

**Review of research conducted in Rocky Mountain National Park of CO, USA and the
Tatra National Parks of Poland and Slovakia**

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Introduction

History of park interactions

Rocky Mountain National Park (ROMO), a unit of the U.S. National Park Service (NPS), the Tatra National Park, Slovakia (Sprawa TANAP and Statne Lesy TANAP are further referred to as TANAP), and the Tatra National Park, Republic of Poland (TPN) have had a sister park relationship since 2006. The formal partnership agreement identifies commonalities in biological communities, geologic setting, and visitor issues. All three parks are recognized as International Biosphere Reserves by the United Nations.

While maintaining and strengthening this partnership numerous staff visits and jointly held meetings between the three parks have laid the groundwork for a more substantive collaboration. In the summer of 2011 research teams from the University of Wroclaw, the Slovakian Academy of Sciences, and Colorado State undertook projects investigating riparian community response to climate change and recovery of areas previously grazed. The success of this and other collaborations suggests future international work will provide ongoing exchange of scientific ideas and management plans. The literature summary provided in this document is intended to better define areas of possible future scientific exchange and collaboration for researchers in the United States, Poland and Slovakia.

Current and future park interactions

Our initial goal was to highlight research conducted in ROMO and in the Tatra mountain range (both TANAP and TPN) as it relates to major research objectives, and to examine whether there are similarities or differences in the types of content categories being used to address those objectives. Research objective categories focused on for the purposes of this review included 1) natural history, 2) conservation, 3) management, 4) diversity, 5) response to disturbance, and 6) visitor-park interactions. Within these research objectives, subject content was further divided into categories including A) vegetation cover and change through time, B) herbivore-plant interactions, C) animal and insect ecology, D) hydrology, E) pollution F) carbon fluxes, sinks and sources, G) changes in soil quality, carbon accumulation, nutrients, H) physical processes: climate and geology, and I) effect of land-use changes and/or changes of pulse disturbances. Our final goal was to determine whether projects and results from these two similar mountain environments are of mutual relevance and to recommend areas of potential joint projects.

Rocky Mountain National Park

Background

Research studies have been conducted in and around Rocky Mountain National Park (ROMO) on a wide range of topics, questions, temporal and spatial scales. Results and findings associated with the main research questions and content categories outlined in the abstract are summarized here, including studies conducted within the ROMO, the Colorado Front Range, Niwot Ridge Long Term Ecological Research (LTER) site and Green Valley Lake to name specific examples. Summaries herein include results and conclusions from published, peer reviewed, articles available to the general academic community and the public.

Natural history: vegetation cover and change through time

Studies focusing on the vegetation structure and distribution within the different ecosystems of the Colorado Front Range and ROMO have emphasized areas of key cultural or social importance, in addition to areas susceptible to disturbance. Such areas include

measurements at the forest-treeline ecotone where visitors often frequent and changes associated with climate are anticipated to become discernible. Other systems studied include canopy species within the subalpine forest (lodgepole pine), peatlands, and species frequently used as browse for large ungulates. Plant community processes examined include effects of invasive or exotic species, and the influence of vegetation on soil characteristics in the alpine.

Research examining vegetation distribution at the forest-tundra ecotone, particularly of tree species, has focused on the potential for advancement of krummholz into the tundra or open forest into the krummholz associated with changes in climate. This potential shift in dominant canopy has been examined using historic data with tree rings, and results have shown krummholz expansion related to increases in mean annual temperature and May snow depth (Hessl & Baker, 1997). Areas with the greatest potential for changes in distribution and growth, determined using GIS, were wet meadows where non tree species could facilitate micro-habitats that enable growth of krummholz individuals (Baker & Weisberg, 1997). Tree seedling density and krummholz leader growth measurements show potential evidence for response to climate change, with krummholz patches growing more rapidly than seedlings (Weisberg & Baker, 1995). Research at neighboring Niwot Ridge LTER examined the spatial patterns of trees in three different forest-alpine tundra ecotone types, and determined that areas of most patchy distribution were associated with heterogeneous topography, while areas with little disturbance (such as wet meadows) showed the least patchy assemblage of trees (Humphries et al., 2007).

Studies examining the distribution of species within the subalpine forest have been related to canopy tree species and wetland species growing in mountain peatlands. A study examining changes in forest dominance and the influence of environmental factors along ecotones in ROMO determined that lodgepole pine distribution is described by elevation and moisture gradients and to a lesser extent by soil characteristics (Stohlgren & Bachand, 1997). Water availability through the position of the water table was also implicated as a key environmental control on vegetation composition in a treed peatland fen within ROMO where other factors included hummock height, degree of shading, ground water temperature and conductivity (Johnson, 1996). Further vegetation sampling in subalpine fens followed gradients of vegetation (hummocks and hollows, treed, vs. open) determined that productivity also varied with composition along this gradient such that treed areas and hummocks facilitated the highest growth rates (Johnson, 1997).

Distribution, regeneration and age structure of vegetation typically used as browse for large ungulate species in winter and summer ranges has been closely monitored within and around ROMO associated with the changes in the elk population size. Age distributions of aspen and regeneration have been estimated using a variety of methods and across many spatial scales including areas with little or no elk presence, to areas of high density use during winter months (Binkley, 2008; Kaye et al., 2003; Suzuki et al., 1999). Results from surveys of stand age indicate that in current stands within ROMO no decade from 1855 through 1965 showed divergence in rates of regeneration from levels expected from the long-term trend, however the number of aspen dating 1975-1995 at low elevations (winter range) on the eastern side of the Continental Divide fell 80-90% below the level expected from long-term trends (Binkley, 2008). Despite the potential decline in the winter range cover by aspen within ROMO was estimated at 5.6% of land area surveyed with no significant differences in aspen basal area, density, regeneration, patch size or amount of browsing between areas of concentrated elk use and areas of dispersed elk use (Kaye et al., 2003). Earlier measurements of regeneration rates in aspen in specific, however, found that only 20% of aspen stands within Estes Valley contained

regenerating stems, as compared with 45-75% across the larger landscape of the Colorado Front Range (Suzuki et al., 1999). An initial study focusing on distribution of willow suggested that decreases in distribution and abundance may be connected to a number of factors, including a decline in beavers, reduction of river branching and a large flooding disturbance, in addition to increases in the elk population. These combined factors resulted in losses up to 55% for tall willow individuals and 20% decline in riparian shrub cover between 1937/46 and 1996 (Peinetti et al., 2002). More recent work has examined the hydrology, geomorphic, and climatic processes associated with willow establishment in ROMO and determined that the role of peak flow varied dependent upon land form (Cooper et al., 2006). In particular, point bars and abandoned channel establishment were driven by 2-5 year return intervals while beaver dams were associated with >5 year intervals (Cooper et al., 2006).

The potential influence of invasive or exotic vegetation species has been touched upon in a few studies, especially relating to the occurrence of sweet clover in the alpine meadows. Research from a study examining soil properties associated with successful invasion determined that soil moisture and soil temperature were instrumental in the establishment of the nitrogen fixer *Melilotus officinalis* at high elevations (Wolf & Rohrs, 2001). Further study discovered that the successful introduction of sweet clover then facilitated other exotic species establishment (Wolf et al., 2003). Effects of invasive species on native communities and soil properties, and the impacts of management practices removing them, were examined in a recent study where introduction of exotic species did alter nutrient cycling, however herbicide treatments produced increases in area of bare ground within the larger plant community (Pritekel et al., 2006).

Vegetation influence on soil processes, animals and invasive species aside, have been estimated within forests and the alpine zone of the Rocky Mountains. Measurements determining the nitrogen release from litter decay in the forest floor found correlations with total net nitrogen mineralization, while rates of decomposition were linked to litter chemistry (Stump & Binkley, 1993). At a moist meadow in the alpine tundra of Niwot Ridge LTER small scale variation in soil N cycling was associated with two different dominant vegetation community members with differences in litter quality, litter quantity and resulting soil quality (Steltzer & Bowman, 1998).

Natural history: herbivore-plant interactions

While there are multiple common herbivores within ROMO, studies focusing on the interactions of herbivores with plant communities have highlighted elk-aspen or -willow cycles. Studies of ungulate herbivory on willow and aspen in ROMO have historic roots, beginning with the personal observations and concerns of Packard (1942) and have continued to be of interest into current times associated with increases in elk population. A publication reports that elk influence on aspen in their winter range has produced increased mortality of aspen stands and reduced the density of living suckers, while historic evidence shows that aspen cohorts regenerated only when there were fewer than 600 elk in the winter range (Baker et al., 1997). Modeled interactions of elk and aspen show that younger stands of aspen are affected at lower concentrations of elk, and regeneration only occurs at densities below 3-5 elk/ km² (Weisberg & Coughenour, 2003).

Beyond the direct impact of changing vegetation structure and abundance, some work has been done on the potential for indirect effects associated with changes in nutrient cycling and ecosystem processes. Results showed that elk browsing had different effects on nitrogen processes dependent on the vegetation community, with a reduction in nitrogen pools and lowered mineralization rates in a willow community, but no impact on upland grass or shrub

areas (Schoenecker et al., 2002). Nitrogen input levels were reduced by half in grazed willow sites, and aspen sites showed high transport of nitrogen away from the site associated with elk (Schoenecker et al., 2002).

Natural history: animal and insect ecology

Surveys and studies of the fauna in ROMO generally focus on species in the public eye; including elk, bighorn sheep, mule deer, black bears, beaver, ptarmigan, and amphibians (especially species endemic to the Rocky Mountains). Information about each species is widely varied, and ranges from current population numbers, to predictions of population dynamics associated with changes in climate, or human-animal interactions and how this may affect animal populations in general.

Many studies have examined past, present and future elk population dynamics in and around ROMO. At present there are two main populations influenced by separate stressors controlling population dynamics. The ROMO herd was considered at a size comparable to ecosystem carrying capacity with little population change since 1991 (there is evidence for a recent decline in unpublished data), as compared to a rapidly expanding population in Estes Park (Lubow et al., 2002; Recent unpublished data show this population is declining). Modeled impacts of climate on elk populations showed that density was the main limitation of population growth, while high levels of summer precipitation accelerated the population growth and higher summer minimum temperature slowed growth (Wang et al., 2002a). Future climate changes with warmer winters and wetter summer could increase populations by 100%, while warmer winters combined with drier summers could increase the population by 50% (Wang et al., 2002b). Finally, aside from direct interactions with vegetation, there are a number of indirect effects associated with elk herbivory and general grazing patterns that include the potential for changes in soil properties. These alterations in soil were examined using elk exclosures in a number of ecosystem types within ROMO. Results showed that elk influence reduced extractable nutrients in sagebrush areas and increasing soil pH in areas of aspen (Binkley et al., 2003). Current management policies associated with elk include some herd culling, in an effort to maintain a healthy population that does not degrade the supporting ecosystem.

Another charismatic large herbivore that visitors to ROMO frequently hope to see are the bighorn sheep, located in general at higher elevations than the larger, more numerous elk. Population estimates of the number of sheep in and around ROMO were originally conducted around 1939, where the numbers were approximately 300 individuals (Packard, 1946) and a mark-re-sight study in the recent past estimate the current numbers at 390 in 2003 and 366 in 2006 (McClintock & White, 2007). An additional current concern comes from results showing increased vehicular stress in bighorn sheep at the access point to a historically important mineral lick (Keller & Bender, 2007).

Evidence for human effects on other species within the park are alluded to in a study examining levels of lead contamination in roadside vegetation favored by park mule deer, where results showed that safe levels of lead were exceeded for deer consuming only 1.4% of daily forage from roadsides (Harrison & Dyer, 1984). Not all species have been negatively influenced by increases in human activities, and in contrast to many other national parks within the region black bears appeared unaffected into the 1990s. Black bears in ROMO exhibited human avoidance and in general remained secretive (McCutchen, 1990). Den site selection however began to become affected by increased human presence during the 1990s and 2000s, with a shift from selecting specific vegetation cover types to canopy height and distance from road, although

steep slopes and areas of deep snow have been continuously favored (R. A. Baldwin & Bender, 2008). A recent study examining bear diet and nutrition found that the main source of gross energy and nitrogen for ROMO bears was animal matter, with crude fat correlated with berries and ungulates (Baldwin & Bender, 2009). Of concern however, was the finding that contemporary diets contain greater prevalence of anthropogenic foods than historic records found, contributing to increased size, condition and productivity of the existing bear population at ROMO, suggesting a need for increased management intervention with the food access of local bears (Baldwin & Bender, 2009).

