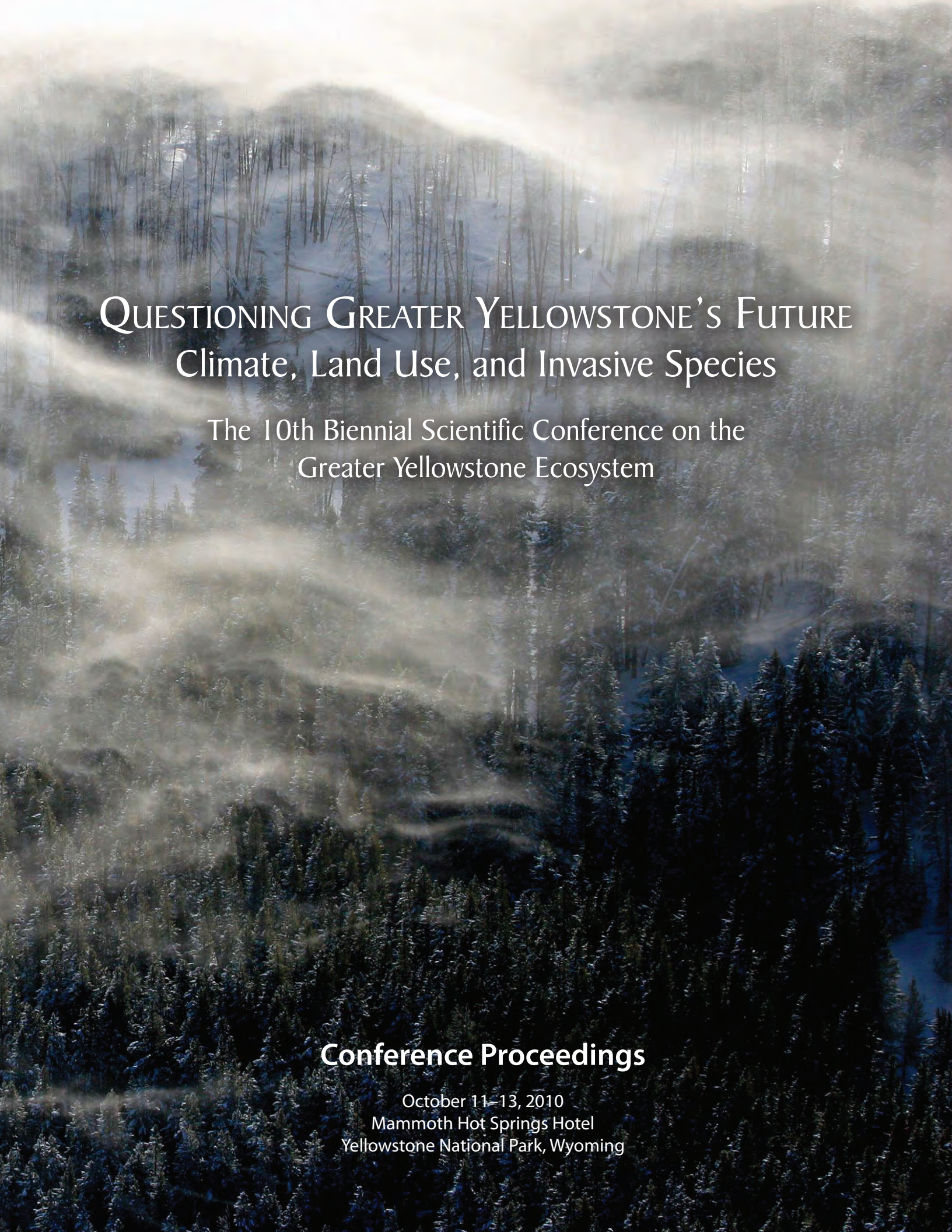


An aerial photograph of a dense evergreen forest covered in a thick layer of snow. Sunlight filters through the canopy, creating a hazy, ethereal atmosphere with rays of light visible. The trees are dark green and densely packed, with snow covering the ground and their branches.

QUESTIONING GREATER YELLOWSTONE'S FUTURE Climate, Land Use, and Invasive Species

The 10th Biennial Scientific Conference on the
Greater Yellowstone Ecosystem

Conference Proceedings

October 11–13, 2010
Mammoth Hot Springs Hotel
Yellowstone National Park, Wyoming



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Editing and layout by Chamois Andersen

with editing assistance from Anne Jakle and Emily Yost
and design assistance from Tana Stith

Program Committee

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Northern Rocky Mountains Science Center, chair
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Cathy Whitlock, Montana State University, Department of Earth Sciences

Planning Committee and Support

Emily Yost, Tami Blackford, Tom Olliff, Glenn Plumb, Tobin Roop,
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Cover: Winter in the Pelican Valley, Yellowstone National Park, 2005. NPS/Dan Stahler.



Conference Mission

The mission of this conference was to generate discussion on changes in three external drivers—climate, land use, and invasive species—that could dramatically alter Greater Yellowstone’s public and private lands. This conference offered participants an opportunity to help shape this region’s future regarding key issues such as:

- How is the Greater Yellowstone climate likely to change in the near future and how do climate projections compare with historical patterns?
- What ecological changes are underway as a result of changing climate and land use, and what will be the consequences for human and natural systems?
- In what ways do increasing demands on public and private lands threaten a sustainable future?
- Which non-native species pose the greatest threat for the region and what are some of the anticipated environmental, social, economic, and human-health consequences of invasive species?
- What new administrative, technological, and scientific tools and strategies are required to address the challenges of changing climate and land use and the threats from invasive species?

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Foreword

“If Yellowstone’s historical record can shed light on the current situation [of science and management], one ray of hope shining from the past might be that Yellowstone has a capacity for infecting its public with a curiosity for science and scientific endeavors, a love and respect for tradition, and with a sense of social responsibility to protect and preserve this place.”

— Judith L. Meyer, Aubrey L. Haines Lecturer,
Department of Geography, Geology, and Planning,
Missouri State University

Since Yellowstone National Park’s establishment, its extraordinary resources have been protected largely through the efforts of generation after generation of park managers, employees, and the many other people who care about the park’s future. The challenges facing national parks have grown increasingly complex, and effective protection of their natural and cultural treasures requires active, informed management based on good science—science conducted by researchers outside as well as inside the National Park Service. It also requires partnerships to increase communication and collaboration on efforts that could not be carried out by the National Park Service alone.

The purpose of the biennial scientific conference on the Greater Yellowstone Ecosystem series, instituted in 1991, is to encourage awareness and application of wide-ranging, high-caliber scientific work on the region’s natural and cultural resources. The wealth of subjects and issues to be explored in the Greater Yellowstone area provides both an unbounded font of research possibilities and an unflagging need for their results. This conference series provides a much-needed forum for knowledge sharing among park managers, the hundreds of researchers doing work here, and the general public.

The goal of the “10th Biennial Scientific Conference on the Greater Yellowstone Ecosystem, Questioning Greater Yellowstone’s Future: Climate, Land Use, and Invasive Species,” was to generate discussion on how changes in climate, land use, and invasive species are altering the ecology of Greater Yellowstone’s public and private lands. More than 45 presentations were given on topics that included the past, current, and future possible effects of these ecosystem drivers on vegetation, wildland fire, land use, alpine glaciers, amphibians, aquatic resources, butterflies, elk, grizzly bears, mountain goats, pronghorn, wolves, plant and wildlife diseases, and human adaptations to the environment. Other conference highlights included interagency, interdisciplinary, and international keynote speeches, an extensive poster session, and a panel discussion of the 2009 “Greater Yellowstone Area Science Agenda Workshop,” at which approximately 90 land managers and scientists identified priorities for ecosystem management in the region over the next 10–20 years.

The 200 participants at the conference—agency managers, scientists, university researchers and students, the public, and media representatives—shared an opportunity to help shape our understanding of some of the key ecological challenges this region faces and the strategies needed to address them. We hope that these conferences and their proceedings continue to contribute to professional knowledge and debate on the many aspects of this extraordinary area during an exceptionally challenging period in its history.

10th Biennial Scientific Conference on the Greater Yellowstone Ecosystem,
Planning Committee

Introduction and Welcome

Suzanne Lewis

Superintendent, Yellowstone National Park

Note: The text that follows is an edited transcription of the speaker's remarks at the conference.

Good morning. My name is Suzanne Lewis and I am superintendent of Yellowstone National Park. It is my great pleasure to welcome all of you here today for this exciting and important conference.

We want to make sure your visit is as fulfilling and fun as possible, so please let us know if you need anything Tami Blackford, Emily Yost, and Janine Waller, or check at the conference registration desk in the hotel lobby.

We in the National Park Service are realistic enough to know that it isn't just our sparkling personalities that attract so many people to these conferences. Yellowstone is a wonderful place to meet, and I hope you have all built some extra time into your schedules to get out in the park while you're here. But Yellowstone does present some hazards you won't encounter in most conference venues. Be careful out there. Some of our most famous scientific topics are wandering around on the lawns here at park headquarters right now. They get pretty worked up this time of year, so please be careful and keep your distance. When you leave a building, or if you're walking somewhere and must turn a blind corner, take a look around first, to avoid big surprises.

Today we celebrate a milestone in this conference series. This is the tenth time we have gathered to report and deliberate on the scientific issues of our region. Those of you who have been involved from the beginning know how much these conferences have contributed, not just to our management dialogues, but also to the knowledge and wonder we can impart to the millions of people who care about Yellowstone. The proceedings of the first nine conferences in this series amount to an encyclopedic resource for future visitors, managers, and researchers, and we're very proud of that. You are part of the most productive generation of researchers in Yellowstone's long and distinguished scientific history, and I thank you for all you've done to enrich the Yellowstone experience.

If we stand back a little farther from all this hard work and conversation, we can see that these conferences track the prevailing moods and priorities of their times. The very

first conference in the series revealed our intense preoccupation with one of Yellowstone's most venerable controversies, the effects of our magnificent ungulate populations on our equally magnificent landscapes. Another time, we focused our energies and insights on the roles and fates of the charismatic native predators, whose future depends upon those controversial ungulates. In other conferences we have explored the place of humans in this landscape; we have penetrated the depths and mysteries of Yellowstone Lake; we have chronicled the reshaping of our ecosystem by non-native species; we have invited our African counterparts to share their experience and insights from living in close company with wildness at least as spectacular as Yellowstone's. And on three memorable occasions we have convened here to consider the effects and lessons of the monumental fires of 1988.

And yet for all of the intensity of the focus of each conference, we have fostered an interdisciplinary breadth, not just across scientific disciplines but across the humanities as well. I'm a historian by training, and I've always been pleased that we could attract so many leading figures



Figure 1. Yellowstone National Park Superintendent Suzanne Lewis.

from the social sciences into the Yellowstone conversation.

That interdisciplinary breadth is, I believe, our best hope for the future of places like Yellowstone. As the agenda for this tenth conference indicates, we are going to need to muster wisdom from all corners of our community if we are to successfully confront the demands of the future. It's easy to see that the preceding nine conferences have been preparing us for this one.

The three topics of this conference—climate, land use, and invasive species—command a great sense of urgency not just in Yellowstone but in American society and the world. Those of us in this room are collectively responsible for helping many other people come to terms with a future that is sometimes only dimly perceptible. But it is certain that whether the changes we foresee will be catastrophic or merely dramatic depends in good part on the strength of our science, and on our success in conveying the meaning of that science to a challenging variety of people—many of whom do not yet even believe that the changes we are concerned with are happening or are worthy of their notice. While I am sure that many of us in this room signed on to our respective careers with some idealized notion that we

were going to try to *help* the world, I doubt that many of us realized the extent to which we might be called upon to help *save* it.

How's that for an opening charge for a conference? No pressure there, right? But I wouldn't put it so bluntly if I didn't have such high confidence that you have the necessary information, wisdom, and humility to do the job. I wish you well in your deliberations here, and I congratulate you again for all your good work on behalf of Yellowstone.

Thank you.

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Opening Keynote

Seeing Things Whole: An Ecosystem Approach to Yellowstone Science

Marcia McNutt

Director, U.S. Geological Survey

Note: The text that follows is an edited transcription of the speaker's remarks at the conference.

Introduced by Suzanne Lewis

Good evening. Thank you for inviting me to be part of this wonderful event.

What a matchless treasure is Yellowstone. The first national park in the world is the setting for the most spectacular display of geothermal features anywhere. It contains one of the largest high-altitude lakes in North America. Its vast tracts of forests and grasslands support very nearly the same suite of wildlife that America's early-European explorers saw—grizzly bears, wolves, and free-ranging herds of bison and elk. Yet, this is a fragile beauty. Yellowstone's complex ecosystem can be easily altered by human missteps, even if they are well intentioned...as we have seen in the past.

You'll hear about many new developments in wildlife and ecological science during the next two days at this conference. Tonight, as your opening speaker, I would like to take a broader view and discuss with you, first, how fundamental we at USGS [the United States Geological Survey] consider an ecosystem approach to be to any natural science endeavor; secondly, how recent science initiatives at the Department of the Interior can support your work in creating a deeper understanding of the Greater Yellowstone Ecosystem; and third, how ecosystem research thrives best when we work in partnership.

At USGS we believe that the starting point to understanding the complexity of Earth systems is the concept of ecosystems. Ecosystems are the building blocks of the Earth's biosphere and support human existence. The plants, animals, microbes, and physical products from ecosystems provide people, as components of those ecosystems, with the energy, water, biomass, medicine, and mineral resources needed to sustain human societies.

Ecosystems are inherently "interdisciplinary," with geographical, biological, geological, hydrological, and other components. The USGS, by the way, is the only federal agency that combines scientific expertise in biology, hy-

drology, geology, and geography. Thus, we are well-positioned to investigate and predict ecosystem change.

More and more land- and resource-management agencies throughout the U.S....and the world...are recognizing the critical need for ecosystem science as they increase their emphasis on sustainability and ecosystem-based management. We stand with you in advocating for the importance of "seeing things whole" from an ecosystem perspective...we know that if we pull one of them out of the chain that it can have unintended consequences and that the whole ecosystem can reform in complex and unintended ways.

This is one beauty of the USGS...by combining scientists that work on the rocks and the water and on all of the animals in the system, we can take an ecosystem approach to looking at these problems. And by working together with our sister agencies within the Department of the Interior we can take that science and put it into actual application in helping managers manage these ecosystems. The USGS also not only has an integrated approach, but we also have a very long history in looking at these problems.

USGS scientists have studied Yellowstone Park for a long time. Actually, [they studied Yellowstone] even before the USGS was formed. The 2007 study, "Integrated Geosciences Studies of the Greater Yellowstone Area" is a 130-year review of the foundation of extensive field studies that include the Hayden Survey of 1871, a precursor to the USGS. It goes through the Hague studies of the 1880s and foundation studies of the 1970s that were NASA supported.

The view of the DOI [Department of the Interior] is that individuals and organizations can accomplish so much more when we work together for the same goals—around the country and the globe. The USGS works with 2,000 different agencies, all the way from the local to the state to the federal...working with tribes, academic communities, NGOs [non-governmental organizations], and the private sector. Here in the Yellowstone area we have a number of key groups we work with including the Greater Yellowstone Coordinating Committee, the Interagency Grizzly

Bear Committee, and the Greater Yellowstone Aquatic Invasive Species Cooperative, among others.

Now, the icons of Yellowstone in the popular imagination are many and they run the gamut from geysers such as Old Faithful, big game animals that are iconic of the old West, such as the bison, elk, and grizzlies, and of course, wolves, which were reintroduced to Yellowstone recently and not without controversy. The wolves have had an impact on livestock and game populations, which leads to continuing debate and restrictions on land use. Over the last 15 years, their reintroduction has been heralded as a great success by some, but also it was hoped that it would help restore a healthier ecosystem by cascading indirect effect[s] on different species by bringing the elk herds into a healthier balance. Recently the USGS and two university partners investigated how land cover change might be improved through the interaction of wildlife in Yellowstone National Park...the concept of landscape in aiding the aspen grove recovery.

This was such an interesting proposal when I was still doing marine research. This argument was being used in the importance of sharks in coral reef ecosystems for keeping a healthy population of foraging fish. The hope was to stop the destructive practice of shark finning. So, the reintroduction of wolves in Yellowstone was having a positive influence on shark population[s] in the ocean.

Now, the research on the wolves in YNP [Yellowstone National Park] is showing at this point that this is not having as positive an impact on the aspen as was hoped for initially. But we shouldn't over interpret the results to necessarily discount the view that a complete ecosystem from the predators on down is a bad idea, and that reintroducing the wolves was a bad idea in keeping an intact ecosystem in Yellowstone.

What I want to talk about tonight is three great pressures that are emerging that we really have to keep an eye on in managing ecosystems in Yellowstone:

1. Land-use changes,
2. Invasive species, [and]
3. Climate change.

These three are being quantified as having an immense impact on Yellowstone and are ones that are very hard to reign in. In November 2009, there was a workshop endorsed by the Greater Yellowstone Coordinating Committee that developed a scientific research agenda for the GYE [Greater Yellowstone Ecosystem] intended to be a strategic framework with flexibility to incorporate continuing research and adaptive management. The science

agenda focuses on these three overarching external ecosystem drivers.

Now if we look at the first of these, land-use changes, there certainly has been a lot of development in the Greater Yellowstone area. The counties in the area have increased in population by 65 percent, but that belies the fact that the rural areas have increased developed land by 350 percent. And that is the statistic that is really disrupting the landscape and the wildlife corridors which are so important to migration. It's the roads that are disrupting the survival of bears because it's impacting the river valleys. There are, of course, new ideas for how one can develop in more sustainable ways that increase the amount of corridors that remain open for wildlife. If these techniques can be used, then it can be beneficial to wildlife.

One Landsat image shows the boundary of YNP as compared to Targhee National Forest, and from it you can see the effect of the clear cutting of the national forest in the patchwork pattern on the landscape; you can see the difference in the land management practices of the two areas. There's little impact in the park, but outside the park you can see the difference right up to the park boundary.

Another large impact is with invasive species. And again, this is something that is very hard to control even in an area as large as YNP. Aquatic invasives have significantly changed the dynamic of native aquatic species such as the cutthroat trout. The native Yellowstone cutthroat trout are impacted by predation from introduced lake trout, while other native fish species are also impacted by non-native fish species, specifically rainbow trout and Eastern brook trout. In addition, there have been introduced New Zealand mud snails that have been brought in on the boots of fishermen and are inadvertently introduced when they are brought into the streams by wading. They also consume a majority of algae, which is primarily a food for native aquatic invertebrates. These types of cascading food chain effects are common with invasive species.

Whitebark pine is a source of food for many animals in the GYE, from squirrels to grizzly bears. An immediate and serious threat to the whitebark pine is an introduced fungal disease—whitebark pine blister rust—which is causing heavy mortality to the species. There are occasionally resistant individuals, but in the short to medium term a significant population decline is predicted.

One problem that is compounding these other problems is climate change. Climate influences every aspect of life on Earth: our own health and wellbeing, our water, our energy, agriculture, forests, our landscapes, our air qual-

ity, and sea level. But global climate change also allows the ability of these non-native species to gain a toehold in a place like Yellowstone. It has increased the temperature by 2 degrees Celsius. More of the precipitation is falling as rain instead of snow in places such as Yellowstone, but in higher elevations the precipitation is melting sooner. We are having peak runoff occurring many weeks earlier, plants are blooming sooner, and the fire season is more frequent and longer.

These problems with climate change are not limited to Yellowstone. Ken Salazar, our DOI secretary, has pointed out that climate change affects every corner of America. The glaciers in Montana's GNP [Glacier National Park] have been melting and are predicted to disappear by the year 2020. Around the globe we're seeing longer fire seasons. We're changing plant and animal species in both the terrestrial and marine environment due to climate. Many of the changes here in Yellowstone are examples of what we are seeing nationwide.

We are going to have to learn to adapt to these changes in climate and we're going to have to use more connected ecosystems and landscapes in order to find corridors for animals to migrate.

The conventional approach in even the basic questions of natural resource management is being transformed by these broad-scale ecosystem changes. We're going to have to be asking different questions and we're going to have to have new management approaches. We're going to have to understand the complexity of global climate issues and we're going to have to manage in new ways under the pressure of climate change. The time for debating climate

change has ended. We have to accept it as reality and manage accordingly.

Fortunately, we have some new tools at our disposal. Recognizing the critical need for more certainty concerning the local effects of climate change, we have the department's first ever coordinating climate change strategy as of September 2009. In Secretarial Order 3289, the Secretary established a network of landscape conservation cooperatives that engaged federal agencies, local and state partners, and the public in crafting practical landscape-level strategies for managing climate change impacts on natural resources.

You've all probably seen this map, which shows how the nation is organized into a framework...a patchwork of these natural landscape cooperatives [Figure 1]. Yellowstone falls under the Great Northern Landscape Cooperative. The partnerships have been established and will allow the partners to work with the managers in Yellowstone with like-minded partners to figure out how climate change will affect wildlife migration patterns and how it will affect wildfire risk, drought, and invasive species. We'll work together with university partners, NGOs, etcetera. From everybody I've talked to, everyone is truly excited about how these changes can be truly transformative.

Part and parcel to these landscape partnerships are the climate science centers. The first climate science centers have already been announced. For the Northwest it's a consortium that includes the University of Idaho, the University of Washington, and Oregon State University. The North-Central is being competed and will be announced soon. These climate science centers will work in partnership with the landscape conservation cooperatives [LCCs] to provide the science necessary to help the LCCs do their job. Together, these two will form the cornerstone of the department's climate change strategy.

Now, ecosystem restoration, whether it's in the Everglades, or Chesapeake Bay, or here in Yellowstone, typically takes place in complex partnerships staffed by professionals with varied backgrounds working through several layers of organization. That's what is really important... nothing is going to work without the partnerships. The science of ecosystem restoration does not point to distinct popular solutions. It works as a common basis for action, bringing groups with widely varied goals together to engage constructively. For science to work well as a basis for action it must be recognizably top quality and it must be completely impartial. It must have relevance to planning and to policy. And the science must have input



Figure 1. Map of the landscape conservation cooperatives.

from all stakeholders to ensure that it has the information and data to address the societal and environmental challenges at hand. Large-scale ecosystem restoration is as complex as it is by necessity. The sheer extent of the science, planning and policy development, implementation, and management required of any large restoration effort greatly outweighs the capability and resources of any one agency or any one level of government. It really takes an entire village, and it takes a village united by a shared belief. It takes everyone believing that science is important, and it must be conducted effectively on restoration of a large-scale ecosystem.

I'd like to thank all the state, local, tribal, and federal agencies involved in conservation efforts in the Greater Yellowstone area. I can't thank everyone here personally, but I want to recognize you all in earnest. Specifically, the Greater Yellowstone Coordinating Committee and the Yellowstone Grizzly Bear Coordinating Committee, and thank you all for your cooperation with the USGS and your contributions to keeping the true nature of Yellowstone. This is truly a great place and you all wouldn't be here if you didn't love it...and it's a great place to live.

Just in closing here tonight: I think we're all here because we want to keep this place as beautiful as it is for the next generation. When I opened here tonight, I said that the mix of animals here and even Old Faithful is much as it was when the first explorers found this place centuries ago, and wouldn't it be nice if centuries from now the gen-

erations that come after us could say the same thing? If that's to be the case, it's going to take a real commitment. It's going to take understanding of what the problems really are, not just what politics thinks the problems are. It's going to take standing together as true partners and agreeing together what the goals are and standing firm on an agreed set of outcomes. It's going to be keeping our eye on a long-term outcome and refusing to compromise on that outcome. Yellowstone, like many of America's great places, is many things to many people. But what it can never be is a failed scientific experiment. So, thank you all for your time here. It's very important that you're all here. Happy to take questions, thanks.

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Superintendent's International Lecture

Moose, Humans, and Climate Change in Arctic Sweden—5,800 Years of Coexistence and Adaption

Göran Ericsson

Professor, Department of Wildlife, Fish, and Environmental Studies,
Swedish University of Agricultural Science

Note: The text that follows is an edited transcription of the speaker's remarks at the conference.

Introduced by Suzanne Lewis

Thanks for the extremely warm welcome, Superintendent Lewis.

Getting an invitation to Yellowstone National Park for a Swede is almost like getting the Nobel Prize. We don't really have a Nobel Prize. Actually, when I got the letter I sat down, I looked at it, and it still was my name the second time I read it. So, it was true...I'm here. I'm honored and extremely flattered.

The tradition goes on...we have a lot of interchange between our societies both in terms of science, but also in terms of the very management ideas in the society. So, following Yellowstone we erected our first national parks in 1909, which was a landmark year in Swedish conservation. We also started our conservation movement in 1909. By then, we started to follow mostly in the footsteps of both Germany and the States in the case of conservation and the national parks.

In the introduction it seems like I am a moose guy, and I have been trying all my life not to work with moose. I am always dragged back to this animal. I try to work for the government, I try to do something else, but eventually always the moose emerges in front of me. So, what I will focus on today is moose as a model species. If I get this right...

Seeing it as a typical animal in that it will be both a winner or a loser of the climate change that we might see in the future...when I was preparing this talk I had this alternative title about how moose didn't make it in New Zealand, and for those of you who know the history of moose it is a cool, climatic model animal and it's mostly in the northern part of the world. It's fairly adaptive—it's in fairly warm climates and fairly cool climates. But then in the '40s they tried to send a few moose to New Zealand and they didn't make it. So, why didn't they make it, and why do they thrive in Sweden and have been doing that for the past 6,000–7,000 years?

That is basically the key topic of my talk today. If you look worldwide, moose have been adaptive to relatively cool summers, cold winters, and throughout this range seems to be adaptive to adaptation. So, what I will guide us through here is some current research data, but those are some data that are gathered together with some friends that are archeologists and geographers. So, we're trying to put these climate change concepts into a 6,000–7,000 year perspective.

When preparing for this talk, I didn't get any direction whether I should speak in Swedish or in English, so I decided to speak in English. So, when storing this talk I asked if they had a Swedish filter so I could take out my accent, but they couldn't. But you can be safe—I learned most of my English from the Muppet Show and the Swedish Chef.

So, my backyard is basically Scandinavia. Being a Swede, you have to acknowledge that Scandinavia is not a country, it's three countries: Norway, Sweden, and Finland. The whole of Sweden is basically 495,000 square kilometers. We have about 9 million inhabitants, which is three times the annual visitors of Yellowstone National Park. The average population density is 20 persons per square kilometer in the southern part. Up north it's less than one per square kilometer. So, this is basically a human desert up there. We call the part of Lapland the "true north," and in terms of moose this is the true north. It was protected early in 1909, and as Yellowstone is iconic for conservation it's also the model for where you really want to go for your vacation. See, once in your lifetime you have to go there and go to the highest peaks and climb Mount Kebnekaise and send a postcard to your relatives. You've been there, you've done it!

So, imagine this is the Yellowstone for many Swedes that we'll be visiting now. So, as with Yellowstone there were some early pressures of land use around these protected areas. Hydroelectric power...at the first we loved hydroelectric power in our national park because it was so important and of course we could restore nature later. Today, this is



Figure 1. Superintendent's International Lecturer, Göran Ericsson.

contested land. There is a lot of reindeer herding still. The natives, the Sami people, herd reindeer, but mining pressure is more and more to come into the national park or into the fringes of national parks. We are even moving a couple of towns up north because there are so many mines under these towns and we need to move the towns. So, this is a contested area.

Also, it is a heterogeneous area with extremely strong seasonal components. It's a cold, dark winter. We are about two hours north of the Arctic Circle and there's no sun for a couple of months, but contrast that to the summers where we have 24 hours of sunlight... extremely good breeding conditions for both mammals and birds and for moose. Of course, they will be affected by climate change.

So, what I've been battling now with in my research is to

understand how life adapted to this seasonal environment and what I'm doing now is basically following the moose. Instead of following the archives I use GPS collars, which are a familiar venue for most of you. When I left this area 10 days ago we were in the peak of the rut, the first snow had come, [and] we were doing a couple of TV specials... at that time during the peak of the rut and the peak of the breeding season...it was a "maladaptation" said the British television crew. They said, "Why mate now and give birth later when you have to starve five or six months and sustain the cold and darkness up here?" So, what I will now explore is a few contrasting elements in our current research and base that on my traditional way of getting data, GPS collars, and a non-traditional way, using archeological data.

Now, I will put this into a wider context. What I established in my research and with my research group is that we basically work with moose and moose behavior in this latitudinal gradient. Going from latitude 57 in the south up to 67-68-69 in the north...what we focus on, of course, [is] climate, but [also] site fidelity...why come and use an area over time? Wintertime, summertime, calving, etcetera. This latitudinal gradient is close to 1,500 kilometers, and there's a fair amount of size variation along this gradient. Of course we can relate it to Bergmann's rule. Most of my talk will be on the area around latitude 67 and 68.

Today's data...when the models work for us, when the moose work...is quite familiar. You use moose, you put a collar on them, and then hopefully have good American satellites up there. It's even better if you have a war so that you get some precision out of it. What we do a lot is use our cellphone network to get realtime access to data. We can manipulate the data flow, we can have high resolution, shorter duration, sampling, etcetera, and then we do the traditional way of getting data into computers and using them for mapping and putting them on the Web, basically.

But the problem we started to discover is that there were no collars on moose 6,000 years ago. That was a key problem. So, when I started to explore this, I made statements like this and this is from a coming paper, and we start to look at collar sensor temperature and we look at simple things like average movement per hour. So we have the average collar sensor temperature and we have the average movement and you start to see patterns and you start to see how this could be related to temperature stress. Ah, it seems like they thrive when the collar temperature is around 20 degrees Celsius. We adjust that and

it gets down to roughly 10 degrees Celsius. You start to see heat stress around 15 degrees Celsius, which is derived from the literature. We expect severe heat stress to affect the animals when you get well over to 30 degrees Celsius. But when you posed this to an older professor (I won't say his name, you might recognize Sheldon Allison) they ask, "What about history?" They are retired, they can ask this. I couldn't answer that. So, then I went to my friend and he said, "Well, let's see what I can help you with."

So, what can history tell us about adaptation versus climate change versus human use as well? Moose came into the Scandinavian Peninsula at least 6,800 years ago. We have a complete skeleton that we found and dated it back to 6,800 years ago. We started to have a few clues that population [wa]s varying over time. They were almost extinct during the 1700s and 1800s and early 1900s, but now we have a lot of moose. There's basically one moose per square kilometer...300,000 to 400,000 moose up there. So, if we put this into some kind of political rhetoric is seems that change has been the norm for moose at least in the last 6,000 years, but then we see if we can have some data from that.

Adapted to variations, if you look at moose, they are long lived, they learn, they can store energy, they have a fairly late reproductive start in life. Up north of the Arctic Circle most of the time when they start to breed they are between three and five years old. They have a large body, which is good if it's cold. They have a lot of fat (I could have needed it this morning...I thought it was fairly cold here in Yellowstone), which conserves heat. It's important to conserve heat up north and if you use this energy loss through winter. They're a good capital breeder, which means they can miss one or two breeding seasons and still be a part of the population. We touched on the size dimorphism along its distributional range.

So, given the simple data we had in terms of temperature we start to think and model what will happen with size, what will happen with migration, what will happen to start with reproduction if we get warmer weather and more precipitation. Of course, we can look at this distributional range, but if we look at the distributional range we can see an extreme size dimorphism. We actually see some of the parts where moose thrive in a warming climate and others parts like in Minnesota and here where they are declining slightly or even fast.

A crash course of the research is a crash course in change. So, change seems the norm for moose. There's



Figure 2. Pitfall trap.

a big annual change between winters and summers, like that. There's a strong seasonal component within and between years and then you have the change imposed by human activities and most of the country is used for humans' sake, in this case forestry. We know that change has been part of moose history for 6,000 years, because they employ a partly migratory strategy because there's an extreme environment up there. Basically, now we're dealing with a question of "should I stay or should I go?" here.

We still find moose up on the very barren ecological desert in the snow there. Year after year they'll stay on the top of a hill and never leave there. They starve for five to six months and then have a lush green pasture for the rest of the year, but they don't move. They just stand there. To the right or left of them, they have a friend that might migrate up to 250 kilometers in extreme cases. Why do



Figure 3. Distribution of pitfall traps in northern Sweden. Pitfall traps in black.

they do that? And they become even harder to understand when we start to realize that moose have been absent from this landscape for periods of time. We also see that humans have followed in the footprints of moose for many, many decades over the last 3,000 years. Humans have also adapted to very cold winters...what will happen now? Will we be adapted to warmer winters?

Back to the snapshots of reality...we couldn't deal with this with the snapshots of reality. Well, 20 years is how far back the data goes in some cases. I still could not see how we could find moose in this ecological desert, starving for five to six months. What would climate change mean to them? Would they still stay or would they disappear from the landscape? We have a fair understanding that they are adapted to the food shortage. They can store [fat] for a long time as I've said a couple of times, but what will happen if there is more food in the winter due to a longer growing season, shorter winter, better condition to move in? With that all said, they are adapted to a rich summer environment, but some of the models actually predict that we will see a richer summer environment. We'll see more pine, more broadleaf, we'll even see aspen moving up. One of the trends that we see here is that we see the aspen

moving uphill. They're not disappearing, they're moving uphill. We see pine getting back again.

The last 100 years of data have said that when there were warmer times, warmer periods of time, the moose came back in these environments. We started to deal with some of the cool summers thing. We did some modeling and published a few papers beyond that. We started to see in the short term with adaptation to warmer summers... well, you could figure out quite easily, this is well known for many species: that you will get a fairly simple model where you have a warm and dry pre-summer resulting in an early flowering and that will lower the concentration of nitrogen in the plants, and you normally see a reduced base of calves in the summer here. So, that will speak in the evolution of smaller moose...not that they will disappear from the landscape.

So, finally we got some data from our friends the archeologists. So, back to our question of what do 6,000 years of data of moose variation tell us when we combine that with other background and other data? Before I give you the full story, I have to sidetrack and get back to this interesting hole in the ground. That's a pitfall [Figure 2]. Pitfalls have been extremely important for humans and moose up north here. This is how foresters view pitfalls today: as an interesting hole in the ground. But imagine a whole valley covered with structures that hinder all animals' paths through the valley. They have no chance but



Figure 4. Pitfall traps in relation to moose movement, as determined by GPS tracking. The red lines indicate pitfall traps, and the black/gray lines track moose movement.

to move to the pitfalls. They have been used up to the late 1800s up north in Sweden. They [were] actually forbidden in 1864. So, instead of using GPS we will use data from pitfalls to target the migratory moose here because, as I said, migration is a natural phenomenon in this landscape and moose are the true animals that have been able to adjust to this landscape change.

Sometimes you get disappointed. Well, I don't think moose are democrats...they might be conservatives because they seem to use the landscape in the very same way for the last 6,000 years. At least, since when we could put the GPS collars on them. I have to give you the background on this first...here is a small settlement of 2,000 people, and here's a river coming down from the north like that that...the black lines or dots are pitfall traps [Figure 3]. So, imagine in this area if a moose comes down, historically it would pad through the pitfalls and this pitfall system probably took about 1,200 years to develop. It was the key resource in human society here.

In the past, humans used to wait for [them] to get into the pitfall. They were migrating along the river valley and more moose [were] coming down because the migration was very predictable. What we started to understand when we put GPS collars on is that even if the moose had been absent in the landscape they seem to be very conservative landscape users. They seem to follow the very same structures. They seem to follow the very same migration routes. It became extremely evident when we put the overlay on our data from our GPS collars.

When we look at our Swedish landscape and the Norwegian landscape (but this just deals with Sweden), most of northern Sweden was covered in pitfalls following the migration routes. So, to get back to our research area in the small town of Sorsele...we started to see when we caught up to this system that you don't see much of it today, but when you put a GPS collar on the moose you could actually predict where the pitfalls were. Getting into the archeological archives we see that they have been in use many hundreds of years. It seems to be industrial processing. If you look at the size of the settlement along the river valley and the bones in the sediments, 95–98 percent of the sediments come from moose. If you move out from the river valleys into the forested land, 65 percent of the bones come from beavers. There are heaps of bones, there are hides underneath, there have been structures, and there have been buildings there...instead of waiting for their arrival they've been waiting by the pitfall waiting for the moose to come.

This is what we experience when we put GPS collars on moose. Now, instead of having black lines I use red (I don't know why), but here are the pitfalls and structures and the lines here are GPS collars of moose here from just one season in this area [Figure 4]. They [the moose] walk the same way...they follow the same migration route as they did 6,000 years ago. When we got down to the archives we established that moose had been absent in landscape for many periods of time, but still they used the landscape in this part of Sweden the same way. But they could have done it differently.

So, in a way nothing new under the sun except this... instead of killing moose with very simple objects, humans now kill them effectively because when we start to look on today's situation the hunters use the same structures. They were not sitting down in the pitfalls, but they were using the same area because it was so predictable that the moose would come there.

So, back to the key question: what did the migration data combined with the archeological data tell us? Well, it told us this: conservatives change slowly. A graph found in Davis 2003 shows summer temperature versus winter temperature and the deviation from the last 12,000 years from now. When we look at our archeological archive we can see that the moose came in the system basically here about 6,800–7,000 years ago, and they are prominent in the archeological records up to basically here. Then, they disappeared suddenly and that coincides extremely well with when we had a rapid change in winter temperatures. And we start to see them again in the pitfalls and the sediment when the temperatures started to stabilize again and we got more back to normal. So, we had rapid change, moose disappeared completely from the system, but were probably still on the northern part of the Scandinavian Peninsula, but not in our pitfalls. So, it seems that moose adapted to change, of course, but they adapted extremely slowly to this.

Right now we're in the phase of an increasing winter temperature here. It's fairly fast, but it's in the range where moose have existed before and it was not in a decreased phase...it didn't get colder. What we might experience now is that moose don't move north, but that they will become smaller. We will see the size change once again we will see the smaller moose reappear north, but we don't know that because they are quite conservative to change and they have become heavily hunted, they have passed a few bottlenecks; we don't know if there is any genetic

variation left to do this. Compared to North American moose, Swedish or Scandinavian moose have a very narrow genetic range currently. So, you never know.

In terms of the science part what we probably need to do is put [it] in a broader perspective, not only with the moose, but we must look at climate change in relation to human society because we will be an important driver especially if there are animals like moose who use the forest heavily. The turnover in this population is 25–30 percent every year. So, imagine the high turnover in population rate in this corridor caused by humans. It's enormous the impact that humans have, especially in this hunted population. Of course, the trade-off (in life history trade is important) is that they have a latitudinal gradient and worldwide we can look at things like that.

Migration patterns are extremely interesting to us. We've been touching [on] that previously today as well. Will migration patterns change when we have a different climate? Can they actually change? Because some of the migration patterns are not tied to genetics they are tied to behavior adaptations. They are also tied to certain landscape structure that might force animals to move in a certain direction and up in a certain place. My fourth point is what we probably have the easiest way of dealing with, the physiological effects due to climate change. We can fairly easily answer those, but we don't know if the animals have a long-term adaptive strategy to that.

So, what will we see in the future? Well, the next time we may see this up north. So, the next time Suzanne [Lewis] comes to me and we fly up there and we are looking at the huge racks...60 some inches...we'll see this instead. A couple of boots underneath and a couple of small, small moose instead. So, you never know.

So, thank you. There are a lot of acknowledgments here. My program is Wildlife and Forestry. My research program is Swedish EPA [Environmental Protection Agency], my recent program is ICEMOOSE together with Wildlife and Forestry and especially my colleagues. And before I open up the floor for questions, thank you!

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A. Starker Leopold Lecture From Range Management to Ecology

Mary Meagher

Retired National Park Service and U.S. Geological Survey Biologist

Note: The text that follows is an edited transcription of the speaker's remarks at the conference.

Introduced by Doug Houston

Thank you all. As you know, I'm going to talk about the history of range management to ecology in Yellowstone. This is a very interesting period. I freely acknowledge that I don't span the entire history of range management in this place, and I think it useful to trace some of the early things that, I think, led to that period of time.

It really began about 1900, I'd say with the early re-introduction of the bison from the Goodnight and Pablo-Allard herds. The superintendent...the military superintendent at the time...observed that, "It is our intention to manage the new herd of buffalo in the same manner as domestic cattle." In fact, that's one of the problems with bison: too many people think that they're cows or big elk. In any case, I've often thought that at least psychologically/subconsciously these kinds of things laid some groundwork. Also, it was very much just the state of the knowledge. I'd also like to acknowledge that of the people I knew, whatever their background—however we view some of the work now—they were hardworking people and they very sincerely thought they were doing the best that the park needed. To me, that's important to remember. They had Yellowstone as part of them also.

In any case, in 1902 bison arrived in Yellowstone. They were moved to the Buffalo Ranch in 1907, and I think that operation further reinforced the livestock and ranching mentality. At the same time, at this period, there were quite a number of elk. How many? Nobody had aircraft...some counts were made by some of the army scouts, starting down in Gardiner at the first of April and moving right upcountry with the elk. You can count a lot of elk that way. But again, people were trying hard. There was a lot of confusion about the numbers of elk and the different herds. If that interests you, you can trace that nicely in Doug's [Houston's] monograph on the northern Yellowstone elk. And of course the elk were the most visible and most numerous large mammal...whatever their numbers...and that always seems to catch attention.

So, by 1914 we find the first written, observational comments expressing concern about range conditions... this is the northern range that I'm talking about. These observations were made by William Rush...a horseback trip...so, this is what you would call a reconnaissance. Meantime the Buffalo Ranch becomes a very large and intensive operation with all the trappings of livestock management: castration and weaning of calves, separation from their mothers, winter feeding. At a certain point it becomes ironic because management reached a number of bison that even they knew they didn't want to support on the ranch...right around 1,000. But they felt they had to continue winter feeding, so then they produced more bison, and they still have to remove some number.

The Buffalo Ranch had a slaughterhouse, corrals, and all kinds of things that are really divorced from thinking about wildlife populations [Figure 1]. The confusion and concern about the numbers of elk was probably fueled by the drought of the 1930s. There were two staff rangers who were really doing range work to the extent that it was being done at that time...Walt Gammill and Rudy Grimm... and it's interesting that the two of them noted how much the vegetation improved when the drought broke. Fancy



Figure 1. Three mounted rangers separate bison for slaughter at the Lamar Buffalo Ranch in December 1930. National Park Service photo: YELL-15805/G. Baggeley.

that. And yet, there's still this diverse livestock/range management interpretation...the dots don't get connected.

By 1930 there were two small exclosures established on the northern range. Throughout this period the elk and the northern range were the focus of attention [Figure 2]. The only original bison remaining in the interior of the park were in Pelican Valley. They had been extirpated from the Mary Mountain complex of the Firehole and Hayden Valleys, but their former presence was known. So in 1936, bison were loaded on trucks at the Buffalo Ranch and taken to the Firehole and to Hayden Valley...a total of 71, roughly half-and-half...and simply released. There are no written comments, no photographs—there is not a shred of information in the files other than the fact that it was done.

So we don't really know what conditions looked like in Hayden Valley, remembering that the dominant ungulate had been gone for 40 years...vanished from those areas in the latter part of the 1890s. Throughout this period that we're still talking about, the focus on the northern range continued, a number of range evaluation techniques were tried, the Buffalo Ranch operations continued—hay-ing operations, mostly of deliberately introduced pasture grasses. All of these kinds of things, I think, reinforced the livestock mentality.

Then came the war and everything just sort of...oh, what I'd call a hiatus. Some of the personnel were gone in the military, there weren't funds, and facilities for visitors began to come apart. So that was a quiet period until after the war. After the war, the Park Service recognized that a lot needed to be done in terms of facilities and most of the emphasis—a program called Mission 66—was on reconstructing roads, building accommodations for visitors...and this was not just in Yellowstone. The program was service-wide.

However, in Yellowstone at least, one biological position was filled. This was a full-time range management person: Walt Kittams. Walt came in 1947. Not only was he expected to know the northern range with its six species of ungulates and its long history of thinking that things were very wrong there biologically, but he also was expected to look at the southern Yellowstone elk and bison—we now had bison on the three interior winter ranges of Pelican, Hayden Valley, and Firehole. I would say that he was a very dedicated range management kind of person. He set about a lot of fieldwork...tried to establish ways to measure vegetation. In the spring of 1948 he made a ski trip through Hayden Valley. Rangers made sporadic patrol

trips, so there was some sense of what was going on. But again, this was “eyeball reconnaissance” and if the snow was blowing you didn't see much, especially from skis. He also made a spring/early summer trip, several fall trips, and in 1949, he made the first aerial survey of wildlife in the park, for bison, across the interior winter ranges. On the northern range, because of the Buffalo Ranch, people thought they knew what the numbers were, even though the Buffalo Ranch had begun to phase out the most intensive parts of the operation in the early 1930s. They'd ceased castration, they'd ceased weaning calves...they still winter fed the bison, they still rounded them up, and then removed the surplus. That was just the program every couple of years. But Walt looked at the interior ranges and, in addition to the northern range, these became of concern to him, and very early.

He focused particularly on the southwest corner of Hayden Valley, with Pleistocene lakebed soils. There are outcrops of sands and silts, small patches of clays...and relative to the rest of the valley, the area has more up and down, small hills. At that time you could drive a road all the way from Hayden Valley to the patrol cabin at Mary Mountain. So, perhaps that influenced where some of his efforts were made to understand what was going on, because his preliminary report on Hayden Valley for 1949 discusses really only those kinds of sites and in that area. That report is also the first time that we see a number of bison that “should” be in Hayden Valley. The number used was 150; I really don't know why that was the chosen number...because, I guess, that sounded like a good, reasonable number. The thinking was that numbers needed to be cut down somewhat, so that was okay.

Concern for range conditions built very rapidly. Although at the time people began to get a sense that there was some movement of bison across Mary Mountain between the Firehole and Hayden Valley, but the assumption was that it was just a few animals. People had no way of knowing at that time that those two valleys basically functioned on a year-round basis as an ecological unit in terms of bison use of that habitat. These four wintering areas—the northern range, Pelican, Hayden Valley, the Firehole—were all yet viewed as separate entities in terms of numbers of bison. Air surveys, as I've mentioned, had just begun and weren't being made every year, and it was a couple more years before another was made. There were more bison of course. Another one made in 1954 produced the highest count that they had on record, which was 1,477 bison.



Figure 2. Bison and elk grazing on Yellowstone's northern range. National Park Service photo: Jim Peaco.

So, the “magic” numbers became 40 bison in the Firehole, 125–150 each for Hayden Valley and the northern range, and maybe 150 for Pelican Valley. In 1952 these magic numbers were developed a little at a time—I’ve never been able to find a solid basis for the choice of the numbers other than Walt’s initial concern about Hayden Valley, and that 150 bison were about what should live there.

A very interesting aspect developed about the Firehole, however, because the perspective shifted very rapidly from concerns for range management/vegetation conditions to attention to all those big bison feet tromping through the geothermal features. The chief naturalist was especially concerned, and very shortly, in writing, this concern became the reason for determining bison numbers in the Firehole.

A trial field operation to reduce bison numbers was held in 1952. Three bison were shot on the Firehole just to see how a field operation could be set up. After that, there were several shooting reductions in the 1950s. These culminated in 1956 with bison being removed from all three of the interior winter ranges. Something like 120 bison were removed from Pelican Valley, several hundred from the Mary Mountain population, and of course the

Buffalo Ranch removals were still being held every other year.

Then in 1958, Walt was reassigned to the regional office, leaving no biological position in the park. At the time I came...I had had a healthy dose of range management while I was at the forestry school at Missoula...and it certainly never crossed my mind to assume that that was not the way to go. Furthermore, that wasn’t anything that I was involved in, as I was the museum curator. But after I began to look at bison, I also began to have some second thoughts. I’d first like to emphasize how easily these proposed numbers for bison became fixed targets, because I think everyone then assumed there were file drawers of supporting data. A management biologist position was established in 1960. The then-canyon ranger, Bob Howe, was moved into that. He had a degree in biology; his job was to supervise reductions. There was no tone of questioning that these were valid target numbers.

In addition to having no range biologist for four years, there were other changes going on in Yellowstone... particularly in top management, and I think that probably compounded this whole perspective. About all that can be said is that “it was the state of the knowledge.” In 1962, another full-time range management person was

added—Bill Barmore. This was also about the time that I started back to school. As I looked at all of Walt Kittams' information, what struck me in a very crude way, I guess is how I would put it...I was very green, please understand...but I realized because I had already started to do some air surveys, that if these places in Hayden Valley that Walt was concerned about were a biological reality, that they were a biological problem, then one bison was too many. That's where these mature bulls would hang out. They'd keep the soil disturbance continuing on the slopes, and they'd wallow, and in the wintertime they'd stay a month or two at a time at any given site. So, it didn't match...in my very rough way of looking at things...that we had a range problem.

Well, we went through most of the '60s with a range management program, gaining ever more impetus. Very interesting. I'd like to read you a quote from 1963, because this one to me most underscores the information problem of "never connecting the dots." This is the assistant state range conservationist, H.W. Cooper: "A primary problem of maintaining both numbers of animals and good-to-excellent range conditions is even or uniform distribution of grazing. With game animals this is difficult to obtain. I have no suggestions as to how it might best be accomplished."

Something of a classic! Meantime the range juggernaut continued and what started as biological concerns became political, social...whatever tag you choose to put on it. It was my first exposure to a sense of mob violence, very tame by present-day standards, I know. But I had never listened to anyone before just going up and down a drugstore aisle ranting, not talking to anybody. A few Butte miners were making noises about coming over and shooting park rangers. The elk removals were field shooting reductions initially, just as had been with the bison. And bison, of course, were cows, so that didn't generate a furor, but the elk certainly did because, "Oh, if you're going to shoot elk, we should be hunting in Yellowstone Park."

It finally reached a point...perhaps there's a trace in files in the National Archives...we don't have anything on paper of which I'm aware...potential for an actual bill in Congress that would indeed authorize sport hunting of elk in Yellowstone Park. As some of you know, Grand Teton National Park has used deputized park rangers in some areas for removal of elk, although it didn't seem to set a precedent. But the elk reduction topic was getting really hot by 1967. There were hearings held. Senator McGee was the prime mover, and the whole thing had

shifted from the field shooting...I never knew a single person who enjoyed it, by the way. It was a teeth-gritting operation, shooting elk with access via oversnow vehicles [surplus army weasels] and dragging the carcasses back to the road...but the reduction program began to shift first, theoretically, to restocking suitable areas wherever in the country. Eventually the live removal program became very clearly, simply put-and-take hunting, because those suitable ranges were full...such as places in Wyoming. So, elk would be live shipped from Yellowstone and the elk season at the receiving end would open, and a good number of elk would be shot.

But the politics about this whole thing were fairly ugly and in the 1967 hearings there was a commitment on the part of the director that no more elk would be shot in Yellowstone. The park also acquired two more live-capture elk traps. One we dubbed "Senator McGee's elk trap." We didn't want them..."we" being the park operations...didn't feel they were necessary—useful—but here we were with line item budget appropriations. So the two traps were built, used one winter, 1968, and then could not be removed until 1983 because the superintendent of the period (the latter part of the 1970s) said, "Senator McGee might run for president." We did finally get rid of them and cleaned up the park.

Learning experience: there were also some interesting facets going on with the bison, our "cows." For the first time ever, in the early 1960s, the bison removals were done by contract...the first and only time, although it spanned two years. A man named Bud Basolo at the Little Buffalo Ranch in Sheridan, Wyoming, at the time...I think he's listed for a couple of record heads, but those heads were captured first in Yellowstone...then he removed them from his ranch. In any case, the operation was pretty interesting because the ranch people thought they were going to round up bison with horses. Now this had been attempted once by the Park Service in 1935. Park personnel thought the bison in Pelican Valley, which is south of the Lamar [northern range] across the Mirror Plateau...that those bison had come from the Buffalo Ranch so they should be amenable to going back—this to reduce the number of bison in Pelican Valley.

The files are pretty blunt about the bison didn't, they wouldn't, and there was no way. So, this was explained to the Little Buffalo Ranch foreman and his crew. They did make a trip up on the Mirror Plateau with Bob Howe; wisely they concluded there was no way they were going to be rounding up bison there with horses. However, there

were trap facilities, live capture facilities on the northern range, so the ranch people got permission to use those. But there was still the question of Hayden Valley. They did try horses. But they didn't try them very long. The superintendent noted that the Little Buffalo Ranch people were very resistant to any kinds of advice or information.

There were a lot of politics in that contract. The grapevine, at least, said that the assistant secretary in the Department of Interior who wrote letters on behalf of Mr. Basolo inquired if Mr. Basolo had gotten the contract—this a week before the notices for bid were posted. That episode was the only experience Yellowstone had with working with a contractor to do reductions before the Park Service said: “No, whatever we feel we need to do, we will be doing it.”

That experience certainly underscored the park's perspective when there began to be talk about hunters shooting elk in the park. Fortunately, that did not happen. Although bison were secondary to the elk issue, the last bison reduction was in 1966, not because decisions had been made to cease, but because at that time target numbers had been met. So it was simply “we're putting this aside and not doing anything for this year.”

Then, we get into the whole business of “natural regulation”...as Doug [Houston] and I observed [in the comparative photo book], that is a very misunderstood phrase. It actually was not a policy—initially—handed down from on high, contrary to what is stated by a number of hardworking historical research people. Perhaps that's the way that they received the information. But it started, really, as a moratorium on reductions, because—as I said—things were rather hot and “let's see what our data is that really supports these programs.” Doug had made a very interesting observation: he had been looking at the series of attempts to measure vegetation on the northern range beginning with the exclosures of 1930. He said, “You know, because there are a whole series of different kinds of things being tried...it wasn't telling them anything, and so they'd try a new method or whatever the newest idea was.”

Some of the methods created their own problems. For instance, the fences of the small exclosures trapped snow, creating a micro-climate that would influence the vegetation, so that wasn't going to take you anywhere. But we really ended the reductions by starting with a moratorium, at least on the park end. I was not a party to what the superintendent might have discussed with Washington, and the Park Service did have the recommendations of the Leopold Report. However, that

did not specify “hands off,” which [is] what some people equate with “natural regulation,” if the data justified it... an active management program could be established. The yardstick was data and when we went looking to see what we had...I've already told you what we had for bison. We had a 1956 memo for a total of 425 bison park-wide. We had the word “trial,” which implied evaluation, and all of that disappeared over the span of four years when there was nobody sitting on top of that. All I can say is that there was no data. Walt tried to establish a few plots and that sort of thing, but they had never been in place any amount of time that would tell you anything.

The range management period is interesting in that sometimes it was called “the numbers game.” As it peaked in the 1960s, it was so many acres, so many animals. There was no concern that diet might not overlap completely... elk versus bison versus bighorn sheep. Or, even if there was an overlap, perhaps it did not occur in time or space, so that in fact the species occupied different niches. By the numbers, a bison was considered equivalent to one-and-a-half cows—these were animal-use months—and these were just numbers, points in time. As with Walt Kittams' reconnaissance of Hayden Valley, his draft report of 1949, more reconnaissance on skis, horseback, and use of the then road and then the first air survey in winter—these too were just points in time.

It was a very interesting period in terms of the numbers—it seemed almost mechanical...one plus one equals two. We learned some things from that...aside from human behavior and how hot a topic the elk could possibly be. I think we learned some very fundamental lessons. Doug observed that had we not had that enormous change in elk numbers...basically the population was cut in half on the northern range...and that served unintentionally, but in fact, as an experiment—being able to watch and evaluate and gather more information as the population began to recover. Did we see a change in the aspen? Did we see a change in the willows? Whatever the particular site or topic of concern, were there changes that reflected the big change in the elk population?

Time, to me, has become a very important element. Doug mentioned the comparative photographs—this range management period and these points in time that said, “Hey, you've got a big problem,” underscored that we needed tools to look at time. Time could be a longer period of evaluation, or, given what our human times are, an attempt to give ourselves an even longer span of time to understand what's going on, as comparative photographs

can do. Also in that period the technology was much more limited. There were no computers. We did have aircraft... we were beginning to get a few field drugging tools to mark animals...that was about it.

So our thinking ecologically has come a long way, but in the process of that I think one of the very hard lessons out of range management, certainly for me, is “if it’s simple, be careful.” Nothing I’ve learned in Yellowstone is simple and I know Yellowstone probably better than I’ve known anything else, which also tells me there’s still a lot of Yellowstone I don’t know and I wish I could stay around. But those are important lessons that carry into the present. It’s very easy to get so deep into numbers that you don’t back off and set them in context. To me, by one means or another, researchers need some sense of the land, whether you collaborate with the person who has that or whether your own research project and the methods you’re using give you time and opportunity to do that. I think that’s very important for a lot of work. It doesn’t necessarily apply to some kinds of research...particularly some of the present work that is much broader geographically...

but in a way I think it does because it keeps you grounded with what you’re trying to learn and understand.

So, those are my lessons: time; if it’s simple, be careful; numbers are a tool, computers are a tool, they’re great but don’t let them run you...and that’s what I have to offer for tonight. I wish good chance with your research projects in the future. I wish I could tag along and look over your shoulders. But that will have to be my shade. Thank you.

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Aubrey L. Haines Lecture

Feeling Our Way Beyond the Science

Judith Meyer

Associate Professor, Department of Geography, Geology, and Planning,
Missouri State University

Note: The text that follows is an edited transcription of the speaker's remarks at the conference.

Introduced by Paul Schullery

Thank you, Paul, for the gracious introduction! And a big “thank you” goes out to everyone on the conference committee for organizing this wonderful gathering. I am truly honored and humbled to be here.

As a historical geographer, I may seem the odd person out at a science conference. And, although Paul assured me I would not need to present anything either scientific or connected to this year's conference theme, I felt at least a little pressure to tie historical analysis to scientific analysis. Typically, historical data comes from people, is subjective, and has accumulated over a very short period of time. Most of the data you scientists collect and analyze comes from the natural environment, is quantitative rather than qualitative, and spans thousands if not hundreds of thousands of years. That said, I would like to take a moment to explain the title of this luncheon talk, “Feeling Our Way Beyond the Science.”

The word “feeling” describes how many of us engaged in studying Yellowstone are, in many ways, truly groping, testing, or feeling our way, hoping to grasp onto something that will ultimately help us manage wisely. Looking ahead, we are not really sure what is going to happen in terms of climate change...or societal change for that matter. Ever-changing economic and political conditions affect how many people live, work, and play in the Greater Yellowstone and what they do and how they behave while they are here. This in turn affects the park's ecological systems. Hence, as physical scientists and as social scientists, we are all really just feeling our way, seemingly in the dark.

I suggest we are also feeling our way because we genuinely care about this place, this park, this greater ecosystem. That is why a recent cover of *National Parks and Conservation Magazine* [Figure 1] jarred more than a few Yellowstone folk who read the cover description: “In an artistic rendering of a famous photo, Theodore Roosevelt poses on Glacier Point in Yosemite National Park.”

I am guessing most of the people in this room are familiar with the original photo used as a template for the rendering: the famous black and white image of Roosevelt and Muir in Yosemite probably jumped into your mind the minute you saw the magazine cover. But, looking more closely, the artist's rendering looks more like Yellowstone's Lower Falls than Yosemite Falls. Note the scale of the falls in a mountainous setting, the angle and color of the side slopes, the curve of the river, the shape of the spray. Perhaps it doesn't matter which waterfall this is. Perhaps all national park waterfalls are interchangeable. Perhaps one protected place is the same as all protected places.

This may be true for the general public, but not for us...the people in this room. For us, Yellowstone is not

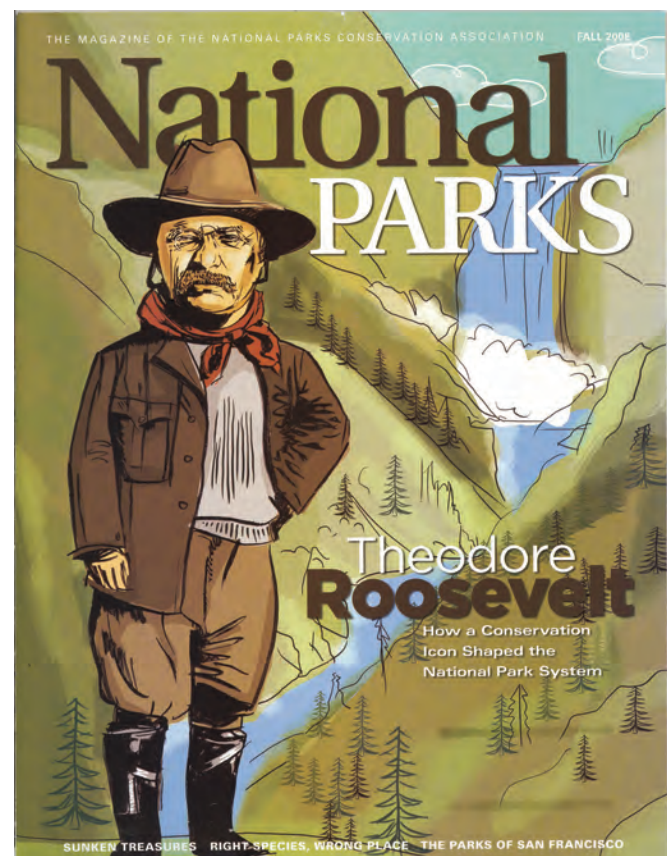


Figure 1. Cover of *National Parks*, Vol. 82, No. 4 (Fall 2008). Artwork by Johanna Goodman.

Yosemite. Nor is it Glacier, Rocky Mountain, or Mount Rainier. Yellowstone is unique. We know it in our heads and feel it in our hearts. Our feelings for this place are real and have value. It is our feelings that guide us down a management path straddling exclusion and alienation of the public on one hand and wanton abuse and degradation by that same public on the other. I don't know about you, but I have come to dread that overused, vacuous phrase, "loving the park to death." Let's get over the fact that 3 million people visit our "wilderness" each year, that the people and the infrastructure it takes to keep them happy are going to have an impact on the environment, and let's figure out how to manage this place as best we can for all the stakeholders, never forgetting that nature itself is also a stakeholder.

Back to the title: we are feeling "our" way, because managing Yellowstone is not about making decisions just for the people attending this conference. We are privileged to be able to work here only because Yellowstone matters to people outside this room. Whether each of us realizes it or not, the world recognizes Yellowstone, or at least the idea of Yellowstone.

The day the U.S. Congress passed a new law allowing guns in national parks, a cartoon showing Yogi Bear with a gun chasing Mr. Ranger appeared in newspapers nationwide. The picture really was worth a thousand words. The public knew exactly what Yogi and "Jellystone" represent, because Yellowstone is a symbol for all national parks. Hence, a lot is riding on what we do here and how we do it. We need a big tent to hold all of Yellowstone's audience, and we can't afford to shut anyone out...not now and not into the future.

Increasingly, demographers point out that the United State's future population will be quite different from the country's first 250 years. Looking at the country as a whole, the white population is graying and is only one of several minority populations with the Hispanic and Latino, African American, and Asian populations right behind. Will Yellowstone be relevant to the new, more diverse "us"? Yellowstone's success as a national park depends on its wonders being relevant to this new, more colorful audience: old, young, black, white, Hispanic, Asian, tribal, white collar, blue collar, over-educated, under-educated, wealthy, poor, urban, rural, texters and tweeters, wolf haters and wolf lovers, and gun haters and gun lovers. If the Yellowstone we know and care for is to survive, we need to welcome and engage its entire public. If we cannot appeal to a broad constituency, if Yellowstone cannot be a truly

national park with something for all Americans, Yellowstone as place and as concept will fail.

Continuing with an explanation of the title, we are feeling "our" way beyond the science. I do not mean against science or opposed to science, but accepting what science tells us and then moving a bit farther. As important as science is...and it is not only important, it is the very foundation of all we do here...we need to recognize there are questions science cannot answer. Measuring snowpack, counting animals, and examining lake sediments are all important, but there is a very real part of Yellowstone that cannot be measured if we limit ourselves to objective, analytical science.

Thinking beyond the science to the subjective, affective, and emotional dimensions of the park should also play a role in arguing for the park's protection and management. Having a "sense of place" means having an understanding of the physical attributes of a place combined with what it means to people. Naturally, different people will respond to a landscape—a place—differently, but that does not make understanding a shared sense of place impossible. Whereas science relies on a prescribed protocol, a control group, and repeated experimentation, historical analysis relies on circumstantial and anecdotal evidence which as a body or as a collection suggests that out of all the possible human responses to a place, there is often a common, shared experience lying just beyond the science.

Okay, back to this year's conference theme and historical geography: is there a historical perception of climate change, land use, and invasive species in the Greater Yellowstone? Let's start with historical perception of land use as part of our Yellowstone sense of place. Consider all the land-use changes made in this park over the past century or so: bear feeding stations, bison show pens, all the fabulous old hotels, Bridge Bay Marina, and the Old Faithful highway interchange. Yellowstone has undergone tremendous changes in land use since its establishment, and manipulating wildlife populations and building roads and hotels is only part of the story. The park was barely a decade old when Superintendent Norris felt it his duty to try to improve even the thermal features! He had a wooden trough built to carry water from active springs on the Mammoth Terraces to Devil's Thumb, an extinct thermal feature, in the hope it would repair and strengthen its cone and rejuvenate the spring...bring it back to life!

As far as historical perception of invasive species is concerned, the term does not appear in park literature

until fairly recently, and even then there is the problem of writers not being able to differentiate between natural change and unnatural change, or how long something needed to be in the park before it changed from being “invasive” to being “endemic” or “quaint.” Even so, visitors and managers alike wrestled with the notion of whether we should (or could) do something about it or not. Further, the historical record suggests this may a “pot calling the kettle black” situation.

As Pleistocene glaciers retreated, were the first plants and animals to move in “invasive”? Were the first people who wandered into Yellowstone an “invasive species”? As academics, we accept that tribal peoples probably had an impact on local if not regional flora and fauna. But, Euro-Americans certainly were and are invasive, and each new generation of park-goers has looked askance at the newcomers. The park’s historical record is full of complaints by horse-and-buggy tourists who considered automobile tourists invasive, exotic, and disruptive of Yellowstone’s natural order.

One of the perks of working in historical time spans and with human institutions, which is what Yellowstone National Park is, is that often we can still save parts of the traditional, bone-deep, historically appropriate experience before it is too late. Ecologists brought back the wolf, and concessionaires brought back the touring car [Figure 2]. Parts of the unique Yellowstone experience have not been

lost despite the invasion of private automobiles, hot tubs, and cellphone towers. Instead, an appreciation for tradition keeps us mindful of our role to protect our collective sense of this place. It is why we keep touring cars on the road and the Boiling River open to bathers. It is why we keep building new visitor centers and running campfire programs. We know these things are not natural, but they are somehow right and true to this place at this time.

At some level, the only difference between the modern human presence in Yellowstone and that of Dalmatian toadflax and lake trout may be that we are aware of our presence, aware of our impact on the park, and aware of the park’s impact on us. Yellowstone’s disappearing amphibians may be aware at some level of an increasingly confined and hostile environment. We humans are also aware of the park’s immediate physical environment. We know summers are hotter, peak runoff occurs earlier, and whitebark pine is dying off. Like the frogs, we are aware of changing environmental conditions.

But we are also aware of what the park means to us. Yellowstone is an example of what a democracy can do when people put their minds to it. It is a laboratory for science and a yardstick for measuring change. It is a place for recreation and camaraderie, a place for contemplation and artistic expression, a place to connect with Mother Nature, Vishnu, God, Buddha, Allah, aliens, or whoever or whatever is “out there.” We are aware of environmental



Figure 2. Touring cars return to Yellowstone to celebrate a reunion at Lake Butte, September 2010.

change and capable of making decisions about how to deal with it. We cannot stop global climate change or the next caldera eruption, but we can prepare for the future.

And finally, what role, if any, does climate play in our collective sense of this place? Historical analysis may not follow the protocol of scientific analysis, but it isn't haphazard or unscientific, either. I know some scientists who think history is too malleable...that history is about myths rather than facts, that science uses facts to dispels myths. A problem with myths is that once they get started, they can have tremendous inertia, especially when the loudest voices telling and retelling them are simply making things up to promote an unrelated agenda. Today, some people believe global climate change is a myth put forward by faceless, nameless "scientists"...the bad guys...who really want to take over the government, cut jobs, raise taxes, and force us to give up our big cars and warm houses. These climate change naysayers want us to go back to "the good old days" when things were right with America. But, those good old days were a time when our legal system did not bring abusive husbands and fathers to trial, our judicial system did not allow people of color to vote or sit on juries, and our educational system did not recognize dyslexia or other learning disorders. We tend to have deep, abiding affection for the past when "factoids" are woven together with "truthiness" and then presented to us whole cloth to convince us that something is true that is not.

In Yellowstone, myths are part of our sense of this place. The myths are endearing and make us feel special for recognizing them as such. Old Faithful erupts every hour on the hour. Lewis River runs uphill. Obsidian Cliff can be shattered by heating it and then spraying cold water on it. The Grand Canyon is so deep it is dark at the bottom and you can see the stars even at noon. Yellowstone's geysers and hot springs release as much carbon dioxide as cars do. Yellowstone employees are really well paid.

Many papers at this conference provided hard evidence that climate change is not a myth. Well, good historical analysis dispels myths, too. Aubrey Haines, Paul Schullery, and Lee Whittlesey did an incredible job putting the campfire myth to rest, but it was not easy. We love our cultural mythology; it makes us feel so good about ourselves. It is hard to give up the myth if it supports other things we want to be true. But myths divert us from looking for the real causes, real effects, and real solutions.

So, let's agree that climate change is not a myth. Does Yellowstone's historical record provide evidence of people's response or reaction to weather events or climate condi-

tions? Of course it does! And, this response or reaction can be quantified to some extent. Superintendents Langford and Norris, the park's first superintendents, were not men of science...they were administrators. Yet something about this place roused their personal and professional sense of both curiosity and responsibility. Both gathered climate data, but Norris left the best record of his thoughts and observations.

When colleagues at Missouri State heard I was giving a talk at a science conference, several offered their services to help me "crunch the data." They knew I had spent the winter looking at early superintendents' reports and that some of these documents contained climate data. Their offer of help reminded me of a favorite passage written by a tourist who camped in the park with several friends, all of whom were fishermen. The tourist, after valiant attempts to join his friends in their endeavor, declared, "I am not a fisherman...nor do I fish. Not that I revile you especially for being fishermen. No, sir. Every man to his own notion of pleasure, whether it's cutting out paper dolls or endowing libraries. I do not seek to reform you to my way of thinking. But personally I fish not, neither do I angle" [Smith 1924, 38-39]. Well, I am not scientist, nor do I crunch numbers. What interests me in the early climate observations and data is that it exists at all as well as the lengths to which early park managers went to secure it.

For example, in his Superintendent's Annual Report to the Secretary of the Interior for the 1878-1879 season, Norris wrote, "Mr. B.F. Bush, an early and enthusiastic member of the scientific association...accompanied me as assistant at a mere nominal salary, purposing to remain in the park during the winter to keep a regular weather record, and explore and sketch its main wonders, at present but little known at that season of the year" [Norris 1878, 979].

In the next year's report, Norris expressed genuine concern for keeping good climate data when he wrote, "I greatly regret the breakage of our thermometers and consequent want of weather records until they were replaced, but the records given in the Appendix have been kept with great care and are deemed accurate and reliable" [Norris 1881, 617]. The following year, he wrote, "The unavoidable failure of all my aneroid barometers to register correctly is a source of deep regret and a serious loss; but the thermometer readings, which have been regularly and carefully noted and preserved at the Mammoth Hot Springs during the entire season...will be perused with interest, as greatly increasing our meager knowledge of

the peculiar climate of these regions” [Norris 1882, 755]. And, “A journal of the transactions of each day was regularly kept...and the weather and elevations recorded at least three times a day. Only the size and purposes of this report preclude its publication entire herein, but the...record of weather and elevations (the former accurate, and the latter, for what of reliability in the readings of the aneroid barometer, approximate only)...will be found tolerably correct, and it is hoped will prove of sufficient interest to encourage the attention of scientists better prepared and outfitted than myself to do this wonderful region justice” [Norris 1882, 767].

Often, quantitative climate data is hidden in parts of narratives where the authors do not comment specifically but provide climate information nonetheless. Norris describes seeing ducks late in the winter: “Some of them remain late in autumn, if not indeed during the winter, as I saw them amid the dense fogs of the Norris Geyser Basin late in November of 1879, and on the 16th of November of this year I shot a fine one at the Mammoth Hot Springs, when the thermometer ranged 10 degrees below zero” [Norris 1881, 614]. Referring to days in the month of April, he wrote, “The 4th, 5th and 7th were clear, the 2nd, 3rd, and 6th rainy, and the snow so soft that traveling with my Norwegian snow shoes 14 feet long, was hard work” [Norris 1882, 807]. His narrative describing the tough travel conditions in July provides insight into snow depth and weather phenomena late in the summer: “Crossing the chilly waters of swollen streams...unprecedented depth of snow in the mountain passes...[and] wagons delayed by terrific hail-storms until the 5th” [Norris 1881, 573].

Equally impressive is interest in not just collecting data but “doing science,” hypothesizing about the relationship between thermal features and local climate conditions: “An ambitious scientific signal-officer at the Mammoth Hot Springs or the Geyser Basin, or both, might, with little additional duty or expense, greatly aid science in solving many interesting and practical questions connected with the origin, character, duration, and decadence of each of these various classes of hot springs, the degree of their connection with the earth’s internal fires, and their combined influence upon the climate of the park” [Norris 1878, 844].

Along with quantitative data of what temperature it was on which day, or whether it snowed or not, Norris also made personal observations, providing insight into how people responded to the weather. As one might expect,

Yellowstone’s weather was fickle even back then. Norris writes about his trip into the Hoodoos, a place he referred to as “Goblinland”: “In early September we were terribly annoyed by fogs and storms...during the entire day of September 6 we remained, amid chilling fogs...standing behind our monument of last year with compass and field glass, ready to catch every glimpse of sunshine or opening in the shifting mists below or about us. But the terrific snowstorm, which had kept us in a clump of fir trees at our camp of last year during much of the 4th and all of the 5th, re-commenced with such fury that we hastily descended to where the weather was warm and pleasant, with little snow. With the dawn came a snow-storm so furious that we yielded to the inevitable and descended. The next day, I returned through mingled snow and sunshine” [Norris 1882, 791].

Tourists and employees, too, recorded their perception of Yellowstone’s weather as part and parcel of their park experience: “Storm clouds piling up on the majestic brim of the Continental Divide, rumbling across the gray sky to



Figure 3. Photo labeled “Snow in the Park Forests, June 13, 1899” on page 65 of Hiram Martin Chittenden’s (1912) *The Yellowstone National Park, Historical and Descriptive*.

make a setting for a crashing, Wagnerian storm. A sinister muttering in the tops of the trees. A nervous chattering on Beaverdam Creek. The lonely, frightened cry of a solitary bird darting for shelter. A wet feel in the wind that drives down on the camp—a cold feel, too. The rain makes a friendly obligato of tiny drums on the tent. The tumbling, yellow creek lends it voice. The trees bend closer to catch the harmony—A rainy day in a snug camp. Surely this moment is the best” [Smith 1924, 58]. But it isn’t just a cold rain that tourists note: “The trip this afternoon was strenuous, we suffered from heat—a burning sun—and our progress was retarded by rutted roads and snow drifts; this incongruity is in keeping with the unfamiliar world we are in” [Patton 1917, 3]. One might say, “there’s no accounting for taste,” or “Yellowstone has something for everyone,” but it is Yellowstone’s unique variety and the juxtaposition of ice and steam, wet and dry, blue skies and black storm clouds that endear it to its public. How easy it is to accept the “weirdness” of this place!

Evidence of how people perceived climate appears in the historical record in yet another dimension: as therapeutic. Yellowstone’s air is described as clear, dry, cool, cold, hot, refreshing, bracing, thin, invigorating, good for what ails you, and “healthy” in contrast to air quality and conditions “back home”...wherever home might have been. How lucky we are to have Yellowstone’s fabulous collection of historical images: photographs, sketches, paintings, and postcards to help us understand past climate conditions! Some sources may be sketchy and the sample size small, but the same might be said of finding dinosaur bones, and that hasn’t stopped paleontologists from recreating detailed dinosaur taxonomies.

Some historical photographs provide evidence of very specific meteorological events or conditions. This [Figure 3] is a photograph showing forest composition as well as depth of snow on June 13, 1899. Historical images have found new life and relevance in re-photography studies by providing a baseline for measuring change. Most of you know the famous glacial erratic not far from Canyon Village, which is itself evidence of glacial transport processes and climate change. It appears in a 1904 guidebook [Figure 4], and even a quick comparison with the view today reveals how the forest has changed. Especially evident is new growth from the 1988 fires.

Official reports, tourist comments, photographs, paintings, Ken Burns’ documentary on the national parks: all this becomes part of Yellowstone’s historical record and reminds us that we are continuing to write that history

today by attending this conference. We have become part of that story. When some future academic reads the conference minutes, what will he or she deduce of the power of this place? What myths will dog us into the future: those silly people thought they could exterminate wolves and then simply put them back! Those people thought they could let bears eat garbage and then teach them to be wild again! They thought they could pump carbon dioxide into the atmosphere, and it would not have an impact on global climate!

If Yellowstone’s historical record can shed light on the current situation, one ray of hope shining from the



GRANITE BOULDER, NEAR INSPIRATION POINT.

Figure 4. Photo labeled “Granite Boulder, near Inspiration Point” on page 325 of Hiram Martin Chittenden’s (1912) *The Yellowstone National Park, Historical and Descriptive*.

past might be that Yellowstone has a capacity for infecting its public with a curiosity for science and scientific endeavors, a love and respect for tradition, and a sense of social responsibility to protect and preserve this place. When Yellowstone National Park was only five years old, Superintendent Norris wrote, “The wisdom of Congress in promptly dedicating the National Park has never been seriously questioned...not the dedication of a lofty mountain-girt lava region destitute of valuable minerals, isolated and worthless of all else, but matchless and invaluable as a field for scientists and a national health and pleasure resort of our people” [Norris 1879, 992].

Science and people: the two have been intertwined—inseparable—in Yellowstone from the very beginning. Let us not forget that. When we are counting beetles or measuring rainfall, let us not forget the awe and wonder of this place. When we are watching Old Faithful erupt standing elbow to elbow with hundreds of people, let us rejoice in Yellowstone’s popularity. Let us not forget what a fragile, rare, and amazing geological confluence of water and heat it is. And let us individually and collectively not forget our obligation to Yellowstone’s future. Each of us has it in us to do so, and we must not sit idly by. Perhaps by “feeling our way,” we will “find a way” to show the world the true power, purpose, and promise of this very special place, this Yellowstone National Park.

Suggested Citation

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Keynote

Long-Term Perspectives on Climate Change and Ecological Impacts in the Greater Yellowstone Ecosystem

Steve Gray

Director, University of Wyoming Water Resources Data System, and
Wyoming State Climatologist

Note: The text that follows is an edited transcription of the speaker's remarks at the conference.

Introduced by Indy Burke

Thank you very much. I appreciate the opportunity to be here. It's such a wonderful time to be in Yellowstone.

All right, a couple things I want to talk about today. First off, given this theme of questioning our future in the Greater Yellowstone area, I'd like to take a few minutes to consider what the pathway to that future might look like. Or, what it's going to look like headed out from today to somewhere out 20, 50, 100 years from now. And first, I'd like to look at our working model...or our operational model...for how we think climate and ecosystems might change over time. We can think of this as the trajectory, or the shape of the trajectory, or the slope, or the character of that line if we're graphing this out through time in, again, how climate or ecosystems might change. Then I'd like to talk about the geographic footprint...or spatial footprint...of how these changes might play out over time. An example of that might be how we expect species to move across the landscape or across the region in response to warming, or, perhaps, how we would expect the species on a mountainside to change as a result of an altered climate. And, really, most of all, to think about—or challenge you to think about—how the working model or the operational model that you have in your brain, of how we're going to change over time and how that affects the decisions that you make and your ability to adapt to or, in some cases, mitigate the changes that might be coming down the pike.

So, in order to do that, I'd like to do it in a little different way. I'm sure that you've seen many, many presentations on say, predictive modeling for what the future might look like or things of that nature. I want to step back (and way back in some cases) and look at how climate has changed in the past and how ecosystems and species have responded to those climatic changes...with the very important caveat, that, as they say in the stock market, "past performance is no guarantee of future performance."

But rather that, we don't have many good examples of how climate and ecosystems are going to change based on our experience. So, if we expand our window and go back in time, then we can get some sense for how climate and species, for example, have changed in the past. I'm going to talk a little bit about how migration and vegetation have changed, changes in ecosystem structure and function, as well as a little bit on the characteristics of natural or inherent climate variability with a particular focus of what happens when we experience drought. And the reason why weaving drought into everything is actually a pretty good one, in that in the future we can expect it's going to be warmer in the western United States. That's just a given. That's a fact. That's basic chemistry and physics. We know that it's going to be warmer.

But, precipitation could go one of two ways. It could get drier overall or in certain seasons, and that means that—because of the "one-two punch" of additional warming and drying or transpiration, plant water use, and evaporation and so forth—that in many cases what we think of as drought today could more or less become



Figure 1. Wyoming State Climatologist Steve Gray.

the norm in the future. Now, on the other hand, that if it could get wetter in some seasons at some time in the future, but it's still warm, the fact of the matter is that inevitably we're going to experience drought conditions. Also, failure of snow or other types of precipitation... and with the added warming...that's going to mean the potential for more intense droughts, perhaps droughts of longer duration, and more chance for drought impact. So, that's why drought is an underlying theme of what we're going to talk about today.

So, just to jump into things here, let's talk about how a species migrated in the past in response to climate change and how this has led to fundamental change to vegetation out there on the landscape. This is just one example from many in the western United States, but one that I happen to be familiar with: looking at how Utah juniper got to where it was hanging out at the end of the last ice age to where its current northernmost distribution—just right at the edge of the Greater Yellowstone area—is today...up in areas of the Bighorns [Bighorn Mountains] and the Pryor Mountains, for example.

And to tell this story, I'm going to use information that we get from this little guy: this is the bushy-tailed woodrat [Figure 2]. It has this fantastic property: it has the capacity to be the greatest vegetation ecologist on the planet. This guy goes out and does a fantastic job of sampling all the vegetation in the area around its nest site, brings little bits of it back to its nest, urinates and defecates on it (does some dirty little business there), but that actually serves to preserve those little bits of vegetation over time. And, after a while it forms a nice hard rind around the little bits of seeds or leaf material that it brings into the nest. You can actually find well-preserved middens, or nests, essentially fossilized out there in caves or overhangs. In one case, there is a 35,000-year-old specimen from northeastern Utah with very little bits of identifiable plant material in it. If you go to many different locations and gather these, you can have very precise radiocarbon techniques to find out when a plant is present on the landscape and you can get a fantastic idea of how the vegetation has changed over time.

Now, the story of the Utah juniper and how it was hanging out at the end of the last ice age to where it currently resides...its northern distribution...there's some interesting stories there of how climate and in particular cycles of wet and dry really paced this migration over time. The story really gets interesting for our purposes when we look at the spatial progression of it, or the geographic migration of it, over time. Now, all things being equal,



Figure 2. The bushy-tailed woodrat (*Neotoma cinerea*; also known as the pack rat).

what we would expect...or what I would expect at the beginning of this process...was that we would go from where it was hanging out at the end of the last ice age and then we would have this nice progression to where the oldest populations would be closest to that hangout and then the youngest populations would be, for instance, in the Pryor Mountains. But what actually happened is a lot different.

We actually got to the middle of this distribution 6,500 years before present, and the second oldest population is the northernmost population today. So, it made a leap of many hundreds of kilometers, defying the great degree of this wonderful, practical model of how species migrate through time. It's a demonstration of the complexity of some of these migration events or the course that these migration events can take over time.

Now, things can get even more complicated when we look at the infilling or backfilling of this distribution over time. A very interesting event such as the fact that or features such as the fact that, say, up in the northernmost area in the Pryor Mountains it took something like in the neighborhood of 3,000 years to get from one side of the Pryors to the other. Or, right next to our oldest population is one of our youngest populations. So, an enormous amount of spatial and temporal complexity in the way that this migration event played out over time is evident.

Now, we can explain some of these patterns based on the fact that up in the Pryor Mountains it's very warm, it's very dry, and it probably made an excellent target for Utah

juniper to land on back in the mid- to late-Holocene. No problem there, but some of these other features...like how it took Utah juniper so long to get from one side of the Pryors to the other...it's either something due to dumb luck or it's something we don't understand well enough to put into a predicted model. And it comes out to be, in a practical sense, something similar to what might happen in the future.

Ecologists love to make up words for this kind of stuff and the terms that come out in the literature when you look at studies like this are first "ecological legacies" and "historical contingencies." And that's simply a way of saying that what we see on the ground today is just a long stream of events, whether it's disturbance, whether it's drought, whatever it might be...that leaves its imprint on the system. And second, what we see on the ground today is not just a product of what happened a few years ago, but it's the sum total of what we had on the ground to begin with, what species were on hand at different points in time, as well as factors such as soils and topography that mediate or control the progression of these events. And over and over again...and this is just one study typical of many throughout the western United States...this points to the fact that there is tremendous potential for what you might think of as threshold-type responses or non-linear-type responses of vegetation, species, whatever it might be, to climate change or forcing by climate.

