



Small Mammals as Indicators of Climate, Biodiversity, and Ecosystem Change

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Climate is a driving evolutionary force for biodiversity in high-latitude Alaska. This region is complex and dynamic with high annual variation in temperature and light. Throughout history, Alaska has experienced major climate extremes over much longer periodicity. For example, the Quaternary Period (the last ~2.5 million years), commonly known as the Ice Age, was punctuated by more than 20 major glacial-interglacial cycles.

During glacial phases, water was locked up in ice sheets that covered much of North America, and the resulting lower sea levels exposed a land connection between Alaska and Siberia, a combined region known as *Beringia* (Figure 1). This isthmus provided vast expanses of land for species to inhabit, provided they could withstand potentially harsh polar conditions. Each extended glacial phase periodically transitioned into a shorter interglacial warm phase. These climate reversals melted continental ice sheets to expose corridors for reinvasion of terrestrial species, particularly those associated with forested habitats further south. Those species that survived at northern latitudes through



Figure 1. Map of Beringia indicating in shades of brown the extent of land including exposed continental shelf during glacial climate phases. Not shown is the corresponding extent of continental and local ice sheets that covered northwestern Canada and southern Alaska during these times. Map courtesy of NPS.

repeated glacial-interglacial cycles formed the Arctic's tundra communities that persist today.

At present, Alaska supports diverse communities associated with both tundra and forests (Figure 2). These communities often interact with one another across latitudinal and elevational gradients, with tundra species generally found further north or higher in elevation. Alaska's climate is continuing to change today, strongly

influencing local environments and the distribution and dynamics of wildlife species.

Methods to Understand Changing Ecosystems

One of the central challenges for the National Park Service (NPS) is to understand how natural resources (particularly biodiversity) are responding to change through time (Marcot et al. 2015). Understanding how species have responded to past episodes of environmental

change provides comparative knowledge for current changes and predictive ability to envision future trends. One way we can access evidence from different temporal scales is by combining knowledge from multiple sources. For instance, we can compare fossil evidence of the extent of ancient distributions with present species' ranges, often suggesting dramatic distributional shifts through time. Field specimen collections spanning multiple decades (Cook et al. 2004), provide valuable samples through time for DNA or isotopic analyses that can highlight changes in regional diversity. Evolutionary histories of species leave predictable signatures within DNA sequences that can indicate how species have responded to changing environments through movement, population size changes, adaptation, or often through complex interactions between species. Ecological modeling and analyses can assess recent changes in populations as they react to current climate.

Monitoring Small Mammals

Small mammals are useful for understanding fine-scale responses to environmental change. Twenty-three years of monitoring in Denali National Park and Preserve yielded critical information on population and community changes (MacCluskie and Oakley 2005). Small mammals in Alaska are diverse for high-latitudes and have evolutionary origins from both Eurasia, further south in North America, including unique populations that are a consequence of local adaptation over multiple glacial phases. Small mammals are also intermediate trophic components of communities because they rely on vegetation, seeds, and arthropods for food, and interact with other wildlife through competition for resources or as a source of prey (Krebs et al. 2014). They have rapid generation

times and are often found at exceptionally high abundances, making them relatively easy to locate, capture, and collect, which is particularly valuable considering the many logistic challenges associated with field access and inventory through Alaska. Unlike most birds that migrate