Changes in climate and the impact this may have on park fauna have been extended not only to elk, but also for ptarmigan- a hen sized bird that feeds on seeds and berries. Ptarmigan population dynamics modeled with climate indices suggest that median hatch dates advanced significantly between 1975 to 1999 in response to increases in April and May temperatures, while high winter temperatures slowed rates of population growth (Wang et al., 2002). Further winter warming is predicted to induce greater decline in ptarmigan populations. Other species, such as beaver, may help offset changes in precipitation patterns through engineering of hydrologic processes within streams. Beaver in ROMO have acted as ecosystem engineers with main effects on hydrologic processes occurring downstream of dams, and dams and ponds enhancing the depth, extent, and duration of inundation associated with floods (Westbrook et al., 2006). Additionally beaver ponds and dams attenuate expected water table declines, and maintained higher waters during floods while also increasing water flow during low-flow periods.

Beyond human induced and climate stressors influencing the population of the native fauna in ROMO there are also studies reporting disease driven population declines in native frogs. Surveys of amphibian population distribution, abundance and potential for decline have found no environmental causes for population reduction (Corn et al., 1997). However, disease driven population declines were measured in boreal frogs with mark-recapture survival rates of male toads averaging 78% from 1991-1994, 45% in 1995 and 3% between 1998 and 1999, suggesting that this toad is in danger of extinction (Muths et al., 2003).

Natural history: hydrology

Measurements of hydrology within and around ROMO have included precipitation, snow pack, stream, and pond/lake characteristics and chemistry- all of which often associated with ambient levels of nitrogen deposition. Long-term monitoring of precipitation chemistry at Niwot Ridge has shown an increase in annual precipitation, amounting to a gain of 300 mm from 1951-1996, coinciding with a doubling of inorganic N wetfall between 1985-1988 and 1989-1992 (Williams et al., 2002). Modeling techniques for winter distribution of precipitation (snow) has been developed at Loch Vale in ROMO where the depth of snow was related to net solar radiation, elevation, slope and vegetation cover type and these parameters were used to estimate snow water equivalent (Balk & Elder, 2000).

Precipitation chemistry, especially the components of compounds within the snowpack has been monitored as a main link between ambient atmospheric deposition and introductions of pollutants, particularly nitrogen, into watersheds and ecosystem processes. Compounds deposited via precipitation enter surface and subsurface water sources and continue to interact within an ecosystem before potentially being exported to systems further downstream. These compounds may have drastic consequences on each ecosystem, and therefore numerous studies have sought to examine this interaction between atmosphere and water, and water and terrestrial processes.

Levels of deposition in winter precipitation, through measurements of snowpack chemistry, across the Rocky Mountains have been collected at National Atmospheric Deposition Program (NADP) wetfall sites, showing consistent trends in deposition concentrations for ammonium, nitrate and sulfur across the region (Ingersoll et al., 2008). Once the snow meltwater enters surface waters measurements at Loch Vale watershed (ROMO) have shown a depression in pH and acid neutralizing capacity at the beginning of spring snowmelt (Denning et al., 1991). Samples of meltwater from the base of the snowpack were found to be acidic and contributed to pulses of nitrate and sulfate to streams and soils, however, infiltration of meltwater into soils and variation in timing of meltwater across the basin prevented stream or lake waters from becoming acidic (Denning et al., 1991). Other studies at Loch Vale have shown that while hydrographs show a rapid response to snowmelt, implying that there may be little interaction of meltwater with soil minerals before entering stream channels (Sueker, 1995), pulses of soil porewater contributions containing dissolved organic carbon (DOC) and total Al have been measured within streams at the beginning of snow melt (Denning et al., 1991).

The contribution of snowmelt to streamflow, and by extension the potential influence of atmospheric deposition onto stream and downstream ecosystem processes, has been estimated in a number of studies across the Colorado Front Range. In one study at ROMO, elemental tracers were used to determine that subsurface water contribution to streamflow during snowmelt was between 33-80% for the duration of the melting period (Sueker, 1995). Further studies at ROMO using hydrograph separation indicated that streamflow contained 42-57% direct snowmelt runoff, 37-54% subsurface water and 4-13% direct rain run-off for May through October, with main differences between basins dependent on surficial material in the basin (Clow & Sueker, 2000). Measurements of source contributions to streamflow at Niwot Ridge found that the majority of streamflow was snowmelt that had infiltrated the subsurface and undergone subsequent biological and geological reactions (Williams et al., 2009). Additional research at Niwot Ridge determined that during initial phases of snowmelt a substantial quantity of nitrate is transported downhill into forested subalpine without assimilation by soil microbes (i.e. directly from snowmelt to streamflow), while seasonally later inputs of nitrate into streams were microbial in origin (Darrouzet-Nardi et al., 2011).

After snowmelt has entered streamflow or surface waters within a pond or lake, deposited compounds may either amplify by draining into the same basin and therefore alter the chemistry of the water body, or have little to no effect due to a strong acid neutralizing capacity (ANC) in the surface waters. Measurements of snowpack solutes at Niwot Ridge have showed that the solute levels were at the upper range for other northern hemisphere areas ($11 \mu \text{eq L}^{-1}$), with a storage of inorganic N in the snowpack averaging 2 kg-N ha^{-1} (Williams et al., 2009). However, the inorganic nitrogen in the surface waters of the stream were at or below detection levels suggesting that this area remained N-limited despite the high levels of deposition and potential for nutrient amplification within the watershed (Williams et al., 2009). While Williams et al. worked in a watershed with an intact ANC, temporal trends in stream chemistry at Green Lakes Valley in the Colorado Front Range showed a declining trend in ANC over the last 25 years (Caine, 1995). This decline in ANC was associated with increased rates of strong acid anion deposition from the atmosphere, especially at high elevations with little soil or vegetation cover, and suggests that the potential for surface water acidification associated with snowmelt pulses is increasing (Caine, 1995).

Beyond the direct influence of deposited compounds on snowmelt and streamflow, there are also landscape contributions to water body chemistry. Studies on landscape controls on

stream chemistry in ROMO have shown that the presence of steep slopes, unvegetated terrain and young surficial debris are negatively correlated with concentrations of base cations, silica and alkalinity and were positively related to nitrate, acidity and runoff (Clow & Sueker, 2000). Many of these factors may be indirectly associated with atmospheric deposition, related to areas of snow accumulation or thin soil horizons that prevent compound uptake in subsurface processes during snowmelt.

Seasonal and elevational gradients of water chemistry, associated with landscape and levels of atmospheric deposition, have also been measured in a number of studies. Stream solute content shows high values in late winter/ early spring that decrease during summer and return more slowly through the fall, controlled by elution of the snowpack by meltwater and changing proportions of surface and sub-surface water contributions to streamflow (Caine & Thurman, 1990). In watersheds with permafrost or the presence of rock glaciers, there are further seasonal contributions to stream solute levels, mainly associated with increasing concentrations during the warm season. Nitrate content of rock glacier outflow at Green Lake Valley, for example, increased over the season with highest concentrations in October (Williams et al., 2007). At Green Lakes Valley concentrations of nitrate decreased between the alpine and treeline, as deposited compounds were assimilated within the stream (Hood et al., 2003). Simultaneously, the contribution of dissolved organic N to total N increased between the alpine and treeline, while ammonium and particulate organic N lacked variation with elevation of streams (Hood et al., 2003).

Natural history: pollution

Long-term measurements of atmospheric nitrogen deposition in the Rocky Mountains show a general increase during the 20th century; however data from NADP Clean Air Status show no clear region-wide increase during the past two decades (Burns, 2003). At the same time, nitrogen loads in atmospheric wet deposition have increased since the mid 1980s at high elevations on the eastern side of the Continental Divide, related to increased sources of ammonium from developing agricultural areas and vehicle traffic (Burns, 2003). Present day deposition maps for the Rocky Mountains were created at 1 km resolution and show an increasing trend in concentration and deposition from north to south throughout the range and hot-spots associated with combined local and regional sources of air pollution (Nanus et al., 2003). Following this map of deposition, isotope analysis of deposited nitrate show a trend of enriched nitrogen in lakes and precipitation from the southern Rockies and at higher elevations as compared to more northern areas (Nanus et al., 2008).

A overview of ecosystem responses shows that nitrogen deposition simulated through nutrient fertilization has changed plant composition, however the alpine and subalpine areas remain N limited in general (Burns, 2004). Additionally, no regional trends have been observed of increasing nitrate concentrations in surface water, despite changes in lake photosynthetic community composition (Burns, 2004). Impacts of atmospheric deposition to ecosystem processes have been quantified by setting critical loads for inorganic nitrogen in the Colorado Front Range beyond which drastic changes are expected (Williams & Tonnessen, 2000). The critical load has been set at 4 kg ha⁻¹ yr⁻¹, to be maintained by federal land managers. Current levels were determined at 2.5-3.5 kg ha⁻¹ yr⁻¹ for elevations above 2500 m, and less than 2.5 kg ha⁻¹ yr⁻¹ for lower elevations, with an increase in inorganic deposition at a rate of 0.32 kg ha⁻¹ yr⁻¹ (Williams & Tonnessen, 2000). Measurements collected at Niwot Ridge/ Green Lakes Valley and Glacier Lake indicate that these catchments are at the threshold of nitrogen saturation

(Williams & Baron, 1996). While not all areas in the alpine or subalpine are saturated, studies have shown that there is less than 50% retention of the nitrogen in some watersheds on the eastern side of the Continental Divide, mostly relating to low biomass and short growing seasons relative to the timing and load of deposition (Burns, 2004).

Tracing the impact of atmospheric deposition within watersheds shows that wet deposition of nitrogen generally accumulates in the snowpack of high elevation ecosystems, therefore storing and releasing pulse increases of potentially strong acid anions with the snow melt into surface water (Williams et al., 2002). This snowmelt enters stream waters and can influence solute chemistry throughout the stream length. Research has shown that the majority of streamflow was of snowmelt origin that infiltrated the subsurface and then entered the stream, however a lack of measurable inorganic nitrogen in surface waters at Niwot Ridge suggests that this area remains N-limited (Williams et al., 2009). A second study in the Colorado Front Range reported downhill transport of nitrate from alpine to the subalpine associated with initial phases of snowmelt, however atmospheric sources of nitrate were not exported from the site due to consumption within a short portion of the stream (Darrouzet-Nardi et al., 2011). Other water bodies do exhibit episodic acidification in surface waters with acid-neutralizing capacities below 0 $\mu\text{mol/L}$ (Williams & Tonnessen, 2000). The Loch Vale watershed within ROMO has been reported as nitrogen saturated, with evidence for an explicit shift in ecosystem dynamics with a switch between being N-limited and N-saturated. As such, only modest atmospheric loadings of nitrogen are necessary to induce nitrogen leaching to surface water (Williams & Baron, 1996). Changes in phytoplankton biomass and nutrient abundance were evident between lakes with elevated deposition ($> 6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) and low deposition ($< 2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), with increased total N concentrations and higher total N: total P ratios (Elser et al., 2009).

Natural history: carbon fluxes, sinks and sources

Ecosystem losses or gains of carbon can have global ramifications associated with greenhouse gases and warming potential. While there are limited long-term records of carbon exchange in the Colorado Front Range, some research has been conducted examining year-long sources of ecosystem respiration or carbon loss. A study in the subalpine at Niwot Ridge using stable isotopes of carbon dioxide (CO_2) showed that the microbial community remained active under a 1 m deep snowpack, which contributed to ecosystem respiration losses during the winter and into the spring (Bowling et al., 2009). Winter measurements of CO_2 and methane (CH_4) in subalpine soils of ROMO show a net source of CO_2 through the winter, while saturated soils were net emitters of CH_4 and soil adjacent to wetland areas consumed CH_4 (Mast et al., 1998). Generally, winter gas flux diffusion was controlled by gas production or consumption in the soil and by physical snowpack properties, with snow providing insulation of soil necessary for continued microbial respiration (Mast, Wickland, et al., 1998).

Wetland carbon fluxes are of particular importance on a global scale due to long-term accumulation and storage of carbon in saturated peat layers. Carbon exchange measurements of a southern Rocky Mountain wetland, modeled for annual flux rates, was found to be a net source of carbon gas to the atmosphere in all three years of the study, although the long term accumulation trend at the site suggested long term carbon storage (Wickland et al., 2001). A long-term model for a Rocky Mountain fen showed sensitivity to anaerobic conditions and predicted that future conditions with lower water table position may create a loss of carbon despite an increase in plant production associated with roots in the surface peat (Chimner et al., 2002).