Now, step back for a minute again and think about what I'm talking about here. I'm talking about species migration in response to climate that plays out over many hundreds or thousands of years. What we're talking about with future climate change are events that are going to be taking place on the time scales of decades. And we have the added complication of land-use change, exotic species, and all of these other factors that are going to be playing out on the landscape. That is going to be the sum of the changes of vegetation and system that we're going to be dealing with in the future.

So, the bottom line from this and many other studies throughout the western United States is that migration in response to climate change can be very messy. That means it can be hard to predict in a practical sense...but that's just the reality of the situation. So, imagine how complicated it is when we have this playing out over many thousands of years...what's going to happen when we have a world with exotic species, land-use change, etcetera? And that's the problem that we're faced with.

Talk a little bit about the role of vegetation change,

ecosystem changes...however you might think about it. And, in this case I'm going to switch species a little bit and talk about a similar problem and that's how pinyon pine reached its northernmost distribution in northeastern Utah at a place called Dutch John Mountain, where a lot of this type of work has been done. And again, we're going to be using information from those pack rats, those bushy-tailed little creatures called woodrats, but supplementing that information from the large and small patterns from the rings in trees that can give us insights into past climate as well as using tree rings to date when individual plants and trees showed up on the landscape.

And we're talking about a system from where we go from a landscape or watershed, where we go from essentially no pinyon on that landscape to pinyon dominating the landscape...being the main player in terms of biomass or individuals. It's happened in a very short, short period of time...in just a matter of decades, really. One particular area, the Dutch John area watershed, it had basically been dominated by Utah juniper from about 9,000 years before present, but then pinyon arrives at nearby sites—in neighboring watersheds—about 800 A.D. or so. But then we go from no pinyon to pinyon domination around 1300 A.D. Now, we get the sense of how this might play out in relation to climate if we compare it to the tree ring record of drought in this area, and what we see is where pinyon pine shows up in other areas (other watersheds) around 800 A.D., we don't have much chance for pinyon pine to move into this particular watershed as we go through a period or a series of extended, very deep, very severe droughts. It's just not the right conditions for the establishment of a new species.

Then, we do have a very small population of pinyon pine that shows up on Dutch John Mountain about 800 A.D. or so, but as you might expect, things don't really get going here because we go back into another extended drought period. A drought that many of you may be familiar with that's associated with many vegetation and social changes in the western United States (the Anasazi abandonment, for example). And then we go into this period here where we go into this rapid vegetation change and that switch over to pinyon domination in this area that happens to coincide with a wet event. So, this, and many other studies from the western United States, point to a recipe for how you can have this type of rapid vegetation change and it essentially looks like this: that in cases where you have extended dry regimes, where you have extended droughts, you can have through mortality or other kinds

of means. You can open up niches or resources out there on the landscape that allow new species to come in. In some cases you can't see these step-like changes in the vegetation and ecosystem. Add another wrinkle to this and if you follow up that drought with an extended dry regime you set the stage for low mortality, rapid recruitment, and in many cases you can see fundamental ecosystem change or turnover if you have this recipe or set of circumstances.

When we think about the future, the recipe—or the potential recipe—changes in that not only are we thinking about dry regimes that are likely to be intensified by warming...more plant water use, more evaporation and so forth...increased disturbance, as well as the fact we're very well dealing with warm and wet conditions in the future that can, in turn, set the stage for cold-intolerant species as well as facilitating the rapid recruitment of new species that come in. And I think it's worth asking the question: if this is a recipe for wholesale vegetation change in some parts of the western United States. But the bottom line is that ecosystems can change in what you might call "fits and starts." At the timescales that you're interested in, that you're going to be doing management activities at (multiple years to decades), it's going to look like nothing is happening over time in many cases. Then, there is the chance that you can have many rapid changes out there on the landscape and, frankly, that's going to be difficult for us to deal with given the way we operate today. And, again, in this study and many others from the western United States—and worldwide for that matter—we see the potential for threshold-like behavior and non-linear change in these systems.

To wrap up with some ideas about natural climate variability or the characteristics inherent to climate variability that are out there...to do this, we can look at tree rings as a measure of what's happened in the past, and one particular example comes from the Yellowstone area. What you see is—over time, going back 800 years or so—a tremendous amount of year-to-year variation in precipitation, but that year-to-year variation is also embedded in longer-term changes and shifts that happen over multiple years and decades. You start to get a sense of that when we, say, smooth that reconstruction with a 15-year moving average, [and] you begin to see periods where it is predominantly wet or predominantly dry, and we tend to switch between these two different states and, in many cases, don't spend much time around the mean.

The poster child for this is when you look at flow

variability in a large watershed like the Upper Colorado River, but the lesson is the same from record to record, in that you see time and time again that the underlying natural climate is non-stationary in and of itself. Instead, that it is characterized by switching by persistent wet and dry regimes, warm and cold regimes, whatever it might be. This is what really characterizes natural climate variability over time...it is non-stationary in and of itself.

A couple things to note:

1. Elements of this non-stationary activity are with us for the foreseeable future, because in many times they're tied to natural variations in how the oceans, say, move heat from the equator to the poles and things of that nature. So, it's built into the system and it's going to be with us for the foreseeable future.
2. At the same time, these same components of the climate system that bring us this non-stationary activity, they're essentially run on heat...it's a "heat engine"...so, adding more heat to this system is likely to alter the characteristics of that variability and there's the potential that it's going to ramp up or amplify portions of that variability that is with us all the time.

So, going back to our model of how climate changes over time. [What] I would submit to you based on my discussions with many resource managers in the western United States is that the way we tend to think about climate change over time is basically this linear trend from where we are today to where we are likely to be in the future. But the fact of the matter is that the inherent non-stationary/built-in variability will be with us for the foreseeable future. It's the combination of that trend and the variability that is going to dictate what we deal with on an operational basis from year to year and decade to decade. And how that natural variability and that trend are combined is really going to be responsible for that climate that we experience and deal with on an operational basis as well as determining the overall impacts that we see on these systems.

We can map out, or graph out, the history of the climate of Yellowstone by going back a thousand years. Basically, we take reconstructive precipitation records from tree rings, and then temperatures, and put them on a common scale and plot them out. And essentially what one sees when they do this is that sometimes we're cool and wet and sometimes we're warm and dry. We spend a lot of time going back and forth between these different general

climate types in the Yellowstone area. We can then add on what has happened in the twentieth century and then we can see that we are moving toward that warm end of the spectrum...but most of what we've experienced is within the bounds of what we've experienced over the last thousand years. Where things get interesting is when we, say, introduce 1 degree Celsius of warming to the system. In that case, we start to move outside the bounds of anything we've experienced over the past thousand years. That's 1 degree Celsius. If we were to map this out using a 3 to 4 to 5 degree Celsius temperature increase...and that's within the realm of possibility toward the middle to end of the century...then we start to look at something that graphs out over here. We're really talking about a fundamental change in the climate of this area.

So, bring this back to what it might mean, or some suggestions or thoughts on what this might mean for management of the Greater Yellowstone Ecosystem. So, back to that concept of how we think about climate change over time. If we're honest with ourselves, the way many of us think about climate change is a linear trend into the future where we take what we've got today and "jack it up" or "ramp it up" a little bit, but essentially we're dealing with the same animal through time. Or, we think of the change as being what we experience with our southern neighbors. The fact of the matter is, based on the best available science, what we know of the potential for climate change in the future is that we're essentially dealing with a completely different animal at some point in the future. What that point might be it's difficult to say, but it will be fundamentally different than anything that we've ever dealt with.

Really, here, we're just talking about changes in average conditions. Changes in average conditions are not really going to have much of an impact on how you do business and the way that you work to manage these systems. But because of that combination of changes in the averages, because of the trends combined with the inherent variability...and variability because of human impacts on the climate system...we're bound to see a wide array of climates in an operational sense, in a year-to-year sense, in a day-to-day sense. Some of them will be like what we've experienced in the past and some may be radically different from what you've dealt with in an institutional sense. That is what we should be thinking about as the reality of what we're going to be dealing with on the ground as a result of climate change.

So, what I would suggest are the "Big Three" implications for management:

1. Species, ecosystems, and components of ecosystems are not necessarily going to move in a nice orderly way from the south to the north. Folks from Yellowstone are not going to be able to take the playbook from Rocky Mountain National Park and just play off of that at 2050. It's not going to work that way.
2. Change on operational timescales is not likely to be gradual or steady. We can be out there monitoring for three, five, seven years, and should we expect to see any change? I would say, not necessarily so, but it may happen very rapidly. And there is a chance from the potential of threshold responses and non-linear actions or interactions that we're going to get surprised...and that's just the fact of the matter.
3. Overall, if we're talking about a new climate here, we're talking about a new ballgame. We're not talking about the end of the world, but we're talking about a different set of rules. I think it's worth asking: as we go through this process and in particular thinking about our future, whether some of the options or the policies that we use to do business today are going to be viable in the future. The fact is because of that trend and because of that inherent variability, climate itself and many of the management goals that we are pursuing are likely to be moving targets. Climate changes, but not in a simple, easy fashion. It's going to be continually changing through time.

It's not just climate, it's climate plus. It's climate change plus exotic species change plus land-use change. It's the mix, the interaction between these that we're going to have to manage in the future. We have to keep that in mind...we can't just say "it's really climate that we have to focus on." We have to think about these challenges jointly.

And then, finally, for the good news: it is a complicated picture. There is a tremendous amount of uncertainty out there, but we have tools to deal with it. It's just that...land managers, scientists...we're not used to dealing with problems like this in ways that the future is going to require, but we can learn from others. Think, for example, of some of the problems and issues that we've dealt with in the past. Say, the Cold War...we didn't know if the Soviets had enough grain to make it through the winter...

at the same time that they were doing some crazy stuff like manipulating world markets to keep us from knowing how much grain they might have on hand. We didn't know if the government might be toppled and then we might have a bunch of hungry, crazy people with a huge nuclear stockpile. But the way we dealt with highly uncertain situations like that—we can borrow ideas from, for example, the military and how they dealt with those situations. Or, look to examples in the business world. UPS [United Parcel Service] could not have known about the Iceland volcanoes, but their customers expected them to have a backup plan. The techniques that are used in business to deal with uncertainty and complexity...we can borrow and learn from that.

One example might be how Leigh Welling and the climate change group are using scenario planning to look at some of these issues. That's only one example of how we might borrow work from those who have gone before us. It might, in some ways, seem like the easy way out, but the fact is...or in my opinion...we can't lose if we do a better job of monitoring the systems that we're in charge of managing. Whether we're talking about managing the climate itself or changes in the ecosystem (or components of ecosystems) that matter to us, this is a win-win in that it helps us prepare for climate change and it helps us prepare for

problems that we know we're always going to face whether it be drought, or regulatory, or legal challenges that might be out there on the horizon.

And then finally, I'll submit to you that you cannot lose when you improve ways to share data and information with the people who need it: the people who are making decisions, the people who are thinking about the future of a place like Greater Yellowstone. It seems like a cheap answer, but if you examine what we're doing today I think you'll find many opportunities in how we pass data and information around and get it to the people who need it. So, I appreciate your attention and thank you very much.

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Keynote

Developing Priorities for Managing Invasive Species in the Greater Yellowstone Ecosystem

Bob Gresswell

Research Wildlife Biologist, Northern Rocky Mountain Science Center,
U.S. Geological Survey

Note: The text that follows is an edited transcription of the speaker's remarks at the conference.

Introduced by Jeff Kershner

Well, thank you, it's really a great pleasure to be here this morning and an honor to be invited. I thank the planning committee for having me here. Also, [I] want to say a special thanks to Emily Yost and Tami Blackford for putting up with all the missed deadlines and so forth over the last six to eight months. Thanks.

Today, I am going to talk about invasive species. My title is very broad, but I'm going to focus on what I feel is one of the biggest priorities for managing invasive species in the Greater Yellowstone.

The issue of invasives is strongly influenced by human values associated with native species. Estimates suggest that over 50,000 alien species, species not found in North America, have been introduced into this country. As a matter of fact, 98 percent of the food we eat comes from plants and animals that were introduced into North America from other places in the world. This currently contributes \$800 billion to our economy. Furthermore, when you think of all the other exotics that were brought into this country for landscaping and other commercial interest, it is apparent that while we may damn invasive species one hand, we often have no one to blame but ourselves.

On the other hand, I think that we have to recognize that these invasive species are the cause of the decline of many of our native species and the cause of many ecological problems across North America. They have a substantial effect on the economy: over \$97 billion had been spent for just 79 exotic species up to 1991, and that was the most recent figure that I found. This figure has undoubtedly doubled that in the last 20 years.

It's really hard to estimate the exact ecological damage that has been done by invasive species in North America. It has been estimated that there are over 750,000 native species, but the life histories of the majority of these species remains unknown. Therefore, it is often difficult to assess

the effects of invaders on the native flora and fauna. It is well documented, however, that over half of the 958 species that are listed under the Endangered Species Act are there because of either competition or predation by non-native species. I think this is an important fact to remember.

Recently I completed a publication in which I discussed the negative effects of invasive species, and the editors wanted me to be very careful about defining "invasive species" because of the values involved with the word. It was suggested that I refer to rainbow trout, a species that was native to watersheds along the western coast of North America and subsequently introduced to waters across North America, as a "non-indigenous" species because it had been introduced on purpose by land managers, and rainbow trout had a great value to the angling public. They felt that the word "invasive species" should be left to the plants and animals that had no socially redeeming value. This example illustrates the difficulty associated with identifying a species as invasive, especially when we talk about non-native fishes which are important to many anglers. These introduced fishes are often referred to as wild trout. For instance, brown trout that now occur in many streams in Yellowstone National Park were not historically present anywhere in North America.

For the remainder of the talk, I would like to focus more specifically on the native Yellowstone cutthroat and some of the issues that threaten its persistence in the Greater Yellowstone Ecosystem. Yellowstone cutthroat trout evolved in the Great Basin over the last 3–6 million years, most recently in the pluvial lakes in that basin that occurred during the Pleistocene. It is estimated that 14 different subspecies of cutthroat trout during that time evolved, and one of those, the Yellowstone cutthroat trout, occurs throughout the Greater Yellowstone area. During the Pleistocene, however, the Yellowstone area was under about 5,000 feet of ice in some places, and 20,000 years ago, there weren't too many Yellowstone cutthroat trout in the region. Apparently, Yellowstone cutthroat trout inhabited Lake Bonneville during the Pleistocene, and at the end

of the glacial period, when that lake began to drain and the lake was receding, the Yellowstone cutthroat moved up the Snake River and over the Continental Divide area and into Yellowstone Lake.

It is important to note that when the area was originally surveyed by David Starr Jordan, one of the first fishery biologists in this country, about 40 percent of the steams in Yellowstone National Park were totally devoid of fish. Apparently, physical barriers, such as waterfalls, blocked upstream movement of fishes, including Yellowstone cutthroat trout and mountain whitefish that were moving into the area following the Pleistocene glaciations. It didn't take us long for this to change, however. In 1889, the same year that Jordan made his survey, some of the first non-native brown trout and brook trout were introduced into the Yellowstone National Park.

Currently, genetically unaltered Yellowstone cutthroat trout in Yellowstone National Park are restricted to the headwaters of the Yellowstone River and Snake River watersheds. The remaining populations of Yellowstone cutthroat trout reflect genetic mixing with introduced rainbow trout. The westslope cutthroat trout and grayling that were here in the Madison River have been totally extirpated. Now non-native rainbow trout and brown trout dominate that system. Many of the smaller headwater streams that were originally barren of fish now support populations of non-native brook trout.

In Yellowstone Lake, an area where I worked over 17 years in the 1970s and '80s, there were only two native fishes: Yellowstone cutthroat trout and longnose dace. Although Yellowstone cutthroat trout were found throughout the lake and some of its tributaries, the longnose dace were found in the tributary streams and the mouths of those streams and in some of the lagoons in the lake. Management activity through the early part of the twentieth century included non-native fish introductions, spawning operations, and angler harvest, and all these activities had a negative effect on the Yellowstone cutthroat trout in the lake. For instance, the hatchery operation alone led to the removal of over 800 million eggs in the first half of the twentieth century. These eggs were all used in the hatchery system and most were stocked back into Yellowstone Lake, but...as we know from some of the activities that occur with salmon in the Columbia River system...this is not something that generally enhances the wild stocks. Although there was substantial effort to keep eggs collected from individual tributaries separated, there was the potential for mixing the 68 individual spawning



Figure 1. Non-native lake trout (*Salvelinus namaycush*). The smaller fish in photo are native Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) removed from lake trout stomachs. National Park Service photo.

populations around the lake. Those of you who have been around hatcheries realize that despite all the great intentions, mixing can occur, especially during the stocking... [which] commonly lead to this mixing. Most importantly, the number of Yellowstone cutthroat trout that were allowed to move upstream to spawn naturally was greatly reduced during that period of time.

There were also unofficial fish introductions, including the longnose sucker, the redbside shiner, and the lake chub. The longnose sucker first appeared in the 1920s and the shiner and chub in the 1950s. In 1985, brook trout were found in Arnica Creek. There was no evidence that the brook trout were in Yellowstone Lake, and therefore, the National Park Service and U.S. Fish and Wildlife Service rapidly initiated eradication efforts. That year piscicide was applied to Arnica Creek, and a second application was completed the following year. All subsequent monitoring suggests that the brook trout were completely extirpated from the system.

By 1990, when I left the park, a series of restrictive angling regulations had resulted in numerous positive changes in the Yellowstone cutthroat trout population, and size and age structure appeared to be approaching levels observed when Americans first came to Yellowstone Lake.

Then things changed. In 1994, the first lake trout was identified in Yellowstone Lake [Figure 1]. And I remember it well. Cathy [Whitlock] and I were visiting in the park, and one of the rangers from Bridge Bay brought this lake trout to the fisheries office. I felt like somebody

just punched me in the stomach, because I knew that at that point the Yellowstone Lake ecosystem would probably undergo significant changes. Although it was possible that the young of the two trout species might compete for food, predation of cutthroat trout by lake trout would be the most disturbing consequence. Lake trout grow to immense size and they eat cutthroat trout. In order to determine the most effective means of dealing with this predaceous invader, the National Park Service convened a workshop in the spring of 1995 that included scientists and researchers and managers from all over in North America.

Although numerous techniques for lake trout suppression were discussed, it was apparent that gillnetting was probably the most suitable method in the short term. Gill nets have been used in commercial fisheries and inland waters for centuries. Furthermore, many of the scientists at that meeting were involved with programs to maintain and restore native lake trout populations in the Midwest, and many of those populations had been severely depleted by commercial fishing with gill nets. The lake trout have prospered in Yellowstone Lake. Many lake trout exceed 15 pounds, and the largest captured to date was almost 27 pounds.

At the same time, however, the cutthroat trout has not fared well. The lake trout were first found in 1994. Clear Creek is one of the tributaries on the east side of Yellowstone Lake. The cutthroat move into the stream in the spring run-off—usually in May or June or [the] early part of July—and spawn and then return to the lake. We had a monitoring system there since the 1940s. It's the longest solid monitoring of Yellowstone cutthroat in Yellowstone Lake. We also had a fall gillnetting program where we sampled the same areas every year during September and we had the average number of fish per net. So, in the '70s and '80s and up until 1990 the numbers were quite high. But then beginning when these lake trout were first discovered in the lake there was this vast decline. The number of spawners in Clear Creek that during the '70s and '80s averaged about 50,000 running into Clear Creek every fall. During the last five years that number has been closer to 500...substantial effect on the cutthroat trout.

The anglers have also seen a great change. The number of fish caught per hour by anglers has drastically dropped by well over 75 percent since the introduction of lake trout. The average size has increased to sizes we never saw before in Yellowstone Lake and that's because there's so few of those cutthroat left. There's been a substantial trophic shift in the structure of that lake. We now see larger zoo-

plankton because the cutthroat trout are so few and far between in that lake now. The zooplankton are larger, they graze more greatly on the phytoplankton, the water clarity has increased...there have been substantial ecosystem-level changes beyond just the reduction of cutthroat trout. At the same time, the lake trout are almost up to the level of cutthroat trout in terms of the angler catch.

Now, as I alluded to there, the fact that these cutthroat trout have been depressed in Yellowstone Lake has a lot bigger issues than angler satisfaction. In the 1980s up until 1990 when we had some good estimates, about 300,000 park visitors per year would stop at either Fishing Bridge or LeHardy Rapids just to watch spawning cutthroat trout. There were more people watching cutthroat trout than there were people angling for all species park-wide during that period. And that has all changed now. If you've been to Fishing Bridge you'll be lucky to see any trout. And not only that, the ecosystem extends well beyond our human values. The grizzly bear, otter, several mammals in the system, over 40 different birds, moved into the lake area each spring for breeding and counted on these cutthroat trout to be accessible for feeding. Lake trout spawn in the fall and in the lake and are not a substitute for the Yellowstone cutthroat trout.

Bear activity in Clear Creek and the number of fish in the trap are correlated, and there is a parallel between number of bears feeding and populations of cutthroat trout. We're going to hear a lot more of this later this morning. Currently there are very few bears feeding on fish in the lake area.

As Jeff [Kershner] mentioned, in 2008 we had a review after 14 years of the lake trout removal program, and we brought together scientists from across North America (quite a few of those folks had been there at the initial meeting) to discuss the lake trout gillnetting activity and to determine what we felt that the program had been accomplishing [Figure 2]. We had [been] asked to evaluate what the effectiveness of the lake trout suppression program [was]. We also [were] asked to evaluate the emerging technologies program at different opportunities, and were there other activities besides gillnetting that could be done...and also to provide some idea of how things might be different in the future.

When we looked at this it was obvious that the predation by lake trout had been reduced and that the growth of the lake trout population had been decreased somewhat. On the other hand...it was pretty obvious also that the cutthroat trout would be even smaller had there not been this gillnetting activity during that period of



Figure 2. The 2008 scientific review panel that evaluated the park's lake trout suppression program and provided direction for future suppression and recovery activities. National Park Service photo.

time. On the other hand, it was also believed that based on the evidence that we saw that the Yellowstone cutthroat trout population would continue to decline and that to date there was no solid evidence what exactly the effect had been on the lake trout population. There were many other options in suppressing lake trout and although none of those technologies were ready to implement at this time, the panel felt there should be more effort to looking for alternatives to gillnetting and these new emerging technologies should be integrated into the program. Not as a substitute to gillnetting, but to be used with it.

In terms of alternatives for the future, we felt there [we]re substantial data gaps to be filled. The intensified lake trout program could bring about the decline of lake trout, but it would take a substantial effort. The level of harvest that would be necessary to do that...again, we were unable to determine what that level would be because there were so few data available to even identify the...for instance, we don't know what the population level [is], the number of lake trout in Yellowstone Lake. We don't know where they spawn. We know a couple of areas that are being used, but these lake trout which were initially found in the West Thumb of the lake are now found all through the lake and we have no clue (other than some areas around West Thumb) where the spawning occurs.

So, what are the top priorities for the lake trout suppression program? Well, there were four recommendations that were made.

1. First of all, to intensify the lake trout suppression for at least six years. The panel felt that the effort should be doubled during that period of time.
2. Monitoring of the Yellowstone cutthroat trout population should continue, but should also be upgraded.
3. Institute a robust lake trout monitoring program.
4. Develop a plan—which had not been done to date—that could be used as a holistic plan for this suppression program.

A few more details, in terms of intensifying the lake trout suppression, the current personnel, and fiscal resources available needed to be increased and employ professional fishers...people who did this commercially... beginning to integrate them into the program. Again, not as a substitute to National Park Service personnel, but to augment their work.

We didn't have any data on where these fish spawned, so it felt that it was important to institute a telemetry study to begin to identify the movement patterns of these fish in Yellowstone Lake and where they spawn to try to set some benchmarks for the lake trout control program and to experiment with alternatives for suppression. In terms of maintaining and enhancing monitoring programs, the trap at Clear Creek washed out in 2008. So, that long-lived monitoring program that dates back to the 1940s was ended in 2008. That has not been replaced to date. So, that is one method of monitoring the Yellowstone cutthroat that is not available to us at this time.

The fall gillnetting program has been continued also, and to look for the whirling disease, which [has] also been found in Yellowstone Lake, to follow that and to try to identify the potential for spread. The work that has been done suggests that it is not a major issue in the lake system at this time.

In terms of a statistically robust lake trout monitoring program, we felt that there should be a marked recapture estimate initiated so that we could get some idea of how many lake trout there were out there and use a review in statistical analysis of existing data to try to identify where the data gaps were. That hadn't been done in 2008. To continue the distribution netting, which is their assessment of lake trout...that is something that is ongoing still.

In terms of developing a lake suppression program, or plan, we felt that the panel was unanimous that there should be a science advisory committee or something of that type. Three or four people who would work closely with the Park Service on an annual basis to help review and advise folks working in this lake trout suppression program. It was also felt that the facilities and policies

in the park at Yellowstone needed to be altered when necessary to help support the suppression program. At least for this period of six years, when we felt we should really double the effort...and at least [create] an effort to work with outside partners, I think this is important, to increase funding for this program. I think there are lots of opportunities for that.

And in terms of the suppression plan, the other thing that we felt was important was to actively manage against lake trout in all other waters...and that would be Lewis Lake and Shoshone Lake and Hart Lake. Lewis Lake would probably be the lake where the lake trout introduced into Yellowstone came from.

So, in summary then, the panel believed that the scope of the Yellowstone cutthroat trout decline would require a rededication of National Park resources and an expansion of partnerships and programs in order to fully restore the Yellowstone cutthroat trout. These are some recommendations we made to say, "Okay, this is 2008, August of 2008...in September, we should start these activities, and this is what should be done in 2009." These are what got done in 2008 and in 2009. The Park Service has been very successful in finding some additional funding to bring in commercial fishers, and that has made a substantial difference in the increase in the number of fish harvested, but that is [only] one of the recommendations that has been able to be attained so far.

The Park Service now sews around 12–15 miles of gill net every night from the time the ice goes off the lake until mid-October in most years. The added effort of the commercial fishers allows them to focus on the larger spawning-size fish. They set their nets and are able to pull them daily and they catch more cutthroat since they are fishing in shallower waters and are able to catch more lake trout when they are cruising for food. But, because they are pulling their nets they are able to release them and the mortality of the cutthroat are no higher than the Park Service net. Park Service nets, because they soak for a much longer period of time, are set deeper and the bycatch is much lower, but they have a much lower chance of releasing more cutthroat because most of the time they are dead by the time they are captured.

A graph that was put together based on some work by John Syslo, who just finished his masters at Montana State University—a graph put together by Park Service staff—shows the level that it would take if the lake trout population...that there would be about a 75 percent reduction in the population at this level. The charts project

the level of the lake trout as of 2008, and the level of lake trout as of 2020 under the current level of effort. To bring lake trout populations down to a 75 percent reduction... that would be the National Park Service effort plus an entire season worth of effort by these contract fishers. If you had multiple contract fishers plus the Park Service crew, they thought they could bring it down to this level within the next six to seven years.

Jackson Gross, who is a colleague of ours at the Rocky Mountain Science Center, is currently exploring alternative methods focused on the early life stages of the lake trout. So, we can begin to go in and, once these spawning locations are located, go in and increase the mortality on the eggs and developing embryo and larvae in these areas during the fall, during the spawning period. And also, focus on the spawning lake trout at that time. Just a small increase in the mortality of these young fish would have a substantial change in the recruitment to the adult population in the lake trout. Some of the techniques that Jackson has been looking at include electricity and suction blowing, which we actually tried in the fall of 2009. We were at least able to suck some lake trout eggs out of these different areas that we were able to locate. He is in active pursuit of ways to successfully use these technologies and apply them in Yellowstone Lake.

I guess this is where I get a little more religious because I think that really, in my mind, the lake trout invasion into Yellowstone Lake really is one of the most significant resource issues in the Greater Yellowstone Ecosystem, and I don't think that failure is really an option. When we think about the bigger picture of Yellowstone cutthroat trout, the subspecies, we have to recognize that currently only 43 percent of their stream habitat is currently occupied...by what the scientists and managers involved in this assessment call Yellowstone cutthroat trout. What's significant is that only about 28 percent—a quarter of the historical range of Yellowstone cutthroat trout—still has genetically unaltered cutthroat trout. Slightly more than half of the stream-dwelling Yellowstone cutthroat trout are already found in places where there are invasive species that share that water with them, and the densities of these fish are under 150 fish per mile. These are not robust populations.

I've put together a little schematic that shows what the distribution of cutthroat trout in Yellowstone Lake will look like if we do fail. There are few tributaries where there are year-round resident populations of cutthroat trout. The one thing to remember is that above the falls of the Yellowstone River, the Yellowstone Lake ecosystem of that falls is the last

remaining intact network of Yellowstone cutthroat trout that still maintain that migratory life history and are not threatened by hybridizing rainbow trout.

We still have time, but as Pat Bigelow said, we have no time to waste. Another thing we have to recognize is that this is not simply a Park Service problem. This is a national problem. I think that this it is important to recognize a few facts, or at least thoughts, that if the suppression was initiated immediately early on, that the Yellowstone Lake ecosystem is a relatively simple ecosystem, but is considered one of the most pristine ecosystems in the United States even with the perturbations that have occurred...that it is a relatively simple system and that it is closed.

The program cannot succeed on the current budget. All that funding does not have to happen inside the Park Service. This is a long-term problem that will require some improvements in the short term and for long-term strategies. We should again emphasize that the budget is not sufficient to be successful and that the long-term problem is going to require improvements in these tactics and strategies, but this issue is going to require a rededication of the Park Service resources and an expansion of partnerships. And again, I

can't say too much about that...that these partnerships can make us successful in Yellowstone Lake.

Again, despite all the doom and gloom, I believe and the panel believes that if we continue to act and continue this program and begin to supplement the current program with new technologies and so forth, that we do have an opportunity to accomplish the removal of this invasive lake trout and restore this large aquatic ecosystem.

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Keynote

Land-Use Change in the Greater Yellowstone Ecosystem: Past, Present, and Possible Future Patterns and Consequences

Andrew Hansen

Director, Landscape Biodiversity Lab, Professor of Ecology, Montana State University

Note: The text that follows is an edited transcription of the speaker's remarks at the conference.

Introduced by John Varley

Good afternoon, folks. I wonder if we could start by thanking the folks that put this all together. This conference has been just great...particularly the planning committee of Tami [Blackford] and Emily [Yost] and Janine [Waller] and Mary Ann [Franke]. Great job.

The program committee is varied. They selected a really good group of folks...lots of interesting topics. I'd like to thank all of you...yesterday I was sitting in the audience and thinking that this is one of the most special meetings that I ever get to attend. What is it about these meetings that I like so much? Well, they're all about Yellowstone and it's always good science, but the main attraction is that we all feel like we're part of a community, part of a research management community that is based on this place, and that's a really special thing.

I've noticed that over the years that there's kind of a turnover in who is doing the work in Yellowstone, and I don't know if it's a five-year longevity or eight-year, or whatever, but it's really critical for a new wave of people to be coming in and picking up these really important studies and continuing the work. So, it's always fun for me to see the new folks that are at these meetings...I really appreciate it.

And finally, it's really important to highlight the incredible quality of the science and the outreach that has come out of the YCR [Yellowstone Center for Resources]...at least for 20 years. And many have said that it was true for years before that as well. That doesn't just happen, you know. It happens because there are very good people working hard to make it happen and so, among others it's John Varley, and it's Tom Olliff, and it's Glenn Plumb, and it's Don Despain, and Roy Renkin, and it's Doug Smith, and P.J. White, and so forth...it's anything but guaranteed that that will continue in the future. You don't get really great programs that just continue without a whole lot of work. So, I'm just hoping that we'll all help to emphasize

the real benefits of trying to ensure that we have this super high quality program here in the park in the future. So, anyway, I'd just like to thank all of you for what you've done for all of us and the park over the last several decades. So, again can we give them a round of applause?

Okay, let's look at some of the history of the area and bring it up to the present and take it up to the future. I'd like to speak to why Yellowstone is so special and how we might try to sustain it into the future given its very special qualities. I think we all know that it is fairly unique in the Lower 48 in terms of being an area that was the latest to have Euro-American settlement and the earliest to have a national park. And, of course, it continues to have that wilderness character, but in addition to climate change there is also a big influx of new residents and substantial land-use intensification.

So the topics that I will talk about today are these:

- Looking at the period of change in human populations and land use from about 1860 to present and projected into the future. Why does this matter ecologically and how might land-use change influence changes within the park? How does the land-use story compare to other parks around the country?
- I'd like to then talk a little bit about how the park and the state of the ecosystem here might influence the human communities in terms of economics, attitudes, and wellbeing.
- And then, finally, end with a few comments on how we might sustain this system.

Mike Huston wrote an interesting paper that basically put forth that Euro-American settlement in the U.S. was first driven by natural resource constraints. People needed to live where resources allowed them to...particularly agricultural lands. Then, once transportation allowed the movement of resources, people tended to move along transportation corridors. And, of consequence, right around 1870—the time Yellowstone was established—the distribution of population in the U.S. was heaviest along

the Eastern Seaboard and the Midwest and the good agricultural lands, and some communities starting to form on the West Coast. The whole intermountain area was fairly sparsely populated. And when we focus in on the area that was around what would become Yellowstone Park, notice that there were small settlements of Euro-Americans. For example, in the Gallatin Valley, but most of the area around the park, was either Native American reservation or these interstitial lands that were occupied by Native Americans that refused to go to the reservations.

To get here at the time, people had to travel on the Oregon Trail just west of us into Utah and Idaho and then backtrack into the Yellowstone area. Because this was a very long route, the Bozeman Trail was built in 1864 as a way of allowing access into this area from the east. It was only open for four years before it was closed under the Treaty of Laramie, and it remained closed until 1876... just after the Battle of Little Bighorn. The following year was the Nez Perce War. These two battles represented the last Native American resistance across North America, and it is notable that that happened right here in our system.

So, this area stayed wilderness and unsettled while most of the rest of the country had been well settled with permanent infrastructure for more than a hundred years. How did the human population size change in the years after that? Well, it grew fairly quickly in 1900–1920 as settlers came in, but then there was this many decade period of very slow growth up until the 1980s, and then growth rates increased... particularly in the last two decades. So, now we're at around 425,000 people in Greater Yellowstone.

If we look at density of rural homes (those outside the towns) starting in 1880, there were very few and the increase was very slow up until the 1970s. So, the rate of growth spikes in the '70s and then again in the '90s. There was a continued boom in Montana up to 2005,

and the current recession probably accounts for the slight decrease in numbers of...in the growth rate of homes in this area [Figure 1].

So, what might explain that growth? This is a wilderness-type landscape, why did all of a sudden people start coming here? Well, Huston put forward that the third major driver of land use across the country was natural amenities. That, as of the 1980s and '90s, wealth increased, education levels increased, transportation opportunities increased, information transfer became easier through the Internet. Of course, people could move to where they used to have to live for their job to places where they really wanted to live, and a lot of people chose to live in wilderness-type settings—exactly the sort of place like Yellowstone that people avoided earlier due to all the reasons that I mentioned.

So, consequently, if we now look at the distribution of rural homes around the Greater Yellowstone Ecosystem... the parks, the light-green public lands, and then the gray are the private lands; blue represents the density of rural homes...and notice that rural homes pretty much ring the public lands, not only in places like the Gallatin Valley where there is a university, airport, etcetera, but even in some of these river valleys like the Woods River that are



Figure 1. Exurban development (center) and forest dieback (bottom left) in the Gallatin Valley of Montana, in the Greater Yellowstone Ecosystem. Photo by Andrew Hansen.

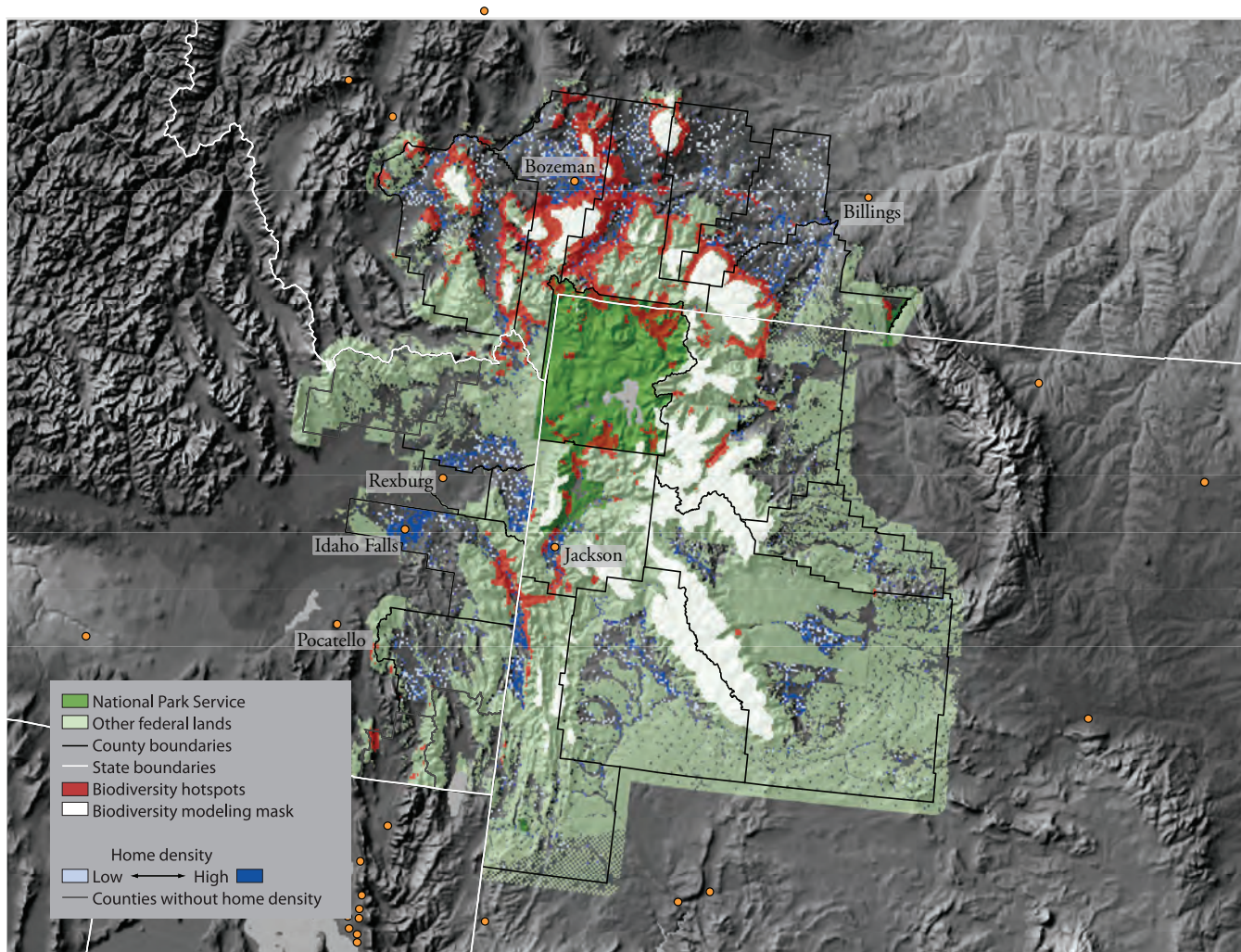


Figure 2. Distribution of rural homes across the 20 counties of the Greater Yellowstone Ecosystem in 1999.

a long ways from any town or airport [Figure 2]. A lot of these people are coming here for the natural amenities... that's what was determined by a study that Patty Gude, Ray Rasker, and I and others did. We did a statistical analysis of correlates with rural home growth and found that it was statistically associated with traditional things that Mike Huston hypothesized with agricultural suitability and with transportation factors and with past development, but also with natural amenities. It's a combination of all these that are contributing to this growth.

What about the future? Well, more of the same. Projected to 2040, the population under this particular one of the IPCC [Intergovernmental Panel on Climate Change] scenarios would go to 725,000 here...almost a doubling. Our projection of rural homes up to 2020 shows a mid-range scenario of almost a 100 percent increase in rural homes. So, we expect to see a fairly dramatic continuation of these patterns into the future.

Okay, so what does this matter from an ecological point of view? We did a general synthesis of how land-use change can affect ecosystems and biodiversity and identified these four groups of mechanisms related to [it]: habitat change, change in ecological processes, biotic interactions, and human disturbance. These can affect the population dynamics of individual species and, in turn, influence community structure and diversity.

Let's look at a few examples of these from our system. First, the habitat change. In the GYE [the Greater Yellowstone Ecosystem] 88 percent of land is public. That alone is important because we know you can't build houses on public land and so intense land use is less likely in those lands. So, we might think that the system is fine. Areas that are urban, or exurban, or suburban cover just 11 percent of the system at present.

How has that been changing over time? Well, the ag lands have been fairly stable over most of the century in

terms of their area and decreasing over the last couple of decades. The big increase has been in the area of exurban development and under urban and suburban development. But again, only 11 percent, so maybe we're okay. Those lands especially are far from Yellowstone and Grand Teton Park, so maybe [are] not a problem. Well, there's a couple of ways where there is potential for negative impacts...one of these being that it just so happens that we're building homes in areas that are disproportionately important ecologically. It's going to be low elevation, well watered, longer growing seasons, high primary productivity.

Bird hot spots, places of particular[ly] high numbers of bird species—which also coincide with high tree and shrub diversity—significantly overlap in places of rural homes. The homes are built just in the bird hot spots. So, the notion is that although much of the system is public and is not converted to intense land uses, that land that has is the most important land in the system ecologically. That's also true from a migration perspective, where many of the ungulates that migrate out of Yellowstone Park are passing through these areas that have rural home development.

If we look at a whole variety of indices of habitat ranging from individual species like pronghorn to habitat types like Douglas fir to what I like to call indices of habitat like bird hot spots or migration corridors or irreplaceable areas...the message here is that some of the habitat types that are largely in the public land, like pronghorn and moose, have undergone very little destruction as a result of this land-use development, but others that tend to be down in the valley bottoms like bird hot spots and riparian habitat have undergone almost a 20 percent decline as of 1999, and under the projections up to 2020 it will be more up to [a] 20–30 percent reduction. So, there are particular habitat types that are indeed getting substantially fragmented by this land use.

But, perhaps even more important are what we might call the “longer distance effects.” The effects on the natural part of the landscape that might be some distance from the lands that have the more intensive land use. With regard to ecological processes, we know that natural disturbance is critical to the maintenance of ecosystem function and biodiversity in the system creating habitats that many species require like cottonwood and aspen and flooded riparian zones and early burn patches for things like woodpecker and (again) aspen. We know that the ability of land managers to allow disturbance to occur are dramatically constrained by the presence of these rural homes and so

the notion of a “let burn” policy in Greater Yellowstone... maybe it might still be on the books, but I don't think it's happening anywhere. I mean, any fire that is threatening homes, we're trying to put out. There's also been a lot of controversy about the extent to which flooding might need to be controlled to protect homes. For example, like in the Paradise Valley.

One other ecological process that you might not think about being susceptible to land-use change is primary productivity and its spatial and temporal distribution across the landscape. Nate Piekielek, a student of mine, has recently been working in the Yellowstone watershed from about the Pelican-Hayden portion of the northern range down the valley to Livingston. We've broken it up into six sections and [are] looking at patterns of NDVI [Normalized Difference Vegetation Index]. Averaged for the last 10 years, the start of the growing season is generally earlier in the valley bottom [near Livingston]. As we long thought the case, the data are confirming that. For those months of March, April, May...there's substantially higher green vegetation in that portion of the study area.

But then, of course, there is a flip over in July, August, parts of September, where it's the upper portion of the northern range where the fast-growing green grass is found, and this is likely the really limiting time of year... having green forage in summer, which requires summer rains and is only happening up in the higher elevations where you have the summer rains. So, these patterns of chronology explain the migration patterns from winter range to summer range and back.

Well, is land use influencing this at all? So, Nate is now focusing on just the portion of the Paradise Valley below the public lands...Nate did a similar plot for undisturbed grasslands, but also for rural home density, suburban, urban, and areas of irrigated agriculture. He found that green-up in the spring is happening a lot earlier in the areas of intense land uses than on the natural [lands] and it's continuing later in the fall. And also, the irrigated agriculture over most of the growing season is way more highly productive than those natural grasslands.

We think that this likely explains the change in the spatial distribution of the elk, in particular, over the course of a year, with many more of them staying lower in the valley over parts of the summer and especially in the fall. Bigger implications of these higher densities and reduced migration in terms of spread of disease like brucellosis...and of course that spread to cattle. In terms of the location of predators like wolves, perhaps bringing wolves down into

more contact with domestic livestock and creating those kinds of problems and in reducing the ability of management agencies to use hunting as a tool to reduce herd size. A lot of these herds are just hanging out on private land where there's not good hunter access. So, this might be a good example of where land use pretty far down out of the park is probably having fairly strong impacts on migration and spatial distribution of ungulates, including the time they spend in the park, in ways that strongly influence policy.

Okay, let's move on to another example that involves biotic interactions. Now if we go from a wildland setting to an increasingly urbanized one through these land-use types, in general the literature suggests that you tend to get changes in types of species present with the reduction of top predators fairly early as the system leaves being a wildland. A variety of predator-sensitive natives tend to drop out and that's because a lot of mesocarnivores tend to be more abundant, like raccoon, skunk, magpie, raven, for example...as indicated by these human-adapted natives. And then, of course, weedy species tend to increase. This can have big consequences for the distribution of biodiversity across the landscape.

Just one example that goes back 10 years or so: we've looked at neotropical migrant bird population dynamics...in this case the yellow warbler. We found that hot spots that were near high densities of rural homes...within those there was much lower reproductive success for those birds than areas with lower home densities. And the main mechanism of that was the expansion of the mesocarnivore community like ravens and magpies. Also, cowbirds that of course lay their eggs in the nests of species like yellow warbler and have very dramatically reduced the reproductive success of yellow warbler and several other species.

When you project rates of reproduction and rates of survival across the landscape as a function of rural home densities and habitat types, you come up with some interesting things. We found that for American robin—a species that is not susceptible to these mesocarnivores or cowbirds—that these riparian, low-elevation areas are population source areas where there's lots of reproduction. The areas up in the park where their species are found have fairly low reproduction some years due to climate limitation, and so it appears to be a system where there are population source areas in the valley bottoms that are probably maintaining vital populations up in the park.

We think that in pre-settlement times that was likely the case for yellow warbler, too, and other neotropical mi-

grants that are very sensitive to these mesocarnivores. But when we model the population growth currently under the current distribution of rural homes, we find that all of these hot spots are population sinks and there's mild sources in the foothills of the Gallatin National Forest, say, but the park is a mild sink due to climate limitation. And this suggests that the conversion of this area from source to sink has flipped the whole system over to a sink. It's an example of where land-use intensification, in this case 40–60 miles away from the park, could be affecting population viability within the park.

Now, I know that yellow warblers are high on your list of most important species, but allow me to divert attention to a less important species like the grizzly bear. Chuck Schwartz and his many colleagues have done really beautiful work asking similar questions for the bears across the system. Just to summarize, they find that mortality is the main driver of population growth for this species. They find that 85 percent of the mortality was human-caused in their study that summarized the last 20–30 years. The rates of survival were decent within the park, a little bit lower in the recovery area outside the park, and in the private lands outside the recovery area substantially lower. They found that these mortality rates were correlated with some natural things like winter severity, but also with several land-use factors, like stuff related to roads and home density. They then modeled population growth over the system...similar to what we did for birds. The maps they've put together are pretty alarming because on one hand, the population is growing overall right now and especially growing on the public lands, but it raises totally the question of: if we do get that doubling of population and of rural homes, at what point does the mortality in the private land for bears become sufficient to force the entire system to become a sink...and put at risk the species in the park?

If we simply overlay the projected 5 degree Celsius change in temperature over 100 years that David Westland just mentioned, which I found amazing, and effect on whitebark and fire, we can really expect that the bears are going to want to be on these lower-elevation lands. So, this is an example of where land use alone might have an effect on a charismatic species. Match that with climate change [and] some really serious challenges [emerge].

Okay, now let's move on to a comparison with other parks across the country. Cory Davis, another student in my lab, has been analyzing the 60 larger parks in the Lower 48 in terms of land-use change using a variety of metrics dealing with population density and housing density and

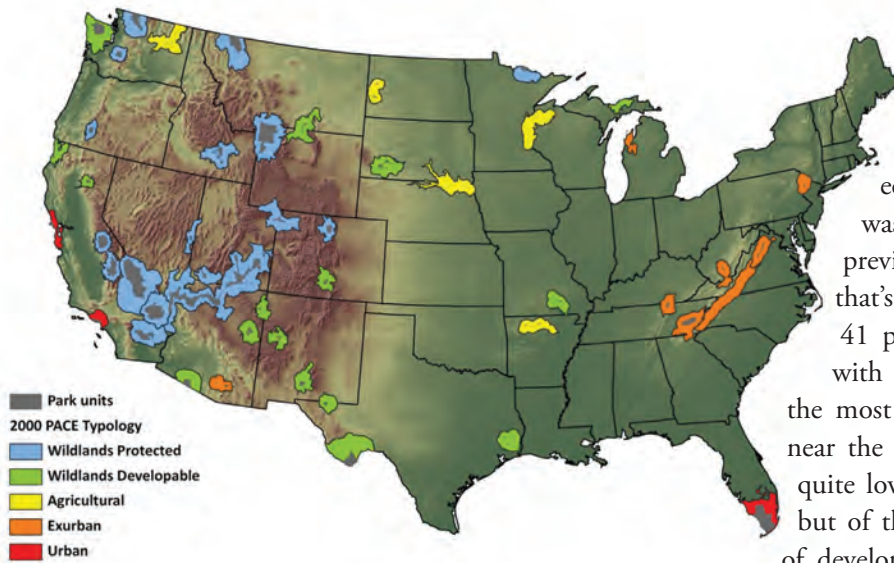


Figure 3. Results of land-use cluster analysis for 60 national parks (Davis et al. in prep.).

impervious surface and roads and change in those from about 1900 or so. Basically, we'd like to show how Yellowstone stacks up relative to other parks in terms of all of these land-use metrics...but before doing so I need to point out that in doing this kind of analysis you have to define what area around the park you're going to do the analysis for. We spent a fair amount of time coming up with a way to do this. In particular, our conceptual model is that these national parks are often connected to some larger surrounding ecosystem through migratory animals and through source/sink dynamics and through fire and these sort of things that I've been talking about. And land-use intensification in that surrounding ecosystem can alter those flows and lead to degradation of the national park. What we set out to do was to quantify and come up with objective criteria to map that surrounding ecosystem. I won't go into any details, but we used criteria related to watershed, to disturbance, to crucial habitats, to species area relationships, and to edge effects from human development.

What we're calling "park-centered ecosystems" show how many of the criteria overlap and where we think criteria overlap...we have high confidence that that's a really important place. But these tend to be fairly large for some of the parks and they reflect what we think of the area around the park where land-use change could be expected to have impacts within the park. So, that's what we used as the area to quantify land-use change.

Comparing Grand Teton and Yellowstone to the mean for the 60 parks in total...one thing that really stood out was the percentage that's in private land. The actual park-centered ecosystem for Grand Teton–Yellowstone was actually quite a bit smaller than we previously thought...some 6 percent, and that's way below the mean for all parks of 41 percent. And when you list the parks with the least amount of private [land] to the most amount, Yellowstone's right in there near the top. Population density is also rather quite low relative to the average for all parks, but of the lands that are private the intensity of development is fairly similar to the average for these other parks. So, we're largely a wilderness park because there's so much public land, not so much because there's relatively little development here on those private lands.

We used statistical clustering techniques to try to put those 60 parks into groups that made sense in terms of their land-use topology or land-use attributes, and the classes that we ended up with were called wildland protected areas, wildland developable, agriculturally surrounded parks, exurban surrounded, and urban parks [Figure 3]. And again, I won't go into any of this here, but point out that Yellowstone–Grand Teton are in that wildland protected class, as are many of the intermountain area parks. These parks are most distinguished by this majority of public land and from that protected area-centered ecosystem with relatively little ag. The private land is largely undeveloped, but that's changing quickly, particularly with exurban development. The types of issues that are fairly unique to these parks are trying to maintain or restore the land species that are present there. That's also true of the wildland/ecological processes like fire management. Wildlife-human conflicts like bear-people interactions are quite common here, spread of disease like brucellosis...many of these parks because they're in harsher western landscapes have the private land in the more equitable part of the landscape and, hence, protection of those hot spots is a particularly important issue. Some of the mineral and gas development [and] resource extraction are important issues.

I guess the main message here is that Yellowstone really stands out as special among all the parks in the country as being really emblematic of this wilderness/wildland-type

protected system. It's got the full complement of native species and even parks like Rocky Mountain and Sierra-Yosemite are dependent on Yellowstone for source areas for things like wolverines. So, again, the park has a really special role nationally and that's all the more reason why trying to sustain it is important.

So...so lastly, we've talked so much about how people affect natural systems; let's try to step back a little bit and ask "is there a feedback loop?" and "what's the whole system look like?" Various people at this conference have mentioned this concept of this coupled natural/human system. It's a term that getting a lot of attention lately, and it's really meant to emphasize these feedbacks. Of course, the way humans affect natural systems is through land management and other impacts as I've talked about, but the feedback involves certain things like goods and services including those natural amenities that Liz Shanahan mentioned earlier this afternoon and some others...as well as risk involved with disease and fire and so forth.

This model is really particularly applicable to our system because we've said that we're [a] natural amenities-based system, but a lot of the people that are moving here are doing so because of the high quality of the nature and presumably they're getting positive feedback from those natural amenities in terms of things like values of their properties, and so forth. And so, the real question is: how do you sustain a natural amenities-based system, one that is very different from a traditional system where natural amenities aren't part of the equation? You know, it's past population growth, access to transportation, etcetera.

I think there are two scenarios that are most obvious. One is what you might call "love it to death," and that is the people that move here because they're so much attracted to the nature just use it too hard...too many rural homes, too many interactions with bears...and it leads to a degradation of the natural system and a decrease in those natural amenities. But, does the population then drop? I suspect not...I suspect once a town reaches 100,000 it's going to grow no matter what the natural amenities are and take that more traditional route. So, my question would be: what would prevent a Bozeman from becoming a Salt Lake City in our lifetimes? I think it's exactly as we would expect. I think there's an alternative possibility and that's what we would call "love it to health." Which is basically to see it as a unique type of system...natural amenities-based system where the challenge is to maintain those natural qualities that are so important to the residents in terms of their quality of life and to their livelihood and to their property values and so

forth...to come up with ways to do that.

What are some of those factors that [determine] whether we sustain the natural system or degrade it? Well, we know that it's related to policy. There's been a huge amount of discussion about that, like land-use planning, and we know that in Greater Yellowstone there's been very highly effective land-use planning in many parts of the system leading to, for example, dramatic increase in conservation easements in really high priority places. So, lots of progress there. We know that our effect on the ecosystem is heavily affected by stuff from elsewhere. Markets, for example...the current recession is leading to a slowdown in exurban development. Now, there's not much we can do about that in terms of management. Population size? I won't dwell too much on this here. I sometimes like to...it's something we don't talk about. I think we can sustain Greater Yellowstone at the current population size. It's easy enough. I think we can sustain it at 700,000, but quadruple that number or 16 times that many? No way. Population size does matter. Can we think about incentive-based systems for communities to move toward target population sizes?

What I would like to spend another minute more on is this last one that relates to us and our attitudes and behavior. I think there's a real opportunity to move toward that more sustainable approach. I'll just give you an example of a study that [Liz] Shanahan and I and others are just starting on that really tries to simplify the very complex human-coupled system down to a more manageable level, and that is to deal with the people that live in individual rural properties such as this subdivision and ask, basically, "why do they live there?" To what extent do natural amenities and ecosystem properties influence why they live there? To what extent do their attitudes and values influence how they manage the property in terms of things like weeds or water or roads or livestock? How do those various property management practices influence the ecosystem? Like the likelihood that weeds will jump from a yard into this adjacent burn area, this logged area, and really become established in the wildlife? Then, how will that affect the natural amenities and their value and how they're perceived back by the people? Might the appreciation of natural amenities get eroded if people tend to degrade the system? Or, if they enhance the system, might those values increase?

Those are the kinds of questions we're asking. And then, very importantly, we're asking: if people are provided good information on these connections, might

they manage their properties differently in order to have a lighter touch on the landscape? If rural homeowners are taught what the weeds are in the system that are a problem and how can you manage them effectively and try to minimize them jumping in the wildlands, will people be more likely to use those practices and limit their effect on weeds?

If these hypotheses are correct, they offer a basis for living more sustainably on the land. And this would apply to exurban homeowners to backcountry recreationalists and the many ways that we interact with nature in this system. To do this kind of work, these are the kind of people on our team: political scientists, economists, education specialists, weed people, system modelers, statisticians, ecologists...and I think that this really represents that a real integrated approach is required to tackle these types of problems. I think there are great examples of this right out of Yellowstone Park. Basically, the way the park teaches people to interact with bears in the backcountry is a fabulous example of a highly effective education program that leads to a dramatic reduction in the negative interactions in the park between bears and people. I think there's real hope for this.

Okay, so just to close out then, what I've tried to communicate is this system is special because it was so wild and so remote that it took so long to develop. And relative to other parks across the country, this one is really special in

that regard. We've got special obligations to the nation in how we manage it, but this wilderness character is now attracting a bunch of people and it's really going to be challenging to maintain the natural part of the system under this increased number of people and land-use intensification, particularly with climate change. We probably have a real opportunity to try and be creative in more sustainable approaches to the system that involve land-use planning, but then also involve questions of population size and involve questions of education and human behavior.

So, thanks so much for your attention and I'd like to just thank these colleagues and students and these various NASA programs for their support for this work over these years. Thank you.

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Panel: Greater Yellowstone Area Science Agenda Workshop

Tom Olliff

Great Northern Landscape Conservation Cooperative,
National Park Service

Cathy Whitlock

Montana State University, Department of Earth Sciences

Yvette Converse

Great Northern Landscape Conservation Cooperative,
U.S. Fish and Wildlife Service

Jeff Kershner (moderator)

U.S. Geological Survey

Note: The text that follows is an edited transcription of the panelists' remarks at the conference.

Opening Remarks of Jeff Kershner

This morning I'm going to lead a panel that will talk about an effort that was started almost two years ago in Bozeman after the last science conference, where we discussed the challenges that were facing managers in the Greater Yellowstone area that were evolving not just as individual events, but as cumulative effects, if you will. We had all been pretty aware of the threat of invasive species within the Greater Yellowstone area. In the midst of 2005–2008 we were undergoing amazing land-use change around the Greater Yellowstone, and on top of that there was this emerging issue of climate change that everyone was concerned about. So, two years ago we discussed pulling together a panel to have a round table discussion on anticipating the challenges that we're going to face in the Greater Yellowstone and then developing a science agenda to deal with some of those challenges.

This discussion occurred last November when we convened a group of managers and scientists in Bozeman to build a science agenda describing the challenges that managers are facing and identifying the science needed to address those challenges. This morning I'm pleased to bring together a panel of folks that were intimately involved to give you their perspective on the important issues we identified in the Greater Yellowstone Ecosystem and how we built part of the science agenda.

Tom Olliff is the National Park Service co-lead of the Great Northern Landscape Conservation Cooperative [LCC]. The National Park Service co-leads the Great

Northern LCC with the U.S. Fish and Wildlife Service, so Tom and Yvette [Converse] co-lead the LCC. As many of you know, he's been around this area for the last 32 years and held various positions with the Park Service. In the recent past, he was the Chief of Resources [at Yellowstone] and then part of the [Greater] Yellowstone Inventory and Monitoring Network. Tom's going to talk a little bit this morning about the science agenda and the steps we've made past the agenda that is discussed in the most recent issue of *Yellowstone Science* in your packet.

Before I introduce Cathy Whitlock, I want to thank Scott Bischke, who's sitting back here in the audience because Scott was really instrumental in pulling this whole thing together and did an amazing job from the standpoint of organization and developing the final product. So, Scott, even though you're not on the panel, you're with us up here.

The next person I'm going to introduce is Cathy Whitlock, professor of Earth Science at Montana State University [MSU]. Cathy came to MSU in 2004, and her research really concerns ecological consequences of past climate change and long-term linkages between vegetation, fire, and climate. The Yellowstone fires of '88 inspired her scientific endeavors of the next 20 years that looked closely at using the layers of charcoal in lake sediments to retrospectively look at past climate change effects. Cathy works all over the world using these techniques, including Argentina, Australia, and New Zealand.

And finally, the next panelist is Yvette Converse, who is currently with the U.S. Fish and Wildlife Service as the co-lead of the Great Northern Landscape Conservation Cooperative along with Tom Olliff. Yvette has worked for



Figure 1. Panelists Tom Olliff, Cathy Whitlock, and Yvette Converse.

15 years in aquatic ecology and conservation in the area of endangered species biology and river conservation and management. She received her master's degree from Utah State in aquatic ecology and watershed science and was the assistant director of the Bozeman Fish Technology Center prior to taking this job.

So, with that, I'm going to let Tom start it off and talk a little bit about where we've been. Cathy will follow with some perspectives on the climate side of the workshop, and Yvette will follow with sort of a long-term landscape conservation perspective and maybe how we attack some of these problems.

Remarks of Tom Olliff

Thank you, Jeff. Those of us working to conserve natural and cultural resources have been dealing with large landscape stressors for a long time. For instance, land-use change and fragmentation have significantly reduced habitat for wildlife and the extent of home range for dozens of wildlife species. We have seen loss of connectivity, disrupted migration corridors. While a lot of the impacts of land-use change happened a long time ago, it is still going on. For example, one out of three acres that has been developed in the United States was developed between 1982 and 2007. Every year, we lose almost 1.6 million acres of our working farms, ranches, and forests to development and fragmentation. Closer to home, work coming out of Andy Hansen's lab at Montana State University shows the

rapid growth in population and rural homes in the Greater Yellowstone area.

Exotic species, the same thing. Yellowstone's first exotic management plan was written by Sue Consolo-Murphy in 1986. Exotic plants have been a management priority for quite a long time, but we also recognize the steep rise in aquatic nuisance species. For example, in 1985 and 1986 we found and began to remove brook trout in the Arnica Creek lagoon in Yellowstone Lake; then, in 1994, we discovered exotic lake trout in Yellowstone Lake, which was probably the signature species of exotic invasion in the Yellowstone region: analysis shows that, without intervention, the Yellowstone cutthroat trout population will be reduced to 10 percent of its former levels by lake trout. New Zealand mud snails, whirling disease, and now we are looking at zebra mussels arriving in the GYA [Greater Yellowstone area]—in 2010, Teton County found two zebra mussels in the livewells of boats that had been at Lake Mead. In the last 20 years, exotic wildlife disease has become a priority issue for the Yellowstone area: brucellosis, of course, has greatly influenced management of buffalo, and now we are dealing with increasing levels of canine distemper, mange, and chronic wasting disease is only 130 miles away.

Recently, we have become acutely aware of the current and projected impacts of climate change. We have already seen a rise in water temperatures, dead fish in rivers and creeks, spawning streams that become disconnected from Yellowstone Lake late in the season due to low water in

the streams and the lake, and less spring runoff to flush out the gravel bars at the mouth. Roy Renkin has analyzed SNOTEL [SNOWpack TELemetry] data and has shown and increase in the growing season of around 25 days in the last decade. And, of course, increased frequency or intensity of natural disturbance regimes—all the brown trees from the mountain pine beetle, for instance. And the largest changes are projected to arrive in the future. Dan Fagre's lab in Glacier modeled changes in vegetation and glaciers in Glacier National Park. They found that by 2030, all of the glaciers in their namesake park disappear; at the same time, vegetation shifts upward—the grassland expands from the valley bottoms to mid-mountain. Potential changes to the landscape, and impacts to resources, are vast.

Since Jeff [Kershner] explained the purpose and venue of the workshop so well, I am going to jump right to the conclusions, that is, the science agenda for the Greater Yellowstone area, the foundational science that we need to promote to give managers information to make the best decisions in light of these large landscape stressors that we are experiencing.

One of the first issues is to help managers make better use of climate data and models, including better regional models downscaled from the Global Circulation Models, which includes more accurate projections of temperature and precipitation, scaled to an area of management relevance, with modeled ecologically relevant data such as snowpack, phenology, productivity, evapotranspiration, and water budget. We currently have two efforts that are providing such data for the GYA, one out of the Climate Impacts Group at the University of Washington and one out of the USGS with Steve Hostetler leading that effort. Many of those data are becoming available on the Ecoshare Web site (www.ecoshare.info) and Steve Hostetler is planning to set up a server at Montana State University with both sets of data, as well as other datasets.

Second, we need a major push on completing vulnerability assessments—how do ecosystems and species, natural and cultural resources, respond to these large, landscape stressors like climate change? There is so much uncertainty with the effects of these large landscape stressors, especially climate change, that managers need this information to help prioritize conservation actions. Priorities for the GYA include the vulnerability of water and aquatic systems, alpine systems, including whitebark pine, and then species, habitats, and ecosystems. We need to understand the synergistic correlations: for example,

how does increased water temperature affect invasive species? How do changes in species distributions affect connectivity? How are these main stressors affecting primary productivity? How does exurban development affect invasive species? The northwest [vulnerability] assessment, led by Sarah Shafer from the USGS and Josh Lawler from the University of Washington, will be one of the first that will help to assess resources in the GYA.

Next, we need synthesized information. One of the issues that managers deal with is simply information overload, especially when it comes to this surge of information that is being developed about large landscapes, and particularly with climate change. Simple summaries of projects and the products being developed by scientists, is a first step in that direction. A synthesis of the different kinds of research being conducted, with an annotation about results, would be beneficial to managers, who already have too much on their plates. Synthesized information about projected changes in climate and land use, and the ecological impacts of those changes; science on resilience, thresholds, and management approaches; predicting new states and ecological systems; information on best management practices, things like “What’s going to be effective?” “What can we manage?” “What do we have very little chance of managing?” All of these are priorities for synthesized information.

Scientists can help us understand and project changes in land use, and really again the synergy between land use and ecological impacts, and identifying specific linkage areas in corridors that need to be maintained or promoted. Highest priorities for invasive species science include the rate of spread not only of existing invasives but species that are new to the region, or about to be new to the region. For instance, quagga mussels were found in Teton County, Wyoming, a couple boats coming from Lake Mead. How can we best prevent invasion or detect in early enough to control? And invasive species and ecological impacts—it takes sometimes a long time to get the concepts in my head, but the botanists in Yellowstone have been telling me that the invasive plants that we prioritize for management is due to concerns of the agricultural sector. From an ecological perspective, we should be more concerned about things like the non-native timothy, which is of course on nobody's radar screen.

And then, finally, what I want to call the “really unknowns”...the effect on our cultural heritage of these large landscape stressors. I have been trying to think about the impact of cultural resources from a very large landscape

strategic impact and what's interesting is that there is a lot of information in scientific literature about ecological impacts and very little on cultural resources. Social scientists need to become more involved. For example, I think it's fascinating that an article in the *Proceedings of the National Academy of Sciences* reported that 97 percent of scientists conducting research in climate change believe in anthropogenic forcing of climate change, but only about 50 percent of the public does. How can social scientists help us understand the link between large landscape conservation and public perception?

I just hit the high points here for the sake of brevity, but in your packet or online the article that we wrote is in *Yellowstone Science* and it really expands on the questions that we hope to have answered.

I think that the good news is that in the last year...or even before that...there is a lot of this work going on, a lot of this science going on, and it is becoming available. Three particular syntheses that will help in the Yellowstone area are the Isabel Ashton synthesis on the ecological effects of climate change with some conceptual models that I think are pretty interesting. Dave McWethy and several people in the audience have actually done a similar synthesis for changes in climate that are being observed and projected for the areas of Greater Yellowstone to southern Rockies to the lower Columbia Basin. Currently, this is in draft, but should be available sometime in the next few weeks. Another resource that is being developed in the GYA is a synthesis of impacts in the Shoshone National Forest. Janine Rice is the primary author, working with Linda Joyce. Janine is here at the conference and will be sitting in with Bryan Armel, who is reporting on that effort later in the conference. So, there is information becoming available that is going to be very valuable to managers.

There is a lot of effort being expended on downscaled climate data; two of the most promising are work that Steve Hostetler is conducting with the USGS and that the Climate Impacts Group at the University of Washington is conducting. Both efforts cover the five-state Great Northern Region. I'm not going to talk about this in any detail because Cathy will have this information in her presentation.

A lot of work is beginning to be focused on vulnerability assessments. For instance, Scott Christensen is going to be talking about some work going on with water and fisheries assessments in the Greater Yellowstone. The Park Service is doing a large pica vulnerability assessment in eight national parks across this Great Northern landscape.

BLM [the Bureau of Land Management] is doing regional ecosystem assessments. [The] Forest Service has some water vulnerability assessments and one of them is on the Gallatin [River]. NatureServe has its own vulnerability assessment tool that you can go online and do your own vulnerability assessments. I tested it out and for it to be really robust you'd really have to have a lot of information, but it is interesting because it really does make you think about it. And I have already mentioned the northwest vulnerability assessment.

How do we as managers approach climate change and other large landscape stressors? The U.S. Climate Change Science Program has developed a review of adaptation options and published it in their Synthesis and Assessment Product Series (this particular one is Section 4.4). They have outlined seven adaptation approaches that work well for conserving resources in the face of any large-scale impact, including: protecting key ecosystem features; reducing anthropogenic stressors; representation (protecting variant forms of a species or ecosystem); replications (maintaining more than one example of each ecosystem or population); restoration; refugia (maintain areas less affected by climate change or other landscape stressors); and relocation (human-facilitated translocation of organisms from one location to another).

Finally, there is this final step of trying to link science with management and to do that you need some kind of framework. I think of it as a blueprint. I think of us as having a lot of tools, such as having hammers and saws, but we need a blueprint in order to build a house, if you will. I like the blueprint from the Glick and Stein's *Scanning the Conservation Horizon* document, including Element 1, Identify Conservation Targets; Element 2, Assess Vulnerability; Element 3, Identify Management Options; and Element 4, Implement Management Options. The science that we identified in the agenda for the GYA fits nicely into this framework. For example, the synthesized information and the social science contribute to Element 1. In Element 2, the vulnerability assessments, we need the climate change modeling, vulnerability assessments, synergistic effects, and effects on cultural heritage. As we look into management options in Element 3, we bring in the resiliency thresholds, management approaches, and land-use changes and invasive species work. Finally, the monitoring of adaptive management into Element 4, which is just the implementation and then the monitoring.

So, the next thing that we are planning to do is to take what is really science focused and bring it into some kind

of framework that helps managers step through it and incorporate it into their work to understand what kinds of things we can do on the ground that might help us think about strategic management issues. And finally there is the scale issue. One of the things that I was able to do and was privileged to do in my time in Yellowstone was work in the district and then in the park level and then scale-up to the ecosystem level and work with the Greater Yellowstone Coordinating Committee and do several things, but I never did scale-up to a landscape or eco-regional level and I never worked across landscape boundaries. For instance, while I know Jack Potter up in Glacier [National] Park, we have never worked on a project together, though we manage similar resources. This is the kind of scale we need to bring to these emerging landscape issues. Think about scaling-up to a large landscape, all of the partnerships involved, all of the different conservation organizations. This is not a trivial question: how do you scale-up from a unit national forest/park/refuge to an ecosystem? How do you scale-up to an eco-region? How do you scale-up to a landscape? And maybe just as important if you work in a landscape: how do you scale-down to a unit? Those are difficult questions that we're wrestling with right now. One way we are thinking about scaling at large landscapes is through this international network of Landscape Conservation Cooperatives or LCCs. Yvette will be talking about the Great Northern LCC, one of 21 LCCs envisioned for North America. So, I am going to turn it over to Cathy to expand on the climate issue in this panel.

Remarks of Cathy Whitlock

Well, thank you. I want to start by saying what a privilege it has been to help develop the Yellowstone science agenda, and I want to thank Suzanne Lewis, Tom Olliff, and Glenn Plumb for having the vision to think big about Yellowstone research over the next 10 years. I also appreciate that they brought so many voices into the conversation to develop this agenda.

I want to talk about the science agenda from my own area—climate change in the past, present, and future. I think after hearing Steve Gray's talk...and as you all know, this is a bigger issue than just the Greater Yellowstone area. Climate change will impact our ecosystems, water availability, and ecosystem goods and services within our wildlands and managed lands. It has major consequences for the socioeconomic wellbeing of the region. So, part of the challenge in developing an agenda is thinking about the interface between the Greater Yellowstone, the surround-

ing regions, and the communities that live here.

The science agenda for the Greater Yellowstone area identified three areas that will be important in the future: climate change, invasive species, and land use. I want to talk to you a little bit about the climate change challenges that were identified in the science agenda. Basically, the science agenda asked, "How will future climate change affect various ecological processes?" Several topics emerged as areas of concern: How is climate change going to impact the biota and functioning of cold-water aquatic ecosystems? How is it going to impact surface water, snowmelt, water availability, water quality, and water temperature? What will be the role of groundwater as a compensating factor?

How about species, habitats, communities, and ecosystems of special concern? Which ones should be targeted for a study and protection? Most people at the workshop recognized that alpine communities are highly threatened as warmer annual temperatures push these ecosystems off our mountaintops. Changing disturbance regimes is also a concern, particularly since we've seen more fires in recent decades in the western U.S. than in the previous century. How are fire activity, insect outbreaks, disease, and other natural perturbations of the system going to change in the future?

The general agreement from the workshop was that efforts to monitor climate need to be expanded to increase our coverage of climate measurements, including SNOTEL sites. Steve Gray touched on the importance of understanding climate variability in the future. We know the mean state is changing, but what about the variability around that mean and the climate surprises that are likely as we take a non-stationary path from the present to future? The workshop also discussed some of the ecological interactions that are likely to occur between climate change and the spread of invasive plant and animal species and land-use change. What positive and negative feedbacks are likely to occur, for example, between fire occurrence, beetle-killed trees, and non-native species. As Tom [Olliff] said, there's a need to think about the Greater Yellowstone Ecosystem as a coupled natural-human system, so that we can understand how decisions that focus on Yellowstone National Park impact the greater region.

What issues concern me for the future? Well, one is this basic question of can species respond to the sorts of climate changes that we're projecting? This is a very basic concern, the idea that species occupy a particular niche but the location of that niche is changing rapidly. For example, think about the climate space of a species along two

gradients of climate: temperature and aridity. Some species are generalists existing under a broad range of temperature and precipitation conditions, and others are specialists with narrow climate requirements. Under today's climate, the geographic range of species may overlap, allowing them to live together in the Greater Yellowstone Ecosystem. As the climate becomes warmer and effectively drier, however, the climate space for some specialists will disappear and those species will become locally extinct. The region may get communities that we've never seen before, so-called novel communities, and we may see new opportunities for invasive species.

When you look at projections of how species' geographic ranges may change with future climate change, it's a pretty scary business. Bartlein et al. [1997] explored the effects of a doubling of carbon dioxide (2xCO₂) on the climate and vegetation of the northern Rockies. They compared the differences between the geographic range of species at present and under 2xCO₂ climate, assuming that species will be able to stay in equilibrium with projected climate change. These equilibrium projections suggest that some species will do fine in the future. Lodgepole pine, for example, tolerates a broad range of climate conditions and may not be too impacted by projected climate change. On the other hand, whitebark pine disappears from Yellowstone as a result of warmer conditions. The study also suggests that the 2xCO₂ climate in Yellowstone will be suitable for species that currently do not grow in the area. For example, western larch may shift its range southward as a result of warmer, wetter winters, and Gambel's oak may expand northward as a result of warmer and drier summers.

So, the projected changes in species distributions are going to be complicated throughout the northern Rocky Mountains. Some species will not shift their range, others will move upslope or be regionally extirpated. Some may expand southwards and others northwards. The net outcome will be assemblages of species that have no modern counterpart. I should add that such simple equilibrium projections don't address whether species will be able to keep pace with future climate change, especially if plants have to move across fragmented landscapes and compete with non-native species.

Another consideration in Yellowstone is that geology has a big influence on our ecosystems, and the importance of soil conditions is not often examined in studies that look at the ecological consequences of climate change. Central Yellowstone is underlain by rhyolite, which is a

very infertile, well-drained substrate. Eastern Yellowstone is dominated by Tertiary andesitic volcanic rocks—soils are richer in nutrients and better developed than on rhyolite. Areas of calcareous glacial sediments, such as Hayden Valley and the Lamar Valley, support grassland communities. Fossil pollen records suggest that lodgepole pine forest has grown on rhyolite substrates for the last 10,000 years almost without change. Andesite substrates have supported spruce, fir, whitebark pine forests, and calcareous substrates have been generally treeless since the last ice age [Whitlock 1993]. So, geology will modulate how plant species respond to future climate changes in Greater Yellowstone to a greater or lesser degree.

There will likely be more fires in the future as well, and the fires of 1988 were perhaps the beginning of a new fire regime associated with warmer climates. A paper came out in 2006 [Westerling et al. 2006] that suggests that middle- and high-elevation forests in the northern Rockies will be most vulnerable for future fires, because they will be affected by warmer temperatures and earlier loss of snowpack. This includes most of Yellowstone's forests. We've examined past fire-climate linkages in Yellowstone by comparing charcoal, pollen, and tree-ring records. Paleofire records from central Yellowstone indicate that the fires of 1988 were large and unprecedented over the last 800 years, although there have been multiple decades when nearly equivalent amount of forest burned [Higuera et al. 2010]. A charcoal and pollen record from Cygnet Lake in central Yellowstone extends fire history information back 17,000 years to the end of the last ice age [Millsbaugh et al. 2000]. Those data indicate that fires were much more frequent during a prolonged warm period between 7,000 and 11,000 years ago, when summers were 2 degrees Celsius higher than at present. During this period, 10–15 fires occurred every 1,000 years, which means a fire every approximately 50 to 75 years. So, current fire-climate linkages may be unprecedented in recent centuries, but not on a longer timescale. Paleoecological data, such as these, can provide important insights for understanding how ecosystems and disturbance regimes may respond to climate changes in the future.

There are, from a scientific point of view, a lot of "black boxes" in our knowledge of how ecosystems function, and the scientific community still has much to learn about climate change impacts within the Greater Yellowstone area. For example, we don't know much about the role of microbes in regulating the consequences of climate change. If you look at watershed models that consider

climate change effects, the microbial activities are usually “black boxed.” We also don’t know how ecosystem processes observed at single sites aggregate to broader patterns at the regional scale. And, we’re still trying to understand how ecosystem dynamics and composition are tied to the hydrologic cycle, ecological legacies, and current and past energy balances. These questions are interdisciplinary and require new ways of thinking about systems ecology.

In conclusion, the ecological stresses discussed in the Yellowstone science agenda are hierarchical, not equivalent, because future climate changes will alter the significance of invasive species and the influence of outside land use. I think we’re also leaving out another theme from this agenda and that’s the fact that visitation in Yellowstone is continually increasing. We’ve reached 3.5 million visitors this year, and visitation during bench seasons is now astronomical. People are loving the park to death—they want to be here year-round and they want access everywhere. How this growing human footprint is going to affect a science agenda focused on climate change, invasive species, and land-use change should also be included in the discussion.

Thank you. I’ll turn it over to Yvette.

Remarks of Yvette Converse

I’m Yvette Converse and I work for the U.S. Fish and Wildlife Service. I’ve been with the Fish and Wildlife Service since about ’99. I was with the State of Utah before that, and I worked in consulting for a number of years. I knew Jeff Kershner from Utah State University and a number of others in the room too, but I’ve only been in Montana since ’04, and I actually know very little in terms of the context of my career and probably in terms of the context of what all of you know about Yellowstone and this whole Greater Yellowstone area. But what I have learned over the last decade or so is about government, and I sure some of you know about that as well.

Let me ask the question: how many folks have never heard of landscape conservation cooperatives? Just raise your hand if you’ve never heard of it. Okay. How many have heard of it, but really have no idea what it’s about? It’s okay. How many people have heard of it and maybe seen this talk before and maybe have a vague notion of what it’s about? How many people know what it’s about? Two, great. That’s consistent, and don’t feel bad about that because it’s really kind of a moving target, and so I’m going to talk a little bit about this and I was really trying to figure out how this fit into the panel, but after seeing what Tom [Olliff] had to say,

and Steve Gray, and then Cathy [Whitlock], hopefully this will make sense because we’re kind of scaling-up. But we’re also talking about administrative obstacles and that’s a huge thing when you work for the government and when you work on government-managed lands.

So, a little about “why”...I think we’ve heard a lot about climate change and the other issues that are going on. I’m going to refer to a report that came out this past spring or maybe in June. It’s authored by Matt McKinney, Lynn Scarlett, and Dan Kemmis and you can find this on the Web site at the Lincoln Institute. It’s called “Large Landscape Conservation: A Strategic Framework for Policy and Action,” but to me after working on this for the past 15 months this really speaks to “why LCCs?” So, if you have a chance, take a look. It’s not very long. Just read maybe the intro or a couple of recommendations in there, because it really gives you an idea of why we are talking about landscape conservation cooperatives. There is a gap in governance and a corresponding need to create formal and informal ways to work more effectively across boundaries and, so, we understand that we have to do this biologically, ecologically, and administratively and this is a huge challenge.

The barriers that they identified in this report include lack of scientific information, lack of capacity to organize... which is part of what we’re trying to do, lack of strategy, and fragmented fiscal investments...basically our money and our programs do not align. The recommendations that they include (and this is an independent report, this report had nothing to do with LCCs) are:

- Multi-scaled: local to global. Local is what you guys do every day if you work in Yellowstone or you’re working at the local level...that’s where stuff gets done. We all know that, we’ve all had that experience. But we also know that if at the highest scale that if at a continental scale or even a regional scale that if folks don’t know what you’re doing then what your recommendations are or what you’re doing is less effective and it’s less useful in terms of getting the money and getting the programs to that area.
- Gathering and sharing information.
- Encouraging a network of practitioners.
- To improve federal effectiveness:
 - Identifying top priorities.
 - Common performance metrics.
- Facilitating multi-agency and public-private coordination.
- Flexible funding.

This puts everyone to sleep including myself, but it's hugely important, and I'm going to take just a second to add a caveat to what Steve [Gray] said about "we have nothing to lose with sharing information, we have nothing to lose by doing more monitoring"...if we do that in a strategic way that's adding. Because what we have to lose is our money and we've all seen it happen in cycles as administration changes, and we have some opportunities here to use money in a strategic way to get at some specific answers—and if the information we provide doesn't do that then we'll lose that money and that's because of the way we do our metrics and the way we share that information. Not just with our constituents in the public, but with our funders in Congress. And that's boring stuff, but it is reality.

So, more science, and I was talking with Andy Hansen this morning on the drive down, and I don't call myself a scientist really. I got as much of a science background as I could get to be effective at making management decisions and so I don't practice science. I did my master's and I've overseen a bunch of PhDs at the [Bozeman] Fish Tech Center, but I specifically do not practice science. So, I'm the first one to say, "Let's do as much science as we need to answer the management questions, because there's limited dollars out there." But when you talk about science and adaptive management you are never done. Okay, so we just have to come to terms with that in society and we have to convey that to our public. Science is never done. We are always refining and learning and adjusting. But what we can do is become more effective at how we do science and how we use that science in our management decisions... and that's what is really important...and ensuring also that that gets transferred to our management actions. The word "adaptive management" has been a buzzword in government over the last 10 years or so and it's what has been brought in to these landscape cooperatives.

One more point on the "why." We have billions of dollars going into the conservation on the ground. Some of us see this in our daily jobs, some of us don't see as much of it, but there's literally billions of dollars coming through different funding entities. Department of Interior alone in the Land and Water Conservation Fund, the North American Wetland Conservation Act, the National Fish Habitat Action Plan, State Wildlife Grants, and the list goes on, spends...and this may be conservative, but...\$500 million. [The] Department of Agriculture in the Farm Bill, which has a huge conservation budget...and if you don't know about the Farm Bill, it would behoove you to learn if you work with private landowners at all...billions of dollars for

conservation. EPA...it goes on. So, we're spending billions of dollars on conservation, and are we being effective? In some cases we are, and in some cases we could do better, and part of what government is not good at is working across our institutional silos and, so, we need to do that as we're facing this change. Part of the change we need to make is an institutional change in the way we do business.

So, the Fish and Wildlife Service had landscape conservation cooperatives in our national climate strategy, and it was really kind of focused on fish and wildlife, and the idea was to get at this adaptive management approach with all agencies working together and focus on specific science and outcomes that are quantifiable that we can then show Congress "this is how we're being effective in how we deal with these focal species." There were other climate initiatives that also happened. The Department of Interior and Ken Salazar, our Secretary of Interior, and in particular David Hayes under him, really wanted to bring some coordination into what was going on in Interior and develop the department's climate response, and under that they decided that the LCC and the USGS climate science center's models were what they wanted to latch onto. So, they did through the Secretarial Order last September and called out LCCs and climate science centers as part of the Department of Interior's response... adaptation response.