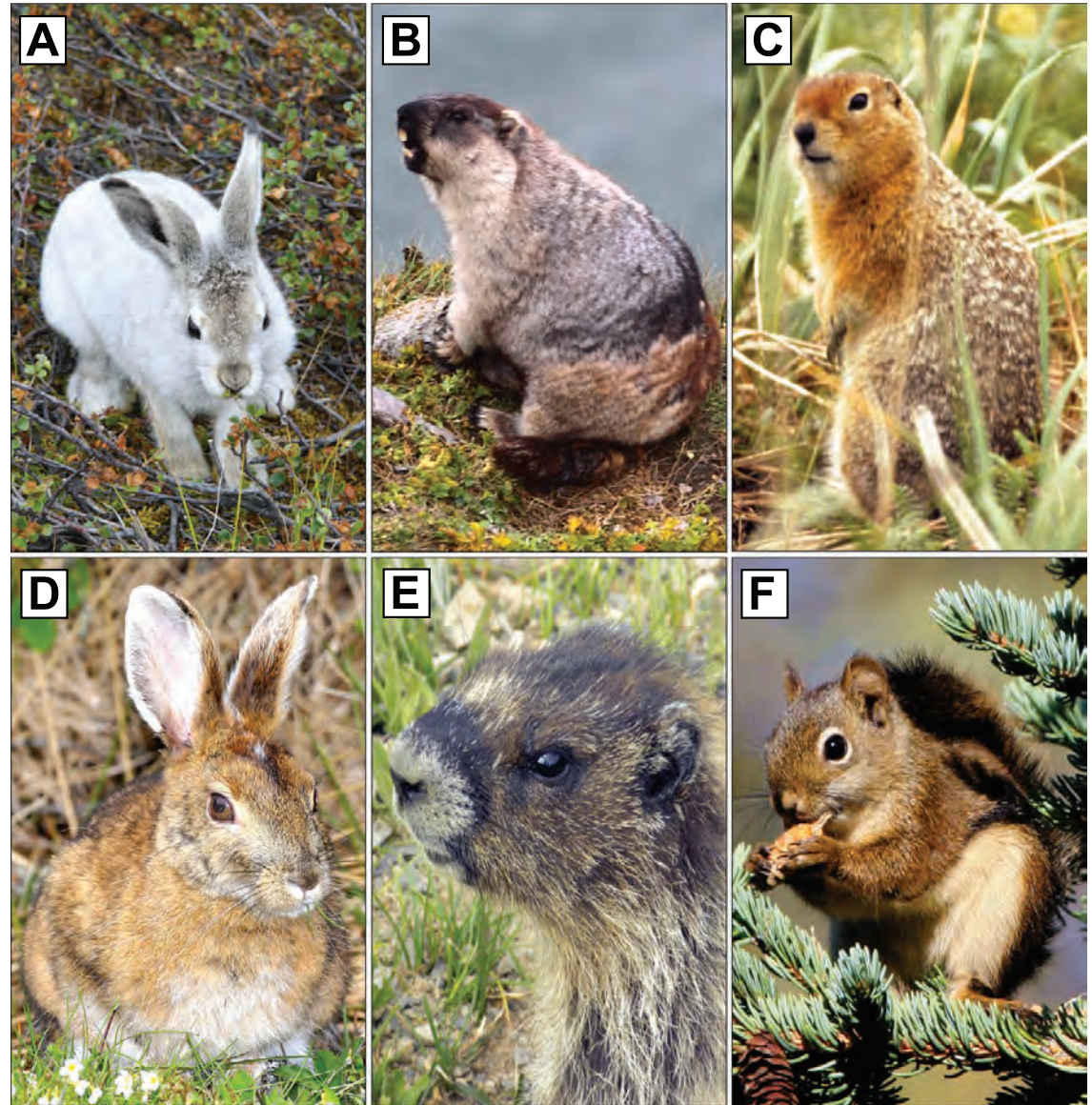


Figure 2. Small mammal ecological counterparts of tundra (top) and forest (bottom) communities within Alaska's national parks. (A) Alaskan hare and (D) snowshoe hare; (B) Alaska marmot and (E) hoary marmot; (C) Arctic ground squirrel and (F) North American red squirrel. Photos courtesy of Creative Commons (creativecommons.org)

seasonally to compensate for fluctuating climate and food resources, small mammals are resident and most do not hibernate, meaning that they respond and adapt to year-round conditions.

An Integrated Analytical Framework for Community Assessments

A key advantage of monitoring small mammals is the “library” of accumulated specimens archived in museums and associated ecological data resulting from decades of standardized field sampling and analysis. As a consequence of robust field efforts (Cook et al. 2004, 2005), knowledge of the evolutionary and natural history of small mammals in Alaska is relatively comprehensive. We can now begin to interpret how whole communities change through time for a given region.