Coupled carbon-nitrogen cycles also may create fluxes of nitrous oxides (N_2O) and nitrogen oxides (NO_x) in areas of high nitrogen availability and aerobic conditions. Measurements of seasonal changes in these emissions showed a peak in N_2O emissions in the spring, which dropped as the soil water content increased from the release of snowpack meltwater and continued to decrease through the dry-out period after snowmelt, while NO_x and CO_2 did not exhibit this change (Filippa et al., 2009).

Natural history: soils

Gains of nutrients into soils is generally associated with atmospheric deposition, chemical weathering or in water sources from upstream. Many studies in the Rocky Mountains have attempted to track how these introductions alter soil quality and composition. Surveys of regional and local patterns of soil nutrients at treeline within the Rocky Mountains showed that these areas are a hotspot for wind driven snow based deposition. Areas with greater snow accumulation also had higher levels of total soil N, especially evident on the eastern side of the Continental Divide and on eastern facing aspects (Liptzin & Seastedt, 2010). Additionally, exchangeable calcium was higher on east facing aspects and at sites west of the Continental Divide (Liptzin & Seastedt, 2010). Research examining the direct impact of deposition on soil N content at Niwot Ridge found that deposition levels were most closely associated with snowpack, with a greater abundance of N-fixing plants in areas with less snow and substantial snow inputs in areas with low N-fixer abundance (Darrouzet-Nardi et al., 2011).

Chemical weathering as a source of soil solutes and contributions to surface waters was examined in the Loch Vale Watershed in ROMO and found to contribute nearly 40% of cations within the basin (Mast et al., 1990). The high levels of cation weathering were associated with the high chemical reactivity of the bedrock material and a high rate of physical erosion in the alpine environment (Mast et al., 1990). Water transport of both eroded and deposited compounds influences the distribution of nutrients within the soils, and soil concentrations therefore frequently follow elevational trends. One study at Green Lakes Valley showed decreased concentrations of nitrate along elevational gradients specifically between the alpine and treeline, accounting for 40-90% of total N along the transect (Hood et al., 2003). Similarly, soil characteristics measured along an alpine topography/ snow gradient showed that levels of snowmelt affected soil moisture and controlled the spatial pattern of major soil attributes such as texture, organic carbon, weathering index, bulk density, non labile and labile phosphorus (P) pools and P availability (Litaor, 2005).

Losses of soil quality or changes in composition may result from a number of different mechanisms, including via gas fluxes or as particles/compounds dissolved in water. Losses of carbon and soil nutrients through gas flux have been measured in ROMO and surrounding areas using ecosystem respiration and gas exchange rates. Soil respiration emissions of carbon dioxide, nitrous oxide, and nitrogen oxides in the subalpine continue during winter months enabled by snowpack temperature insulation and controlled by soil moisture (Filippa et al., 2009). A model of net carbon flux exchange from a fen in the Rocky Mountains showed an increase in carbon losses from carbon pools in roots within the peat, while there was no carbon loss or slight gain of carbon present in the organic matter pool and in the above-ground pools of C (Chimner et al., 2002). Losses of soil nutrients through water flow have been measured in lake basins and in streams, however it appears that all exports of nitrogen are associated with dissolved organic nitrogen and particulate N (Darrouzet-Nardi et al., 2011). Further, research at Niwot Ridge found that the dominant form of N in the soil was dissolved organic N and any inorganic N that was

transferred to surface waters within the local creek were immediately immobilized (Williams et al., 2009). These results are supported by measurements of nitrogen concentrations measured along an elevational gradient in Green Lakes Valley showing a relative increase in the proportion of DON to total N between the alpine and treeline (Hood et al., 2003).

Interactions between soil and vegetation may also control soil quality and composition, and research conducted in forests of the Rocky Mountains found that nitrogen release from plant litter decay was correlated with total net nitrogen mineralization (Stump & Binkley, 1993). Vegetation composition, and subsequent differences in litter chemistry, were also measured as creating small-scale variation in soil N cycling in association with soil microclimate in a moist meadow of alpine tundra at Niwot Ridge (Steltzer & Bowman, 1998).

Natural history: physical processes- climate and geology

Long-term climate records measured at Green Lakes Valley-Niwot Ridge suggest that there has been an increase in annual precipitation resulting in a total gain of 300 mm from 1951-1996, with the most substantial increase occurring since 1967 (Williams et al., 2002). Changes in climate associated with the El Nino Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) in the Rocky Mountain subalpine forests have shown a historic relationship with drought induced fire occurrence between 1700-1975 (Schoennagel et al., 2005). Studies found that large fires in ROMO occurred during extreme La Nina years, while PDO was predominantly negative in high fire years (Schoennagel et al., 2005). Constructive phases of ENSO and PDO were significantly associated with large-fire events, such that combined warm phases co-occurred with large fires in the central and northern Rockies, and combined cool phases promoted large fires in the southern Rockies (Schoennagel et al., 2005).

Geological controls on ecosystem processes within ROMO have focused on the interactions between basin and bedrock characteristics and stream chemistry. Parameters negatively influencing concentrations of base cations, silica, and alkalinity in stream water chemistry included land area covered by steep slopes (> 30 degrees), un-vegetated terrain, and young surficial debris (Clow & Sueker, 2000). These same geographic features were positively correlated with nitrate, acidity and runoff (Clow & Sueker, 2000). Other factors influencing geological contributions to stream chemistry include erodibility of the parent material. This is supported by measurements from the Loch Vale Watershed, where the easily erodible calcite dominated the bedrock and contributed cation concentrations as high as 40% of the total compounds present (Mast et al., 1990).

The interaction of climate and geography (and in some cases vegetation) also controls the presence and distribution of ground that is permanently frozen otherwise known as permafrost. Models of the distribution for past and future permafrost indicate that in the Colorado Front Range 12% of the study range is underlain by permafrost, however a decrease in ambient air temperature of 4 degrees C would allow 74% of the study range to have permafrost, and an increase in ambient temperature by 4 degrees C would reduce permafrost to being almost non-existent (Janke, 2005a). Alternative modeling techniques based upon correlations with rock glacier activity classes, the -1.0 degree C MAAT isotherm, and winter snow temperature measurements less than -3.0 degrees C determined a spatial area of 8.9% of the land area in the Colorado Front Range underlain by permafrost (Janke, 2005b). Modern relict rock glacier distribution indicates that mean annual temperature was once 3-4 degrees cooler during the Pleistocene and permafrost extending some 600-700 m lower than today (Janke, 2005a).

Rock glaciers have been examined as a potential source of nutrients into watersheds downstream, and the structure of these glaciers is important to understand implications of how thaw will impact the surrounding ecosystems. Measurements of the structure within a rock glacier has shown a top thin layer (0.7- 1 m) of fine sediments and soils underlain by a thicker zone (1-3 m) of ice-free blocky active layer, and a third layer that extends to about 5 m includes unfrozen, fine and wet sediments and below 5 m an ice-rich permafrost zone above the bedrock (Leopold et al., 2011). Surface sediments containing carbon in a rock glacier feature at Green Valley Lake may contribute to a mean outflow concentration of dissolved organic carbon of 0.85 mg L⁻¹ (Williams et al., 2007). Additionally, the ice rich zone of the rock glacier may be the source for a seasonal signature of nitrate concentrations increasing in streamflow throughout the growing season (Williams et al., 2007).

Evidence for thaw of existing areas of permafrost has been measured within the Green Lakes Valley associated with an increase of water flow in late season hydrographs not found in watersheds known to lack permafrost (Caine, 2010). Additional evidence from an increase in base cations and silica and particularly calcium and sulfate ions in stream discharge suggest degradation of ice-rich permafrost on the north-facing slopes of the valley below 3700 m (Caine, 2010). Direct measurements of permafrost thaw has been performed at sites in the Colorado Front Range where permafrost was confirmed in the 1970s that now contain only ice lenses, in coordination with soil temperature measurements suggest thermal degradation has altered permafrost distribution (Leopold et al., 2010).

Natural history: effect of land-use change and/or changes of pulse disturbances

Fire is frequently considered a menace by humans living in areas prone to this type of disturbance, threatening livelihoods, homes and property. From an ecological perspective, however, fire brings a start to secondary succession for vegetation and microbial communities, and provides a diversity of habitats for wildlife in a heterogeneous matrix of areas with different fire intervals. In the area of ROMO, almost 70% of large fires occurred during La Nina events that coincided with a negative Pacific Decadal Oscillation, although these phases co-occurred during only 29% of the 1700-1975 period (Schoennagel et al., 2005). Using dendochronology and geographical information system mapping there is evidence for a historic dominance of infrequent, extensive, stand replacing fire events, while surface fires affected only 1-3% of the forest area (Sibold et al., 2006). Canopy tree species in the Rocky Mountains have different fire return intervals, with modern lodgepole pine stands originating following fires in the last 400 years, while spruce-fir stand generation has not been affected by fire in the past 400 years (Sibold et al., 2006). Other research on stand succession after a fire 260 years previous showed that initial colonization was by spruce and lodgepole pine but that subalpine fir increased in abundance during the past 100 years with future changes in tree canopy dominance dictated by windthrow events (Veblen, Hadley, & Reid, 1991). Local studies in and around ROMO have shown that the low incidence of fire associated with fire suppression in the 20th century is not unique in comparison with the previous 300 years of fire history, and lasting consequences associated with this practice are not likely in this region (Sibold et al., 2006).

In addition to windthrow or blowdown, there are many types of secondary disturbance operating within the forests of ROMO, and some work has been done to examine how these disturbances may influence lodgepole pine stand development. Examination of the effects of blowdown, surface fires, and mountain pine beetle outbreak on demographic processes in post-fire lodgepole pine stands in ROMO showed that surface fires don't affect tree dominance in the

canopy nor trigger pulses of recruitment and therefore do not have detectable influence on stand development (Sibold et al., 2007). At the same time, mountain pine beetles and blowdown trigger pulses of regeneration of both lodgepole pine and subalpine fir, especially in stands altered by thinning prescriptions to reduce fuel ladders thereby increasing tree density within 15-20 years following treatment (Sibold et al., 2007).

Conservation: vegetation cover and change through time

Studies focusing on the conservation of vegetation within ROMO have focused on methods of identifying changes in plant community structure in relation to changes in disturbance, specifically with fire for tree species and invasive understory species. Stand dynamics for the ponderosa pine were monitored following established criteria to identify cause of tree regeneration and mortality events, especially related to fire events. Researchers determined that dense even-age stands were related to pre-EuroAmerican settlement crown fires and a lack of crown fires will create a fire regime outside the historic range of variability (Ehle & Baker, 2003).

Invasive species are another threat to conserving existing rare and endemic species, frequently associated with outcompeting and replacing native flora at a cost of species diversity and richness especially in disturbed areas. A recent study examining plant communities in areas of restoration of endemic species found that there was higher species richness and cover associated with native species in areas that were not invaded by exotic plants (Pritekel et al., 2006). This same study found that attempts to eradicate invasive exotics, whether by mechanical means or using herbicides, increased the area of bare ground thereby also altering natural levels of nutrient cycling, belowground community functioning and plant community composition. These studies suggest main limitations and setbacks to continued conservation of existing flora within ROMO, given changes in conditions required for plant community maintenance.

Conservation: hydrology

Conservation of wetlands and waterways within ROMO has been examined in relation to draining by ditching associated with construction proceeding from the growth of the park. In a study focusing on restoration of an impacted fen the water table was successfully restored by increasing surface sheet water flow, however the results from this study highlight the potential damage induced in wetland areas by ditching or simple water diversions (Cooper et al., 1998). The authors of this study also noted that similar fens in the southern Rocky Mountains are sensitive to summer precipitation and hydrologic changes associated with the timing of surface runoff, all likely to be influenced by changes associated with climate in addition to future developments directly associated with human expansion.

Conservation: pollution

Efforts to reduce impacts of pollution on park natural processes, and thereby conserve existing biogeochemical processes within the park, have focused on translating known scientific results into public policy. Work by Porter and Johnson (2007) established a target level of nitrogen deposition, to be achieved associated with emission reductions in areas identified as sources of nitrogen in the surrounding foothills and beyond. This work is an excellent example of how conservation in protected areas is dependent on policies far beyond the borders of the park proper. Without jurisdiction to control these outside influences, it is likely further difficulties in conserving existing systems for future public use will arise.