This changed a couple things. It changed the Fish and Wildlife's original view of what the LCCs were, and I think for the better, but it broadened it and also made the game change...as we go things are changing and we're not sure exactly what that means when folks like the Park Service who have missions and mandates for cultural resources and BIA [Bureau of Indian Affairs] for Native American resources and Bureau of Reclamation for water infrastructure [are involved]. How does that change how we think about landscape conservation in terms of this cooperative effort with those agencies? So, we're still figuring that out, but the good news is that we're starting to think about how to make it work and, I think, turned a corner from complaining about another new program.

So, a couple things, and the one thing I want to emphasize is that this is a partnership of organizations... not just government, but hopefully of other organizations as well...and it's going to take some time to try and bring those circles together. If you think about the math...and I'll show you in a minute...the Hawaiian Islands ha[ve] an LCC. For the most part, those folks are all in the same city or in the same office building, right? In our part of

the world we have much larger administrative diversity going on across our areas. That doesn't mean, you know, they have much more ecological challenges and we have huge ecological opportunities in this part of the world. So, there's going to be differences in how we approach this LCC, but having a partnership is the root of this. Then, the second part of this is that there is some funding that the Fish and Wildlife Service received and is putting that toward that partnership to determine how to use [it]. To me the funding has been a little bit of a distraction because people see that and say, "How can I get that money?" instead of focusing on what's really important here, which is the partnership and the foundation that it is we build to be more effective at what we do.

With that I'm going to talk about how we're spending our money and how we're hoping to build this up. So, you've seen the map of the LCCs. The map was based on bird conservation regions and some other things. No map is perfect and really it's just a framework for organizing. There's really nothing about the map that says we can't go outside our boundaries and, in fact, really we're working on subjects that overlap a lot of these areas all the time. So, more detail there...

Some things we accomplished this year: the Park Service came forward and said they'd like to be a leader on the Great Northern, and this is important because the Department of Interior said "Okay, Department of Interior agencies that said they want to step up and take part in this LCC thing since it's a Department of Interior initiative..." And so the Park Service looked around and saw this area, the Great Northern area, as being one where they had a lot of issues, and so now, fortunately enough, I have Tom [Olliff] working as a co-lead with me in organizing this. It's been really great having the Park Service community behind this because there are a lot of great resources that are brought in.

We have a steering committee with a lot of partners and a partner base that's growing all the time. We developed a goal statement. We have an advisory team that is kind of the working group that has also grown and is multi-agency. We have a governance charter and we spent about \$1.5 million on science and information products this year. But again, the focus here is that we have this partnership and this base to develop a network.

Our goal statement, I think, is pretty good. The steering committee level is regional director, so two Park Service regional directors, two Fish and Wildlife Service regional directors, five state wildlife directors, five BLM

[Bureau of Land Management] state directors, the list goes on to about 35 or 40 people. But these folks agreed to this, which I think is pretty good, because if you see in there the words "...build resilience in the face of climate change and other landscape-level stressors," it's not just about climate. Our money is through climate change through this new administration, but this is really about the whole landscape approach and what we can bring to bear. It's not just about climate.

I'm just going to really quickly talk about this because it really sort of set the stage for us. What we have in this Great Northern area compared to Hawaii—the difference in broad diversity of issues and resources going on—but that also brings us some opportunities with these partnerships. And, so, in the scale in that I'm thinking about this from the Great Northern, there's a lot of really good landscape-level partnerships. They might be species or place based, but they're working at a landscape scale and those are opportunities for all of us...including Yellowstone...to plug into those because when we start to think about the things that Steve [Gray] talked about, and Cathy [Whitlock] talked about with shifts in distribution of species and vegetation, we're going to need to work outside of our comfort zones and areas that we know.

I'd like to give you an idea of the kind of structure we're talking about for the LCC. We have a coordinator, staff (not much of a staff right now, it's me and Tom [Olliff] and Rich Sodja of USGS), and we have the advisory team really working with the staff to build this whole model, but the steering committee has only met once. They've had a couple phone calls and they're going to meet again this fall. But the real value here is linking into that partnership network and the way we plan to do that is through these eco-geographic forums, or we're calling them "eco-forums." So, we split our LCC...or not split it but kind of summarize it...as three different areas: Columbia, sage-steppe, and Rocky Mountain. So, the idea there is that the mountains are not outshining the Columbia, or we don't focus on any one, and it also gives this a way to kind of convene around ecologically relevant issues. So, folks that are working on sage-steppe issues here might be talking to folks working on sage-steppe or arid lands issues in Washington.

So, the idea is that we plan to roll out a process to engage this partnership network through these eco-forums and that would be where most of folks like you, or some partnership that you work in, would engage and start to drive the priorities for this level.

In the past year we did a quick assessment in “getting the horse in front of the cart,” because we got our money our first year without having a lot of planning behind us. So we did a quick assessment on informational needs and really we were looking at this landscape level of information. We had some webinars; we’ve got some feedback on that. Some of you may have participated. We also talked to a number of partnerships including GYCC [the Greater Yellowstone Coordinating Committee] and others and asked them what information needs do you have at sort of a landscape scale and these rose to the top. They’re not the only ones. I would add invasives and some other things. But really when you think about foundational information we can all share across the landscape, these came into the top. The highlighted blue is what our steering committee prioritized for this year. Part of the reason they didn’t prioritize climate is that they feel there are some more imminent issues that we had to get on board with first and partly because they’re still unclear as to the role of LCCs versus the climate science centers.

So, I’m just going to give you a couple of examples of some of the projects we’ve funded this year, but you can go to our Web site and there’s a full list there, and it explains the process that we used and where that money is going. But these are the kinds of projects we have and I’m going to show you three of them. They all follow the same model. This one is of the aquatic, sort of watershed-scale, pilot that Clint Muhlfeld is doing in the Crown of the Continent, North Flathead region. He’s doing that with the Flathead Biological Station and it’s the same model and I’m sure some of you are involved in this sort of work. Basically getting your GIS or spatial information layers together, doing some kind of a classification of species or ecological relevance information or modeling in the middle, and doing your vulnerability and the end.

Same thing with some of the work they do with the IGBC [Interagency Grizzly Bear Committee] or what Chris Servheen does with the University of Montana...it’s the same model...corridor analysis, ecological modeling, species validation. This is some of the work and then you end up being able to identify critical areas and linkages... in this case with grizzly bear.

This is the Washington Connected Landscapes Project. So, this is another big effort going on within the Great Northern area, but same model: corridor analysis, species...they do the DNA and telemetry work and validate species information, and then the ecological modeling and model validation, and then apply [it] to management. So, that’s just to give you some ideas.

Our next step is to give you some more information of what we talked about. We’re going to roll out these eco-forums in the next six months to a year and hopefully you’ll learn more about that and it’ll be a good way for folks like you to engage and get on to a long-term strategy. But Tom [Olliff] is somebody that you guys know well and can ask any questions about this as well. He and I have been working on this together. So, that’s all I have.

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Air Quality Monitoring in the Teton and Gros Ventre Wilderness Areas: A Mixed Methods Approach

Andrew R. Allgeier¹ and Stephen E. Williams²

¹ Executive Director, Yellowstone Receptions Foundation (Sleeping Giant Ski Area), 4019 Somerset Circle, Casper, WY 82609, 307-699-1064, aallgeier@gmail.com

² Professor, Department of Renewable Resources, College of Agriculture and Natural Resources, University of Wyoming, 1000 E. University Ave., Laramie, WY 82071, 307-766-2683, sewms@uwyo.edu

Abstract

Water and soil samples were collected from 40 lake basins in the Teton and Gros Ventre Wilderness Areas of western Wyoming during the summers of 2005 and 2006, respectively. Analysis of water samples led to a baseline for further sampling to determine levels of atmospheric NO_x deposition. Acid neutralization capacity (ANC) of these lakes was used as an indicator of susceptibility to acidification from atmospheric deposition. Also examined was the contention that water quality is a function not only of air quality but also of abiotic and biotic characteristics of lake catchment basins. Interviews with six permitted outfitters were conducted in March 2008. These interviews generated a baseline of observed phenomena relating to Air Quality Related Values (AQRVs) and the feasibility of using local, long-term resource users as a monitoring tool. Five lakes in each the Teton and Gros Ventre Wildernesses had less than 200 µeq/L ANC. These 10 lakes are at risk of acidification according to U.S. Environmental Protection Agency (EPA) guidelines. When integrated with the 1984 EPA Western Lakes Survey data, basic trends of air quality emerged. Increases in NH₄⁺ and decreases in SO₄²⁻ were shown. Parent material was found to have a significant correlation with ANC ($p = 0.007$). The interview process showed that outfitters are a source for historic resource conditions and can prove to be a valuable part of the monitoring process by noticing visible changes in the resource.

Introduction

Alpine environments around the globe are showing signs of stress and change (Vitousek et al. 2000). Extensive research by Williams et al. (1996) in the Colorado Front Range indicates nitrogen saturation occurs in alpine environments. Prior research in alpine areas of Wyoming has included long-term air quality monitoring at several sites in the Wind River Range (WRR) as well as the Glacier Lakes Ecosystem Experimental Site (GLEES) in the Snowy Range. Data from the WRR sites suggest that there is an unusually high and potentially damaging amount of nitrogen deposition in alpine ecosystems such as those of the Wind River Range (Svalberg 2005). Wilderness areas adjacent to the Teton and Gros Ventre, such as the Bridger and Fitzpatrick, are showing signs of increased levels of air pollution from upwind changes in land use (Svalberg 2005). Changes in development west of these areas include urbanization of Teton County, Idaho, and wind-blown agricultural particulates (Story et al. 2005). Gas and oil development in areas of western Wyoming may have negative impacts on air quality in surrounding and downwind areas as well.

As of 1977, Clean Air Act (U.S. Congress 2004) amendments established all existing international parks,

federally designated wilderness areas greater than 5,000 acres, national memorial parks greater than 5,000 acres, and national parks greater than 6,000 acres, as Class I airsheds. As a result of the 1977 and 1990 amendments to the 1970 Clean Air Act, federal land managers have the affirmative responsibility to manage areas of the highest air quality (Class I airsheds) for minimal change and protection of Air Quality Related Values (AQRVs; U.S. Congress 2004). Class II airsheds are defined by the 1977 Clean Air Act amendments as areas that received park or wilderness designation after 1977 or other areas as designated by the governor of the state in which the area lies, as attainment of meeting the National Ambient Air Quality Standards (NAAQS) or as unclassifiable due to lack of air quality data. The Teton and Gros Ventre Wildernesses in northwestern Wyoming fall into these two categories, respectively. The Teton and Gros Ventre Wildernesses at present have no current baseline for air quality standards.

AQRVs are elements of the resource that may be degraded by air pollution and include flora, fauna, soils, water, cultural resources, geologic features, and visibility (Berg et al. 2005). AQRVs in the Teton Wilderness and

Gros Ventre Wilderness Areas fall into two categories: water and visibility (USFS 2002). This study primarily addresses the water AQRVs and, secondarily, soil and visibility.

A principal indicator of the water quality AQRV is lake chemistry. This is measured as a trend over time for the acid neutralization capacity (ANC) of any given lake and is a measure of the ability of the lake to buffer inputs of acid from wet deposition usually in the form of nitrate (NO_3^-), ammonia (NH_4^+), and sulfate (SO_4^{2-} ; Aber et al. 1998). Lakes with low ANC, associated acidification/pollution of perennial streams, and soil/geological properties of sampled lake basins were targets of this effort. The concern threshold is a change from baseline and this study in part establishes that baseline.

Acidification of watersheds is often associated with changes in microbial and macroinvertebrate communities and increased metal availability and toxicity (Fenn et al. 1998). As the ANC of water bodies decreases due to

acidification, additional inputs of nitrates and sulfates are no longer buffered and the biological activity, including nutrient cycling changes (Baron et al. 2000).

Acidification of soils will modify solubility of some chemical constituents and accentuate leaching of others. Further increases in inorganic nitrogen have the potential to deteriorate stability of alpine soils (Matson et al. 2002). Other changes in the alpine environment include increased nitrogen in the soil, increased mineralization, and altered species composition in lake microbiota (Baron et al. 2000). Palmer et al. (2007) suggested that micronutrients including selenium decreased in areas of increased acidic deposition. If left unchecked for long periods, acidic deposition has the potential to change the tree species' composition and type (Fenn et al. 1998).

In addition to the basic air quality survey, the role of soils and parent material on water quality measurements should be determined. The chosen sampling sites in both wilderness areas have widely differing lithologies despite their relative geographic closeness. This expands on the research done on nitrogen-saturated soils in the central Rocky Mountains of southern Wyoming and northern Colorado (Baron et al. 1994).

Description of Study Area

Both the Teton and Gros Ventre Wilderness Areas are primary components of the Greater Yellowstone Ecosystem (GYE). The Teton Wilderness is the origin of both the Yellowstone and Snake Rivers. The Teton Wilderness' 284,899 hectares (ha; 585,238 acres) extend from the northeast border of Grand Teton National Park to the southeast corner of Yellowstone National Park (Figure 1). It is a component of the Teton-Washakie-Yellowstone (TWY) Wilderness Complex. This complex includes 236,837 ha (585,238 acres) in the Teton Wilderness (Bridger-Teton National Forest), 284,899 ha (704,000 acres) in the Washakie Wilderness (Shoshone National Forest), and about 163,493 ha (404,000 acres) of southeast Yellowstone National Park, managed as *de facto* wilderness. These contiguous wilderness areas form the largest wilderness zone in the Greater Yellowstone area (GYA) at more than 688,000 ha (1.7 million acres) and create one of the largest such areas in the Lower 48 states (Patten 1991). This area is an ecologically non-fragmented system and is mostly composed of volcanic geologic materials in the Absaroka Mountains at elevations ranging from around 2,100 meters (m; 7,000 feet) to more than 3,900 m (13,000 feet).

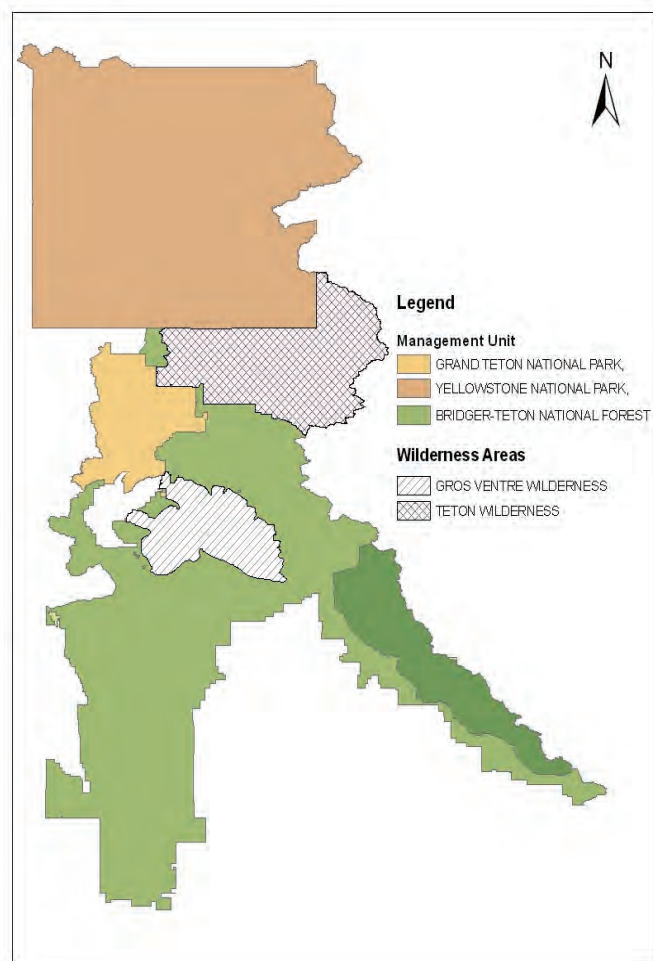


Figure 1. Location map of the Teton and Gros Ventre Wildernesses within the Greater Yellowstone area.

The Gros Ventre Wilderness, about half the size of the Teton Wilderness, is the headwaters of the Gros Ventre River and other streams, including Granite Creek, a major tributary of the Hoback River. The Gros Ventre Wilderness also contributes hydrologically to the upper Green River system. This wilderness, 116,115 ha (287,000 acres) in size, ranges in elevation from 1,900 m (6,500 feet) to nearly 3,600 m (11,700 feet) and is composed of a wide variety of geological parent materials, including numerous sedimentary rocks (mostly limestones) with isolated pockets of igneous and metamorphic lithologies.

This study establishes a baseline of water quality and soils data for the Teton and Gros Ventre Wildernesses in order to identify lakes at risk of chronic and episodic acidification from atmospheric deposition. Without such a baseline, changes in water and air quality cannot be quantified, and management to protect the natural conditions of this ecosystem will be impaired. Land managers need this data to determine whether they are meeting air quality standards and when to put pressure on upwind land managers to change their policies to remediate the problem. A subset of the lakes in each wilderness is recommended for resampling to monitor changes in air quality in a cost-effective manner.

Mixed Methods Design

To address the social component of the issue of air quality, qualitative methods were used in the form of pilot interviews with users of both wilderness areas. Since both quantitative and qualitative methods were used to determine the baseline and probable impacts of air quality in these wilderness areas, this study is designated a mixed methods design.

Tashakkori and Teddlie (2003) define sequential mixed method design as: "A design in which one type of data provides a basis for the collection of another type of data. It answers one type of question by collecting and analyzing two types of data. Inferences are based on the analysis of both types of data." In the case of this study, the qualitative data informs the quantitative study by both examining the collective memory about these wildernesses through their users for episodes of impaired water quality and visibility, as well as to generate possible new study sites based on unique knowledge of the area. It is important to note that the qualitative data was not used to triangulate or confirm the quantitative data but rather to direct and drive it.

Weiss (1994) explained the advantages of this type

of study: "While it can be valuable for the results of qualitative interview studies to be verified by other methods, it can also be valuable for the results of studies done by other methods to be illuminated by qualitative interview studies."

Human Resource Background. Both the Teton and the Gros Ventre Wildernesses have a long history of hunting and guiding. In the Teton Wilderness, ranger patrol cabins were installed in the early twentieth century by the National Park Service, U.S. Forest Service, and the Wyoming Game and Fish Department. Permits are often held by guides for long periods of time and there is fairly low turnover. This can lead to the outfitter having intimate knowledge of the resource, and they may note subtle changes in the condition of the resource that other observers miss. Outfitting and guiding in these wilderness areas is both a profession and a way of life, thus outfitters are invested in maintaining the integrity of the resource.

Shifting demographics have left land managers unsure of the public's attitudes toward national forests. Attitudes can be used to predict behavior (Fishbein and Ajzen 1975), which can help land managers determine how the public wishes to use national forests. Controversy over land-use issues is more common as traditional views are replaced with an environmental orientation (Van Liere and Dunlap 1980; Eckersley 1992).

While research has shown that younger, more educated, urban dwellers tend to de-emphasize traditional commodity uses of nature (e.g., logging, mining, and grazing) and place higher value on issues such as wildland preservation (Rudzitis 1999), less attention has been given to whether or not occupational dependency has affected attitudes toward national forest management. People in service sectors have been shown to be more environmentally oriented than those in production-related industries (Beyers 1999; Nelson 1999; Rudzitis 1999).

Social Impacts. The air quality of the Teton and Gros Ventre headwater areas directly affects the areas downstream including much of the GYA. The water quality of these areas impacts downstream users and systems, including aquatic life, wetlands, waterfowl, recreationists, and other human uses farther downstream, including agriculture. Potential changes to the soil and biota of high alpine systems through atmospheric deposition can have cascading effects on those communities, downstream ecosystems, and land uses.

The social science research herein is in the form of interviews of permitted outfitters and recording their values, attitudes, and behavioral intentions toward change in resource integrity and the management implications thereof, as well as any noted air quality–related resource impairments. The qualitative aspect of the project includes determining the effects of increases in acidic atmospheric deposition on the way of life to stakeholders that are lower in the watershed.

Objectives

This study investigates the management equation by addressing the following:

1. The establishment of baseline air quality data for the Teton and Gros Ventre Wilderness Areas,
2. The establishment of baseline soils and water data for the Teton and Gros Ventre Wilderness Areas,
3. The comparison of air quality, water quality, and soil parameters across differing parent materials,
4. The determination of whether excess nitrogen is coming from atmospheric deposition,
5. The evaluation of water and soil data to determine lakes at risk of acidification, and
6. The determination of effect of acidification on dominant user groups' way of life in study areas.

Section I. Quantitative Analysis

Relevant Literature Summary

Acidification Case Studies. Significant acidification was documented in central and eastern Europe from the time of the Industrial Revolution through the 1980s (Fott et al. 1994; Kopacek et al. 2001). Montane forest ecosystems in

the eastern United States have shown signs of nitrogen saturation (Mayer et al. 2002). Fenn et al. (1998) compared the responses of multiple ecosystems in North America to nitrogen excess. They concluded that symptoms of N saturation were most noticeable in high-elevation, spruce-fir ecosystems in the Appalachian Mountains and West Virginia. This may be due to differences in geology or perhaps increased temporal exposure to elevated N levels. Aber et al. (1989) used these instances of acidification of temperate forests to develop a continuum of nitrogen saturation (Figure 2). Aber et al. (1989) was also the first to formally define nitrogen saturation as the availability of ammonium and nitrate in excess of total combined plant and microbial nutritional demand.

Despite the focus on deposition in the eastern United States, there are multiple examples from the central Rocky Mountains. Alpine ecosystems adjacent to the Front Range of Colorado have already begun showing multiple signs of N saturation (Williams et al. 1996). Williams and Tonnessen (2000) examined chronic additions of nitrates along the Colorado Front Range in alpine environments. They documented significant increases in deposition of inorganic nitrogen at higher elevations. Burns (2003, 2004) re-analyzed this data and suggested that continued monitoring of atmospheric nitrogen deposition may reveal more trends in the future. ANC of lakes in the Colorado Front Range has decreased as a response to chronic atmospheric nitrogen deposition (Williams and Tonnessen 2000). Deposition from volatilized agricultural nitrogen (NH_4^+) in adjacent alpine environments has been documented by Collett et al. (2007) as part of the RoMANS study in Rocky Mountain National Park. Baron et al. (2000) showed that the majority, 75 percent,

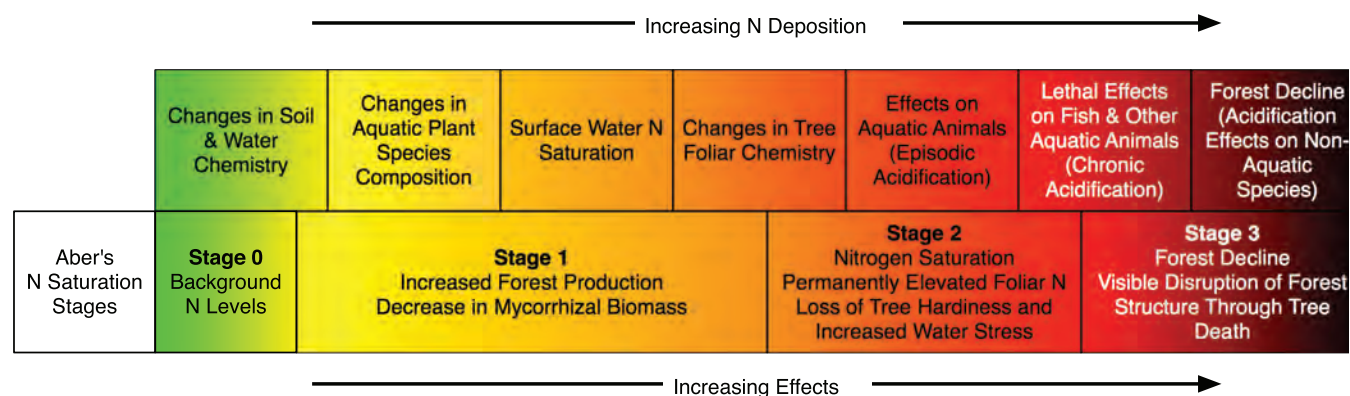


Figure 2. Continuum of nitrogen deposition effects in terrestrial ecosystems. Stages of nitrogen saturation were developed by Aber et al. (1989).

of N deposition in the east side of the park was from anthropogenic sources.

Other findings suggest this trend extends into the northern Rocky Mountains as well. Currently, an increasing trend in N deposition in alpine environments in the GYA has been documented by Svalberg (2005). Sampling of glaciers in the Wind River Range (50 to 80 kilometers [km] to the southeast of the areas in the present study) by Naftz et al. (1996) revealed nitrogen deposition during the late 1980s and early 1990s at levels nearly one-hundred fold above levels during the previous several hundred years.

Water Chemistry. Aquatic biota, including fish and invertebrates, can be impacted by poor water quality (Burns 2003). Sullivan et al. (1997) showed that nitrogen deposition (especially chronic) has a greater influence on acidification of freshwaters than originally thought. Increased NO_3^- in surface waters has been shown to change algae species composition and negatively affect amphibian populations (Burns 2003, 2004). Isotopic analysis of $\delta^{15}\text{N}$ and $\delta^{18}\text{O}$ by Campbell et al. (2002) determined that most of the measurable nitrate in surface waters in the alpine system has been cycled microbially or chemically and thus differs from the original precipitation form. This does not, however, change the effects of the quantity of N added to a given catchment.

Effects on Aquatic Species. Increased nitrogen deposition from anthropogenic sources has also been shown to change the microbial community structure in alpine lakes with a marked increase in the diatom fraction (Wolfe et al. 2001, 2003), indicating that even modest increases in N deposition can result in biogeochemical changes that likely represent the beginning of a stronger response to N deposition. Kelly et al. (1982) showed the importance of bacterial processes in regulating the rate of lake acidification, finding that energy normally devoted to carbon dioxide retention (or methane production) is diverted to nitrate and sulfate reduction in the presence of excess nitrate and sulfate.

Soil Chemistry and Microbiology. Sickman et al. (2002) showed that soils accounted for up to 82 percent of the nitrogen variability within surrounding surface waters in high-elevation ecosystems in the western United States. Locations in the Front Range of Colorado show that as a result of long-term loading from atmospheric deposition,

alpine soils have a decreased capacity to retain additional N inputs into the system (Baron et al. 1994; Williams and Tonnessen 2000). Such increases in nitrogen have the potential to impair nutrient cycling, resulting in decreased bioavailability of micronutrients.

Additional atmospheric nitrate can upset the seasonal nutrient and growth dynamics of the sensitive alpine community. Lipson et al. (1999), Miller and Bowman (2003), Nemergut et al. (2005), Schmidt and Lipson (2004), and Schmidt et al. (2004) all address the spring surge of nutrients and nitrogen and the interaction of the microbe-plant communities with respect to the pulse of nitrogen. Egerton-Warburton et al. (2001) noted a decrease in arbuscular mycorrhizal activity as a result of increased nitrate deposition. Microbes and plant/microbe symbioses that fix N_2 in nitrogen-limited environments lose their competitive advantage in systems where N is abundant (Aber et al. 1989).

Effects on Terrestrial Species. Further effects of increased nitrogen deposition occur in the plant community. Miller and Bowman (2003) showed a change between species use and growth of increased nitrogen and its implications for eventual change in species and community diversity. Change in forest species composition has also been shown to be a function of over-saturation and deposition of anthropogenic sources of nitrogen (Matson et al. 2002).

Vitousek et al. (1997) listed in detail the probable responses to increased nitrogen deposition, which included accelerated losses of biological diversity, especially in those plants adapted to efficiently use nitrogen and other species that in some way depend on those plants. Ecosystem response to nitrogen deposition was also investigated in Colorado by Baron et al. (2000), who showed that deposition rates and biogeochemical cycling rates vary widely among catchments but with some level of predictability.

Influences On and Of Climate Change. The interaction of nitrogen and the microbial community also has impacts on larger biogeochemical cycling processes for carbon and nitrogen. Schmidt et al. (2004) investigated how chronic nitrogen additions affect the structure and biogeochemical functioning of soil microbial communities and report that the microbial community may provide a seasonal sink for additional nitrogen. Shallow but organically rich alpine soils stressed by high nitrogen loading are experiencing accelerated decomposition rates (Retzer 1974). An increase

in the rate of decomposition results in increased release of CO₂.

Climate change may also play a role in changes of pH of high alpine lakes (Koinig et al. 1998). Koinig et al. (1998) established that temperature affecting the timing and duration of snow and ice cover of alpine lakes had a mediating role in the lake's chemistry. Temperature also had an effect on chemistry through changing the rate of weathering and erosion of parent material in the catchment (Rogora et al. 2003). Higher nitrogen levels measured in alpine soils of the northern Wind River Range (30 times as much as levels reported in 1985 by Williams et al. from similar sites) combined with significantly higher temperatures will result in soil degradation and compromise the mountains' hydrological function.

Sampling. Water quality of headwater regions is partly a function of air quality. A manifestation of air quality is water quality and can be assessed by sampling lakes from particular areas over time. Surface water samples from lakes in high, alpine watersheds provide a good indication of air quality, as any pollutants such as nitrate or ammonia provide condensation nuclei for water. By sampling high alpine lakes rather than lower-elevation waters, the chemistry more accurately reflects that of the original precipitation by minimizing time and biogeochemical opportunities to change (Berg et al. 2005; Nanus et al. 2005). Lakes in Yellowstone National Park on volcanically derived soils greater than 2,590 m (8,500 feet) in elevation were shown to have the greatest probability of having a low ANC (Nanus et al. 2005). Changes in the chemistry of these lakes can more accurately reflect changes in air quality.

Statistical analysis of ANC and other parameters should take into account the mediating variables shown by Berg et al. (2005), who listed watershed characteristics such as acreage, lake perimeter to area ratio, lithology, vegetation cover, and catchment to lake area ratio. Catchment characteristics were shown to be correlated to levels of total nitrogen and phosphorus by Kopacek et al. (1995).

Management Implications. Use of wilderness areas as areas of research to help assess more developed areas, especially in the use of determining anthropogenic versus natural change, was examined by Graumlich (2000) and Vitousek et al. (2000). They suggest that large-scale changes such as air quality rely on pristine areas such as

wilderness to gain a complete view of what is actually occurring. The EPA took a national survey of lakes from 1983–1984. The Western Lakes Survey of 1984 yielded data for two lakes—one in the Teton Wilderness and one in the Gros Ventre Wilderness (EPA 1984). This data may be useful in establishing long-term trends in air quality.

As noted by Story et al. (2005), managers of Class I airsheds must manage to protect the air quality of these areas, as mandated by the Clean Air Act (U.S. Congress 2004). Usable management frameworks to address the issue of air quality include the Limits of Acceptable Change (LAC) framework developed by Stankey et al. (1985). LAC is based on the use of indicators and standards (Stankey et al. 1985; Nilson and Tayler 1997). It is at this level that it can be incorporated into the management of air and water quality. Indicators are set for areas of concern or significance. Standards are set to yield the desired future conditions. If the critical threshold for a standard is met, a remedial management action must take place. This study provides a baseline for standards of air and water quality.

Methods

Conceptual Background. The interrelatedness between the biotic and abiotic components of the air quality system stems from Jenny's (1941) soil state equation. Jenny states that soil is a function of both the individual and combined actions of parent material, topography, organisms, and climate at a given site and integrated over time. Using the same format to examine the factors that influence air quality, water quality is related to air quality. Water quality in turn also is a function of topography, climate, parent material, and organisms. Comprehensively water quality is a function then of air quality and is further attenuated by Jenny's other factors of climate, parent material, topography, and organisms. Water quality is then, succinctly, a function of air quality and soils. A visual representation of this is provided in Figure 3 and takes into account that air quality parameters do not always interface first with soil.

Water and soil parameters were chosen for measurement due to the existing Forest Service air quality monitoring program, which uses water samples to determine air quality. Soil samples were taken due to their unique functional role between atmospheric deposition and any surface waters.

Air/Water. Sample sites for both wilderness areas were selected in accordance with the standards set by the Forest

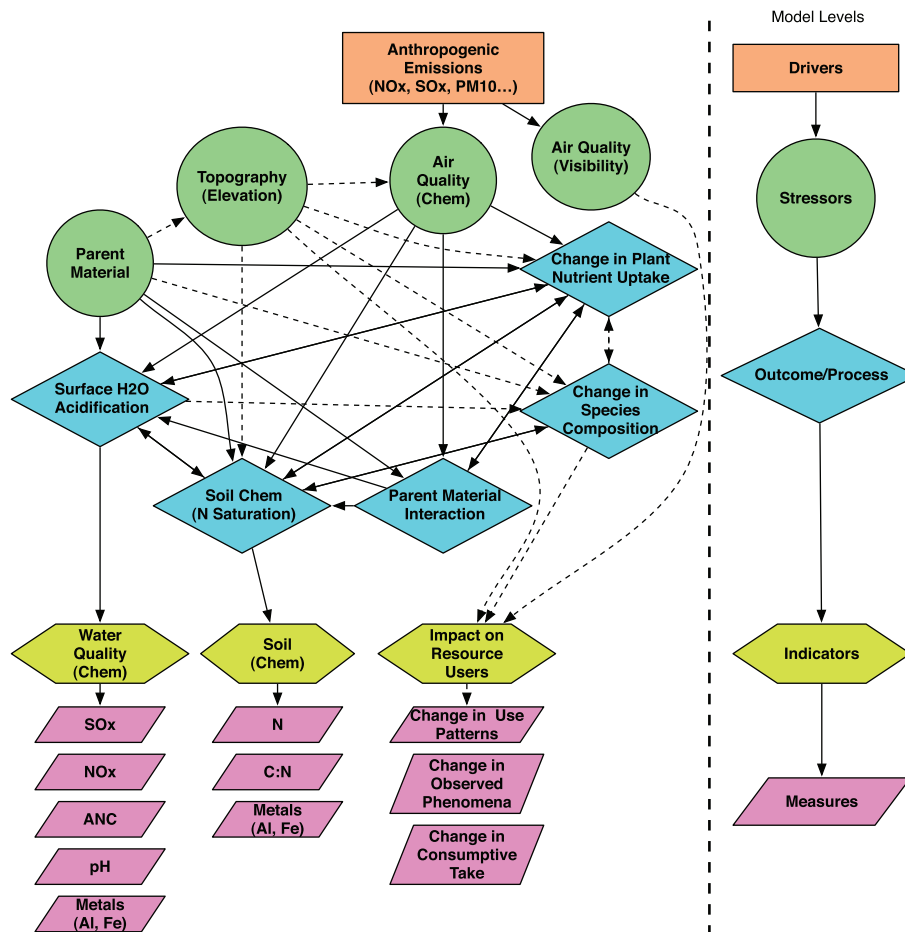


Figure 3. Conceptual path model of atmospheric deposition and analysis. The model follows any anthropogenic emissions from source through any ecosystem processes or factors to a measurable and monitorable output of the system. Arrows with dotted lines represent functional linkages and relationships. Arrows with solid lines show the movement of matter through the system. For elaboration of model level definitions, see Allgeier (2009). This model was developed for this study by the authors.

Service and those recommended by the Rocky Mountain Research Station (RMRS) water and soils laboratory in Fort Collins, Colorado (USFS 2002a). Lakes were chosen based on their depth, presence of a flowing outlet for sampling purposes, their geographic position high up in the watershed, and for having no lakes above them in their catchment zone. The influence of organisms on the samples was mitigated through selection of high-elevation lakes above 2,400 m (8,000 feet), preferably above treeline. Lakes were also chosen to ensure a wide geographic distribution across each wilderness area. Ease of access was also taken into consideration to facilitate re-sampling. The data for lake selection came from United States Geological Survey (USGS) topographic maps, the Bridger-Teton National Forest Geographic Information System (GIS) database, and the firsthand knowledge of

employees of the Forest Service and Wyoming Game and Fish Department.

Samples and subsequent measurements were taken from 21 lakes that were sampled between June 19 and August 19, 2005, in the Teton Wilderness. The geographic representation of these sampling locations included nearly the entire wilderness, with 19 samples from the Snake River watershed and two samples from the Yellowstone River watershed. A third sample from the Yellowstone watershed was taken during the 2006 field season. Sampling was done on foot during seven sampling trips covering a distance of approximately 64 km (40 miles) and five horseback trips that covered approximately 563 km (350 miles).

Measurements were taken from 17 lakes sampled between June 19 and August 4, 2006, in the Gros Ventre Wilderness. Once again, the geographic representation

of these sampling locations included nearly all of the wilderness area with six lakes in the Hoback/Snake watershed, nine lakes in the Gros Ventre/Snake, and two samples from the Green River watershed.

One sample taken during the 2006 field season was taken from the Teton Wilderness in the Upper Yellowstone watershed; this sample was missed during the 2005 sampling season due to hazardous trail conditions.

Sampling of the Gros Ventre was accomplished by three horse pack-supported trips covering approximately 241 km (150 miles) and seven sampling trips on foot covering a distance of approximately 193 km (120 miles).

Sampling methodology followed was that prescribed by the U.S. Department of Agriculture (USFS 2002a). To keep samples at a stable and low temperature during horse transport in the wilderness, the bottom half of a hard-sided, aluminum, bear-resistant pannier was lined and covered with 2.54 cm (1 inch) rigid polystyrene foam insulation and stocked with blue ice packs. For foot sampling trips, samples were kept cool using an insulated, soft-sided cooler bag with blue ice packs. Sample temperatures were kept a few degrees above 0°C in this manner. Once out of the backcountry, samples were moved to a refrigerator with a constant temperature near 0°C. For shipping to the laboratory for analysis, samples were packed into a hard-sided foam cooler with multiple frozen blue ice packs and shipped by standard U.S. Postal Service registered mail. Samples were shipped early in the week in order to arrive at the laboratory before the weekend. Analysis was done at the biogeochemistry laboratory at the Rocky Mountain Research Station (Fort Collins, Colorado) for analysis. Methodology followed for water is that of the USFS (2002a).

Water analysis included filtering, pH, alkalinity (including ANC), conductivity, anions (F^- , Cl^- , NO_3^- , PO_4^{3-} , SO_4^{2-}), and cations (Na^+ , NH_4^+ , K^+ , Mg^{2+} , Ca^{2+}). To determine ANC, the Gran analysis technique (Gran 1952) was used. We measured pH using the EPA method 150.1 (electrometric; EPA 1983a). Conductivity was measured using the specific conductance method (EPA 1983b). An ion chromatograph (IC) with separator was used for measuring anions and cations via the EPA Method 300.0 (EPA 1993).

Soils. Soil samples came from upslope of the area immediately surrounding the sampled lakes. Soil samples were taken at 20 lakes in the Teton Wilderness and 17 lakes in the Gros Ventre Wilderness. At each lake location, three

samples were taken to a depth of 15 cm. Samples were taken from a variety of aspects and vegetation types that best represented the catchment basin. Soil was cooled and transported in the cold storage pannier or soft-sided cooler along with the water samples. Once they were out of the wilderness, soil samples were stored at 1°C and maintained at that temperature until analysis. Soils were analyzed for extractable nitrate, extractable ammonium, extractable potassium, pH, organic carbon, extractable phosphate, texture, and electrical conductivity. Soil analysis was done by the Soil Testing Laboratory at the University of Wyoming (Laramie, Wyoming), according to methodology of Williams et al. (1985).

Statistics. All statistics were performed in Microsoft Excel V.11.5. Analysis of soil versus water parameters as well as the influence of elevation was carried out using linear regression analysis. Analysis of parameters as a function of parent material was done with a one-way ANOVA followed by a Tukey's HSD post hoc test in Microsoft Excel using innerSTAT-a v2.0 (Instituto Nacional de Enfermedades Respiratorias, Mexico). Analysis of parameters as a function of wilderness area was done using two sample t-tests. A significance level of $\alpha = 0.05$ was used for both ANOVA and t-tests. Statistical results are reported using the following notation: ANOVA: (F value, degrees of freedom, p value), t-test: (mean, standard deviation), and two sample t-test: (t, degrees of freedom, p value).

Results

Water. Analysis of the 22 lakes in the Teton Wilderness are shown. Levels of NH_4^+ ranged from $< 0.01 \mu\text{mol/L}$ to $62.42 \mu\text{mol/L}$. NO_3^- levels ranged from < 0.007 to $62.043 \mu\text{mol/L}$; SO_4^{2-} levels ranged from $< 0.05 \mu\text{mol/L}$ to $68.34 \mu\text{mol/L}$ (Table 1). Duplicate samples from Emerald and Tri-County Lakes showed up to a 10-fold difference in NH_4^+ , and Tri-County had a 10-fold difference in NO_3^- . ANC levels also showed high variability ranging from $45.0 \mu\text{eq/L}$ to as high as $2,889.3 \mu\text{eq/L}$ (Table 1). Lake chemistry for the Gros Ventre Wilderness showed levels of NH_4^+ ranging from $< 0.01 \mu\text{mol/L}$ to $28.83 \mu\text{mol/L}$, and NO_3^- levels from $< 0.007 \mu\text{eq/L}$ to $15.160 \mu\text{mol/L}$. SO_4^{2-} levels ranged from $< 0.05 \mu\text{eq/L}$ to $99.5 \mu\text{mol/L}$ (Table 2). ANC levels ranged from $51.6 \mu\text{eq/L}$ to $4228.9 \mu\text{eq/L}$. The duplicate sample at Upper Farney Lake showed a 10-fold difference in NH_4^+ .

A total of 10 lakes from both wildernesses (Table 3) were found to be below the $200 \mu\text{eq/L}$ ANC threshold set

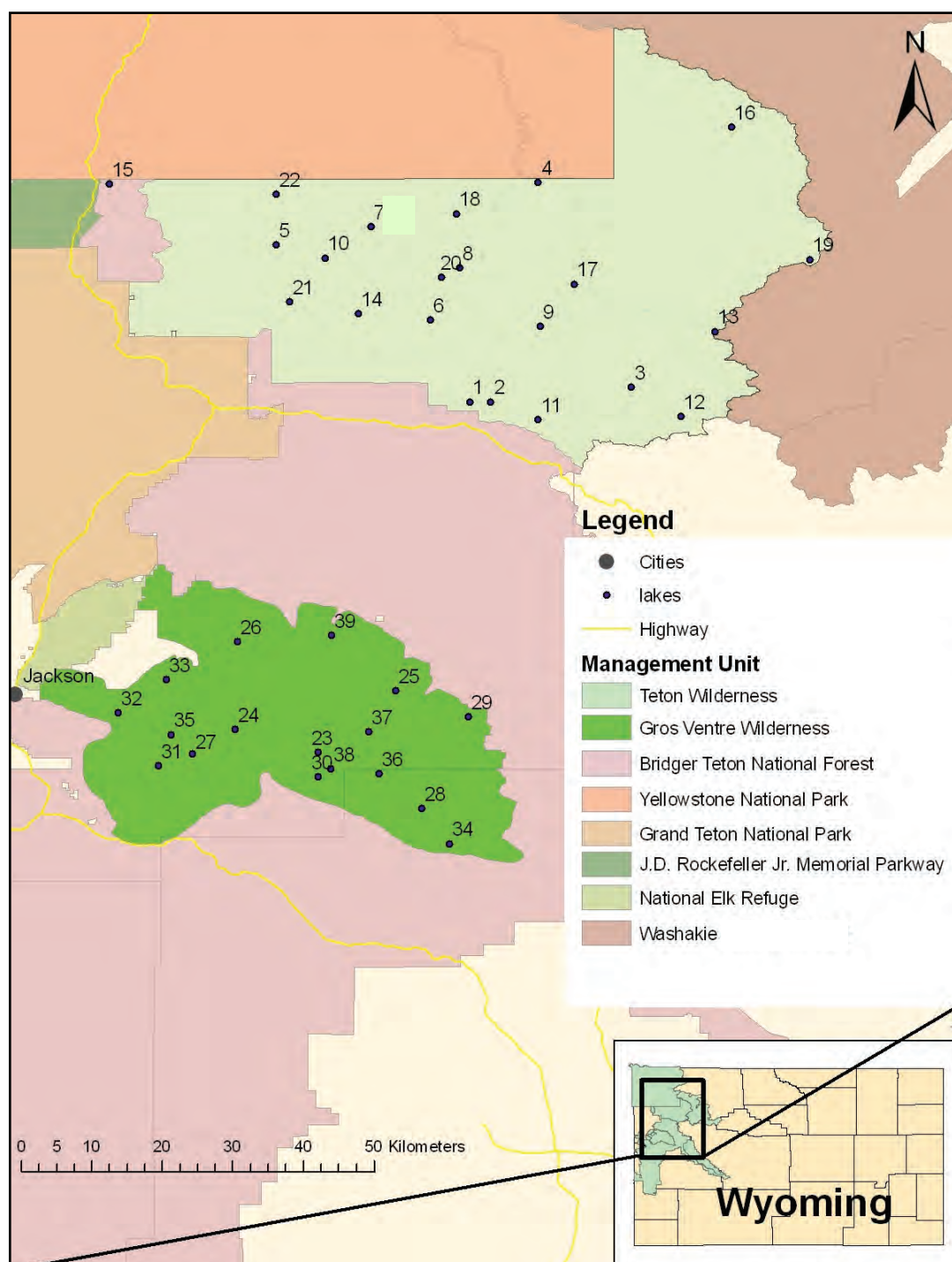


Figure 4. Sample distribution map of lakes; see Allgeier (2009) for GPS coordinates.

Table 1. ANC, NO_3^- , NH_4^+ , and SO_4^{2-} for lakes sampled in the Teton Wilderness. Lake numbers correspond to point locations (Figure 4).

Lake & Number	ANC $\mu\text{eq/L}$	NH_4^+ $\mu\text{mol/L}$	NO_3^- $\mu\text{mol/L}$	SO_4^{2-} $\mu\text{mol/L}$	Parent Material	Elev. (m)	Sample Data
Bear Cub Lake (2)	499.8	5.21	<0.007	68.34	Granitic	2291	06/22/05
Holmes Cave Lake (11)	45.0	2.38	<0.007	3.08	Limestone	2981	08/03/05
W. Enos Peak Lake (20)	1499.8	5.04	<0.007	8.82	Limestone	2512	07/11/05
Valley Fork Lake ² (19)	342.0	1.00	0.919	13.94	Volcanic	3278	06/30/06
Lewis Lake (12)	177.6	4.88	<0.007	3.59	Volcanic	3130	07/25/05
Marston Lake (13)	83.8	2.33	<0.007	1.60	Volcanic	3091	07/27/05
Tri-County Lake (17)	233.1	7.26	6.548	3.32	Volcanic	3062	08/11/05
Tri-County Lake ¹	227.5	60.15	62.043	3.37	Volcanic	3062	08/11/05
Silvertip Lake (16)	181.7	0.83	<0.007	8.42	Volcanic	3059	08/16/05
Ferry Lake (9)	180.6	3.77	<0.007	3.60	Volcanic	3037	07/27/05
Two Ocean Lake (18)	420.1	4.16	0.258	3.60	Volcanic	2834	08/18/05
Bertha Lake (3)	811.7	5.82	2.226	15.19	Volcanic	2728	07/26/05
Gravel Lake (10)	1329.8	<0.01	<0.007	33.03	Volcanic	2665	07/15/05
Emerald Lake (7)	554.2	18.52	<0.007	22.78	Volcanic	2652	07/14/05
Emerald Lake ¹	539.3	7.43	<0.007	22.96	Volcanic	2652	07/14/05
Divide Lake (6)	2039.7	3.88	0.387	<0.05	Volcanic	2621	06/29/05
Coulter Lake (5)	343.0	10.15	<0.007	10.42	Volcanic	2545	07/12/05
Wolverine Lake (22)	1573.9	<0.01	<0.007	24.19	Volcanic	2542	07/26/06
Moss Lake (14)	276.8	2.99	<0.007	10.46	Volcanic	2537	07/01/05
Enos Peak Lake (8)	357.8	3.60	<0.007	4.51	Volcanic	2524	06/29/05
Whetstone Lake (21)	2603.0	5.21	0.952	34.21	Volcanic	2371	07/13/05
Bridger Lake (4)	771.8	62.42	1.564	20.22	Volcanic	2358	08/17/05
Angles Lake (1)	2889.3	4.99	0.355	<0.05	Volcanic	2254	06/22/05
Sheffield Lake (15)	722.5	5.10	3.919	20.02	Volcanic	2219	08/01/05
Field Blank	1.4	<0.01	<0.007	<0.05	N/A	N/A	07/02/05
Field Blank	-4.4	1.00	<0.007	<0.05	N/A	N/A	07/16/05
Field Blank	3.3	2.16	<0.007	<0.05	N/A	N/A	07/29/05
Field Blank	4.3	0.72	<0.007	<0.05	N/A	N/A	08/19/05
Valley Fork Blank	3.0	1.22	<0.007	<0.05	N/A	N/A	07/27/06

¹ Indicates duplicate sample for quality control purposes. Every 10th lake sampled included a duplicate.

² Valley Fork Lake sampled during the 2006 field season.

by the EPA indicating sensitivity to acidification. Lakes with less than 100 $\mu\text{eq/L}$ ANC are at risk of episodic acidification while lakes with < 50 $\mu\text{eq/L}$ ANC are at risk of chronic acidification. Complete water analysis for both wildernesses and soils for the Teton Wilderness results are available (Allgeier 2009).

T tests showed no significant differences ($p = 0.05$) between the mean of ANC, pH, NH_4^+ , NO_3^- , and SO_4^{2-} for the Teton versus the Gros Ventre lakes. Stratifying lakes by parent material showed no significant difference between water pH categorized by parent material, NH_4^+ so categorized, or SO_4^{2-} . However, ANC differed highly significantly for all water samples categorized by parent material ($f(2,38) = 5.58$, $p = 0.007$).

Post hoc comparisons using Tukey's HSD test revealed that ANC in limestone lithologies ($\bar{x} = 1,478$, $sd = 1,125.8$) was greater than both that of volcanics ($\bar{x} = 702.8$, $sd = 728.2$) and granites ($\bar{x} = 189.3$, $sd = 186.1$). ANC was significantly lower in granitic parent material ($\bar{x} = 111.6$, $sd = 77.4$) than in limestone ($\bar{x} = 1,579.8$, $sd = 1,137.2$) in the Gros Ventre ($t(16) = -2.52$, $p = 0.01$). There was no difference in ANC in the Teton Wilderness between volcanics and limestone ($t(20) = 0.13$, $p = 0.9$).

Where correlations were examined between elevation and water pH, ANC, NO_3^- , NH_4^+ , or SO_4^{2-} in either wilderness area or as a whole, there were not significant correlation coefficients and r^2 values were all < 0.07.

Table 2. ANC, NO₃⁻, NH₄⁺, and SO₄²⁻ for lakes sampled in the Gros Ventre Wilderness. Lake numbers correspond to point locations (Figure 4).

Lake & Number	ANC μeq/L	NH ₄ ⁺ μmol/L	NO ₃ ⁻ μmol/L	SO ₄ ²⁻ μmol/L	Parent Material	Elev. (m)	Sample Data
MacLeod Lake (30)	215.8	1.55	<0.007	81.24	Granitic	3110	08/04/06
Upper Shoal Lake (38)	54.0	<0.01	0.258	5.26	Granitic	3100	07/19/06
Pinnacle Lake (31)	125.1	<0.01	15.160	15.69	Granitic	3045	07/06/06
Gros Lake (27)	51.6	<0.01	12.160	7.98	Granitic	3044	08/01/06
Black Peak Lake (23)	1197.5	2.94	2.161	25.29	Limestone	3200	07/19/06
Upper Brewster (36)	910.3	1.77	2.726	30.67	Limestone	3168	07/18/06
Tosi Lake (34)	138.7	4.77	1.710	4.27	Limestone	3106	06/27/06
Hodges Lake (28)	261.1	5.65	1.290	4.51	Limestone	3072	06/27/06
S. Twin Cr. Lake (32)	1556.5	2.72	6.693	9.32	Limestone	2972	07/10/06
Upper Farney Lake (37)	1668.1	<0.01	0.339	6.56	Limestone	2969	07/17/06
Upper Farney Lake ^{1,2}	1637.9	2.05	0.419	6.38	Limestone	2969	07/17/06
E. Miner Cr. Lake (26)	1039.1	<0.01	11.515	4.54	Limestone	2938	07/13/06
Turquoise Lake (35)	70.2	<0.01	2.435	8.69	Limestone	2930	08/01/06
Bridge Creek Lake (25)	2712.5	<0.01	0.629	4.76	Limestone	2920	06/20/06
Upper Slide Lake (39)	4228.9	11.09	4.000	2.77	Limestone	2873	06/19/06
Table Mtn. Lake (33)	2535.8	10.53	11.128	7.39	Limestone	2839	07/11/06
Jones Creek Lake (29)	2307.9	28.83	2.500	99.50	Limestone	2672	06/21/06
Box Lake (24)	1852.4	2.55	0.194	9.17	Limestone	2650	08/02/06
Field Blank	-6.1	<0.01	<0.007	<0.05	N/A	N/A	06/28/06
Field Blank	-4.4	<0.01	<0.007	<0.05	N/A	N/A	07/13/06
Field Blank	3.8	<0.01	<0.007	<0.05	N/A	N/A	07/20/06
Field Blank	2.9	<0.01	<0.007	<0.05	N/A	N/A	08/03/06

¹ Indicates duplicate sample for quality control purposes. Every 10th lake sampled included a duplicate.

² Indicates a possibly contaminated sample as noted by the Rocky Mountain Research Station Water Lab.

Table 3. Summary of lakes sensitive to acidification.

Lake	ANC μeq/L	pH	NH ₄ ⁺ μmol/L	NO ₃ ⁻ μmol/L	SO ₄ ²⁻ μmol/L	Parent Material	Elev. (m)	
Holmes Cave Lake	45	6.7	2.38	<0.007	3.08	Limestone	2981	Teton Wilderness
Lewis Lake	178	7.3	4.88	<0.007	3.59	Volcanic	3130	
Marston Lake	83.8	6.9	2.33	<0.007	1.6	Volcanic	3091	
Silvertip Lake	182	7.4	0.83	<0.007	8.42	Volcanic	3059	
Ferry Lake	181	7.4	3.77	<0.007	3.6	Volcanic	3037	
Upper Shoal Lake	54	6.5	<0.01	0.258	5.26	Granitic	3100	Gros Ventre Wilderness
Pinnacle Lake	125	6.5	<0.01	15.16	15.69	Granitic	3045	
Gros Lake	51.6	6.4	<0.01	12.16	7.98	Granitic	3044	
Tosi Lake	139	6.3	4.77	1.71	4.27	Limestone	3106	
Turquoise Lake	70.2	6	<0.01	2.435	8.69	Limestone	2930	

There was some question that timing of sampling may have had an influence on water chemical parameters, thus ANC as a function of sample date was analyzed using a linear regression analysis. There was a significant correlation for the Teton ($r = 0.480$ [$p = 0.05$], $r^2 = 0.237$, $n = 22$) but

not the Gros Ventre ($r = 0.408$ [ns], $r^2 = 0.17$, $n = 17$; Figure 5). ANC was also analyzed with regard to sampling date by parent material and correlation coefficients did not change, including significance (Figure 6).

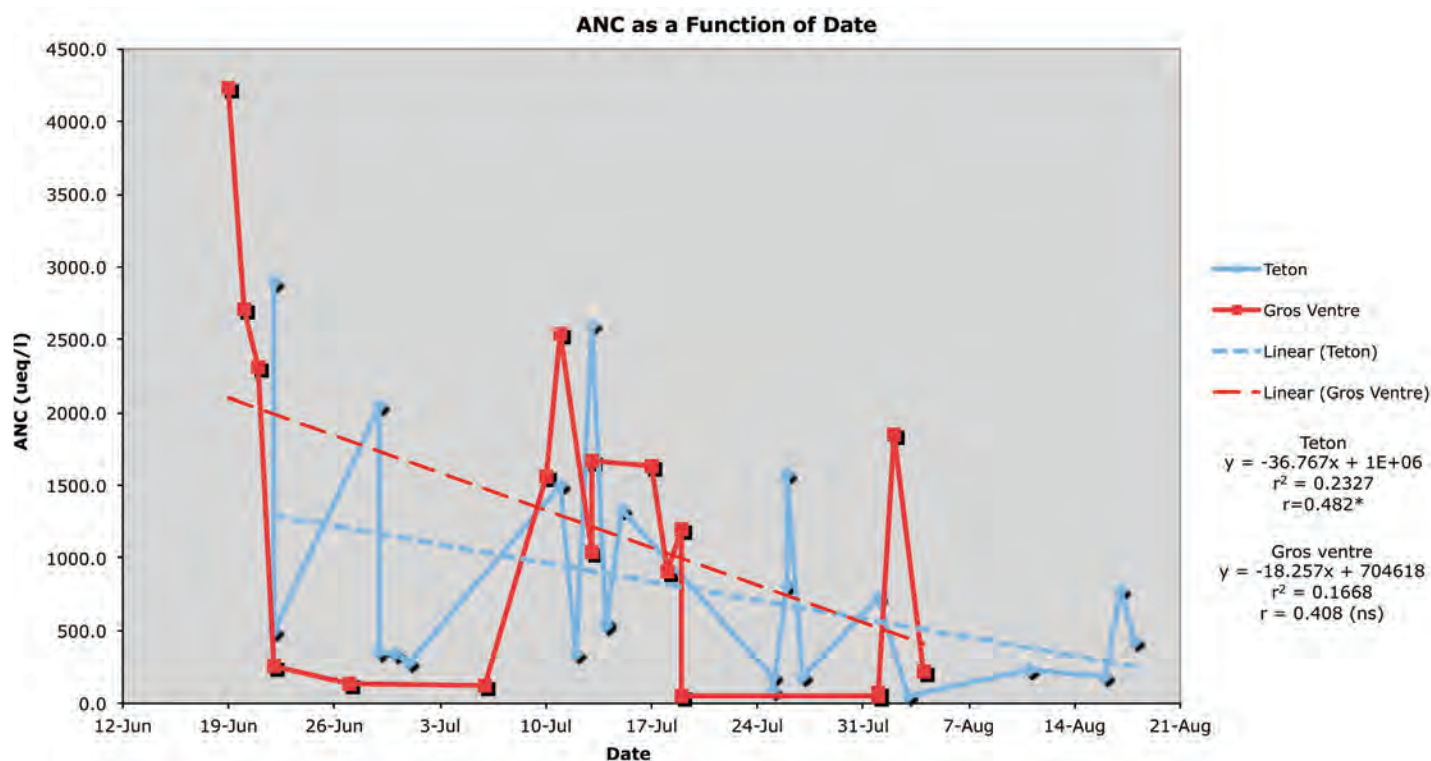


Figure 5. Acid Neutralization Capacity (ANC) as a function of sampling date.

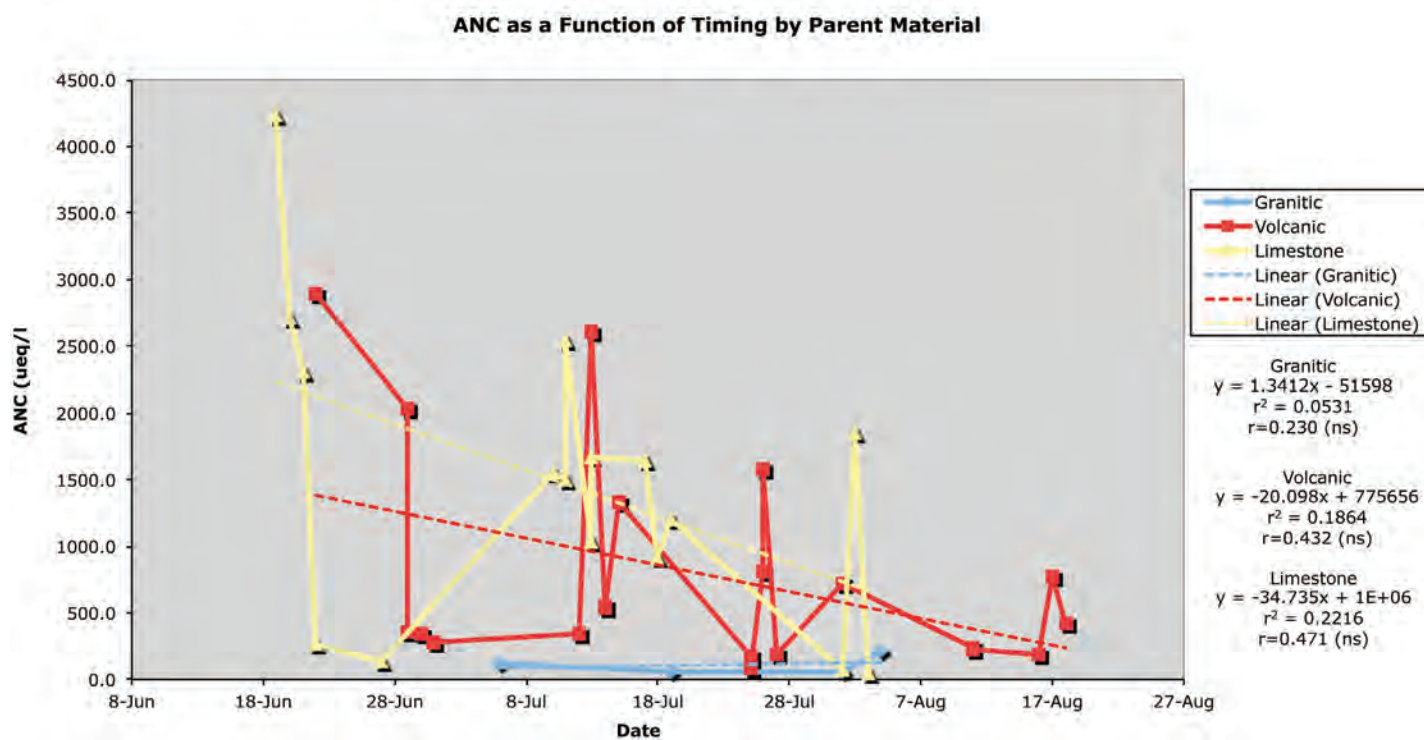


Figure 6. Acid Neutralization Capacity (ANC) as a function of sampling date by parent material.

Western Lakes Survey Trends. Two lakes, Ferry Lake from the Teton Wilderness and Table Mountain Lake from the Gros Ventre Wilderness, were sampled by the EPA as part of the 1984 Western Lakes Survey. As such, preliminary trends for pH, NH_4^+ , NO_3^- , SO_4^{2-} , and ANC have been established.

Ferry Lake pH increased from 6.2 to 7.4. NH_4^+ increased from < 0.01 to $3.77 \mu\text{eq/L}$. NO_3^- decreased from 0.17 to $< 0.01 \mu\text{eq/L}$. SO_4^{2-} decreased from 9.37 to $7.20 \mu\text{eq/L}$ (Figure 7). Table Mountain Lake pH increased from 7.4 to $8.3 \mu\text{eq/L}$. NH_4^+ increased from 0.50 to $10.53 \mu\text{eq/L}$. NO_3^- increased from 0.49 to $11.13 \mu\text{eq/L}$. SO_4^{2-} decreased from 15.83 to $14.78 \mu\text{eq/L}$ (Figure 8). Ferry Lake ANC decreased to 180.6 from $214.6 \mu\text{eq/L}$, while Table Mountain Lake ANC increased to $2,535.8$ from $2,492.6 \mu\text{eq/L}$ (Figure 9). Between the two lakes, common trends are limited to similar decreases in SO_4^{2-} and marked increases in NH_4^+ and pH.

Soils. Soils from the Teton Wilderness showed a wide range of variability consistent with varying parent material and altitude (Table 4). Soil pH varied from 4.5 to 8.0 , NH_4N ranged from 0.8 to 33.6 mg/kg , NO_3N ranged from 0.1 to 28.0 mg/kg , and PO_4P ranged between 1 and 144 mg/kg . Total N ranged from 1.0 – 34.6 mg/kg . The C:N ratios were all $10:1$ or greater with a range of 13.0 – $39.9:1$.

Soil results for the Gros Ventre Wilderness also showed a wide range of variability consistent with varying parent material and altitude (Table 5). Soil pH varied from 4.3 to 7.7 , NH_4N ranged from 0.1 to 14.4 mg/kg and NO_3N ranged from 0.2 to 80.9 mg/kg . The C:N ratios were all $10:1$ or greater with a range of 10.4 – $55.01:1$. Total N ranged from 2.0 – 81.1 mg/kg .

Parent Material. There were no significant differences in total soil N between parent materials ($f(2,108) = 0.6$, $p = 0.5$). Soil pH was significantly different between parent materials ($f(2,108) = 15.4$, $p < 0.001$). Post hoc comparisons revealed that granitic soils had lower pH ($\bar{x} = 5.1$, $sd = 0.5$) than volcanic soils ($\bar{x} = 5.5$, $sd = 0.7$), and volcanic soils were lower than limestone soils ($\bar{x} = 6.3$, $sd = 1.1$). Carbon to nitrogen ratio was significantly different among parent materials ($f(2,108) = 3.5$, $p = 0.03$). A post hoc comparison showed that this difference was between granitic ($\bar{x} = 13.9$, $sd = 2.5$) and limestone ($\bar{x} = 22.0$, $sd = 12.9$) soils only. There was a significant difference in soil NO_3^- -N ($f(2,108) = 4.6$, $p = 0.01$) between parent materi-

als. A post hoc comparison showed that this difference was only significant between limestone ($\bar{x} = 11.0$, $sd = 13.4$) and volcanic ($\bar{x} = 4.9$, $sd = 7.2$) derived soils. There was also a significant difference in soil NH_4^+ -N and parent material ($f(2,108) = 9.9$, $p < 0.001$). Post hoc comparison showed that the differences occurred between granitic ($\bar{x} = 2.9$, $sd = 4.2$) and volcanic ($\bar{x} = 6.9$, $sd = 6.3$) and between limestone ($\bar{x} = 2.8$, $sd = 2.8$) and volcanically derived soils. Significant differences occurred in soil PO_4^{3-} -P between parent materials ($f(2,108) = 19.4$, $p < 0.001$). Post hoc comparison showed that differences occurred between granitic ($\bar{x} = 6.6$, $sd = 4.1$) and volcanic soils ($\bar{x} = 47.4$, $sd = 36.2$). Differences also occurred between limestone ($\bar{x} = 15.5$, $sd = 21.1$) and volcanically derived soils.

Elevation. There were no significant correlations between elevation and soil: pH, NO_3^- -N, NH_4^+ -N, PO_4^{3-} -P, or C:N ratio (all $r^2 > 0.05$, $r < 0.230$ [ns]).

Wilderness Area. Soil pH varied significantly ($t(109) = -2.7$, $p = 0.008$) between the Teton Wilderness ($\bar{x} = 5.6$, $sd = 0.078$) and the Gros Ventre Wilderness ($\bar{x} = 6.0$, $sd = 1.1$). NO_3^- -N was significantly different between the two areas as well ($t(110) = -3.4$, $p < 0.001$). The Teton samples had lower nitrate ($\bar{x} = 4.7$, $sd = 6.9$) than the Gros Ventre ($\bar{x} = 11.1$, $sd = 12.6$). There were significant differences in NH_4^+ -N ($t(110) = 4.8$, $p < 0.001$) between the Teton ($\bar{x} = 7.2$, $sd = 6.6$) and the Gros Ventre ($\bar{x} = 2.4$, $sd = 2.9$). There were significant differences in PO_4^{3-} -P ($t(109) = 6.4$, $p < 0.001$) between the Teton ($\bar{x} = 45.9$, $sd = 37.1$) and the Gros Ventre ($\bar{x} = 10.9$, $sd = 11.2$). The carbon to nitrogen ratio did not vary significantly between wilderness areas ($t(109) = 0.6$, $p = 0.6$) nor did soil nitrogen ($t(109) = -0.7$, $p = 0.5$).

Water Chemistry Compared to Soil Chemistry. Water to soil chemistry regression revealed that water:soil pH had a significant correlation ($r = 0.469$, $r^2 = 0.22$, $n = 36$). Water NO_3^- was not significantly correlated with soil NO_3^- ($r^2 = 0.02$, $n = 36$), as was water and soil NH_4^+ ($r^2 = 0.12$, $n = 36$). In the Teton Wilderness, pH showed significant correlation ($r = 0.592$, $r^2 = 0.35$, $n = 17$), NO_3^- showed very little ($r = 0.22$, $r^2 = 0.05$, $n = 17$), and NH_4^+ showed little as well ($r^2 = 0.14$, $n = 17$). In the Gros Ventre, none of the chemical constituents showed any significant levels of correlation, all r being non-significant at pH ($r^2 = 0.10$, $n = 19$), NO_3^- ($r^2 = 0.15$, $n = 19$), and NH_4^+ ($r^2 = 0.10$, $n = 19$).

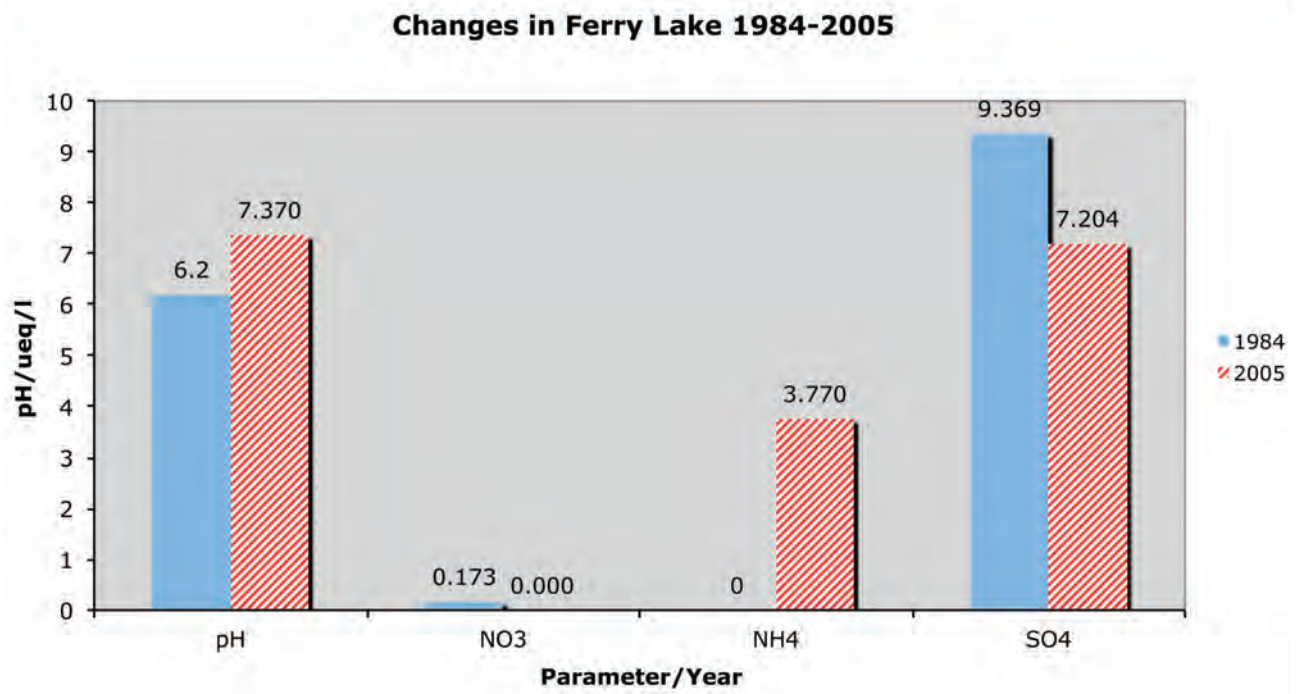


Figure 7. Ferry Lake trends. pH is measured in standard units. NH_4^+ , NO_3^- , and SO_4^{2-} are measured in $\mu\text{eq/L}$.

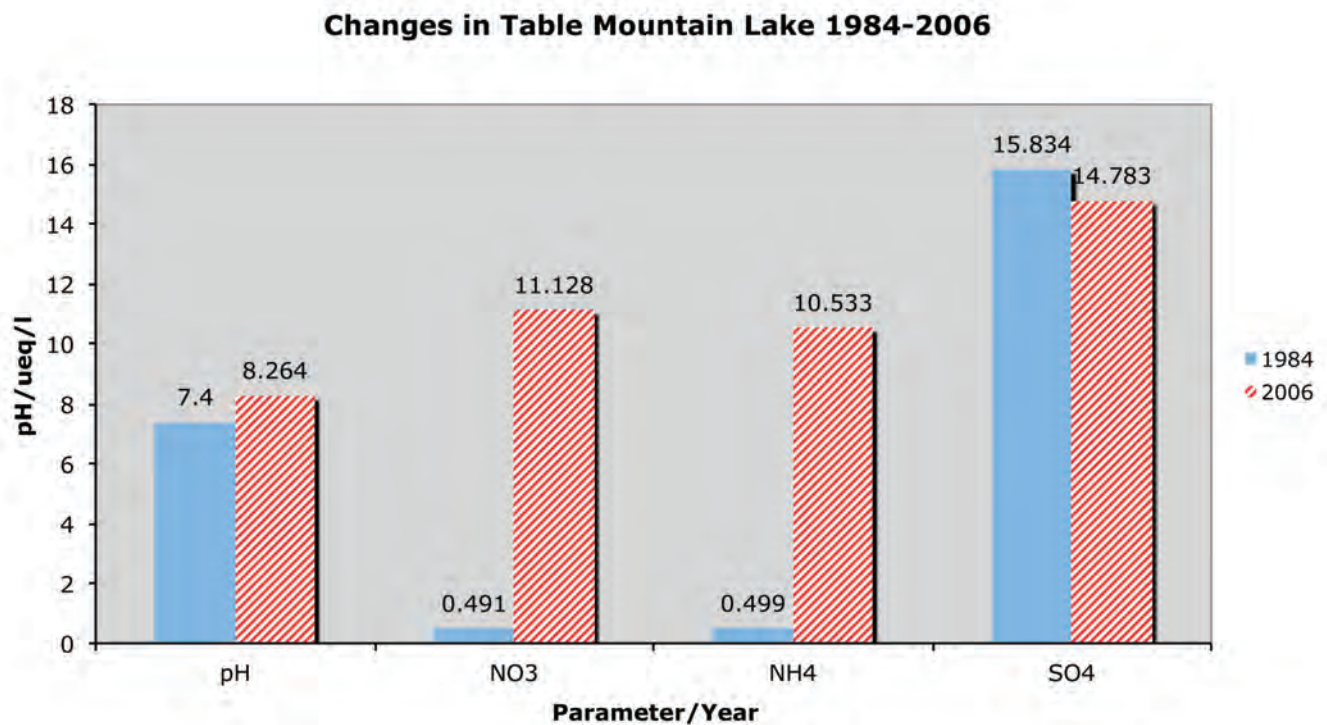


Figure 8. Table Mountain Lake trends. pH is measured in standard units. NH_4^+ , NO_3^- , and SO_4^{2-} are measured in $\mu\text{eq/L}$.

Changes in ANC 1984-2005/06

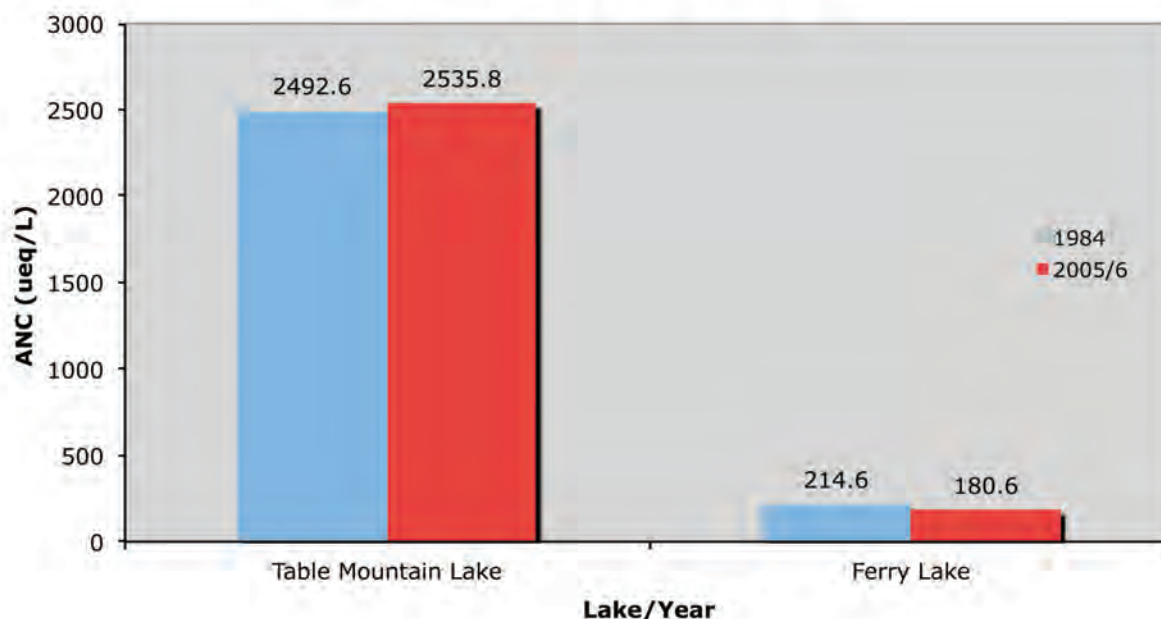


Figure 9. Acid Neutralization Capacity (ANC) trends for Western Lakes Survey sites.

When water and soil parameters were analyzed in parent material groups (granitic, volcanic, and limestone) with both wilderness areas pooled, slightly stronger relationships emerged (Table 6). For the granite group, pH ($r^2 = 0.57$, $n = 4$) and NH_4^+ ($r^2 = 0.60$, $n = 4$) showed the strongest relationship and had correlation coefficients of 0.75 and 0.77, respectively, but neither of these are statistically significant probably due to such a small n . In the limestone group, pH ($r^2 = 0.23$, $n = 15$) showed a weak but significant relationship with a correlation coefficient of 0.48. In the volcanic ($n = 18$) and limestone ($n = 15$) groups, there were no significant correlations.

Discussion

Water Chemistry. While overall water levels of inorganic N throughout the Teton Wilderness are low, ammonium is more prevalent than nitrate, suggesting that this nitrogen is originating from sources other than combustion. In the Gros Ventre, nitrate was greater than ammonium, suggesting the Gros Ventre receives more nitrogen from combustion sources.

The direct inverse relationship between elevation and ANC is consistent with previous research done by Williams and Tonnessen (2002) and Blankenship (1990) that indicates higher altitude communities with less vegetation

and more precipitation and deposition are less able to utilize the increased nitrogen.

NO_x levels are below those shown to be nitrogen saturated, such as those of the Colorado Front Range (high of $20.2 \mu\text{mol/L NO}_3^-$, $4.8 \mu\text{mol/L NH}_4^+$; Baron et al. 2000), but at a few lakes NO_x levels are high enough for concern. ANC values are low enough to also be near or below those seen in nitrogen saturated areas.

Parent Material. Overall, the ANC values of Gros Ventre lakes showed higher variability and are generally higher than those of the Teton Wilderness. The Gros Ventre samples' variability likely stems from variable parent materials in the area. Those samples originating from granitic soils in the core of the range, such as Gros Peak Lake, Pinnacle Lake, Upper Shoal Lake, and Turquoise Lake, showed noticeably lower ANC than those located on limestone. ANC also showed variability by drainage without regard to parent material. The lakes in Tosi Basin that drain into the Upper Green River showed low ANC, despite being on a limestone parent material. The wide variability in ANC value in lakes on limestone parent material may stem from geologic differences in material hardness, i.e., older Paleolithic limestones are much more resistant to weathering. The remaining lakes displaying low ANC were all in soils of granitic

Table 4. Summary of Teton Wilderness soil chemistry. $\bar{x}$ is the average and sd the standard deviation.

Lake		NO ₃ N mg/kg	NH ₄ N mg/ kg	pH	x- PO ₄ P mg/kg	%N	%C	C:N	Total N mg/ kg	Parent Material	Elev. (m)
Enos Peak	$\bar{x}$	1.7	6.8	5.7	89.3	0.1	3.2	25.0	8.5	Volcanic	2524
	sd	2.7	5.5	0.3	31.0	0.0	0.5	5.1	3.3		
Divide	$\bar{x}$	8.5	6.7	7.7	32.3	0.3	7.9	28.9	15.2	Volcanic	2621
	sd	6.4	6.1	0.3	37.0	0.1	1.8	6.9	11.3		
Moss	$\bar{x}$	0.2	6.1	4.8	75.0	0.1	3.4	26.5	6.3	Volcanic	2537
	sd	0.2	2.2	0.2	32.4	0.0	0.4	2.6	2.4		
W. Enos Pk.	$\bar{x}$	3.4	5.4	6.9	49.0	0.2	3.7	19.1	8.8	Limestone	2512
	sd	1.9	1.9	0.7	61.5	0.1	0.8	5.0	3.3		
Coulter	$\bar{x}$	1.3	3.7	4.9	86.7	0.1	3.6	24.3	5.0	Volcanic	2545
	sd	2.1	2.0	0.2	40.8	0.1	0.6	2.4	4.0		
Whetstone	$\bar{x}$	0.9	9.4	5.6	30.0	0.3	5.1	20.7	10.3	Volcanic	2371
	sd	1.3	6.8	0.6	30.4	0.1	0.5	3.6	6.1		
Emerald	$\bar{x}$	3.0	5.7	5.6	88.0	0.2	3.7	21.0	8.7	Volcanic	2652
	sd	2.1	2.8	0.7	48.5	0.1	2.2	3.9	4.6		
Gravel	$\bar{x}$	0.7	4.5	5.9	81.0	0.1	3.7	24.2	5.2	Volcanic	2665
	sd	0.8	2.0	0.3	26.0	0.1	1.2	2.6	2.8		
Lewis	$\bar{x}$	2.0	5.2	5.4	22.3	0.3	3.6	15.7	7.2	Volcanic	3130
	sd	0.9	2.6	0.8	3.8	0.2	1.9	4.1	3.1		
Bertha	$\bar{x}$	0.2	9.4	5.5	48.7	0.1	4.6	29.0	9.6	Volcanic	2728
	sd	0.1	8.8	0.1	19.7	0.1	1.1	4.5	8.7		
Wolverine	$\bar{x}$	2.6	4.6	5.1	57.0	0.2	3.1	22.7	7.2	Volcanic	2542
	sd	3.9	1.2	0.2	24.3	0.1	1.3	7.9	3.8		
Fairy	$\bar{x}$	1.4	7.8	5.5	43.0	0.5	7.5	15.7	9.2	Volcanic	3037
	sd	0.9	3.8	0.6	29.4	0.5	6.7	1.7	4.5		
Marston	$\bar{x}$	1.0	12.0	5.4	9.7	0.5	7.3	14.6	13.0	Volcanic	3091
	sd	1.1	9.6	0.5	3.5	0.3	3.6	0.7	9.4		
Sheffield	$\bar{x}$	0.3	2.8	5.5	37.0	0.2	5.2	33.2	3.1	Volcanic	2219
	sd	0.2	3.0	0.3	32.9	0.2	4.4	6.2	3.2		
Holmes Cave	$\bar{x}$	1.0	6.7	5.3	23.7	0.2	5.5	25.4	7.8	Limestone	2981
	sd	1.2	1.4	0.4	31.8	0.1	1.8	8.2	2.6		
Tri-County	$\bar{x}$	17.5	5.5	5.1	10.0	0.3	3.9	15.0	23.0	Volcanic	3062
	sd	6.1	4.7	0.7	3.6	0.2	2.6	2.1	10.1		
Silvertip	$\bar{x}$	15.4	14.8	5.0	19.3	0.2	2.3	16.3	30.2	Volcanic	3059
	sd	13.2	16.8	0.2	12.9	0.1	0.5	1.1	29.4		
Bridger	$\bar{x}$	12.6	13.0	5.7	70.7	0.4	5.7	16.3	25.5	Volcanic	2358
	sd	3.4	15.7	0.5	3.8	0.1	1.8	2.3	18.8		
Two Ocean	$\bar{x}$	14.6	13.5	4.9	10.3	0.3	4.1	16.4	28.2	Volcanic	2834
	sd	12.8	6.0	0.3	0.6	0.2	2.0	3.2	18.6		
Valley Fork	$\bar{x}$	4.8	1.1	5.9	6.7	0.4	5.2	13.2	5.8	Volcanic	3278
	sd	4.4	0.1	0.7	1.5	0.2	2.6	1.5	4.5		

Table 5. Summary of Gros Ventre Wilderness soil chemistry. $\bar{x}$ is the average and sd the standard deviation.