Analysis of accumulated data is facilitated by new statistical and genetic methods not possible only a decade ago (Hope et al. 2013). To demonstrate, we gathered genetic sequences and locality information from museum databases for over 25 species of small mammals occurring within Alaska, including tundra and boreal forest species, and representing shrews, voles, squirrels, rabbits, and small carnivores. Our results indicate that species associated with forests in Alaska arrived here together through rapid range expansion since the end of the last glacial phase as climate warmed (Hope et al. 2015). Many are still experiencing population growth and continued range expansion. Tundra species, however, exhibited more idiosyncratic responses, whereas some species recently expanded their range, others exhibited stable or declining populations.



Student interns live trapping within Denali National Park for the Central Alaska Inventory and Monitoring Network small mammal monitoring project. (A) Jenna DiFolco and (B) Vida Torres handle specimens of *Microtus oeconomus*, the tundra vole; (C) Heather Stewart sets a Sherman® live trap baited with rolled oats.

Photos courtesy of NPS.



Graduate students Dianna Krejsa and Donovan Jackson working with Alaska specimens archived in the mammal collections of the Museum of Southwestern Biology at the University of New Mexico, Albuquerque, NM.



Sarah Arguello and Robert Nofchissey, working with the Beringian Coevolution Project, process small mammal specimens within a field laboratory.

In addition to interpreting genetic information from museum specimens, we performed ecological analyses of climate data associated with the current distribution of each species. Climate tolerances of species (e.g. temperature or rainfall extremes) for the present time are often a strong predictor of where they occur. We used these climatic “envelopes” to verify the genetic and fossil evidence and better understand how distributions have changed through time, and how they may be expected to change into the future. Future predictions indicate the possible trend (increase or decrease in population size), magnitude, and physical location of species ranges into the next several decades. Finally, by overlaying predictions for multiple species, we mapped changes in small mammal diversity through time, independently for both tundra and forest communities (Figure 3) and with all study species combined (Figure 4).