Management: vegetation cover and change through time

A key management concern in ROMO at present is related to the presence and spread of exotic or invasive plant species introduced from beyond the park boundaries. One species in particular, sweet clover, has become common in montane grasslands where it now acts as a facilitator for other exotic species into the community (Wolf et al., 2003). In the 1990s a study was conducted to examine the means of movement for introduced species within the ROMO to aid in management decisions. This study determined that plant community composition and introduction of exotic species were significantly influenced by distance from trail edge, level of trail use, and distance from trailheads as a point of introduction (Benninger-Truax et al., 1992). Some attempts to manage invasive species, however, have been determined to negatively impact native plant communities in a similar manner as the presence of actual exotic species, by altering the availability of bare ground (Pritekel et al., 2006).

Management: herbivore-plant interactions

National parks, particularly ROMO, face management issues relating to wild ungulates with small park sizes, incomplete protection of winter ranges, and an absence of predators. At ROMO management decisions within the park to allow elk populations to grow until naturally limited through ecosystem carrying capacity have produced cascading effects on vegetation and soils within the park. Measurements conducted on aspen regeneration in the 1990s showed that high densities of elk in the winter range have increased the mortality of aspen stands in addition to reducing the density of living suckers (Baker et al., 1997). A study looking at the age distribution of aspen in the park found that between 1855 and 1965 there were no decades with higher or lower regeneration than that expected from the long-term trend, however modern aspen regeneration on the lower elevations of the eastern slopes within the park were at levels 80-95% below recruitment expected from the same trend (Binkley, 2008). Given that aspen appear to be facing extreme densities of elk that may be limiting regeneration, the sustainability of this trend was assessed across vegetation browse communities in the late 1990s. Results from this study pointed to changes in nutrient cycling associated with elk browse in willow and aspen tree communities, and changes in biomass for shrub communities (Schoenecker et al., 2002). Modeling approaches have been applied to determine a level of elk density that would be sustainable at the ecosystem level, and it was determined that aspen regeneration succeeded when elk populations were between 300-600 in the winter range- as compared to current levels of 1000-1200 (Weisberg & Coughenour, 2003). Current (2012) management of elk in ROMO does include some herd culling, to maintain healthy populations without degrading the supporting ecosystems. Additionally fencing has been installed to allow willow and aspen recovery.

Management: animal and insect ecology

Modeling exercises conducted in ROMO to illuminate strategies of controlling elk population dynamics determined that lifetime contraceptives required treating the fewest animals but increased population variability and increased risk of extinction (Bradford & Hobbs, 2008). Year-long contraceptives required treatment of more animals but had no extinction risk, whereas culling produced intermediate levels of both extinction risk and number of animals treated (Bradford & Hobbs, 2008). Results from models may be particularly useful for determining future actions within the park and for the neighboring elk herd in Estes Park, as the elk of

ROMO have approached a carrying capacity of 1,069 individuals that has remained constant since 1991, while the Estes Park population continues to increase at rates as high as 5.2% (Lubow et al., 2002). The herd in ROMO is currently being managed for population size using the culling method.

A second major management concern for animals in the park relates to a recent trend of black bears relying on anthropogenic sources of food such that individual animals have gotten larger in size, while also being in better condition and therefore able to have higher productivity for offspring (Baldwin & Bender, 2009). The authors of this study highlighted the need for land managers to increase the quality and quantity of natural food sources, while also reducing bear dependence on anthropogenic sources of food (Baldwin & Bender, 2009). It should be noted that managing for a particular species is not a component of the mandate for national parks in the United States, however this information may be of use to areas managed by such agencies as the Department of Fish and Game (title varies by state).

Management: hydrology

On the eastern slopes of the Rocky Mountains pollution deposition has created a number of management problems related to hydrology and potential long term influences on water quality. Current hydrologic conditions in high elevation basins are associated with a general decline in acid neutralizing capacity and pH of streamwater (Caine, 1995). Recovery of these systems will be associated with changes in the rates of deposition, and largely controlled by political decisions removed from the park.

Management: pollution

Measurements of pollution levels related to deposition in Rocky Mountain National Park have been applied to the establishment of a target level of nitrogen deposition associated with resource protection within the park, with recent advances in local public policy (Porter & Johnson, 2007).

Diversity: vegetation cover and change through time

Many studies have highlighted the overall diversity of plants in areas within ROMO, and a number of studies have included examination of the controlling factors limiting or causing levels of diversity. Traditional studies comparing plant diversity between areas influenced by fire, proximity to riparian areas, or associations with elk have supported trends identified in other regions and helped identify landscape patterns of diversity (Stohlgren et al., 1997). Studies performed at Beaver Meadows within ROMO examined the field based methodology used to determine species richness and diversity, determining that a new technique (pixel nested plot) was comparable to previous methods and required less time investment (Kalkhan et al., 2007). Other studies have focused on applying models, which include environmental factors related to topography and elevation, for scaling diversity and richness trends to larger areas of the landscape (Kalkhan & Stohlgren, 2000). Environmental factors have also been examined for playing a role in the success of exotic species invasions within ROMO. Factors such as soil nitrogen concentrations, percentage of bare ground as well as physical characteristics such as distance from trailhead or level of trail use have been found to increase the likelihood of successful introduction of exotic species (Benninger-Truax et al., 1992; Kalkhan et al., 2007).

Aside from environmental controls on plant diversity and richness, many biotic factors, such as competition and facilitation, also influence the number and type of plants present in an

area. Studies examining competition and facilitation between native and non-native species have shown that areas with high native species richness are more likely to become invaded by exotic species, such as low elevation riparian zones (Kalkhan et al., 2007; Stohlgren et al., 2002). Additionally invaded areas show changes in species richness as well as changes in underlying environmental conditions such as nutrient losses in soils (Pritekel et al., 2006).

Diversity and richness analysis and variation within specific ecosystems of ROMO have included subalpine wooded fens (Johnson, 1996, 1997). Environmental factors identified as contributing to species composition included water table depth, hummock height, availability of light and soil/water temperature (Johnson, 1996). The genera and species of algae present in alpine lakes was also examined in the 1960s, although associated environmental conditions were not the focus of the study (Whitford & Kim, 1971).

Diversity: animal and insect interactions

Investigations of insect diversity within ROMO appear limited to a study examining spatial heterogeneity in butterflies. This study determined that butterfly richness was correlated with increased plant species richness and amount of available shrubland (Kumar et al., 2009). Studies of animal diversity, or the factors related to animal diversity and richness are perhaps a point of future study for ROMO.

Response to disturbance: vegetation cover and change through time

The potential for climatic disturbance on vegetation patterns and processes in ROMO have focused on changes in the alpine at the forest-tundra ecotone. Measurements of seedling density, seedling establishment and increases in krummholz height in ROMO have suggested that changes in vegetation cover are most closely associated with high snow depths in willow wet meadows (Baker & Weisberg, 1997; Hessel & Baker, 1997a, 1997b; Weisberg & Baker, 1995). Warmer temperatures for soil associated with deep snow packs in this area have allowed a release of krummholz leader growth and initiated higher seedling densities since the end of the Little Ice Age (Weisberg & Baker, 1995). At Niwot Ridge a similar study showed that highest density of tree and seedling distributions were associated with areas of low topographic relief and the presence of meadows and wetlands along the forest-alpine tundra ecotone (Humphries et al., 2007). Climate may also be a main factor in observed reductions in aerial extent of floodplain willow, as changes in climate associated with early spring runoff, lower summer and fall flows and decreased snowpack will contribute to reduced return intervals of peak flow levels necessary to initiate recruitment of willow on point bars, beaver ponds or abandoned channels (Cooper et al., 2006).

Further down slope studies have shown that climate becomes only a secondary factor related to the disturbance of greatest importance: fire. At present, Ponderosa pine regeneration appears to be influenced by fires from the 1860s, in addition to a release from grazing pressure in the 1970s-1980s (Mast et al., 1998). However, a continuation of the current frequency of crown fires would create a fire regime outside the historical range of variability and would therefore alter pine recruitment (Ehle & Baker, 2003; Mast et al., 1998). Studies specifically examining changes in the frequency and severity of fire in the Colorado Front Range have used Engelmann spruce, subalpine fir and lodgepole pine to determine that historically the fire regime was dominated by infrequent, extensive stand replacing fire events, however no change in fire frequency was detected beyond the variability of a 300 year fire history (Sibold et al., 2006). Fire was shown to influence the recruitment of different tree species differently however, and

research has shown that subalpine fir has increased in abundance for the past 100 years, with further changes in tree community composition determined by secondary disturbances such as windthrow (Sibold et al., 2006, 2007; Veblen et al., 1991). The fir species is generally increasing due to advantageous gap creation associated with windthrow and mountain pine beetle kill, as compared with lodgepole pine (Sibold et al., 2007; Veblen et al., 1991). Surface fires do not appear to influence changes in tree composition, although ectones for lodgepole pine in ROMO are controlled by elevation and soil moisture- both features associated with limiting fire severity (Stohlgren & Bachand, 1997).

Disturbance related to the effect of pollution on plants in ROMO has focused on the impact of nitrogen deposition. Research has shown that tree tissue chemical components vary between the eastern and western slopes of the Rocky Mountains, corresponding to increases in N deposition on the eastern side (Baron et al., 2000). In the alpine zone a manipulation experiment determined that critical loads of nitrogen deposition change individual species at levels of 4 kg N ha⁻¹ yr⁻¹; changes in plant community occur at levels above 10 kg N ha⁻¹ yr⁻¹ (Bowman et al., 2006).

Physical disturbance has also been considered as influencing plant communities within ROMO. Trail erosion and changes in bare ground coverage in areas of high use have promoted the introduction of exotic plants within ROMO (Benninger-Truax et al., 1992).

Response to disturbance: herbivore-plant interactions

The relationship between herbivores and plants can be altered by changes in population levels, water or nutrient availability, etc. However mechanisms that produce those disturbances for either the herbivore or plants may also alter the nature of the relationship between the two. Changes in disturbance patterns of fire and human predator control have been compounded by increases in elk numbers and decreases in elk predators in controlling the distribution and regeneration of aspen in the Rocky Mountain National Parks of North America (White et al., 1998).

Response to disturbance: animal and insect ecology

Climate as a driver of change on animal populations in ROMO has been examined as a potential amplifier for local elk populations. Warmer winters and wetter summers predicted with future climate in the region could increase the population of elk by 100%, while warmer winters and drier summers would still increase the population by 50% (Wang et al., 2002a). Historic data on population dynamics of the white-tailed ptarmigan at ROMO has shown an advancement of hatch dates in response to increased April and May temperatures, while high winter minimum temperatures appear to retard the growth rate of the population (Wang et al., 2002b).

Non-climate-based disturbances to animals of ROMO include habitat acidification from pollution deposition and disease dispersal. Both of these disturbances have been examined as contributors to a decline in amphibian populations within the park; however there appears to be low risk of levels of acidity necessary to kill embryos of amphibians (Corn & Vertucci, 1992). Biotic agents have been identified as a main culprit in a mass die-off of local amphibians, specifically a fungus has been responsible for a sharp decline in egg masses of the boreal frog (Muths et al., 2003).

Response to disturbance: hydrology

By virtue of mountain meteorology much of the hydrology within the ROMO region is influenced by elevated levels of deposition in precipitation. A study focusing on precipitation chemistry in relation to this phenomenon found that strong acid anions, ammonium and high salt concentrations originate to the east of ROMO, and are transported via up-valley funneling winds at different times of the year (Baron & Denning, 1993). The compounds present in precipitation originating beyond the boundaries of the park are therefore of potential concern and influence for all levels of water supply downstream in the watersheds.

Target elements or compounds of concern include those toxic to humans and ecosystems, or those that may become so at high rates of deposition. Measurements of the concentrations of mercury in precipitation were 3-4 times higher during summer months at Loch Vale in ROMO, when precipitation has an easterly origin, and levels were comparable to concentrations across the Midwestern and Northeastern US (Baron & Denning, 1993; Mast et al., 2005). Other toxic compounds measured within remote lakes, including PAH fluoroanthene and PCBs from sediment samples, indicate the connectivity of anthropogenic sources to wilderness areas within ROMO (Heit et al., 1984). Identification of specific sources for sulfate and nitrate in the snowpack and in lake samples have shown that winter deposition of sulfate is of anthropogenic origin, specifically coal from electric plants (Mast et al., 2001). Nitrate sources showed a trend of enriched delta ^{15}N (produced in association with industrial operations) in the southern Rockies and at higher elevations when compared to lake and precipitation samples from the northern Rockies in areas more removed from point source contributors (Nanus et al., 2008).

In mountainous areas the majority of precipitation falls as snow, forming a snowpack that accumulates during the winter and then melts in a comparatively short time period, thereby releasing all stored compounds in pulses during the spring. Dust may also accumulate in the snowpack and influence radiative forcing during the melting period and therefore alter the timing of peak runoff and rates of evapotranspiration during the early spring (Painter et al., 2010).