Lake		NO ₃ N mg/kg	NH ₄ N mg/ kg	pH	x- PO ₄ P mg/kg	%N	%C	C:N	Total N mg/ kg	Parent Material	Elev. (m)
Bridge Creek	$\bar{x}$	7.4	2.9	6.3	22.3	0.3	3.5	16.2	5.6	Limestone	2920
	sd	9.3	2.8	1.0	9.3	0.2	2.1	8.1	6.4		
Jones Creek	$\bar{x}$	1.7	6.1	5.3	39.3	0.1	2.7	17.9	5.8	Limestone	2672
	sd	1.4	4.0	0.7	12.7	0.1	1.1	2.8	6.7		
Tosi	$\bar{x}$	8.1	5.5	5.7	5.0	0.2	2.7	16.3	4.9	Limestone	3106
	sd	9.0	4.2	1.0	3.6	0.2	2.1	7.7	28.5		
Hodges	$\bar{x}$	23.9	4.7	5.2	3.3	0.1	1.9	19.0	34.1	Limestone	3072
	sd	10.0	2.0	0.1	0.6	0.1	1.6	7.7	32.6		
Pinnacle	$\bar{x}$	2.9	2.6	5.1	6.0	0.1	1.4	15.6	3.4	Granitic	3045
	sd	2.1	1.5	0.4	6.9	0.1	1.0	4.5	9.2		
South Twin Cr.	$\bar{x}$	12.5	1.0	7.0	8.7	0.4	6.0	15.0	16	Limestone	2972
	sd	3.3	0.5	0.6	1.5	0.2	3.4	2.3	14.5		
Table Mountain	$\bar{x}$	12.1	0.6	7.0	8.3	0.3	4.6	19.6	11.2	Limestone	2839
	sd	1.8	0.3	0.7	2.1	0.1	2.1	6.1	13		
East Miner Cr.	$\bar{x}$	10.4	0.7	7.5	6.3	0.3	11.2	44.7	11.7	Limestone	2941
	sd	3.7	0.2	0.5	1.5	0.1	5.2	17.8	6.9		
Upper Farney	$\bar{x}$	28.9	1.6	5.4	22.3	0.2	10.6	35.6	3.2	Limestone	2969
	sd	45.1	1.3	0.6	21.0	0.1	13.5	34.8	81.1		
Upper Brewster	$\bar{x}$	10.0	0.9	7.5	6.0	0.3	7.2	24.6	14.2	Limestone	3168
	sd	7.1	0.4	0.4	3.6	0.1	5.7	16.9	2.3		
Upper Shoal	$\bar{x}$	6.5	5.6	5.1	10.3	0.2	2.1	12.4	3.3	Granitic	3100
	sd	7.5	7.6	0.7	2.3	0.1	1.1	2.0	29.6		
Black Peak	$\bar{x}$	11.9	1.1	7.5	5.7	0.5	6.8	16.2	33.5	Limestone	3200
	sd	16.9	0.9	0.4	3.8	0.7	6.7	7.3	3.7		
Turquoise	$\bar{x}$	14.2	2.8	5.2	4.3	0.3	4.5	16.7	21	Limestone	2930
	sd	1.5	3.6	0.3	1.2	0.1	0.9	2.1	16.8		
Gros	$\bar{x}$	10.6	2.8	4.7	6.3	0.3	4.1	13.7	17.5	Granitic	3044
	sd	7.5	2.7	0.1	1.5	0.1	1.3	1.4	19.6		
Box	$\bar{x}$	9.5	0.8	6.0	10.3	0.3	4.6	19.5	12	Limestone	2650
	sd	7.6	1.1	1.4	4.9	0.1	1.1	5.4	3		
MacLeod	$\bar{x}$	6.8	0.2	5.4	4.3	0.3	3.9	14.2	6.2	Granitic	3110
	sd	5.2	0.1	0.5	2.9	0.2	2.2	0.8	12.7		
Upper Slide Cr.	$\bar{x}$	10.7	1.3	7.1	23.0	0.2	6.6	25.0	16.9	Limestone	2873
	sd	7.3	0.1	0.2	11.4	0.1	2.6	2.1	3.7		

Table 6. Summary of water:soil regression analysis by parent material.

		Water		
		pH	NO ₃	NH ₄
Soil	Granite	pH	r ² =0.57	
		NO ₃	r ² =0.02	
		NH ₄	r ² =0.60	
	Limestone	pH	r ² =0.23	
		NO ₃	r ² =0.00	
		NH ₄	r ² =0.12	
	Volcanic	pH	r ² =0.06	
		NO ₃	r ² =0.14	
		NH ₄	r ² =0.10	

origin. Overall, ANC values in the Gros Ventre were lower than expected in many lakes.

Duplicate Variability. The three duplicate samples (Emerald and Tri-County in the Teton and Upper Farney in the Gros Ventre) showed significant variability in NH_4^+ measurements. The Upper Farney duplicate sample was tagged by the lab as having “possible contamination.” The duplicate variability could originate from a number of factors, including sampling error, sample contamination, laboratory contamination, and intrinsic variability in surface water chemistry. Laboratory error is highly unlikely as the RMRS water laboratory follows strict quality control protocol and the samples only varied significantly in this one parameter. Biological activity may account for some of the variability. Field notes indicate that there was significant vegetation at the outlet to Upper Farney and algae present at Emerald. Tri-County Lake showed no such biological activity near the sampling point.

Timing. Timing of sample collection did not affect ANC values. As shown in Figures 5 and 6, ANC generally decreased over the course of each summer, but these were very weak or non-significant decreases. This ties in with a general correlation between sampling date and elevation. Higher elevation lakes were generally sampled later in the season, as access to them became available only after snow-melt. The ANC values are therefore more correlated with elevation, and as a consequence with orographic precipitation magnification, than with timing.

1984 Western Lakes Survey Trends. While not statistically significant, the base trends from the Western Lakes Survey sites (Ferry Lake, Table Mountain Lake) mirror national trends (National Atmospheric Deposition Program [NADP] 2008). These trends include decrease in the deposition of sulfate ion and “a clear dramatic increase in nitrogen deposition, largely from ammonia, to many ecosystems at the same time that acidity and sulfate were being reduced” (NADP 2008). The similarity of these trends in sulfate and ammonium strengthens the validity of the data from the initial sampling effort in the Teton and Gros Ventre Wildernesses.

Soils. All soil samples had a carbon to nitrogen ration of greater than 10:1. This represents a loose limit for nitrogen saturation. Many sites in the Gros Ventre Wilderness (15

of 17) were near this threshold, having at least one soil sample at or below a ratio of 15:1, while only 9 of 22 sites in the Teton Wilderness had a sample at or below 15:1. That all of the C:N ratios were well above 10:1 suggests these systems remain N limited.

Water Chemistry Compared to Soil Chemistry. The significant correlations between pH of water and pH of soils is likely due to the contact between precipitation that falls in the lake basins and picks up the pH signature as it flows over and through the soil in route to the lakes. It seems logical that the pH would be a function of parent material, but none of these correlations were significant except for the weak relationship regarding limestone. Of other correlations, some were near the significance cutoff, which suggests a larger n may have shown a significant relationship.

Recommendations

To establish if the AQRV of water quality is at risk in the Teton and Gros Ventre Wilderness Areas, annual sampling of a few lakes that are low ANC and that are in areas susceptible to acidification is recommended. Historical baseline data on Ferry Lake and Table Mountain Lake from the 1984 EPA Western Lake Survey represents an essential starting place for establishing any trends in water quality. Good indicator lakes in the Teton Wilderness include Marston, Lewis, Silvertip, Holmes Cave, and Ferry. Lakes in the Gros Ventre Wilderness for long-term sampling are Tosi, Turquoise, Gros Peak, Upper Shoal, Table Mountain, and Pinnacle. With the exception of Table Mountain, each of these lakes has an ANC value of less than 200 $\mu\text{eq/L}$ and is above 2,900 m elevation. Table Mountain Lake is included due to its historical data from the 1984 EPA survey. If possible, these lakes should also be monitored for the diversity of benthic macroinvertebrates, which give a good indication of air quality (Blankenship 1990). Changes in composition and abundance of invertebrates at these lakes would be a good early indicator of chronic acidification. Soil samples should continue to be taken at each lake sampled. Soil chemistry may indicate nitrogen saturation long before it is exhibited in surface water chemistry. This is especially important because of the variability in parent material in both wilderness areas.

Changes in Sampling Procedure. The poor repeatability shown in the duplicate samples can be addressed by small changes in sampling procedures. Since the number of lakes

has been reduced, duplicate, or preferably triplicate, samples should be taken at each lake. This would allow for the elimination of any one outlier sample. If future duplicates show greater reliability, the number of duplicate samples may be pared back to the original 1 in 10 sample rate. To further aid reliability of the findings, it would be greatly beneficial for the sampling team to collect additional data in the field at the time of sampling. This would include water pH, conductivity, and on-site filtering. The pH and conductivity measurements will allow for computer model speciation of chemical constituents through the EPA's MINTEC program. This program determines what constituent(s) control the water chemistry for a given sample. This in turn would allow for much more accurate extrapolation of actual air quality and the mediating role of soils between atmospheric deposition and surface water chemistry. The pH and conductivity may be measured with a small, affordable multimeter or probe. The filtering materials are available from the Rocky Mountain Research Station for a nominal fee. Additional changes in sampling should begin to address the timing of nitrogen fluxes into surface waters. Sampling of the subset of lakes in each wilderness should occur as closely as possible to peak runoff. This would have a greater probability of capturing any peaks in surface water nitrogen. Ideally, this would mean sampling a week or two before the cresting of the major river in the sample's drainage. The Upper Snake, Yellowstone, Gros Ventre, Upper Green, and Hoback all have available flow data to establish optimum sample timing.

In addition to the continued sampling of select surface waters and their associated soils, collection and analysis of atmospheric deposition would greatly aid in determining the amount and impact of air quality. The USGS has demonstrated that bulk collectors in the form of ion-exchange resin collectors are effective in Rocky Mountain National Park (Clow et al. 2007). This would allow for collection of unaltered precipitation nitrogen chemistry. This would be very helpful in establishing critical nitrogen loads for both wilderness areas.

Possible future collaborative air quality monitoring efforts include investigation of possible emission sources of NO_x in western Wyoming, northern Utah, and eastern Idaho via an emission inventory similar to that done by the Colorado Regional Air Quality Partnership and a comparison of surface water data collected in Grand Teton National Park.

Section II. Qualitative Analysis

Introduction

Qualitative research informs quantitative research in that it raises new questions from qualitative conclusions and generates new questions for both qualitative and quantitative evaluation. Qualitative research is concerned with process, meaning, and understanding. It seeks to clarify how individuals make sense of their lives, their experiences, and their structure of the world. The use of qualitative interview research is a relatively new phenomenon when compared to the lengthy history of the "hard sciences." Researchers use qualitative methods "to study things in their natural setting, attempting to make sense of, or interpret natural phenomena in terms of the meanings people bring them" (Greenhalgh and Taylor 1997). This approach is particularly effective in that it uses "a holistic perspective which preserves the complexities of human behavior" (Greenhalgh and Taylor 1997). In even simpler terms, interviewing provides access to the observations of others and allows researchers to capture events that would otherwise be lost (Weiss 1994).

Integration of Social Science into Management. The use of social science in the context of resource management has been, to a large extent, aimed toward satisfying user demands on the resource while meeting biophysical management goals (Manning 2001).

By the early twentieth century, scientific knowledge had superseded folk knowledge in the minds of resource managers (Dyer and Leaerd 1994; Lopez 2001). Weeks and Packard (1997) have shown that locally based stakeholders may not understand the science behind the biophysical processes of the resource, but they have adapted their observations and behaviors to sustainably manage it. In contrast, Lucas (1979) found that visitors not limited to those in close proximity to the resource were lacking in observational capacity to recognize resource damage or deficiencies compared to trained land managers. Indigenous groups where folk knowledge of fisheries has been passed down through multiple generations have shown to be more effective than scientific groups in management of the Gulf Coast oyster fisheries. As a result of this understanding, Dyer and Leaerd (1994) recommended that agencies should explore and include the experiential knowledge of natural resource users, where applicable, and the agencies should recognize that community skills can be as important as scientific skills in reaching management goals.

There have been several examples of local, long-term stakeholders being able to see small changes within an ecosystem:

I have watched these changes in Greater Yellowstone for most of my adult life....I hold the old fashioned view that to understand how nature works in a particular place you have to spend many years there on the ground and in the water, in all seasons, creating a baseline by which to measure change. Theories, models, and statistics are of limited use; indeed, they are often a place to hide from reality. You have to see things with your own eyes—no one can do it for you. New arrivals and tourists passing through cannot understand what has been lost. (Turner 2008)

This new management paradigm of treating local stakeholders as a valuable management partner allows for the stakeholders to better understand the science behind management decisions and for the resource managers and scientists to make management decisions that incorporate the social context to which they are applied. Ruddle (1994) concluded that local knowledge can provide a shortcut to pinpoint essential applied research needs, especially in localities where a traditional conservation ethic exists.

Incorporation of Indigenous/Local Knowledge into Natural Resource Management. Ruddle (1994) sees the integration of local knowledge into resource management as a largely untapped resource:

Local knowledge is of great potential value in the modern world. It can provide an important information base for local resources management... where conventionally used data are usually scarce to nonexistent, as well as providing a shortcut to pinpoint essential scientific research needs.

This is not to say that local knowledge can do away with traditional science; rather, it provides a wealth of qualitative observations for scientists to use in the generation of research questions and hypothesis testing. Many of the important features of local resource knowledge were summarized in Ruddle's (1994) common characteristics of local knowledge where he concluded the following about local populations:

1. They are based on long-term, empirical, local observation that is adapted specifically to local conditions, embraces local variation, and is often extremely detailed.
2. They are practical and behavior oriented, focusing on important resource types and species.
3. They are structured, which makes them somewhat compatible with Western biological and ecological concepts.
4. They are often dynamic systems capable of incorporating an awareness of ecological perturbations and of merging this awareness with an indigenous core of knowledge.

The importance of indigenous resource knowledge in natural resource management also has been documented by Johannes (1978), Klee (1980), Ruddle and Johannes (1985), the National Research Council (1986), and McCay and Acheson (1987).

Ruddle (1994) does, however, place limitations on use of local knowledge in management: "First, however, it must be systematically collected and organized and then evaluated and scientifically verified before being blended with complementary information derived from Western-based sciences, so as to be useful for resources management." These limitations are key in that they recognize the many other cases where the reliability of memory and "folk science" has clearly been shown to be far from infallible.

Ruddle (1994) notes that any practical usefulness of local knowledge is rarely exploited, largely due to disparagement. He termed the process of discounting local knowledge by scientists as "the bias of elite professionalism." Thus local knowledge of resources and environments is rarely used to assist the design of development projects or management systems.

By incorporating the long-term observations of a spatially rooted user group (outfitters), the Limits of Acceptable Change (LAC) will be able to incorporate more relevant indicators into the management policy thus providing a superior standard of management and resource integrity. In addition, this investigation into the values, attitudes, and behaviors of a major user group will directly benefit wilderness managers by connecting them with their constituents. This can be done in the LAC steps of defining and describing opportunity classes and evaluating and selecting an alternative for management actions.

Management Implications. As noted by Story et al. (2005), managers of Class I airsheds have an affirmative responsibility to manage to protect the air quality of these areas. Usable management frameworks to address the issue of air quality include the LAC framework developed by Stankey et al. (1985). LAC is based around the use of indicators and standards (Stankey et al. 1985; Nilsen and Taylor 1997). It is at this level that it can be incorporated into the management of air and water quality. Indicators are set for areas of concern or significance. The indicators come from a distribution of social, biophysical, and managerial measures. Standards are set to yield the desired future conditions. Once the standard reaches a critical threshold, a remedial management action must take place to stop the degradation of the resource and raise the condition back to the desired level.

The inclusion of input from outfitters into the LAC planning framework is possible at several stages throughout the process developed by Hendee et al. (1978). Specifically, input from this research can be used to identify area concerns and issues, inventory resource and social conditions, and monitor conditions. This study serves to determine the potential for incorporating outfitters and other local resource users as a management tool in monitoring the effects of air quality.

Methods

Approval of these interviews was granted from the University of Wyoming Institutional Review Board on July 31, 2007 (details appear in Allgeier 2009). This was done to meet the standards of the Code of Federal Regulations, Title 45 CFR § 46.101. This study was exempted from full review as it is interview research.

Six interviews were conducted between February and April 2008. Of these interviews, three each were from outfitters from the two wilderness areas. Outfitters were chosen as the target group because of their potential extensive knowledge and experience in their respective wilderness area. As a group, they simply have more contact time with the resource than anyone else. The outfitters also have a vested interest in maintaining the integrity of the natural condition of the wilderness. Outfitters were also the easiest population of users to contact in these areas due to established contact information with the Forest Service. The recreational specialization of the sampled outfitters was intentionally kept as diverse as possible. Specializations included: hunting/fishing, youth backpacking, ranching,

and sightseeing trips. The length of experience in their current wilderness area also varied, ranging from a few years to three generations.

Disclosure and Confidentiality. Subjects' participation was entirely voluntary and was limited to answering the researcher's questions. Subjects received full disclosure about the nature of the research project. Subjects were advised that their participation or non-participation would have no effect on their status as a permitted outfitter of the Bridger-Teton National Forest. Subjects signed a consent form prior to participating in the interviewing process. The sources of all data were kept confidential. Pseudonyms were used to ensure anonymity. Any potentially identifying characteristics of the subject's responses were aggregated and reported in a composite fashion to maintain anonymity.

Interviews. Interviews were conducted in a semi-structured style from a standardized list of questions, though deviation from the list occurred frequently for follow-up questions or clarification (Allgeier 2009). All interviews were conducted at a place of the subject's choosing. All interviews were recorded on minicassette tapes for later transcription. In addition, the interviewer took notes as the interviews progressed.

Once all of the interviews were transcribed, the researcher coded the subjects' responses according to themes that emerged in the interview and coding process as prescribed by Weiss (1994).

Results

Themes. The following five themes emerged from the interview process:

- I. Resource observations,
- II. Appreciation of the ecological complexity of the resource,
- III. Biocentric valuation of the resource and similar desired future conditions,
- IV. Lack of dependency on the resource, and
- V. Desire for better interaction with management.

Each theme will be described and then supported with outfitter responses.

I. Resource Observations. Outfitters, especially those who have a long history with the resource, showed an ability to monitor changes in the resource as it relates to their busi-

ness, particularly those that are intrinsic to the wilderness experience (noise, litter, man-made intrusions, etc.). Outfitters were very sensitive to changes in use patterns, especially within their permit area. With regard to AQRVs, outfitters were also able to note changes in water quality as it relates to fisheries and visibility.

"There's a lot of physical change. Primarily from fire and bugs. The '88 fires were a big change. Beetle kill—10 years ago, I'd never heard about it. Now, our whole area has problems with it. In the Teton Wilderness, we've pretty much lost the fishing. The whole Yellowstone drainage is gone. It's gone to hell in a hand basket. Used to be the finest cutthroat trout fishery in the world and in the last 17 or 18 years, it's deteriorated to virtually nothing. As far as visibility is concerned, the only problem we have up here is from fires and dust storms out of Idaho."

"A lot of the trees are ringed, you know, their roots have been stumped. The trails look like 10 feet wide and there's a dozen trails through every meadow. You slowly see a trail start to merge into four or five and that's what I've seen the most. I've seen more of other people's trash as time goes on."

"Now there's sound pollution. More and more planes over the Gros Ventre on their descent into Jackson. Also more scenic flights over the wilderness. I would say the best fishing I've had was nine years ago. The worst fishing I've ever done was about last year, same spot. If you talk to people who have been there longer, they'd say that the fishing was unbelievable 20 years ago, 30 years ago."

"The snowpack up there has been bad because of the drought in the last few years. There was a huge difference in precipitation from the trailhead to the top of the mountains."

"We don't typically see smog in the wilderness."

II. Appreciation for the Ecological Complexity of the Resource. The interviewed outfitters had a significant understanding of scientific resource management. They also recognized the limits of their own expertise and were willing to share their knowledge. They were aware of the pressures on the Greater Yellowstone Ecosystem as a whole, including energy development, land-use change, invasive species, and climate change.

"You get out on foot and it's big, it's huge, but if you draw back and look at the U.S. or North America, Yellowstone is a dot, just a pin prick. Everything else is fenced and people living all over it and it's not as big as it appears when you're on the ground. You can look on a map and see it's surrounded by development."

"You have lots of different problems going on in that ecosystem: acid deposition, siltation. You have to manage the predators if you are managing the game. You can't do one without the other. I don't know why the fishery is gone. I don't know if my theory is better than anyone else's theory. How do you know what's air quality or pollution related, what's high precipitation or lake trout affecting the cutthroat. For an outfitter to ride by and know that is difficult to know, I think. The more you know, the more I find out that I don't know. When you can't see something, a lot of people tend to overlook it or don't think about it."

III. Biocentric Values Regarding the Resource and Similar Desired Future Conditions.

The outfitters of the Teton and Gros Ventre Wilderness Areas are extremely dedicated to these areas and demonstrate strong resource loyalty and specificity. There is little to no chance of spatial substitutability. Outfitters have a shared vision of their desired future conditions for both wilderness areas. Keeping a pristine environment, maintenance of a primitive experience, and stability are universally held attitudes.

"It's an area that's grown on me. The longer you're here, the more it grows on you. I'm a third generation outfitter. It's hard to leave. I've been packing into the wilderness since I was four. It's a tremendous lifestyle, a tremendous way to raise a family."

"I like it being wild. I don't mind wolves, I don't mind the bears, I don't mind the mountain lions. That's the whole point! It all has to do with being out there and the wildness of it. I really enjoy the wildness of it."

"I'm willing to let my way of life change with everybody else's so we don't have to disrupt the ecosystem up there."

"In the future, I would like to see it like it was 25 or 30 years ago: less fire damage, more game, less regulations. More decision-makers on the ground."

"Keep things primitive up there."

"I'd just like to see the use more evenly distributed."

IV. Lack of Dependency on the Resource. None of the outfitters was completely dependent on outfitting as a means of income. They are committed to these areas because they want to be, not because they have to be.

"The majority of our business is here at the ranch. The park also gives us some of our business."

"I don't think there's a lot of guys that make all their money out there. A lot of them are electricians or construction or something to supplement their income."

V. Desire for Better Interaction with Management. Nearly all outfitters found room for improvement with the current management of the resource. Most complaints were centered on the social-managerial interface and less so with the managerial-biogeophysical interface. Many outfitters who have held a permit historically have favorable memories of a better relationship with management in the past.

"It's difficult to get started as an outfitter. They need to make it easier to understand the process of becoming an outfitter, not make it easier for it to become an outfitter. They like to think of their permittees as one in the same and they're not. Small number operations don't have the same impact as those with many, many user days. There's not a whole lot of consistency when it comes to enforcement. I've been ticketed and rewarded for doing the same thing by different people. It sends a very mixed and confusing message."

"I think that the Forest Service should pay more attention to those people who use the forest on their own as opposed to concentrating on the commercial operator. They need to put the people they have to work instead of sitting around picking their nose. They need to get them out there and do something and do it right. Clear trails!"

"I try to participate in the forest plan process but if you're not there at every step of the planning process to have your input, then you don't have say into the plan."

Discussion

Weiss (1994) categorized good interview subjects into two categories: people who are uniquely able to be informative because they are an expert in an area or were a privileged witnesses to an event and people who, taken together, display what happens within a population affected by a situ-

ation or event. In the case of this study, both descriptions apply. Permitted outfitters in many cases have been so for years or decades, giving them a unique and expert knowledge of the resource. They are also capable of postulating the consequences of a change to the resource to them and their clients, whether it is air quality or otherwise. It is important to note that these results apply only to outfitters from these two areas that were willing to participate. The results may not be applicable to outfitters who were not willing to participate or those from other wilderness areas.

None of the outfitters could identify any problems with air quality outside of smoke from forest fires and the occasional "dust storm" from Idaho. This absence of evidence should not be mistaken for evidence of absence. No significant water quality issues that could be positively linked to air quality were found. The "dust storms," while not quantitatively connected to air quality, or linked to particulate matter measures, were the kind of unique data that can provide a starting point for a quantitative study. If, in fact, particulate matter is coming from Idaho and into western Wyoming, it is likely that any NH_4^+ or NO_3^- is also being transported by the same wind events. Furthermore, this would also indicate sub-regional air movement patterns that connect significant agricultural NH_3 use with surface water sampling sites. Reported declines in the productivity of the fisheries of both the Upper Gros Ventre and Thorofare Creek indicate that there is something affecting these aquatic ecosystems that should be investigated. This could be linked to invasive species productivity, as reported by Hall et al. (2006).

While research has shown that younger, more educated, urban dwellers tend to deemphasize traditional commodity uses of nature (e.g., logging, mining, and grazing) and place higher value on issues such as wildland preservation (Rudzitis 1999), less attention has been given to whether or not occupational dependency has affected attitudes toward national forest management. People in service sectors have been shown to be more environmentally oriented than those in production-related industries. Support for this argument can be found in several articles by Beyers (1999), Nelson (1999), and Rudzitis (1999). This is also supported by Theme V, which points out that no outfitter is occupationally dependent on their respective wilderness area. When combined with Theme III, their values regarding the resource, these outfitters are outfitting in these particular areas because they enjoy it.

Summary of Abilities of Outfitters as a Monitoring Tool. Outfitters are able to notice changes in wilderness infrastructure (trails, campsite impacts) that a more causal user would not (Lucas 1979). Outfitters are likely to observe changes indicative of the latter stages of nitrogen saturation including changes in forest composition (beetle kill, fire) and changes in fisheries. Outfitters are therefore capable of informing natural resource managers of possible air quality management issues that relate to the limits of acceptable change framework. Outfitters fill a unique role due to extended experience and observation of the biogeophysical resource that is otherwise difficult or impossible to fill, especially given the “transfer and advance” system currently in place within the Forest Service.

When dealing with indigenous or local knowledge, Ruddle (1994) warned against “the bias of elite professionalism,” that is, when resource managers or scientists view local knowledge as lacking legitimacy in mainstream thought, regarding Western science as superior. Local knowledge does not fit into formal scientific models or challenge conventional theories. Ruddle (1994) states: “Such attitudes remain deeply embedded both in individuals and institutions, such that persons wishing to pursue unconventional projects and research often face ridicule and occasionally, job loss.”

Recommendations

The use of outfitters as tools or partners in monitoring aspects of management of the air quality resource is feasible within limits. It must be remembered that the qualitative nature of their observations should remain qualitative and that it should trigger a quantitative scientific management response.

Inclusion of permitted outfitters in the monitoring process helps establish a resource-based dialogue instead of an authority/control-based dialogue much in the manner of using the authority of the resource technique for resource-based law enforcement (Wallace 1990). This empowers resource users to become involved at a stewardship level. Having a positive, open dialogue may also transfer to other areas of the manager-permittee interface.

Expansion of the pool of monitoring sources beyond outfitters will increase the chances of catching a sign of impaired air quality. This should be a voluntary inclusion process targeted at non-permitted, long-term resource users (locals). Setting up a Web page linked from the main forest Web site that lists a few of the visible signs of impaired water quality or visibility (mass fish kills, algal

blooms, poor visibility, etc.) with a comment box would reach a wide audience of forest users and be cost effective. Placing signage at trailheads with the same information would also increase meaningful participation in air quality monitoring and awareness.

This overall mixed methods study presents considerable data on water chemistry of high elevation lakes so as to establish a baseline for further monitoring and tracking of water quality trends in the future. The lake chemistry is viewed as a surrogate for air quality parameters connected to climate change. Although the quantitative part of this study does identify 10 lakes most likely to be affected by air quality changes, it stops very short of identifying positive or negative air quality parameters. Table Mountain Lake in the Gros Ventre Wilderness and Ferry Lake in the Teton Wilderness were sampled by the EPA in 1984 and both were sampled again in this study. Even though there are some similar trends between the two lakes in terms of change in water parameters, these two lakes are a considerable distance apart and are on very different parent materials. Therefore, it is difficult to draw many conclusions from this low number of lakes when only one sampling has been done.

So what is left? In the absence of hard data over the more than 20-year interval between the 1984 EPA survey and this one, we have no choice but to look to those observers that have the long-term perspective on both wilderness areas. Their observations are therefore crucial and of great value. Even in the future, when more quantitative data is forthcoming, the observations of the long-term observers will continue to be of great value. Even in hard science there is much merit for making an observation and then discovering the data to support or refute the observation.

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Vegetation Monitoring to Detect and Predict Vegetation Change: Connecting Historical and Future Shrub/Steppe Data in Yellowstone National Park

Geneva Chong¹, David Barnett², Benjamin Chemel³, Roy Renkin⁴ and Pamela Sikkink⁵

¹ U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715, 307-733-9212 ext. 5, geneva_chong@usgs.gov

² NEON, Inc., 1685 38th Street, Suite 100, Boulder, CO 80301, 720-746-4858, dbarnett@neoninc.org

³ U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715, 307-733-9212 ext. 5, dr.chemel@gmail.com

⁴ Yellowstone Center for Resources, PO Box 168, Yellowstone National Park, WY 82190, 307-344-2161, roy_renkin@nps.gov

⁵ U.S. Forest Service Rocky Mountain Research Station, Fire, Fuel, and Smoke Science Program, 5775 W. U.S. Highway 10, Missoula, MT 59808-9361, 406-829-7343, psikkink@fs.fed.us

Abstract

A 2002 National Research Council (NRC) evaluation of ungulate management practices in Yellowstone specifically concluded that previous (1957 to present) vegetation monitoring efforts were insufficient to determine whether climate or ungulates were more influential on shrub/steppe dynamics on the northern ungulate winter range. The NRC further recommended that the National Park Service employ more contemporary and acceptable “range” monitoring efforts in the future that allow for deterministic analyses of vegetation change. In response to these recommendations, we have begun to develop and test new, more robust methods for sampling vegetation on Yellowstone National Park’s northern range, while maintaining a connection to over 50 years of historical data. In 2009 we sampled transects associated with existing vegetation exclosures using historical (transects) and new (multi-scale circular plots) methods simultaneously. In 2010 we expanded our methods comparison and collaborated with the National Ecological Observatory Network planning and design phase to map the occurrence of several non-native species of interest to the park. The overall objectives of the project are to provide: 1) a comparison of sampling methods, particularly their ability to detect changes in native and non-native species presence/absence and cover; 2) an expanded monitoring design that samples “missing” vegetation types and considers the landscape scale and the National Ecological Observatory Network northern range site; and 3) example forecasts of the presence of native and non-native species of interest under climate change scenarios. Here we provide an overview of the project to date.

Introduction

The northern range of Yellowstone National Park, comprised of the Lamar and Yellowstone River drainages, is important winter habitat for many of the ungulates that reside in higher-elevation areas of the park during summer. These wintering grounds extend beyond the northern edge of the park into Montana and are commonly thought to be essential to the fitness of the ungulate populations that utilize them. The ecology of the northern range has long been, and continues to be, at the center of debates over the Park Service’s management of these populations (Huff and Varley 1999).

The composition and integrity of vegetative communities on these grazing lands has been the subject of extensive research (Yellowstone National Park 1997),

and this landscape has changed considerably over the past century. It remains unclear, however, which factors are responsible for driving these changes and how the driving factors will alter this ecosystem in the future. A 2002 National Research Council (NRC) evaluation of ungulate management practices specifically concluded that previous (1957 to present) vegetation monitoring efforts were insufficient to determine whether climate change or ungulates were more influential on shrub/steppe dynamics on the northern ungulate winter range. The NRC further recommended that the National Park Service employ more contemporary and acceptable “range” monitoring efforts in the future that allow for deterministic analyses of vegetation change.

In response to these recommendations, we have begun to test new, more robust methods of sampling vegetation and groundcover on Yellowstone's northern range, while maintaining a connection to over 50 years of historical data. In 2009 (Chong et al. 2010) and 2010 we sampled transects associated with existing vegetation exclosures across the northern range using historical (transects) and new (multi-scale circular plots) methods simultaneously. Here we present preliminary results from two sets of data from these exclosures, Gardiner and Blacktail, that were obtained using a contemporary, multi-scale circular plot sampling technique (Barnett et al. 2007). We also mapped distributions of several non-native species of interest, which were incorporated into models of spatial distribution variability. The spatial distribution models are being developed in order to forecast the presence of native and non-native species of interest under climate change scenarios and to help locate additional vegetation sampling locations.

Our research aims to integrate three influences that can profoundly impact this important landscape: land use, climate change, and invasive species. Many researchers have studied these interrelated topics from a variety of angles and more will continue to do so. We present one option for how vegetation data might be collected and analyzed to provide managers, scientists, and the public with possible answers to the question: "what plants might grow on Yellowstone's northern range in a future with a different climate and with varied resource management actions?"

Methods

Multi-Scale Circular Plot Vegetation Sampling. In July and August 2009 we sampled 36, 168-m² circular, multi-scale vegetation plots modified from the National Forest Service Inventory and Analysis (FIA) Program (Frayar and Furnival 1999; Barnett et al 2007; Figure 1). Species composition, foliar cover and height, and cover of abiotic variables (e.g., rock, litter, bare soil) were recorded in three 1-m² subplots nested within the 168-m² plot. (Species codes and species nativity follow the PLANTS Database [USDA NRCS 2011].) Species composition was also recorded for the entire 168-m² plot. The circular plots were placed in and adjacent to four grazing exclosures that were constructed in 1957 and 1962. These 2-hectare exclosures are located on the Blacktail Plateau (two exclosures, nine plots) and on the Gardiner Bench west of the Roosevelt

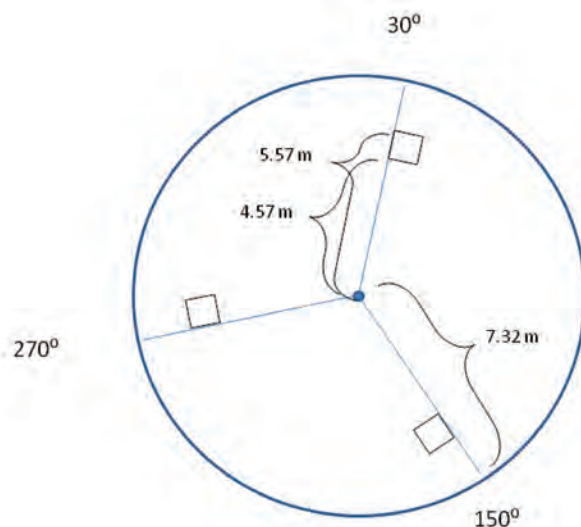


Figure 1. Multi-scale circular plot. Square subplots are 1 m x 1 m.

Arch (two exclosures, 19 plots). These plots were centered on the midpoint of historical 100-foot transects. Eight additional plots were sampled in and around the Blacktail Plateau exclosures in July 2010.

Non-native Plant Species Mapping. In July and August 2010, we used global positioning system (GPS) receivers to locate and record the presence of non-native species of concern (pale madwort, *Alyssum alyssoides*; desert madwort, *Alyssum desertorum*; annual wheatgrass, *Agropyron triteceum*; and cheatgrass, *Bromus tectorum*). Our mapping efforts were largely limited to easily accessible areas along roads or trails, but, when possible, we surveyed away from these areas until the limit of occurrence was reached. We also acquired mapping data for these species of interest collected on the northern range that were compiled and distributed by the Greater Yellowstone Coordinating Committee's Invasive Species Working Group (Greater Yellowstone Coordinating Committee 2006).

Vegetation Modeling. By integrating field data with descriptions of the landscape and climate, models provide an opportunity to understand the processes (causation) associated with observed patterns (description) of vegetation (Kerr et al. 2007; McMahon et al. 2009). Habitat suitability models describe the environmental conditions that most overlap a species' distribution and project that relationship across a defined space. The accuracy of habitat suitability models depends on the number and distribution of observed presence locations, the completeness of the species surveys, and the resolution

and relatedness of predictor layers in the models (e.g., climate, geology and soils, vegetation, and remote sensing layers). Once a habitat suitability map is generated, it can be validated by withholding some of the occurrence data for testing, or through new survey data.

We used a Maxent (Elith et al. 2006; Phillips et al. 2006) species-habitat matching model to estimate the distributions of the non-native species of interest under current climate and land use. Maxent employs a machine learning method based on the principal of maximum entropy to probabilistically describe locations (grid map cells) with conditions conducive to species occurrence based on individual environmental variables. Environmental variables we used included: topographic characterizations, remotely sensed Landsat 7 data, and 19 bioclimatic variables (Hijmans et al. 2005) derived from monthly total pre-

cipitation and monthly mean, minimum, and maximum temperature as compiled by WorldClim (www.worldclim.org). Climate data reflect averages from 1960–1990. Cross-correlated environmental variables were removed ($r > 0.8$), and we report the Maxent test area under the curve (AUC) values generated from 25 model iterations with 15 percent of the location data withheld to test the accuracy of the model.

Results

We identified the same number (63) of total plant species in our 168-m² circular plots at the Gardiner and Blacktail grazing exclusion sites. The Jaccard's coefficient of similarity between sites was 0.24, which means 24 percent of the species found occurred at both sites ($J = 1.0$ is complete similarity). The Jaccard's coefficient comparing species

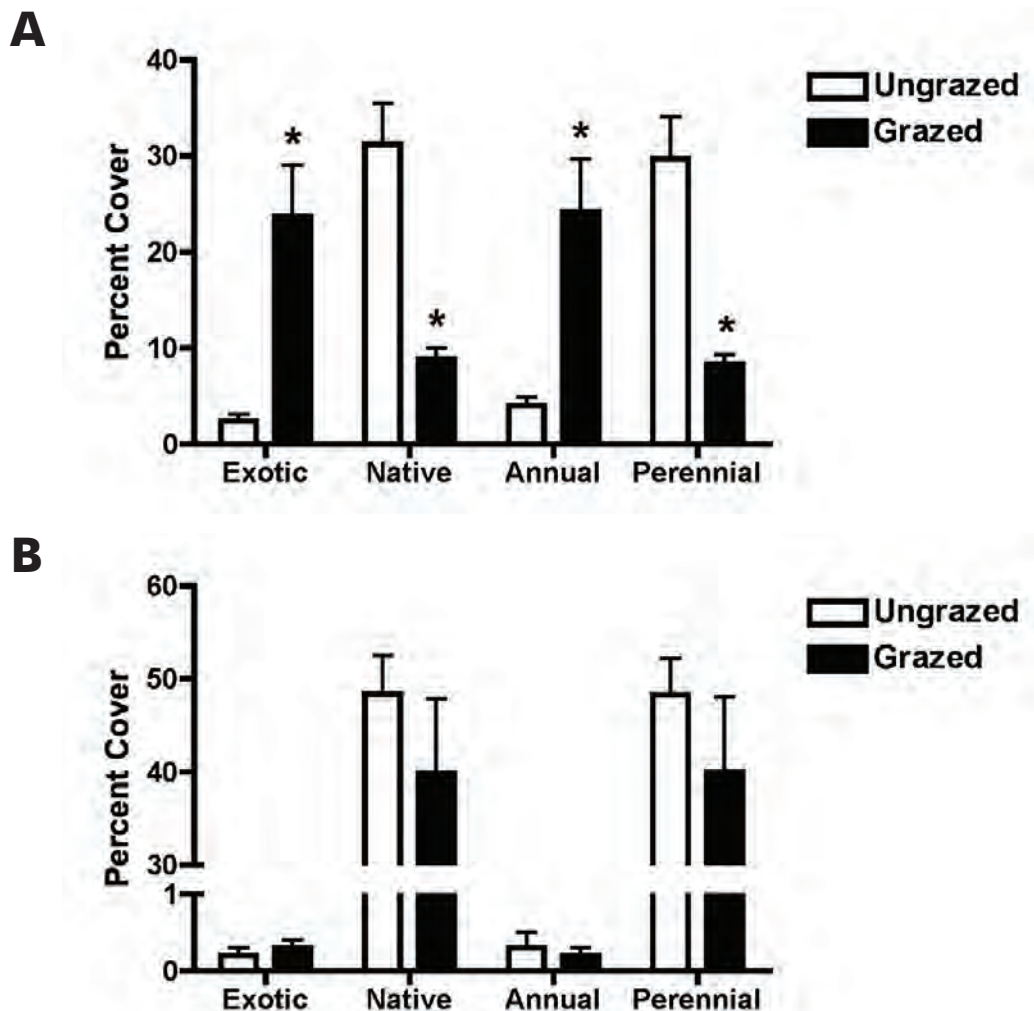


Figure 2. Percentage cover data from A) Gardiner and B) Blacktail exclusions in Yellowstone National Park. Asterisk indicates significant difference between grazed and ungrazed ($p < 0.001$, two-tailed t-test).

Table 1. The mean $\pm$ standard error of the mean (SEM) number of plant species sampled in circular plots in and around exclosures in Yellowstone National Park. The number of plots sampled for each treatment are listed in parentheses.

	Species per plot (mean $\pm$ S.E.M)			
	Gardiner		Blacktail	
	Ungrazed (11)	Grazed (8)	Ungrazed (10)	Grazed (7)
Total	21.5 $\pm$ 1.9	23.1 $\pm$ 1.7	18.6 $\pm$ 1.5	22.1 $\pm$ 1.8
Native	18 $\pm$ 1.6	16.5 $\pm$ 1.0	18.0 $\pm$ 1.5	21.1 $\pm$ 1.6
Non-native	3.5 $\pm$ 0.5	6.6 $\pm$ 0.8	0.7 $\pm$ 0.2	1.2 $\pm$ 0.2

Table 2. Percentage cover data from exclosures in Yellowstone National Park. Asterisk indicates significant difference between grazed and ungrazed ($p < 0.001$, two-tailed t-test).

	Percentage cover (mean $\pm$ S.E.M)			
	Gardiner		Blacktail	
	Ungrazed	Grazed	Ungrazed	Grazed
Vegetation	33.6 $\pm$ 4.6	32.6 $\pm$ 5.7	48.6 $\pm$ 4.1	40.2 $\pm$ 8.0
Veg: Native	31.2 $\pm$ 4.3	8.9 $\pm$ 1.1*	48.4 $\pm$ 4.1	39.9 $\pm$ 8.0
Veg: Non-native	2.4 $\pm$ 0.7	23.7 $\pm$ 5.3*	0.2 $\pm$ 0.1	0.3 $\pm$ 0.1
Veg: Annual	4.0 $\pm$ 0.9	24.2 $\pm$ 5.4*	0.3 $\pm$ 0.2	0.2 $\pm$ 0.1
Veg: Perennial	29.7 $\pm$ 4.3	8.4 $\pm$ 0.9*	48.3 $\pm$ 3.9	40.0 $\pm$ 8.0
Abiotic	69.3 $\pm$ 5.5	66.0 $\pm$ 9.7	57.9 $\pm$ 5.1	59.1 $\pm$ 8.8
Abio: Litter	11.8 $\pm$ 4.7	11.5 $\pm$ 6.3	11.9 $\pm$ 2.7	6.6 $\pm$ 2.3
Abio: Rock	34.3 $\pm$ 4.2	21.9 $\pm$ 4.5	27.4 $\pm$ 3.9	34.5 $\pm$ 7.2
Abio: Soil	19.8 $\pm$ 3.5	29.0 $\pm$ 6.5	16.4 $\pm$ 2.7	16.0 $\pm$ 2.2

Table 3. Top species by percentage occurrence. Species codes (USDA, NRCS 2011): *Agropyron spicatum*, Agsp; *Agropyron triteceum*, Agtr5; *Alyssum desertorum*, Alde; *Allium textile*, Alte; *Antennaria microphylla*, Anmi3; *Artemesia frigida*, Arfr4; *Artemesia tridentata*, Artr2; *Atriplex gardneri*, Atga; *Camelina microcarpa*, Cami2; *Elymus elymoides*, Elel5; *Festuca idahoensis*, Feid; *Koeleria cristata*, Kocr; *Poa secunda*, Pose.

Percentage Occurrence							
Gardiner				Blacktail			
Ungrazed		Grazed		Ungrazed		Grazed	
Alde	77.3	Agtr5	100.0	Feid	95	Kocr	89.3
Agsp	68.2	Alde	93.8	Kocr	85	Feid	78.6
Artr2	65.9	Elel5	71.9	Artr2	82.5	Agsp	75.0
Pose	65.9	Atga	59.4	Agsp	77.5	Arfr4	71.4
Alte	61.4	Cami2	53.1	Anmi3	67.5	Pose	64.3
				Pose	67.5		

Table 4. Top five species by average cover. Species codes (USDA, NRCS 2011): *Agropyron spicatum*, Agsp; *Agropyron triteceum*, Agr5; *Alyssum desertorum*, Alde; *Antennaria microphylla*, Anmi3; *Artemesia frigida*, Arfr4; *Artemesia tridentata*, Artr2; *Atriplex gardneri*, Atga; *Festuca idahoensis*, Feid; *Koeleria cristata*, Kocr; *Opuntia polycantha*, Oppo; *Poa secunda*, Pose; *Sarcobatus vermiculatus*, Save4.

Average Cover							
Gardiner				Blacktail			
Ungrazed		Grazed		Ungrazed		Grazed	
Artr2	12.9	Agr5	10.9	Artr2	20.9	Feid	13.5
Pose	2.9	Alde	10.5	Feid	8.4	Agsp	5.8
Agsp	2.8	Atga	1.5	Anmi3	4.4	Artr2	5.3
Atga	2.4	Pose	1.5	Agsp	2.8	Kocr	2.4
Oppo	2.0	Save4	1.0	Kocr	2.0	Arfr4	2.3

Table 5. Average cover of non-native species of interest. Species codes (USDA, NRCS 2011): *Agropyron triteceum*, Agr5; *Alyssum desertorum*, Alde; *Bromus japonicus*, Brja; *Bromus tectorum*, Brte.

Average Cover				
Gardiner			Blacktail	
	Ungrazed	Grazed	Ungrazed	Grazed
Agr5	0.06 (0.06)	10.9 (2.6)*	0.0	0.0
Alde	1.4 (0.4)	10.5 (3.0)*	0.0	0.0
Brja	0.71 (0.35)	0.85 (0.69)	0.0	0.0
Brte	ND	0.79 (0.74)	0.0	0.0

similarity in and around the grazing exclosures was 0.54 and 0.60 for the Gardiner and Blacktail areas, respectively. We sampled similar numbers (approximately 50) of total species inside and adjacent to the exclosures at each of the sites. The mean values of plant species found per plot were similar across treatment areas (approximately 20, Table 1). In general, though not statistically significant, more non-native species were encountered at the Gardiner site, and, about twice as many non-natives were found in the grazed plots than the ungrazed plots at this site (Table 1).

Cover data from the 1-m² subplots from the Gardiner exclosures illustrate significant differences between the cover of native or non-native species in grazed and ungrazed areas (Figure 2A). The Gardiner exclosure had significantly more non-native vegetation cover, more annual cover, and less perennial cover (Table 2). In contrast, similar differences were not found in and around the Blacktail exclosures (Figure 2B). No statistically significant differences were found in the cover of total vegetation or various abiotic cover types between grazed and ungrazed areas at either site (Table 2). The differences in vegetation between the grazed and ungrazed areas of the Gardiner site

are further highlighted by examining the top species by occurrence (Table 3) and cover (Table 4). In grazed areas at the Gardiner site, three out of the top five species by occurrence were non-native, with *Agropyron triteceum* and *Alyssum desertorum* occurring in 100 percent and 94 percent of the measured areas, respectively. Additionally, these two non-native plants averaged 10 percent cover (Tables 4 and 5). In contrast, in ungrazed Gardiner plots *Alyssum desertorum* occurred with less frequency and was the only non-native species listed in the top five species by occurrence (Table 3). Furthermore, the top five species by cover inside the Gardiner exclosures (ungrazed) were all native species. We also found that *Artemesia tridentata* (big sagebrush) occurred with greater frequency (Table 3) and had greater cover (Table 4) in ungrazed areas at both sites. It is notable that non-native species are absent from the top five species lists for occurrence and cover at the Blacktail site (Tables 3 and 4).

The Maxent analysis of the contribution of independent variables to describing cheatgrass (*Bromus tectorum*) distribution shows elevation was the most influential in the cheatgrass model (Figure 3). The logistic

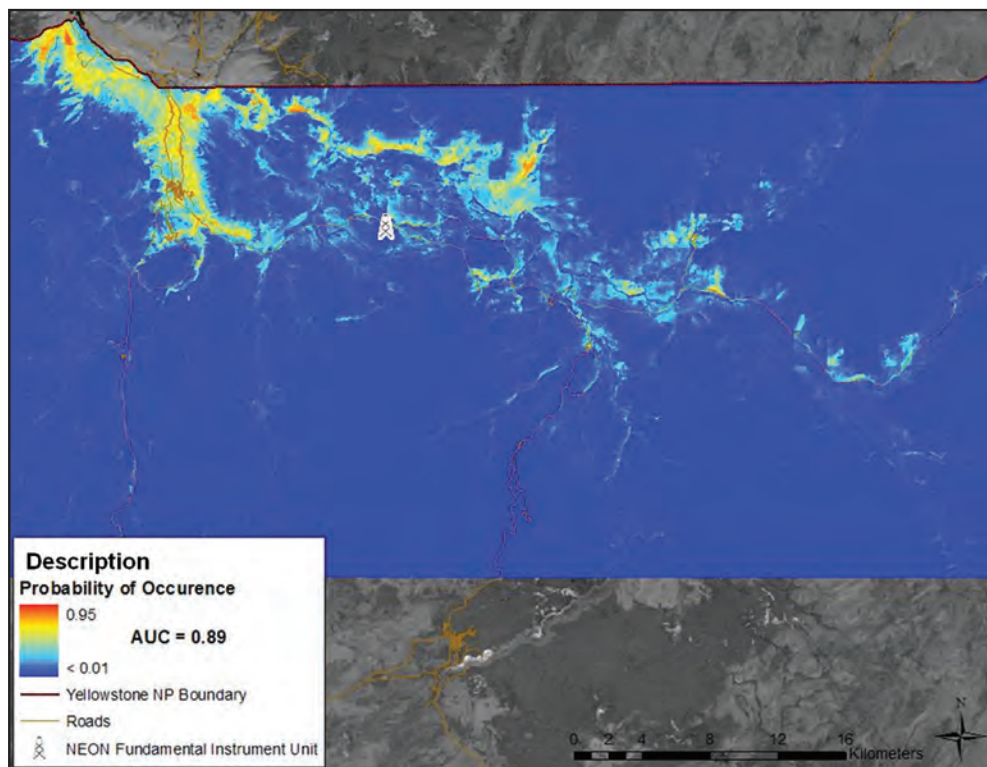


Figure 3. The probability of occurrence of cheatgrass as described by maximum entropy modeling with a variety of climate, topographic, and biotic descriptors of the landscape as influential independent variables. The National Ecological Observatory Network (NEON) Fundamental Instrument Unit indicates a potential area of location, not an actual location. The area under the curve (AUC) is an indicator of the amount of variation explained by the model.

response curve for elevation (describing logistic response as each elevation is varied, keeping all other independent variables at average sample value) reached a maximum at 1,700 m (Figure 4), which indicates that cheatgrass is currently most often observed around 1,700 m elevation. Other influential variables in the model included tassel cap soil brightness (a moisture index), vegetation type, precipitation of the wettest annual quarter, landform, and the annual range in temperature (Figure 3).

Discussion

To best detect and forecast change in response to climate variability and management actions, vegetation monitoring designs should consider needs for field data collection, management, and multi-scale analyses. The National Ecological Observatory Network (NEON) Northern Rocky Mountain domain includes Yellowstone National Park's northern range and provides an opportunity to collaborate with NEON's investigations into scaling models of plant species distributions from plots, to landscapes, to regions, and forecasting changes in species distributions related to climate change.

Spatial analyses of species distributions, such as the example we presented here of the current distribution of the non-native, annual cheatgrass, will provide information on where additional sampling sites should be established. The Maxent model to describe current cheatgrass distribution, for example, could be used with climate change scenario data (e.g., changes in precipitation and temperature) to describe potential future distribution and thus direct management action. Models of other species' current distributions could be used to test the strength of existing data and thus guide the placement of new monitoring sites.

Because long-term exclosures reflect inherent site differences and effects caused by grazing and the exclusion of grazing, our data are descriptive and not explanatory. Although extensive sampling techniques are not necessary for the trained eye to perceive differences in grazing effects between the current, predominant vegetation in the Gardiner and Blacktail areas, differences must be quantified to allow comparisons through time and space to detect and respond to change. Our initial analyses confirm that there are significant vegetative differences between the Gardiner and Blacktail exclosure sites. That the cover of native and

non-native species was found to be significantly different between grazed and ungrazed plots for the Gardiner exclosures, but not the Blacktail exclosures suggests that these differences are not solely attributable to ungulate grazing effects. Rather, they likely reflect a variety of factors including, but not limited to, climate, soil chemistry, human influence, and grazing. However, *Artemesia tridentata* occurred with greater frequency (Table 3) and had greater cover (Table 4) in ungrazed areas at both sites, suggesting that grazing may be a driving factor for this species.

Mapping efforts to determine the extent of four non-native annuals, including two mustards, *Alyssum desertorum* and *A. alyssoides*, and two grasses, *Agropyron triticeum* and *Bromus tectorum* (data compiled by the Greater Yellowstone Coordinating Committee), laid a foundation for modelling efforts to predict where these species may spread under various climate change scenarios. We were concerned about these species dominating and expanding because they degrade rangeland. Issues with range degradation include reduced palatability (e.g., phytoliths), nu-

trition, productivity (carbon sequestration), soil fertility and water holding capacity, increased fire frequency, and, related to climate change, phenology or timing of resource availability (e.g., early green-up and early senescence result in reduced forage availability in the winter). The current probable distribution of cheatgrass (Figure 3) is of concern because of its potential to spread in the northern range at the expense of native vegetation that provides more valuable forage and other ecosystem services.

The Gardiner Bench area, which is the hottest and driest part of the park, has become dominated by a few annual, non-native plant species (e.g., *Alyssum alyssoides*, *A. desertorum*, *Agropyron triticeum*, and *Bromus tectorum*). Our mapping efforts suggest that while *Bromus tectorum* is relatively widespread throughout the northern range, the range of *Agropyron triticeum* does not currently extend up the Gardiner River drainage beyond the Boiling River. Similarly, while both species of *Alyssum* occur sporadically throughout the northern range from Gardiner to the Lamar Valley, *A. desertorum* dominates vast expanses at the

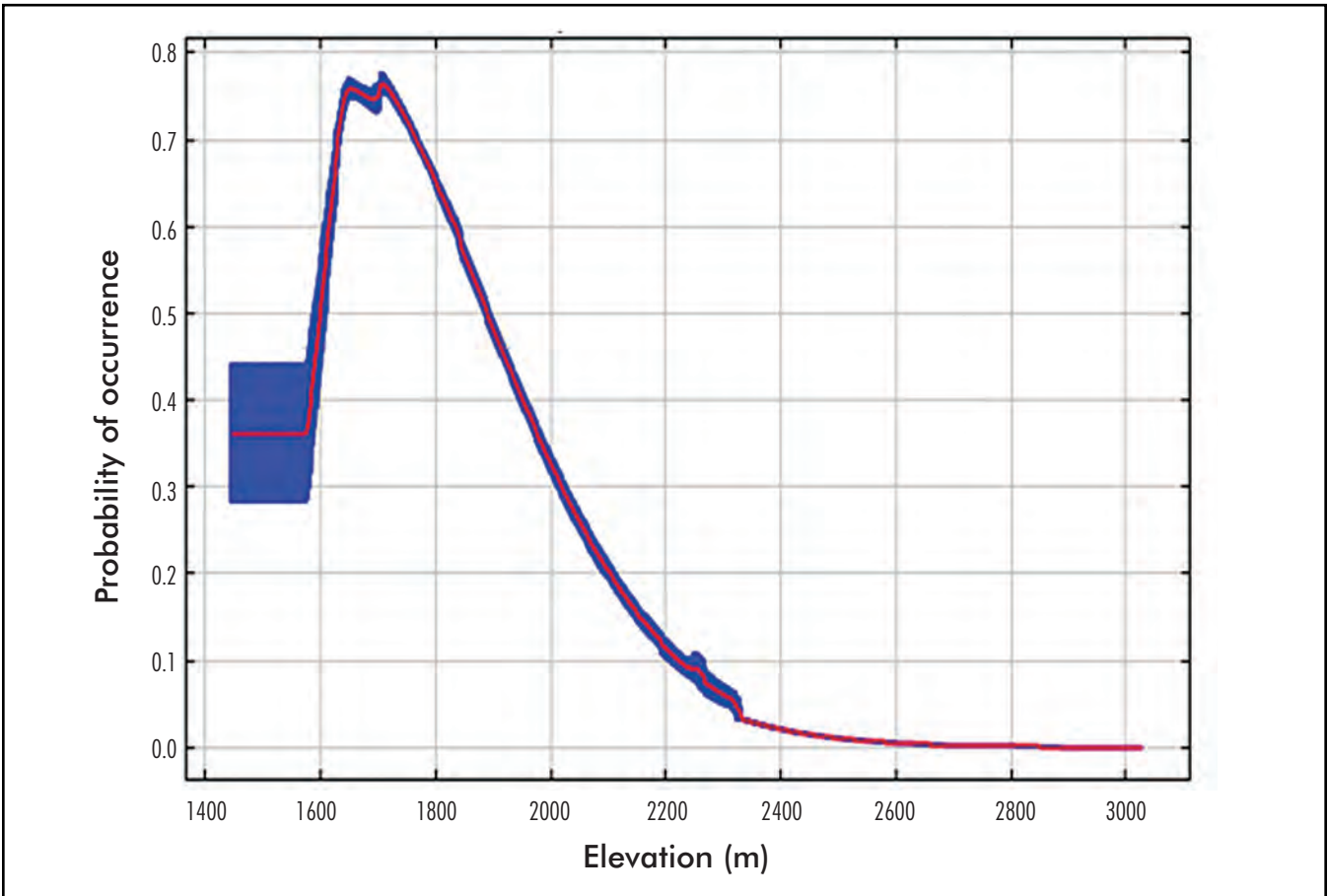


Figure 4. The probability of cheatgrass occurrence as described by elevation. The curves show the mean response of the 25 replicate Maxent runs (red) and the mean +/- one standard deviation (blue).

lower elevations of the Gardiner area. Under certain climate change scenarios these species may expand into other portions of the northern range, with potentially negative consequences for critical winter habitat.

In summary, ecosystems change in response to climate, land use, and invasive species. Species distribution modeling is a tool that integrates knowledge of how vegetation has already changed and predictions of how it may change in the future to manage risks to critical habitat. For example, managers could use spatial distribution models to develop non-native species control and native species restoration plans. The connections between field-based data and modelling are critical to provide natural resource managers with methods of sampling vegetation that detect change and with hypotheses of the drivers of change, and thus ways to model future vegetation distributions. Here we have presented one possible use of plot and ground-based vegetation data in non-spatial analyses and spatial models. We hope that advancing correlations between past and present sampling techniques and using modelling techniques to explore how plants may be distributed under changes in climate will allow natural resource managers to make decisions that allow for adaptation to change and/or risk management.

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Climate Change and Greater Yellowstone's Native Trout: Potential Consequences and Management in a Warmer World

Scott M. Christensen

Greater Yellowstone Coalition, PO Box 1874, Bozeman, MT 59771,
406-586-1593, schristensen@greateryellowstone.org

Abstract

Four subspecies of cutthroat trout (*Onchorhynchus clarkii*) inhabit the waters of the Greater Yellowstone Ecosystem and are likely to be impacted by warmer water, changes in stream flow, and the increasing frequency of other disturbances associated with climate change. We examined how four climate change-driven effects—increased summer temperatures, winter flooding events, increased wildfire risk, and long-term persistent drought—threaten the broad-scale persistence of Yellowstone cutthroat trout (*O. c. bouvieri*), Bonneville cutthroat trout (*O. c. utah*), westslope cutthroat trout (*O. c. lewisi*), and Colorado River cutthroat trout (*O. c. pleuriticus*) within this region. Our overall analysis of population vulnerability combined the climate change evaluation with a population-specific assessment of persistence for each subspecies. Our results suggest the potential for significant declines of suitable habitat for native trout in the Greater Yellowstone Ecosystem. Large portions of ranges either currently lack the basic persistence criteria to sustain trout or are at high risk from climate change, and in some cases both risks apply. Existing stressors such as habitat degradation and non-native species competition and introgression will be exacerbated by climate change impacts. Rapid changes in habitat conditions will reduce habitat resiliency and the ability of native trout to successfully adapt. The threat posed by climate change warrants new management strategies and an increased commitment to maintaining native trout populations. Prioritization of habitats and populations for immediate restoration actions is critical as changes in climate occur over the next 50 years.

Introduction

The Greater Yellowstone Ecosystem (GYE) is home to many of the most iconic rivers in the American West. The Yellowstone, Snake, Madison, Henry's Fork, Green River, and others provide high quality recreational opportunities and critical aquatic habitat for fish and wildlife. The headwaters of the Missouri, Colorado, and Columbia Rivers all begin on the high, rugged peaks of the GYE, prompting some to refer to this landscape as “the headwaters of the continent.”

The rivers and streams of the GYE are home to a diversity of native fish. This ecosystem is the only place on Earth where four distinct cutthroat trout subspecies are found. Divided by major watersheds, the Yellowstone cutthroat trout (*O. c. bouvieri*; Figure 1), Bonneville cutthroat trout (*O. c. utah*), westslope cutthroat trout (*O. c. lewisi*), and Colorado River cutthroat trout (*O. c. pleuriticus*) inhabit the waters of this biologically rich region. Each of these fish have been petitioned for listing under the Endangered Species Act due to habitat degradation and fragmentation, as well as competition and hybridization with non-native trout. Currently, none of the four subspecies is protected under the act.

On top of the existing suite of threats to trout populations, the climate is warming in the GYE and aquatic systems are showing a response. As temperatures have warmed, snowpack has been on a downward trend and average peak spring runoff in the Intermountain West is occurring 10 to 20 days earlier than the historical average (Yellowstone National Park 2010). In the GYE, temperatures have tracked the regional trend and in some areas have outpaced warming trends of the Northern Rockies. Average July temperatures at Mammoth Hot Springs have increased 3.5°F between 1940 and 2007, and models predict a 4–13°F increase in the region over the coming century (Greater Yellowstone Resource Brief 2009; IPCC 2007). When water temperatures warm, thermal thresholds for native cutthroat trout are exceeded, suitable habitat is diminished, and warm-water fish species such as smallmouth bass are able to access new stream segments.

Climate warming is driving disturbance regimes that have historically shaped habitat for native trout in the GYE. The increasingly uncharacteristic nature of extreme temperatures, wildfire, winter flooding, and persistent drought, combined with the present state of degraded and



Figure 1. Yellowstone cutthroat trout in the Grand Canyon of the Yellowstone River. Photo courtesy of FishEyeGuy Photography.

fragmented habitats and populations, pose a significant threat to the cutthroat trout subspecies that have evolved in the GYE.

Analysis of Climate Change Impacts on Native Trout.

Scientists from the U.S. Geological Survey's Northern Rocky Mountain Science Center, the U.S. Forest Service's Boise Forest Sciences Laboratory, and Trout Unlimited are engaged in a collaborative effort to assess climate change impacts on interior species of native salmonids. The first phase of this effort is a coarse-scale assessment conducted in a geographic information system (GIS) environment that makes use of the best available information in the West. The analysis is conducted as a spatially distributed model at 800-meter spatial resolution. The recently completed open file report (Haak et al. 2010) detailing the larger project is available at: http://www.nrmc.usgs.gov/research/climate_trout.

The Greater Yellowstone Coalition partnered with Trout Unlimited and the U.S. Geological Survey to produce the Greater Yellowstone Ecosystem portion of the larger project, which is the basis for this paper and presentation. The coarse-scale assessment analyzes four potential impacts caused by climate change to populations of native trout in the GYE: increased summer temperature, increased winter flooding, increased wildfire risk, and long-term persistent drought (see Figures 2–6). Additionally, a composite map was produced that depicts the interaction of all four climate change–driven impacts. A 3°C temperature increase was assumed, which is consistent with global circulation 2050 model projections for the western United States. The results

of the analyses for each factor were summarized by sub-watershed (6th Hydrologic Unit Code). This allowed analysis of the interaction of potential climate change–induced environmental change with data on population and habitat conditions for native trout.

A greater explanation of methodology is available in the open file report referenced above and in Williams et al. (2009). For the purposes of this paper and presentation, the coarse-scale maps are presented to describe potential consequences of climate change impacts on native trout and to give context for the management

approach outlined further in this paper.

Management in a Warmer World. The results of this analysis forecast a challenging future for native trout in the GYE. Populations are already fragmented and isolated in many locations, and climate change will exacerbate existing stressors. As those responsible for managing and stewarding the lands, waters, and species of the GYE grapple with the impacts of warming temperatures, the following climate change adaptation principles should guide management strategies:

1. Reduce existing stressors;
2. Protect water quality and quantity;
3. Protect and enable natural movement and migration;
4. Improve capacity to predict;
5. Manage collaboratively at the ecosystem level; and
6. Interventions/treatments should be well informed and monitored.

In addition to these general principles, three others that are more specific to native trout populations should be considered:

1. Preserve existing diversity;
2. Improve resilience to change; and
3. Promote immediate and prioritized habitat restoration.

Specifically, preserving diversity applies to several key areas, such as genetics, life history, and geographic distribution. Improving resilience to change focuses on

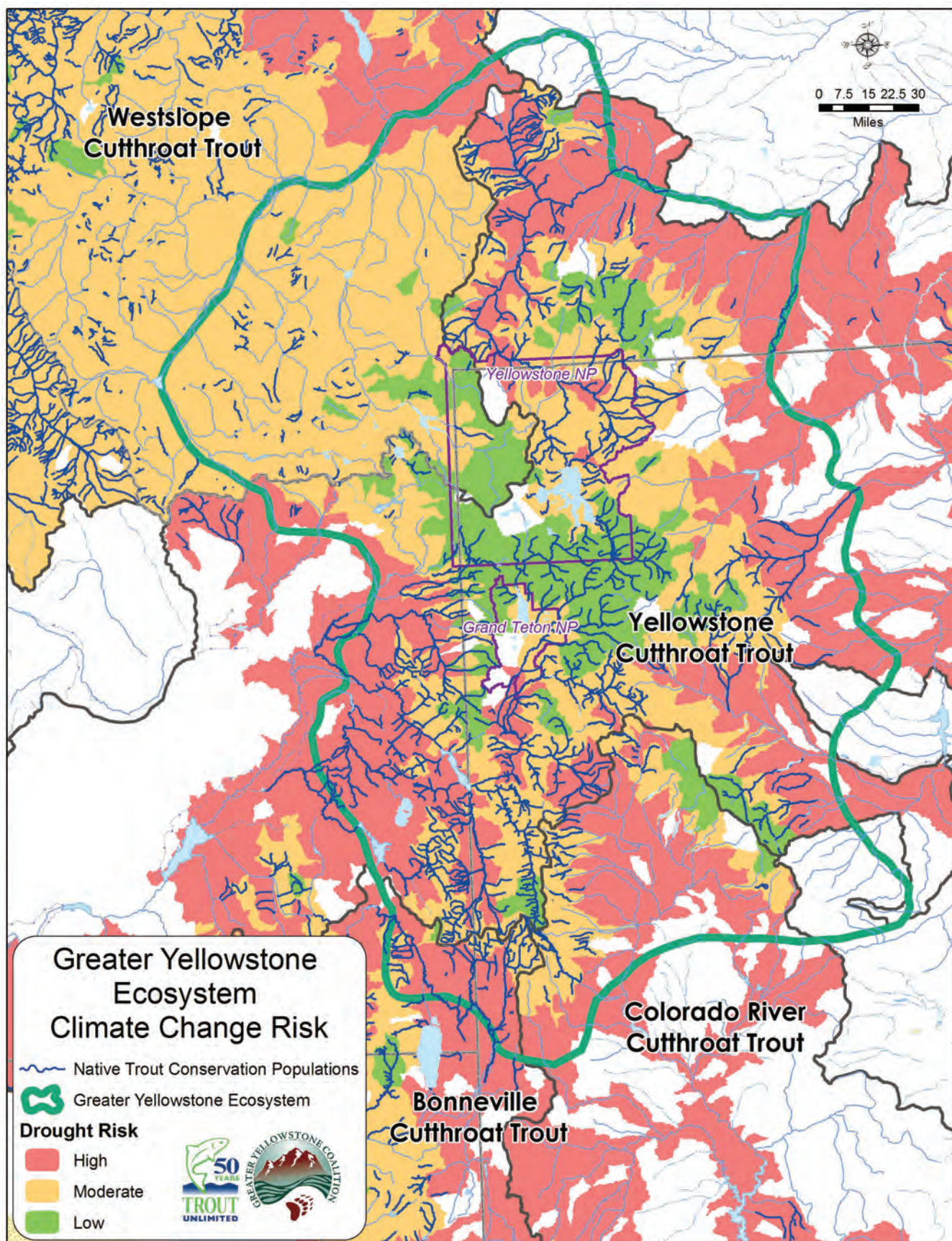


Figure 2. Drought risk.

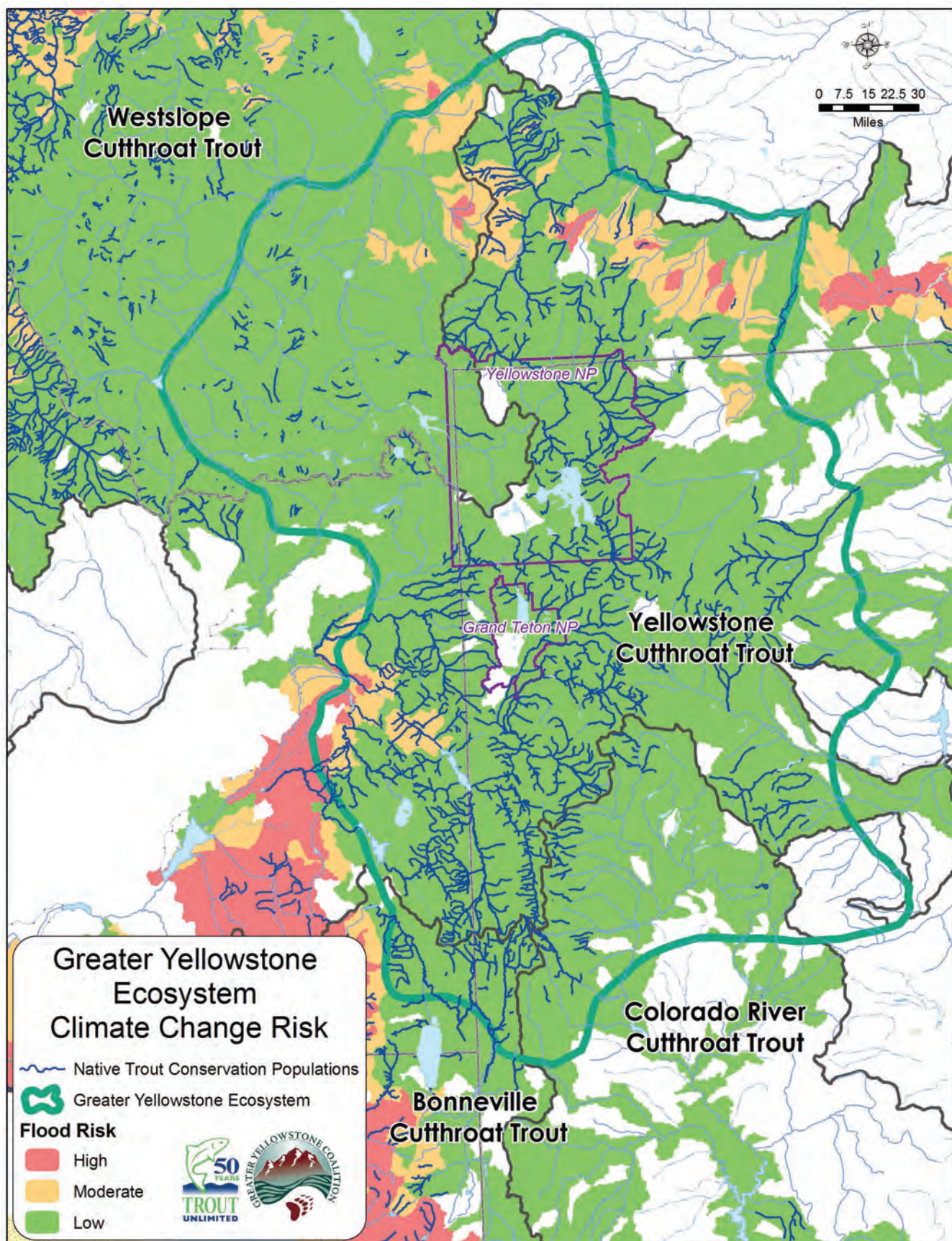


Figure 3. Winter flooding risk.

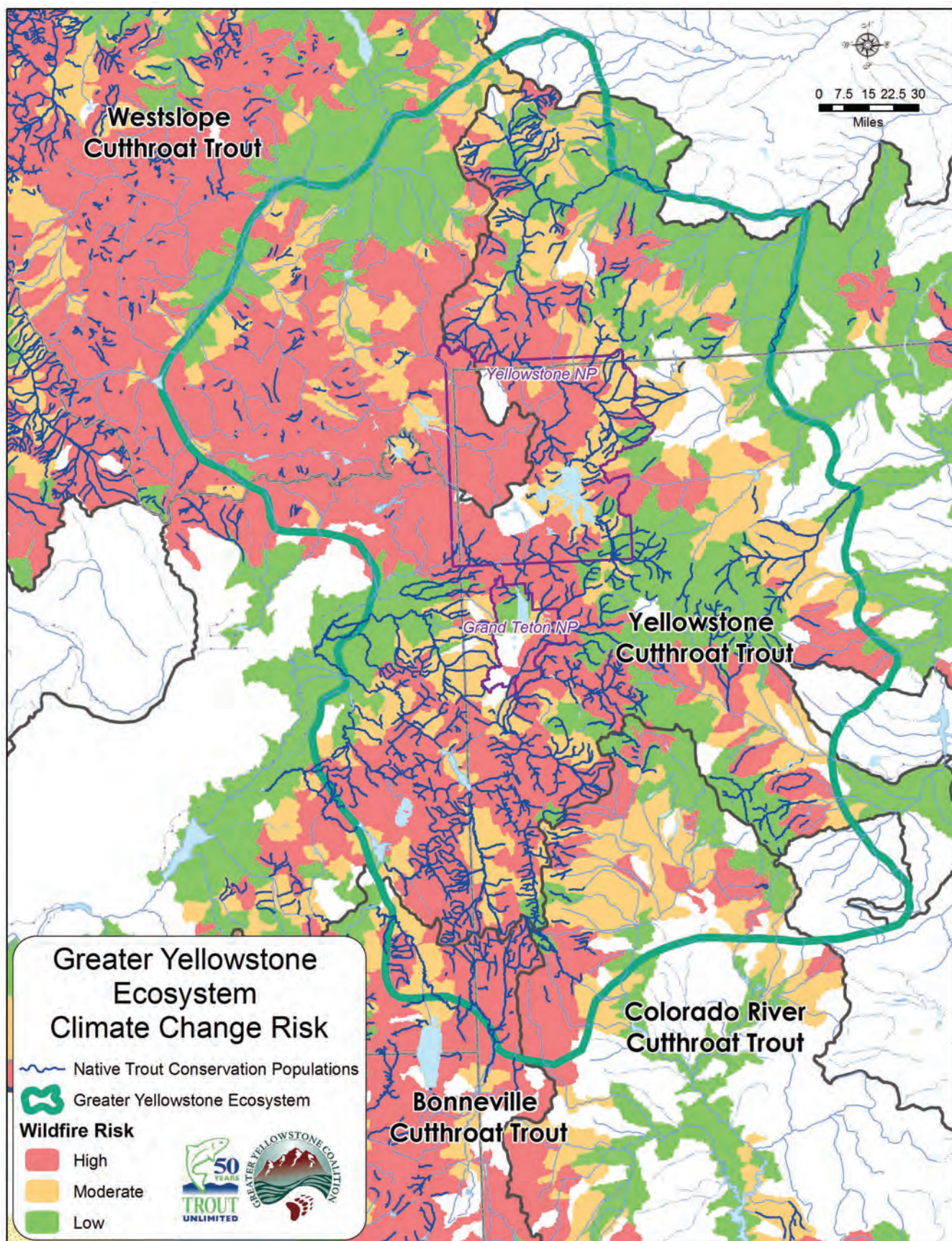


Figure 4. Wildfire risk.

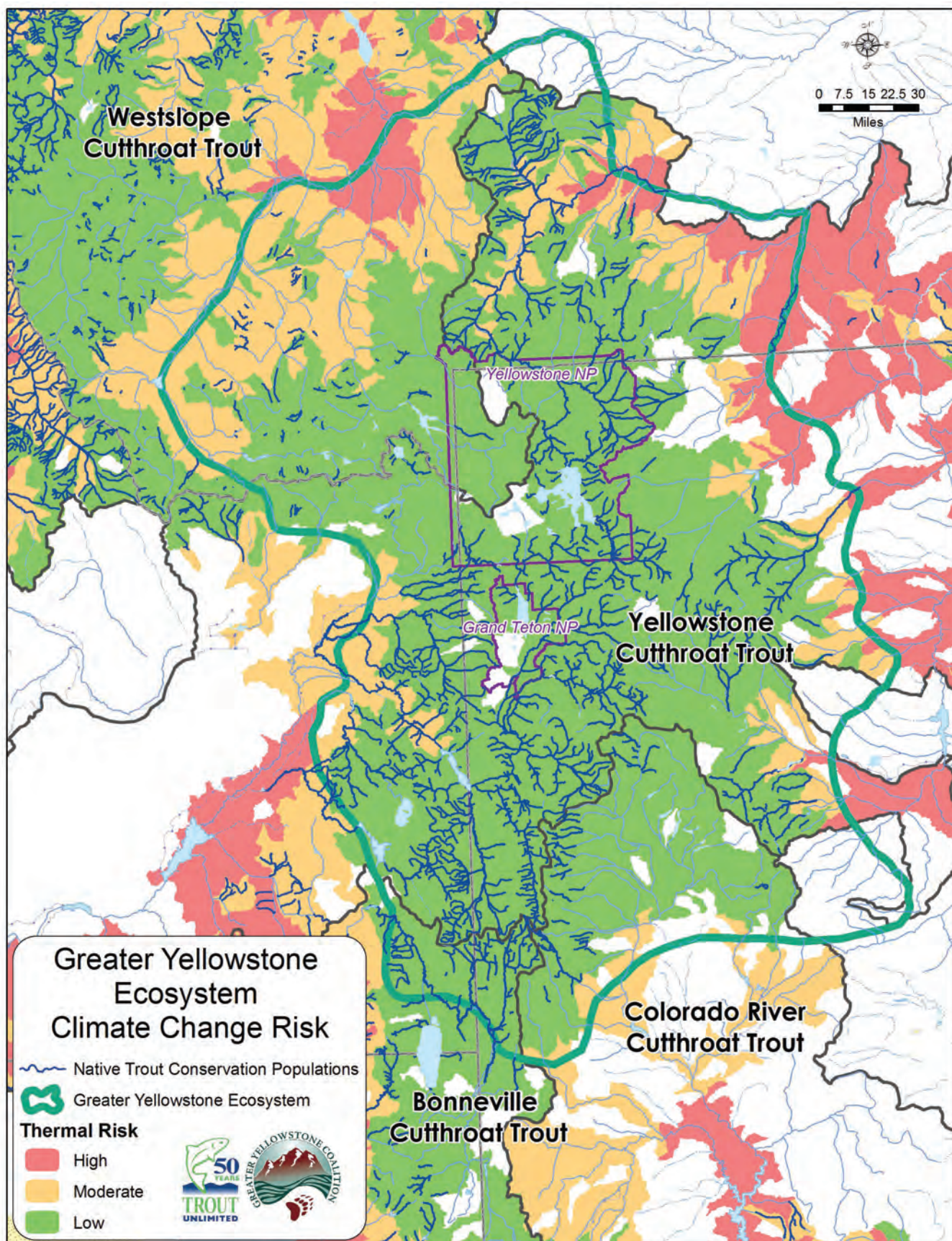


Figure 5. Thermal risk

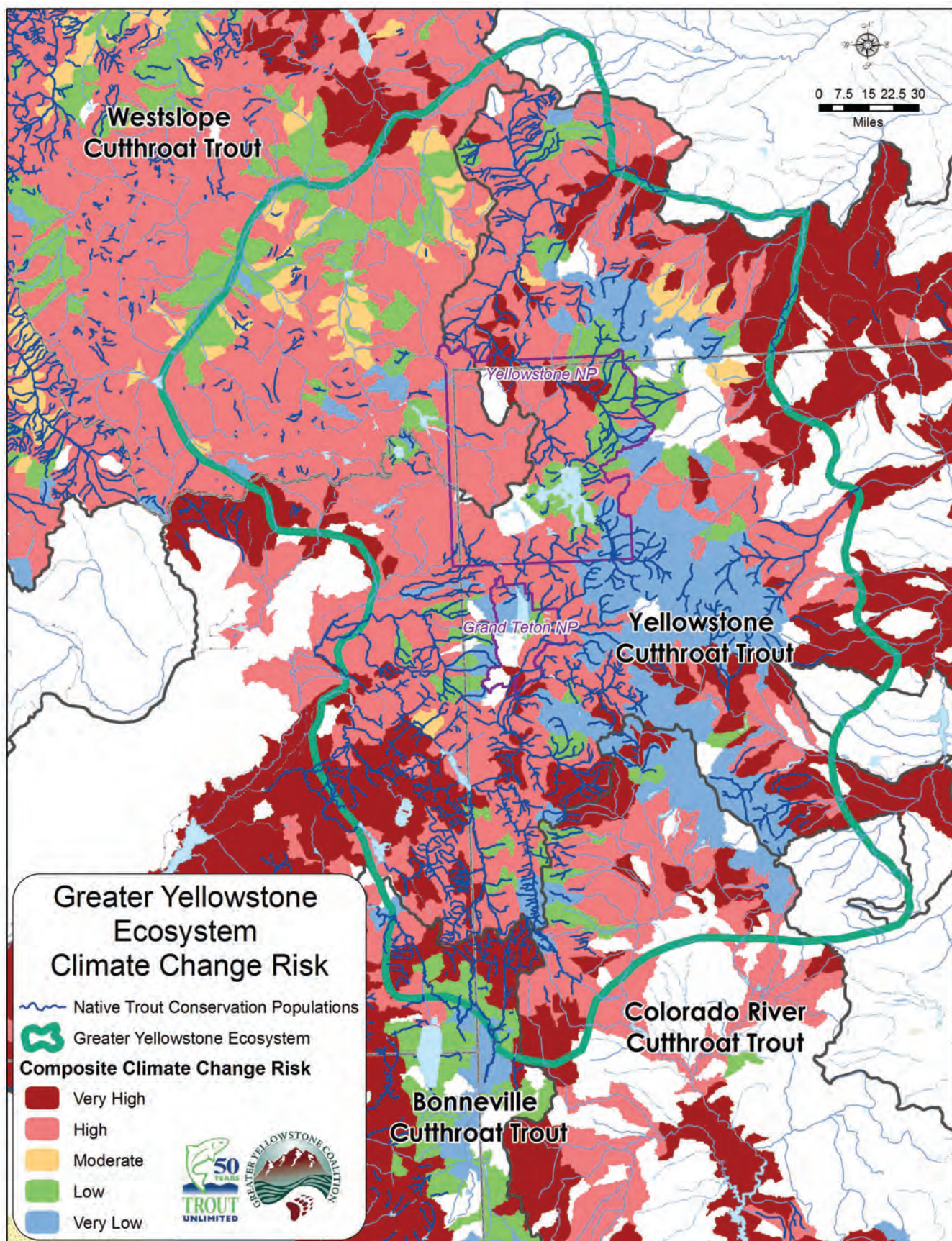


Figure 6. Composite climate change risk

maintaining sufficiently large populations and intact, connected habitats that allow species to survive significant disturbances and environmental change. Finally, the current extent of habitat degradation and fragmentation will limit managers' ability to sustain native trout populations in the future. A thoughtful and well-planned approach to habitat restoration that includes an assessment of vulnerability to climate change impacts, understanding of watershed-wide connectivity, analysis of non-native trout distribution and core native trout populations, and evaluation of key sites and existing stressors should be considered in new, large-scale restoration programs. Due to the uncertainties of watershed-scale climate change impacts, these principles provide a solid strategy geared toward preparing and buffering native trout populations as the climate warms.

Conclusion

Global climate change is real and is affecting native trout in and around the world's first national park. This trend will continue into the future as warming temperatures compound existing challenges to trout populations such as habitat degradation and fragmentation and hybridization and competition from introduced, non-native trout species. The efforts of the U.S. Geological Survey, U.S. Forest Service, and Trout Unlimited have demonstrated that coarse-scale modeling and mapping of climate change risk to native trout is possible and may be an effective guide for managers at an ecosystem scale. Clearly there are areas where native trout will fare poorly as temperatures rise. Conversely, there are likely to be significant areas of refuge in places like the Beartooth and Absaroka Ranges, the Wind River Range, and several other high-elevation areas of GYE watersheds.