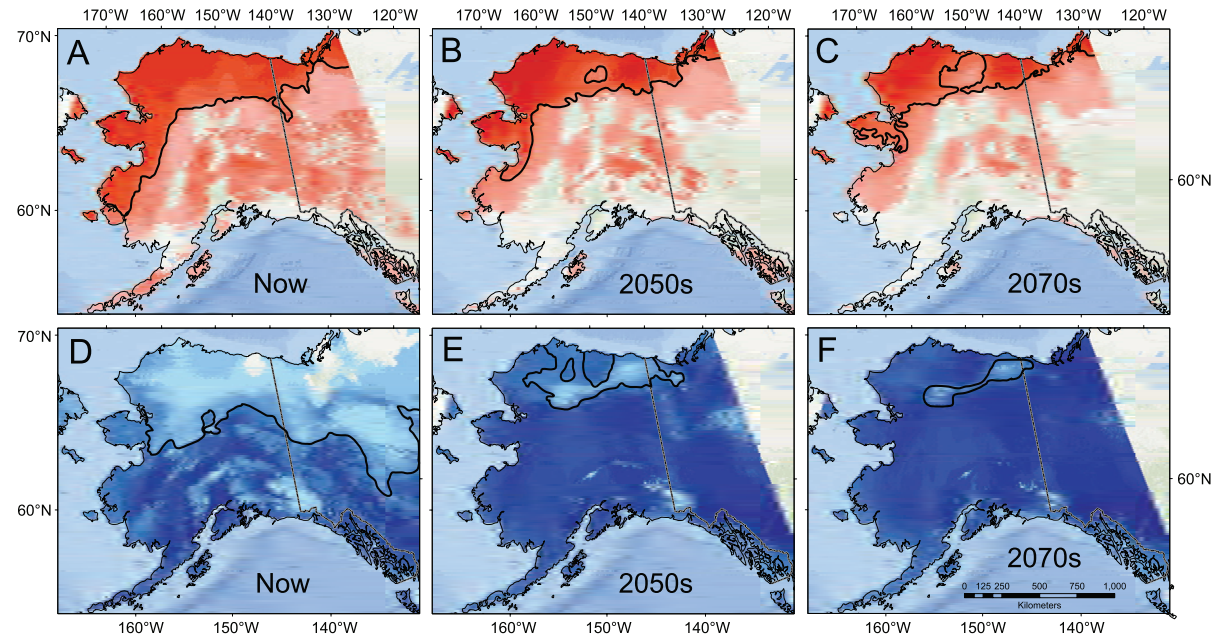


Figure 3. Climate envelope model predictions for tundra taxa (top; red) and forest taxa (bottom; blue) based on (A) and (D) current (now), (B) and (E) 2050s, and (C) and (F) 2070s climate projections. The color gradient reflects areas of low (light) to high (dark) diversity. Distribution of diversity reflects compilation of predictive maps for 12 boreal and 7 tundra/alpine-associated species. Black lines provide a guideline to the extent of $\geq 50\%$ of the diversity within boreal and tundra biomes respectively during each timeframe. Adapted from Hope et al. (2015).

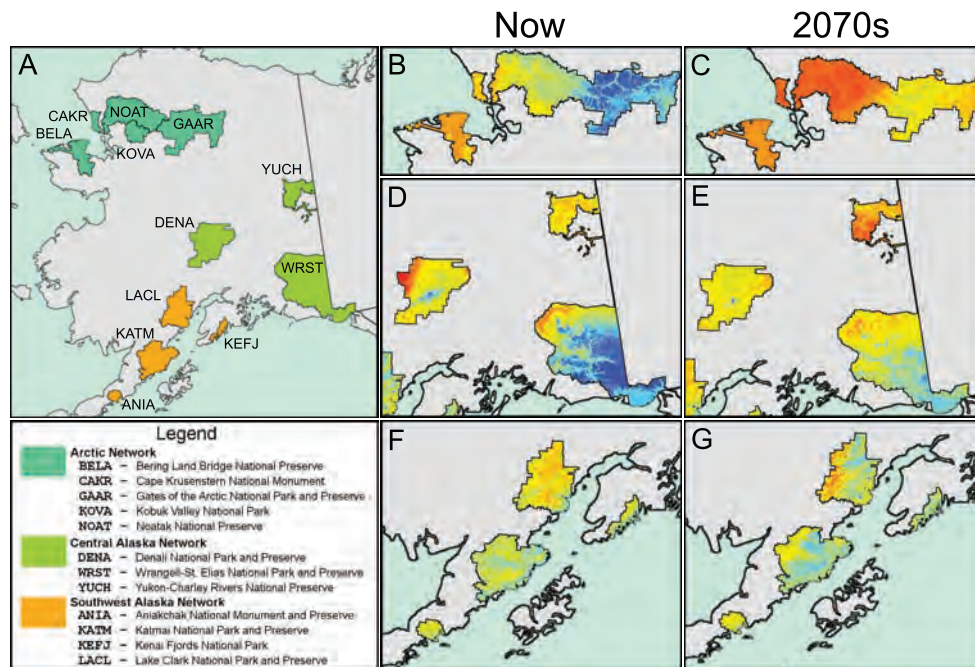


Figure 4. Climate envelope model predictions for all taxa for the current time (now) and the future (2070s) within Alaska parks. The grouping of parks within inventory and monitoring (I&M) networks within Alaska is shown in (A). Diversity change is shown in (B) and (C) the Arctic I&M Network, (D) and (E) the Central Alaska I&M Network, and (F) and (G) the Southwest Alaska I&M Network. The color gradient reflects areas of low (blue) to high (red) richness. Adapted from Hope et al. (2015).