Monitoring of snowpack chemistry between snowpack sites and National Atmospheric Deposition Program wetfall sites have showed similar trends in the concentrations of ammonium, nitrate and sulfate between 1993 and 2004 (Ingersoll et al., 2008). The release of solutes from the snowpack and into the watershed at Niwot has been quantified as being in the upper end of concentration values for other northern hemisphere areas (Williams et al., 2009).

Numerous studies have examined the fate of solutes after entry into the soil matrix, and at Niwot Ridge the majority of streamflow has been determined as snowmelt, including inorganic forms of nitrogen that are rapidly processed into organic compounds in the soil or stream (Darrouzet-Nardi et al., 2011; Williams et al., 2009). Similar studies at ROMO in the Loch Vale watershed support an influx of snowmelt based water runoff into the stream systems with depressions in pH and acid neutralizing capacity (Denning et al., 1991). The amount of snowpack originated nitrogen solutes that leach from the alpine zone has been linked to vegetation cover, where nitrate declines in the greater presence of plants and dissolved organic nitrogen increases in the presence of plants (Hood et al., 2003).

Runoff from meltwater and streamflow accumulates in basins with lakes and ponds in the mountain areas, and here numerous studies have examined the effects of atmospheric deposition on lake chemistry and ecological functioning. A prime concern relates to the acidity of said lakes, and the factors of a lake that may result in dramatic changes in pH with deposition. A study of the sensitivity of high-elevation lakes across the National Parks of the Rocky Mountains found that lakes with a high probability of having a low acid neutralizing capacity were located

in basins with elevations greater than 3000 m, less than 30% of the catchment having a northeast aspect and a bedrock with low buffering capacity- specifically lakes in ROMO (Nanus et al., 2009). There is hope however, as evidence for recovery of acidification indicates a reduction in lake surface sulfate concentrations relating to regional reductions in SO₂ emission (Mast et al., 2011).

Aside from the effect of acidifying lakes, deposition has the additional issue of altering chemical composition and thereby increasing nutrient availability, particularly of nitrogen. Lakes receiving high levels of deposition have higher concentrations of nitrate and total nitrogen, in addition to higher total nitrogen to total phosphorus ratios than lakes with low levels of deposition (Elser et al., 2009). Short term enrichment of nutrients showed that lakes with higher deposition exhibited instances of phosphorus limitation, thereby being near a saturation point for ambient levels of nitrogen (Elser et al., 2009). The Loch Vale watershed has been measured as nitrogen saturated, with a shift in aquatic ecosystem dynamics from an N-limited system to an N-saturated system where only modest atmospheric loadings of nitrogen are sufficient to induce nitrogen leaching (Williams & Baron, 1996). Lake nitrate concentrations have been measured as higher in lakes on the eastern side, where nitrogen deposition rates are higher, with evidence for shifts in diatom community composition over the past 50 years (Baron et al., 2000). Additionally, changes in the assemblages of diatoms and records of N, C and H isotopes from sediment cores in lakes have shown a substantial shift in nitrogen cycling over the past ~60 years (Enders et al., 2008). Sediment analysis of alpine lakes across the Colorado Front Range were determined to share a synchronous shift in diatom communities associated with an increase in depleted delta ¹⁵N, with no previous evidence of an equal shift in a 14,000 year post glacial history (Wolfe et al., 2001; Wolfe et al., 2003).

Measurements of the retention of nitrogen added as a result of deposition showed that aquatic algae were responsible for immobilizing 15% of total N deposition (Baron & Campbell, 1997). Even so, increasing amounts of inorganic nitrogen through deposition is causing episodic acidification in headwater catchments of the Green Lakes Valley in the Colorado Front Range with acid neutralizing capacities below 0 µmol/L, suggesting a need for management of water quality in high elevation watersheds (Williams & Tonnessen, 2000).

Response to disturbance: carbon fluxes, sinks and sources

The effects of climate on carbon sequestration or loss has been examined in Rocky Mountain fens, where future conditions with lower water table levels are likely to release carbon despite potential increases in plant production (Chimner et al., 2002). Changes in seasonal snowpack and levels of soil moisture in subalpine meadows will also alter nitrous oxide and carbon dioxide fluxes, where increased water availability stimulates flux rates (Filippa et al., 2009).

Response to disturbance: soils

The deposition of pollutants through precipitation and Aeolian deposits, particularly of nitrogen and other ecosystem nutrients, is of particular concerns in mountainous areas with traditionally low levels of nutrient availability. A review of published studies conducted in the Rocky Mountains confirmed retention levels less than 50% in watersheds on the eastern side of the Continental Divide, despite altering plant composition, biomass and productivity (Burns, 2004). Other studies have targeted the potential source of deposited nitrogen, and suggest that deposition on the eastern slopes of the Continental Divide are related to ammonium produced

from agricultural areas and increasing vehicular traffic (Burns, 2003; Davis et al., 2008). One study estimated that 75% of the increased soil nitrogen pools on the eastern slope of the Rocky Mountains could be accounted for by increased nitrogen deposition associated with human settlement and expansion in the last several decades (Baron et al., 2000).

Deposition within the alpine and subalpine regions is not ubiquitous, and instead follows snowpack distribution of nutrient concentrations. Treeline in the alpine has been predicted to be a deposition hotspot, and research has shown higher total soil nitrogen along treeline for the eastern slope and for eastern aspects on the western slope of the Rocky Mountains than on the western slope in general (Liptzin & Seastedt, 2010). Additionally, forest and tundra soil samples were drastically different within the same site, confirming an influence of deposited nitrogen (Liptzin & Seastedt, 2010). These results suggest that while regional deposition levels may be reported below threshold points, individual sites and ecotones may experience deposition levels beyond identified critical levels. A manipulation study examining nitrogen critical loads necessary for ecosystem responses found that increases in chemical leaching from soils, in addition to net nitrification into the atmosphere, occurred at deposition levels above $20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Bowman et al., 2006).

The transfer of deposited nitrogen from soils to waterways is related to the storage and release of solutes and is largely controlled by spring flushing events with the melting of the snowpack. Nitrogen immobilized by soil after deposition increases the amount of dissolved organic nitrogen, allowing these biologically available compounds to enter the streamflow (Williams et al., 2009). This has been shown in measurements of surface water and soil for concentrations of ammonium, nitrate, dissolved organic nitrogen, and particulate organic nitrogen along elevational gradients, where nitrate decreases between the alpine and treeline (Hood et al., 2003). During initial phases of snowmelt, however, a substantial quantity of nitrate is transported downhill without assimilation by soil microbes, suggesting that changes in amount and timing of snowmelt will alter soil-nutrient interactions and response to deposition (Darrouzet-Nardi et al., 2011).

Response to disturbance: physical processes- climate and geology

At Green Lakes Valley- Niwot Ridge measurements of annual precipitation report a total gain of 300 mm from 1951-1996, with the greatest increase in precipitation occurring since 1967 (Williams et al., 2002). Increases in winter precipitation increase snowpack and insulation for alpine soils, thereby creating compounding effects of mountain permafrost thaw associated with climate warming. Evidence for permafrost, and that it is thawing, has been found using stream hydrographs where an increasing trend of water flow is evident in September and October, while the trend has not been found in watersheds lacking potential for permafrost thawing (Caine, 2010). These results suggest that ice-rich permafrost on north-facing slopes below 3700 m may be thawing, and thereby responsible for measured changes in water flow late in the fall before winter freezing (Caine, 2010).

Models of permafrost distributions suggest that mountain permafrost and rock glaciers exist in ~ 12% of the Colorado Front Range, however an increase in ambient temperature by 4 degrees (Celsius) would reduce permafrost to being almost non-existent (Janke, 2005a). The potential for widespread thawing is already evident under existing climate conditions, with measurements of soil temperature and permafrost distribution in the Rocky Mountains reduced such that permafrost identified in the 1970s are now designated ice lenses (Leopold et al., 2010).

Response to disturbance: effect of land-use changes and/or changes of pulse disturbances

Fire as a means of disturbance is traditionally characterized as a pulse disturbance, and in Colorado has been subject to a number of suppression techniques since the arrival of Euro-American settlers. Historic fire frequency and patterns were examined using tree rings in a high-elevation forest within ROMO and identified 41 fire events beginning in 1533 (Buechling & Baker, 2004). Of these fires, 22 were high-severity crown fires, with a return interval of 346 years for these stand replacing fires- although the aerial expanse of fires was shown to increase since 1700 associated with summer drought (Buechling & Baker, 2004). Other studies in ROMO have suggested potentially contradictory advice associated with fire suppression, first that suppression by humans has created fuel hazards that threaten ecosystem characteristics, and second that managed fires may not be appropriate for all ecosystem types (Keane et al., 2002; Schoennagel et al., 2004). Conclusions from these studies suggest that management plans associated with fire ought to consider the specific ecosystem type and historic return interval, rather than a blanketed approach to fire suppression.

Land-use change related to human expansion has created the potential for disturbance at ROMO in a number of different ways. Climatically, transformation of grasslands into dry and irrigated agricultural fields has altered summer temperatures and diminished low-level upslope winds over the plains, while lowering summer temperatures in higher elevations (Chase et al., 1999). Additionally, increases in conversion of plains to agricultural land has increased the application of fertilizers, thereby creating volatilized ammonia that is estimated to contribute 20% of total nitrogen deposition within ROMO (Davis et al., 2008). Finally, dormant agricultural fields have led to increases in dust loading in snowpacks supporting the Colorado River thereby altering the timing and magnitude of meltwater runoff within the entire watershed (Painter et al., 2010).

Visitor-park interactions: vegetation cover and change through time

As a National Park dedicated to providing public access to natural places, ROMO is faced with a difficult task of providing means for exploring wilderness without having visitors degrade the wilderness in the process. Degradation comes in many forms, and includes physical changes such as erosion, but also inadvertent introductions associated with exotic or non-native species. Trail corridors have been identified as a source of exotic species within ROMO, with higher levels of non-native plants found in proximity to high-use trails, junctions and campgrounds (Benninger-Truax et al., 1992). Physical destruction of plants was identified as an early problem associated with human activities in the alpine tundra where visitors ventured off trail or into areas surrounding designated viewing areas (Willard & Marr, 1970). Differing impacts of human activities on communities within the alpine tundra, and recovery after protection from human degradation, suggested that a lengthy recovery was necessary for tundra plants particularly in areas with historic high use by visitors (Willard & Marr, 1971). Continued protection and recovery of damaged vegetation in the alpine zone showed an increase in species richness, however a decline in plant cover suggests that unassisted regeneration will take longer than a century (Willard et al., 2007).

Visitor-park interactions: animal and insect ecology

Visitor concentration around roads, trails and campgrounds can have a negative effect on animal activities, particularly large mammals. Despite this, bear activity in ROMO appear to be relatively unaffected by human development, both for den-site selection and in previously

avoiding areas with humans thereby remaining secretive without interfering with park services (Baldwin & Bender, 2008; McCutchen, 1990). More recently, however, increases in the proportion of anthropogenic food in bear diets is a concern, particularly with observed increases in bear size and productivity that could increase human-bear interactions within the park, particularly near food sources such as campgrounds and picnic areas (Baldwin & Bender, 2009). Presence of roads and human frequency has not been as benign for all mammals in ROMO, and for roadside grazing mammals such as mule deer concentrations of lead in roadside vegetation has been identified with high concentrations of lead (Harrison & Dyer, 1984). Bighorn sheep have also been shown to be displaced by vehicular traffic near mineral licks, a feature that may compromise the health and productivity of local bighorn sheep (Keller & Bender, 2007)..

Visitor-park interactions: effect of land-use changes and/or changes of pulse disturbances

The potential for an influence of long term changes in weather and regional climate for mountain areas has great ramifications for visitor use of ROMO. Generally changes in factors that influence species habitat, snow and water availability and the quality of tourism seasons may be a point of future development within ROMO (D. Scott, 2003).

Tatra National Parks

Background

Research studies have been conducted in and around the Tatra National Parks of Poland and Slovakia for decades on a wide range of topics, questions, temporal and spatial scales. Results and findings associated with the main research questions and content categories outlined in the abstract are summarized here, including studies conducted within the Polish Tatra National Park (TNP), the Slovakian Tatra National Parks (Sprawa Tatra National Park and Statne Lezy: TANAP), the Tatra Mountain range generally- including the Low and High Tatras, and the Carpathian Range. Summaries herein include results and conclusions from published, peer reviewed, articles available in English (or at least the abstract) to the general academic community and the public. The authors acknowledge that this dramatically reduces the number of articles available for review, as many articles are published in either Polish or Slovak, however as none of the authors are fluent in either of these languages English was elected as the limiting requirement. An attempt has been made to include articles for which an English abstract is available, particularly associated with the European journal *Ekologia* and the Polish Journal of Ecology.