The core question related to native trout management in a warmer world is this: is the current level of investment and commitment adequate for these highly sensitive species to persist? The reality of climate change demands a new, more robust, and well-funded approach to conserving native trout—one that brings new urgency and new thinking to how managers sustain species in a warmer world.

For more information, visit http://www.nrmc.usgs.gov/research/climate_trout.

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Long-Term Observations of Boreal Toads at an ARMI Apex Site

Paul Stephen Corn¹, Erin Muths², and David S. Pilliod³

¹ U.S. Geological Survey, Northern Rocky Mountain Science Center, Aldo Leopold Wilderness Research Institute, 790 E. Beckwith Ave., Missoula, MT 59801, 406-542-4191, scorn@usgs.gov

² U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Ave., Building C, Fort Collins, CO 80526, 970-226-9474, muthse@usgs.gov

³ U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Snake River Field Station, 970 Lusk St., Boise, ID 83706, 208-426-5202, dpilliod@usgs.gov

Abstract

The U.S. Geological Survey's Amphibian Research and Monitoring Initiative (ARMI) is a national project with goals to monitor the status and trends of amphibians, conduct research on causes of declines, and provide information and support to management agencies for conservation of amphibian populations. ARMI activities are organized around extensive inventories and place-based monitoring (such as collaboration with the Greater Yellowstone Inventory and Monitoring Network), and intensive population studies and research at selected locations (apex sites). One such site is an oxbow pond on the Buffalo Fork near the Black Rock Ranger Station east of Grand Teton National Park. We have been conducting mark-recapture of boreal toads (*Anaxyrus boreas*) at Black Rock since 2002. In concert with studies of other toad populations in the Rocky Mountains, we have documented a high rate of incidence of the chytrid fungus *Batrachochytrium dendrobatidis* (Bd) and a negative rate of growth of the toad population, but not the population crash or extinction observed in other populations with high prevalence of Bd. Long-term observations at other ARMI apex sites have proven invaluable for studying effects of climate change on amphibian behavior, and the Black Rock site has been upgraded with onsite recording of weather data and auditory monitoring of other amphibian species. Continued research at Black Rock will be critical for understanding the interrelated effects of climate and disease on amphibians in the Greater Yellowstone Ecosystem.

The ARMI Effort

The Amphibian Research and Monitoring Initiative (ARMI) of the U.S. Geological Survey (USGS) is a national effort to document status and trends of amphibian populations on federal (mainly Department of Interior) lands, conduct research into causes of amphibian declines and malformations, encourage partnerships to expand the scope of monitoring efforts, and provide information that will assist land managers in protecting amphibian populations (Corn et al. 2005a). Monitoring and research is conducted by ARMI in a hierarchical manner, conceptualized as a pyramid, with relatively less effort at relatively more sites (for example, inventory work) forming the base, greater effort at a restricted number of sites in the middle (for example, monitoring occupancy in a defined area of inference such as a national park), and intensive effort at a few sites at the apex of the pyramid (Corn et al. 2005a).

ARMI in the Rocky Mountain Region. Nationally, ARMI is divided into seven regions, and USGS research zoologists Steve Corn and Erin Muths are the principal in-

vestigators in the Rocky Mountain Region (Montana, Wyoming, Colorado, and New Mexico). At the middle level of the ARMI pyramid, amphibian populations are monitored in the national parks on the Continental Divide: Glacier, Yellowstone, Grand Teton, and Rocky Mountain National Parks (Corn et al. 2005b). ARMI partners with the National Park Service Greater Yellowstone Inventory and Monitoring Network (GRYN) to conduct monitoring in Yellowstone and Grand Teton National Parks, where amphibians are considered one of GRYN's vital signs. Analysis of trends in amphibian populations is accomplished by examining the change in occupancy by each species in small drainages (catchments). Each catchment encompasses several individual wetlands that are searched for evidence that breeding has occurred. Multiple visits are conducted so that detection probabilities can be estimated to account for the possibility that a species could have bred at a site but been missed by the surveys (MacKenzie et al. 2006).

Middle-level occupancy monitoring targets all the amphibian species that occur in the study area, but monitoring at apex sites is usually focused on a single species and



Figure 1. West arm of the Black Rock apex monitoring site. Photo by Steve Corn, U.S. Geological Survey.

often employs intensive capture-recapture methods to estimate demographic parameters, including population size and survival. Research often addresses the environmental influences that affect populations. The ARMI Rocky Mountain Region conducts apex studies at several locations in Montana, Wyoming, and Colorado. For example, populations of boreal chorus frogs (*Pseudacris maculata*) near Cameron Pass in northern Colorado have been studied since 1986, making this one of the longest continuous amphibian studies in the world. Data from this site have contributed to our understanding of how exposure of amphibian embryos to ultraviolet radiation varies from year to year, driven by the dependence of breeding phenology on mountain snowpack (Corn and Muths 2002). At another apex site, ARMI has supported studies by two University of Montana graduate students on a population of Columbia spotted frogs (*Rana luteiventris*) occupying a high-elevation fishless basin in the Bitterroot Mountains. Frogs have been marked since 2000, and annual survival of post-metamorphic life stages is higher in years with smaller snowpacks (McCaffery and Maxell 2010). Such results are important in predicting responses of amphibian populations to climate change.

The Black Rock ARMI Apex Site. In the Greater Yellowstone Ecosystem, ARMI maintains an apex site east of Grand Teton National Park at an old oxbow of the Buffalo Fork near Bridger-Teton National Forest's Black Rock Ranger Station (Figure 1). This site, which we name Black

Rock, supports breeding populations of four of the five amphibian species known to have occurred in the Jackson Hole area (Figure 2). Only the northern leopard frog (*Lithobates pipiens*), which has likely been extirpated from the area, is missing (and we have no evidence that this species ever occurred at Black Rock). The boreal toad is the primary species monitored at Black Rock. Studies began in 2003 after two of the authors (EM and DSP) received a grant from ARMI to examine the distribution of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis* [Bd]) in the Rocky

Mountains and its effects on the population dynamics of boreal toads. Adult toads are sampled on several occasions during the breeding season in May or June each year, and individuals are identified by their passive integrated transponder (PIT) tag that is inserted under the dorsal skin upon first capture. Some toads are sampled for Bd by running a cotton swab over the ventral skin. Swabs are submitted to a laboratory for detection of Bd DNA using polymerase chain reaction (PCR) analysis.

Amphibians are in decline worldwide and Bd is considered a leading cause (Collins and Crump 2009). Bd is suspected as the primary cause of the collapse of boreal toad populations in the southern Rocky Mountains, including the crash to near extinction of toads in Rocky Mountain National Park in the mid-1990s (Muths et al. 2003). The first component of the ARMI study documented that Bd is common throughout the Rocky Mountains, including at Black Rock. Muths et al. (2008) detected Bd at 64 percent of 97 study sites (clusters of wetlands within 3 km of one another) and in 23 percent of 1,151 boreal toads sampled. Despite the high prevalence of Bd, toad populations in the northern Rocky Mountains did not seem to be undergoing the sudden and steep declines seen in Colorado.

In the second component of the ARMI study, Pilliod et al. (2010) addressed the population-level effects of Bd infection by comparing demographic parameters at two sites with Bd present (Black Rock and Lost Trail National Wildlife Refuge, Montana) to a site free of Bd (Denny Creek, in the Sawatch Range, San Isabel National Forest, central Colorado). This study found high annual survival

(0.73–0.77) of adult toads that were not infected with Bd at all three locations, but at Black Rock and Lost Trail, toads that tested positive for presence of Bd had lower survival (0.42 and 0.53, respectively). As a consequence, the population at Denny Creek was stable, but numbers of adult toads at Black Rock and Lost Trail were declining 5–7 percent per year.

Black Rock has served as a site for related studies. One of the authors (PSC), with Sophie St.-Hilaire and Peter Murphy from Idaho State University, obtained research grants in 2006 and 2008 through the USGS Park Oriented Biological Support (POBS) program to document Bd in and around Grand Teton National Park and study the apparent differences in the consequences of Bd infection between toads in the northern and southern Rocky Mountains. Murphy et al. (2009) found Bd present at all

10 boreal toad breeding sites sampled, with a mean prevalence of 64.5 percent. In the laboratory, Bd isolated from toads collected at Black Rock killed toads as effectively as Bd isolated from Colorado, but recently metamorphosed toads from Black Rock survived longer than toadlets from Colorado. Papers describing the results of the second POBS study, involving field and laboratory data on behavioral characteristics of toads from Black Rock and Colorado that might affect the outcome of Bd infection, are currently in preparation. This study included radio telemetry of adult toads at Black Rock in 2008.

We intend to continue data collection at Black Rock for the foreseeable future, with several enhancements. We began using an automated recording system in 2009 to document breeding activity by boreal chorus frogs and Columbia spotted frogs. Because temperature is impli-



Figure 2. Amphibians that breed at Black Rock. Clockwise from upper left: boreal toad (*Anaxyrus boreas*), barred tiger salamander (*Ambystoma mavortium*), Columbia spotted frog (*Rana luteiventris*), and the boreal chorus frog (*Pseudacris maculata*). Photos by Steve Corn, U.S. Geological Survey.

cated in the presence and expression of Bd (Muths et al. 2008; Pilliod et al. 2010), we installed a weather station in 2009 to provide more precise climatic data. In 2010, we began marking both boreal toads and boreal chorus frogs at a newly constructed pond 400 m west of the oxbow. Finally, we have begun using quantitative PCR analysis of the Bd samples, which provides an estimate of zoospore density, rather than qualitative analysis, which provides a categorical assessment of the degree of infection. These additional data may prove useful, because population-level effects of Bd infection may be related to the severity of infection of individual animals (Briggs et al. 2010). The data collected at Black Rock already have proven extremely valuable to the study of amphibian populations in the Rocky Mountains. Because lengthy time series of amphibian population data are relatively rare, the longer we collect these data, the greater the contribution is likely to be.

We would like to thank the Buffalo Fork Ranger District of the Bridger-Teton National Forest for permissions and logistical support, Rick Scherer for population analyses, and Deb Patla, Blake Hossack, Sophie St.-Hilaire, Peter Murphy, and Chuck Peterson for observations, data on Bd, and assistance with fieldwork. Research has been conducted under Wyoming Game and Fish Department Chapter 33 Permit and Research Permits from Yellowstone and Grand Teton National Parks. This is contribution 368 of the U.S. Geological Survey Amphibian Research and Monitoring Initiative.

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CO₂ Exchange of Native and Exotic Plant Communities in Gardiner Basin, Yellowstone National Park

C. Eric Hellquist¹, Douglas Frank², Kimberly W. Ryan³, and E. William Hamilton III⁴

¹ Department of Biological Sciences, State University of New York Oswego, Oswego NY 13126, 315-312-2523, eric.hellquist@oswego.edu

² Department of Biology, Syracuse University, Syracuse NY 13244, 315-443-4529, dafrank@syr.edu

³ Department of Biological Sciences, State University of New York Oswego, Oswego NY 13126, kimwahl001@gmail.com

⁴ Department of Biology, Washington and Lee University, Lexington VA 24450, 540-458-8890, hamiltone@wlu.edu

Abstract

Exotic plant species change patterns of succession that affect the rates of integrated plant and soil feedbacks. Gardiner Basin (Yellowstone National Park) is an important migratory corridor that has been impacted by agricultural disturbance and subsequent colonization by non-native mustards and grasses. These plant invasions have degraded habitat quality in Gardiner Basin to such an extent that a vegetation restoration project is now underway. We studied carbon dioxide (CO₂) exchange patterns to understand functional differences between adjacent native and exotic plant communities in Gardiner Basin. We sampled dry sites including former agricultural fields ($n = 2$) and mudslides ($n = 2$), as well as moist streambank sites ($n = 2$) that pass through the former agricultural fields. Net ecosystem productivity (NEP) was low ($< 2.0 \mu\text{mol CO}_2/\text{m}^2\text{s}$) in dry sites and was not different ($p > 0.05$) between native and exotic plots. However, along streambanks, NEP in native plots was 2–3 times greater than in exotic plots ($p < 0.05$). Very little CO₂ was released via soil respiration in dry soils (ca. -0.6 to $-2.0 \mu\text{mol CO}_2/\text{m}^2\text{s}$). There was no difference in soil respiration between native and exotic plots in former agricultural field or mudslide sites. However, native plots along streambanks had soil respiration rates that were approximately five times greater than exotic plots. Despite their dominance in Gardiner Basin habitats, exotic plant communities did not have consistent CO₂ exchange patterns in relation to their native neighbors. Despite the lack of consistent generalizations related to CO₂ exchange processes in Gardiner Basin, these data provide site-specific background that can contribute to assessing the progress and the effectiveness of current vegetation restoration protocols being tested in Gardiner Basin.

Introduction

Integrated interactions between aboveground (plants) and belowground (plant roots, archaea, bacteria, fungi, and invertebrates) communities are recognized as important determinants of ecological relationships in terrestrial environments (Reynolds et al. 2003; Wardle et al. 2004; Bardgett and Wardle 2010). Tens of thousands of plants rely on symbiotic relationships with bacteria and fungi for growth (van der Heijden et al. 2008). Plants also rely on microbially mediated biochemical processes to release nutrients into the soil for eventual uptake for growth (e.g., nitrogen; van der Heijden et al. 2008). The introduction of exotic plants can alter plant-soil feedbacks (Bardgett and Wardle 2010; Kardol and Wardle 2010), which has important implications for restoration strategies of impacted habitats (D'Antonio and Meyerson 2002; Kardol and Wardle 2010).

Measuring transitions in plant-soil feedback processes can provide managers with an understanding of the effects of exotic species on ecosystem function (Callaham et al. 2008; Eviner and Hawkes 2008; Heneghan et al. 2008; Kardol and Wardle 2010). If changes in plant-soil feedbacks are persistent following invasion, control, and during restoration, these ecological legacies must be overcome for habitat restoration to be successful (D'Antonio and Meyerson 2002; D'Antonio and Hobbie 2005). Knowledge of ecological dynamics within native and exotic communities can provide important insight into the efficacy of plant removal and restoration techniques (D'Antonio and Meyerson 2002; Kulmatiski et al. 2006; Eviner and Hawkes 2008; Heneghan et al. 2008; Kardol and Wardle 2010). Evaluating ecosystem function as well as community composition provides managers with a basis for assessing the progress of vegetation restoration from multiple

scales at sites with unique ecological contexts (Eviner and Hawkes 2008; Kardol and Wardle 2010).

The Gardiner Basin of Yellowstone National Park (YNP) extends from the vicinity of Gardiner, Montana, along the Yellowstone River northward to Yankee Jim Canyon. This area is an important wildlife corridor for migratory ungulates, including bison, elk, and pronghorn (National Park Service 2005). The use of Gardiner Basin for agriculture through the 1930s has left a lasting ecological legacy on the landscape (National Park Service 2005). Tilling and irrigation of rangeland facilitated the introduction of several Eurasian plant species into Gardiner Basin. Today, the Gardiner Basin is the most invaded landscape in YNP, and its grasslands are characterized by stands of *Alyssum desertorum* Stapf (desert alysium, an invasive mustard), *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass), *Bromus tectorum* L. (cheatgrass), and *Eremopyrum triticeum* (Gaertn.) Nevski (annual wheatgrass), among several other exotic mustards, grasses, and chenopods (National Park Service 2005). The establishment of these invasive plants has altered the community and ecosystem properties of the basin and has degraded the rangeland for migratory ungulates such as pronghorn (National Park Service 2005). In order to enhance the quality of the Gardiner Basin migration corridor, the National Park Service and its partners have initiated a comprehensive habitat restoration effort. Restoration strategies include the removal of exotic species, improving soil quality, and replanting native plant species (National Park Service 2005).

Despite the central importance of plant-soil feedback relationships in terrestrial ecology and the utility of combining plant-soil feedback studies with restoration ecology, few studies have brought these related fields together (Eviner and Hawkes 2008; Kardol and Wardle 2010). Our ongoing research is studying linkages between plant community succession and plant-soil feedback in the context of vegetation restoration within Gardiner Basin. In this paper, we summarize data related to CO₂ exchange in adjacent native and exotic plant communities to understand how ecosystem function related to carbon exchange is related to plant community composition. Understanding patterns of aboveground and belowground interactions prior to comprehensive vegetation restoration will provide benchmarks for understanding the efficacy of restoration protocols in Gardiner Basin grasslands.

Materials and Methods

We sampled six sites across Gardiner Basin (vicinity of 45°2'3'' N; 110°44'23'' W) in May–July 2007. We classified sites into two categories based on plant biomass and soil moisture. Low-production, dry sites were located in agricultural fields and mudslides while high-production, moist sites were found along Landslide Creek and Stephens Creek. Within each site, distinct community patches were identified that were dominated by native and exotic species. These sampling locations were established in immediate proximity to each other to control for substrate conditions. Paired exotic and native plant communities differed between sites. At dry sites, native species consisted of *Carex duriuscula* C. A. Mey. (*Carex stenophylla* Wahlenb.), *Poa secunda* J. Presl., and *Pascopyrum smithii* (Rydb.) A. Löve, while exotic communities consisted of *Agropyron cristatum* and *Alyssum desertorum*. At moist, mesic locations in close proximity to streams (Landslide Creek and Stephens Creek), native communities were characterized by *Juncus balticus* Willd. and *P. smithii*, while *Elymus repens* (L.) Gould and *Bromus tectorum* dominated exotic plots.

We measured three CO₂ exchange parameters (net ecosystem production, ecosystem respiration, and soil respiration). Net ecosystem productivity (NEP) and ecosystem respiration (R_{eco}) was measured within a clear chamber (50 cm x 50 cm x 50 cm) made of transparent, non-CO₂-absorbing polycarbonate plastic (Risch and Frank 2006, 2007) mounted on a frame inserted into the ground. The CO₂ exchange chamber was attached to a closed pathway portable infrared gas analyzer (LI-6262, Licor Biosciences Inc., Lincoln, Nebraska, USA). Methods related to chamber temperature, soil temperature, and photosynthetic photon flux density (PPFD) followed Risch and Frank (2006, 2007). R_{eco} was measured in the same chamber as NEP with a shade cloth covering the entire chamber to block all ambient light. Non-CO₂-absorbing polycarbonate cylindrical chambers (20 cm high x 10 cm diameter) were fitted within two 10-cm diameter PVC collars anchored in the soil to measure soil respiration (R_{soil}). All vegetation was clipped to the soil surface within each PVC ring so that no aboveground CO₂ exchange was occurring through plant tissue. Two replicate R_{soil} measurements were taken at each circular subplot (n = 4) and averaged.

CO₂ exchange parameters were measured simultaneously in paired, equilibrated CO₂ chambers for 150 s between 0930 and 1530 hrs. CO₂ exchange

was calculated by averaging two CO_2 fluxes during measurement intervals of 120 s each. Between each sampling period chambers were vented until the internal chamber CO_2 concentrations returned to ambient levels. Calculations of NEP, R_{eco} , and R_{soil} followed Risch and Frank (2006, 2007).

Results

There were differences in CO_2 exchange in native and invaded plots for NEP and R_{soil} when all sites had their CO_2 flux data pooled into native and invaded plant communities (Figure 1). There were no differences for R_{eco} (Figure 1). However, when sites were examined individually, CO_2 fluxes varied between native and invaded plots between sites (Figures 2–5).

In the former agricultural fields and vicinity, NEP was minimal (range of mean values 0.54 to 0.52 $\mu\text{mol}/\text{m}^2\text{s}$), with no differences between invaded (*Alyssum* and *Agropyron cristatum*) and native plots (*Poa* and *Carex*; paired t-test; $p \geq 0.30$). However, in communities located along streambanks where soil moisture was higher, NEP was positive, indicating a net uptake of CO_2 by vegetation (Figure 2). At Landslide and Stephens Creek, uptake of CO_2 by native plants (*Juncus* and *Pascopyrum*) was approximately two to three times higher than plots with invasive plants (*Elymus repens* and *Bromus tectorum*; Figure 2).

Ecosystem respiration fluxes were context dependent both within and between sites. The two low-productivity sites did not show a difference for R_{eco} ($p = 0.70$ and $p =$

0.31, paired t-tests, range of means 1.84–2.44 $\mu\text{mol}/\text{m}^2\text{s}$). However, on the slopes of mudslide deposits (low biomass, dry sites) invaded plots had significantly greater overall CO_2 release ($p < 0.0001$ and $p = 0.002$, paired t-test) than native plots (Figure 3). At the more mesic sites (Landslide Creek), R_{eco} was greater in native plots than exotic plots ($p = 0.05$, paired t-test; Figure 4). However, at Stephens Creek there was no difference between R_{eco} fluxes between communities ($p = 0.82$, paired t-test; Figure 4).

Soil respiration at low biomass, dry sites (agricultural fields and mudslides) was minimal (data not shown). There were no differences in native and exotic plots ($p > 0.05$, range of means 0.62–1.95 $\mu\text{mol}/\text{m}^2\text{s}$) at dry sites. At the moister Landslide Creek site, R_{soil} was approximately four times greater than the invaded plots (Figure 5). At Stephens Creek, there were no differences in R_{soil} between the native and invaded communities (Figure 5). Carbon fluxes at Stephens Creek were much lower than Landslide Creek ($p < 0.001$, paired t-test; Figure 5).

Discussion

Gardiner Basin has the highest concentration of exotic plants in YNP, and the proliferation of species such as *Alyssum desertorum* is having consequences across scales of ecological interactions. Species traits uniquely contribute to ecological interactions and ecosystem processes (Bardgett and Wardle 2010 and references therein). Due to the unique circumstances of each ecosystem, plant-soil feedbacks are defined by the attributes of the species (plants and microbes) that are present over the course succession

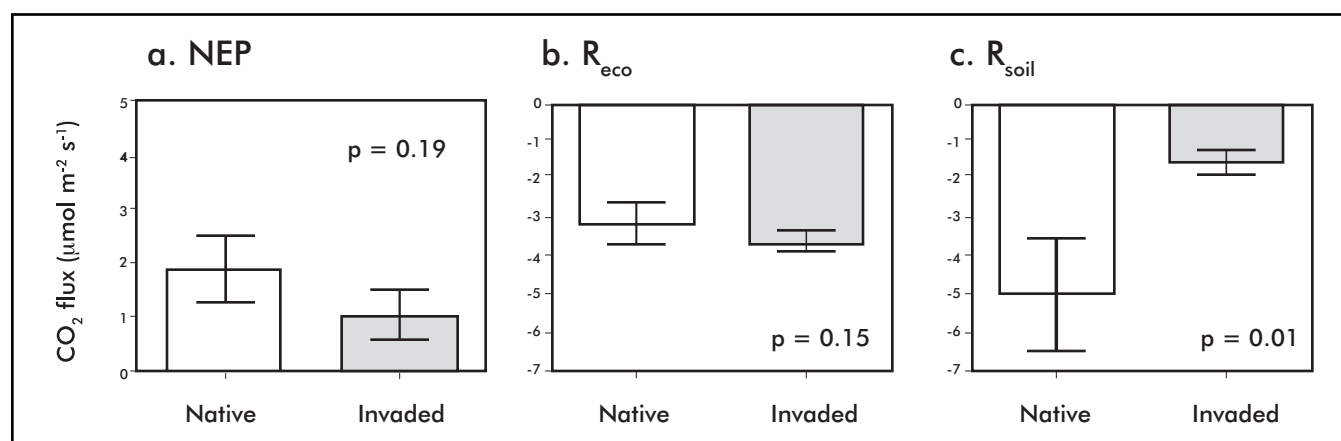


Figure 1. CO_2 fluxes in native and invaded plots pooled across all sites in Gardiner Basin. a) Net ecosystem productivity (net CO_2 flux into plant biomass); b) Ecosystem respiration (CO_2 flux from plants and soil into the atmosphere); c) Soil respiration (CO_2 flux from plant roots and soil organisms into the atmosphere). R_{soil} values presented are from the small cylindrical chamber and are not calibrated with the volume of the cuboidal chamber used for NEP and R_{eco} fluxes. P-values are for paired t-tests. Error bars are standard error of the mean.

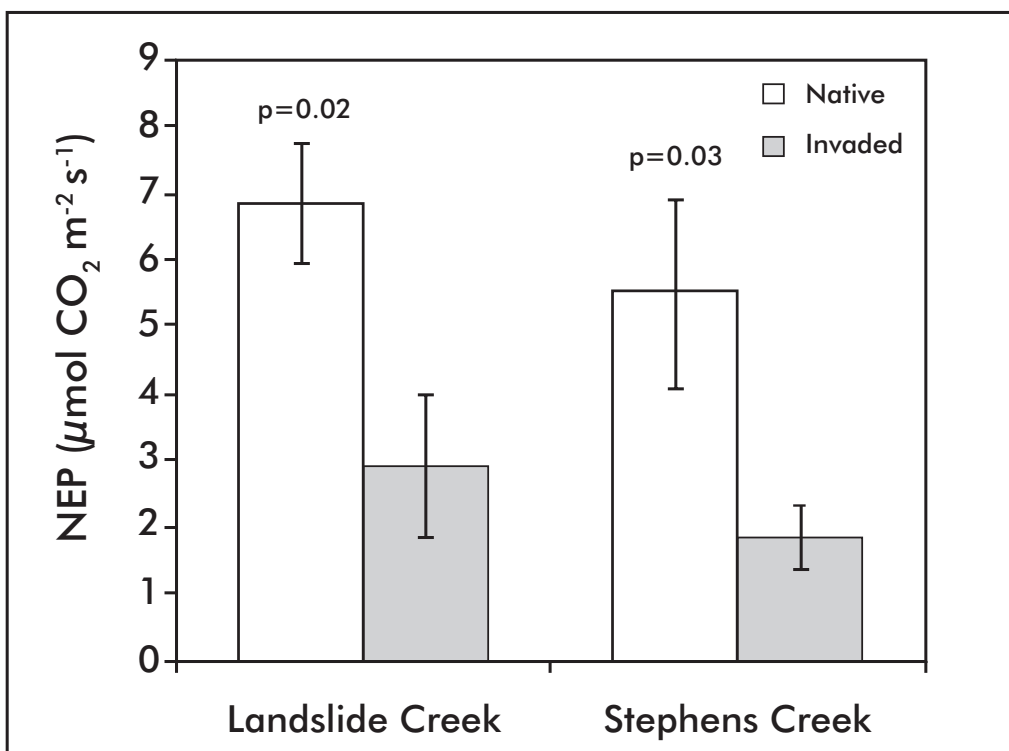


Figure 2. Net ecosystem productivity (NEP) for two streamside sites in Gardiner Basin. P-values are for paired t-tests comparing native to invaded plots within in each site. Error bars as in Figure 1.

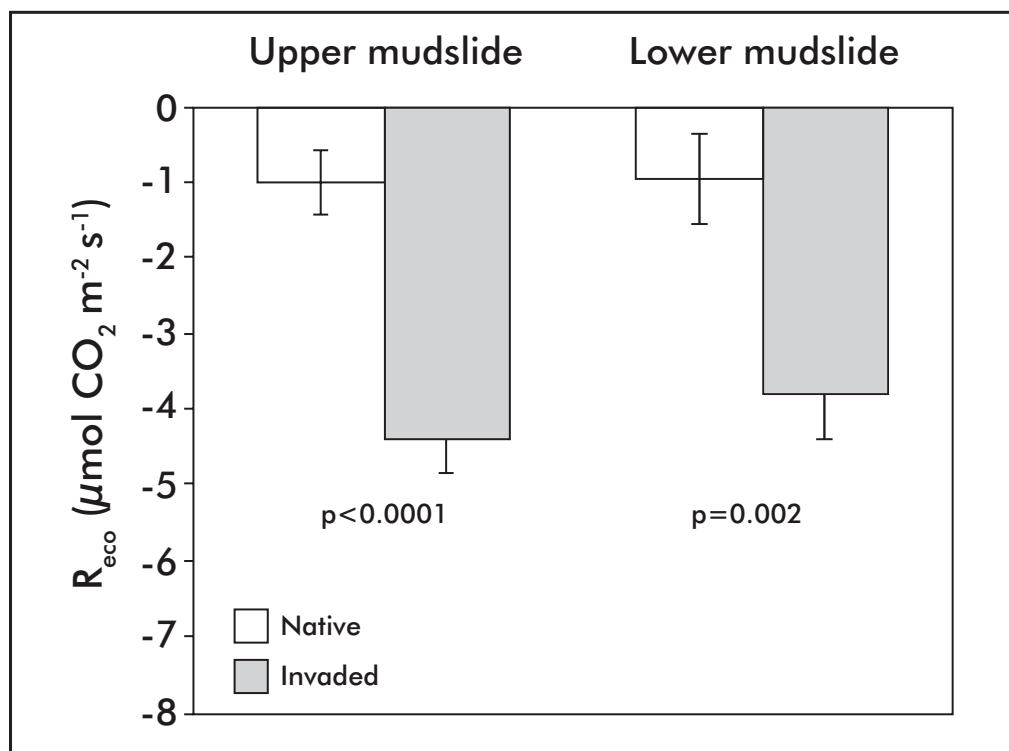


Figure 3. Ecosystem respiration (R_{eco}) for two dry sites in Gardiner Basin located on the mudslide deposits south of Landslide Creek. P-values are for paired t-tests comparing native to invaded plots within in each site. Error bars as in Figure 1.

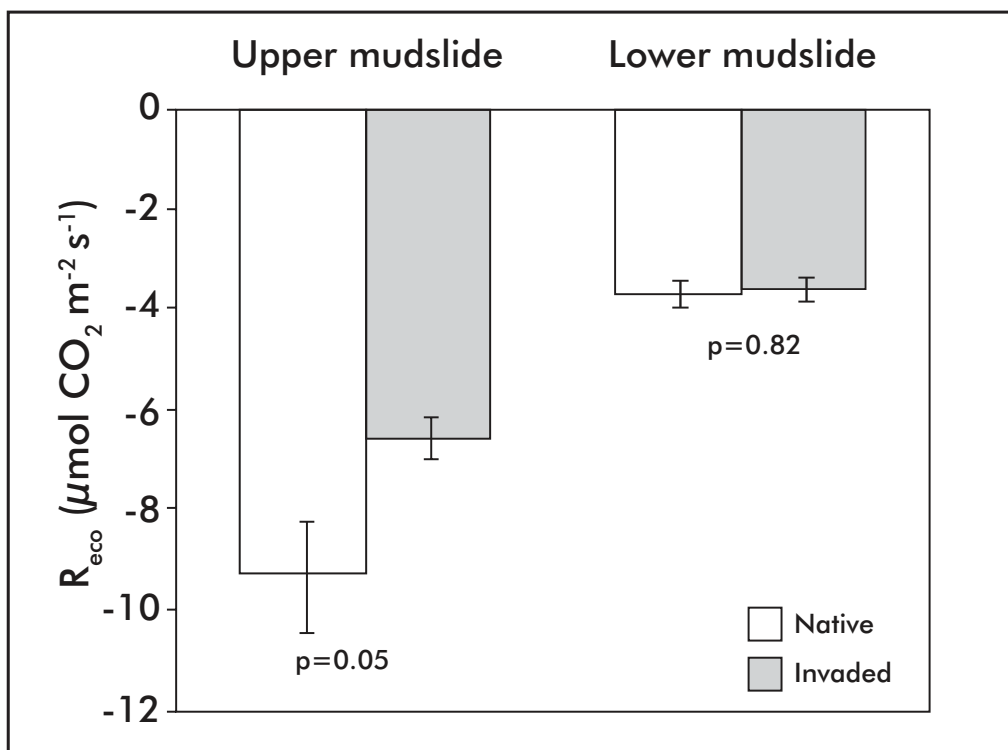


Figure 4. Ecosystem respiration (R_{eco}) for two streamside sites in Gardiner Basin. P-values are for paired t-tests comparing native to invaded plots within in each site. Error bars as in Figure 1.

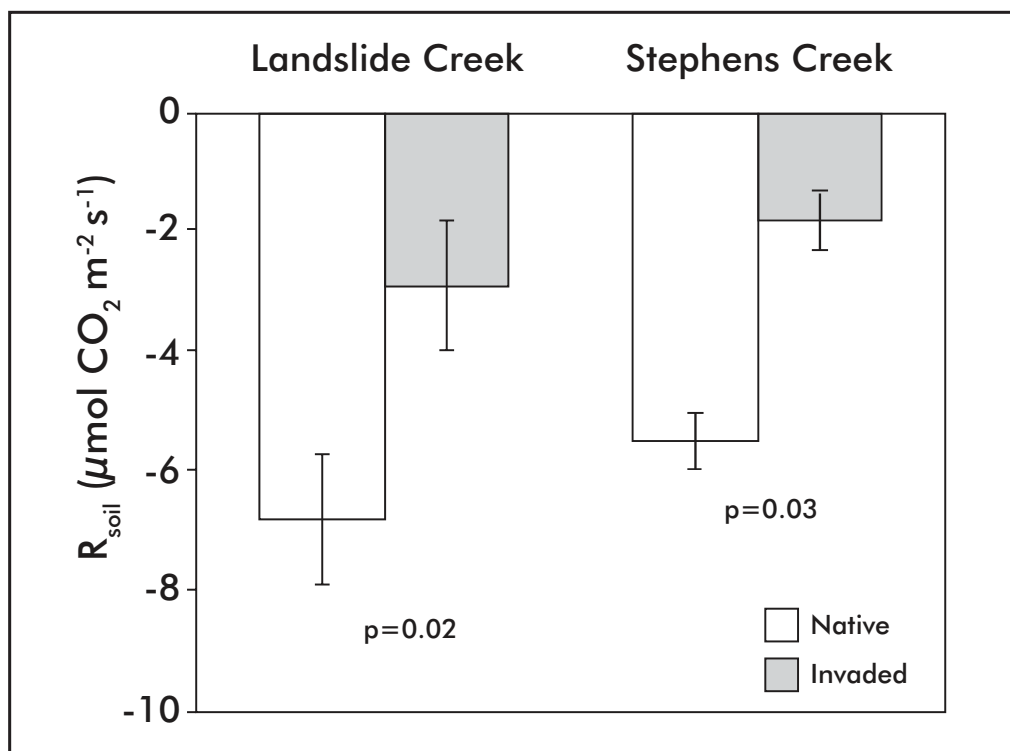


Figure 5. Soil respiration (R_{soil}) for two high plant biomass sites in Gardiner Basin. P-values are for paired t-tests comparing native to invaded plots within each site. Error bars as in Figure 1.

at any one site (Eviner and Hawkes 2008; van der Heijden et al. 2008; Bardgett and Wardle 2010; Kardol and Wardle 2010). Restoring plant communities will depend on not only removing exotic plant species, but also on successfully restoring belowground interactions (Eviner and Hawkes 2008; Kardol and Wardle 2010). Therefore, understanding species traits that influence ecosystem responses (such as CO_2 exchange) will contribute to understanding current ecosystem function in habitats where restoration is desired. Our data describe components of CO_2 exchange influenced by plant-soil community feedbacks in relation to community composition that can be measured over time as plant restoration (i.e., human-mediated succession) proceeds so that ecologists and managers can evaluate ecosystem recovery from plant invasion.

Plants affect carbon cycling across ecological scales through rates of photosynthesis, litter decomposition, soil respiration, and net ecosystem productivity (Raich and Tufekcioglu 2000; Robertson and Paul 2000; Huxman et al. 2004). The extent of these processes will vary based on the plant (Bardgett and Wardle 2010; Kardol and Wardle 2010) and microbial (Reynolds et al. 2003; van der Heijden et al. 2008) community composition as well as environmental conditions that may change over time (Eviner and Hawkes 2008). The relative importance of CO_2 uptake will depend on the relative carbon exchange capacities (photosynthesis and respiration) of plants in relation to the magnitude of belowground respiratory processes related to decomposition of plant litter. Thus, plant attributes such as litter quality affect nutrient availability within soils (Ehrenfeld 2003, 2004; Bardgett and Wardle 2010) as well as CO_2 exchange patterns.

When pooled across sites ($n = 6$) in the Gardiner Basin, native plots had greater carbon exchange for NEP and R_{soil} (Figure 1). However, when sites were examined individually, relationships between CO_2 exchange processes between native and invasive plant communities were not consistent (Figures 2–4). Carbon exchange processes varied across Gardiner Basin as well as within sites at sample plots that were only meters apart. At both of these scales, plant communities and presumably the associated soil communities were different. The variation in CO_2 fluxes observed was expected based on the role of variable soil conditions (e.g., moisture; Huxman et al. 2004; Risch and Frank 2007), plant species characteristics, and plant-soil feedbacks (Wardle et al. 2004; Bardgett and Wardle 2010; Kardol and Wardle 2010) that can influence rates of carbon exchange (Bardgett and Wardle 2010).

Higher rates of photosynthesis can contribute to the success of invasive plants (Kloeppel and Abrams 1995; Pattison et al. 1998; McAlpine et al. 2008) and would be expected to lead to higher rates of NEP on invaded plots depending on the abundance of respiring microbes in the soil. In Gardiner Basin, NEP (net fluxes of CO_2 into plant biomass) was variable across the landscape, but was greatly reduced in the former agricultural fields and mudflow sites. Meanwhile, streamside locations had NEP values that were higher in native compared to invaded plots (Figure 2). Former agricultural fields (the target of vegetation restoration) had very little net CO_2 intake, indicating that overall photosynthetic capacity of plants (native or introduced) at these sites was less than in streamside habitats. In addition, soils of the former agricultural fields (native or invaded plots) respired very little CO_2 . The lack of carbon flux in the degraded agricultural soils is related to the physiology of the resident plants in combination with reduced organic matter quantity and microbial abundance in these soils (Hamilton et al. unpublished data). In semi-arid Arizona grasslands, NEP was higher for native plants (Huxman et al. 2004), but in a later study (Hamerlynck et al. 2010) the same invasive grass (*Eragrostis lehmanniana*) was found to have greater NEP values than a native grass (*Muhlenbergia porteri*). Hamerlynck et al. (2010) concluded that increased soil moisture under the canopy of invasive *Eragrostis* facilitated carbon uptake and growth during seasonal dry periods.

In Gardiner Basin, R_{eco} and R_{soil} showed greater CO_2 fluxes in native plots with *Juncus balticus* compared to the exotic *Elymus repens* at Landslide Creek. However, at Stephens Creek where *Pascopyrum smithii* was paired with exotic *Bromus tectorum*, CO_2 fluxes were either equivalent (R_{soil}) or there was greater R_{eco} in the invaded plots (Figure 4). Huxman et al. (2004) found that R_{soil} was elevated in plots with exotic *Eragrostis* that were exposed to precipitation pulses. Higher R_{soil} rates were also observed in invaded grassland communities in Hawaii (Litton et al. 2008). In our work, the magnitude of R_{soil} was context dependent and likely related to the suitability of soil conditions (such as soil moisture and organic matter content) for microbial growth.

The rates of carbon released during microbial respiration and decomposition will depend on the quality and quantity of organic matter in soils (Luo and Zhou 2006). Attributes of exotic plants including litter quality have been linked to changes in microbial communities (Kourtev et al. 2002; Duda et al. 2003; Holly et al.

2008). Initial vegetation restoration efforts in Gardiner Basin have begun in three exclosures (3.0–10.5 hectares [ha]) situated on former agricultural fields. Initial steps of the restoration are focused on removing exotics followed by restoring soil organic matter. Once organic matter has accumulated in the soils, native vegetation will be planted. To date, exotic species have been removed in the exclosures and ‘Hays’ barley (*Hordeum vulgare* L.) has been established (2009–2010). By augmenting the soils of the agricultural fields with barley detritus, organic matter subsidies should increase carbon fluxes on these fields. Planting of Hays barley has increased soil organic matter by approximately 20 percent in restoration exclosures and should positively affect the abundance and diversity of microbial communities (Hamilton et al. unpublished data). Improved organic matter quality over the course of restoration should lead to increased microbial biomass, enhanced decomposition, and higher rates of R_{eco} and R_{soil} as restoration proceeds.

Differences in our carbon exchange patterns can be explained partially by belowground communities. Bacterial abundance data from Gardiner Basin indicates that Landslide Creek has over twice the microbial carbon of the agricultural fields, mudslides, or Stephens Creek sites (Hamilton et al. unpublished data). In poor quality soils like the former agricultural fields, bacterially mediated processes that contribute to plant productivity (e.g., nitrogen fixation, or release of nutrients through decomposition) should be high because of the scarcity of nutrients and the importance of bacterial metabolism necessary to release nutrients for plants (van der Heijden et al. 2008). Our Gardiner Basin data show greater bacterial diversity in native plant soils than invaded soils across our sites based on the abundance of molecular markers in the soil as determined by quantitative polymerase chain reaction methods (Hamilton et al. unpublished data).

Our ongoing research is investigating how plant and microbial identity determine ecosystem function (carbon and nitrogen allocation) during restoration. Understanding how exotic plant species influence ecosystem processes determined by plant-soil feedbacks will enhance the effectiveness of vegetation restoration in Gardiner Basin. We anticipate that patterns of microbial abundance and community composition determined with molecular techniques in the Hamilton laboratory will contribute to our understanding of site-specific carbon fluxes. The variation in CO_2 fluxes measured in this study across spatially complex habitats has been noted in other YNP

CO_2 exchange studies (e.g., Risch and Frank 2006). The importance of ecological context (species composition and habitat heterogeneity) are critical for determining the direction and magnitude of plant-soil interactions but can limit the identification of unifying generalizations (Eviner and Hawkes 2008; Kardol and Wardle 2010). However, generalizations can oversimplify and mislead restoration interventions (Eviner and Hawkes 2008). Contrary to our usual search for generalities, for restoration projects to be successful, an understanding of ecological interactions and functions unique to each restoration site are critical (Eviner and Hawkes 2008; Kardol and Wardle 2010). The success of restoration projects will be greatly enhanced by cooperative efforts of ecologists and land managers who can work together to create restoration strategies suited to the unique suite of interacting ecological processes that are characteristic of each restoration site (Eviner and Hawkes 2008). We hope that our data that links aboveground and belowground processes to vegetation restoration will help managers assess habitat restoration strategies in Gardiner Basin, other YNP grasslands, and similar locations in the Greater Yellowstone Ecosystem.

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Monitoring Insect and Disease in Whitebark Pine (*Pinus albicaulis*) in the Greater Yellowstone Ecosystem

Cathie Jean¹, Erin Shanahan², Rob Daley³, Shannon Podruzny⁴, Jodie Canfield⁵, Gregg DeNitto⁶, Dan Reinhart⁷ and Chuck Schwartz⁸

¹ Greater Yellowstone Network, National Park Service, 2327 University Way, Suite 2, Bozeman, MT 59715, 406-994-7530, cathie_jean@nps.gov

² Greater Yellowstone Network, National Park Service, 2327 University Way, Suite 2, Bozeman, MT 59715, 406-581-3398, erin_shanahan@nps.gov

³ Greater Yellowstone Network, National Park Service, 2327 University Way, Suite 2, Bozeman, MT 59715, 406-994-4421, rob_daley@nps.gov

⁴ Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, USGS, 2327 University Way, Suite 2, Bozeman, MT 59715, 406-994-2607, shannon_podruzny@usgs.gov

⁵ Gallatin National Forest, U.S. Forest Service, PO Box 130, Bozeman, MT 59771, 406-587-6739, jecanfield@fs.fed.us

⁶ USDA Forest Service Forest Health Protection, PO Box 7669, Missoula, MT 59807, 406-329-3637, gdenitto@fs.fed.us

⁷ Yellowstone National Park, National Park Service, PO Box 168, Mammoth, WY 82190, 307-344-2145, dan_reinhart@nps.gov

⁸ Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, USGS, 2327 University Way, Suite 2, Bozeman, MT 59715, 406-994-5043, chuck_schwartz@usgs.gov

Abstract

White pine blister rust (WPBR) and a recent mountain pine beetle (MPB) outbreak associated with above normal winter temperatures jeopardize whitebark pine in the Greater Yellowstone Ecosystem (GYE). In response to concerns over the health of this keystone species, a long-term interagency monitoring program unified through the Greater Yellowstone Coordinating Committee was initiated to assess the status and trends of whitebark pine trees > 1.4 meters (m) tall. Between 2004 and 2007 we randomly sampled 150 stands with whitebark pine and established 176 permanent transects in which 4,774 individual trees > 1.4 m tall were marked and are being monitored over time. Based on data from our initial establishment of transects, we estimated the WPBR infection rate as 0.20 ($\pm$ 0.037 se). We began resurveying transects in 2008 and the most recent assessment of tree status took place in 2009 and 2010 when all transects were resurveyed for tree mortality and evidence of mountain pine beetle infestation. Based on this resurvey, we estimated that near the end of 2010, 16.4 percent of all marked whitebark pine trees within our monitoring transects had died and that mortality was much greater in trees > 10 cm at diameter breast height. Barring severely cold temperatures sufficient to kill larva, high levels of MPB may continue to threaten whitebark pine until the large diameter host trees are diminished. Long-term monitoring will record these changes through time.

Introduction

Insect and disease outbreaks in forest ecosystems can be linked to local weather and regional climate patterns. Warm temperatures and the loss of extreme cold days reduce winter overkill of insects, speed up life cycles, and lead to range expansions (Logan et al. 2003). When favorable conditions exist, mountain pine beetle (*Dendroctonus ponderosae*) populations can quickly increase to epidemic proportions.

The dispersal and germination of white pine blister rust (*Cronartium ribicola*) is also linked to weather and

climate. Dispersal of the fungus is influenced by wind, temperature, and humidity (Van Arsdell et al. 2006). White pine blister rust germination and infection of pine occur when nighttime temperatures stay cool (below 68°F), free moisture is available on the needle surface, and relative humidity is high for at least two consecutive days (Koteen 1999). The low natural resistance of five-needle pines, including whitebark pine (*Pinus albicaulis*), along with favorable climatic conditions, has enabled white pine

blister rust to spread to higher elevations and more recently to a greater number of pine tree species (Ashton 2010).

The combined effects of insect and disease on whitebark pine in the Greater Yellowstone Ecosystem (GYE) have research scientists, plant ecologists, and wildlife biologists working together to address the status and trends of this important tree species. Through the Greater Yellowstone Coordinating Committee, the Greater Yellowstone Network, and the United States Geological Survey

(USGS) Interagency Grizzly Bear Study Team, experts have completed an unprecedented level of monitoring to document and report on levels of blister rust infection and the proportion of trees dying during the current outbreak of mountain pine beetle. This report summarizes monitoring data collected from 2004 through 2007, the sampling period when transects were first established, and from 2007 through 2010, the sampling period when transects were resurveyed for trend information.

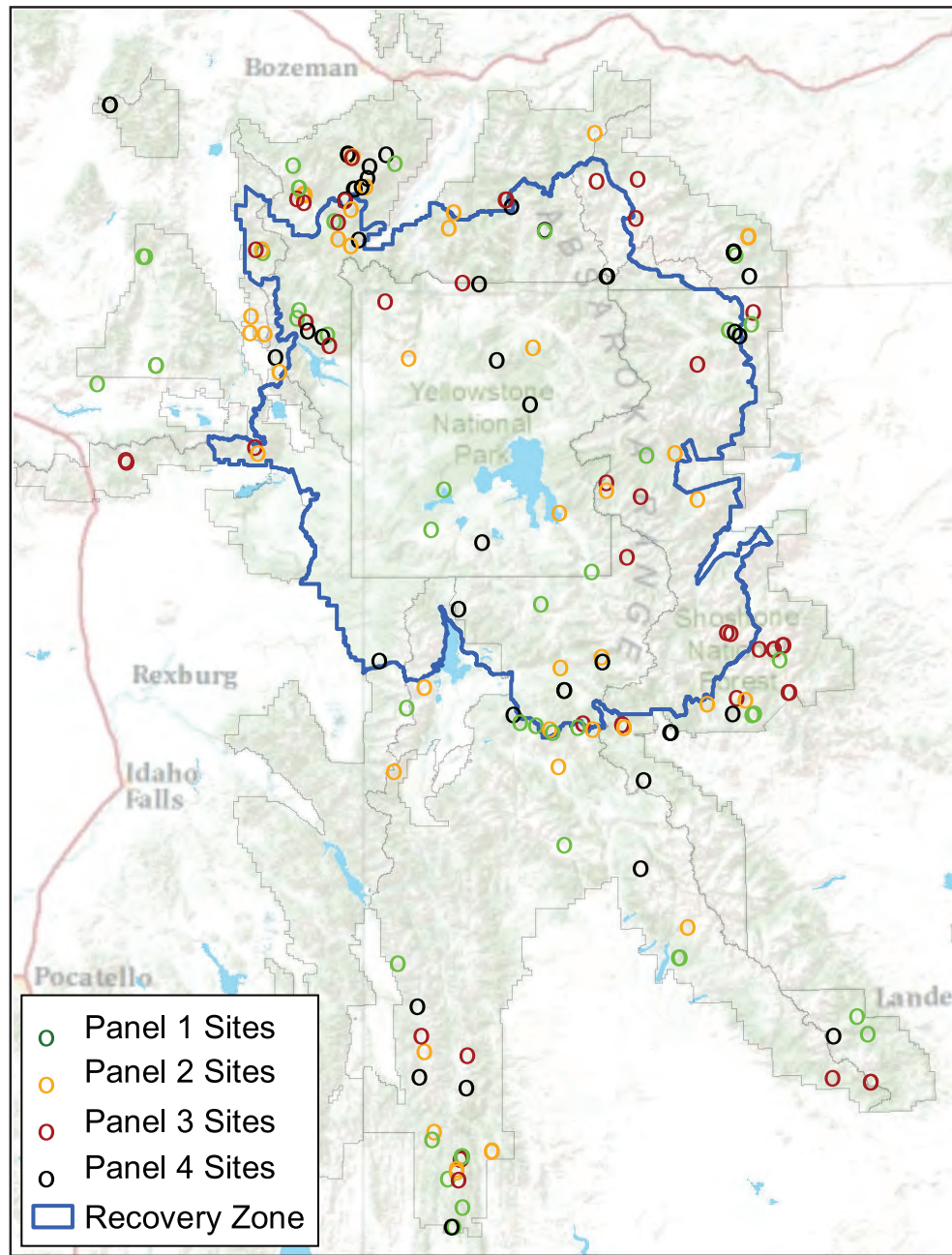


Figure 1. Location of whitebark pine survey transects ($n = 176$) in the Greater Yellowstone Ecosystem in Idaho, Montana, and Wyoming. A panel is a subset of the total sample size that was visited within a given year.



Figure 2. Live, dead, and recently dead whitebark pine in the Greater Yellowstone Ecosystem. National Park Service photo.

Purpose and Background

The purpose of our long-term monitoring program is to determine the status and trends of whitebark pine forests throughout the GYE. To date, the principle focus of the Interagency Whitebark Pine Monitoring protocol (Greater Yellowstone Whitebark Pine Monitoring Working Group 2007) has been the presence and severity of white pine blister rust and mortality of whitebark pine > 1.4 m tall.

Our target population is all whitebark pine (regardless of habitat type) in the GYE on federal lands (six national forests and two national parks; Figures 1 and 2). The sample frame includes forest stands ≥ 2.5 hectares (ha) within and outside of the U.S. Fish and Wildlife Service's Grizzly Bear Recovery Zone (GBRZ) that have a component of whitebark pine in the species composition. Forest stands that burned in the 1988 wildfires or later were excluded from the sample frame, as these stands were considered too young to have whitebark pine trees > 1.4 m tall.

We selected our sampling units using a two-staged probability-based sampling design that allows for statistical inference to the entire GYE. Our primary sampling units are randomly selected forest stands and our secondary sampling units are 10 x 50 m randomly selected transects from each stand. At least one whitebark pine tree > 1.4 m tall was required for a permanent transect to be established.

Between the years 2004 and 2007, we established 176 permanent transects and permanently marked 4,772

individual live trees > 1.4 m tall so that we could follow the incidence of white pine blister rust and survivorship of individual trees over time. Within each 5 x 10 m transect, we measured diameter breast height (DBH) of all permanently tagged live whitebark pine trees. We also measured the DBH of standing dead and recently dead whitebark pine trees > 1.4 m within the transect, but we did not permanently tag these trees.

Each live whitebark pine tree > 1.4 m tall was surveyed for white pine blister rust cankers based on aecia (the active, fruiting body of the canker), which is the definitive symptom of white pine blister rust (Tomback et al. 2005). We also surveyed for auxiliary signs of infection, including rodent chewing, branch flagging, swelling, roughened bark, and oozing sap (Hoff 1992). If three of the five auxiliary signs occurred in the same area on a tree, that location was noted as having white pine blister rust infection. The numbers of branch and trunk cankers were recorded for each of the tree sections. For analysis purposes, we considered an individual whitebark pine tree infected with white pine blister rust if one canker (aecia or three auxiliary signs) on either the tree bole or branch was documented/observed.

We also surveyed trees for evidence of mountain pine beetle infestation. We considered an individual whitebark pine tree infested with beetles if we observed pitch tubes and/or frass on a live tree, or the presence of J-shaped beetle galleries beneath the bark of a dead tree.

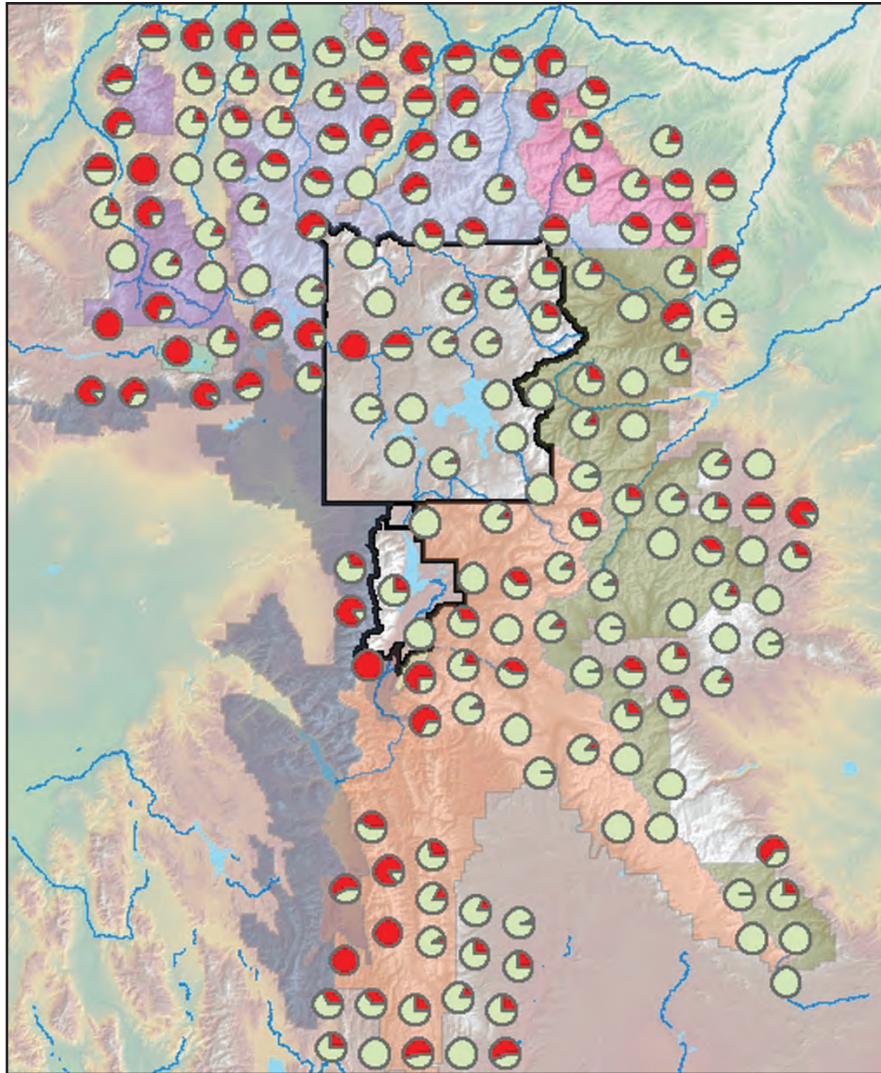


Figure 3. Proportion of whitebark pine trees (> 1.4 m tall) infected (red) and not infected (light green) with white pine blister rust at each transect within the Greater Yellowstone Ecosystem. Due to map scale, the pie charts are distributed for readability and may not be placed on the actual survey location.

Since 2008, we resurveyed transects based on a four-year rotating panel for white pine blister rust and a two-year rotating panel for mountain pine beetle. Each year we resurveyed two panels of 40–45 transects, each to capture rapid changes in tree mortality and evidence of attack during an active mountain pine beetle outbreak. During resurveys, each permanently tagged tree was evaluated for its status as live (green needles were present), recently dead (with non-green needles), or dead (needles were absent). Live trees with a fading crown were noted in the tree comment field. The most recent assessment of tree status took place in 2009 and 2010 when all transects were resurveyed for mortality and evidence of mountain pine beetle infestation.

The proportion of trees infected with white pine blister rust was calculated using a design-based ratio estimator that accounts for the total number of mapped stands within the sample frame and stratified by within and outside the GBRZ (Greater Yellowstone Whitebark Pine Monitoring Working Group 2007). We used data from repeat surveys to document rates of tree mortality. Tree mortality, expressed as a percentage, was calculated by dividing the total number of tagged dead and recently dead trees observed between the years 2007 and 2009 by the total number of live trees tagged between 2004 and 2007, and then multiplying by 100. We used data from repeat surveys to document changes in the size class distribution of live whitebark pine trees in the monitoring sample.

Table 1. Summary data from the Greater Yellowstone Ecosystem showing the increase of standing dead trees over time. Dead and recently dead trees encountered during initial transect establishment between 2004 through 2007 are untagged.

	2004–2007	2009–2010
Live trees (tagged)	4772	4189
Dead and recently dead (tagged and untagged)	888	1674
Total trees (tagged and untagged)	5660	5863
% dead and recently dead trees	16	29

Table 2. Mortality and recruitment statistics for whitebark pine trees > 1.4 m tall within permanent monitoring transects in the Greater Yellowstone Ecosystem. New recruits that have grown > 1.4 m tall since transect establishment were tagged and added to the database during resurveys.

2004–2007 transect establishment	2007–2010 resurvey results		
	Dead and recently dead counted	% mortality	New recruits added
Live trees tagged			
4772	784	16.4	238

Results

What is the proportion of trees > 1.4 m tall with white pine blister rust in the GYE? Using our design-based ratio estimator, we estimated the proportion of whitebark pine trees infected with white pine blister rust was 0.20 ($\pm$ 0.037 se) at the end of 2007 (Greater Yellowstone Whitebark Pine Monitoring Working Group 2008). Our monitoring indicated that white pine blister rust was widespread and highly variable in intensity and severity across the GYE (Figure 3).

What is the increase of standing dead trees > 1.4 m tall within our permanent monitoring transects? Using data from repeat surveys, the percentage of dead standing trees increased from 16 to 29 percent by the end of 2010 (Table 1). We derived the baseline value of 16 percent from the sum of all recently dead and completely dead trees at > 1.4 m tall that we encountered during the initial transect establishment. For example, a tree that recently died was observed with persistent non-green needles, whereas a completely dead tree had no remaining needles. We did not

reassess the status of untagged dead trees and assumed they were still standing because whitebark pine can remain standing for years or even decades after mortality.

What is the mortality in whitebark pine trees > 1.4 m tall within our permanent monitoring transects? Mortality recorded toward the end of 2010 among whitebark pine trees > 1.4 m tall that were originally tagged during transect establishment was 16.4 percent (Table 2).

How has the recent mountain pine beetle epidemic changed the size class distribution of living whitebark pine trees in the monitoring sample? We grouped the DBH of live whitebark pine trees by size class and plotted this frequency to compare the number of trees in each size class during the initial survey (2004–2007), with the most recent survey results (2009–2010; see Figure 4). The decrease in live trees was especially evident in trees > 10 cm DBH that are most susceptible to mountain pine beetle at-

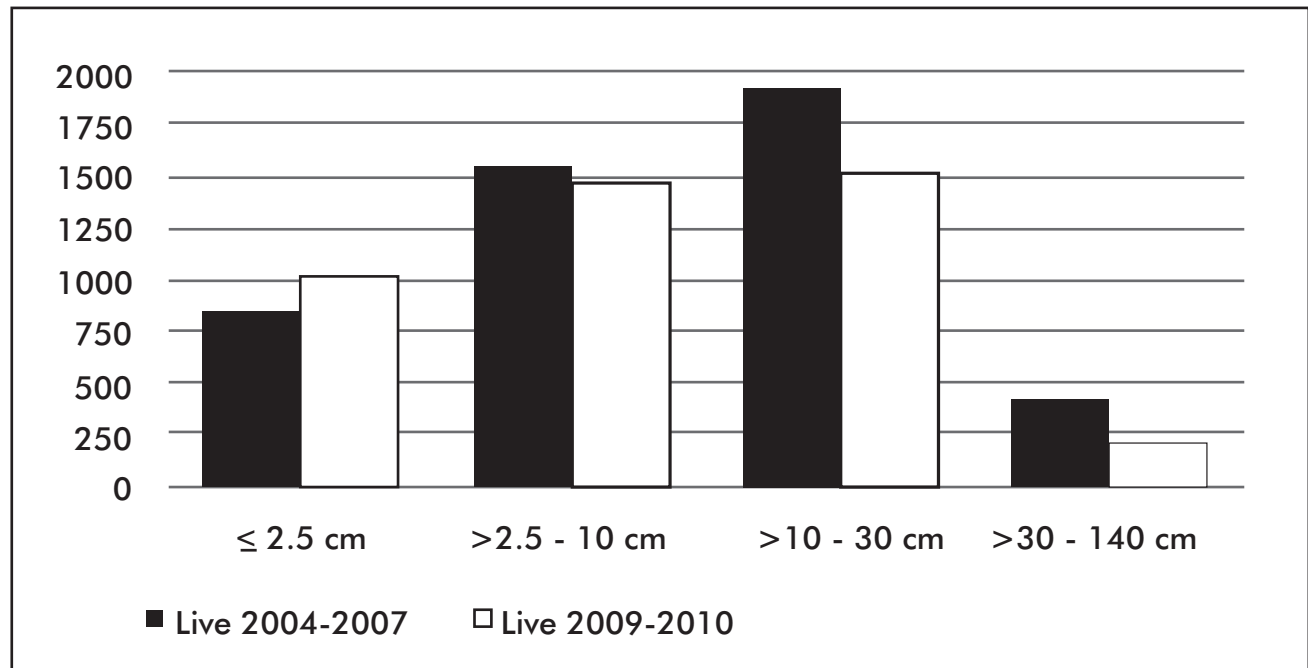


Figure 4. Change in size class distribution of whitebark pine trees >1.4 m tall between our initial survey (2004–2007) and our most recent survey (2009–2010). Data from the Greater Yellowstone Ecosystem.

tack. The increase in the number of trees ≤ 2.5 cm represents the number of trees recruited into our sample as they reached 1.4 m in height (see Table 2).

Conclusion

Weather and climate will continue to play a role in insect and disease outbreaks in forest ecosystems in the GYE. Gibson et al. (2008) anticipate beetle populations to remain high as long as weather conditions are conducive to beetle survival and/or until most mature host trees have been killed. In our monitoring transects, in 2010 a large number of live whitebark pine trees >10 cm DBH are still present (Figure 4). Trees larger than 10 cm DBH are most susceptible to mountain pine beetle attack (Furniss and Carolin 1977). Some whitebark pine surviving the current mountain pine beetle outbreak will continue to be stressed by white pine blister rust. Unlike mountain pine beetle, white pine blister rust infects all size classes. Seedlings and saplings are especially susceptible and are often killed within one to three years of infection (Schoettle and Sniezko 2007). Although not reported here, we are developing protocols to monitor trees < 1.4 m tall to track changes in white pine blister rust infection and survival within this size class.

Our whitebark pine monitoring program provides valuable information to help guide future management strategies, restoration planning, and allocation of scarce funding and other resources (Schwandt 2006; Greater Yellowstone Whitebark Pine Monitoring Working Group 2007). Moreover, the collaborative, interagency monitoring and management efforts of whitebark pine in the GYE are an effective strategy to help this important high-elevation species continue to persist across the landscape.

Suggested Citation

Jean, C., E. Shanahan, R. Daley, S. Podruzny, J. Canfield, G. DeNitto, D. Reinhart, and C. Schwartz. 2011. Monitoring Insect and Disease in Whitebark Pine (*Pinus albicaulis*) in the Greater Yellowstone Ecosystem. In *Questioning Greater Yellowstone's Future: Climate, Land Use, and Invasive Species. Proceedings of the 10th Biennial Scientific Conference on the Greater Yellowstone Ecosystem*. October 11–13, 2010, Mammoth Hot Springs Hotel, Yellowstone National Park. C. Andersen, ed., 114–120. Yellowstone National Park, WY, and Laramie, WY: Yellowstone Center for Resources and University of Wyoming William D. Ruckelshaus Institute of Environment and Natural Resources.

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Postglacial Vegetation Development in the Northern Greater Yellowstone Ecosystem

Teresa R. Krause¹ and Cathy Whitlock²

¹ Department of Earth Sciences, 200 Traphagen Hall, Montana State University, Bozeman, MT 59717, 406-994-6856, teresa.krause@msu.montana.edu

² Department of Earth Sciences, 200 Traphagen Hall, Montana State University, Bozeman, MT 59717, 406-994-6856, whitlock@montana.edu

Summary

The late-glacial to early-Holocene transition, 20,000 to 8,000 years ago, was a period of rapid environmental change in the western United States. At the beginning of this period, the Greater Yellowstone Ecosystem (GYE) supported the largest mountain glacier complex in the western United States, and ice recession after 17,000 years ago put into motion a series of biologic changes that resulted in the present-day terrestrial ecosystem. However, these biologic

events are not well understood; the goal of this study is to understand the temporal and spatial patterns of early plant community development in the northern GYE following ice recession, specifically the patterns and rates of conifer colonization in the region.

Using a network of new and existing fossil pollen records from Dailey Lake, Blacktail Pond, and Slouch Creek Pond, we reconstructed the spatial and temporal patterns of early plant community development following deglaciation in the northern GYE (Figure 1). These vegetation patterns were compared across sites, as well as to the timing of glacial recession in the GYE using established patterns of ice recession (Licciardi and Pierce 2008). Thus, we were able to determine the patterns of vegetation development, the timing of arrival of various conifer species to the GYE, and how quickly those conifer species colonized the region.

Preliminary data suggest alpine tundra communities developed first on the newly deglaciated terrain, followed by open *Picea* parkland and eventually closed subalpine forest of *Abies*, *Picea*, and *Pinus*. The order of conifer species arrival was similar across sites, with *Juniperus* arriving first, followed by *Picea*, *Abies*, *Pinus*, and lastly, *Pseudotsuga*. Rates of conifer colonization ranged from 89 meters/year for *Juniperus* to 27 meters/year for *Pinus* and *Pseudotsuga*. These preliminary results suggest that plant community development occurred quite rapidly following ice recession in the northern GYE, and that the patterns of conifer species arrival in the GYE were strongly controlled by the ecological characteristics of the individual species, with pioneer species such as *Juniperus* arriving at sites first. In addition, postglacial migration rates of conifer species were much slower than the 100 to 1,000 meter/year rates required to keep pace with projected rates of climate change (Davis and Zabinski 1992; Iverson and Prasad 2002).



Figure 1. Researchers collecting fossil pollen records.

Suggested Citation

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Direct Impacts of Changing Climate on Frozen Archaeological and Paleobiological Resources in the Greater Yellowstone Ecosystem

Craig Lee¹, Halcyon Lapoint², Michael Bergstrom³, Molly Westby⁴ and Walt Allen⁵

¹ University of Colorado, Institute of Arctic and Alpine Research, University of Colorado, UCB 450, Boulder, CO 80309, craig.lee@colorado.edu

² Custer National Forest, 1310 Main Street, Billings, MT 59105, hlapoint@fs.fed.us

³ Beartooth Ranger District, Custer National Forest, 1310 Main Street, Billings, MT 59105, mbergstrom@fs.fed.us

⁴ U.S. Forest Service, Rocky Mountain Region, 740 Simms Street, Golden, CO 80401, mwestby@fs.fed.us

⁵ Gallatin National Forest, 9900 Fish Hatchery Road, Bozeman, MT 59715, wallen@fs.fed.us

Abstract

As the Earth's climate warms, archaeological and paleobiological materials are being discovered in areas of melting perennial snow and ice. Although artifacts have occasionally been found in association with glaciers, in North America they have primarily been discovered in association with relatively static snow banks, or "ice patches." Some ice patches were used prehistorically by Native Americans to hunt game animals, for example, bighorn sheep and bison that were attracted to the locations. Preserved organic artifacts that might result from such encounters include arrows, darts, sinew lashing and fletching, as well as basketry, clothing, and cordage. The stable ice in these features retards decay and has kept otherwise perishable materials suspended in virtually unaltered states for millennia. Once released from this protective environment, arrested taphonomic processes resume and organic artifacts rapidly decompose. Ice patch discoveries within the Greater Yellowstone Ecosystem (GYE) include a complete atlatl dart foreshaft, dart and arrow shaft fragments, chipped stone tools, and processed animal remains. The discoveries offer important insights into alpine paleoecology and the use of high-elevation environments by prehistoric humans. Ice patch archaeology is a nascent field in North America, and the GYE ice patches are the most intensively studied in the conterminous United States. This paper: 1) provides a review of the global state of ice patch archaeology; 2) reviews progress made in the last five years to identify and survey prospective locations in the GYE; and 3) highlights directions for building and maintaining resource awareness.

Overview of Ice Patch Archaeology

As the Earth's climate warms, archaeological and paleontological materials are being discovered at areas of melting perennial snow and ice drifts, or "ice patches," in high latitude and high altitude mountain areas (Hare et al. 2004; Dixon et al. 2005; Grosjean et al. 2007), including in the Greater Yellowstone Ecosystem (GYE; Lee 2008a, 2008b, 2009, 2010a, in press). Ice patches characteristically exhibit little internal deformation and/or movement, and consequently they can contain ancient ice that, unlike glaciers, is kinetically stable. Freezing retards the decay of organic material, and in some instances these features have preserved otherwise perishable hunting gear and associated equipment in the context in which it functioned for millennia (Lee 2010a, in press).

Although cultural material has been discovered in association with ice patches for at least the past century

(Keddie and Nelson 2005; Farbrege 1972), the discovery of Otzi, the "Ice Man," and associated artifacts by hikers in 1991 (Spindler 1994) arguably marks the beginning of a modern era of ice patch archaeology. Shortly thereafter in 1993, a significant but essentially unreported artifact was identified by hikers in Olympic National Park: remnant fragments of a loose-weave burden basket melting out of a perennial snowfield within a hundred meters of a previously recorded lithic scatter (D. Conca, pers. comm. 2005; National Park Service 2006). The largest of the basket fragment measures ca. 21 x 28 centimeters (cm; 8.5 x 11 inches), and a sample of the basket was radiocarbon dated to ca. 2,900 years Before Present (BP; National Park Service 1999, 2006). The burden basket may have been used to pack a variety of materials, including snow from the ice patch to the nearby campsite, and may have been abandoned at the ice patch after failing.

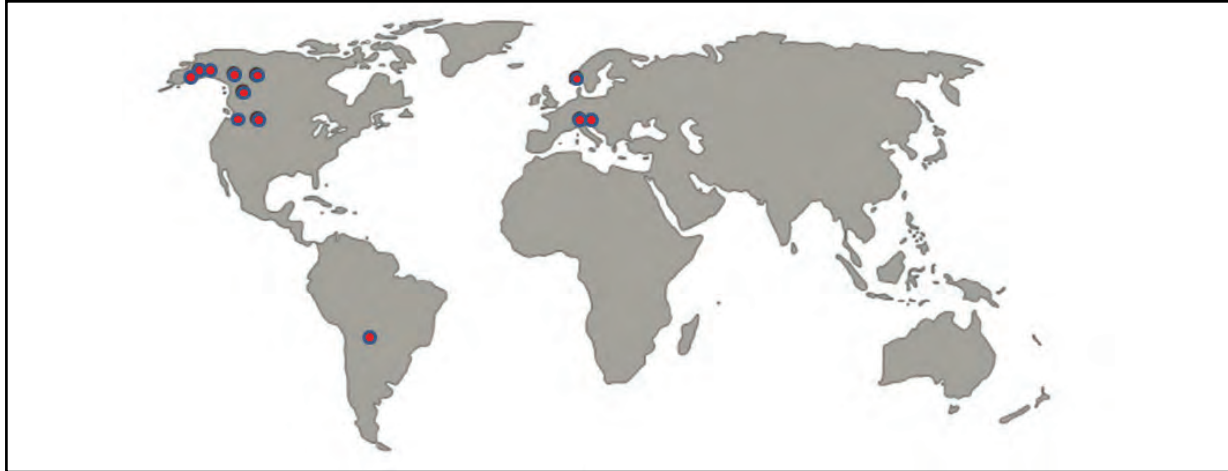


Figure 1. Areas with archaeological finds connected to ice patches (modified from Finstad and Pilø 2010).

The growing database of ice patch discoveries has illuminated some interesting regional differences in the prehistoric use of the features. For example, most ice patch discoveries in North America and Norway are connected to hunting, while finds in the Alps and British Columbia are most often associated with travel and transport through mountain passes (Figure 1). Discoveries in South America are primarily related to sacred activities (Ceruti 2010). A recent master's thesis by University of Wyoming student Rachel Reckin (2011) begins the necessary process of synthesizing the disparate data available on ice patch archaeology.

Survey in the GYE

Ice patches are present throughout the high-elevation areas of the GYE, with most associated archaeological sites occurring between 9,500 and 10,500 feet; however, sites have been identified as high as 11,250 feet (Figure 2). There are a variety of imperfect proxies to gauge survey conditions, including the mass balance of glaciers; however, ice patches “breathe” differently than glaciers and respond more noticeably to vagaries in the seasonal accumulation of snow and summer melting.

Several factors appear to influence an ice patch's potential to contain archaeological material, including: 1) relative isolation of ice patches from one another, which seems to concentrate activity toward a given location; 2) proximity to lower elevation, ice patch-free country; and 3) relative ease of access (e.g., proximity to human and animal travel corridors [passes]). Depending on the degree of melt and local conditions, in some years ice patches

can appear to have a black halo, particularly on their downslope sides, due to the presence of windblown and other organic material (e.g., animal feces).

The techniques used to identify permanent ice patches in the GYE (Lee 2007a, 2007b, 2007c, 2008a, 2008b) have been adapted for use elsewhere, including in Denali (Lee 2010c), Rocky Mountain (Lee 2010b), and Glacier National Parks (Kelly and Lee 2010).

The ice patch identification process involves using virtual globes (VG) and other sources of publicly available satellite and aerial imagery to scan a given area for snow and ice exhibiting the characteristics outlined above and in the introduction (Lee 2009, 2010b). VGs, such as Google Earth (earth.google.com) and NASA's World Wind (worldwind.arc.nasa.gov) play a significant role in this endeavor, but other online utilities such as Flash Earth (flashearth.com) and proprietary imagery are often useful. VGs can easily manipulate complex geospatial data in three dimensions to maximize topographic relief and to focus on the northeast-facing exposures where ice patches persist. At a minimum, before going into the field to conduct a survey, it is advisable to examine the prospective survey area with a VG for ice patches meeting the above criteria.

After prospective locations have been identified, aerial reconnaissance of the target ice patches is conducted prior to pedestrian surveys. Aerial reconnaissance consists of late summer overflight(s) of prospective ice patches that can be used to assess melting. Ice patch archaeological sites have been identified on the Custer and Shoshone National Forests and in Yellowstone National Park (Lee et al. 2009; Lee, in press). Numerous paleobiological sites consisting

of non-cultural, relict wood, for example, spruce (cf. *Picea engelmannii*) as well as animal remains, e.g., bighorn sheep (*Ovis canadensis*) and bison (*Bison bison*), have been identified in these resource areas as well as in the Gallatin National Forest. Most chronometric data for the sites, specimens and artifacts discussed are presented as radiocarbon years (^{14}C) before present. To preserve continuity and utility, this paper uses the radiocarbon timescale throughout in the ^{14}C BP notation. Calibrated ages—those ages derived from comparison of ^{14}C BP ages with calibration curves, for example, IntCal09 are identified as such by the preface “cal yr” or simply “cal.”

Paleobiological Specimens

Two of the first paleobiological samples encountered at a GYE ice patch consisted of tree stumps in growth position melting out of the bottom of an ice patch on Grass Mountain (Figure 3). The ice patch is above modern treeline. The trees were identified as spruce (cf. Engelmann spruce; J. Lukas, pers. comm. 2006). One of the assays returned an accelerator mass spectrometry (AMS) ^{14}C age of $7,935 \pm 15$ years BP and the other returned an AMS ^{14}C age of $7,955 \pm 15$ years BP. These dates are noted in Carrara



Figure 2. The area in green is a composite of contiguous high-elevation landforms and major valley systems that comprise the Greater Yellowstone Ecosystem (duplicated from Lee 2010a).



Figure 3. Mike Bergstrom (USFS archaeologist) examines one of the two ca. 8 ka year-old tree bases exposed in the melting toe of the Grass Mountain ice patch. Photo by Craig Lee.

(in press) as well as Lee (in press). The Holocene thermal maximum (ca. 10,000 to 8,500 cal yr BP) was as much as 6°C warmer than historic summer temperatures (Miller et al. 2005), which allowed trees to grow at this higher elevation. The trees may have met their demise during the rapid cooling that was underway by ca. 8,500 cal yr BP when their micro-environment filled in with snow. Additional discoveries of non-anthropogenic trees/wood have been made at other ice patches, including in Colorado and Wyoming (e.g., Benedict et al. 2008). A survey of dead wood above treeline on Grass Mountain reported no surface wood older than ca. 1,300 ^{14}C years BP (A. Bunn pers. comm. 2007; Bunn et al. 2004).

Archaeological Sites

Inclusive of the 2010 field season, at least seven (but maybe up to nine) prehistoric sites associated with melting “ice patches” have been identified in the GYE. Archaeological discoveries include sites with organic and chipped stone artifacts as well as sites with butchered animal remains exposed by melting ice.

The most remarkable and oldest artifact recovered from the GYE ice patches is a complete wooden dart foreshaft made from a birch (*Betula sp.*) sapling trimmed of its branches (Figure 4). A small sample of wood taken from a break in the foreshaft was AMS ^{14}C dated to $9,230 \pm 25$ BP; calibrated age 10,281–10,497 cal BP ($p = 1.0$). The artifact is contemporary with the late Paleoindian

Cody complex (ca. 9,200–8,400 ^{14}C BP or 11,220–9,445 cal BP) in North American archaeology. Locally, this time period coincides with the Alder complex (Davis et al. 1989). The complete weapon was probably propelled by an atlatl, or spear thrower, which would have provided mechanical advantage by increasing the leverage of the thrower's arm, resulting in greater projectile velocity.

Two groups of three evenly spaced lines on opposing sides of the artifact are inferred to be ownership or property marks (Lee 2010a). Ethnographic observations indicate ownership marks occur on hunting weapons designed to remain in the bodies of large game. They typically consist of simple lines and can be specific to either an individual or community. The lines on the foreshaft appear to be embossed or pressed into the wood with a ca. 1 millimeter (mm)-wide tool on the thinnest portion of the shaft near the projectile point haft. If the shaft broke off inside the animal, this portion could link the hunter with the kill.

The ability to differentiate weapons based on distinctive marks suggests other elements of these artifacts (e.g., projectile points) were not indicative of, or distinctive to, the person using the weapon (Lee 2010a). Particularly skilled individuals within a band or group may have crafted most of the technically demanding points (Lee 2010a).

Protecting Ice Patches

In addition to monitoring productive sites and identifying new ones, stabilization may be a realistic option for the most significant locations. Two potential stabilization techniques have been identified. Snow fences could be used to artificially bolster the amount of snow on the patch. Such fences should not be raised until after the winter cold wave has penetrated the old ice core. A second possibility is to use thermally insulating blankets similar to those used in Switzerland to preserve snow bases at ski areas.

Building and Maintaining Resource Awareness

The ice patch phenomenon transcends the political boundaries that divide the GYE. The goals of our ongoing work are five-fold: 1) to identify and characterize sites currently threatened by climate change that will be lost if not properly identified and recorded (protected) immediately; 2) to provide GYE unit resources managers with a report that may aid in resource management decisions; 3) to generate unparalleled scientific data regarding human adaptations in the GYE through the analysis of unique, ancient, or-

ganic artifacts; 4) to augment and correlate with regional climate studies through the analysis of ancient paleoenvironmental records, such as frozen tree stands; and 5) to promote public education through the use of student/volunteer labor and the dissemination of project results via presentations at professional meetings and publications.

Ice patch discoveries provide an amazing way to capture public interest and integrate education about archaeology, Native American cultures, and modern climate change. We are currently planning to engage a videographer to film,

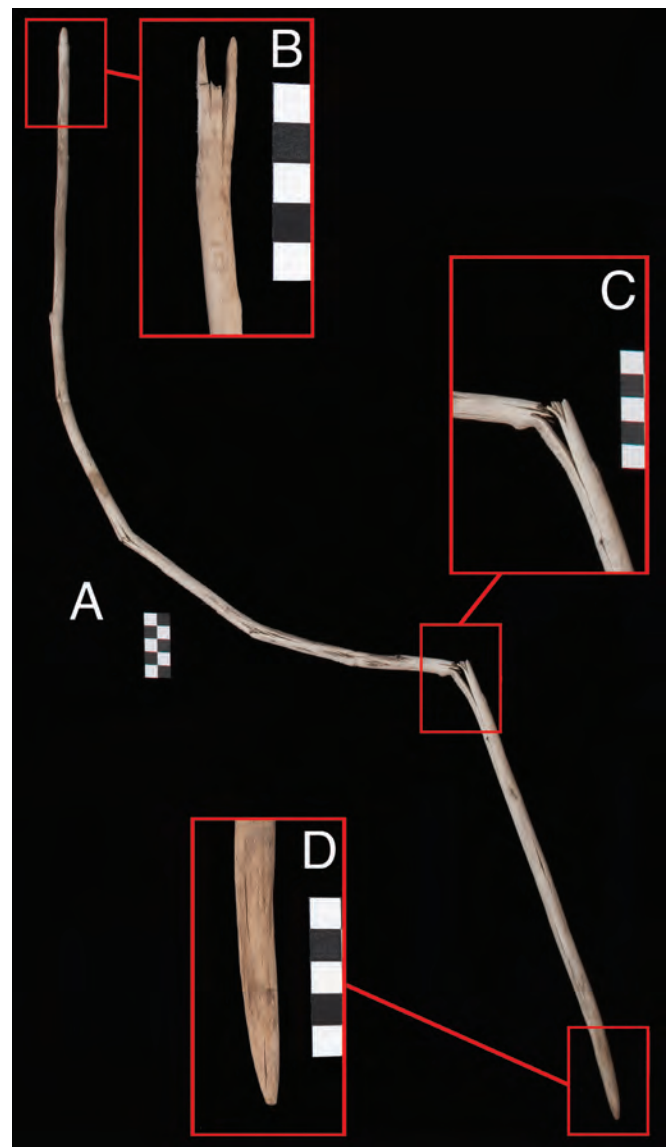


Figure 4. Dart foreshaft. Clockwise from large image: A) the complete foreshaft; B) detail of the hafting element at the tip (the probable ownership marks are visible near the bottom of the image); C) detail of animal damage (probably a trampling fracture that occurred when the artifact was saturated and partially buried in slush); D) detail of the base portion of the foreshaft. Scales in centimeters.



Figure 5. The 2010 Montana Archaeology Month poster; copies are available from the Montana Historical Society.

edit, and produce a 15 minute Web video highlighting the critical thinking and findings of ice patch archaeology in the GYE. The engaging and informative video will serve multiple purposes. The Web link can be shared through informal partners, such as the U.S. Forest Service “Passport in Time” program as well as through Project Archaeology, which has an educational mandate to bring archaeology to middle school classrooms. The video can also be copied to DVD (or streamed) into classroom settings during the annual “Archaeology Month” (or “Archaeology Week”) in GYE and other Rocky Mountain states, and the online content will augment allied educational missions around the globe, including at Klimapark2469 in Norway

(<http://www.oppland.no/Klimapark2469-English>) and the Kwanlin Dun Heritage Center in Yukon, Canada. Additional details about ice patch archaeology in the GYE can be found online at http://instaar.colorado.edu/ice_archaeology. “Ice Patch Archaeology” was the theme of the 2010 Montana Archeology month poster (Figure 5). Poster copies are available from Damon Murdo (dmurdo@mt.gov) at the Montana Historical Society.

Take Home Messages

The effects of climate change are tangible in northern and mid-latitude ice patches. Ice patch discoveries provide a unique way to capture public interest and to educate about other effects of global warming. The ice patch phenomenon is global and transcends the state and government boundaries that permeate the GYE. This research would benefit from supra-level organization, such as might be provided by the Greater Yellowstone Coordinating Committee (GYCC).