Trends in Diversity and Community Turnover

Predicted changes for total small mammal diversity into the next century vary across Alaska parks (Figure 4). In the Arctic parks, mammal diversity exhibits a strong longitudinal gradient with more species predicted in the west. Future predictions indicate an overall increase in diversity, although the distribution of diversity will become more even (Figure 5). Increasing diversity is generally considered beneficial; however, this increase is largely due to the rapid northward movement of forest species, whereas tundra species are contracting their range more slowly. Different velocities of change among forest and tundra species (Figure 3) will broaden overlap between these communities through time and increase the complexity of interactions among them. In the central forested region, the total number of species is not predicted to change, although the distribution of this diversity will change as species are predicted to invade higher elevations and so increasing total occupancy in this region. Within Southwest parks, the number of species is predicted to decrease slightly as total diversity shifts along both latitudinal and elevational gradients. It is possible that other species currently occurring further south, such as Keen's deer mouse (*Peromyscus keeni*), may shift north and west, maintaining or increasing the total small mammal diversity through this region. Recent studies have also suggested that climate changes may reduce the extent of boreal forests further south in Alaska, giving way to other novel habitats such as deciduous forest or grassland (e.g., Wolken et al. 2011), and by extension, changes in the associated mammal communities.

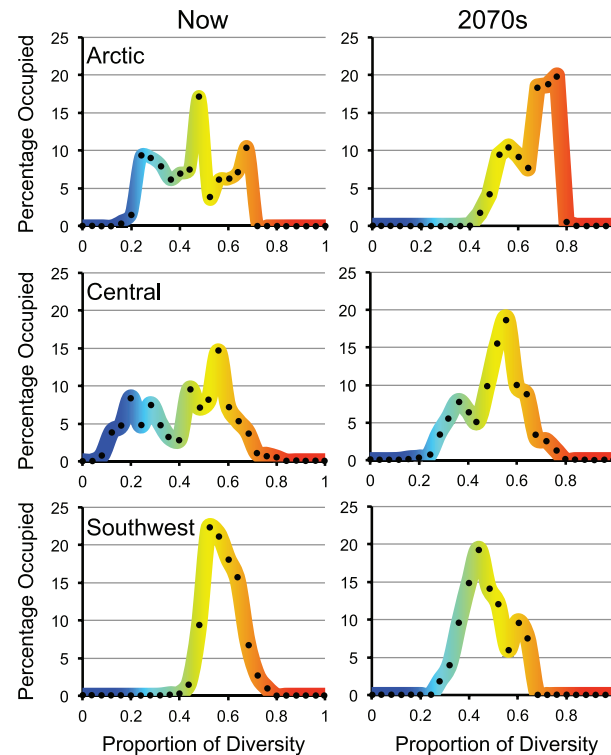


Figure 5. Plots of predicted small mammal community diversity within three networks of Alaska parks analyzed for the current time (left) and future (right) ranging from blue (low) to red (high) where colors reflect climate envelope model predictions of total diversity (Figure 4). Values reflect percentage area (y-axis) of each network's parks predicted to support a given proportion of richness (x-axis). For example, for current predictions within the Arctic I&M Network, almost half of total richness (13 taxa) is predicted to occur across roughly 17% of the management region, whereas peak richness (roughly two thirds of the taxa) is only predicted to occur through roughly 10% of this region. Into the 2070s timeframe, almost four fifths of the species are predicted to occur through 20% of the total area. Adapted from Hope et al. (2015).

Conclusion

This is a time of rapid environmental changes in Alaska and effective management of natural resources benefits from detailed knowledge of the past and present, and our most informed predictions of future biotic responses to these changes (Barnosky et al. 2012). Species that have evolved within tundra habitats over multiple glacial cycles are not only best adapted to high-latitude and high-elevation environments, but may also respond more slowly to change. This equates to a broadening overlap between distinct communities as forest species advance along environmental gradients faster than tundra species retreat. Less certain is how different communities will interact in regions of overlap, so-called contact zones, such as occurs across latitudinal, longitudinal, and elevational gradients through many Alaska parks. High-latitude and high-elevation areas may constitute future refugial areas for tundra and alpine species respectively and these regions within Alaska parks will likely constitute critical areas for future research to inform resource management. Studies of hybridization, competition, disease, associated species such as parasites, physiological tolerances, phenology, and evolutionary adaptation to novel environments could all be facilitated by focusing on small mammal communities and continuing to build spatially extensive and temporally deep archives from parks.

Preserving our natural resources within Alaska parks will remain a challenge, particularly considering the predicted changes in community dynamics and species distributions. We provide a framework for small mammal fieldwork that can be built on through time; similar effort is needed for other facets of biodiversity.

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