Natural history: vegetation cover and change through time

As the Tatra National Parks (for ease both nationalities of parks will be abbreviated TNP unless more specific information is necessary) includes mountainous areas within both Slovakia and Poland in the Carpathian Range, there is a great deal of variation in vegetation and factors governing plant distribution. General classes of the vegetation cover across the Polish Tatra Mountains were determined using the Braun-Blanquet technique in the 1980s, where regions such as lower montane, upper montane, dwarf pine, alpine and subnival were described along environmental gradients (Mirek & Piekos-Mirkowa, 1992). No such attempt at describing the land area associated with major vegetation classes has been published for Slovakia, however for the dominant coniferous ecosystems of the Slovakian TNP, biomass and productivity were estimated over 20 years for the herb and moss layer. These measurements determined that the

greatest levels of understory biomass in the Slovakian TNP were associated with bog-dwarf pine ecosystems (Kupicek, 2001).

A number of studies have been conducted in the Tatra Mountains of Poland examining what happens to trees after death, particularly relating to the formation of coarse woody debris and regeneration associated with decaying logs. One study highlighted the degree of decay and age of dead wood on the forest floor, and determined that coarse woody debris accounted for 30% of the total volume of living and dead trees within a stand (Zielonka, 2006). The high volume of woody debris was also examined as a site for germination and regeneration for tree seedlings and other understory plant species, where the middle stage of decomposition was determined the best substrate (Zielonka & Niklasson, 2001). This estimate of the best substrate for germination was more closely examined for colonization of herbs, and it was determined that ~50 years after tree death the conditions were best for germination and colonization of herbs (Zielonka & Piątek, 2004).

Studies of specific plant (and fungi) species in the Tatra Mountains have ranged from highlighting abiotic habitat conditions for dwarf pine to describing new species of lesser known fungi (Bayerová et al., 2005; Svajda et al., 2011). The application and development of new techniques for examining the relationships between species, especially in determining community characteristics, have also been common using the Tatra Mountain Range as a testing area. In the Polish Tatra Mountains, plant community classification for tall-forb and tall-grass communities were conducted using linkage clustering and detrended correspondence analysis for examining environmental gradients controlling these community types (Šeffer et al., 1989). Later work in the Polish Tatra Mountains focused on using artificial neural nets and hyperspectral data for classifying high-mountain plant communities (Zagajewski, 2010). This same technique was used in the Polish TNP to confirm groups of aquatic bryophytes growing in streams with different bedrocks, where differences in groups of bryophytes were determined based on differences in the concentration of key elements (Samecka-Cymerman et al., 2007).

Many environmental factors influence plant distribution and productivity, and a key concern for foresters in the TNPs relates to the effect of climate on tree growth. The response of tree ring growth to changes in climate were measured in four different tree species across the Tatra Mountain in both Poland and Slovakia and results supported the general rule of growing season temperature controlling high-elevation tree growth (Büntgen et al., 2007). Elevation and tree density also appear to interact with climatic conditions based on a study from the Polish Tatra Mountains, with different responses to summer temperatures related to the elevation of the measured tree (Savva et al., 2006). Associated findings in the Pol'ana biosphere reserve in central Slovakia determined that variation in stand structure and regeneration were associated with altitude (Holeksa et al., 2006). Not only the trees themselves may be affected by changes in elevational climate however, symbionts such as mycorrhizae are both dependent on trees or other hosts and the environmental conditions in which the host grows. One study following elevational gradients in the Western Tatras and the High Tatra Mountains examined root infection by arbuscular mycorrhizal fungi, where types of infection differed with elevation (Zubek et al., 2009). Some work has been done examining historic changes in treeline with climate, using pollen and macroscopic analyses of sediments from high elevation lakes in the High Tatra Mountains of Slovakia. Despite potential changes in climatic conditions, there was no evidence of changes in the treeline during the Holocene, while spruce forests remained dominant below 1000-1400 m (Rybníčková & Rybníček, 2006).

Aside from interactions between climate and elevation, there are also impacts of pollution associated with elevation. Across the greater Carpathian Mountains a series of permanent vegetation plots were established within the vicinity of ozone monitoring stations for use in comparing composition and phytosociological records where it was determined that crown damage corresponded to ambient ozone levels (Grodzińska, Godzik, Fraczek, Badea, Oszlányi, Postelnicu, & Shparyk, 2004a). A study examining the potential for the detection of nuclear pollution (^{137}Cs) in moss and bilberry leaf samples determined that nuclear pollution had reached the two valleys in Poland where measurements were conducted, with the transfer of elements from soil to plants dependent on soil properties (Kubica et al., 2004).

Natural history: herbivore-plant interactions

Studies of large mammal herbivores and interactions with native vegetation appear to be under-represented in the literature, especially considering the presence of native chamois, deer, and moose. Low densities of natural predators have been maintained in the TNPs however, perhaps mitigating some of the concerns observed in ROMO. Sheep grazing has been a historic use of land within the Poland Tatra National Park; however results from a sheep enclosure study between 1965 and 1994 showed transitions into potentially natural conditions (Witkowska-Zuk & Ciurzycki, 2000). Secondary succession proceeded differently depending upon underlying bedrock, ranging from tall-grass vegetation to the introduction of Dwarf pine and meadow communities (Witkowska-Zuk & Ciurzycki, 2000).

A cultural concern for tree health related to forestry in Poland has prompted a number of studies focused on the potential for insect damage for spruce and pine. One study highlighted a tritrophic interaction between insect damage on pine cones, predator insects and parasitoids in controlling the seed eating insects (Kozioł, 2000). Another study focused on the variation in insect diversity associated with the development of Norway spruce cones (Kozioł, 2010). Other insects researched that are dependent on spruce hosts include the *Cephalcia*, which have been found to be influenced by drought (Jachym, 2003). Finally research has been done on the bark beetle *Ips typographus* to examine migration patterns relative to host spruce trees, with no evidence for natural barriers preventing the spread of the spruce pest (Lakatos, 2003).

Natural history: animal and insect ecology

The TNPs are refugia for a variety of native fauna, although many species are in danger of local extinctions and are subject to active management. One such charismatic species is the brown bear, where multiple attempts to maintain a viable population in the Polish TNP have allowed the continuation of this animal (Buchalczyk, 1980; Curry-Lindahl, 1972). Existing bears, in addition to facing growing threats associated with land-use change, climate and potential disturbance from high densities of park visitors, have been identified with infections of *Mycobacterium avium* subsp. *paratuberculosis* (Kopečna et al., 2006). Infection from various parasites can have a drastic limitation on the longevity and success of individuals within the population, and high rates of parasitism have not been limited to brown bears within the TNPs. Other carnivore species in the Slovak TNP have been surveyed for a muscle parasite trichinellosis, with high rates of infection across families of predator types (Hurníková et al., 2007).

Chamois are another charismatic member of the fauna in TNP with a closely monitored population due to multiple potential sources of decline including climate, predator densities and disease. A study focusing on climate and predator control on population levels of chamois

determined that wolf and wild boar densities, as well as snow depth were key predictors of population size (Chovancová & Gomory, 2000). Another study highlighted the high infection rate of lung nematodes in a population of chamois in the Slovak TNP (Stefancikova, 1994), and while little causation was mentioned in this particular study it is possible to expect an impact on the population related to this infection.

Other members of the land dwelling fauna are generally overlooked in the published literature; however there is some information about those creatures that live in the air. Bird species distributions and densities relative to forest habitat type were measured for birds in the Polish TNP, in addition to the environmental factors influencing occurrence of middle and great spotted woodpeckers in deciduous forests (Glowacinski & Profus, 1993; Kosiński, 2006). Other members of the air-borne community- bats- have been monitored using high elevation caves both during hibernation as expected, but also during summer months in the Polish Tatra Mountains (Piksa, 2008).

Both bird and bat communities are related to the insects of the Tatras, which have also been studied in associated with potential timber sources and preventative forestry. As such, the beetle diversity and population dynamics have been studied in the Polish TNP along elevational gradients associated with Norway spruce bark (Tykarski, 2006). Spruce bark beetles, *Ips typographus* have been studied in the Tatra Mountains especially in regard to migration patterns and the spatial patterns of the beetle outbreak in infecting spruce trees (Lakatos, 2003; Jakuš et al., 2003). Other spruce dwelling insects have been a concern of Polish foresters, and the life history and interactions of *Cephalicia* have been documented (Jachym, 2003). Another particular pest of foresters due to the indiscriminate nature of this herbivore is the gypsy moth. A study examining the predation on egg masses for this moth attributed 38% of predation to invertebrate predators and 62% to vertebrata, while also concluding a trend of total predation as inversely density dependent (Turcani et al., 2003). Invertebrates have also been studied in the stream systems of the Polish West Tatra Mountains, where macroinvertebrates influence the decomposition of organic matter (Galas & Dumnicka, 2003).

Natural history: hydrology

For mountainous regions the majority of precipitation falls as snow, and while studies examining rain chemistry have not been published for the Tatra Mountains, there is information available regarding snow distribution and snowpack chemistry. A study examining the variation in snow cover across the Tatra Mountains found that there were different snow conditions between the northwestern and southeastern regions (Lapin et al., 2007). Review of the potential for long-range transport of atmospheric pollutants in snow found that persistent organic pollutants were present at all altitudes, for all compounds examined, highlighting the connectivity between wilderness areas and human development (Arellano et al., 2011). Other measurements of hydrology in the Tatra Mountains have focused on stream, pond and lake chemistry, particularly in relation to the deposition of nitrogen and other forms of industrial pollution that has historically altered the functioning of these systems. Seasonal changes in sources of water including spring runoff from snowpack and stream surface water chemistry remain unpublished; however some work has examined the capacity for streams to accommodate potentially strong flushes of spring runoff with high levels of nitrogen or acidic compounds. Research has shown that in alpine streams lower levels of discharge promote increased rates of ammonium uptake by streambed biota (Kopáček & Blažžka, 1994). This suggests that the high flow and high discharge rates associated with spring melt enable deposited compounds to move

further downstream before assimilation than compounds associated with precipitation events during later in the growing season.

High elevation streams frequently feed into alpine ponds and lakes, thereby transferring and potentially amplifying the effects of deposition as unassimilated compounds accumulate in the surface waters. Lake chemistry is naturally influenced by soil sorption characteristics and bedrock type, and one study targeted a comparison between catchments and the levels of terrestrial phosphorus export, finding that soil concentrations of aluminum and iron were related to phosphorus sorption maxima (Kaňa & Kopáček, 2006). Other factors such as deposition and snowmelt runoff can create seasonal variation of lake chemistry and some studies have highlighted the potential for this variation, especially related to the release of solutes from the snowpack with spring thaw, which can influence both the nutrient status of lakes and also the pH (Kopáček & Stuchlík, 1994; Kopáček et al., 2000; Kopáček et al., 1996).

The relationship between nitrogen and phosphorus in alpine lake waters is traditionally nitrogen limited for productivity, although atmospheric input may alter this relationship and alter the trophic status of the lake (Kopáček et al., 1995). There is a potential for lakes to become nitrogen saturated and instead face phosphorus limitation, a feature reported in the Rocky Mountains of Colorado. Despite this, the retention of nitrogen was shown to increase in two high elevation catchments in the Polish Tatra Mountains, even with continued deposition of nitrogen and no addition of a source for phosphorus (Rzychoń & Worsztynowicz, 2008). These findings were attributed to a decreasing acidification from sulfur derived compounds and global warming- both of which contribute to prolonging the vegetative growing period, alter photosynthetic species composition and stimulate microbial activity in the soil (Rzychoń & Worsztynowicz, 2008). Nitrate leaching from these lakes, however, appears to be limited by percent land cover with meadow and increased soil depth, while steeper grades of terrain, higher levels of annual precipitation and elevation increase the amount of nitrate leaching (Kopáček et al., 2005).