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The Effect of Climate Change and Habitat Alteration on Speciation in *Lycaeides* Butterflies in the Greater Yellowstone Area

Lauren Lucas¹ and Zachariah Gompert²

¹ Department of Botany, 3165, University of Wyoming, Laramie, WY 82071, 307-766-2634, llucas5@uwyo.edu

² Department of Botany, 3165, University of Wyoming, Laramie, WY 82071, 307-766-2634, zgompert@uwyo.edu

Abstract

Climate change and habitat alteration can affect evolutionary processes, including speciation, the process responsible for the origin of new species. Specifically, climate change and habitat alteration can bring formerly isolated species into secondary contact or reduce the efficacy of barriers to inter-specific mating, leading to hybridization and merger into a single lineage. Our research focuses on a pair of recently diverged butterfly species: the northern blue butterfly (*Lycaeides idas*) and the Melissa blue butterfly (*Lycaeides melissa*). These butterflies have come into secondary contact in the Greater Yellowstone area and now hybridize extensively in and around the Jackson Hole Valley. The future evolutionary trajectory of these species (i.e., whether they remain distinct or experience increased hybridization) may be affected by both climate change and habitat alteration. Currently, these species differ in the number of adult flights per summer and the timing of these adult flights. These differences might be eroded with increased climate change, thereby increasing hybridization. Additionally, Melissa blue butterfly larvae now commonly feed on cultivated and feral alfalfa, which was introduced into the United States in the 1800s. This has allowed populations of Melissa blue butterflies to persist where they formerly could not and has likely facilitated contact between the Melissa blue and northern blue, including contact between these species in the Jackson Hole Valley. The continued spread of alfalfa may further increase hybridization rates between these species. This research highlights the importance of understanding the effects of climate change and habitat alteration on the speciation process.

Introduction

Habitat alteration and climate change can affect the distribution, phenology, and abundance of species. Shifts in the geographic range of species have been documented in several well-studied taxonomic groups, including European butterflies and mountain-top species, following changes in habitat or climate (Parmesan 2006). Similarly, Sinervo et al. (2010) documented local extirpation and in some cases global extinction of Mexican *Sceleporus* lizards that was linked to climate change; specifically, extinction was correlated with a change in maximum winter air temperature. Habitat alteration and climate change can also affect the evolutionary trajectory of populations. Reductions in effective population size, including those caused by habitat alteration or climate change, are expected to accelerate the loss of genetic diversity due to drift (i.e., the change in allele frequency in a population due to sampling error). Additionally, changes in the abiotic environment or biotic community a population experiences will create novel selective pressures, which will alter the evolutionary dynamics of the focal population.

Habitat alteration and climate change also have the potential to affect the speciation process. Speciation is a

fundamental evolutionary process that is responsible for the planet's biodiversity. The evolution of reproductive isolation, which is defined as reduced fitness of hybrid offspring or a reduced propensity for inter-population matings between divergent lineages, is central to the speciation process. The potential effects of habitat alteration and climate change on speciation are complex. Habitat alteration and climate change can affect rates of dispersal and gene flow among populations. Increased geographic isolation between populations, and thus a reduction in gene flow, should facilitate the evolution of reproductive isolation. Alternatively, gene flow can occur between formerly isolated populations via secondary contact, which can retard the evolution of reproductive isolation. In this case, rates of hybridization would increase, thereby affecting the efficacy of reproductive isolation. A recent example of the effect of habitat alteration on the process of speciation involves 500 haplochromine cichlids in Lake Victoria (Seehausen et al. 1997). These cichlids diversified from a single common ancestor over approximately 12,000 years. Because of the relatively recent timing of this radiation, there has been little time for intrinsic isolation to evolve among these species. Instead, reproductive

isolation is primarily due to variation in male colors coupled with variation in female preference for male color patterns. Deforestation and agricultural practices around Lake Victoria have reduced its water clarity; consequently, species diversity has decreased and hybridization has increased, because females cannot easily distinguish males by their colors in the turbid water.

Habitat alteration and climate change also have the potential to affect the speciation process in the Greater Yellowstone area (GYA). This paper reports the results of our research as it relates to the effect of these factors on adaptation and speciation with two recently diverged Lycaenid butterfly species: *Lycaeides idas* and *L. melissa*. We begin by describing the natural history of *L. idas* and *L. melissa*. We then discuss three key topics: 1) the effect of Pleistocene glacial cycles (historical climate change) on divergence and hybridization between *L. idas* and *L. melissa*, 2) the potential effect of alfalfa introduction (a form of human-induced habitat alteration) on rates of hybridization between the two species, and 3) the role of phenology in isolating *L. idas* and *L. melissa* and the effect future climate change might have on the integrity of these two species.



Figure 1. *Lycaeides melissa* north of Sinclair, Wyoming. Photo by Lauren K. Lucas.

The Natural History of *Lycaeides melissa* and *L. idas*.

Lycaeides is a holarctic genus of small blue butterflies in the family Lycaenidae. At least two and up to five species of *Lycaeides* butterflies are recognized in North America. These include *L. idas* (the northern blue), which is found throughout the mountainous regions of the western United States and Canada as well as much of Eurasia, and *L. melissa* (the Melissa blue), which occupies the western and northeastern United States as well as portions of southern Canada (Figure 1; Scott 1986; Brock and Kaufman 2003). The ranges of these species overlap in western North America, particularly in the central and northern Rocky Mountains, which include the GYA. *Lycaeides idas* and *L. melissa* populations can be found in close proximity to each other near the Jackson Hole Valley and the Grand Teton Mountain Range of northwestern Wyoming.

In the GYA, *L. idas* and *L. melissa* populations differ ecologically and morphologically. *Lycaeides idas* populations use several native species of *Astragalus* (e.g., *A. miser* and *A. alpinus*) as larval host plants, whereas most *L. melissa* populations feed on cultivated or feral alfalfa (*Medicago sativa*; Gompert et al. 2010a). *Lycaeides idas* populations also tend to occupy more mesic habitat at higher elevations, whereas *L. melissa* populations are found in drier habitat often near agricultural lands. Compared to *L. melissa*, *L. idas* individuals have smaller male genitalia and reduced wing pattern elements (i.e., black spots and orange iridescent aurorae; Lucas et al. 2008; Gompert et al. 2010a).

Pleistocene Diversification and Hybridization of

L. idas and *L. melissa*. Past climate change has almost certainly contributed to the diversification of *Lycaeides* in North America. Mitochondrial DNA sequence data are consistent with a scenario of fragmentation of North American *Lycaeides* into at least three geographically isolated refugial populations during the Pleistocene glacial advances (Nice et al. 2005). This history is also consistent with recent high-throughput nuclear DNA sequence data, which indicates considerable genetic structure among these hypothesized refugial populations (Gompert et al. 2010b). Because of geographic isolation during these Pleistocene glacial advances, the ancestors of *L. idas* and *L. melissa* populations that currently occur in close proximity in the GYA evolved independently. It is likely that many of the morphological and ecological differences,

Table 1. Population information for *Lycaeides* populations in the vicinity of the GYA. Nominal taxonomic identifications are given, although many of the *L. idas* populations are quite admixed. Admixture proportions give the mean proportion of genetic material for each population inherited from *L. melissa*. Further details are given in Gompert et al. (2010a).

Locality	Taxon	Latitude	Longitude	Elevation (m)	Admixture Proportion
Goshen, WY	<i>L. melissa</i>	41.7346	104.2645	1364	0.937
Chugwater, WY	<i>L. melissa</i>	41.7993	104.7490	1577	0.969
Indian Bathtubs, WY	<i>L. melissa</i>	41.2040	106.7714	2214	0.937
Glenrock, WY	<i>L. melissa</i>	42.8662	105.8285	1518	0.986
Bear Mountain, WY	<i>L. melissa</i>	42.2378	107.0492	1982	0.987
Lander, WY	<i>L. melissa</i>	42.6533	108.3551	1787	0.947
Victor, ID	<i>L. melissa</i>	43.6590	111.1114	1850	0.970
Dubois, WY	<i>L. melissa</i>	43.5622	109.6991	2153	0.787
Teton Science School, WY	<i>L. melissa</i>	43.4233	110.7757	1918	0.622
Periodic Spring, WY	<i>L. melissa</i>	42.7468	110.8493	2113	0.036
Swift Creek, WY	<i>L. melissa</i>	42.7251	110.9066	1949	0.516
Bull Creek, WY	<i>L. idas</i>	43.3007	110.5530	2195	0.135
Soda Lake, WY	<i>L. idas</i>	43.5283	110.2573	2359	0.154
East Table, WY	<i>L. idas</i>	43.2249	110.8117	1865	0.059
Upper Slide Lake, WY	<i>L. idas</i>	43.5829	110.3328	2246	0.200
Blacktail Butte, WY	<i>L. idas</i>	43.6382	110.6820	2220	0.292
Shadow Mountain, WY	<i>L. idas</i>	43.6974	110.6102	2180	0.235
Mt. Randolph, WY	<i>L. idas</i>	43.8547	110.3918	2221	0.161
Lozier Hill, WY	<i>L. idas</i>	43.8729	110.5497	2122	0.133
Avalanche Peak, WY	<i>L. idas</i>	44.4860	110.1307	2998	0.156
Riddle Lake, WY	<i>L. idas</i>	44.3617	110.5465	2395	0.075
Natural Bridge, WY	<i>L. idas</i>	44.5278	110.4479	2373	0.162
Trout Lake, WY	<i>L. idas</i>	44.9019	110.1291	2124	0.051
Hayden Valley, WY	<i>L. idas</i>	44.6823	110.4945	2344	0.125
Mt. Washburn, WY	<i>L. idas</i>	44.7832	110.4494	2740	0.038
Cascade Lake, WY	<i>L. idas</i>	44.7550	110.4927	2424	0.067
Indian Creek, WY	<i>L. idas</i>	44.8787	110.7387	2211	0.026
Bunsen Peak, WY	<i>L. idas</i>	44.9337	110.7212	2260	0.094
Jardine, MT	<i>L. idas</i>	45.0747	110.6335	1985	0.043
Watkins Creek, MT	<i>L. idas</i>	44.7849	111.3088	2150	0.023
Garnet Peak, MT	<i>L. idas</i>	45.4323	111.2245	1910	0.024
King's Hill, MT	<i>L. idas</i>	46.8407	110.6990	2239	0.052

some of which might contribute to reproductive isolation between these lineages (e.g., differences in the size of male genitalia; Lucas et al. 2008; Gompert et al. 2010a), evolved during this time. Climate then warmed at the end of the Pleistocene (Pielou 1992). DNA data and current distributions of *Lycaeides* butterflies indicate that this warming likely facilitated range shifts and expansions of

Lycaeides from the hypothesized refugial populations (Nice et al. 2005; Gompert et al. 2008). Since this time, *Lycaeides* descendents from each of these refugial populations have come into (secondary) contact (Nice et al. 2005; Gompert et al. 2010a). Because reproductive isolation between these lineages is incomplete, secondary contact following the retreat of Pleistocene glaciers has resulted in hybridization

and gene exchange (i.e., introgression). One region of extensive secondary contact and hybridization between *L. idas* and *L. melissa* is the GYA. Much of the Jackson Hole Valley, Yellowstone Plateau, and surrounding area was glaciated until approximately 14,000 years before present (Wisconsin glaciation; Harris et al. 1997). With warming and the retreat of glaciers, eastern and western groups began to move through the mountains, particularly along low-elevation passes, which served as conduits between formerly isolated groups (Hewitt 1996), facilitating hybridization.

Nabokov (1952) described individual *Lycaeides* butterflies from several populations in the GYA (e.g., at Blacktail Butte in Grand Teton National Park) with male genitalia intermediate in size between typical *L. idas* and *L. melissa* individuals. He thought it quite likely that this intermediacy was the result of hybridization between *L. idas* and *L. melissa*. Since Nabokov's work, considerably

more evidence has amassed that documents extensive hybridization between *L. idas* and *L. melissa* in the GYA. First, *L. idas* and *L. melissa* populations in this region have identical mitochondrial DNA sequences (Gompert et al. 2008), which were likely passed from *L. idas* populations to *L. melissa* via interbreeding. More recently, Gompert et al. (2010a) demonstrated extensive hybridization between *L. idas* and *L. melissa* populations in the GYA based on hundreds of genome-wide genetic markers and two morphological characters: male genitalia size and aspects of wing pattern.

Admixture proportions (i.e., statistical estimates of the proportion of genetic variation in each population inherited from *L. melissa*) indicate that many populations in the GYA classified as *L. idas* have experienced gene flow with nearby *L. melissa* populations (Table 1). For example, *L. idas* populations from Blacktail Butte, Upper Slide Lake, and Lozier Hill have inherited between 13 and 29 percent of their genetic variation from *L. melissa*. Moreover, geographic patterns of admixture suggest that hybridization between *L. idas* and *L. melissa* has led to the formation of a hybrid zone that extends north from the Jackson Hole Valley to Hayden Valley. Specifically, admixture proportions and morphological characters vary from *L. melissa*-like to *L. idas*-like along a geographical transect, from south to north (Figure 2). Interestingly, the admixed populations generally occupy sites with similar habitat to *L. idas* populations and feed on *L. idas* larval host plants (e.g., *Astragalus* sp.), hence their taxonomic classification as *L. idas* populations.

As evidenced by patterns of morphological and genetic variation, historical changes in climate during and after the Pleistocene have been central to diversification and hybridization in North American *Lycaeides*. Thus, climate change has directly affected the speciation of these butterflies by altering rates of gene flow and thus the degree of evolutionary independence between these lineages. The future evolutionary trajectory of these taxa is unclear. The speciation process could culminate in complete reproductive isolation, or hybridization could further erode genetic differences between these taxa and they could merge into a single lineage. Much of our current work explores the specific morphological, ecological, and behavioral characters that might be involved in reproductive isolation (e.g., male genitalic morphology, male and female wing pattern morphology, female oviposition [i.e., host plant] preference, mate preference, and phenology), which will shed further light on the expected evolutionary trajectory

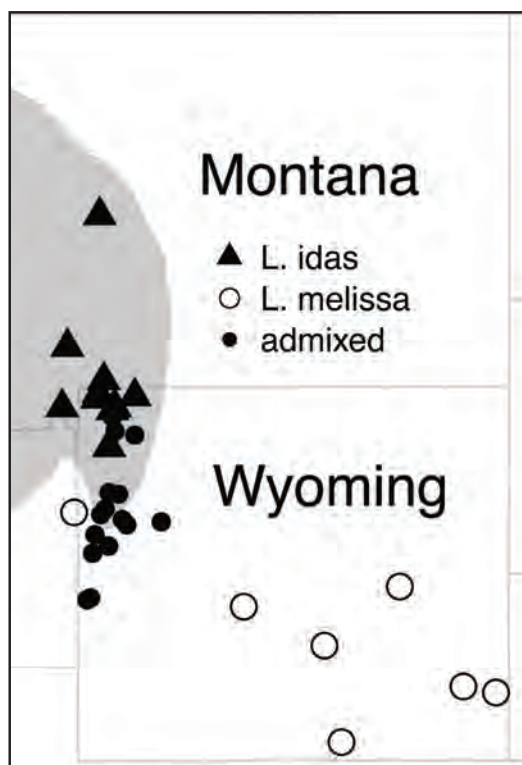


Figure 2. Map depicting region of secondary contact and hybridization between *L. idas* and *L. melissa* in the GYA. Populations are denoted with symbols. Populations were classified as admixed if their mean admixture proportion was between 0.1 and 0.9 (Gompert et al. 2010a). The gray shaded region denotes the range of *L. idas* within the displayed area. *Lycaeides melissa* occurs over the entire region depicted in the map.

of these taxa. As part of this research we have identified two key aspects of *Lycaeides* natural history that have an effect on the speciation process and have been or likely will be impacted by habitat alteration and climate change. We discuss each of these in following sections.

The Effect of Habitat Alteration on *Lycaeides* Speciation in the GYA. As discussed extensively in the preceding section, secondary contact and subsequent hybridization between *L. idas* and *L. melissa* was due in part to warming climate and the retreat of glaciers from the GYA at the close of the Pleistocene. However, without the contribution of other factors, the geographic range and abundance of *L. melissa* might have been substantially reduced relative to its current range and abundance. Many *L. melissa* populations currently use cultivated and feral alfalfa, *Medicago sativa*, as a larval host plant. Historical records indicate that alfalfa is not native to North America, and it was intentionally introduced to North America approximately 200 years ago for agricultural purposes (it is a common component of hay). Since its initial introduction, alfalfa has spread over large portions of North America (Michaud et al. 1988). Butterfly populations cannot persist in an area in the absence of a suitable larval host plant, and in most cases a given butterfly species can only feed on plants from one or a few genera (Scott 1986). For example, *Lycaeides* generally specialize on legumes from a few genera (e.g., *Astragalus*, *Lupinus*, or *Glycyrrhiza*). In areas where *L. melissa* are currently quite abundant, the only potential host plant available is alfalfa, and it is not clear that an alternative host plant would have been available in the absence of agriculture. Thus, *L. melissa* would not likely be in many places where it currently is found without human-induced habitat alteration, specifically the introduction and cultivation of alfalfa.

The introduction of alfalfa also likely has contributed to the extent of secondary contact between *L. idas* and *L. melissa* in the GYA. Alfalfa is found in several regions in and near the GYA, such as the Mormon Row/Antelope Flats area of Grand Teton National Park; Jackson, Wyoming; Victor, Idaho; Dubois, Wyoming; and Gardiner, Montana. These same regions are quite near current areas of secondary contact and hybridization between *L. melissa* and *L. idas*. Moreover, in most of these regions native host plants fed on by *L. melissa* are either absent or low in abundance. This situation suggests that the presence of alfalfa has increased rates of hybridization in the GYA. Interestingly, most regions of secondary contact and hybridization

in the North American *Lycaeides*, including regions of hybridization outside of the GYA (i.e., in the Sierra Nevada, White Mountains, and near Lake Michigan), involve alfalfa-feeding *L. melissa* and *L. idas*, or Karner blue butterfly populations feeding on native host plants.

The Effect of Climate Change on *Lycaeides* Speciation in the GYA. As previously discussed, past climate change likely facilitated diversification of *Lycaeides* during Pleistocene glacial advances. As the climate warmed, divergent *Lycaeides* populations came into secondary contact and hybridized (Nice et al. 2005; Gompert et al. 2010a). Our research suggests that ongoing climate change, particularly increased temperatures, might further erode a major source of reproductive isolation between *L. idas* and *L. melissa*. In general, patterns of hybridization based on molecular and morphological data indicate that reproductive isolation between *L. idas* and *L. melissa* is relatively weak (i.e., matings between *L. idas* and *L. melissa* can occur and result in, at least in some instances, viable and fertile offspring). However, perhaps the strongest component of reproductive isolation between *L. idas* and *L. melissa* is temporal and due to differences in phenology, specifically differences in adult flight time and voltinism (i.e., number of broods per year). In the GYA, *L. melissa* populations have at least two broods each year, whereas *L. idas* populations, as well as admixed populations (i.e., populations with many hybrid individuals), have a single brood per year (Figure 3). Moreover, the timing of offspring flights differs between *L. idas* and *L. melissa*. Adult butterflies for the first *L. melissa* brood can generally be encountered from the very end of May until about the middle of July, and adults from the second brood are present from early- or mid-August until as late as the end of October. Conversely, adult *L. idas* butterflies from the single brood can be found from approximately the middle of July until the middle of August (Figure 3). A similar flight time occurs for the admixed populations. Because there is little overlap in the flight time of adult *L. idas* and *L. melissa*, there is a decreased probability for them to encounter each other and thus a reduced probability of inter-specific mating and hybridization. This separation in time is connected in part to diapause or hibernation. *Lycaeides* diapause as eggs following the final brood each year and do not emerge as larvae until the following spring. Eggs laid by the first adult *L. melissa* brood do not diapause, but instead develop directly as larvae after spending only about a week as eggs (personal observation of the authors). This makes the sec-

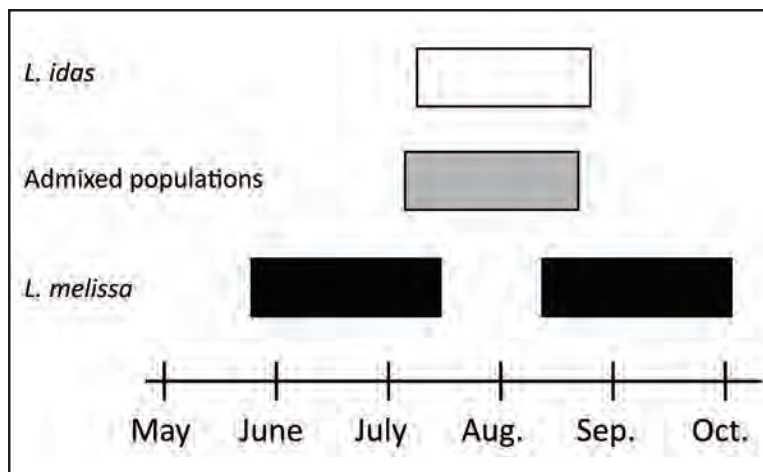


Figure 3. Approximate adult butterfly flight times for *L. idas* and *L. melissa* populations in the GYA. Flight times are based on field observations by the authors during 2008, 2009, and 2010. Tick marks denote the first day of each month.

and *L. melissa* brood possible. Conversely, *L. idas* and admixed populations diapause directly after the first brood.

Ongoing climate change has the potential to alter the efficacy of temporal isolation between *L. idas* and *L. melissa*. Warmer climate in the future could select for an earlier first brood for *L. idas* or multivoltinism (i.e., multiple broods per year) in *L. idas*. Either of these changes would increase temporal overlap in the adult flights of *L. idas* and *L. melissa*, and thus would increase the probability of inter-specific matings and the rate of hybridization. Increased gene flow would reduce genetic differentiation between these lineages and further erode genetic differences responsible for reproductive isolation.

Conclusion

The history of diversification and hybridization in North American *Lycaeides* butterflies has been strongly influenced by climate change during and following the Pleistocene. This includes *L. idas* and *L. melissa* populations in the GYA. Rates of hybridization between these two species were likely increased by the introduction of alfalfa to North America, including in the GYA. This is because alfalfa is now often used as a larval host plant by *L. melissa* populations and allows these populations to persist in areas where they would not likely be able to survive otherwise. Finally, *L. idas* and *L. melissa* currently are isolated to a large extent because of phenological differences. However, if the climate in the GYA warms, selection will likely favor phenological changes in *L. idas* that could reduce this temporal isolation and further increase rates of hybridization.

Humans have the potential to affect evolutionary processes, including speciation, through habitat alteration and contributions to climate change. The potential effects of humans on the speciation process are complex and could lead to an increase or decrease in biological diversity. This is because humans have the potential to increase or decrease rates of gene flow and hybridization among differentiated lineages. In the case of *L. idas* and *L. melissa* in the GYA, the most likely effect of further habitat alteration and climate change will be increased hybridization and the potential collapse of these species into a single lineage. Nonetheless, outcomes of secondary contact and hybridization are often quite complex and the specific outcome in this case is uncertain. In fact, hybridization in *Lycaeides* has even led to the formation of novel species, as was documented in alpine habitat of the Sierra Nevada (Gompert et al. 2006).

The case we have described of hybridization between *L. idas* and *L. melissa* in the GYA is not unique. The GYA is an interesting geographic region with a notable number of species forming regions of secondary contact or hybrid zones. For example, Swenson and Howard (2005) found evidence for dense clustering contact zones in the Rocky Mountains of Idaho, Wyoming, Colorado, and New Mexico between closely related taxa using data from hybrid zones as well as from species range maps of trees, birds, and mammals and from the position of phylogeographic breaks within species. Furthermore, Hewitt (1996) denoted the strong barriers to dispersal represented by mountain chains and noted that low mountain passes would provide corridors for dispersal during periods of climatic warming; hence, hybrid zones should cluster in such corridors. Thus, the GYA represents a hot spot of secondary contact due to its unique geographic location and topography. Therefore, the effects of habitat alteration and climate change on the speciation process in the GYA might be particularly pronounced.

Suggested Citation

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Prehistoric/Historic Ecology and Land Restoration within the Gardiner Basin, Yellowstone National Park, Montana

Douglas H. MacDonald¹, Elaine S. Hale², Pei-Lin Yu³, Mary Hektner⁴ and David S. Dick⁵

¹ Department of Anthropology, University of Montana, Missoula, MT 59812, 406-243-5814, douglas.macdonald@mso.umt.edu

² Branch of Environmental Compliance, Yellowstone Center for Resources, PO Box 168, Yellowstone National Park, WY 82190, 307-344-2156, Elaine_Hale@nps.gov

³ Rocky Mountain Cooperative Ecosystem Study Unit, University of Montana, Missoula, MT 59812, pei-lin.yu@cfc.umt.edu

⁴ Branch of Environmental Compliance, Yellowstone Center for Resources, PO Box 168, Yellowstone National Park, WY 82190, mary_hektner@nps.gov

⁵ Department of Anthropology, University of Montana, Missoula, MT 59812, 406-243-5814, davidsdick@charter.net

Abstract

Archaeological data collected within the Gardiner Basin of Yellowstone National Park provides an excellent window into changing land-use patterns during the Holocene within the Greater Yellowstone Ecosystem (GYE). The Gardiner Basin is the lowest-elevation portion of Yellowstone National Park and is located between the city of Gardiner, Montana, and northward to Yankee Jim Canyon along the Yellowstone River. While various environmental and ecological changes occurred during the Holocene—including oscillating precipitation and temperature trends—Native American hunter-gatherer use of the area remained consistent for 11,000 years until the onset of Euro-American homesteading. The homestead era disrupted the well-established cultural ecology of the Gardiner Basin. Archaeological work at the former railroad town of Cinnabar, Montana, provides key information regarding the effect of homesteading on the environment and the economic challenges faced by early Euro-American settlers. Yellowstone National Park recognizes the deteriorated condition of the Gardiner Basin's ecology due to the Homestead Era. The Gardiner Basin Restoration Project is an attempt to reestablish native plant communities within the basin, in essence bringing it back to the ecological conditions present during much of prehistory.

Introduction

The Gardiner Basin is the lowest-elevation portion of Yellowstone National Park and is located between the township of Gardiner, Montana, and Yankee Jim Canyon, a distance of about 10 miles along the Yellowstone River (Figure 1). While various environmental and ecological changes occurred during the Holocene—including oscillating precipitation and temperature trends—Native American hunter-gatherers used the area for 11,000 years until the onset of Euro-American homesteading. The homestead and national park eras disrupted the well-established cultural ecology of the Gardiner Basin. Recently, Yellowstone National Park recognized the deteriorated condition of the area. The Gardiner Basin Restoration Project is an attempt to reestablish native plant communities within the basin, in essence bringing it back to the ecological conditions present during much of prehistory.

This paper will provide an overview of the pre-European paleoenvironment of the Gardiner Basin, as well as a

brief overview of Native American use of the area during the last 11,000 years. We then discuss historic data, as well as results of archaeological excavations at Cinnabar (Yellowstone's original train station) and other archaeological sites in the area, to provide insight into how land use changed during the last century. Finally, we discuss Yellowstone's efforts to restore the former agricultural fields to native vegetation. We use site-specific archaeological, paleoenvironmental, and historical data to better understand the Gardiner Basin's historic and prehistoric ecology from a landscape perspective. By building data from specific sites, we hope better grasp the changing ecology and human adaptation within the entire landscape.

Ecology and Environment of the Gardiner Basin

On its surface, the Gardiner Basin appears to be an area in which human habitation has been a struggle; certainly the historic use of the area might reflect some difficulty in

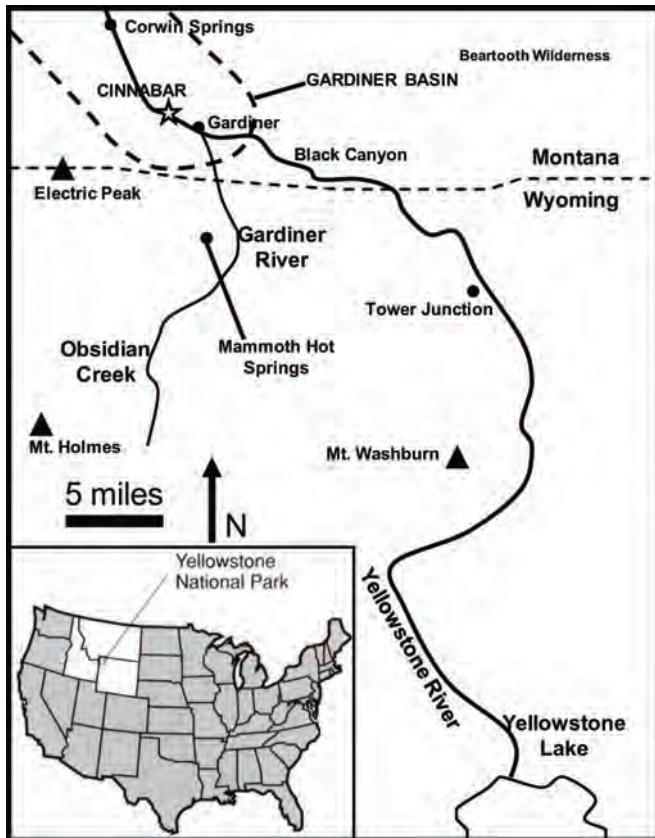


Figure 1. Map of Gardiner Basin study area.

adapting to the brutal heat of the summer, contrasted by the sometimes harsh winters. However, does the prehistoric record show a similar human struggle? How did people use this landscape prior to the arrival of Europeans? What would the Gardiner Basin look like today if Europeans had never arrived? What is a “pristine” Gardiner Basin? Is it when hunter-gatherers were present, say prior to 300 years ago? Is it when no people were present, say prior to 12,000 years ago? Obviously, figuring out what “pristine” means is difficult; however, for the purposes of this paper, we mean ground conditions as they were prior to the arrival of European-Americans, or approximately before 1800 A.D.

As discussed in numerous papers in these proceedings, landscapes are composed of various interconnected resources, including rivers, mountains, springs, plants, insects, and animals, including humans. The current composition of resources in the Gardiner Basin includes a variety of species adapted to a marginal environment. The Gardiner Basin is ecotonal in character, with the Rocky Mountains bordering it to the west and east, the Yellowstone Plateau bordering it to the south, and the Great Plains bordering it to the north. The basin is thus surrounded on three sides—east, south, and west—by high-

elevation landforms. It is for this reason that the Northern Pacific Railroad decided to proceed no farther than Gardiner in its installation of tracks into Yellowstone National Park along the Yellowstone River. Beyond Gardiner, to the south, the rugged conditions of the Black Canyon of the Yellowstone and the steep terrain of the Gardiner River to Mammoth Hot Springs effectively marked the town of Gardiner as the last stop. Today, it is the last stop for tourists entering the park through the North Entrance. After Gardiner, the wilds of Yellowstone begin.

This modern use of the area is reflected in its historic use. The Gardiner Basin has always been used as a staging area to enter the park. Early brochures tout Gardiner as the ideal location through which to enter the park. Beginning in 1903, the railroad stopped there and people then used wagons and eventually motorized vehicles to venture southward into the park. Even today, the Gardiner Basin is home to Yellowstone’s northern corral operations, evidence of the continued use of the adjacent geography for trip staging. For many people who live in Gardiner, Montana, the area of our study is often referred to as the “Boundary Lands.”

The Boundary Lands is a fitting name for the area, not just for the historic, but also for the prehistoric, period. Native American hunter-gatherers used the basin as a launching point from which to obtain obsidian tool stone from Obsidian Cliff, among a host of other natural resources. Historically, late nineteenth- and early twentieth-century Europeans focused on alleviating the harsh setting of the Boundary Lands. The Boundary Lands—or Gardiner Basin—is generally hot and dry in the summer and cold and fairly dry in the winter. Ideally, it is composed of sagebrush/grassland steppe vegetation, but historic use of the area has resulted in mostly non-native weeds.

The Yellowstone River flows northwesterly through the basin, acting as Yellowstone National Park’s northern boundary (Figure 2). Reese Creek is a free-flowing stream that marks the dogleg of the park boundary, a few miles north of the North Entrance arch. The Rocky Mountains—including the majestic Electric and Sepulcher Peaks at 10,992 and 9,652 feet (ft) above mean sea level—mark the Gardiner Basin’s southwest boundary. One can literally walk straight east, west, or south into the heart of the Rocky Mountains from the Boundary Lands. A northward trek brings you through Yankee Jim Canyon to the Paradise Valley and into the grasslands of the Great Plains.

Other interesting geological features of the Boundary

Lands include glacial moraines and outwash features, reflecting the melting and receding of the glaciers more than 12,000 years ago. Glacial melt water washed through the Gardiner Basin, leaving behind huge piles of glacial debris in the otherwise flat glacial valley of the Yellowstone River. After the retreat of the glaciers, a large landslide of waterlogged soils washed over the Gardiner Basin just north of Gardiner, pushing the Yellowstone River northward to its current channel. Evidence of this landslide is apparent today as one drives along Route 89 just north of Gardiner. Landslide Creek borders the gigantic landslide feature to its north. Numerous small ponds and spring seeps characterize the landslide area above the Gardiner Basin.

The elevation of the Gardiner Basin is approximately 5,300 ft, compared to the elevation of Mammoth Hot Springs of 6,500 ft and of Yellowstone Lake at 7,800 ft. At this comparatively low elevation, the Gardiner Basin is within the rain shadow of the Madison and Absaroka-Beartooth mountain ranges. The area typically receives less than 10 inches of precipitation per year and stays relatively free of snow. Summertime temperatures can exceed 100°F. In winter, the Gardiner Basin is somewhat of an oasis for a huge array of ungulates, including bison, antelope, elk, and deer, because of its relatively mild winters compared to the bordering landscapes, making vegetation available year round; in summer, the situation reverses and the oasis is the high-elevation Yellowstone Plateau and the low-elevation Gardiner Basin is harsh, dry, and hot.

Prehistory and Paleoenvironments of the Gardiner Basin

Because of its low elevation and relatively warm weather compared to the surrounding area, the Gardiner Basin not only always served as a wintering ground for ungulates, but also for hunter-gatherer peoples—Native Americans between 11,000 and 300 years ago. In the following section, we characterize more fully the human use of the Boundary Lands, in light of archaeological, paleoenvironmental, and historic data. Dates utilized in this discussion are in uncalibrated radiocarbon years.

Until at least 12,000 years ago, the Gardiner Basin was filled with glaciers, and melt water formed the incipient Yellowstone River. Global warming caused the melting of the glaciers, and by 11,000 years ago hunter-gatherers occupied or travelled through not just the Yellowstone Valley and the GYE, but also all of the Americas. Most of the Upper Yellowstone region probably resembled glacial-edge

landscapes that are visible today in places like the Brooks Range in Alaska, with melt water streams, swamplands, and otherwise harsh conditions. Paleoenvironmental data indicate that emergent tundra was dominant in the post-glacial Yellowstone Plateau (Huerta et al. 2009).

For reasons of scanty populations that kept on the move and a dynamic environment that erased archaeological sites, Early Paleoindian sites are fairly rare in the GYE. Only two 11,000-year-old Clovis projectile points have been found in the Gardiner area, one during construction of the post office and one by University of Montana (UM) researchers near the old townsite of Cinnabar (MacDonald and Livers 2010). A very small number of Clovis points of Obsidian Cliff obsidian indicate that the earliest human use of the GYE was in part motivated by the need for high quality stone for projectile point manufacture. The closest substantial Clovis site to the Gardiner Basin is the Anzick Clovis burial site, north of Livingston (Lahren 2006). Certainly, Clovis people were in the GYE, but their population densities were very low.

There is little evidence of intensive use of the Yellowstone Park area until the Late Paleoindian period, approximately 9,000 years ago. Until that time—between 11,000 and 9,000 years ago—paleoenvironmental data suggest that the Yellowstone Plateau and the far upper reaches of the Yellowstone River (including the Gardiner Basin) were in a period of environmental transition from tundra to pine and spruce parkland. Summer temperatures and winter moisture both increased at this time. By 9,000 to 8,000 years ago, however, those transitional, post-Pleistocene conditions gave way to a more stable environment which was exploited by Native American hunter-gatherers at sites like Osprey Beach on the southern shore of Yellowstone Lake (Johnson 2001; Shortt 2003). As reported by Whitlock et al. (1991, 1995), pollen profiles for ponds and lakes in northern Yellowstone indicate a climate that was wetter than today, with more pine, juniper, and birch and less Douglas fir. Forest fire frequency was also fairly low at this time (Huerta et al. 2009). Native Americans hunted and gathered a wide variety of resources within the Yellowstone region, including bison, deer, bighorn sheep, bear, and rabbit, among others (Sanders 2001). Fish was not a significant portion of the diet, even at sites along rivers and lakes.

Between 8,000 and 5,000 years ago, climate conditions changed throughout the region, bringing a fairly hot and dry climate; this time has been dubbed the altithermal climatic period (Antevs 1953). The altithermal

has been documented in other regions throughout North America, particularly the Great Plains (Meltzer 1999). In the Gardiner Basin and the northern range of Yellowstone, paleoenvironmental data collected by Whitlock et al. (1991), among others, suggest advancing forest and steppe vegetation after 7,600 years ago. Sagebrush and native shortgrass prairie pushed into the area at the expense of the pine parkland.

After 8,000 years ago, human occupation of the GYE was focused in the uplands to escape the hot and dry lowlands. For example, Mummy Cave (Husted and Edgar 2002) near the East Entrance to the park—at an elevation of 6,215 ft—and the Fishing Bridge Point Site at Yellowstone Lake (MacDonald and Livers 2010)—at an elevation of 7,800 ft—indicate fairly active use of high-elevation river valleys and lake resources during this period. At Yellowstone Lake, grassland steppe vegetation dominates during this period, whereas prior to 8,000 years ago pine and spruce are much more common (Huerta et al. 2009).

The dominance of grass pollen is a testament to the dramatic climate change that occurred during the altithermal period at high-elevation settings like Yellowstone Lake; it was so severe that forests in uplands around the lake were replaced by grasslands. Forest fire frequency also increased during the mid-Holocene, likely due to the increased summer insolation of the altithermal (Millsbaugh et al. 2000). The increase in fire frequency is likely attributable to both cultural and natural mechanisms. Natural fire events increased due to the hot and dry climate; however, the role of Native Americans should be considered as well. It was common for Native Americans to use controlled fire to improve forage for prey species or for other purposes.

In the Gardiner Basin, grasslands faltered under increasing summer temperatures of the altithermal, forcing game, and in all likelihood people, into uplands. During the UM archaeological survey of the Gardiner Basin in 2007–2008 (Maas and MacDonald 2009), researchers did not recover any Early Archaic (altithermal period) artifacts in this hot low-elevation landscape. In contrast, UM recovered several projectile points and a hearth feature of Early Archaic age at the high-elevation Yellowstone Lake (MacDonald and Livers 2010). These data support the hypothesis that hunter-gatherers probably travelled through places like the Gardiner Basin in their quest to get to cooler, more biodiverse locations like Yellowstone Lake. It was during this period that Pleistocene bison—

Bison antiquus—became extinct, while the modern *Bison bison* emerged due to its ability to adapt to the altithermal's harsh conditions.

After 5,000 years ago—during the Middle Plains Archaic Period—large bison herds emerged on the landscape, with the ameliorating climate and increased biomass of improved grasslands. During this period, paleoenvironmental data indicate increased moisture and decreased summer insolation, bringing back shortgrass prairies to the Gardiner Basin, with decreasing sagebrush and increasing stands of pine in well-watered areas (Huerta et al. 2009). Pollen profiles at Middle Archaic and Late Archaic sites in the Gardiner Basin show a dominance of pine, sagebrush, and grass, a similar type of pollen profile that we would see in undisturbed areas today (Gish 2010). Thus, it is at this time—between 5,000 and 3,000 years ago—that the essentially “modern” or “pre-contact” landscape emerged in the Gardiner Basin, as well as throughout the Plains and Rockies. The essential character of the environment at 4,000 years ago more or less resembled that of roughly 300 years ago, prior to the arrival of Europeans.

The most intensive period of use in the Gardiner Basin during all of prehistory was the last 5,000 years, peaking between 3,000 and 1,500 years ago, when grasslands sustained large herds of ungulates. Blood residues on projectile points, as well as faunal remains from archaeological sites, indicate that a variety of game were hunted by Native Americans living in the Gardiner Basin and Greater Yellowstone (Sanders 2001). While the period between 3,000 and 1,500 years ago marks the emergence of the classic Plains bison-hunting culture, people living in the GYE utilized a wide range of hunted and gathered resources.

While prior research suggests a drop-off in use of the GYE during the 1,500 years prior to European-American contact (Johnson 2001), UM's recent research suggests active use of the Gardiner Basin and Greater Yellowstone during this period (MacDonald and Livers 2010). UM researchers have excavated several Late Prehistoric features—mostly fire pits and hearths, and also projectile points—which indicate active use of a variety of Late Prehistoric resources, including widespread use of plants, such as chenopods (herbaceous forbs from the goosefoot and pigweed families) likely used as a flavoring or moisture protectant during the roasting of game. *Chenopodium* seeds are edible as well.

Research certainly indicates that Yellowstone was used by Native Americans until Euro-American encroachment in the area. Two of UM's three excavated hearths from the



Figure 2. The Yellowstone River in Hayden Valley. National Park Service photo.

2008 work at the Airport Rings stone circle site just north of Gardiner show use of tepee structures as recently as 250 years ago (Livers and MacDonald 2009). Two hearths at Yellowstone Lake near Fishing Bridge yielded dates within the last 250 years as well. Archaeological data from these sites in the GYE show continued hunting and gathering of the vast variety of resources in the region, including active use of Obsidian Cliff obsidian and a variety of game and plants.

Pollen and ethnobotanical analysis of those Late Prehistoric features' contents provides an interesting window into the types of plants in the area just prior to European contact with native peoples (Gish 2010). Pollen profiles contain a variety of native arboreal species, including pine, spruce, Douglas fir, juniper, and elm, likely representing wind-blown pollens from trees in nearby uplands. Non-arboreal pollen within the Late Prehistoric features native grasses, greasewood, sagebrush, and goosefoot (*Chenopodium*), all of which might have been used as wild resources by Native American hunter-gatherers. Macrobotanical plant fragments were also recovered in the features, indicating processing of prickly pear cactus and goosefoot as food and sagebrush as firewood. This suite of native plants suggests that the Gardiner Basin, despite its dry and arid condition, provided ample vegetation for hunting and gathering people to live quite comfortably.

However, while we have abundant archaeological and ethnographic evidence which indicates active use of the

park's land by Native American hunter-gatherers, linking specific tribes to the park's prehistory continues to be challenging. There are few historic accounts of Native American use in northern Yellowstone National Park after the park's creation in 1872. This is mainly due to efforts by the early administrators of Yellowstone National Park to downplay or eliminate Indian involvement and usage of the park, which was intended to encourage American and European tourists to feel safe after the 1877 Nez Perce encounter in the park and the 1878 Bannock War. In general, though, most of the more contemporary sites, dating from about A.D. 1500 onward, are dominated by Shoshone, Blackfoot, Crow, and Salish tribes (Nabokov and Loendorf 2002).

At 1500 A.D., the overall ecological setting of the Gardiner Basin was similar to today, with the exception that at that time the vegetation was dominated by a variety of native grasses and shrubs. Today, as described below, while sagebrush remains, ever-present non-native grasses and invasive weeds dominate the former agricultural fields.

Historic Use of the Gardiner Basin

The introduction of European-Americans into the Gardiner Basin was fairly devastating to the local ecology. Agriculture (plowing and irrigation for crops) and cattle grazing removed most native vegetation on the tillable, non-rocky areas, and non-native weeds now dominate the abandoned fields. To track this change, we now provide a brief overview

of the historic use of the Gardiner Basin, with an eye on the major differences of its use compared to the prehistoric period.

While a definitive date for the establishment of the first Euro-American settlement in the Gardiner Basin is unknown, Lee Whittlesey's research suggests that James Henderson and his brother A. Bart Henderson established residence in 1871 when they built their "Bozeman toll road" along the Yellowstone River (Whittlesey 1995). The next recorded settlement in the project area was George W. Reese in April 1875. In 1880 the town of Gardiner was founded at the mouth of the Gardiner River by James McCartney after he and Harry Horr were evicted from their illegal hot springs bathing business site near Mammoth Hot Springs. One of the first structures erected in the Gardiner area was a horse-racing track on the southern side of "Gardiner Flats," southwest of the North Entrance station (Whittlesey 2008).

During their ownership of the ranch, George Reese and his sons had at least three different ranch houses in the area. A portion of Reese's property (likely a right-of-way) was sold to the Northern Pacific Railroad (NPRR) in June of 1883 (Whittlesey 1995). The right-of-way allowed the Northern Pacific Railroad to bring its tracks to within three miles of Gardiner. During this same year, Hugo John Hoppe established his homestead just south of the Cinnabar town site on August 4th and moved his family there (Dick and MacDonald 2010).

Historic accounts and early photographs of Cinnabar confirm the rather bleak aesthetics of the town. A visitor who passed through Cinnabar in August 1884 stated that the town consisted of "four houses and a depot in a box car," which indicates that the town had not grown much in the year since its founding. By 1885, an actual building had been established as a depot, while a traveler to the town described Cinnabar as "a few ranches, a hotel, two or three stores, twice as many saloons, a few private houses, and the railroad depot" (Whittlesey 1995). One saloon was located just south of the hotel. It is not clear where the other saloon was located. Hoppe eventually owned a hotel with a dining room, a saloon, large barn, warehouse, and general store. The store was run by Billy Hall who founded the Hall Company in Gardiner. Later that summer, Hoppe built a livery stable, blacksmith shop, mill, icehouse, and other homes (Dick and MacDonald 2010).

The NPRR was finally extended to Gardiner on December 15, 1902, which signaled the collapse of

Cinnabar. After the Park Line extension of the railroad into Gardiner, several businesses left Cinnabar and relocated to Gardiner. In 1903, President Theodore Roosevelt visited Yellowstone and his train was parked for 16 days at Cinnabar instead of Gardiner (Whittlesey 1995). The Cinnabar Hotel became the "temporary White House" during his visit. Roosevelt held many of his cabinet and presidential details in the hotel. After Roosevelt's stay, however, Cinnabar was largely abandoned and the area quickly reverted to ranchland.

In the 1930s, over 7,000 acres of this area were added to the northwest corner of Yellowstone National Park through purchase and eminent domain to provide key low-elevation winter range for elk, pronghorn, bison, and deer. Approximately 700 acres of the addition were irrigated agricultural fields. Following acquisition, the park ceased irrigation and seeded the fields to crested wheat-grass (*Agropyron cristatum*), an exotic perennial grass which was recommended because it was aggressive, would crowd out weeds, was drought resistant, undergoes early green-up and was (erroneously) thought to provide better forage than native plants. It thrived and for many decades was almost the only plant species present.

Fixing Historic Damage to the Gardiner Basin

The overall effect of this historic use of the area was a complete removal of nearly any native vegetation in the lowland tillable flat areas along the Yellowstone River. Without vegetation to hold the soil in place, wind can cause significant soil movement and degradation of the soils. The University of Montana's archaeological excavations at Cinnabar revealed the extent of the wind erosion in the Gardiner Basin. UM's excavations focused on the basement of Hoppe's hotel, abandoned in the early twentieth century soon after Roosevelt's stay. At the time of the abandonment, the hotel was removed, leaving the basement open to the elements. During the next 100 years or so, the five-foot-deep and 2,500 square foot basement filled with approximately 12,500 cubic feet of sediment, evidence of extreme erosion due to westerly winds blowing through the basin.

Figure 3 shows a profile of UM's excavations within the hotel foundation, revealing layer upon layer of eroded, wind-blown sediment. Other evidence of the historic use of Cinnabar has been nearly erased from the ground surface, with most former building locations completely invisible on the ground surface. UM's use of sub-surface

imaging technology facilitated the identification of buried house features that were otherwise not observable on the ground surface at Cinnabar (Sheriff et al. 2010).

As revealed by UM's archaeological work at Cinnabar, while the Gardiner Basin was utilized for agriculture for less than 60 years, the effect was fairly devastating. Today, the former fields are dominated by non-natives: crested wheatgrass, a remnant of the park's post acquisition seeding efforts, and an exotic mustard, desert alyssum (*Alyssum desertorum*). In drought years even those weeds suffer in the heat of the Gardiner Basin, leaving large patches of un-vegetated soil, vulnerable to even more wind erosion. The current vegetation provides poor forage for ungulates and the physical and ecological condition of these sites continues to degrade. The park has attempted a variety of native revegetation experiments that have failed. In retrospect, they were too small in scale, too short term, and failed to recognize the special remedial actions needed to repair

these degraded semiarid soils so that they can again sustain the native vegetation.

Restoring a Ruined Landscape

In recognition of the deteriorated condition of the area, Yellowstone National Park has begun a long-term pilot restoration project for the former agricultural fields. The goal of the project is to restore ecologically sustainable native plant communities. While revegetation projects had been successfully completed in other areas of the park, none were in as dry and hot a landscape as the Gardiner Basin.

Led by Mary Hektner and colleagues from the Yellowstone National Park Center for Resources, the Gardiner Basin Restoration Project proposes to restore native plant communities to approximately 700 acres of former agricultural fields between Gardiner and Reese Creek. Recognizing that the park staff did not have the experience in arid land restoration that was needed, the park joined with

Gallatin National Forest and the Montana State University-based Center for Invasive Plant Management to convene a restoration workshop in April 2005. Ten specialists in arid land restoration were invited to help Yellowstone and Gallatin National Forest (which acquired similar former agricultural lands for wildlife habitat adjacent to the park) develop recommended long-term restoration/management plans for approximately 1,200 acres of former agricultural fields within Yellowstone and Gallatin National Forest.

The workshop resulted in recommended strategies and extended timeframes to restore a mosaic of sustainable native plant communities that provide wildlife habitat and forage. Desired species include, but are not limited to, Sandberg's bluegrass (*Poa secunda*), bluebunch wheatgrass (*Elymus spicatus*), needle and thread (*Hesperostipa comata*), Junegrass (*Koeleria macrantha*), Indian ricegrass (*Achnatherum hymenoides*), wild onion (*Allium textile*), winter fat (*Krascheninnikovia lanata*), saltsage (*Atriplex gardneri*), rabbit brush (*Ericameria nauseosa* and *Chrysothamnus viscidiflorus*), greasewood (*Sarcobatus vermiculatus*), western wheatgrass (*Elymus*

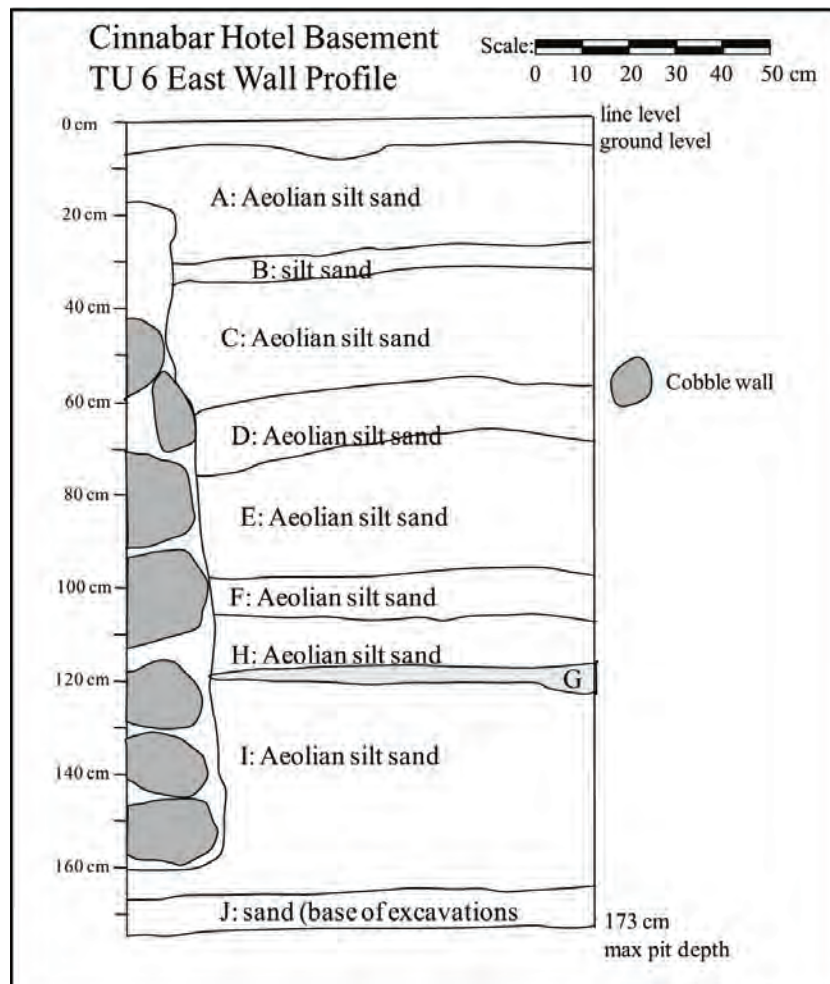


Figure 3. Cinnabar basement wall profile. Note the five feet of wind-blown sediment accumulated against the cobble basement wall.

smithii), Wyoming big sage (*Artemisia tridentata* var. *wyomingensis*), and prickly pear cactus (*Opuntia polyacantha*). As discussed above, archaeological features from the Airport Rings stone circle site just north of Gardiner contained several of these very species.

Four pilot areas totaling 50 acres were fenced in 2008 and 2009. The first 23-acre site, which was fenced in 2008, was treated with herbicides and no-till drill seeded to a cereal barley crop in the spring of 2009. It and a seven-acre pilot site was no-till drill seeded to winter wheat in September 2009 and barley in May 2010. The other two pilot sites were treated with herbicides in May 2010. All four units were seeded to winter wheat in September 2010. No-till drilling of the native grass seed is scheduled for the fall of 2011 and fall of 2012.

Ultimately, the Gardiner Basin Restoration Project has noble goals, especially in a setting as hot and dry as Gardiner Basin. Once the native plants take hold, the portion of the Gardiner Basin within Yellowstone National Park will greatly resemble the world inhabited by Native American hunter-gatherers prior to European-American contact. The project may become a model for other agencies with similarly disturbed, high and dry landscapes. Park management is thus an important, and enduring, phase of human occupation that has shaped the Gardiner Basin in the Late Holocene, and will provide an interesting phase for our descendants to consider in the long history of Yellowstone National Park.

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Managing Yellowstone for Ecosystem Resilience in the Age of Human-Forced Climate Change

Tom Olliff¹ and Paul Schullery²

¹ NPS Coordinator, Greater Northern Landscape Conservation Cooperative, 2327 University Way, Suite 2, Bozeman, MT 59715, 406-994-7920, Tom_Olliff@nps.gov

² 1621 South Black, Bozeman, MT 59715, 406-585-5337, pds@bresnan.net

Abstract

The most fundamental strategy of climate change adaptation management—that is, adjusting land management in response to changing climate variables and ecological response—is managing for ecosystem resilience, or increasing the amount of change or disturbance that an ecosystem can absorb without undergoing a fundamental shift to a new system. Of several approaches to build resilience, three have particular relevance to land managers in the Greater Yellowstone Ecosystem: protecting key ecosystem features, reducing anthropogenic stressors, and restoring functionally intact ecosystems. Since Yellowstone National Park was established in 1872, the fundamental strategies of natural resource management have evolved to focus on restoring resilience to the ecosystem. This evolution in management strategies can be described over five stages or eras: 1) the “Wide-Open” Era in which park resources were treated similarly to corresponding resources elsewhere in North America (1872–1883); 2) the Game Preservation Era in which preferred wildlife species were favored at the expense of the rest of the ecological community (conservatively 1883–1916, liberally 1883–1974, or even 1883–1994); 3) the Agricultural Era, in which park managers embraced established commercial standards for measuring resource-management success (1918–1968); 4) the Ecological Management Era (popularly known as “natural regulation,” 1968–1984); and 5) the Native Species Restoration Era (1984–present). We propose the possibility of a sixth era, of landscape-scale conservation, that is now beginning. Understanding the context of Yellowstone’s present resource management strategy—and the driving forces behind the evolving strategies—can provide valuable tools to apply to today’s challenges.

Introduction

Human management of the Greater Yellowstone Ecosystem (GYE) landscape is an ancient endeavor. Various groups of native people who lived in or visited the present GYE are known or assumed to have had a variety of effects on plant and animal communities. Archeological and historical evidence indicates that native people hunted a variety of native animals and gathered numerous plant species (Haines 1977; Schullery 2004; Nabokov and Loendorf 2004; Loendorf and Stone 2006). Perhaps the most persistently discussed human effects on the GYE landscape prior to the arrival of Euro-Americans involve fire. It is known that native people in the American West intentionally set fires for several purposes, but like other activities of native people prior to Euro-American settlement of the GYE, our knowledge of the specifics of these activities, and how these activities may have changed over time, is regrettably slight: “Direct evidence still remains too thin to make a solid case about the degree to which Yellowstone National Park (YNP) proper was subject to alteration by intentional Indian fires, though some scholars have tried” (Nabokov and Loendorf 2004, 2008).

The present paper focuses on management ideologies and strategies since the creation of Yellowstone National Park (YNP) in 1872. However, it is essential to recognize that in modern land-management dialogues in the GYE that “prehistoric” ecology has been an important and controversial point of debate. The extent and meaning of native peoples’ activities and effects on the GYE, and on national park landscapes generally, are still a matter of intense interest and disagreement among researchers, managers, and advocates attempting to select or influence future management direction (Craighead et al. 1995; Kay 1995; Yochim 2001; Vale 2002; Schullery 2004; Cole et al. 2008).

Any attempt to break a historical continuum of events into distinct segments or “eras” as we do here must begin with an admission of the fundamentally artificial nature of the enterprise. While such chronological organizations are often helpful, they always involve a certain amount of arbitrary dating of ideas, processes, and movements that are not really that tidy. History does not periodically restart itself with a clean slate: the seeds of each successive era were sown in the previous era.

That admitted, there is still great worth in identifying general trends in the thoughts and actions that have shaped our management of the GYE and YNP. The identification of such eras is a valuable device for clarifying past and future directions of thinking.

Era 1. 1872–1883: The Wide-Open Era

The act creating the park gave little direction to the Secretary of Interior regarding the park's biological features, beyond requiring that they be protected in their "natural condition," a mandate and a term we have spent the last 138 years debating (U.S. Statutes at Large, Vol. 17, Ch. 24, 32–33; Haines 1974; Pritchard 1999; Wagner et al. 2006; Cole et al. 2008).

Because of the widespread slaughter of thousands of animals in the new park, in 1883 the Secretary of the Interior established a policy forbidding hunting in the park—in one stroke creating the world's foremost public wildlife preserve (Hampton 1971; Haines 1977; Schullery 2004). The park was created to preserve geological wonders, but from 1883 on, biological values dominated management attention, and initiated the second of our management eras.

In the park's first 11 years of existence a number of forces combined to set later managers up for difficult quandaries about management of this pioneering experiment in natural resource stewardship. Exclusion of native people and their activities became progressively more thorough, thus ensuring that whatever their influences on the landscape had been prior to the creation of YNP, those influences diminished or disappeared (Nabokov and Loendorf 2004). The Little Ice Age, a cooler period of about four centuries, ended at mid-nineteenth century, thus ensuring that the ecological setting of the GYE was in for a period of adjustment and change even if Euro-Americans and their influences had not visited the region. And Euro-Americans, appearing in increasing numbers, began a wholesale overhaul of large portions of the landscape, including the sustained destruction of large mammals. It is only in the past four decades that intensive attention has been paid to the long-term consequences of such dramatic changes that occurred in the park's first years.

Era 2. 1883–1918: The Game Preservation Era

The Game Preservation Era was characterized by protection and promotion of favored animal species. Few predators were protected, and the destruction of the others was better organized (Schullery and Whittlesey 1999). Popular

non-native fish were widely introduced (Varley and Schullery 1998; Franke 1996, 1997). Non-native plant species were increasingly introduced, both accidentally and intentionally (Despain 1990; Whipple 2001; Olliff et al. 2001). Introductions of other European and North American game animals were planned or attempted. Favored scenery was likewise nurtured (Schullery and Whittlesey 2001). The suppression of natural fires was initiated by the U.S. Army in 1886 (Barker 2005; Franke 2000). With hindsight, we may be inclined to see these early managers as short-sighted or misguided, but their grasp of their responsibilities was often quite nuanced. It is difficult for us to fully imagine the intellectual and political realms they inhabited.

Except for the first three years under civilian administration, the Game Protection Era as we define it coincided precisely with the 32-year stay of the U.S. Cavalry in YNP (1886–1918; Haines 1977; Bartlett 1985; Broadbent 1997; Barker 2005). The army provided the necessary discipline and muscle to see the struggling young park through its early years, and army officers activated much of the resource-management policy that was continued by the National Park Service (NPS) when that agency assumed full control of the park in 1918.



Figure 1. Ranger Ted Ogsten and Chief Ranger Sam Woodring with coyote pelts collected during predator control operations in Yellowstone National Park in 1927. National Park Service photo.

Era 3. 1918–1968: The Agricultural Management Era

We have named this era “agricultural” because many management practices tended at first to reflect prevailing professional agricultural values. But this era witnessed the slow, comprehensive, and often bitterly resisted departure of park policies from mainstream agricultural thinking (Pengelly 1963; Tyers 1981; Houston 1982; National Park Service 1997; Klein et al. 2002). Established army programs such as predator killing (Figure 1), ungulate feeding, ungulate population control, fire suppression, bear feeding, and fish stocking were at first embraced, but eventually met with increased scrutiny and disapproval (Schullery 2004). By 1968, the end of this era, all such programs were either eliminated or were circling the drain.

Ecological thinking eased in slowly, but by the 1930s, biologist George Melendez Wright and his colleagues laid out a series of essentially modern ecological rationales for national park management (Wright et al. 1933). The influential Leopold and Robbins reports of the early 1960s reinforced the earlier work of Wright et al. (Leopold et al. 1963; Robbins et al. 1963). By the late 1960s, political crises in the management of several charismatic wildlife species became irresistible forces for abrupt changes in policy and led to a comprehensive and controversial reimagining of the park’s potential as an institution (Houston 1982; Schullery 1992; Craighead et al. 1982; Craighead et al. 1995; National Park Service 1997; Barmore 2003).

Era 4. 1968–1983: The Ecological Management Era, Popularly Known as “Natural Regulation”

This is the first era in which the goal of managing for “naturalness,” a concept implicit in the NPS 1916 Act, and reflective of the spirit of the 1964 Wilderness Act, came to be a dominating policy. The concept of “naturalness,” like the earlier term “natural condition,” is constantly still discussed and debated (Boyce 1991; Wagner et al. 2006; Cole et al. 2008). In this era, a goal coalesced around the principle of heightening wildness, that is, of allowing ecological processes as much independence and as little obstruction by humans as possible (Despain et al. 1986). The flagship issue of this era, in fact the issue that more than any other launched it, was management of Yellowstone’s northern range. After several decades of intractable controversy, in the 1960s park rangers killed thousands of elk to satisfy prevailing but erroneous concepts of appropriate popula-

tion size and range condition. This crossed public and political thresholds of tolerance, forcing management change just as new thinking in wildland ecology arose (Houston 1982; Barmore 2003). In 1971, ecologist Douglas Houston laid the groundwork for a new and enormously productive scientific inquiry and debate with a hypothesis for ecological management of the northern herd, predicting that the herd would be limited by intraspecific competition for food and associated winter mortality with no “negative” effects on other ecosystem elements (Houston 1971). More than 100 scientific studies later, the analysis and controversy continue (Despain 1994; National Park Service 1997; Wagner et al. 2006). This flagship issue was accompanied by a hefty fleet of other equally vexing and stimulating issues. Restoration of the essential functions of wildland fire began in the park’s centennial year and seemed a model of policy success until the fires of 1988 revealed how socially, politically, and scientifically challenging authentic wildland fire processes could be (Figure 2; Franke 2000; Wallace 2004; Barker 2005). Brucellosis in Yellowstone bison, as historically venerable an issue as elk management, likewise tested attempts to break down the famous “boundary mentality” that so often frustrates advances in ecosystem management (Meagher 1973, 1989; Franke 2005; Gates et al. 2005; GAO 2008). And the separation of grizzly bears from human food sources, while revealing a sea-change in public and management attitudes, has only been accomplished and sustained through continued intensive research and monitoring (Schwartz et al. 2006). The scientific legacy of the Ecological Management Era is infinitely richer than that of its predecessors. It heralded an unprecedented intensity of scientific scrutiny on the Greater Yellowstone landscape, perhaps best exemplified by the three occasions on which the National Academy of Sciences has been called upon to analyze and arbitrate Yellowstone’s scientific conversation (Cowan et al. 1974; Cheville and McCullough 1998; Klein et al. 2002). It is also exemplified by this successful biennial scientific conference series.

Era 5. The Restoration Era: 1983–Present

In 1976, the National Park Service made an unsuccessful attempt to restore grayling to a small stream in the Madison River drainage, but we begin this era in 1983 because of the high-profile success of peregrine falcon restoration beginning that year (Baril et al. 2010). There followed a



Figure 2. Firestorm approaching the Old Faithful development during the famous 1988 fire season, when the full implications of the restoration of natural fire to Yellowstone became evident. National Park Service photo.

second unsuccessful attempt at grayling restoration in the mid-1990s (Kaya 2000); restoration of abandoned mine lands beginning in 1990 (Olliff, pers. comm.); of wolves beginning in 1995 (Smith 2005); of bald eagles in 2005 (Baril et al. 2010); of abandoned agricultural fields in the Gardiner Basin in 2008 (NPS 2010); and of westslope cutthroat trout in the Gallatin River drainage in 2008 (Koel et al. 2008). Concurrently, a series of projects aimed to protect native species from non-native invasives included eradication of clandestinely introduced brook trout from Arnica Lagoon and Creek in 1985–86 (Gresswell 1991); intensive efforts to control exotic plants (1986–present; Olliff et al. 2001); lake trout control in Yellowstone Lake (1995–present; Varley and Schullery 1995; Koel et al. 2008; Gresswell 2009); and implementing the Interagency Bison Management Plan to control the spread of the exotic bacteria *Brucella abortus* (2000–present; Plumb et al. 2009; Cross et al. 2010). Contrary to a common perception of natural regulation as a passive, hands-off policy, these programs reveal a forcefully intrusive management effort to restore and preserve ecosystem functions. The environmental legislation of the 1970s took hold slowly in Park Service culture and greatly increased the complexity of all management processes. Ironically, despite the tremendous increase in research since the 1960s, it wasn't until the passage of the National Parks Omnibus Management Act in 1998 that the 82-year-old agency was actually required to use science as a basis for management decisions (National Parks Omnibus Management Act 1998).

Interagency ecosystem-level management became common during this era despite strong political resistance. The Greater Yellowstone Coordinating Committee, composed of park superintendents and forest supervisors, was formed in 1964, but paid very little attention to ecosystem issues until the mid-1980s, by which time Yellowstone staff were already quietly involved in dozens of cross-boundary initiatives (Congressional Research Service 1987; Greater Yellowstone Coordinating Committee 1991; Barbee et al. 1991). Today, with high-profile management programs like grizzly bears and bison, the roll call of involved agencies, tribes, and other entities is more of a directory than a list.

Era 6? A Guess about the Future: Are We Entering the Landscape Conservation Era?

In 2009, Secretary of the Interior Ken Salazar mandated that because of the breadth of impacts of climate change, all Interior Department bureaus must contribute to large-landscape conservation. It is almost uncanny how the eras of “Ecological Management” and “Restoration” anticipated the large-landscape conservation approaches suggested in the recent scientific literature. The National Park Service now has co-leadership of the Great Northern Landscape Cooperative, which covers much of Wyoming, Montana, Idaho, Washington, and parts of Oregon; it is one of 21 such science-management partnerships established to promote large-landscape conservation (DOI SO 3289). To-

day, throughout the realm of natural-area management, there are calls for a fresh look at the inherent ambiguities of traditional and even more recent management strategies (Cole et al. 2008; Jackson and Hobbs 2009). Pluralistic strategies for future management direction include various combinations of managing for naturalness while conserving biodiversity and resilience. Yellowstone will no doubt play an important role in these deliberations and in the management experiments that grow from them.

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Spatial and Temporal Dynamics of Recent Forest Disturbance in the Greater Yellowstone Ecosystem

Scott Powell

Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 59717,
406-994-5017, spowell@montana.edu

Abstract

Forest fires and insect outbreaks are common forest disturbance agents in the Greater Yellowstone Ecosystem (GYE), but the cumulative effects of forest management and climate change have potentially exacerbated these disturbance dynamics in recent years. I quantified the patterns and rates of conifer forest cover change across the northern portion of the GYE to better understand how and where disturbance regimes were changing. I examined a nearly 40-year time series of aerial photographs between 1971 and 2009 to understand how the frequency, type, and location of forest disturbances have changed. The most notable change was the increase in the frequency of insect outbreaks across the northern portion of the GYE over the past 10 years, compared to the period 1971–1999. The next step in this research will be to use the aerial photo data as reference and validation for satellite remote sensing–based analyses of forest disturbance between 1984 and 2010. For this effort I will assemble a dense time series of Landsat imagery and employ novel time series change detection techniques to quantify the location, type, and timing of forest disturbance events on an annual time scale. The goal of this study is to improve our understanding of recent forest disturbance dynamics in the GYE and to help formulate hypotheses about the interactions among forest disturbance processes.

Introduction

Forest structure and composition are governed by dynamic processes, including forest succession and disturbance events like insect outbreaks and fire. Quantifying the spatial and temporal variability of forest dynamics and elucidating the factors that shape the patterns and trends we see across our landscapes remains a major challenge for science and land management alike.

In some parts of the Greater Yellowstone Ecosystem (GYE), namely lower elevation forests, historical land management practices, including fire suppression, livestock grazing, and forest management, have contributed to widespread increases in the density and extent of conifer forest (Gruell 1983; Meagher and Houston 1998). Variability in the rates of conifer encroachment across the GYE (Powell and Hansen 2007) has resulted in altered forest structure and composition in places. I hypothesize that these changes, along with changing climate, have created favorable conditions for insect outbreaks. However, interactions among forest dynamics and disturbance processes remain untested at broad spatial and temporal scales, warranting a more synoptic and spatially expansive analysis.

This study seeks to address two primary questions:

1. How have the spatial and temporal patterns of forest dynamics changed in the GYE over the past several decades?

2. What are the interactions among forest dynamics? Specifically, does conifer encroachment influence subsequent patterns of insect outbreaks?

The methodological approach to address these questions relies on a long-term retrospective dataset of aerial photographs spanning nearly 40 years from the early 1970s through the modern era. This proceedings paper briefly documents the initial stages of this research effort and presents preliminary results based upon a limited analysis of the data. I have only begun to analyze the 40-year aerial photo time series and present preliminary results based on that effort.

Methods

I quantified the changes in forest structure and composition using a nearly 40-year time series of aerial photographs (1971, 1999, and 2009). I previously documented forest dynamics in the GYE between 1971 and 1999 with a large sample of over 2,000 plots (Powell and Hansen 2007). For this proceedings paper, I present preliminary results of photo interpretation from 1971–2009 from a 20 percent random subsample of 0.81 hectare (ha) photo plots ($n = 209$) from the northern transects of the GYE (labeled transects north of Yellowstone National Park; Figure 1). Aerial photo interpretation methods relied on

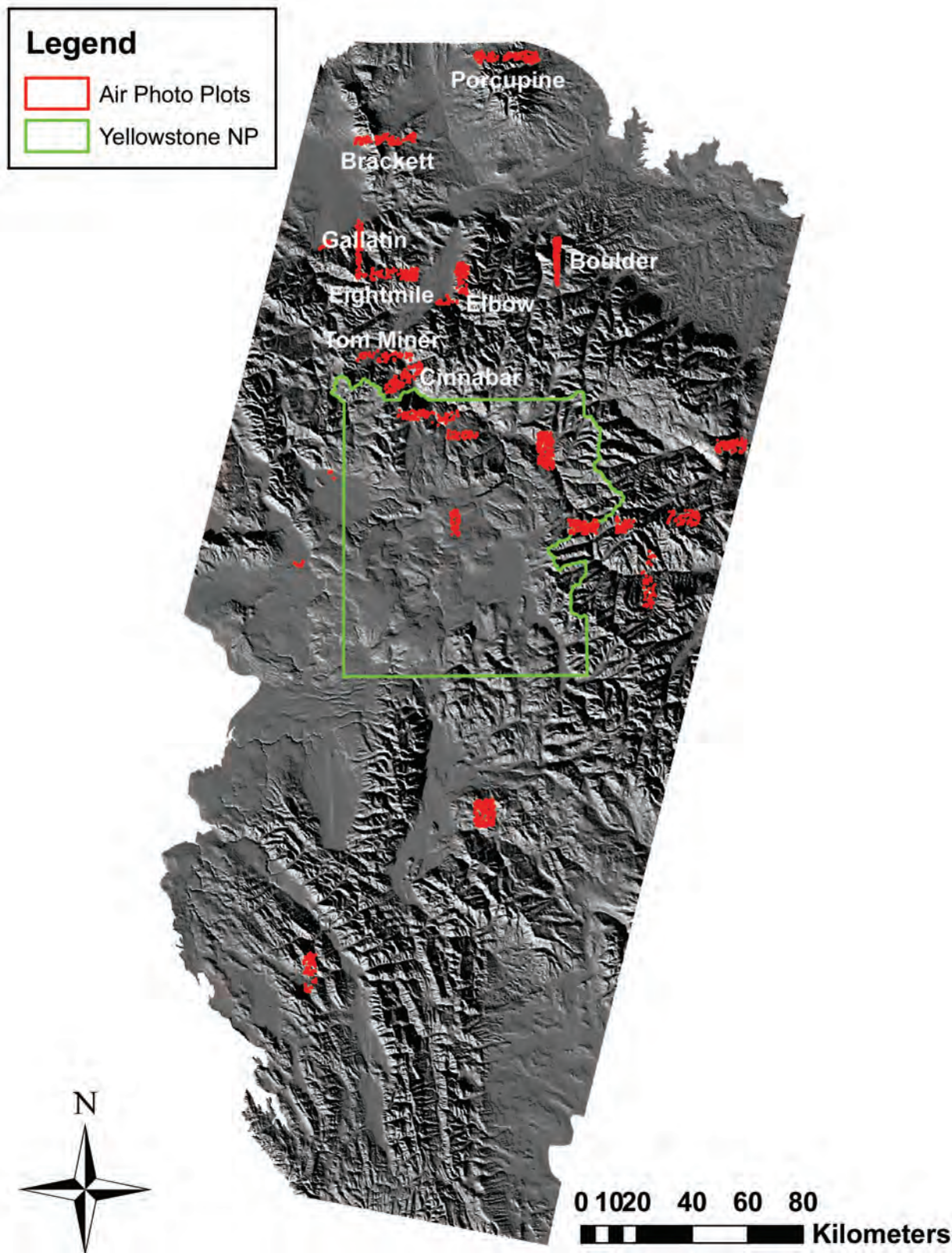


Figure 1. Aerial photo sample plots within transects across the GYE. Over 2,000 plots were previously interpreted for the time period 1971–1999. For the purposes of this paper, a random sample of 20 percent of the plots within the northern transects (labeled transects north of Yellowstone National Park) were resampled ($n = 209$) to include the time period 1999–2009.

the use of the point-intercept method for determination of the percentage composition of conifer forest (Powell and Hansen 2007). For each photo plot sample, I interpreted the trajectory of conifer forest cover and classified it accordingly as no-change, conifer expansion (conifer cover increase from zero), conifer densification (conifer cover increase), burn, harvest, or conifer decrease (insect outbreak, other mortality). I then compared the type and frequency of various forest dynamics for 1971–1999 with 1999–2009.

Results

Comparing the frequency of forest dynamics for the period 1971–1999 to the period 1999–2009, the biggest change was the dramatic increase in the conifer decrease category, which included various types of insect activity (Figure 2). In the 28 years between 1971 and 1999, only about 8 percent of samples exhibited mortality associated with insect outbreaks. That percentage increased to nearly 25 percent during the period 1999–2009. The other notable change that I observed was the decrease in conifer densification, which went from 30.5 percent of the samples between 1971 and 1999 to 11.9 percent of samples between 1999 and 2009.

To better understand the spatial variability of these changes, I examined the forest dynamics within each of the eight transects from the northern portion of the GYE (Table 1). For this analysis, I grouped conifer expansion and conifer densification into one category termed “conifer encroachment,” and grouped insect outbreaks, fire,

Table 1. Changes in conifer encroachment (expansion + densification) and disturbance (insect outbreaks, fire, and harvest) compared between two time periods (1971–1999 and 1999–2009) for eight transects in the northern portion of the GYE.

Transect name	Sample size	% Change in conifer encroachment	% Change in disturbance
Boulder	31	-12.9	+6.5
Brackett	14	-28.6	+35.7
Cinnabar	24	-20.8	+12.5
Eightmile	37	-32.4	+40.5
Elbow	32	-2.6	+9.9
Gallatin	18	-21.1	+37.8
Porcupine	27	-18.5	+18.5
Tom Miner	17	-29.4	+5.9
Average	200	-20.8	+20.9

and harvest into another category termed “disturbance.” Across all eight transects, the average change in percentage of samples exhibiting conifer encroachment between the two time periods was -20.8 percent. In contrast, the average change in percentage of samples exhibiting disturbance was +20.9 percent. As expected, there was variability among transects. The Elbow transect exhibited the smallest decrease in conifer encroachment (-2.6 percent), while the Tom Miner transect exhibited the smallest increase in disturbance (+5.9 percent). In contrast, the Eightmile transect exhibited both the largest decrease in conifer encroachment (-32.4 percent) as well as the largest increase in disturbance (+40.5 percent).

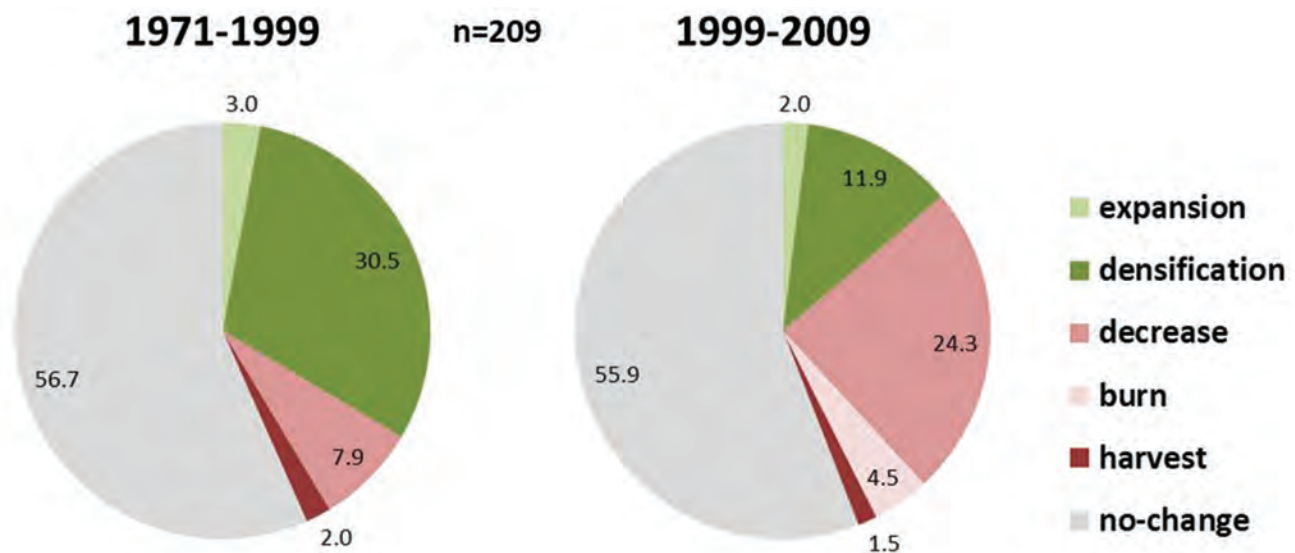


Figure 2. Comparison of forest dynamics between two time periods: 1971–1999 and 1999–2009.

Two transect examples are further illustrated here in greater detail. The first is the Eightmile transect, located between the Paradise Valley and the Gallatin Valley and encompassing the Hyalite region south of Bozeman, Montana (Figure 3). During the period 1971–1999, this transect was dominated by conifer densification (over 40 percent of samples), especially in the lower-elevation forests adjacent to the Paradise Valley. The most recent 10-year period, between 1999 and 2009, tells a very different story. First, the Fridley Fire of 2001 occurred within part of this transect, resulting in a large increase in the burn category. Second, there was a large increase in the conifer decrease category associated with insect activity. Third, there was a large decrease in the conifer densification category.

The second example of the spatial variability of forest dynamics is the Tom Miner transect, near the southern end of the Paradise Valley, encompassing Yankee Jim

Canyon of the Yellowstone River (Figure 4). Here, the most significant change between periods was the notable decrease in conifer densification. Between 1971 and 1999, nearly 60 percent of samples exhibited conifer densification, in contrast to only 35.3 percent of samples between 1999 and 2009.

These preliminary results suggest the possibility of interactions among disturbance processes. I investigated the occurrences of insect outbreaks in the most recent decade (1999–2009) relative to 1971–1999 dynamics. Specifically, for a given sample plot that exhibited insect activity between 1999 and 2009, I quantified the previous trajectory of conifer cover between 1971 and 1999. The results of this analysis indicated that over one third (34.7 percent) of all recent insect activity occurred in forests exhibiting recent conifer densification (Figure 5). In 2009, the average conifer cover of these plots was 75 percent. The

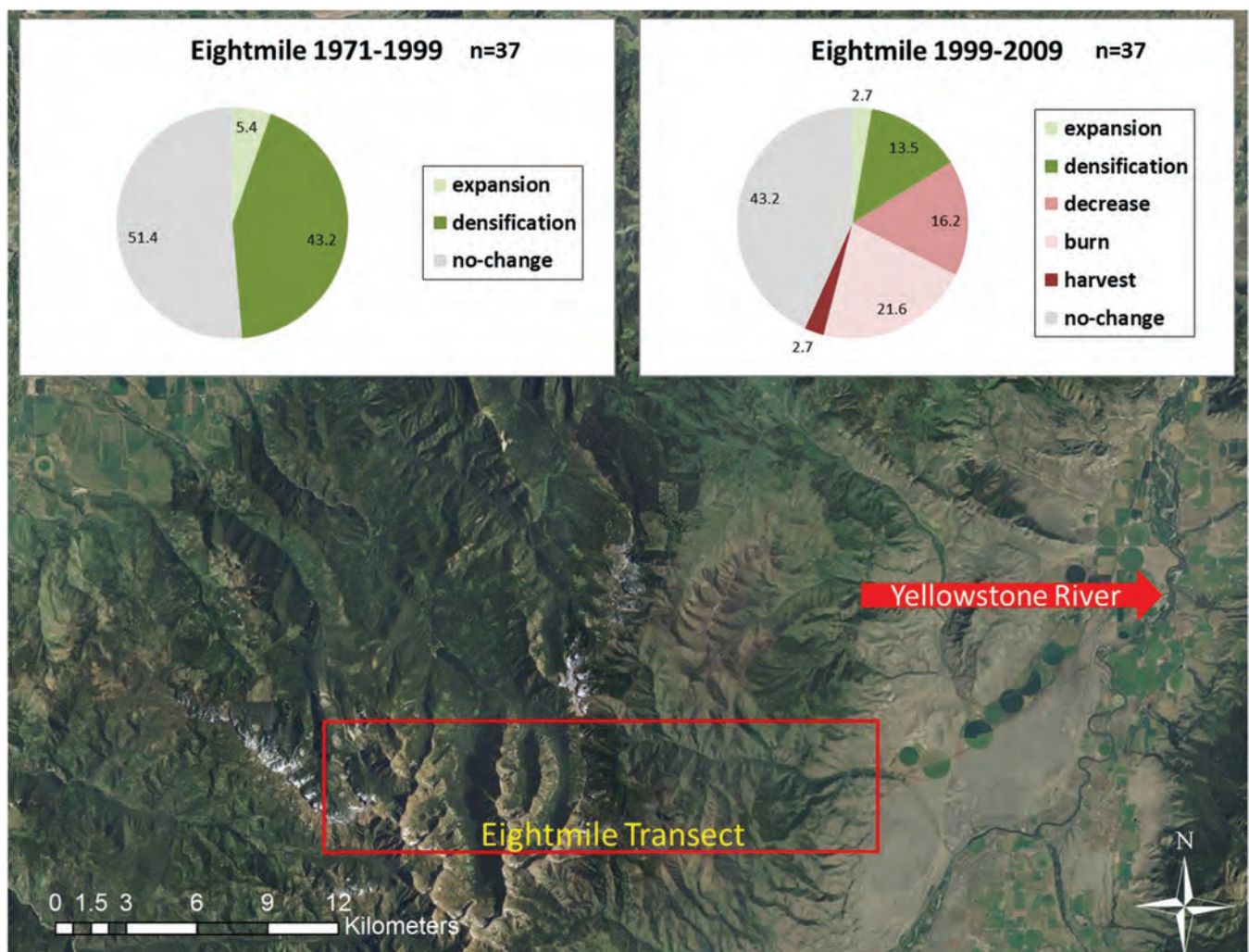


Figure 3. Comparison of forest dynamics for the Eightmile transect between two time periods: 1971–1999 and 1999–2009.

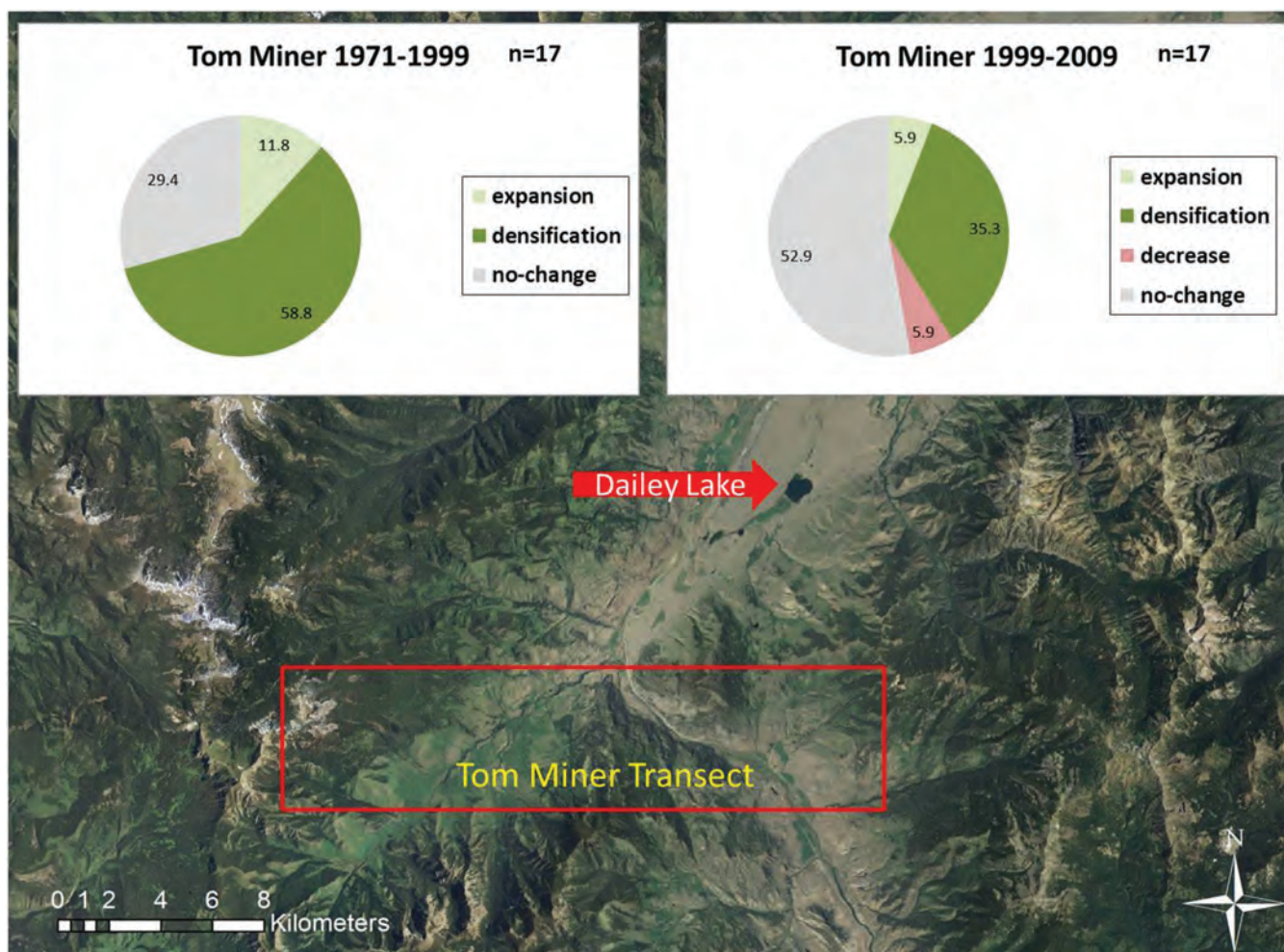


Figure 4. Comparison of forest dynamics for the Tom Miner transect between two time periods: 1971–1999 and 1999–2009.

majority (55.1 percent) of insect activity occurred in areas classified as “no-change” between 1971 and 1999, with an average conifer cover of 86 percent.

Discussion

The rates of forest dynamics and disturbance have varied significantly over recent history according to forest type and bioclimatic setting. From a relatively small sample of aerial photo plots over a nearly 40-year time period, I can conclude that the rate of disturbance associated with insect outbreaks has risen notably since 1999. This is consistent with an abundance of observations from the GYE and across western North America that have shown dramatic increases in mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the past decade (Raffa et al. 2008; Logan et al. 2009; Bentz et al. 2010). By historical standards, widespread insect outbreaks are not unprecedented in the GYE (Romme et al. 1986; Lynch et al. 2006), but the current scope of infestation may be larger than those previ-

ously documented. Some of the observed outbreaks are also due to a suite of other insects, including the western spruce budworm (*Choristoneura occidentalis*), which causes defoliation and mortality in Douglas fir (*Pseudotsuga menziesii*) and other tree species. The data also show a small increase in the frequency of fire, which is consistent with other regional observations (Westerling et al. 2006).

I can also conclude from a small sample of aerial photos that the rate of conifer encroachment has decreased (from 33.5 percent to 13.9 percent of samples), but this is likely at least partially attributable to a shorter time period of observation (from 1999–2009) compared to the initial 28-year time period (1971–1999). Given relatively slow conifer growth rates in the GYE, it is possible that 10 years is insufficient for detecting subtle changes in conifer density. Another potential factor that must be considered, however, is that drought conditions during much of the past decade (Crabtree et al. 2009; Debinski et al. 2010) rendered conditions less favorable for conifer reproduction,

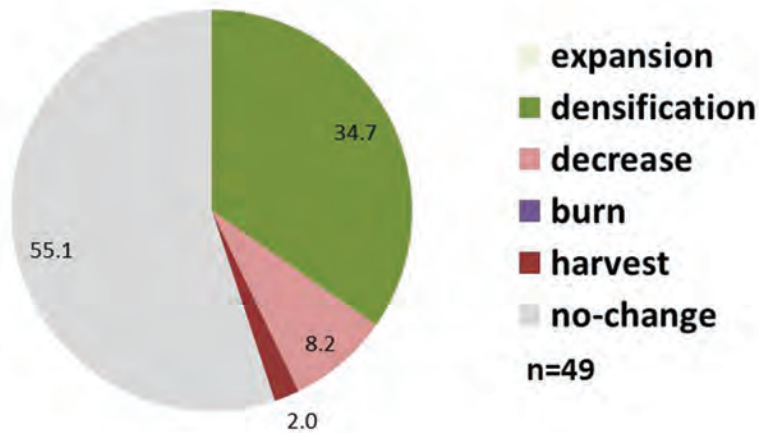


Figure 5. Frequency of recent (1999–2009) insect outbreak locations in relation to prior forest dynamics (1971–1999).

seedling establishment, survival, and growth, though Debinski et al. (2010) documented increases in woody plant cover in some montane meadows in the GYE during that time period.

I have demonstrated in previous work that there is significant spatial variation in rates of conifer encroachment (Powell and Hansen 2007). Examination of recent forest dynamics within specific transects from this current study corroborates this earlier finding, as demonstrated by the spatial variability of disturbance and conifer encroachment across the sample transects. The Eightmile transect exhibited large increases in disturbance (fire and insects), while the Tom Miner transect did not exhibit a large increase in either type of disturbance. One likely explanation for this spatial variability is simply due to differences in forest type, structure, and biophysical settings between these two transects. The Eightmile transect contains more mid- to high-elevation, even-aged, mixed coniferous forest (including lodgepole pine [*Pinus contorta*]), which is highly vulnerable to mountain pine beetle infestations. In contrast, the Tom Miner transect contains more lower-elevation, ecotonal forest dominated by Douglas fir, which is vulnerable to spruce budworm defoliation but not to mountain pine beetle infestation. These differences are not surprising, but they do underscore the spatial variability associated with forest disturbance dynamics.

Interactions among forest dynamics are similarly governed by forest type, structure, and bioclimatic setting. I can conclude from a small sample of aerial photos that a large percentage (34.7 percent) of the currently observed

(1999–2009) insect activity has occurred in stands previously (1971–1999) exhibiting conifer densification. Across all recent observations of insect activity, the average conifer cover in 2009 was 81 percent. The relationship between stand density and the likelihood of bark beetle mortality has been shown previously in ponderosa pine (*Pinus ponderosa*) forests in Arizona (Negron et al. 2009) and is potentially related to reduced tree vigor with higher stocking rates. Covington and Moore (1994) also portend the likelihood of increased insect infestations in ponderosa pine forests associated with fire exclusion and subsequent increases

in stand density. Similar associations among tree size, stand age, and likelihood of mountain pine beetle infestation have long been noted in Rocky Mountain lodgepole pine forests (Amman et al. 1977), where bark beetles tend to preferentially infest larger trees (Pfeifer et al. 2011).

The majority of the observations (76 percent) of recent insect activity in conifer stands exhibiting densification were likely associated with mountain pine beetle infestations. The remaining observations (24 percent) were likely associated with spruce budworm infestations in Douglas-fir stands. There is evidence that young Douglas-fir trees, especially seedlings and saplings in the understory of larger trees, are particularly vulnerable to spruce budworm infestation (Hadley 1994), underscoring a potential relationship between recent conifer encroachment and spruce budworm outbreaks. Conifer defoliation associated with outbreaks of spruce budworm does not strictly lead to tree mortality, though in some cases it does, but the reduction in live needles can greatly reduce canopy cover and appear to an air photo interpreter as a decrease in conifer cover.

Management Implications

The relationship between conifer encroachment and insect outbreaks has obvious management implications. It begs the question: should conifer encroachment be actively managed (e.g., by thinning or prescribed fire) to reduce stand density and hence vulnerability to insect outbreaks? The answer to this complex question depends in large part on two factors: 1) the degree to which the forest land in question is relied upon for timber production, and 2) the relationship between insect outbreaks and subsequent fire

risk. If a particular area is planned for future timber harvest, then management strategies designed to reduce stand densities and hence vulnerability to future insect outbreaks might be warranted. With regards to the latter factor, despite the popular assumption that insect-related mortality necessarily leads to increased fire risk, the literature suggests a more nuanced relationship that is wholly dependent upon forest type, disturbance regime, and time since outbreak. For example, a study of spruce budworm defoliation in British Columbia Douglas-fir forests showed a significantly reduced risk of fire following infestation (Lynch and Moorcroft 2008). A number of other studies have also shown little to no relationship between insect outbreaks and subsequent fire risk (Kulakowski et al. 2003; Kulakowski and Veblen 2007; Jenkins et al. 2008; Tinker et al. 2009). However, most of these studies were conducted in relatively mesic subalpine forests where the occurrence of fire is generally limited by drought rather than by fuels.

Conclusions and Future Research Directions

One of the barriers to effective analysis of disturbance interactions is the lack of spatially and temporally detailed maps of disturbance at broad scales. The USDA Forest Service's Aerial Detection Survey (ADS) provides some of the most comprehensive maps of insect outbreaks, but the spatial detail is lacking in these maps and precludes their effective use for fine-scale analysis of disturbance interactions. Air photo time series analyses, such as the one described in this paper, provide only a temporally detailed sample of disturbance dynamics. The next step in this research will be to complete the aerial photo interpretation for the full sample of over 2,000 plots across the GYE. Multiple lines of evidence are important, including the ADS and aerial photo time series, but satellite image analysis will be essential for providing detailed, large-area maps of disturbance dynamics. The next step in this research will be to analyze a dense time series of Landsat satellite imagery to quantify forest disturbance and dynamics in a spatially and temporally detailed manner. The LandTrendr algorithm is especially well suited for forest disturbance detection and is capable of accurately detecting both abrupt forest disturbance (e.g., harvest, fire) as well as subtle forest growth and disturbance processes (e.g., conifer encroachment, insect activity; Kennedy et al. 2010; Powell et al. 2010).

With the spatial and temporal detail that can be achieved with satellite image analysis, the interactions

among forest disturbance processes will be more rigorously analyzed. I will investigate the statistical likelihood of co-occurrences among conifer encroachment, insect outbreaks, and fire. This will facilitate improved understanding of the nature of ecosystem dynamics and shed light on management implications.

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Monitoring Alpine Climate Change in the Beartooth Mountains of the Custer National Forest

Dan Seifert¹, Edward Chatelain², Craig Lee³, Zach Seligman⁴, Don Evans⁵,
Hans Fisk⁶ and Paul Maus⁷

¹ Custer National Forest, 6811 U.S. Highway 212 S., Red Lodge, MT 59068, 406-446-4520, dseifert@fs.fed.us

² Department of Physics, Astronomy & Geosciences, Valdosta State University, 1500 North Patterson St., Valdosta, GA 31698, 229-333-5758, echatela@valdosta.edu

³ Institute of Arctic and Alpine Research, University of Colorado, Campus Box 450, Boulder, CO 80309, 303-735-7807, craig.lee@colorado.edu

⁴ University of Montana, Department of Geography, 303-902-1040, seligmanz@hotmail.com

⁵ USDA Forest Service, Remote Sensing Applications Center, 2222 West 2300 South, Salt Lake City, UT 84119, 801-975-3750, dtevens@fs.fed.us

⁶ USDA Forest Service, Remote Sensing Applications Center, hfisk@fs.fed.us

⁷ USDA Forest Service, Remote Sensing Applications Center, pmaus@fs.fed.us

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Abstract

The U.S. Department of Agriculture Forest Service's Remote Sensing Steering Committee awarded funding to investigate methods to measure and quantify the effects of climate change on alpine glaciers. Four glaciers within the Absaroka-Beartooth Mountains were selected for analysis. Five to nine dates of stereo photography, spanning the years from 1952 to 2003, were analyzed for each site. The photos were orthorectified in Leica Photogrammetry Suite (LPS). However, digitizing the changing glacier boundaries from the orthorectified imagery was surprisingly subjective and inexact. Still, the changing boundaries of these glaciers tell a compelling story about glacial retreat despite the inexactness of the interpretation. The LPS block files were also imported into ArcGIS Stereo Analyst to create 3-D profiles of the glacier surfaces. These profiles show dramatic ice loss at all four sites—thus, the surface profiles proved to be better indicators of glacier change than the boundary delineations. The methods used in this project can be a cost-effective means to monitor the effects of climate change on alpine glaciers.

Background

The Earth's climate is warming, leading to smaller ice caps and glaciers. This loss has significant impact on the planet—not the least of which is a potentially catastrophic rise in sea level. The scientific community is focusing a good deal of attention on mapping and monitoring globally significant ice caps and ice fields.

Generating only slightly less interest are the tens of thousands of smaller alpine glaciers in mountainous areas around the globe. These alpine glaciers make critical contributions to local ecosystems and economies. They serve as reservoirs that release water in the summer and early fall when it is most needed. Glaciers cool the local environment, creating critical terrestrial microhabitats and cool the stream runoff, producing critical aquatic habitats

(Figure 1). The reduction and loss of these alpine glaciers will profoundly alter affected ecosystems and economies.

In 2008 the U.S. Department of Agriculture (USDA) Forest Service's Remote Sensing Steering Committee awarded funding to pursue a proposal submitted by the Custer National Forest to investigate methods to quantify the effects of climate change on the alpine glaciers of the Absaroka-Beartooth Mountains.

There have been a number of successful efforts to map alpine glaciers. Many of these have focused on spatial extent or planimetric (X,Y) mapping (Hoffman et al. 2007). However, the decrease in ice depth, or elevation (Z), can be far more significant than indicated by the reduction in ice surface area (Pochop et al. 1990).



Figure 1. Alpine glaciers make critical contributions to local ecosystems, but they are currently threatened by a warming climate. USDA photo.

There are two general remote sensing methods to measure the Z dimension: 1) using stereo imagery, or 2) using an active return system such as radar or lidar. Lidar may prove to be the most effective method for current and future monitoring, but, since it is a new technology, there is currently no historical data. Radar data have been used to map ice elevation surfaces (Scheifer et al. 2007); however, historical data sets are spotty, hard to come by, and virtually nonexistent prior to the mid-1980s.

Stereo imagery allows investigators to see and measure elevations and their differences. By definition, stereo imagery works by obtaining images of the same feature from two different vantage points. Some current satellite and airborne sensors can obtain digital stereo coverage—but, once again, these sensors are relatively new and don't provide an historic perspective.

The Forest Service has been systematically collecting stereo resource photography of all the lands it manages since the 1940s and, in some areas, as far back as the 1930s. Typically, photo acquisition repeats on a 5 to 10 year cycle. Programs such as the National High Altitude Photography (NHAP) program, the National Aerial Photography Program (NAPP), and the current National Agricultural Imagery Program (NAIP) greatly supplement the available dates of resource photography. In addition, the USGS is a terrific resource for additional special-project

stereo photography. Thus, aerial photography is the best source of historical stereo imagery.

Using photography to map elevations is not new; it provides the fundamental data to create the national series of 7.5 topographic quadrangles. However, traditional methods of deriving elevation information from photography are both specialized and cumbersome. Despite that fact, traditional photogrammetric techniques were used to measure the area and elevation changes of glacial surfaces in the Wind River Range in Wyoming (Pochop et al. 1990). The project analysis was restricted to two dates of imagery and two sites, thus making the effort more manageable.

A fortunate convergence of technologies and availability of data now allow anyone in the Forest Service to use historical aerial photography to map and measure changes in alpine glaciers. This project's objective was to develop a cost-effective procedure that demonstrates the efficacy of this approach.

Methods

The general methodology consisted of selecting suitable alpine-glacier sites, identifying and locating available stereo photography, scanning the photography or obtaining already-scanned imagery, orthorectifying photography, delineating glacier boundaries, measuring ice elevations for each site and date, and analyzing the results of those measurements.

Selecting Suitable Alpine-Glacier Sites. Four alpine glacier sites within the Absaroka-Beartooth Mountains were selected for analysis: 1) the East Grasshopper Glacier, 2) the West Grasshopper Glacier,¹ 3) the Castle Rock Glacier, and 4) the Rearguard Glacier. These four glaciers had different sizes, aspects, elevations, and locations.

¹ Despite having similar names, the East and West Grasshopper Glaciers are very different from each other—separated by more than 25 kilometers with distinctive cirques and glaciers between them.

Identifying and Locating Available Stereo Photography.

The project used three sources of aerial photography: 1) the Aerial Photography Field Office (APFO), 2) the USGS EROS Data Center, and 3) existing prints from the Custer National Forest, Beartooth Ranger District.

The APFO has archived the original film for all USDA-contracted photo projects since 1955 (currently more than 50,000 rolls). Five dates of photography for each site were identified within the APFO holdings: 1951–52, 1971, early 1980s, early 1990s, and 2003. To facilitate selecting the correct photos, project personnel scanned the aerial-photo project flight-index map for each date, georeferenced each map, and overlaid it with the selected alpine-glacier sites in ArcGIS. This allowed easy identification of the film rolls and exposure numbers that corresponded to the four sites. Combining four study sites, five dates, and approximately four photos per date (ranging from two to six), produced approximately 80 photos that were obtained from the APFO.

Because of the dramatic changes that appeared at Castle Rock Glacier, four more dates of imagery were obtained for this site from the USGS EROS Data Center (10 additional photos). These supplemental images resulted in nine dates of stereo imagery: 1952, 1971, 1976, 1981, 1987, 1991, 1995, 1998, and 2003 and a total of approximately 90 individual photographs. Note: the most notable dates turned out to be the earliest and the latest—they gave the most complete summary of glacier change. The intervening seven dates were included to provide a more complete change record and investigate correlations with regional climate records.

One other date of photography was located and used—the Custer National Forest discovered aerial photo prints from the 1930s in its archives. However, this photography covered only one site—the Rearguard Glacier.

Scanning the Photography. The resource photography obtained from the APFO was originally acquired at nominal scales of 1:15,840 to 1:24,000. All of these resource photos were scanned at 700 dpi on a desktop scanner. This produced nominal pixel sizes ranging from 0.6 to 0.9 meters and an uncompressed file size of about 120 megabytes each. The photography that came from the USGS was smaller scale—ranging from nominal scales of 1:35,000 to 1:48,000. The USGS scanned these images on a photogrammetric scanner at approximately 1,800 dpi, resulting in nominal pixel sizes ranging from about 1.5 to 2 meters.

Orthorectifying Photography. The photos were orthorectified using ERDAS Imagine's Leica Photogrammetry Suite (LPS). LPS requires digital elevation models (DEMs) and reference imagery that cover the project area. LPS also requires camera reports² for each date of photography. Camera reports were created for any photographs that didn't have them. Using LPS, we defined the photogrammetric orientation parameters for each set of stereo photos (each date and site). These definitions were saved in what LPS terms "block files." After preparing the block files, orthophoto mosaics were also created.

Delineating Glacier Boundaries. The nine orthophoto mosaics of the Castle Rock Glacier were used to digitize the approximate glacier boundary for each date. This seemingly simple task was actually quite difficult and inexact. The main glacier surface was always easy to identify; however, it sometimes seamlessly graded into seasonal snowfields, rock glacier, and rock outcrops that made the boundary very indistinct. Digitizing the glacier boundary for the other sites was not attempted because the distinction between the obvious glacier surface and surrounding surfaces was even less apparent than it was in the Castle Rock Glacier. Despite the difficulties this technique encountered with the Castle Rock Glacier, clear trends revealed significant shrinking over the 51 years captured by this imagery (Figure 2).

Measuring Ice Elevations. Each LPS block file was imported into ArcGIS Stereo Analyst. Then a line that approximated the major axis of the glacier was digitized for each site. For each date of stereo imagery, a set of 3-D points along the axis (± 5 meters horizontally) of the glacier was digitized. These were saved as ESRI shapefiles with Z values. The 3-D points required identifying the same exact feature on the stereo pair in Stereo Analyst and manually adjusting the parallax to define its elevation before digitizing the point. Automated (image-to-image correlation) methods did not work well for two reasons: 1) the

² Mapping cameras are periodically calibrated by the USGS Optical Sciences Lab. These reports provide precise measurements (to 0.001 mm) of the characteristics of each camera system including lens distortion, calibrated focal length, and fiducial measurements (fiducials are known locations on the film that become image control points in the orthorectification process). Camera reports became a requirement for all mapping cameras in 1973 but are essentially non-existent prior to that date.

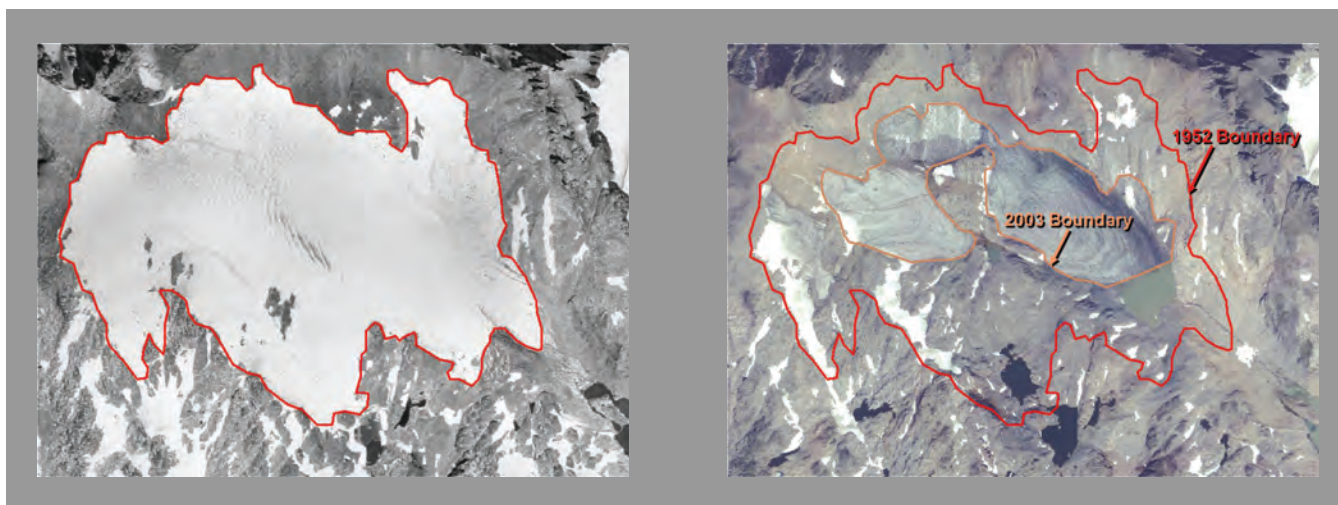


Figure 2. On the left is the Castle Rock Glacier in 1952, with its boundaries outlined in red. On the right is the Castle Rock Glacier in 2003, with its present boundaries outlined in gold along with the 1952 boundary in red. The shrinkage is dramatic—especially when considering the additional loss in depth.

amount of parallax in this steep mountainous terrain is extreme, and 2) often there were very few distinct features on the snowy glacier surfaces that allowed image-to-image matching. For each date 40 to 80 3-D points were digitized along the major axis of the glacier.

By using the 3-D analyst tools in ArcToolbox, the 3-D point shapefiles were exported to comma-delimited ASCII text files with *UTM X*, *UTM Y*, and elevation values in meters above mean sea level. These text files were imported into an Excel spreadsheet for analysis.

Analyzing the Data. Once the data were gathered and prepared, the analysis was fairly direct. It consisted of simply plotting the ice-surface elevations so they could be compared, computing the differences in surface elevation between dates, and deriving summary statistics from the difference calculations.

Comparing the profiles of different dates required converting each X,Y position of each profile to a distance from a single, fixed X,Y position, which was located just beyond the toe of the terminal moraine. Again, to facilitate comparison, an Excel add-in interpolated values so that every distance value from the fixed X,Y position at the toe of the glacier had a corresponding ice-surface elevation value for all dates of imagery (Figure 3).

Errors can enter this procedure at nearly every step; however, on two occasions, the entire process (for a site and date) was repeated and produced nearly identical results. This correlation indicated the high precision of the measurements. In spite of the measurement accuracy,

however, a bias could not be ruled out. An elevation bias could have resulted from allowing the LPS program to solve the block-file triangulations by giving too much latitude to the Z component. Fortunately, that bias was easily corrected by adding a constant to each profile that made the initial part (which was on bare ground—except in 1952, when it was snow covered) match the true elevation of that area.

Results and Discussion

The project revealed a dramatic decrease in ice depths—especially in the case of the Castle Rock Glacier, which lost an average of 60 meters of ice in the 51 years from 1952 to 2003 (Figure 4). This amounts to an average surface loss of 1.2 meters of ice per year. However, this rate has been far from consistent. The periods from 1987 to 1991 and 1995 to 2003 showed mean ice losses of 2.5 meters per year (well above the average), while the period between 1995 and 1998 revealed a mean loss of only 0.3 meters per year (well below the average). Results for the Castle Rock Glacier are summarized in Table 1.

The other sites exhibited less dramatic ice losses (Table 2). The East Grasshopper Glacier lost an average of just over 16 meters of ice in the 51 years from 1952 to 2003, averaging 0.3 meters per year.

The Castle Rock Glacier has a south-southeastern exposure. Its profile (for all dates) was measured over 1,500 meters of horizontal distance with an elevation ranging from 3,400 to 3,620 meters. By contrast, the East Grasshopper Glacier has a northeastern exposure, a 2,700 meter

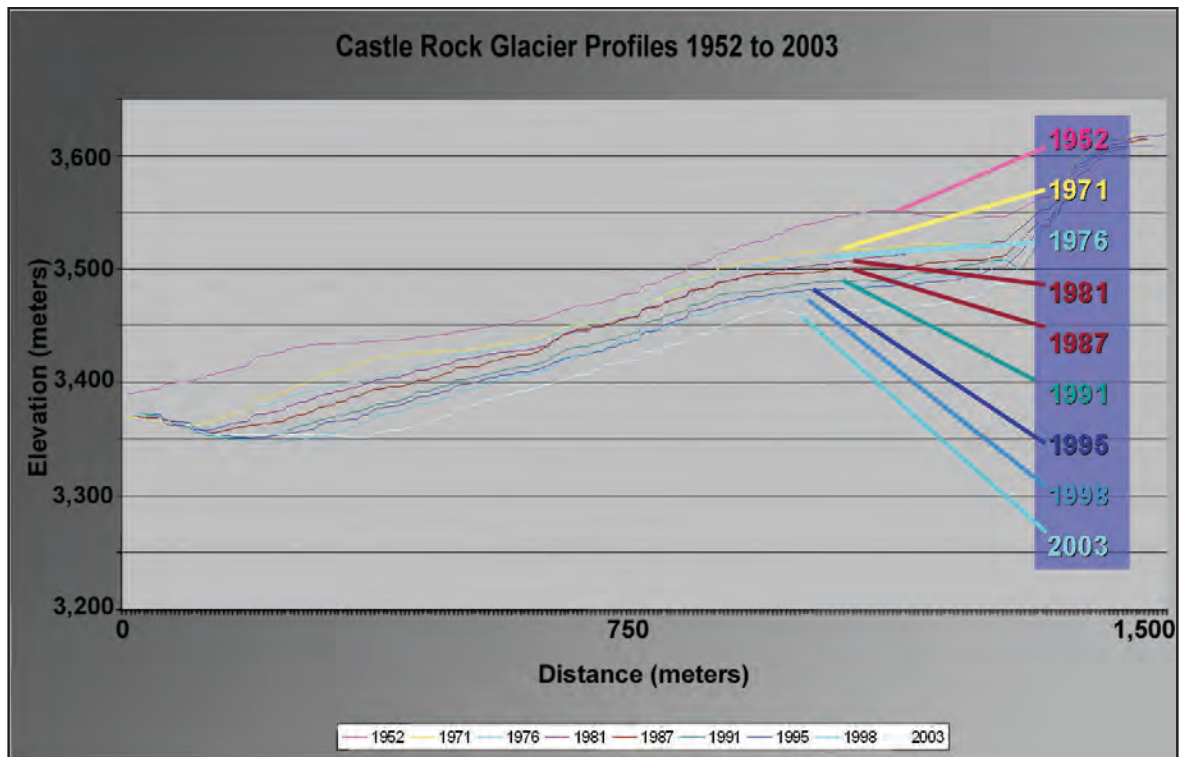


Figure 3. Surface profiles along the major axis of the glacier for each date of imagery. The surface profiles decrease after each time interval.

profile distance, and elevations ranging from 2,900 to 3,500 meters. It seems that the northeastern exposure of the East Grasshopper Glacier allows it to be longer and lower than the southern exposure of the Castle Rock Glacier. The incoming solar radiation for the Castle Rock Glacier is much higher than the East Grasshopper Glacier (Table 3).

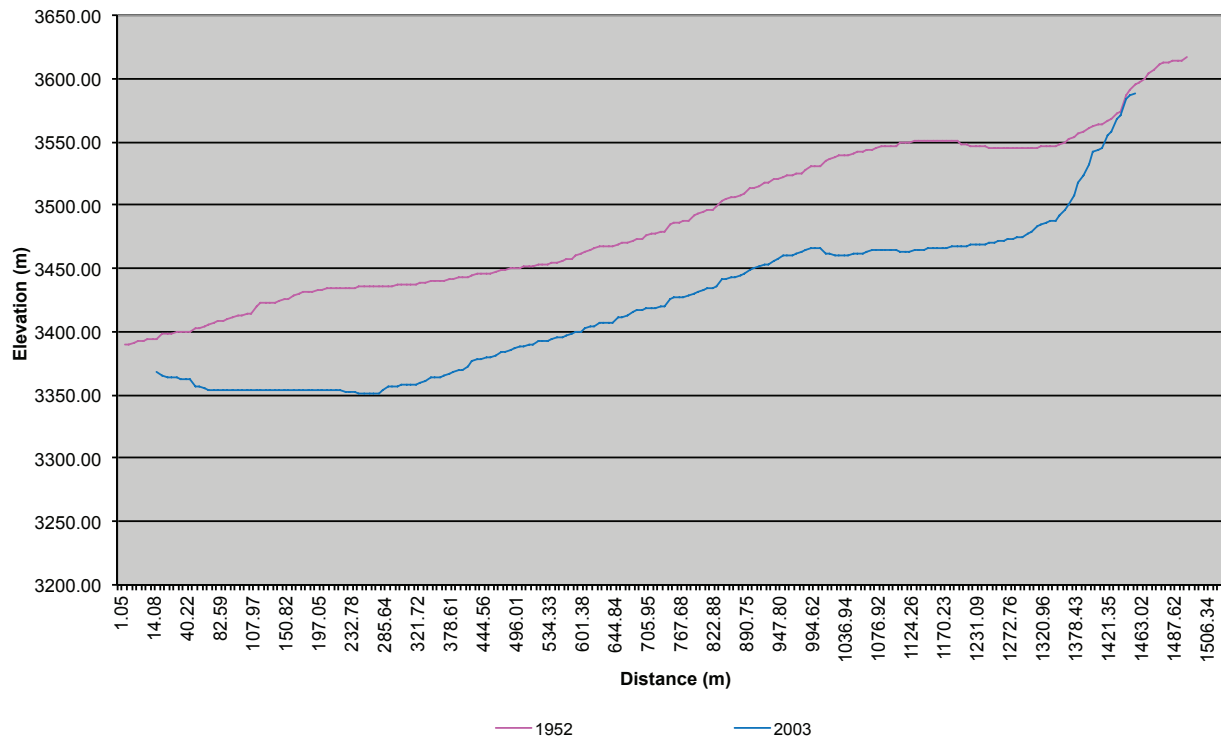
The character of the two glaciers is quite different as well. The East Grasshopper Glacier exhibits a very indistinct gradation from an ice/snow surface at the upper elevations to rock glacier and then moraine at the lower elevations. By contrast, the Castle Rock Glacier has a very distinct snow and ice surface—with little or no transition to rock glacier or moraine conditions. The exposure and characteristics of the East Grasshopper Glacier may be attenuating the effects of global warming compared with the Castle Rock Glacier. Alternatively, because the East Grasshopper Glacier has a far larger rock component, the loss of ice may simply be less evident. The inconsistency between these two glaciers indicates that it may be unwise to extrapolate ice-loss values to other glaciers in the Beartooth Mountains—much less other mountain ranges—without further study.

Costs. With several caveats, the approximate total cost for one date of imagery at a typical glacial site is \$2,120. As already detailed, the tasks include identifying and locating

available stereo photography, scanning the photography or finding already-scanned images, orthorectifying the photography, measuring ice elevations for each site and date, and analyzing the results of those measurements. There are several ways of accomplishing many of these tasks, and consequently costs can be quite variable. To keep things simple, assume one glacier site for one date—requiring four photographs for complete stereo coverage. Here is the estimated breakdown:

- Identifying and locating available stereo photography (assumes access to flight-index maps): 6 hours
- Scanning the images: 6 hours
- Orthorectifying the photography (including finding or making a camera report and downloading the DEMs and reference imagery): 12 hours
- Measuring ice elevations (includes importing the LPS block file and setting up the stereo model in ArcGIS Stereo Analyst, creating the shapefile, digitizing 3-D points, and exporting the shapefile to an X,Y,Z text file): 8 hours
- Analyzing the data (includes importing the X,Y,Z text file, preparing the data for comparisons, and plotting the results): 8 hours

Castle Rock Glacier Profiles 1952 to 2003



Glacier Profile Change 1952 to 2003

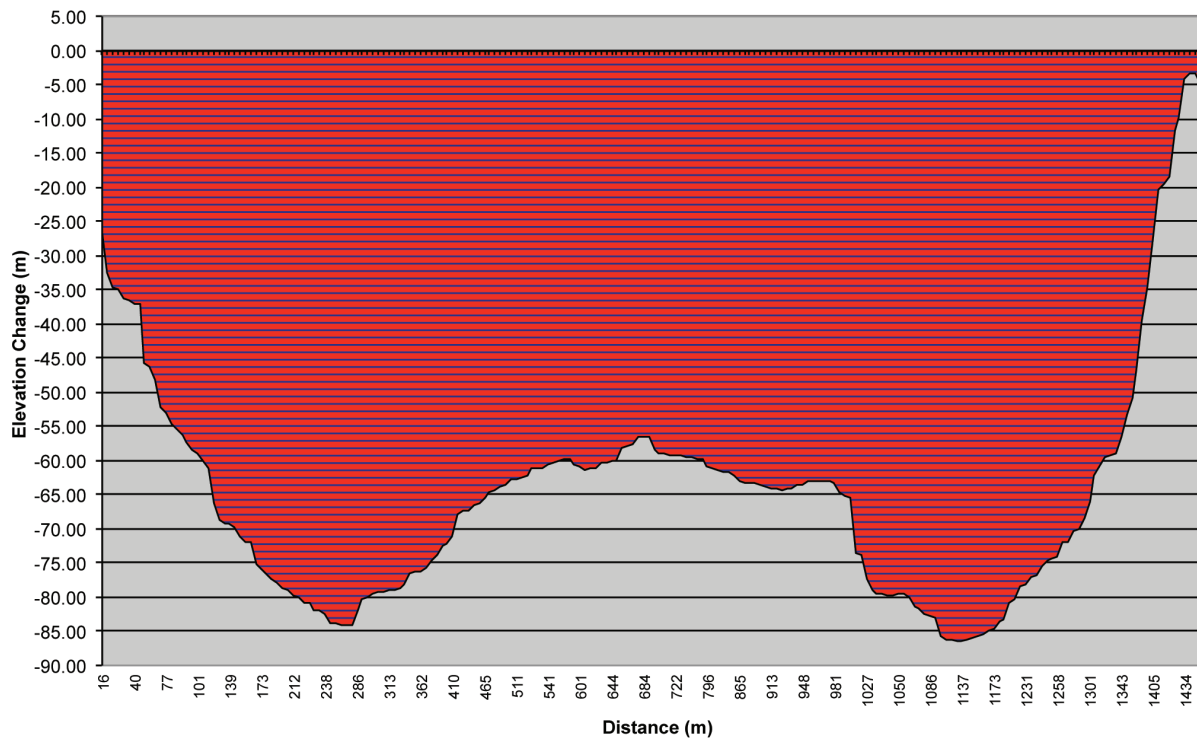


Figure 4. The top portion displays the surface profiles along the major axis of the glacier for 1952 and 2003. The bottom portion graphically shows the loss of ice along the profile between the two dates. In 51 years, the average ice loss has been more than 60 meters.

Table 1. Summary of Castle Rock Glacier surface ice-loss rates.

Mean Surface Ice-Loss Rates (m/yr) — Castle Rock Glacier								
1952 to 1971	1971 to 1976	1976 to 1981	1981 to 1987	1987 to 1991	1991 to 1995	1995 to 1998	1998 to 2003	Overall
-1.06	-0.93	-0.89	-0.95	-2.55	-1.06	-0.28	-2.47	-1.26

Table 2. Summary of surface ice-loss rates at other glaciers.

	Mean Surface Ice-Loss Rates (m/yr) — Other Glaciers				
	1952 to 1971	1971 to 1987	1987 to 1995	1995 to 2003	Overall
E. Grasshopper Glacier	-0.60	-0.04	1.07	-1.55	-0.31
W. Grasshopper Glacier	0.10	0.14	-0.88	-0.33	-0.11
Rearguard Glacier	0.01	-0.16	-0.16	-0.79	-0.20

Table 3. Amount of incoming solar insolation for the Castle Rock and East Grasshopper Glaciers.

Direct + Diffuse Mean Incoming Solar Insolation (watt hours per square meter)		
Day	Castle Rock Glacier	East Grasshopper Glacier
Summer Solstice	7,768	6,338
Spring/Fall Equinox	4,565	3,114
Winter Solstice	1,188	602

Thus, the total labor time is approximately 40 hours, which at \$50 an hour is \$2,120. This estimate assumes that the personnel have the required software, expertise, and familiarity with the procedures and that there are no unforeseen problems. The data have a relatively insignificant cost: four photos at \$30 apiece is \$120, bringing the total cost to \$2,240.

Conclusions

This project demonstrated that current technology and methodology can effectively monitor changes in glacial areas and ice volumes related to climate change. The technology to measure changes in alpine glaciers accurately is widespread within the Forest Service; however, using these technologies effectively may entail a significant learning curve.

The methodology in this project provided the desired information and was cost effective; costs can be even lower if fewer dates of imagery are used in the analysis. This project used nine dates of stereo imagery for the Castle Rock Glacier and five dates for the other three glaciers. Howev-

er, important glacial-change information can be garnered by comparing any two dates of imagery—especially if they are the earliest date and the latest date available.

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Snow Dynamics and Mountain Fox (*Vulpes vulpes macroura*) in Yellowstone: Incorporating Climate in Species-Habitat Models

J. W. Sheldon¹, Robert L. Crabtree², Christopher S. Potter³,
Daniel J. Weiss⁴ and Brandt Winkelman⁵

¹Yellowstone Ecological Research Center, 2048 Analysis Drive, Bozeman, MT 59718, 406-556-1414, sheldon@yellowstoneresearch.org

²Yellowstone Ecological Research Center, 2048 Analysis Drive, Bozeman, MT 59718, 406-556-1414, crabtree@yellowstoneresearch.org

³Senior Scientist, NASA-Ames, Moffett Field, CA 94035, 650-604-6164, christopher.s.potter@nasa.gov

⁴Yellowstone Ecological Research Center, 2048 Analysis Drive, Bozeman, MT 59718, 406-556-1414, weiss@yellowstoneresearch.org

⁵Yellowstone Ecological Research Center, 2048 Analysis Drive, Bozeman, MT 59718, 406-556-1414, winkelman@yellowstoneresearch.org

Abstract

Snow pattern dynamics in northern temperate regions exert a critical regulatory role on a multitude of ecosystem processes. Snow cover onset and ablation, snow-water equivalent (SWE) patterning, snow-pack penetrance (oversnow travel, access to prey in the sub-nivean space), and timing of major snow events are all important to terrestrial animals. As climate patterns shift, changes in patterning of snow dynamics may exert important adaptational influences on animal ecology and energetic budgets. Snow data are available from remotely sensed, in situ measurements, and modeled estimates, but a consistent set of approaches for assessing the ecological impacts of changing snow metrics has not yet been realized. Access to standardized low/no-cost snow covariates for animal-habitat models remains an important goal that has ramifications for both management and research. We investigated the winter use patterns of mountain red fox (*Vulpes vulpes macroura*) on the northern range of Yellowstone National Park (YNP) and evaluated snow cover and SWE alongside more traditional habitat attributes. We found that SWE is an important determinant of habitat use by red fox on the northern range of YNP. Based on SNOTEL (SNOWpack TELelemetry) and observational data, we suggest that snow-hardening events may also play a key role for mountain fox foraging success in YNP and contribute to a mechanistic explanation for why SWE is important.

Introduction

Snow in northern temperate regions (such as Yellowstone National Park [YNP]) governs many organismic processes, including herbivory, across-snow travel and migration, and predation in the sub-nivean space. Snow can be thought of as a highly dynamic landcover type with the potential to exert strong effects on animal space use patterns. Snow cover occurs in Yellowstone from November to June and mean daily minimum temperatures average below freezing for eight months of the year (Newman and Watson 2009). Snow cover's effects on what constitutes available habitat and prey are as yet only generally characterized in the heterogeneous winter environment of YNP.

Red fox are an important medium-sized carnivore in YNP and are one of the three species of canid (along with wolves, *Canis lupus*, and coyotes, *Canis latrans*). During the 1880s numerous fox with a variety of coat colorations were

seen in YNP (Norris 1881), so it is known that fox were present when the park was created. Prior to the 1950s, red fox were rare to absent from the lower elevations of Montana, and it appears that fox ranges were originally restricted to the mountainous, western, and southern parts of the state (Fuhrmann 2002). The indigenous Yellowstone fox appears to be the montane form, and is generally nocturnal and shy. It is common in forested habitats containing adequate densities of essential small mammal prey in and around the Yellowstone region. These fox can be seen mousing along ecotones, foraging at carcasses, especially during winter, and traveling the forest edge, particularly at dawn and dusk periods.

Red fox have been well studied in YNP (Crabtree 1993, 1997; Fuhrmann 1998, 2002; Van Etten 2006; Van Etten et al. 2007). Habitat use is well-characterized at a

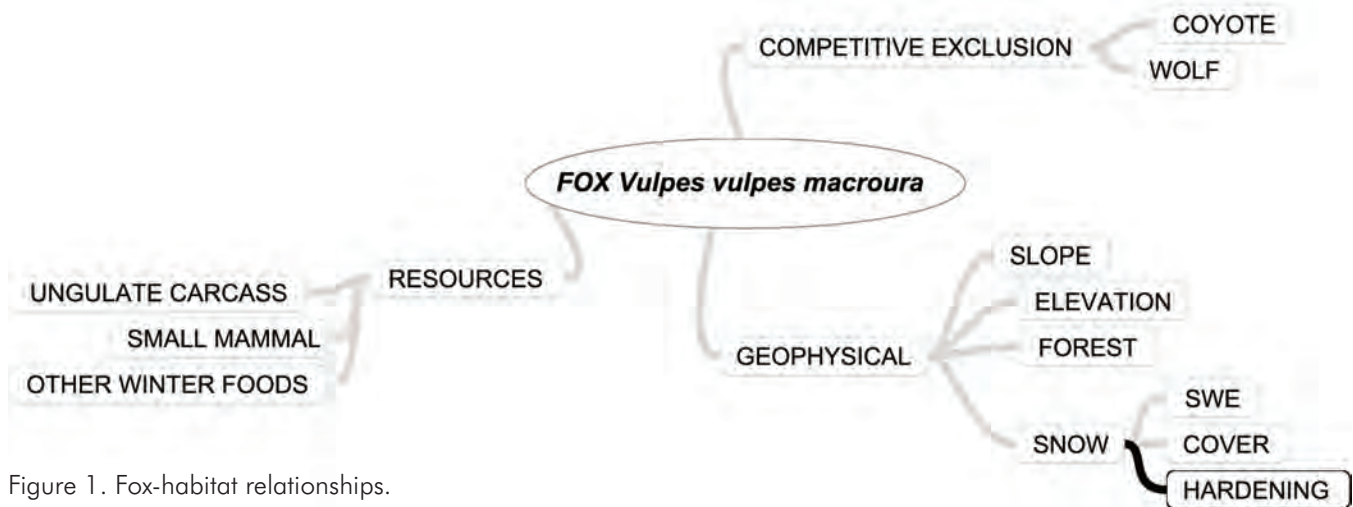


Figure 1. Fox-habitat relationships.

fine scale (Van Etten et al. 2007) and the relationships with prey and competitors have been characterized (Crabtree and Sheldon 1999; Gese et al. 1996).

This highly specialized boreal forest carnivore exists at all elevations throughout YNP, with a continuous distribution through the adjacent wilderness regions of the Beartooth Plateau, and it occurs at elevations up to 10,000 feet during the winter months. From a general ecological perspective it is useful to examine the potential structuring effects of snow on fox spatial use patterns. Furthermore, in snow-dominated alpine and subalpine landscapes, the YNP fox can be seen as a sentinel species for climate change, providing insight into snow ecology in the severe winter environments, within the context of the larger system of predator, prey, and geophysical constraints in this severe winter environment.

We followed the systems approach of Kausrud et al. (2008) who examined mesocarnivore and snow dynamics in Norway. These authors investigated the larger context of an integrated community of predators and prey strongly influenced by snowpack dynamics. They found warm periods during late winter are increasing in their system. At the same time, the cyclicity of small mammal populations has dampened, which in turn appears to be linked to declines in the predator populations. Thus links between global climate shifts and regional to local snow dynamics and concomitant effects on predator-prey dynamics are suggested. In YNP we are interested in beginning to work out characterization of snowpack dynamics with respect to the fox/small mammal populations.

Methods

In working with complex geophysical covariates such as snow, where mechanisms potentially exerting effects on organismic space use or habitat selection are not yet understood, we find it helpful to visualize the fox-habitat system, framed in terms of testable covariate relationships (see Figure 1). We think about the influences on fox habitat use in three general categories: 1) geophysical constraints—these are the classic habitat or landscape metrics used in most animal-habitat models and include slope, elevation, and snow metrics; 2) energetic covariates, or food; and 3) dominant competitors or hazards—in the fox context this includes coyotes, which we know from previous research in YNP and elsewhere can strongly condition where fox spend their time. We then draw the actual model from this idealized universe of possible space-use determinants and define the list of covariates that we actually have on or have the capacity to create (Figure 2).

We evaluated the relative effects of snow cover and SWE within the context of a conventional habitat model for red fox, based on from ground-telemetry data from the Lamar Valley on the northern range of Yellowstone. Data from a single representative winter season (2003–2004) were used, a time period during which eight fox were radio-collared in the Lamar Valley. We used the following covariates (explanatory variables) in the statistical model:

- Elevation (from Digital Elevation Model)
- Slope
- Forest (percentage forest cover)
- Sagebrush cover (percentage)

Table 1. Model output from fox-snow habitat resource selection.

	Parameter Estimates				
	Coefficient	SE (coeff)	t-value	p-value	vif
Intercept	-2.431	4.56	-0.53	0.590	NA
Elevation	-0.511	0.40	-1.28	0.201	4.1
Forest	0.292	0.25	1.18	0.239	1.3
Prey biomass	-0.196	0.08	-2.43	0.016	1.3
Slope	-0.269	0.15	-1.82	0.070	1.3
SWE	-1.857	0.27	-6.86	0.000	2
Snow cover	-0.154	0.08	-1.9	0.058	1.1

- Small mammal prey (a modeled estimate from the preceding summer)
- Snow cover (MODIS snow cover product)
- Snow water equivalent (SWE)

We used resource selection probability function analysis (Lele and Keim 2006) to assess the contributions of these covariates to the patterning of fox space use.

Results and Interpretation

We found that snow, in the form of SWE (snow water equivalent; the amount of water present in a column of snow) was an important influence on where fox spent their time (Table 1). The quadratic form of the response shows that fox do not select for areas of very low or very high SWE, preferring areas of intermediate SWE. We found that snow cover was marginally important. Elevation, which often dominates species-habitat models, was not an important predictor of where fox spent their time. This makes sense ecologically, since fox distribution is continuous from the lowest elevations in YNP (and below) up to the alpine environment on the Beartooth Plateau. Fox selected for habitat characterized by higher biomass of prey, but only up to a point, thereafter avoiding areas of highest prey density that may be associated with higher exposure risk to coyotes. This patterning may also be confounded by competitive avoidance strategy or possibly with SWE effects. Forest was not an important determinant of habitat selection at the 500 meter (m) spatial resolution of the original model; however, when the forest term was run at a 30 m (much finer grain) resolution, it became important, confirming the results from Van Etten et al. (2007), where fox show great finesse with respect to their use of forest and forest-edge habitats.

Finally, outside of the resource selection analysis, we investigated preliminary approaches for modeling snow-transformation (snow-hardening) by looking at data from the adjacent northeast entrance SNOTEL (SNOWpack TELelemetry) site and matching that snow data record to empirically observed fox captures, which typically are associated with periods of food stress (Figure 3). We speculate that an observed snow hardening event (rain-on-snow, accompanied by a warming then freezing temperature oscillation) during late February resulted in a surge in captures due to fox “shut-out” from access to prey in the

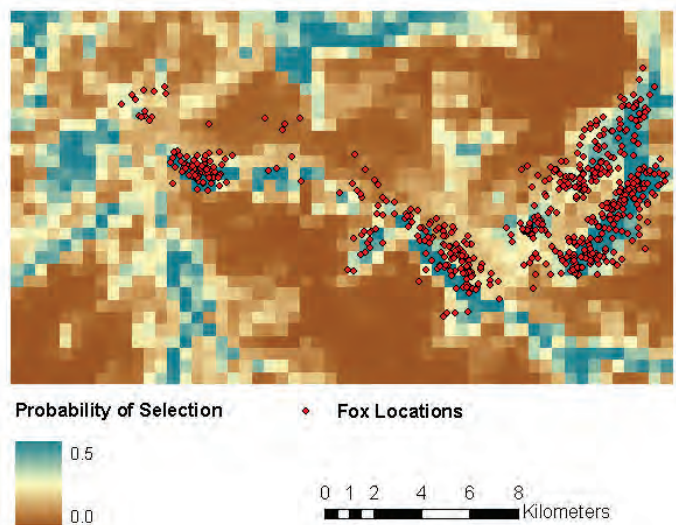


Figure 2. Red fox locations (ground telemetry, winter 2003–2004) are shown as red points, superimposed over the fox resource selection fit surface (tan/blue color ramp). The resource selection model was run in ‘R’ code, within an ArcGIS platform. Probability values indicate the likelihood of fox use, according to the model.

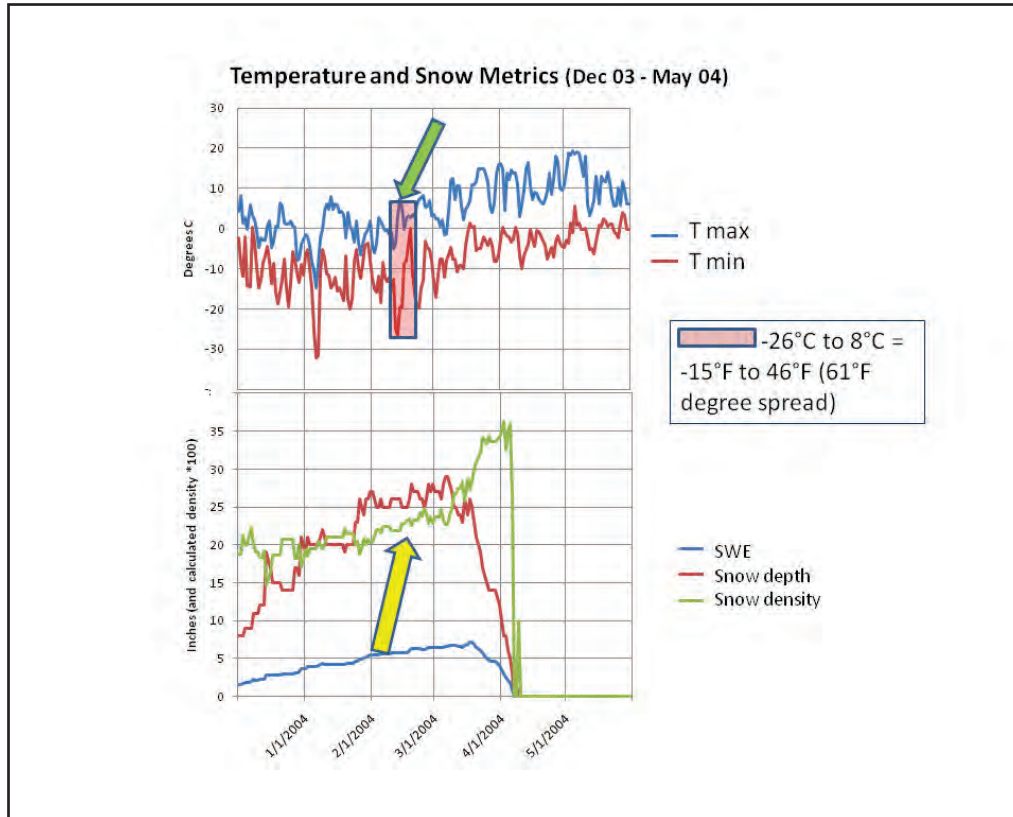


Figure 3. Snow water equivalent (SWE) and snow depth data taken from the northeast entrance SNOTEL site adjacent to the study area in Yellowstone National Park. Snow density was calculated as SWE divided by snow depth. Note the snow hardening events (increased snow density values) that occurred during February and March prior to snow ablation (final meltdown) in mid-April.

sub-nivean space, demonstrating empirically the contribution of snow-hardening events to fox food availability, and pointing toward avenues for further investigation.

Conclusions

Changes in snow-pack dynamics and their effects on ecosystem function and biodiversity may exert strong effects on trophic interactions. Ungulate winter herbivory patterns, as well as prey access by terrestrial carnivores (both over snow and below snow) are affected. The mechanisms through which snow may influence the patterning of animal-habitat relationships is not yet well characterized, or supported by theory.

Climate-driven snow-attribute changes may be relevant to a more comprehensive set of ecosystem dynamics, including carnivore across-snow predation (e.g.,

the wolf-ungulate system) as well as more comprehensive food web interactions. These food web interactions include all predation in the sub-nivean space by other mesocarnivores, such as mustelids, as well as herbivory (winter access to forage) by ungulates.

Snow hardening events, particularly those accompanying springtime conditions, impact fox winter ecology by enhancing snow mobility. During this study, fox were observed making longer range movements during the brief periods that the snow surface “set up.” If, as Kausrud et al. (2008) suggest, changing seasonal temperature and precipitation regimes exert effects on snow subsurface and surface attributes, then we may expect to see a continuing suite of impacts on fox prey access, mobility, and energetics in YNP.

The Snow Model for Yellowstone National Park was developed by Francis Singer, Gary Wockner, and Mike Coughenour of the Natural Resource Ecology Lab (NREL) and Phil Farnes of Snowcap Hydrology in 2001.

Suggested Citation

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Long-Term and Short-Term Invasion of Non-Native Brook Trout into Habitats Occupied by Native Yellowstone Cutthroat Trout in the Shields River Basin of Montana

Bradley B. Shepard¹, Scott Opitz², and Robert Al-Chokhachy³

¹ Montana Cooperative Fishery Research Unit, Ecology Department, Montana State University, Bozeman, MT 59717, 406-223-3011, shepard.brad@gmail.com

² Montana Department of Fish, Wildlife, and Parks, 1354 Highway 10 West, Livingston, MT 59047, 406-222-5105, sopitz@mt.gov

³ U.S. Geological Survey, Northern Rocky Mountain Science Center, 2327 University Way, Suite 2, Bozeman, MT 59715, 435-881-9127, ral-chokhachy@usgs.gov

Abstract

Non-native brook trout (*Salvelinus fontinalis*) have been implicated as part of the reason for the documented decline of native cutthroat trout (*Oncorhynchus clarkii* spp.) populations; however, a question remains as to whether brook trout continue to invade cutthroat trout habitats or whether they rapidly expanded following their initial releases in the early to middle twentieth century and have remained relatively static since that time. If brook trout invasion is still occurring, how might climate change influence rate of invasion? We assessed whether brook trout continued to invade Yellowstone cutthroat trout (*O. c. bouvieri*; YCT) habitats over both moderately long (from 1974 to 2003) and short (2003 to 2009) timeframes in the Shields River drainage of Montana. Sampling of 18 sites that were surveyed in 1974 and two other sites that were sampled in 1989 or 1990 was repeated during 2001–2003. There was no apparent change in the fish community in four sites (YCT remained allopatric in three sites and brook trout were at similar proportions in another site); brook trout had recently invaded three sites or had increased to make up a higher proportion of the fish community in five sites; Yellowstone cutthroat trout made up a higher proportion of the fish community in two sites after rainbow trout disappeared; and brown trout appeared to have recently invaded one site or made up a higher proportion of the fish community in three sites, replacing brook trout in two of these sites. In 2009 a systematic sampling scheme was used to assess short-term invasion in the headwaters of the Shields River drainage. This portion of the drainage had many streams that supported only YCT in surveys conducted around the year 2003, but by 2009 four of these streams had been successfully invaded by brook trout. Additionally, brook trout had totally replaced YCT in three streams and a portion of another stream. No fish were found in portions of three streams that had previously supported YCT. These results appeared to be spatially dependent and fish community dynamics and water temperature may be playing a role. These data suggest brook trout are continuing to invade habitats within the upper Shields drainage and often displace Yellowstone cutthroat trout. This is similar to what has been found for westslope cutthroat trout (*O. c. lewisi*), although this contrasts what was found in the Snake River drainage in Idaho. Climatic changes that are now occurring may be accelerating the rates of brook trout invasion and more research is needed to identify specific factors promoting successful invasion of non-native brook trout.

Introduction

Behnke (1992) described the native inland trout of western North America and recognized 15 subspecies of cutthroat trout. Both Yellowstone cutthroat (*Oncorhynchus clarkii bouvieri*) and westslope cutthroat (*O. c. lewisi*) trout are native to the Greater Yellowstone Ecosystem. The abundance and distribution of Yellowstone cutthroat trout have declined from historical levels throughout their range, and genetically unaltered populations are estimated to currently occupy about 27 percent of their historical

ranges (Hadley 1984; Varley and Gresswell 1988; Behnke 1992; Gresswell 1995; Kruse et al. 2000; May et al. 2003; Meyer et al. 2006; May et al. 2007). Factors associated with these declines include introductions of non-native fishes, habitat changes, and over-exploitation (Hanzel 1959; Behnke 1992). Meyer et al. (2003) suggested that Yellowstone cutthroat trout populations in southeastern Idaho had changed little in abundance, species composition, or size structure from the 1980s to the late-1990s.



Figure 1. Field technician Drew Pearson at upper Shields Basin. Photo by Brad Shepard, courtesy of Montana, Fish, Wildlife, and Parks.

However, they found that rainbow trout were expanding in some areas of the upper Snake River basin and cautioned that this expansion represented a potential risk to existing Yellowstone cutthroat trout populations.

Brook trout (*Salvelinus fontinalis*) are native to eastern North America and were widely introduced into waters within the historical range of Yellowstone cutthroat trout during the early twentieth century. They now occupy many of the headwater habitats previously occupied by many of the native subspecies of cutthroat trout (Behnke 1992; McIntyre and Rieman 1995). Brook trout continue to invade and displace populations of native cutthroat trout (MacPhee 1966; Griffith 1972, 1988; Behnke 1979; Liknes and Graham 1988; Dunham et al. 2002). For invasion to be successful, individuals must not only be able to disperse, but habitats to which they disperse must be capable of supporting a reproducing population (Adams 1999; Dunham et al. 2002; Kennedy et al. 2003; Benjamin 2006; Benjamin et al. 2007). Brook trout appear to have flexible life histories that allow them to successfully inhabit a wide range of habitats from relatively warm, low-elevation sites to cold, infertile, high-elevation sites (Kennedy et al. 2003).

Approximately 96,000 brook trout fry, 1.6 million juveniles, and 5,500 adults were released into streams and rivers in the Shields River drainage of Montana from 1933 to 1954 by the Montana Department of Fish, Wildlife, and Parks (Fish Planting Database, Montana Fish, Wildlife, and Parks, Helena). It is likely that prior to this date the federal government may have stocked some brook trout, but federal stocking records are not available in an electronic format and the senior author has been unable to obtain summaries of federal stocking records. We assume that range expansions of brook trout after 1954 were a result of natural dispersal events. We documented the presence or absence and relative abundances of native Yellowstone cutthroat trout and non-native trout, including brook, brown (*Salmo trutta*), and rainbow trout (*Oncorhynchus mykiss*), within selected tributaries to the Shields River during two time periods (2003 and 2009) and compared these results to earlier sampling (Berg 1975; files of Montana Department of Fish, Wildlife, and Parks, Livingston).

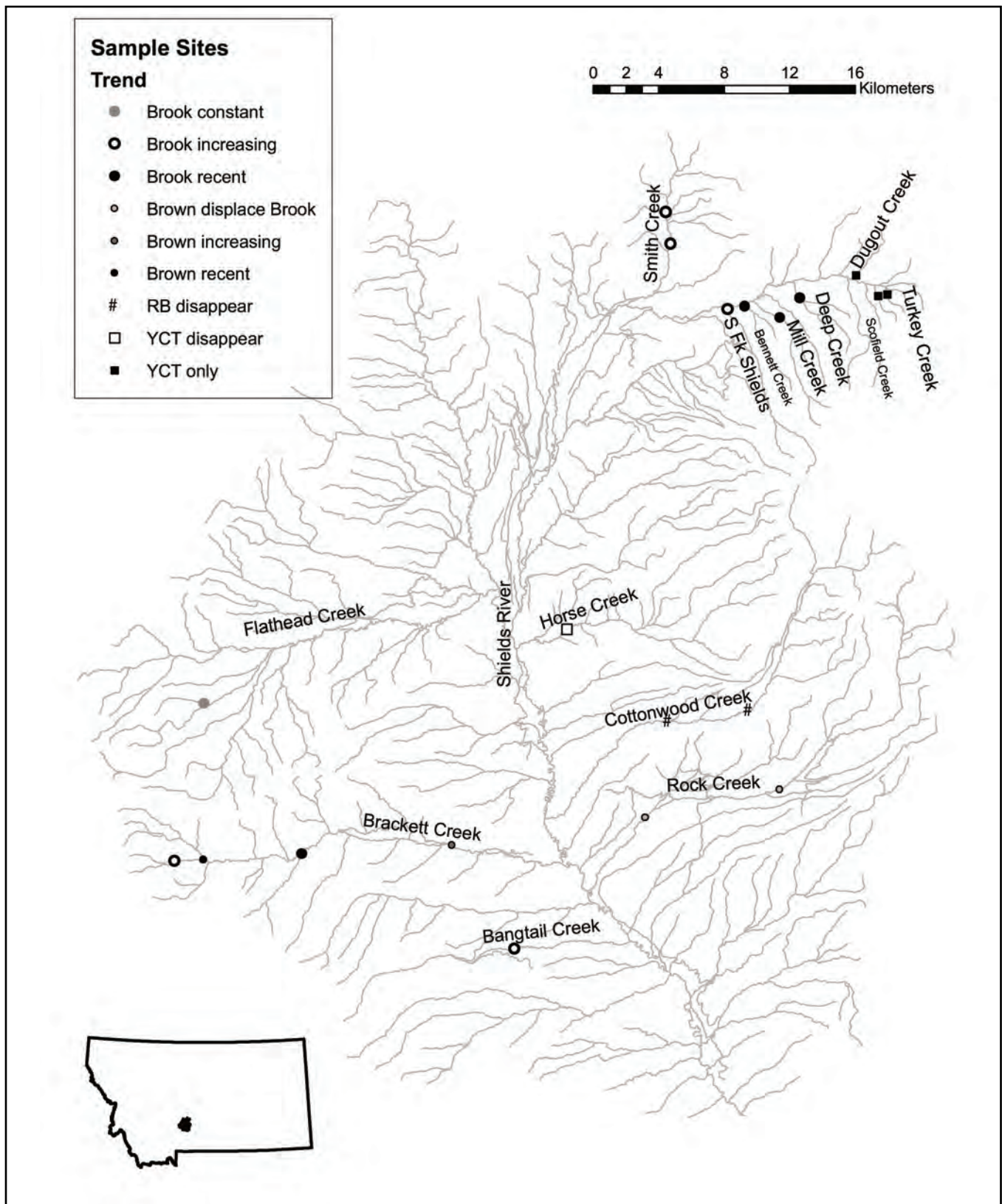


Figure 2. Map of the Shields River drainage of Montana showing sites that were sampled from 1974 to 2003. Different symbols represent different trends observed over time in each sample section (YCT = Yellowstone cutthroat trout; RB = rainbow trout). See Figure 4 for trout species composition information.

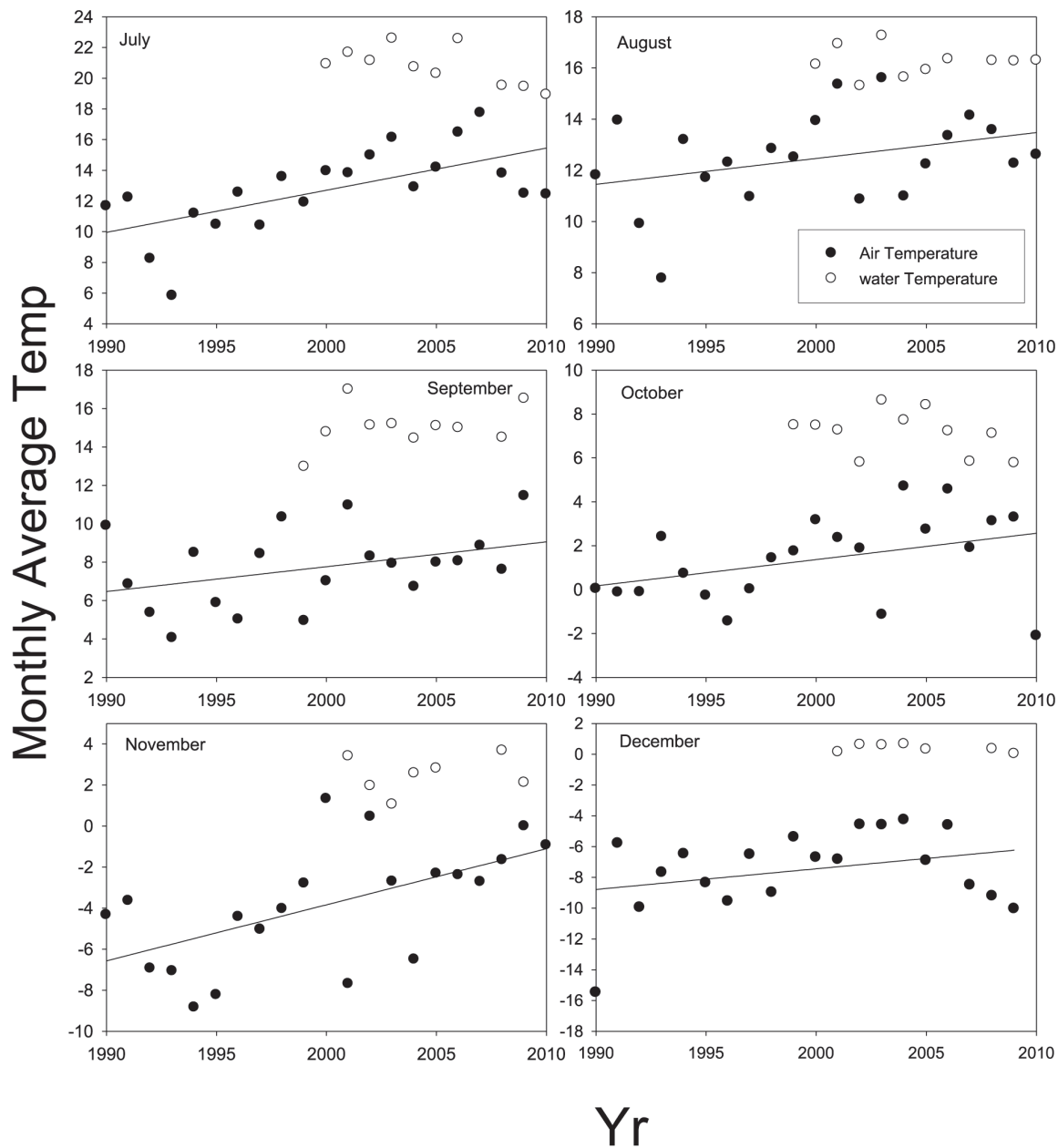


Figure 3. July through December mean monthly air (solid circles) and water (open circles) temperatures from 1990 through 2010 ("Yr" on x-axis) showing trends in annual monthly temperatures. Trends in air temperatures were significantly ($p < 0.01$) different from zero for July and November.

Study Area

The Shields River drains approximately 117,000 hectares (ha) and flows into the Yellowstone River approximately 10 kilometers (km) east of Livingston, Montana, and 785 km above the mouth of the Yellowstone River (Figures 1 and 2). Ecoregions within the Shields River drainage represent the Middle Rockies and Northwestern Great Plains provinces of the Temperate Steppe and Temperate Desert divisions (Woods et al. 1999). The Crazy Moun-

tains bound the watershed on the east and the Bridger and Bangtail Ranges bound it on the west. Elevations range from about 1,310 meters (m) at the mouth of the Shields River to about 3,350 m at the summit of Crazy Peak in the Crazy Mountains. The Bridger Range rises to an elevation of 2,895 m.

Approximately 33 to 38 centimeters (cm) of precipitation falls annually on the lower portions of the valley, while the weather station at the town of Wilsall in

Species Distribution

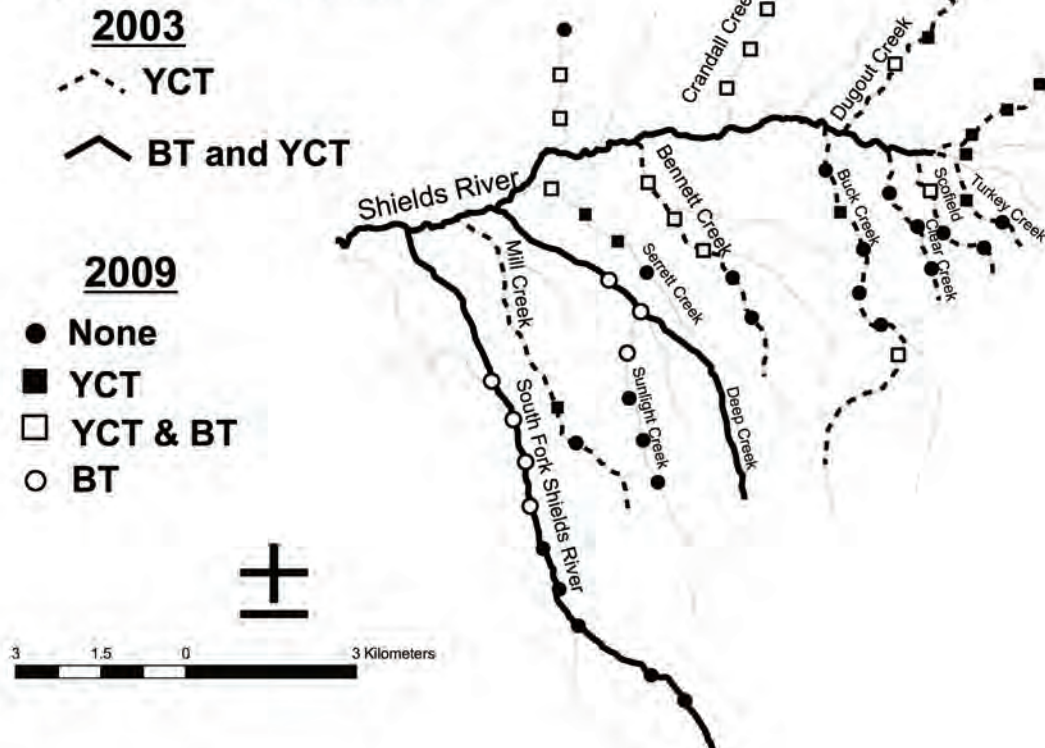


Figure 4. Map of the upper Shields watershed (above Smith Creek) showing distributions of brook trout (BT) and Yellowstone cutthroat trout (YCT) in 2003 (line symbols along each stream) versus 2009 (sample points).

the upper valley reported an annual mean precipitation of about 50 cm for the period of record from 1957 to 2004 (WRCC 2005). The Bridger Range in the west has an annual precipitation of over 127 cm, and the Crazy Mountains in the east average around 152 cm of annual precipitation. About 68 percent of the annual precipitation falls from April through September, with about half this falling in the months of May and June (WRCC 2005). Air temperatures within the Shields basin during the past 20 years have shown a warming trend, with this trend being slightly warmer than worldwide averages (Figure 3; e.g., Intergovernmental Panel on Climate Change 2007; Saunders et al. 2008).

Methods

We captured fish from sample sections that were at least 100 m long using single-pass electrofishing with backpack Smith-Root electrofishers (Models SR-12BP or SR-15B). Presence of each fish species was noted and relative fish abundance for each trout species was calculated as the number of captured fish 75 millimeters (mm) and longer per

100 m of stream length. Sample sections of 91 m (300 feet) originally sampled by Berg (1975) in 1974 were re-sampled in 2003. These sections were located at road crossings, so they were easy to re-locate. However, Berg's (1975) report was not clear as to whether he sampled above, below, or both above and below the road crossings. We sampled 100 m above and below each road crossing, and since relative abundances of each trout species above and below each road crossing were similar, we pooled the above and below road sections for analyses and comparison to Berg's (1975) results. While our sections were slightly more than twice as long as Berg's (1975) sections, we believe that comparing relative abundances and presence/absence results should be valid between these two time periods. We also re-sampled two other sites that were originally sampled by the lead author in 1990. In a few cases these sample sections were also sampled during intervening years and we included summaries of these data (files of Montana Department of Fish, Wildlife, and Parks, Livingston).

In 2009 we systematically sampled 100-m-long sections at 0.8 km intervals in all tributaries to the upper

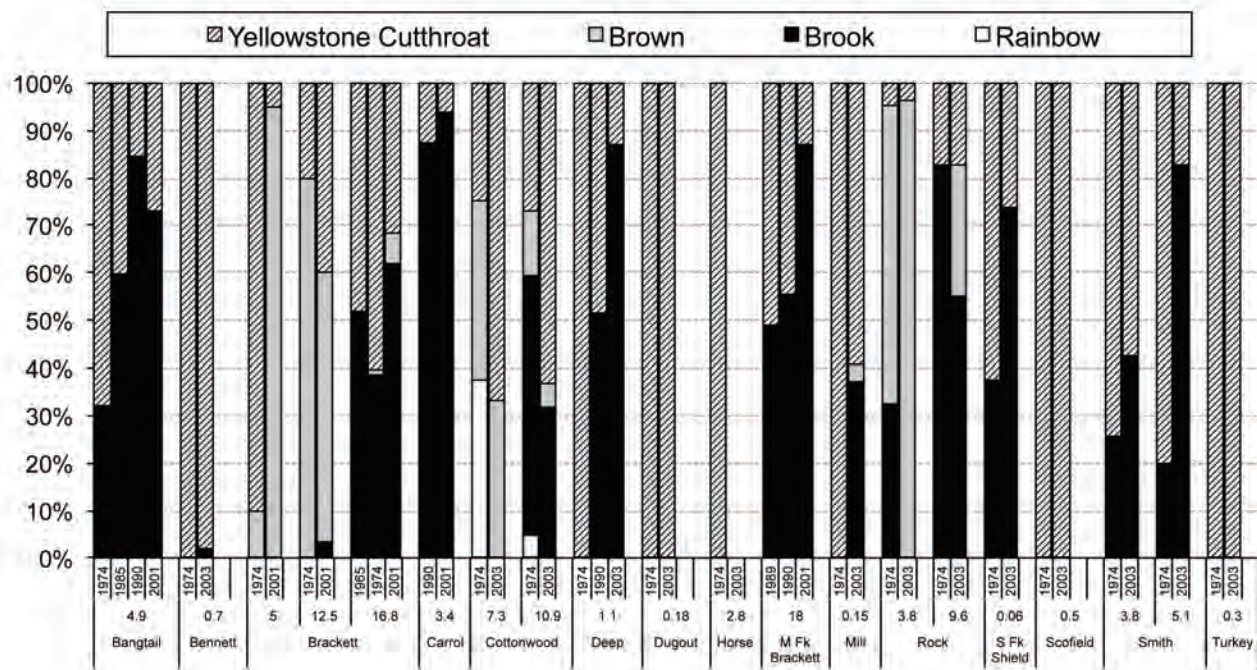


Figure 5. Species composition (%) for trout species in selected sample sites in Shields River tributaries from 1974 through 2003. Year, stream mile, and stream name are shown on the x-axis.

Shields River above Smith Creek to document the distribution and relative abundance of all trout species (Figure 4). We were unable to sample a few sites due to uncooperative landowners. We compared presence or absence and relative abundance of each trout species we found in 2009 to earlier sampling in 2003 and to other sampling done by Montana Fish, Wildlife, and Parks and Gallatin National Forest fisheries biologists (files, Montana Fish, Wildlife, and Parks and Livingston Ranger District, Gallatin National Forest, Livingston, Montana).

Graphs of species compositions for each sampling year by sample site are presented to illustrate changes over time. Classifications of changes in species compositions are also plotted on maps by site to show the spatial arrangement for these changes.

Results

Between Berg's (1975) sampling in 1974 and our sampling in 2003, we observed several different patterns of change in species compositions (Figures 2 and 5). For many sites (8 of 20, or 40 percent) brook trout either invaded between 1974 and 2003 (three sites) or they made up a higher proportion of the trout captured, while Yellowstone cutthroat proportions declined (Figure 5). In only one site did the composition of brook trout and Yellowstone cutthroat trout remain similar between 1974 and 2003. In three sites

Yellowstone cutthroat trout were the only salmonid species captured in both 1974 and 2003. In two sites in Rock Creek the proportion of brown trout increased, and they appeared to displace or reduce the proportion of brook trout, but not Yellowstone cutthroat trout, which made up a relatively small proportion of captured trout in both 1974 and 2003. In lower Brackett Creek the proportion of brown trout increased dramatically as the proportion of Yellowstone cutthroat trout declined, and in upper Brackett Creek brown trout were first documented in 2003. In Cottonwood Creek, following the cessation of rainbow trout stocking in 1967 (Fish Stocking Database, Montana Fish, Wildlife, and Parks, Helena) rainbow trout disappeared and it appeared that the proportion of Yellowstone cutthroat trout increased in response to the disappearance of rainbow trout. In one site Yellowstone cutthroat trout were the only species captured in 1974, and no trout of any species were found in 2003. Spatially, it appeared that from 1974 to 2003 non-native species have invaded primarily in an upstream direction and their proportions increased in many sites. In 2003 allopatric populations of Yellowstone cutthroat occurred only in tributaries located in the headwaters of the Shields watershed (Figure 2).

Systematic sampling of tributaries within the upper Shields watershed during 2009 indicated that invasion of brook trout continued to occur in the upper basin and the

rate of invasion appeared to accelerate during the relatively short time between 2003 and 2009 (Figures 5 and 6). While brook trout continued to invade the upper Shields basin, there was no evidence of rainbow trout or brown trout invasion into the upper basin above Smith Creek.

Discussion

Non-native trout, especially brook trout, invaded many habitats historically occupied by Yellowstone cutthroat trout within the Shields River basin, and invasion of brook trout appears to have accelerated during the past decade. Invasion by non-native trout within the Shields drainage appeared to reduce the proportion of Yellowstone cutthroat trout in many areas. This finding is different than the findings of Meyer et al. (2003) who found that abundances, distribution, and size structure of Yellowstone cutthroat trout populations in southeastern Idaho had not changed much between the early 1980s and the late 1990s.

Shepard (2010) concluded that brook trout and westslope cutthroat trout occupy a similar niche, and because of this niche overlap, brook trout displace cutthroat trout. This conclusion of brook trout displacing native cutthroat trout is supported by many studies (Schroeter 1998; Novinger 2000; Hepworth et al. 2001; Peterson and Fausch 2003; McGrath 2004; McGrath and Lewis 2007).

The three most commonly cited mechanisms for displacement of cutthroat by brook trout are competition, predation, and parasite or disease transmission (Fausch 1988; Dunham et al. 2002). Predation by brook trout on greenback cutthroat trout (*O. c. stomias*) was too low to account for displacement of cutthroat trout by brook trout based on analyses of stomach contents and stable isotopes (McGrath 2004; McGrath and Lewis 2007). Numerous food habits studies conducted on brook trout have found little to no evidence of predation on salmonids by brook trout in streams (Griffith 1970, 1972; Allan 1981; Cummings 1987; Bechara et al. 1992; Dunham et al. 2000; Mistak et al. 2003). However, studies that caged brook trout and cutthroat trout together documented predation on cutthroat by brook trout (Gregory and Griffith 2000; Novinger 2000). Predation by brook trout on cutthroat trout in these cage studies may be an artifact of the cage-treatments (McGrath 2004). Brook trout in several headwater streams of the Greenbrier River, West Virginia, ate brook trout (Webster and Hartman 2005). Salmonids in streams generally do not begin eating fish until they have reached 270 mm (Keeley and Grant 2001), a size at the upper limit of most fish in Rocky Mountain headwater trout populations.