Changes in the chemical composition of high elevation lakes can have cascading effects on the organisms living within, particularly those with narrow ranges of environmental tolerance. Several studies have sought to examine the implications for high levels of acidity on lake dwelling organisms, and how changes may be associated with different environmental conditions. A comparison of phytoplankton across three lakes in the Tatra Mountains with differing levels of acidification found that the highest biomass was found in a small, shallow, phosphorus-rich and acidified lake, while the lowest biomass was found in a lake very poor in phosphorus and was midway between being acidified and neutral (Fott et al., 1999). Aside from the dry mass of phytoplankton associated with acidity levels, levels of phosphorus and chlorophyll A may be associated with pH level. Research by Vyhnálek et al. (1994) found that concentrations of total phosphorus and chlorophyll A were similar to those developed for lakes in other regions, with the exception of lakes with low pH levels where chlorophyll levels were much lower than expected. Smaller bodies of water face similar issues with chemical to biological changes associated with deposition levels, and vernal pools and ponds fed directly via snowmelt showed seasonal variation in pH levels (Kownacki et al., 2006). Even with fairly substantial changes in pH, the composition of the macro-invertebrate communities appeared unaffected by the water acidification occurring in association with snowmelt (Kownacki et al., 2006).

Natural history: pollution

Background historic levels of airborne pollution, and the influence this has had on different ecosystems, has been a main point of concern for research in the Tatra Mountains. One type of pollution of concern for the Tatra Mountains includes the accumulation of tropospheric ozone. In response a network of monitoring stations were established to passively sample ozone throughout the year, finding that there was high spatial variation across the mountain region with some areas identified as hotspots exceeding recommended levels for protecting native forests and vegetation (Bytnerowicz et al., 2004). Many studies have focused on the influence of pollution on water quality, and the evidence for pollution in lake sediments- even in remote high elevation regions where the only source of pollution is long distance airborne particles. One such study found a historical record of the deposition of hydrocarbons dated using radiocarbon from the 1830s reconstruction period to present (Fernández et al., 2000). Another used the snow pack rather than lake sediments, but found persistent organic pollutants across all altitudes for all hydrocarbons tested including aromatic hydrocarbons, organohalogens and PCBs such that concentration increased with elevation in the Tatra Mountains of Slovakia (Arellano et al., 2011).

Long term accumulation of industrial pollutants prompted studies focusing on the potentially accumulated effect, particularly associated with nitrogen and sulfur into mountain forest and alpine lake ecosystems. Results from a study calculating fluxes and budgets for sulfur and nitrogen determined that sulfur outputs from ecosystems were lower than inputs thereby suggesting continued accumulation, while nitrogen outputs were relative to inputs with evidence for some accumulation of N in the soils in areas with high deposition (Kopáček et al., 2001). Prolonged deposition affects the chemistry and accumulation in soils, and a great deal of attention has been placed on changes in acidity of lakes associated with deposition in the Tatra Mountains. Levels of acidification and the impact it has had on lake ecosystem processes was examined in one study using changes in zooplankton communities to separate lakes into three groups where higher, colder lakes exhibited greater changes in acidity (Fott et al., 1994). Studies examining the effect of watershed type and seasonal timing of deposition on concentrations of nitrogen determined that nitrate was the highest contributor to total N in lakes above treeline, while organic N was most common in forest lakes (Kopáček et al., 1995, 1996).

Recent advances in environmental protection, pollution control and laws dictating levels of acceptable air quality have altered the ambient levels of deposition across the Tatra Mountains. As such it has been proposed that a number of ecosystems may begin to recover and return to more pristine processes. Numerous studies documented ecosystem responses to the changing ambient environment as, for example, a Polish study found that changes in precipitation chemistry included a reduction in sulfate and hydrogen ions while there was no change in nitrate, ammonium or total N deposition (Rzychoń & Worsztynowicz, 2008). A study examining trends more broadly across Central Europe concluded that policy controlled reductions in nitrogen and sulfur emissions decreased the deposition of sulfate, nitrate and ammonium by 30-40%, thereby allowing a reduction in lake concentrations of sulfate and nitrate with a slowing of cation leaching and an increase in pH (Kopáček et al., 1998). Later studies confirmed a reduction in sulfate, nitrate and ammonium ions in lake water, despite an initial biological lag in response and recovery (Kopáček et al., 2002). With such evidence in favor of eventual recovery from historic levels of pollution deposition results were modeled for future emission projections from Slovakia and Poland to determine how formerly degraded lakes would respond with time (Kopáček et al., 2003). Later measurements by the same author in the Tatra Mountains found evidence of predicted recovery 15 years after onset of the reduction in

emission, with recovery specific to the acid neutralizing capacity (Kopáček et al., 2006). Recovery on this time scale is certainly heartening for land managers and the stability of the mountain ecosystems, however long term confirmation is necessary particularly given possible interactions with climate change.

Natural history: soil

Spatial and temporal variation in soil characteristics across the Tatra Mountains have historically been linked to the transfer of nutrients and compounds between soils and water bodies, particularly with lakes. The importance of soil characteristics on influencing water chemistry, particularly in response to acidification or addition of nitrogen or phosphorus, was examined through comparison of catchments with differing surrounding soils. Research in two Bohemian Forest lakes found that soils with a higher phosphate sorption capacity were predominantly associated with higher pools of iron oxides (Kaňa & Kopáček, 2006). A general review of the physical, chemical and biochemical composition of soils in the alpine of the Tatra Mountains found that alpine meadows showed considerable variation in amount of soil, while moraines averaged much lower (Kopáček et al., 2006). Chemical components varied between meadows and moraines as well, with lower pools of carbon, nitrogen, phosphorus and sulfur in moraines than in meadows (Kopáček, Kaňa, et al., 2006).

Natural history: physical processes- climate and geology

Measurements associated with physical processes in the Tatra Mountains have ranged from recording cosmic rays (Kudela & Langer, 2009) to tracking permafrost and landslides, evidence of a rich history of ongoing research through the last century. A summary of the general climate in the Tatra Mountains determined that this mountain range includes the greatest range of climatic conditions in Central Europe, with distinct elevational zones and corresponding vegetation community types (Niedzwiedz, 1992). This wide variation in conditions allows the potential for the continuation of mountain permafrost, where elevations above 1990 m with a thermocline of -1 °C in Poland support the existence of discontinuous permafrost with a total area of 100 km² (Dobinski, 1998). Measurements of mountain permafrost in Poland were continued into the late 1990s, where permanently frozen ground was found sporadically in regions above 1900 m on north facing slopes in the High Tatra Mountains, however this permafrost was near a 0 °C isotherm and therefore possibly degrading (Moscicki & Kedzia, 2001).

Ice, snow and frozen ground together also have the capacity to physically alter the landscape in the mountains, by instigating changes in geomorphic events. A study on the natural environment and landform dynamics of the Tatra Mountains determined that the Tatra Mountains had extended above the Pleistocene snowline, which today include areas of alpine meadow (Kotarba, 1992a). Present day slope-rock dynamics above treeline and within the fluvial systems in the valley bottoms are not linked under normal conditions, limiting sediment transfer and physical alterations to local formations and weathering except in the case of extreme events (Kotarba, 1992a). Extreme events that can link these systems were reconstructed using geomorphological mapping over the last 200 years and it was determined that high-energy events were more frequent during the Little Ice Age related to climatic factors and an increase in earthquake occurrence (Kotarba, 1992b).

Conservation: vegetation cover and change through time

The conservation and maintenance of forest for economic means has precluded much research and emphasis within the Slovakian TNP. A massive, and uncommon, windthrow event in 2004 offered an opportunity for examining long term effects of clearing vs. unclearing of fallen trees and how this would affect eventual forest dynamics. Conclusions were striking, and concluded that while the highest recruitment of tree seedlings was in undisturbed forest, the uncleared windthrow areas maintained a high enough seedling density for natural regeneration of the forest, while the cleared areas would require a future management plan to restore the area to natural conditions (Jonášová et al., 2010). This study found that cleared areas were immediately colonized by grasses and other dense vegetation preventing growth of birch and willow, and thereby preventing open soil suitable for future seedling establishment, in direct contrast to uncleared areas (Jonášová, Vávrová, & Cudlin, 2010a). Related work in Poland focused on the uses for dead wood in the larger ecosystem processes and determined that trees left in the understory to decompose, after death or a windthrow, acted as substrate for germination of other vegetation with middle stages of decomposed wood the best suited to herb colonization (Zielonka & Niklasson, 2001; Zielonka & Piątek, 2004). Generally these studies urged the conservation of dead wood within the ecosystem as a means of facilitating continued existence of the natural forest.

Conservation: herbivore-plant interactions

Seeding germination and colonization is limited first by the number of viable seeds able to establish, making seed predators an important concern for forestry conservation. As such research has been conducted focusing on the tri-trophic interactions of seed herbivore insects on Norway spruce, and the influence of a natural parasitoid in limiting population densities (and therefore reducing cone damage) (Kozioł, 2000). In this instance a natural cycle limiting population explosion acts as a means of conserving the dynamics of forest continuation.

Conservation: animal and insect ecology

The conservation of Carpathian fauna has focused on protected and endangered species and habitat types supporting those animals. One study highlighted the connections between land preserved and protected and the distribution of protected mammals across Poland, showing that areas with endangered and protected mammals are associated with habitats of larger forest complexes, higher floristic diversity and valleys (Grabinska, 2007). Of these protected mammals the brown bear was reported in densities as high as 230 in association with the land area of the Tatra National Parks of Poland and Slovakia during the 1970s (Curry-Lindahl, 1972). The protection of other charismatic mammals has focused on understanding Tatra chamois population dynamics associated with predators, climate and disease (Chovancová & Gomory, 2000; Stefancikova, 1994).

Conservation: effect of land-use changes and/or changes in pulse disturbances

Land-use change of surrounding communities and forests appears to be the largest threat to the long-standing boundaries of the Tatra National Parks in terms of immediate effects. Consequently there has been work examining the effects and future of nature conservation in the Carpathian Range in the face of political and ethnic boundaries (Oszlányi et al., 2004). Linkages between the surrounding areas both in terms of land connectivity and distribution of protected areas for mammals, but also the connections between water sources and uses within and beyond

the parks (Grabinska, 2007; Pringle, 2001). These studies show important steps toward advocating for comprehensive plans addressing nationwide conservation.

Management: vegetation cover and change through time

Eastern European protected areas have been exposed to chronic ambient levels of pollutant deposition for decades, and the ramifications of this exposure for forests and ecosystem processes are significant. As a result, a number of studies have looked at quantifying concentrations of heavy metals and other industrial pollutants in nature as preliminary work supporting management decisions. Mercury concentrations and the influence of industrial pollution on elemental concentrations in needles and leaves has shown evidence for pollutant assimilation in forest systems (Mankovska, 1998; Mankovska, 1996).

Other forestry projects designed to enlighten management practices include understanding the effect of wind disturbance on tree species composition during succession and the role of dead wood in forest continuation (Jonášová, Vávrová, & Cudlin, 2010a; Zielonka & Malcher, 2009; Zielonka & Niklasson, 2001). While windthrow appears to be fairly uncommon in the Carpathian Range, studies have examined the historic impact this may have on growth patterns for native tree species, showing that spruce appear unaffected in the long term by windthrow, while larch were recruited only after a major disturbance (Zielonka & Malcher, 2009). After a major disturbance however there is the management concern of recovering lost lumber. The results of a Slovak study examining the consequences of clearing fallen trees shows that despite the possible short term benefit, salvage areas cleared of downed trees lack the natural density of seedlings for regeneration of previously existing tree species (Jonášová, Vávrová, & Cudlin, 2010a). These findings agree with a Polish study reporting the importance of dead wood for the regeneration of seedlings and understory species by providing an ideal substrate for germination (Zielonka & Niklasson, 2001).

Concern over the integration of social-cultural, economic, and ecological aspects associated with protected areas has prompted an evaluation of management practices in Slovak national parks (Svajda, 2011). Results found that while there was a long standing history of management, there is evidence that some fields of activity are creating potential future concerns, particularly related to biodiversity from a planning phase for solution to current problems (Svajda, 2011).

Management: herbivore-plant interactions

Management decisions to act in response to a disturbance can have both economic ramifications and ecological ones, and consequently different Parks faced with similar concerns may respond in drastically different measures. One such disturbance was an outbreak of the bark beetle (*Ips typographus*) during 1993-1998 in the Tatra Mountains, in national park lands in both Poland and Slovakia (Grodzki et al., 2006). Slovakia responded with active pest management, including trap trees, insecticides, salvage cutting, and pheromone traps, while Poland did not initiate a management plan. Despite these drastically different approaches, and therefore different amounts of money invested in the program, tree mortality was not significantly reduced in the Slovak regions and the outbreak ended naturally with unfavorable weather conditions (Grodzki et al., 2006). Results from this comparison study may be of immediate application for management plans in the United States, where bark beetle continues to expand across the Rocky Mountains.