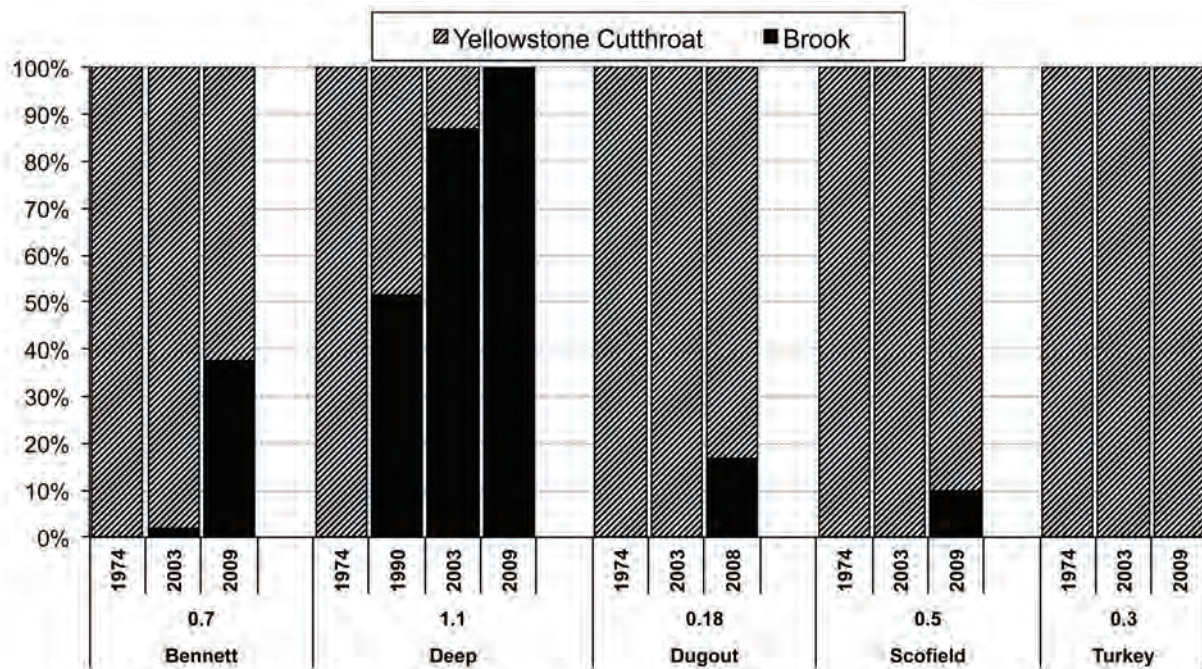


Figure 6. Species composition (%) for trout species in selected sample sites in upper Shields River tributaries from 2003 through 2009. Year, stream mile, and stream name are shown on the x-axis.

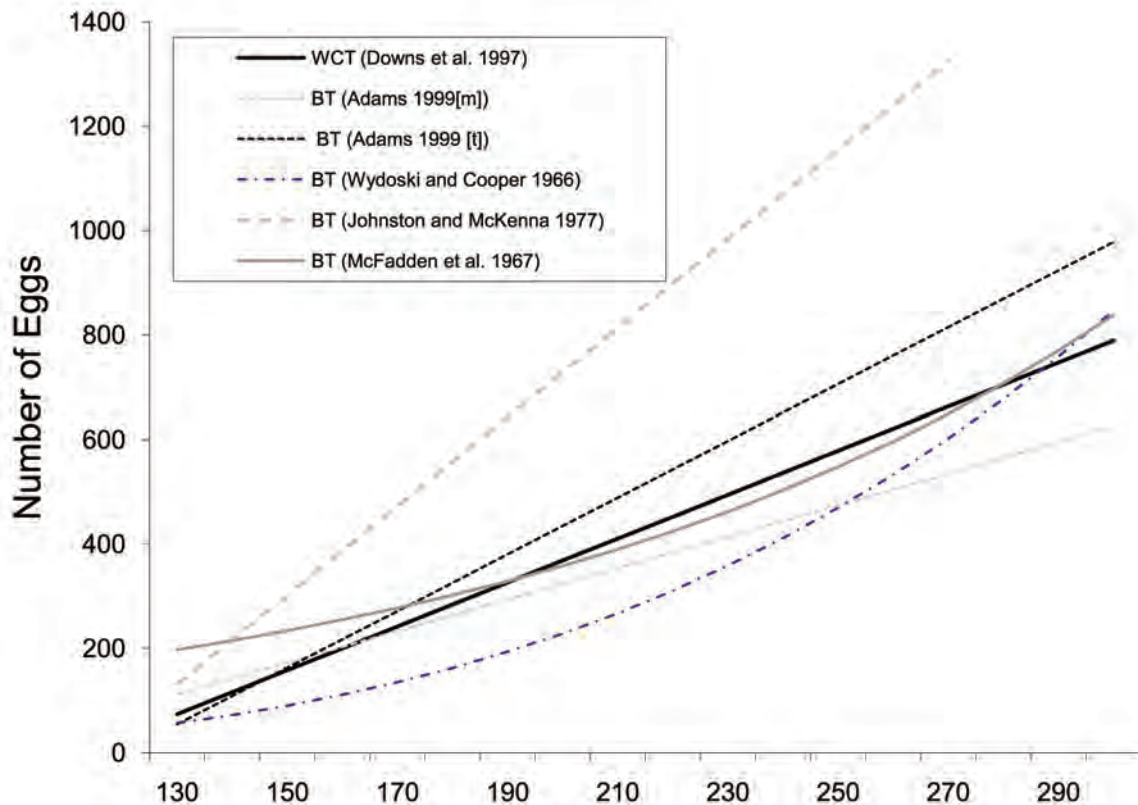


Figure 7. Fecundity (number of eggs) related to total length (TL; mm) for westslope cutthroat trout (WCT) and brook trout (BT) with citations (for Adams 1999 the “m” and “t” in brackets refer to relationships developed for Moore and Twelvemile Creeks, respectively).

Competition appears to be a more likely mechanism than predation for displacement of cutthroat trout by brook trout, and many researchers have suggested that this competition probably occurs at young ages, though few studies have explicitly tested this hypothesis (Novinger 2000; Shepard et al. 2002; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007). Griffith (1970, 1972) documented dietary overlap between brook trout and westslope cutthroat trout and suggested that brook trout could replace westslope cutthroat trout through competition for food, space, or both, but he suggested that replacement of westslope cutthroat trout by brook trout probably occurred after habitat degradation had already reduced or eliminated westslope cutthroat trout. Diet overlap was high between brook trout and Lahontan cutthroat trout (*O. c. henshawi*), but brook trout used larger organisms than cutthroat trout (Dunham et al. 2000). Colorado River cutthroat trout (*O. c. pleuriticus*) consumed a wider range of food organisms than brook trout (McGrath and Lewis 2007). Diet overlap was high between Bonneville cutthroat trout (*O. c. utah*) and brook

trout, but overlap varied by habitat type, with 92 percent overlap seen in beaver ponds, 75 percent in a high-gradient stream reach, and 65 percent in a low-gradient stream reach (Hilderbrand and Kershner 2004).

Brook trout displaced Colorado River cutthroat trout from microhabitats at higher water temperatures in a laboratory setting, but cutthroat trout were able to maintain positions at lower water temperatures (10°C; DeStaso and Rahel 1994). Young brook trout inhibited the foraging efficiency of juvenile Colorado River cutthroat trout in a controlled laboratory setting (Thomas 1996). Thomas (1996) suggested that this inhibition might be the mechanism responsible for decreased growth rates of cutthroat trout that she documented in the wild. Juvenile brook trout excluded juvenile greenback cutthroat trout from more profitable stream positions (Cummings 1987). Brook trout grew faster and moved less than Bonneville cutthroat trout in stream enclosures where both species were introduced at low, ambient, and high densities (Buys et al. 2009). Buys et al. (2009) observed a negative correlation between growth and emigration for cutthroat

trout in the presence of brook trout, leading them to infer a possible competitive response in cutthroat trout caused by the presence of brook trout. Competition by conspecific age-0 brook trout at two different densities resulted in activity rates that were four times higher for the high-density treatments and supported the hypothesis that at higher densities competition can have a negative effect on growth through an increase in activity rates (Marchand and Boisclair 1998). After brook trout were removed from a reach of a tributary to Priest Lake, Idaho, age-0 westslope cutthroat trout that were subsequently stocked into this reach resulted in much higher densities of cutthroat trout than in adjacent tributaries where brook trout were not removed (Strach 1990).

If reproductive potential (fecundities) are different between the two species, the species with a higher reproductive potential could be expected to have a demographic advantage. A review of the literature indicated that fecundities could be highly variable among different populations of the same species, even for populations that occupied similar stream habitats (Rounsefell 1957; Wydoski and Cooper 1966; Lennon 1967; McFadden et al. 1967; Johnson and McKenna 1977; Downs et al. 1997; Adams 1999; Figure 7). These data suggest that fecundities of brook trout and westslope cutthroat trout that occupy small, relatively unproductive streams are either similar, or that fecundities of westslope cutthroat trout in these types of streams may be higher than brook trout. Fecundities for brook trout reported by Johnston and McKenna (1977) were higher than reported for all the other studies cited. This population occupied a river below two reservoirs that flowed through agricultural lands at a low-elevation on Prince Edward Island. Even though the brook trout sampled in this system were less than 250 mm total length (TL), this system probably had much higher secondary productivity than is typically available in mountainous headwater streams that could have increased fecundity rates. We concluded that these data did not provide convincing evidence for a fecundity advantage for brook trout over cutthroat trout in small, relatively unproductive streams.

Whereas fecundities probably are not too different between cutthroat and brook trout, female brook trout in headwater streams can mature at a smaller size than westslope cutthroat trout. Female brook trout from a high-elevation stream in Colorado matured at fork lengths (FL) from 130 to 225 mm, and females from a mid-elevation stream matured at 90 to 170 mm (Kennedy et al. 2003),

whereas female westslope cutthroat trout from moderate to high-elevation streams in Montana first reached sexual maturity at about 150 mm (FL), and almost all females longer than 190 mm were sexually mature (Downs et al. 1997). Smaller size, or earlier age, at first maturation could give brook trout a reproductive edge over westslope cutthroat trout that might allow brook trout to numerically overwhelm westslope cutthroat trout populations over time.

The differences in the timing of spawning and fry emergence between brook trout and cutthroat trout may play an important role in determining whether brook trout can successfully displace native cutthroat trout (reviewed by Griffith 1988). Several demographic consequences arising from these differences in early life-histories are dependent upon the geomorphic and climatic setting. Incubating brook trout embryos are subjected to both winter freezing and winter high flow scour events that can reduce their survival (Lennon 1967; Elwood and Waters 1969; Seegrist and Gard 1972; Strange et al. 1993; Latterell et al. 1998). Winter freezing effects may be moderated by brook trout selecting groundwater recharge areas for spawning (Benson 1953; Curry and Noakes 1995). Incubating brook trout embryos can be crushed or displaced if winter flows are high enough to mobilize the streambed.

Cutthroat trout spawn during the declining limb of spring snowmelt peak flows and embryos incubate over the summer as flows continue to decline and stabilize (Schmetterling 2001). Cutthroat trout fry emerge when flows are near a base level. Thus, they are much less vulnerable to peak flow events. However, because of their late emergence cutthroat trout have much less time than brook trout to grow and put on fat reserves to carry them through the winter. Smaller size of age-0 trout, especially related to low fat, lipid, and protein reserves, have been shown to increase over-winter mortality of fish (Hunt 1969; Rose 1986; Cunjak et al. 1987; Cunjak and Power 1987; Cunjak 1988; Meyer and Griffith 1997; Berg and Bremset 1998; Coleman and Fausch 2007; Webster and Hartman 2007).

Newly emerged brook trout fry can be flushed far downstream by high spring flows that occur shortly after they emerge (Latterell et al. 1998; Warren et al. 2009). Effects of high flows can be magnified or mediated by the geomorphic setting. Steep stream channels in narrow, constricted valleys can magnify the effects of high flows by concentrating flows and offering no off-channel, low-velocity refuges to newly emerged brook trout fry

(Chisholm and Hubert 1986; Fausch 1989; McLaughlin and Noakes 1998). Brook trout recruitment in streams that commonly experience peak flow events in the winter or early spring—common occurrences in environments with maritime climatic influences west of the Continental Divide—would more likely be affected than streams where spring snowmelt dominates the flow regime and results in late spring or early summer peak flows, which occur after brook trout fry have emerged from the stream gravels.

Low-gradient channels that occupy wide floodplains, especially if beaver ponds are located in these floodplains, can mediate effects of high flows on embryos and newly emerged brook trout fry by dissipating high flow energies and velocities and providing off-channel refuge habitats (Benjamin 2006; Benjamin et al. 2007). Beaver ponds probably function as sources for repeated brook trout invasions into steeper and more confined stream reaches (Benjamin 2006; Benjamin et al. 2007). Whereas beaver dams can restrict or prevent upstream movement, beaver ponds can moderate temperatures and provide cover and food resources important for brook trout (Rupp 1954; Allen and Claussen 1960; Winkle et al. 1990; Johnson et al. 1992; McRae and Edwards 1994; Collen and Gibson 2001; Cossette and Rodriguez 2004). Brook trout may be better adapted to pond conditions than many other salmonid species, and Collen and Gibson (2001) found that brook trout dominated Atlantic salmon (*Salmo salar*) in streams with beaver ponds. Beaver ponds may be particularly important as winter habitat, and several studies have indicated that both brook and cutthroat trout prefer beaver ponds during the winter (Jakober et al. 1998; Lindstrom and Hubert 2004).

Moderate levels of fine sediments within spawning areas can reduce embryo-to-emergence survivals (reviewed by Everest et al. 1987 and Chapman 1988). Fine sediment levels affect brook trout and westslope cutthroat trout embryo-to-emergence survivals differently with brook trout apparently being slightly more tolerant of fine sediments (Hausle and Coble 1976; Witzel and MacCrimmon 1983; Irving and Bjornn 1984; Argent and Flebbe 1999; Curry and MacNeill 2004). This embryo survival advantage for brook trout at similar levels of fine sediments may be enough to tip the balance in favor of brook trout, especially in streams with fine sediment levels of 20 percent or higher.

Later emergence timing by cutthroat trout also results in a distinct size disadvantage compared to same-age brook trout, which emerge months earlier and maintain

a 30 to 50 mm size advantage through their first year of life (Griffith 1988). Young (2004) concluded that because coho fry emerged earlier and maintained a size advantage over steelhead fry, interspecific competition was strongly asymmetrical in favor of coho and that habitat selection by both species was strongly dependent upon densities of coho fry. This mechanism may explain the commonly reported dominance of age-0 brook trout over age-0 cutthroat trout (Griffith 1974) and may be a major factor responsible for the displacement of cutthroat trout by brook trout (Novinger 2000; Shepard et al. 2002; Peterson et al. 2004; Hilderbrand 2003; McGrath and Lewis 2007).

Age-0 rainbow trout have been shown to compete for food and space with age-0 brook trout, reducing growth of brook trout during their first summer (Rose 1986). In spite of their smaller size, age-0 rainbow trout were more aggressive than age-0 brook trout in Rose's (1986) study. He suggested that this may result in increased overwinter mortality of age-0 brook trout and be a mechanism by which rainbow trout exclude brook trout. This result was supported by a deterministic model developed and applied by Marschall and Crowder (1996). Displacement of native brook trout by non-native rainbow trout in Rose's (1986) study, where age-0 rainbow trout emerged later and were smaller than age-0 brook trout, was exactly opposite from the effect that the senior author observed for non-native brook trout and native cutthroat trout in streams of the northern Rocky Mountains, where earlier emerging non-native brook trout displaced native cutthroat trout. Could this reversal in competitive advantage, caused by differences in emergence timing between native brook trout and non-native rainbow trout in the east versus non-native brook trout and native cutthroat trout in the west, be related to different behaviors of these different species or to differences between native and non-native species behaviors in these different geographic locations? This question might be a fruitful area for future research.

Numerous mechanisms exist by which brook trout might gain a competitive advantage over cutthroat trout, and these individual mechanisms probably operate synergistically and in complex ways, depending on the local environment. The high degree of diet overlap documented in several studies (e.g., Griffith 1970, 1972; Hilderbrand and Kershner 2004; McGrath 2004; McGrath and Lewis 2007) provides evidence for exploitive competition. Behavioral studies have shown that brook trout are more aggressive than cutthroat trout and will displace them from preferred focal habitats, providing evidence for both

exploitive (competition for space or cover) and interference competition (e.g., Cummings 1987; DeSato and Rahel 1994; Thomas 1996; Schroeter 1998; Novinger 2000; Koenig 2006; Buys et al. 2009). Abiotic variables such as temperature, channel gradient, stream size, and valley confinement can either promote or inhibit displacement of cutthroat trout by brook trout.

One important question is: “Why does the rate of invasion of brook trout within the Shields River basin appear to be accelerating at such a fast pace?” Water temperature has been suggested by many authors as potentially important in mediating the invasion success of brook trout into habitats occupied by native salmonids (e.g., Fausch 1989; DeStaso and Rahel 1994; Dunham et al. 2002; Shepard 2004; McMahon et al. 2007). However, separating influences of temperature from altitude has proven difficult (McHugh and Budy 2005; McMahon et al. 2007; Ohlund et al. 2008). Critical thermal maxima for brook trout range from 27.7 to 29.8°C and are probably related to stock, life-stage, and sex (Benfey et al. 1997). Brook trout have been shown to seek out cooler water provided by groundwater, pool stratification, or tributary inflows when water temperatures approach critical levels (Baird and Krueger 2003).

Relationships between water temperature and daily growth potential have recently been developed for brook trout and westslope cutthroat trout by McMahon et al. (2007), Bear (2005), and Bear et al. (2007). These relationships indicate that optimal temperatures for growth of brook trout are wider and overlap optimal temperatures for growth of westslope cutthroat trout (Figure 8). Westslope cutthroat trout have a very narrow range of temperatures (12 to 16°C) where they have a potential growth advantage over brook trout and their advantage is relatively small. Brook trout grow progressively more than cutthroat trout as temperatures increase or decrease beyond this 12 to 16°C range. Thus, brook trout may have a physiological advantage over cutthroat trout because they can optimize their growth potential over a wider range of temperatures than cutthroat trout.

Air temperature data indicates a dramatic warming has occurred over the last 20 years within the Shields River Basin (Figure 3). We found a strong correlation ($r = 0.96$, $p < 0.01$) between mean monthly air temperatures at the South Fork Shields SNOTEL gauging site and water temperatures recorded at the U.S. Geological Survey (USGS) stream gauging station in the Shields River near its mouth. Thus, it is possible that the recent rapid rate

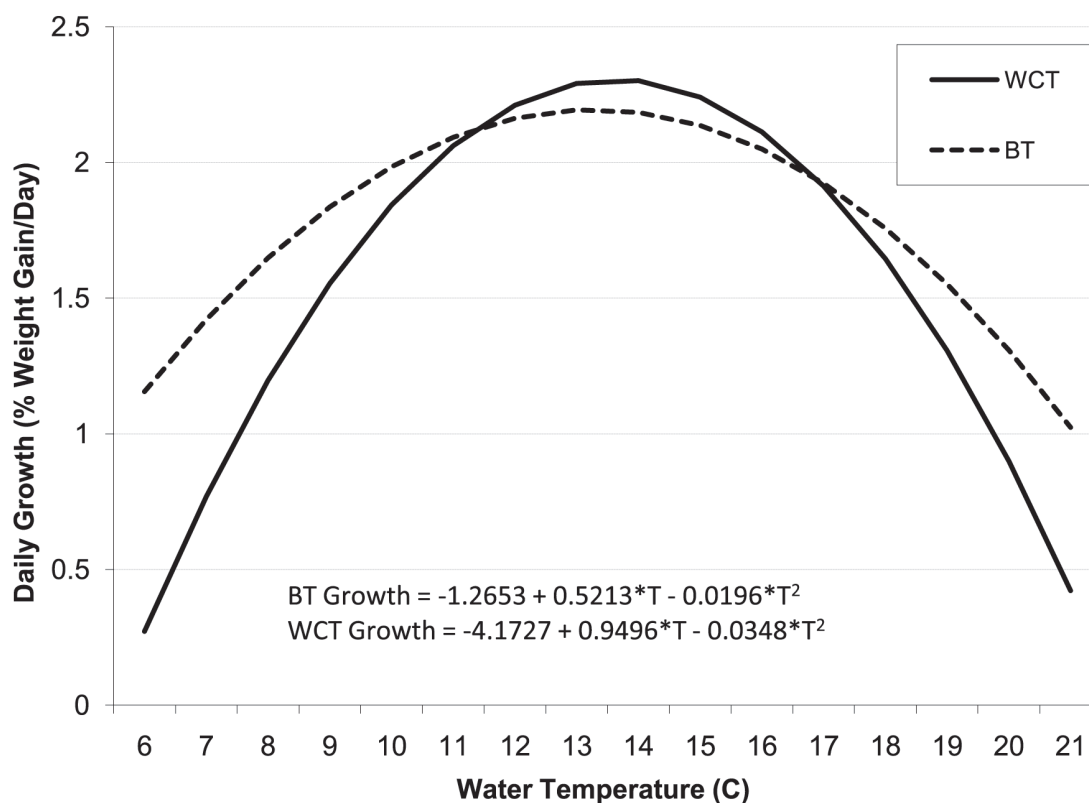


Figure 8. Predicted potential daily weight gain for juvenile westslope cutthroat trout (WCT; Bear et al. 2007) and brook trout (BT; McMahon et al. 2007) based on water temperature (°C; “T” in equations).

of brook trout expansion and displacement of cutthroat trout in the Shields River Basin is related to increases in air and stream temperatures. We plan to continue testing this hypothesis.

Conserving native cutthroat trout populations in tributaries where brook trout might invade will probably require physical barriers to prevent invasion of headwater habitats (Novinger and Rahel 2003; Wofford et al. 2005; Van Houdt et al. 2005; Peterson et al. 2008). Unfortunately, many headwater areas above fish barriers may not provide enough stream habitat to allow native cutthroat trout populations to persist for long periods of time without human intervention (Shepard et al. 1997, 2005; Harig et al. 2000; Hilderbrand and Kershner 2000; Kruse et al. 2001; Harig and Fausch 2002; Hilderbrand 2002; Hilderbrand 2003; Peterson et al. 2008; Fausch et al. 2009).

Consequently, we suggest that a wide range of conservation measures will be needed to conserve cutthroat trout. In locations where no non-native trout occur, large areas of interconnected habitats that support cutthroat trout populations should be maintained. These conservation areas should be as large as possible to 1) protect as wide a diversity of life histories (i.e., migratory and resident) as possible, 2) include both lotic and lentic habitats, and 3) allow metapopulation dynamics to operate (e.g., Rieman and Dunham 2000). Where non-native trout occur, cutthroat trout populations will need to be isolated to conserve their genetic integrity and prevent invasion by non-native competitors that can displace them. Isolation of populations will require replication of many of these isolated populations to protect their genetic legacies and allow for re-founding of these populations should they go extinct. Isolation may also require periodic genetic infusion to avoid inbreeding depression (genetic rescue; e.g., Schonhuth et al. 2003; Letcher et al. 2007; Zajitschek et al. 2009).

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Vulnerability of Landscape Carbon Fluxes to Future Climate and Fire in the Greater Yellowstone Ecosystem

Erica A. H. Smithwick¹, Anthony L. Westerling², Monica G. Turner³,
William H. Romme⁴ and Michael G. Ryan⁵

¹Department of Geography, Pennsylvania State University, University Park, PA 16801, 814-865-6693, smithwick@psu.edu

²Sierra Nevada Research Institute, University of California–Merced, Merced, CA 95343, awesterling@ucmerced.edu

³Department of Zoology, University of Wisconsin–Madison, Madison, WI 53706, turnermg@wisc.edu

⁴Warner College of Natural Resources, Colorado State University, Fort Collins, CO 80523, romme@warnercnr.colostate.edu

⁵USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO 80526, mgryan@fs.fed.us

Abstract

More frequent fires under climate warming are likely to alter terrestrial carbon (C) stocks by reducing the amount of C stored in biomass and soil. However, the thresholds of fire frequency that could shift landscapes from C sinks to C sources under future climates are not known. We used the Greater Yellowstone Ecosystem (GYE) as a case study to explore the conditions under which future climate and fire regimes would result in tipping points of C source-sink dynamics. We asked: How great a change in climate and fire regime would be required to shift conifer forests in the GYE from a net C sink to a net C source? To answer this question, we developed downscaled climate projections for the GYE for three general circulation models and used these projections in a dynamic ecosystem process model (CENTURY version 4.5). We simulated C storage to year 2100 for individual forest stands under three fire-event pathways (fires at 90, 60, or every 30 years) and a reference simulation (no fire, representing the historical fire interval) under both future and current downscaled climate scenarios. Our results show that fire intervals less than approximately 90 years will cause lodgepole pine (*Pinus contorta* var. *latifolia*) forest stands to shift from a net C sink to a net C source, because the time between fires would be less than the time required to recover 85 percent of the C lost to fire. The capacity for fast post-fire regeneration of lodgepole pine from an aerial seedbank (serotinous cones) and the projected increase in lodgepole pine productivity under warmer climate conditions would not counter the consequences of fire-return intervals that were less than 90 years. In all future climate scenarios, decreases in fire-return interval are likely to reduce the potential of the GYE landscape to store C. The magnitude of this shift will depend on the future distribution of forest and non-forest ecosystems across the landscape, other constraints on fire patterns not considered here (fuels, ignition factors, and landscape management), and the accuracy of the fire-climate model as future climate diverges increasingly from the past.

Introduction

Forest managers in the western U.S. are facing more wild-fires than ever before, and it is increasingly important for scientists and managers to anticipate the consequences of this trend. In subalpine forests of the northern Rocky Mountains, the number of large fires has increased in the past 25 years in association with warmer temperatures, earlier snowmelt, and longer fire seasons (Westerling et al. 2006; Running 2006). This trend is expected to continue with global warming (Tymstra et al. 2007; Littell et al. 2010). Yet, the consequences of increased fire frequency and climate warming for western forests remain uncertain. Increased fire occurrence is a prime concern of residents and

land managers from state and federal agencies because of direct effects of fire on life, property, and resources (GAO 2007). More frequent fire may also trigger important ecological changes, and carbon (C) source-sink dynamics may be particularly vulnerable to altered fire regimes (e.g., Kurz et al. 2008; Balshi et al. 2009).

Our previous work, based on intensive field measurements in a chronosequence of 77 lodgepole pine (*Pinus contorta* var. *latifolia*) stands (Smithwick et al. 2009a; Kashian et al., in prep) and simulation models (Smithwick et al. 2009b) has shown that C and nitrogen (N) losses following stand-replacing fire are recovered within 70–100

years, well within the relatively long, average historical fire intervals (135 to 310 years) in lodgepole pine forests of the Greater Yellowstone Ecosystem (GYE; Schoennagel et al. 2003, 2004). When simulating C balance in lodgepole pine forests under projected future climates, our results also suggested the potential for an increase in net C storage (Smithwick et al. 2009b), because lodgepole pine productivity in the GYE may be limited, in part, by temperature and/or length of the growing season. Because C losses to fire are relatively low and C stocks recover within the observed fire-return intervals (FRIs), we surmised that forests in the GYE would need to burn much more frequently than has occurred throughout most of the Holocene, where fire intervals were generally greater than 100 years (Whitlock et al. 2003), for C storage to be substantially altered (Kashian et al. 2006). However, the degree to which fire frequency would need to be increased that would lead to reductions in C storage has not been explored previously.

Our goal in this project was to advance scientific understanding of landscape-scale vulnerabilities of key western forest types to climate change. Our overall question was: *how great a change in climate and fire regime would be required to shift conifer forest communities in the GYE from a net C sink to a net C source?* We aimed to identify the fire frequency at which conifer forests become net sources of C to the atmosphere (i.e., lower C storage in the future when compared to current conditions). The GYE is ideal for this study because its fire regime and vegetation dynamics are reasonably well understood (e.g., Romme and Despain 1989; Whitlock et al. 2003; Turner et al. 2003). In 1988, the extensive Yellowstone fires inaugurated a new era of major wildfires in the western U.S., and 20 years of intensive post-fire research have provided many new insights into the consequences of large, severe wildfires in the Yellowstone ecosystem (Kashian et al. 2006; Schoennagel et al. 2008; Turner 2010). Lodgepole pine, the dominant tree species in Yellowstone National Park, can regenerate rapidly and abundantly after fire due to its serotinous cones (Turner et al. 1997), and the abundance of serotinous cones covaries spatially with elevation and historical fire frequency (Schoennagel et al. 2003). Although canopy fires consume fine litter, branches, and foliage, and kill live trees, relatively little of the C pools in tree boles, downed wood, and soil are combusted (Tinker and Knight 2000; Campbell et al. 2007).

Methods

Our approach combined a dynamic ecosystem model to project future C stocks under different climate scenarios and fire regimes. To identify how great a change in climate and fire regime would be required to shift vegetation from C source to C sink, we ran the ecosystem model CENTURY version 4.5 (Parton et al. 1987; Smithwick et al. 2009b) aspatially for the dominant vegetation communities in the GYE given a large fire event in 1988, and a range of estimated fire-return intervals and current and future climate conditions. Based on our previous work (Kashian et al. 2006; Kashian et al., in prep), we identified general patterns of fire regime and forest regeneration pathways across the region. Our goal was to focus on critical drivers that would be likely to result in observable and representative change across the landscape. We concluded that changes in C stocks would be most significant for transitions of forest to non-forest (rather than forest to forest only). Other studies have shown substantial differences in C stocks with stand age up to about 100 years, but less difference among conifer forest types (Bradford et al. 2008). Thus, our current modeling was focused on lodgepole pine, a representative forest type in the region. The model has to-date been additionally parameterized for warm-dry conifer (primarily Douglas fir [*Pseudotsuga menziesii*] forests in the GYE) and grasslands in the Lamar Valley; as validation data of C stocks in this ecosystem (Donato et al., in prep) become available, we will incorporate these vegetation types into our approach. However, to capture variation in recovery in lodgepole pine, we modeled two recovery pathways: fast (high pre-fire serotiny, more prevalent at elevations < 2,400 meters [m]) and slow (low pre-fire serotiny, characteristic of elevations > 2,400 m; Schoennagel et al. 2003). We expect that the slow recovery pathway will be representative of other vegetation types that lack serotinous cones and are likely to regenerate more slowly, for example, Douglas-fir or spruce-fir forests. All fires were prescribed to be high-severity, stand-replacing events.

To estimate current and future climate conditions, we used historical climate data and general circulation model (GCM) runs downscaled to the North American Land Data Assimilation system 1/8-degree latitude/longitude grid (12 x 12 km resolution). We used three AR4 GCMs (CCSM 3.0, CNRM CM 3.0, and GFDL CM 2.1) forced with the Intergovernmental Panel on Climate Change's (IPCC's) Third Assessment Report: Special Report on Emissions Scenarios (SRES) A2 emissions pathway to

generate a set of plausible climate futures for the western USA. The three GCMs used here are among a larger group that were assessed to adequately represent important aspects of western North American climate, including seasonality of temperature and precipitation and multi-year variability in sea surface temperatures (Daniel Cayan et al., unpublished). This particular subset of models was chosen because daily values for important variables such as temperature and precipitation were available for each GCM run, and these were required to force the hydrologic simulations used. The A2 emissions scenarios have been a frequent focus for impact assessment work because they were thought to represent a plausible high-end emissions scenario. However, for much of the past decade, emissions and atmospheric concentrations of greenhouse gases have exceeded the range of commonly used IPCC emissions scenarios, especially SRES A2. Consequently, given current and past emissions, the long lead times necessary to reduce future emissions, and the long atmospheric residence times of many greenhouse gases, climate projections using the SRES A2 CO₂ trajectory can no longer be considered a plausible representation of the future, nor representative of a “high” emissions scenario, but were used here given their availability.

Because current atmospheric concentrations exceed those represented in the SRES A2 scenarios, the climate scenarios used to derive our results can be considered conservative. GCM temperature and precipitation fields were downscaled using the constructed analogs method with bias correction (Maurer and Hidalgo 2008). Gridded historical climate data (temperature, precipitation, radiation, and wind speed) were obtained from Dr. Lettenmaier at the University of Washington and Dr. Maurer at the University of Santa Clara (Hamlet and Lettenmaier 2005). For the simulations of lodgepole pine forest, we used climate data from the grid centered on the Yellowstone Lake climate station, which is centrally located in the GYE and surrounded by lodgepole pine forest.

Productivity, mortality, and post-fire recovery were parameterized in CENTURY for lodgepole pine and warm-dry conifer trees based on empirical data (Tinker and Knight 2000; Pearson et al. 1987; Ryan and Waring 1992; Stump and Binkley 1993; Smithwick et al. 2009a; Kashian et al., in prep) and previous modeling efforts (Kashian et al. 2006, Smithwick et al. 2009b). The model was run in “savanna” mode, allowing for grass and tree competition for water and nutrients. For all simulations, we assumed a C3 grass parameterization available in CEN-

TURY. Grass represented a small proportion of C stocks in mature stands but was a large and transient component of total C stocks for several years following fire. These large, transient pulses of post-fire grass were likely overestimated and future modeling efforts will be increasingly focused on grass dynamics in early post-fire years.

The fire-return intervals used in the CENTURY and landscape C modeling are based on understanding of the canopy seed bank and its influence on post-fire regeneration. Specifically, Turner et al. (2007) demonstrated that lodgepole pine saplings are producing cones (including a few serotinous cones) by 15 years of age. Cone production begins at about the same age or even later in other conifer species of the GYE, and recent fires that have burned young conifer forests (< 30 years) show minimal tree regeneration (Romme and Turner, personal observations). To encapsulate this rapid but variable trend in development of a canopy seed bank, we used a 30-year fire interval as a conservative estimate of the minimum FRI that would be followed by a very high likelihood of reforestation. If fire recurs at < 60 year intervals, seeds are present but in moderate quantities. By stand age of > 90 years, lodgepole pine trees are generally producing substantial numbers of cones. Although stands are likely to regenerate at different rates following a stand-replacing fire due to patterns in fire severity and pre-fire levels of serotiny (Turner et al. 2004), cone production is not limiting by age 90 years, and even initially sparse stands experience infilling (personal observations; Kashian et al. 2005, 2006). Empirical work along chronosequences of > 77 stands in the GYE (largely in Yellowstone National Park) indicated that most differences in N and C stocks occur at stand ages < 100 years (Smithwick et al. 2009a; Kashian et al., in prep).

Using these parameterizations for vegetation, climate, and fire, we performed a model experiment using a 4 x 4 x 2 factorial design in which we considered four climate scenarios (historical plus the three GCMs), four fire-event pathways (no fires after 1988, a fire 90 years after the 1988 event, a fire 60 years after the 1988 event, and fires every 30 years after the 1988 event), and two recovery pathways (fast or slow).

Model output included live and dead pools (large wood, branches, leaves, coarse roots, fine roots), as well as active, slow, and passive pools in surface and soil, and relevant ecosystem processes such as respiration and decomposition. The time needed for forest C recovery following fire under both current and future climate scenarios was determined by comparing the time to recovery of pre-1988 C stocks (average of 1950–1987) of

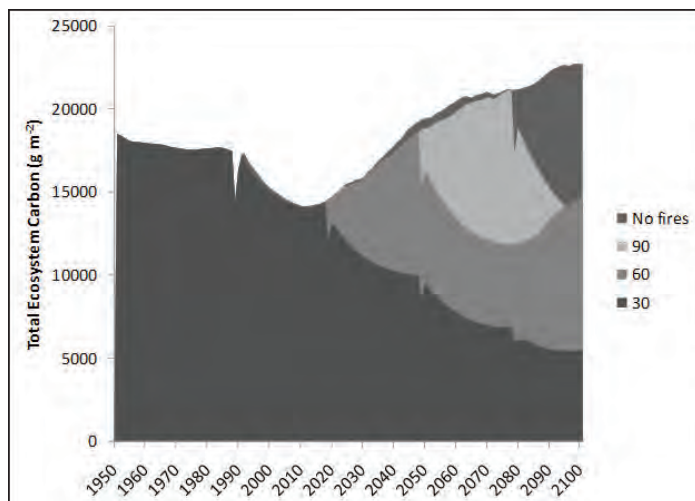


Figure 1. Results from the CENTURY v.4.5 model simulations showing C stocks for total ecosystem carbon (g/m^2 ; sum of live, dead, and soil pools) for four fire scenarios: no fires between 1989 and 2100, one fire 90 years following 1989; one fire at 60 years following 1989; and fires every 30 years between 1989 and 2100. Data are averaged across three different climate scenarios (CCSM, CNRM, GFDL—see text for details).

mature forest stands to that of both future periods (1970–2099), or was averaged across the post-1988 simulation period (1989–2100). Total ecosystem C stocks varied little (< 10 percent) among future climate scenarios for a given fire-event pathway and were therefore averaged for the purposes of demonstrating the large differences in C stocks forecast among fire scenarios. Similarly, fast versus slow regeneration had a much smaller effect on total ecosystem C stocks than the timing of individual fire events. For simplicity, only fast recovery pathways from the CENTURY model are shown here.

Results

The modeled C storage between 1950 and 1987 in lodgepole pine forests averaged $17,900 \text{ g C}/\text{m}^2$ (Figure 1). Simulation of the large fire in 1988 resulted in a 12 percent reduction in total C stocks from pre-fire levels—a relatively small reduction, largely due to the limited amount of biomass in the consumable pools (litter, foliage, fine branches) that was available to burn. Live pools were killed and converted to dead pools, but were not consumed. In the absence of subsequent fire (assuming historical fire-return intervals and therefore no fire in the post-1988 period), prefire C stocks were recovered by mid-century and, on average across the climate scenarios, continued to increase slowly through the end of the simula-

tion. Under future climates and in the absence of subsequent fire, total C stocks were between 17 and 30 percent higher than historical C stocks. Increases in total ecosystem C under the future climates were stimulated by higher rates of net primary production of lodgepole pine with warmer temperature compared to the control simulation, although relative increases in productivity were less for the GFDL scenario (data not shown). For simulations assuming one fire event (90 year FRI), live and total C stocks were recovered following the 1988 fire before the 90-year fire event. However, for scenarios with FRIs at 60 or 30 years, live, dead, soil, and total C stocks did not recover prior to the next fire event, and total ecosystem C storage declined progressively through the future simulation period due to the lack of time for C recovery.

Averaged across the three future climate scenarios for the post-1988 fire period (1989–2099) and assuming fast recovery, total ecosystem C stocks at the end of the simulation period were 28 percent lower than historical stocks for the 60-year fire event and 66 percent lower than historical C stocks for the 30-year fire-interval scenario (Figure 2). In contrast, C stocks were within 5 percent of the pre-fire stocks for the 90-year fire-event scenario. These three fire scenarios suggest that fire events would need to be separated by 90 years or longer for recovery of C stocks, whereas more frequent fire events would lead to C losses relative to the historical average for mature forest stands. However, these simulations represent singular pathways of one or more fire events spaced exactly at 90, 60, or 30 years. In reality, fire sequences at any given location on the landscape will be best represented by a probabilistic distribution of fire events.

Discussion

Recent studies have emphasized the importance of understanding how changing climate and disturbance regimes—including wildfire—will alter the terrestrial C cycle (e.g., Kueppers and Harte 2005; CCSP 2007, 2008; Bond-Lamberty et al. 2007; Bowman et al. 2009; Frolking et al. 2009). Fire and recovery are fundamentally linked to regional C balance in forest landscapes, and other authors have suggested that terrestrial C sinks may be weakening (Fung et al. 2005; Canadell et al. 2007). We had suggested previously but had not demonstrated (e.g., Kashian et al. 2006; Smithwick et al. 2009b) what our current findings indicate: a threshold of fire-return interval beyond which current fire C stocks will not recover to their pre-fire levels. For lodgepole pine forests of the GYE, our simulations suggest this threshold may occur at a fire return interval of approximately 90 years.

Recent studies have documented an increase in the occurrence of large fires during the past few decades, with increases most pronounced in mid-elevation regions of the northern Rocky Mountains (Westerling et al. 2006; Morgan et al. 2008; Littell et al. 2009), due to increases in temperature and drier conditions. If fire frequency is reduced below the threshold identified here, forests will re-burn before they have re-accumulated the C lost in the previous fire. As a result, high-elevation Rocky Mountain forests could become C sources in the global C cycle, which could exacerbate global climate change. More frequent fires would also mean that mature and old-growth forests, which now cover large portions of high-elevation landscapes in the central and northern Rockies, will be increasingly replaced by young forests or even by non-forest vegetation during this century. The degree to which vegetation changes in response to warmer temperatures and longer growing seasons could potentially offset C losses is not known. For example, expansion of warm-dry conifer species or sagebrush steppe into non-vegetated areas could increase C stocks, whereas shifts from forest to non-forest vegetation would reduce C storage.

The capacity for fast post-fire regeneration of lodgepole pine from an aerial seedbank (serotinous cones) and the projected increase in lodgepole pine productivity under warmer climate conditions (Smithwick et al. 2009b) appear unlikely to counter reductions in fire-return interval that fall below 90 years. The magnitude of the shift in C balance due to shorter fire intervals in the future governs

the ability of the forests to sequester C. Thus, the accuracy of future fire-climate models is critical for determining the degree to which C storage will be altered. Importantly, the specific timing of individual fires in a given location is likely to be more critical for determining the likelihood of forest recovery than projections of an *average* fire return interval in the future climate period. For example, net ecosystem production for Yellowstone National Park may be negative for about 30 years after the 1988 fires (Kashian et al. 2006), indicating even one or two additional fires as large as the 1988 fire would likely cause the GYE landscape to be a net C source over management timeframes. However, the specific time-path of the extreme fire years through the coming century must be estimated probabilistically.

Spatial variation in fuel, including potential shifts in dominant vegetation, is critical for understanding the spatial pattern in total ecosystem C stocks across the GYE landscape.

The magnitude of the shift in C balance will depend on the future distribution of forest and non-forest ecosystems across the landscape. A fundamental question is whether the current tree species and forest types will be able to persist in the GYE given projected climatic conditions and fire-return intervals. Some models suggest substantial changes in the geographic distribution of major tree species in the northern Rocky Mountain region, including the GYE (e.g., Bartlein et al. 1997; Coops and Waring 2011). For the work presented here, we assumed that the current dominant species were still present in the GYE at the end of the twenty-first century for three reasons. First, our focus is on what will happen in the next 90 years; broad-scale biogeographic rearrangements like those depicted in Bartlein et al. (1997) probably will occur over a longer time period because of constraints on species migration, limitations to dispersal, etc. Second, we know that lodgepole pine persisted through variable climates and fire regimes during most of the Holocene (Whitlock et al. 2003), and the biogeographic models indicate that lodgepole pine and montane forests will still be present in the GYE a century from now even if their abundance is diminished (Bartlein et al. 1997; Rehfeldt et al. 2006). Finally, even if other conifer species replace the current dominants, the stand-level C dynamics probably will not be hugely different from what we are modeling for lodgepole pine; moreover, if future forests fail to regenerate altogether, then the tipping point from C sink to C source will be even more dramatic than our model predicts.

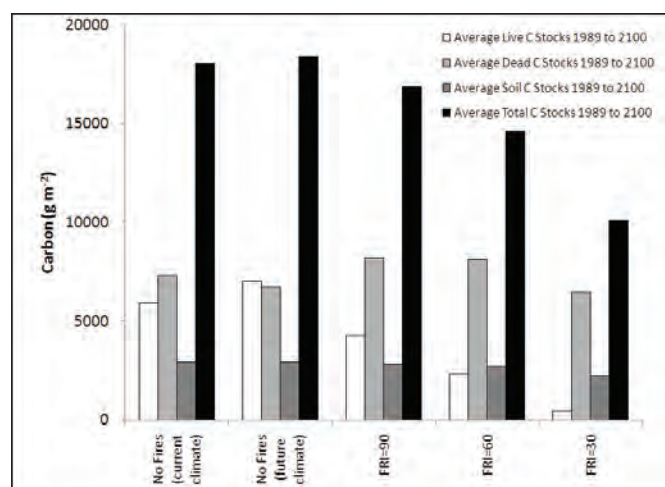


Figure 2. Carbon stocks (g/m²) for live, dead, soil, and total forest pools for historical (no fires between 1989 and 2100) and future fire (90-, 60-, or 30-year FRI) under current or future climate. Future climate was averaged across three climate scenarios (see text).

However, the qualitative shift in fire regime predicted by our model underscores the importance of considering what vegetation types would be better suited to future climates in the GYE. Although projections of future vegetation condition were beyond the scope of the present project, it is an important priority for future work. To better forecast landscape C stocks for the *current* GYE, our next step is to parameterize CENTURY for additional ecosystem types that are present today. Few data exist for validation of C stocks for additional forest types in the northern Rocky Mountain region, although several related efforts are underway (e.g., Donato et al., in prep) that can inform this effort. Integration of these additional vegetation types and fire/climate responses will refine the sensitivity of our projected responses.

Whether we are likely to witness “tipping points” of C storage in the GYE during the twenty-first century, that is, sudden large and/or qualitative shifts in response to gradual or continuous changes in underlying driver variables, depends on the probabilistic projections of fire event pathways in conjunction with dynamic ecosystem modeling. The most striking potential tipping point identified here is that more frequent fire produces a qualitative shift in high-elevation Rocky Mountain forests from functioning as a C sink to a C source. Fire events that occur between 1988 and 2078 (90 years following the 1988 fire) have the potential to reduce C storage through the end of the simulation period (2099) if they re-burn forests that are < 90 years old. We had previously expected lodgepole pine ecosystems to be one of the most resilient Rocky Mountain forest types because of their historically long fire intervals and their capacity for rapid recovery after fire (e.g., Kashian et al. 2006; Smithwick et al. 2009b). However, our analyses indicate that even lodgepole pine forests are vulnerable to projected climate change and the associated increase in burning during the twenty-first century. Ignoring the potential for future state changes, that is, shifts from forest to non-forest and from C sink to C source—and the spatial variation of these changes across heterogeneous landscapes—may lead to erroneous expectations for such values as biodiversity, productivity, and ecosystem C storage.

In conclusion, the modeling results shown here do not include projections of *future* vegetation distributions on the GYE resulting from future climate and fire, nor do the simulations describe well the site-specific time paths of actual fire events and recovery, which are likely to be

heterogeneous over the landscape due to the interactions of ignition, fuels, topography, and microclimate. A major focus of our forthcoming papers will be to define path-specific trajectories of C fluxes that account for probabilistic fire events and variation in recovery rates for current vegetation types. Yet, our results do indicate that the C storage of GYE forests is extremely sensitive to projections in fire events over coming decades. Given recent projections of future fire-climate relationships (Littell et al. 2010; Westerling et al. 2006; Westerling et al., in prep), managers must be increasingly aware of the potential for novel vegetation-fire conditions, their heterogeneity across the landscape, and the potential for tipping points in critical ecosystem function such as C storage.

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Using Virtual Research Learning Centers to Share Climate Information

Janine M.C. Waller¹, Tami S. Blackford², Rob E. Bennetts³ and Tom Olliff⁴

¹ National Park Service, Yellowstone National Park, PO Box 168, Yellowstone National Park, WY 82190, 307-344-2593, janine_waller@nps.gov

² National Park Service, Yellowstone National Park, PO Box 168, Yellowstone National Park, WY 82190, 307-344-2204, tami_blackford@nps.gov

³ National Park Service, Southern Plains Network, Capulin Volcano National Monument, PO Box 40, Des Moines, NM 88418, 719-846-4663, rob_bennetts@nps.gov

⁴ Great Northern Landscape Conservation Cooperative, Bozeman Fish Tech. Center, 4050 Bridger Canyon Road, Bozeman, MT 59715, 406-944-7920, tom_olliff@nps.gov

Abstract

Climate change obligates land managers to communicate local and regional climate information to national and global audiences. Our coalition of partners offers a model for making climate data, synthesis products, and other information available across park and agency boundaries to a wide audience. These groups, including the Greater Yellowstone, Chihuahuan Desert, Southern Colorado Plateau, Sonoran Desert, and Southern Plains Inventory and Monitoring Networks; Greater Yellowstone Science Learning Center, Learning Center of the American Southwest (the above represent 52 National Park units); the Desert Southwest, Rocky Mountain, and Colorado Plateau Cooperative Ecosystem Studies Units; Sonoran Institute, Montana State University, Yellowstone Association, Yellowstone Park Foundation, and Canon U.S.A., Inc., have been collaborating over the past four years to create parallel Web sites that share science information with land managers, researchers, educators, and the public (see www.greateryellowstonescience.org and www.southwestlearning.org). The Web sites are organized by resource and make scientific information available at various levels of detail. As part of an effort to move toward a larger perspective on climate, these Web sites are merging their climate information to make it available on one Web page so users can access the multi-park, multi-Research Learning Centers, multi-network, and multi-regional information from one climate portal. Information collected and analyzed by various groups can be located in one place. The Great Northern Landscape Conservation Cooperative may also become a partner in this effort. These Web sites offer the potential to assimilate climate information across boundaries, support vulnerability assessments and the development of models, and improve communication products and strategies.

It comes as no revelation that climate change is a multifaceted issue. Because climate and weather occur over multiple temporal and spatial scales, any attempt to understand their impact on our planet is, of necessity, a complex undertaking. An issue of such significant reach requires a similarly extensive response, and government, non-government organizations, and educational institutions have all become invested in addressing the causes and impacts of climate change. The impacts of climate change obligate land managers to communicate local and regional climate information to national and global audiences.

In response, the National Park Service (NPS) has developed a climate change strategy that focuses on four elements: science, mitigation, adaptation, and communication. As we look to communicate information about climate change, there are many opportunities to leverage existing partnerships and tools. As an example,

the NPS's Research Learning Centers (RLCs) are well-poised to address each of these elements by effectively and efficiently communicating science information and making it accessible to diverse audiences.

The RLCs were established with the NPS Natural Resources Challenge along with the NPS Inventory and Monitoring Network (I&M) and Cooperative Ecosystem Studies Unit (CESU) programs. The purpose of the learning centers is to facilitate research efforts and support science education opportunities and the exchange of information. They enable science-informed decision making and are supported by partnerships. In short, they connect parks, science, and people. Each RLC meets the unique needs of its park units through a variety of facilities, staff, and activities. RLCs offer different combinations of services, including laboratory space and dormitories for researchers, assistance with research permitting and pro-

posals, support of science education and internships, and science communication services.

There are approximately 20 RLCs nationwide, and they work with a variety of partners both in and outside the Park Service to accomplish their goals. They work to varying degrees with the other NPS Natural Resource Challenge programs, individual parks, and Exotic Plant Management Teams. Their locations overlap with I&M networks and CESUs, creating an ideal opportunity to develop or strengthen regional and national partnerships. The RLCs facilitate communication between and work with park researchers, land and resource managers, resource operations staff, and interpreters.

The Greater Yellowstone Science Learning Center (GYSLC) works with several universities; non-profit organizations, such as the Sonoran Institute and the Yellowstone Association; and also has support from a commercial company, Canon U.S.A., Inc., through the Yellowstone Park Foundation. Many other partners are involved in the research projects themselves. The GYSLC is composed of the same NPS units as its regional I&M network—this isn't the case for all RLCs, but it has enabled the GYSLC to maintain a close working relationship with the I&M program. Our partners help us meet our funding needs, advance Web site development, co-ordinate related science outreach activities, and enable us to creatively reach our goals.



Figure 1. Greater Yellowstone Science Learning Center Web site.

The GYSLC and other Park Service RLCs could play several roles in climate change research and communication. Because they are at the nexus of internal and external NPS programs, they can serve as agents for NPS Climate Change Response Program goals by facilitating research, collaboration, planning, and adaptation to climate change at local, regional, and landscape scales. There is also an opportunity for regional, interagency partnerships on the topics like climate change, particularly between RLCs and Landscape Conservation Cooperatives. For example, four RLCs fall within the boundaries of the Great Northern landscape conservation cooperative. These and other partnerships help RLCs provide an accessible, efficient conduit for implementing responses and partnering in climate change communication, education, and outreach.

The RLCs, including the GYSLC and many other partners, are active in climate change response projects. Examples include a multi-region evaluation of pollinator response to climate change and a multi-region pika vulnerability assessment. The National Science Foundation's Climate Change Education Partnership has also funded RLC proposals to develop formal and informal climate change education programs nationwide.

Over the past five years, the GYSLC has worked as an unfunded RLC in cooperation with the Learning Center of the American Southwest (www.southwestlearning.org) and others to develop Web sites that fulfill their needs for science outreach. The structure that has been developed on these Web sites is presented in this paper as a potential model for meeting an often-articulated need to organize and make available climate data, information, projects, and synthesis products.

The Web sites were developed concurrently and aim for a level of consistency that allows users to easily navigate both (www.greateryellowstonescience.org and www.southwestlearning.org), but the sites also offer flexibility in meeting diverse needs and priorities (Figure 1). The sites are organized around resources rather than programs, but are also sortable by park unit, so users can choose how they prefer to access information. The logos and links to our major partners are included on the sites' main pages to provide recognition and transparency. The audiences for these virtual RLCs are land and resource managers, researchers, educators and students, and interested members of the public and media. In order to communicate effectively with numerous and diverse audiences, it is necessary to provide information that is accessible to a variety of levels of complexity. GYSLC parks host nearly 300 researchers

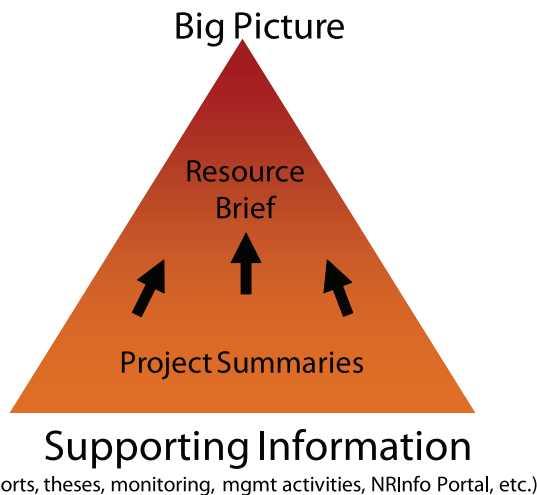


Figure 2. The triangle represents the model for distilling and synthesizing resource information into the products available on the Web sites.

from various agencies, universities, and organizations each year who produce hundreds of papers, manuscripts, books, and book chapters on their work annually; this volume of information is difficult to absorb. A multi-regional topic like climate change has the potential to generate even more research and publications.

Managers and the interested public may not necessarily have the time or the background to process this wealth of information. Because their inquiries are often specific to a particular resource, that is how the Web sites are organized. The different levels of information available on the Web sites can be represented as a triangle (Figure 2). At the bottom are data and detailed information. That information is distilled to report on the status and trends of a resource, which helps managers track resource and ecosystem dynamics. The supporting information includes everything from theses to I&M annual reports and protocols. We also produce summaries of specific projects that encompass all the work being conducted on a resource regardless of which agency or institution conducts it. Farther up the triangle and looking at the resource in a broader context, we have more in-depth overviews. At the top of the triangle we have the ultimate distillation of information: the resource brief, which aims to answer the “so what?” question. The resource brief is based on data collected by park staff and research partners and serves as a venue to put research into context and help managers determine the relevance and interconnectedness of resources.

The resource brief is the core communication product of the Web sites. It tells why a resource is important, describes its status and trend, and provides a discussion of the factors driving the status and trend or other management issues. The managers at parks with virtual RLCs find this product to be especially useful for quickly finding information about the status of a resource. Perhaps most critically, the briefs present this information concisely and in layman’s terms. Hosting these products on the Internet solves issues of availability and accessibility of paper copies, especially when they are filed in desk drawers, staff are working in the field, or managers are working after hours. Though we produce the content primarily for park managers, the information is public and made widely accessible by posting it on the Web sites.

These sites can also be used to connect to a variety of science outreach activities. Through these portals, students and educators at multiple levels are able to access research in parks. The Web sites can also function as an outlet for the data that volunteers and students collect during bioblitzes, or 24-hour inventories of all living organisms. Many of the results from Yellowstone’s first bioblitz, held in 2009, are posted to the GYSLC Web site (Figure 3). Beyond making the data available and accessible to the partners who helped collect it, this enables the results to be used in a meaningful context, such as a classroom. Over time, citizen scientists can see the connections of their work to other research, particularly in a resource



Figure 3. Scientists, park staff, and volunteers participated in a 24-hour bioblitz to inventory as many species as possible in a given area of the park. Many of the logistics for the event were facilitated through the GYSLC Web site. This photo shows a bioblitz volunteer and park visitors looking for aquatic macroinvertebrates in a water sample. National Park Service photo.

brief. The Web sites reach a committed audience and can put them in touch with volunteer opportunities or field institutes that have the ability to increase their investment in park preservation and issues. It can also be an avenue to publicize scholarships and fellowship opportunities.

The GYSLC Web site was used to assist with the logistics for the 2010 Scientific Conference on the Greater Yellowstone Ecosystem. In November 2009, and April and May of 2010, the GYSLC site and Southwest Learning site were used in the facilitation of other workshops focused on several of the issues discussed at the conference. The benefit of this type of facilitation is the fostering of collaborations that result in tangible products. Those earlier workshops generated several reports that will help shape the course of management and research in the region.

The virtual research learning center model is now being implemented by six other RLCs that have started similar sites in partnership with this effort (Figure 4). Two additional I&M networks are planning to go online in 2011, and an additional I&M and NPS unit are in the discussion stages as well. This consortium of modular Web sites provides another opportunity to leverage expertise and funds to improve the model.

Climate information will continue to become available at a rapid pace and can be overwhelming. In the face of this influx, land managers will have an increased need to communicate local and regional climate information to national and global audiences. The RLCs can help to effectively and efficiently communicate this and other science information and make it accessible to a variety of audiences. The Web sites in this model offer the potential to assimilate climate information across boundaries, support

vulnerability assessments and the development of models, and improve communication products and strategies. As part of an effort to broaden our perspective on climate change, the model used by virtual RLCs could provide the ability to access, synthesize, and facilitate climate science from multi-park, -RLC, -network, and -regional sources in one portal.

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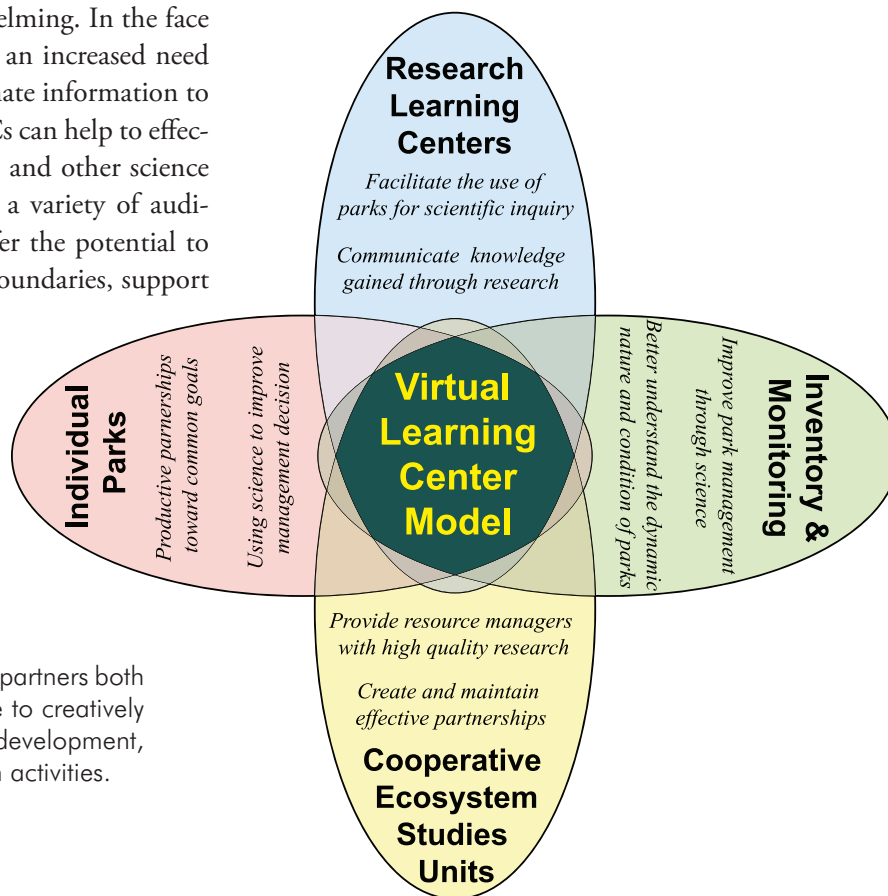


Figure 4. The RLCs work with a variety of partners both in and outside the National Park Service to creatively meet funding needs, advance Web site development, and coordinate related science outreach activities.

Water Transparency to UV Radiation as a Sentinel Response to Climate Change: Implications for Aquatic Foodwebs and Invasive Species

Craig E. Williamson¹, Kevin C. Rose², Andrew J. Tucker³, Jeremy S. Mack⁴, Erin P. Overholt⁵, Jasmine E. Saros⁶, Janet M. Fischer⁷ and Jennifer C. Everhart⁸

¹ Global Change Limnology Lab, Department of Zoology, Miami University, Oxford, OH 45056, 513-529-3180, craig.williamson@muohio.edu

² Global Change Limnology Lab, Department of Zoology, Miami University, Oxford, OH 45056, 513-529-3180, rosekc@muohio.edu

³ Global Change Limnology Lab, Department of Zoology, Miami University, Oxford, OH 45056, 513-529-3180, tuckera2@muohio.edu

⁴ Global Change Limnology Lab, Department of Zoology, Miami University, Oxford, OH 45056, 513-529-3180, mackjs@muohio.edu

⁵ Global Change Limnology Lab, Department of Zoology, Miami University, Oxford, OH 45056, 513-529-3180, overhoep@muohio.edu

⁶ Climate Change Institute, University of Maine, Orono, ME 04469, jasmine.saros@maine.edu

⁷ Department of Biology, Franklin & Marshall College, Lancaster, PA 17604, janet.fischer@fandm.edu

⁸ Department of Biology, Franklin & Marshall College, Lancaster, PA 17604, jennifer.everhart@fandm.edu

Abstract

In clear mountain lakes, ultraviolet (UV) transparency is a particularly sensitive indicator of changes in climate and land use due to its high sensitivity to small changes in nutrients and dissolved organic carbon (DOC) from the terrestrial landscape as well as atmosphere. Using data from several field campaigns in the Greater Yellowstone Ecosystem (Beartooth Mountains, Montana/Wyoming, USA), Lake Tahoe (California/Nevada, USA), and the Canadian Rockies, we report seasonal and interannual shifts in UV transparency, zooplankton, and chlorophyll from several clear mountain lakes. We consider what these patterns indicate about changes in snow, ice, and disturbance within watersheds and implications for aquatic foodwebs and invasive species. Our field data document striking seasonal and interannual differences in UV transparency. For example, UV transparency can more than double from ice-out to midsummer. In Lake Oesa, the depths to which 1 percent of UV (320 nanometer [nm]) penetrated were 12 meters (m) versus 21 m on July 28 in 2008 and 2009, respectively, and these differences appeared to be related to seasonal climate signals. Closely correlated with these changes, peak zooplankton abundance in the water column in these two years was at a depth of 7–9 m in 2008, but exceeded 15 m in 2009. Climate-driven changes in UV transparency, temperature, and phytoplankton may alter the distribution and abundance of zooplankton and the fish that feed on them. Observed decreases in UV transparency may also open niches for invasive fish and invertebrates that now threaten the clear mountain lakes of western North America.

Introduction

As the lowest point in the landscape, lakes and streams are some of the most valuable sentinels of changes in climate and land-use patterns in the surrounding catchment and airshed (Williamson et al. 2008; Williamson et al. 2009a; Williamson et al. 2009b). High-elevation alpine lakes such as those found in the Greater Yellowstone Ecosystem are some of the most sensitive sentinel systems due to their generally undisturbed watersheds, very low nutrient concentrations, high water transparency, low temperatures, and very short ice-free seasons. The physical structure of these lakes

is regulated by ultraviolet (UV) exposure and temperatures that differ markedly compared with even geographically proximate lakes that are below treeline (Rose et al. 2009a). Even small perturbations within the catchments of alpine lakes can lead to dramatic changes in the physical, chemical, and biological characteristics of these lakes. High-elevation lakes are also experiencing much more rapid climate change than lower-elevation lakes (Vinebrooke and Leavitt 2005; Bradley et al. 2006). One of the better established examples of how lakes provide signals of environmental change is the rapid and dramatic shift in diatom species composition that

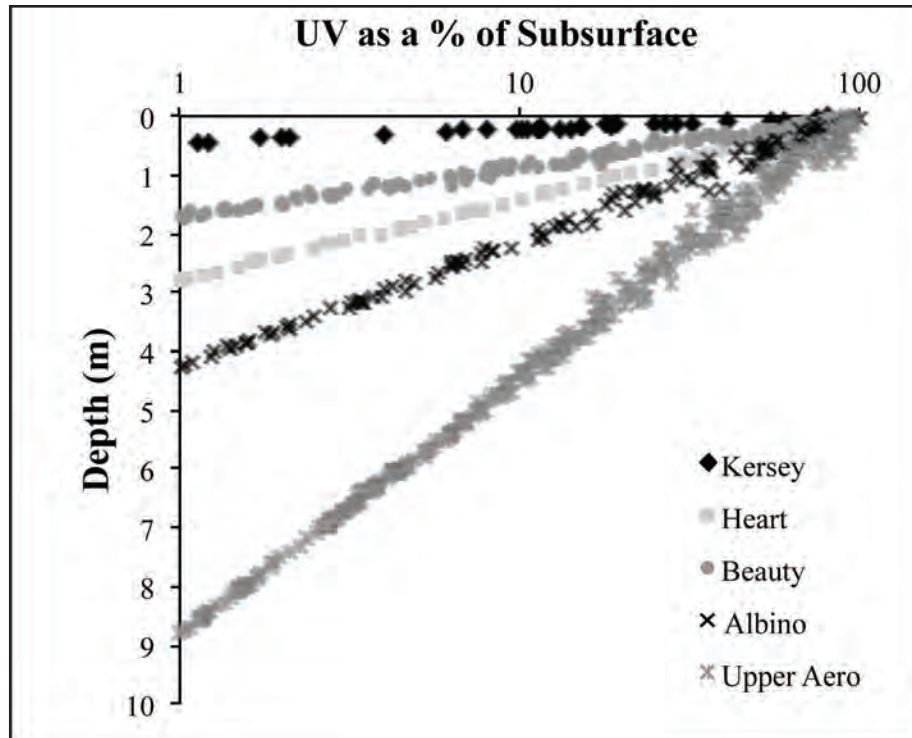


Figure 1. UV transparency (320 nm) of five lakes in the Beartooth Mountains during the summer of 2010. The intersection of each line with the vertical axis shows the depth to which 1 percent of 320 nm UV radiation penetrates relative to the amount just under the water surface, frequently referred to as the 1 percent 320 nm UV depth, or Z1%320nm.

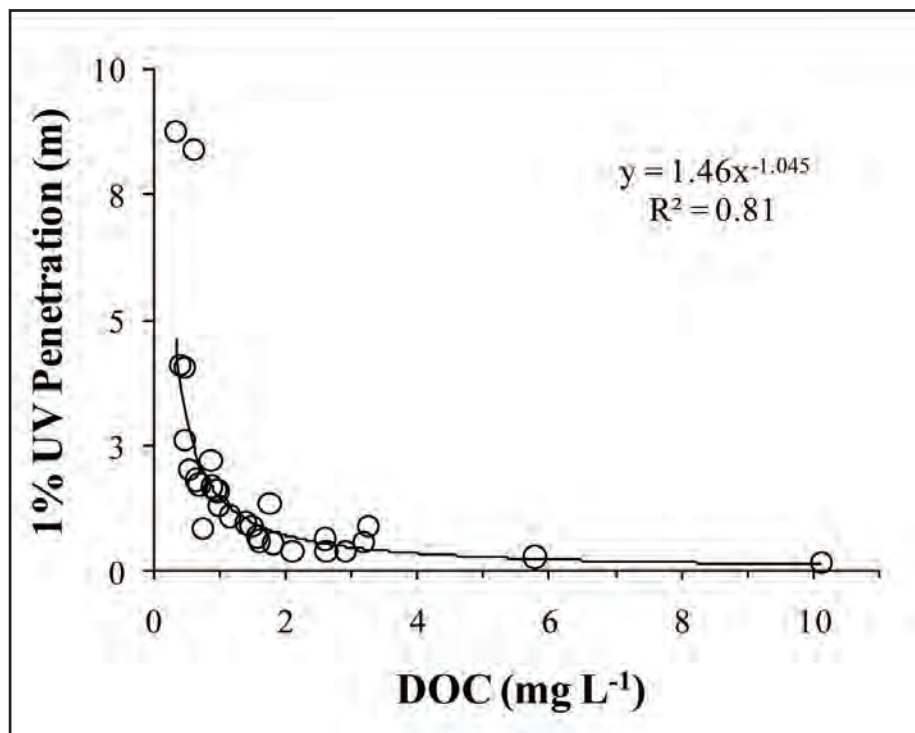


Figure 2. UV transparency as a function of DOC concentration in 29 Beartooth Mountain Range lakes. Note the particularly steep increase in UV transparency when DOC concentrations are below ~1 mg/L.

has been observed in recent decades in lakes of the Beartooth Mountains. These changes appear to be driven largely by changes in climate (thermal stratification) and N deposition (Saros et al. 2003). Here we present data on changes in UV transparency in alpine and subalpine lakes from the Greater Yellowstone Ecosystem (Beartooth Mountains) and other regions and discuss how monitoring UV transparency can provide valuable information on not only the causes of environmental change, but also the consequences for aquatic foodwebs and invasive species of fish and invertebrates.

UV Transparency and Environmental Change

Variations in UV transparency provide a wealth of information on both spatial variations in lake catchment characteristics, as well as environmental change over time (Rose et al. 2009b; Williamson and Rose 2010). The UV transparency of surface waters can vary greatly among lakes within a single region (Figure 1). This variation in UV transparency is driven largely by variations in the concentrations of dissolved organic carbon (DOC). In the Beartooth Mountains,

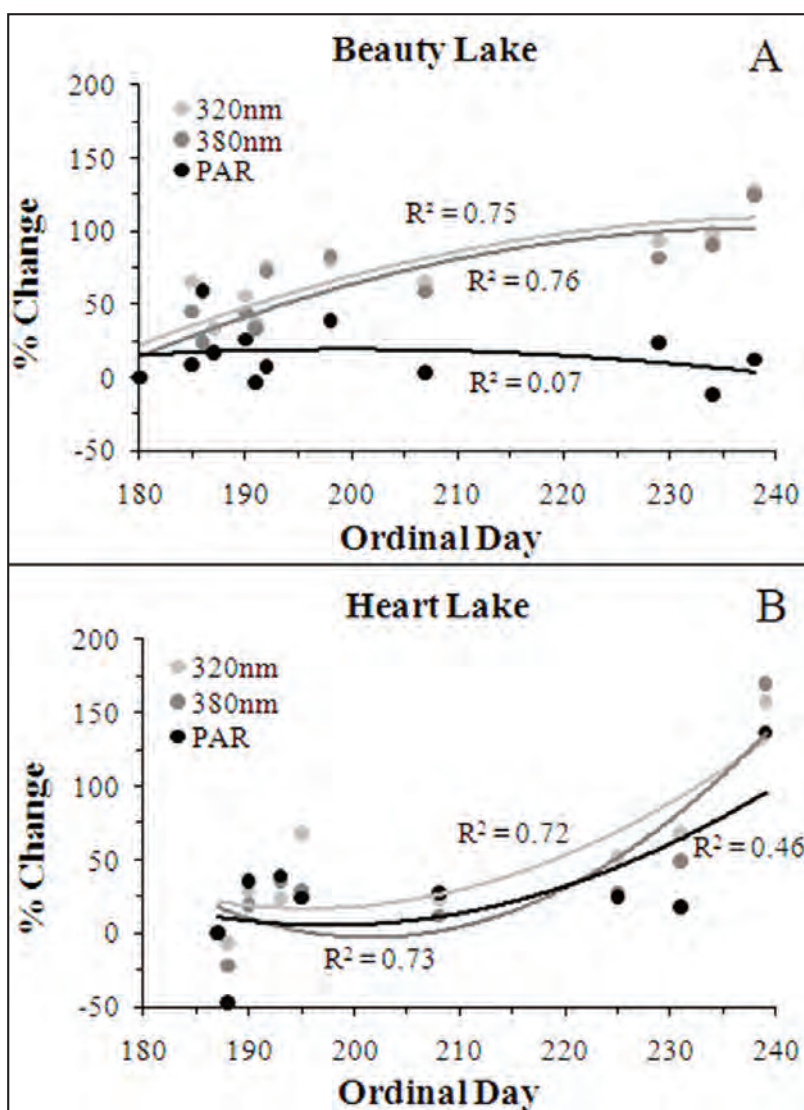


Figure 3. Seasonal changes in water transparency to UV-B (320 nm), UV-A (380 nm) and photosynthetically active radiation (PAR, 400–700 nm) in two Beartooth Mountain lakes. Note that in Beauty Lake (A) UV shows a strong seasonal increase while PAR shows little or no change, while in Heart Lake (B) both UV and PAR transparency show strong seasonal changes. From Rose et al. 2009a.

DOC concentrations alone predict 90 percent of the variability in 320 nanometer (nm) UV transparency (Figure 2). This DOC is largely derived from the surrounding terrestrial catchment, and characteristics of the catchment thus largely determine DOC concentrations. In the Beartooth Mountain lakes, 92 percent of the variation in DOC concentration among lakes can be predicted by just two characteristics of the surrounding terrestrial catchment: the extent of the vegetation coverage (the source of the fixed carbon), and the proportion of the catchment that has a slope of < 5 percent (representing both conspicuous and cryptic wetlands where the DOC is generated; Winn et al. 2009). This dependence of DOC on vegetation and wetlands within the catchment is particularly relevant to climate change and recently observed advances in the treeline and changes in precipitation in many montane ecosystems globally (Harsch et al. 2009).

In addition to being highly sensitive to spatial variation in the characteristics of the surrounding catchment, UV transparency also provides a sentinel response of environmental change. This is due largely to the sensitivity of DOC quality (color) and concentration to changes in hydrologic balance between precipitation and evaporation as well as to atmospheric deposition of nitrogen (N) and sulfur (S). For example, DOC concentrations increase in response to later ice-out dates and to greater spring rains, but decrease with drought (Pace and Cole 2002). DOC concentrations also increase in response to N deposition (Bragazza et al. 2006; Tranvik et al. 2009), and decrease with increasing S deposition (Schindler et al. 1992; Evans et al. 2006; Monteith et al. 2007). DOC thus mediates the effects of multiple types of environmental forcing on UV transparency, making UV a valuable sentinel response to environmental change.

Changes in UV Transparency in the Beartooth Mountains and Canadian Rockies

Multi-season sampling records from lakes in the Beartooth Mountains demonstrate a strong seasonal change in UV transparency, with a doubling of UV transparency from the time of ice-out until late summer (Figure 3). This pattern likely reflects the strong increase in temperature and decrease in precipitation from the time of ice-out to late summer. A more extensive residual analysis looking at interannual variation in UV transparency relative to the prior winter snowfall revealed that UV transparency may be a valuable sentinel response to snowfall in most lakes (Rose et al. 2009a). In one of our study lakes in the Canadian Rockies, we observed very pronounced changes in UV transparency within a single year. Lake Oesa in Yoho National Park was sampled on July 28 in both 2008 and 2009. In 2008, 1 percent of the surface 320 nm UV penetrated to a depth of 12 m, while in 2009 it penetrated to a depth of 21 m. While we do not have enough data to decipher the reasons for these changes, the remote location of this lake in an undisturbed watershed make interannual differences in climate the only likely explanation.

Ecological Effects of UV

UV has a wide range of effects on the ecology of zooplankton (Rautio and Tartarotti 2010) and fish (Zagarese and Williamson 2001). Incident levels of solar radiation at the surface of a lake at middle northern latitudes can kill some zooplankton and larval fish within a day or less (Williamson et al. 1999). Many zooplankton are known to respond to UV radiation by migrating vertically within the water column

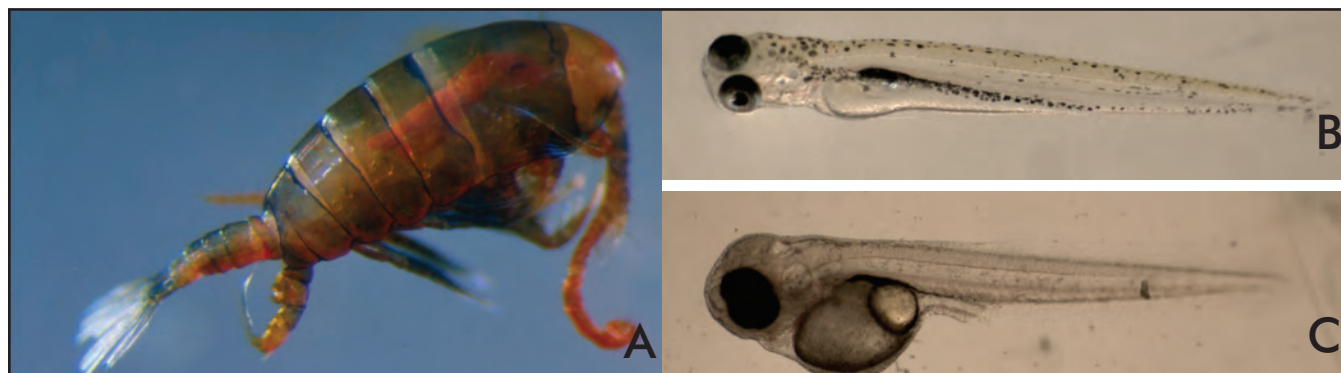


Figure 4. Photographs of some of the organisms in lakes that are influenced by UV radiation including a large (up to 3+ mm), pigmented copepod *Hesperodiaptomus shoshone* (A), larvae of Lahontan redbreast (B), which is native to Lake Tahoe, and invasive largemouth bass (C). Note the more abundant melanin pigment along the dorsal surfaces of the body and gut of the redbreasts. This species also has higher concentrations of UV-absorbing pigments that are invisible to the human eye (Robert Moeller, unpublished data). Photos by Robert Moeller (copepod) and Andrew Tucker (fish larvae).

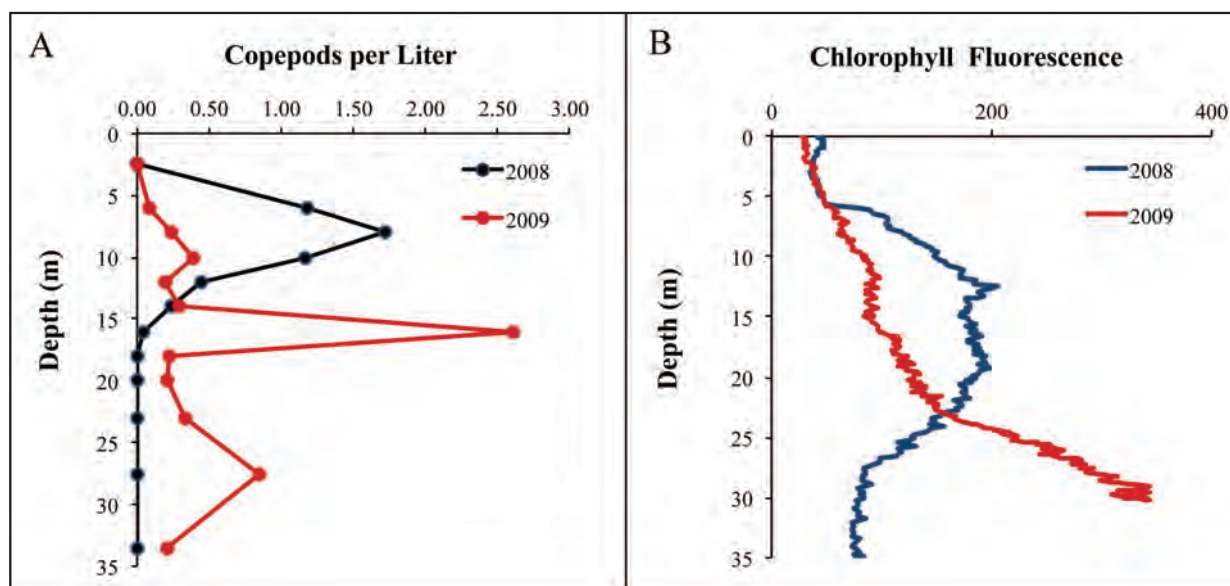


Figure 5. Depth distribution of *Hesperodiaptomus arcticus* (A) and chlorophyll fluorescence (B), a proxy for food concentrations in Lake Oesa during two years of dramatically differing water transparency. The depth to which 1 percent of surface 320 nm UV penetrated in 2008 was 12 m, while in 2009 it was 21 m.

(Leech and Williamson 2001; Leech et al. 2005; Fischer et al. 2006). Thus these strong within and among lake variations in UV transparency have potentially important consequences for the ecology of aquatic foodwebs. Here we give two examples: one that looks at changes in the vertical distribution of zooplankton and their food resources, and another that looks at the ability of UV radiation to exclude invasive warmwater fish.

In alpine lakes where there are no visual predators, the crustacean zooplankton are often a single species of large, highly pigmented calanoid copepod such as *Hesperodiaptomus* (Figure 4A). While these pigments reduce the sensitivity of various species of alpine calanoids to UV damage, the low levels of DOC and higher elevation of alpine lakes may still lead to UV damage and inhibition of reproduction (Zagarese et al. 1997a; Zagarese et al. 1997b; Cooke et al. 2006). In Lake Oesa where UV transparency (1 percent 320 nm depth) was 12 m in 2008 and 21 m in 2009, the peak densities of the dominant zooplankton species *Hesperodiaptomus arcticus* were between 7–9 meter (m) depth in 2008 and 15 m in 2009 (Figure 5A). The vertical distribution of phytoplankton food resources (as estimated from chlorophyll fluorescence profiles) exhibited a broad peak between 5 and 15 m in 2008, but peaked at a much deeper depth of below 25 m in 2009 (Figure 5B). This deeper distribution of plankton in the lake exposes them to colder temperatures and less light, thus potentially reducing growth and reproduction. We do not have enough information to assess the cause of these deeper distributions

of zooplankton and their food resources in 2009, but what is clear is that these changes in vertical distribution of the plankton correspond closely to the increase in UV transparency. This suggests that UV can provide signals of, if not actually influence, the vertical distribution of zooplankton and their food resources.

In Lake Tahoe, which spans the California–Nevada border, there is good evidence that high levels of UV transparency may serve to limit the reproductive success of invasive warmwater fish species (Tucker et al. 2010). The larval stages of fish tend to be highly transparent (Figures 4B and 4C). The lack of ability of these larvae to swim in the early stages of development while on the open and exposed nests makes the larval stage the most UV sensitive life-history stage. Outdoor exposure experiments have demonstrated that the larvae of the native Lahontan reddsides, *Richardsonius egregius*, are six times as UV tolerant as larvae of the invasive warmwater largemouth bass, *Micropterus dolomieu* (Figure 6). Thus, managing lakes to maintain high UV transparency may reduce the availability of low UV nearshore refugia where these invasive species would be able to spawn, while maintaining the integrity of the more UV-tolerant native species (Tucker et al. 2010). From a climate change perspective, one of the important implications of this work is that as treeline advances, the UV transparency of lakes is likely to decrease, potentially creating lower UV transparency and nearshore spawning refugia for invasive warmwater fish as well as other UV-sensitive invaders such as zebra mussels.

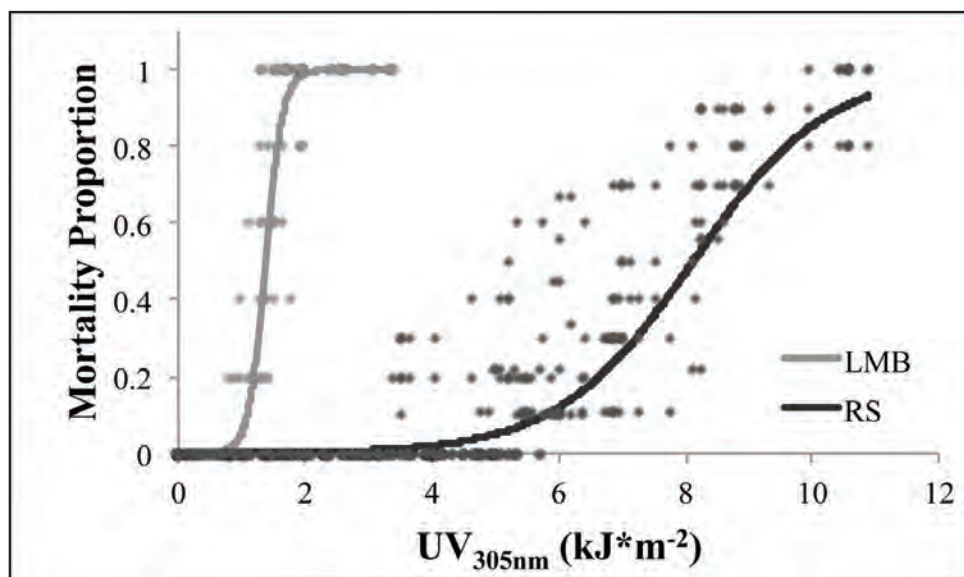


Figure 6. Mortality rates as a function of 305 nm UV exposure for the highly UV sensitive invasive warmwater largemouth bass (A) and the much more UV tolerant Lahontan redbreasted sunfish (B), which is native to Lake Tahoe.

Conclusion

Alpine lakes are fragile ecosystems that are highly sensitive to environmental change. This sensitivity to environmental change makes them both valuable sentinels of change, but also makes them vulnerable to alteration of their foodweb structure and potential for being invaded by warmwater fish and invertebrates. Keeping a close eye on changes in the UV transparency of lakes in the Greater Yellowstone Ecosystem can be a cost-effective and valuable tool for assessing the effects of a variety of environmental forces that range from changes in land use and tourist pressures to climate change and invasive species.

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