Management: animal and insect ecology

Some attention has been spent on the distribution of protected animals relative to areas of protected land throughout Poland. Protected land in the southern and mountainous areas of Poland were found to have the highest number of mammal species present, including area in a number of National Parks suggesting that these parks are operating for managing biodiversity in Poland (Grabinska, 2007). A particular mammal of concern has been the brown bear, with changing population numbers associated with land-use change and active management of population introductions in areas with no viable population (Buchalczyk, 1980; Curry-Lindahl, 1972). The chamois is another well liked mammal of the Carpathian Range that has been considered protected associated with threats from poaching and land-use change. Understanding of population dynamics of the chamois is a particularly important management concern for continued survival of the species, and current concerns include climate change with snow depth and changes in predator numbers (Chovancová & Gomory, 2000). Both the chamois and brown bear have been documented with bacterial and or nematode infection, and while these factors may not play a current role in managing for either species it may become relevant for the future (Kopečna et al., 2006; Stefancikova, 1994).

Other potential targets of management concern include threats to either forestry or fishing, both of which are important as historic uses of the national parks in Poland and Slovakia. A key finding regarding concentrations of PCBs and PCBEs in fish across lakes in high elevation areas across Europe identified a negative relationship between temperature and tissue concentrations (Gallego et al., 2007). These results suggest that the lakes in the Tatras associated with high levels of industrial deposition are more likely to contain fish with toxic concentrations in tissues in cold high elevation areas (Gallego et al., 2007). Forestry related management issues include distribution and occurrence of spotted woodpeckers in Poland, which were determined to avoid young forest stands while preferring old oak-dominated forests (Kosiński, 2006). Conservation efforts related to this species may therefore limit forestry plans; however it is the bark beetle that has caused the most damage and limitations to forests across the Tatra Mountains. Attempts to protect existing forests using pheromone traps were instigated in the Slovak High Tatra Mountains with limited long term success, while mapping of site and stand infestation did remotely estimate levels of outbreak (Jakuš, 1998a; Netherer & Noppmayr, 2005).

Management: effect of land-use changes and/or changes of pulse disturbance

The continued functioning of any of the Tatra National Parks depends both on the management practices and responses to change within the park, and changes in the surrounding forests, communities and even within the country as a whole. National studies evaluating the success of protected areas, particularly in regard to spatial distributions of biodiversity, have been conducted in Slovakia and Poland (Grabinska, 2007; Svajda, 2011). Generally these studies have found that the park system and areas of protected land have acted as refugia for native species, but that more work can and should be done to maintain these areas in perpetuity. One study in particular highlighted the need to encourage ecological stability in the forests of the Tatra Mountains by allowing the persistence of native stand structures before and after new disturbances, acknowledging that existing stands are often superficial and represent historic modifications to nature (Voloscuk, 1998). Another serious concern is the connectivity of waterways with biological reserves, and how these may act as point sources for pollution in otherwise protected areas (Pringle, 2001).

Examples of the impact of management actions within a park, especially relating to decisions regarding forestry and how forests create habitat for desired native species include protection efforts for the middle and great spotted owl (Kosiński, 2006). At the same time there are difficulties with source populations for forestry pests such as the bark beetle (Grodzki et al., 2006). Natural disturbances, both biotic and abiotic in nature, are a common potential change in land cover within the parks that can have lasting effects on park resources depending upon human actions taken (Jonášová et al., 2010b).

Another type of management decision that can have long lasting influence on future land changes in and around the parks relates to visitor use and monitoring through the park area, particularly trail use. Tatra National Park in Slovakia has initiated a visitor monitoring program with the goal of being able to better serve users of the hiking trail system, in addition to giving an estimate of trail usage, which may be related to invasive species introductions or wildlife avoidance (Švajda, 2009).

Diversity: vegetation cover and change through time

Due to the long history of research conducted in the Tatra Mountains multiple floras and guides to vegetation have been created, available even in English, with updates from the 1990s (Mirek & Piekos-Mirkowa, 1992). New species have been described locally, highlighting the importance of the continued protection of refugia land area for native species (Bayerová et al., 2005). Additionally, classification studies examining plant communities through the Tatra Mountains have highlighted spatial distributions of vegetation types from tall-grass to high-mountain meadows (Zagajewski, 2010; Šeffler et al., 1989). Other work has examined plant functional traits, such as the biomass distribution within the herb and moss layer of forest ecosystems and colonization of mycorrhizae along elevational gradients (Kupicek, 2001; Zubek et al., 2009).

Diversity: herbivore-plant interactions

Associated with concerns about forestry practices, diversity studies examining relationships between herbivores and plants have focused on tree and cone insect herbivores. Specifically the cono- and semiphagous insects of the Norway spruce have been described in addition to their parasitoids (Kozioł, 2000). Another study highlighted the variability in cone entomofauna of the Norway spruce, particularly related to the development of the cone (Kozioł, 2010). These and other studies emphasize the multiple linkages between biodiversity and ecosystem function, whether through negative feedbacks associated with parasitoids or the potential for outbreak when controls are absent.

Diversity: animal and insect ecology

Studies examining the community members that move within the Tatra Mountains have highlighted the diversity of creatures from birds to lice, most within the framework of how each species relates to the available forest. One study conducted a survey of the vertical distribution of breeding birds within the Polish Tatra National Park, specifying birds that preferred different types of forest habitat (Głowacki & Profus, 1993). Other studies have focused on the insects of the mountains, with a description of the jumping plant lice (Drohojowska & Głowacka, 2011), and elevational gradients of scolytid beetles in Poland associated with dead bark of the Norway spruce (Tykarski, 2006). A complete entomofauna of the cones of Polish fir and of Norway

spruce included well over 4,600 individual insects from 15 species (Kozioł, 2010; Skrzpczynska, 1988).

Diversity: pollution

The Tatra Mountains have been exposed to historic chronic high levels of ambient nitrogen deposition, associated with coal industry and city development in the 19th and 20th centuries. As a consequence many lakes and ponds in the higher elevations face severe acidification that then acts to alter the species composition of the hydrofauna. Results from a study comparing lake chemistry in the West Tatra relative to the High Tatra in Slovakia found that there was a less pronounced effect of deposition in the West Tatra (Vranovský, 1994). Even so, there was evidence for anthropenically altered chemistry of lakes in both regions producing changes in species composition (Vranovský et al., 1994). The influence of pollution deposition on diversity of plants or animals is less studied within the Tatra Mountains than in ROMO, and could provide support for policy changes at the larger scale.

Response to disturbance: vegetation cover and change through time

The effect of climate on changes in vegetation cover has been touched upon in a range of studies and systems across the Tatra Mountains. A growth response study using tree-rings in multiple tree species in Poland and Slovakia used multivariate statistics to examine factors controlling growth, determining that growing season temperature was the predominant influence in increasing ring size (Büntgen et al., 2007). A similar study targeted the growth of Norway spruce along elevational gradients in Poland, finding that the temperatures in March, April, June and July were important in predicting radial tree growth, although the influence varied with elevation (Savva et al., 2006). This same study found that fall mean temperatures, particularly October, positively increased tree radial size in all elevations suggesting that climate changes expanding the growing season are of particular interest for forestry (Savva et al., 2006). In a different system, lake sediments have been used throughout the Slovak High Tatras to examine changes in pollen and macroscopic remnants associated with sediment accumulation in the Holocene, specifically related to changes in treeline (Rybníčková & Rybníček, 2006). While this study contained only two lakes under differing formation origin (glacial/ non glacial) there was no evidence for changes in the treeline from an elevation between 1000-1400 m during the Holocene (Rybníčková & Rybníček, 2006).

In addition to climate, there are a number of studies examining the impact of physical disturbances on vegetation cover in the Tatras on a number of different time scales. One study used lichen growth on debris flows as a means of determining formation rates within the Polish High Tatra Mountains, using vegetation presence as the measurement of impact rather than the other way around (Jonasson et al., 1991). At the other end of the time scale instantaneous events can have lasting effects on vegetation structure, and a large windthrow disturbance in 2004 in Slovakia allowed an examination of these changes and the human management response to it. Areas disturbed by the windthrow reported lower values of regeneration and seedling density for original tree species than surrounding unaffected forest areas, however the levels were hypothesized to be sufficient for a continuation of tree species in native levels of composition (Jonášová et al., 2010a). Alternatively, in areas where downed trees were cleared after the windthrow event the density of seedlings and rate of regeneration were too low for natural re-growth of native tree composition, and would require active management to return the forest to pre-existing conditions (Jonášová et al., 2010a). Measurements of longer term regeneration after

wind disturbance in the Tatra Mountains based upon dendrochronology determined that spruce trees continued to regenerate throughout succession, while larch were only recruited immediately following the disturbance (Zielonka & Malcher, 2009). Changes in recruitment between tree species following succession suggest a potential for changes in species composition. Changes in composition on longer time scales are important to understand for maintaining viable forests maintained for forestry.

A final physical disturbance associated with vegetation change through time in the Tatra Mountains is the effect of grazing on species composition. While we could find no papers associated with wildlife herbivory, domestic animals particularly sheep have a long history within National Park boundaries. Sheep exclosures were implemented in the mid 1960s and maintained through the 1990s in the Polish TNP, allowing secondary succession in a number of ecosystem types that resulted in a return to tall-grass vegetation in some areas, recovery of meadow systems and in subalpine plots the growth of dwarf pine (Witkowska-Zuk & Cieurzycki, 2000). Exclosures of herbivores in ROMO offer potential comparisons between nations, and current work has been instigated to examine vegetation recovery following historic domestic grazing both in Poland and Colorado.

Air pollution has become a silent but deadly source of disturbance for mountain vegetation across Eastern Europe. Of particular concern are rising concentrations of tropospheric ozone, associated with industrial pollution and automobile exhaust, which follow air currents upward into remote mountain ranges and there damage existing vegetation. An overview of the effect of ozone on *Pinus cembra* across mountain sites in Europe determined that ambient levels of ozone caused visible damage for trees growing in the Carpathian Range (Wieser et al., 2006). Concern for levels of ozone has resulted in a measurement network across the Tatras using both continuous and passive samplers to determine differences between geographic locations and between years (Godzik & Fleischer, 2006). Vegetation surveys conducted adjacent to ozone monitoring stations found that visible damage was evident in both the tree layer and in herbaceous plants, suggesting an impact of concern for forestry but also on cascading foodwebs for wildlife associated with the herb layer (Godzik & Fleischer, 2006). Additional work associated with this network was able to directly link concentrations of ozone measured at a station with levels of crown damage in the canopy (Grodzińska et al., 2004b).

Other deposited air pollutants are problematic for vegetation, particularly vegetation in mountain regions. A transect survey of moss and bilberry in the TNP of Poland found evidence of nuclear pollution (^{137}Cs) in the plant tissues, with exact transfer of elements between soil and plants dependent on the soil type, amount of soil organic matter and soil pH (B. Kubica et al., 2004). Another study examined changes in mercury concentration in needles of forest trees across the mountains of Slovakia, finding that while mountain needles contained lower concentrations than needles found near iron ore mines they were comparable to concentrations found in industrial zones and higher than concentrations on military lands (Mankovská, 1996). Less toxic pollutants have had equal impacts on vegetation disturbance however, including deposition of sulfur (SO_4) and nitrogen (NO_3) that have altered soil pH. One study determined that the interactive effect of air pollution, extreme weather, and biotic agents (the two latter associated with climate) have degraded forest conditions in the Tatra Mountains since the 1990s such that sulfate, nitrate and pH levels are above established critical loads for forests, while ozone levels exceed index levels during large portions of the growing season (Fleischer et al., 2005). Examples of the effects of surpassing critical load limits of pollution on vegetation include changes in the chemical composition of foliage, where one study found these chemical

compositions could be used as an indicator for industrial pollution in Slovakia (Mankovská, 1998). Another study highlighted whole ecosystem changes in the alpine zone associated with air pollutions, including changes in soil chemistry and shifts in the location of plant communities in the Tatra National Park of Slovakia (Rusek, 1993). Specific results found by this study included plant community dependent variation in changes of pH, and that all changes were more extensive in alpine grasslands on limestone than on granite (Rusek, 1993).

Response to disturbance: herbivore-plant interactions

Across the Tatra National Parks, studies examining herbivore induced disturbance associated with vegetation have mainly on the effect of the bark beetle (which does not eat the needles and instead bores into the bark of host trees), and the change in vegetation associated with domestic animal grazing (Grodzki et al., 2003; Witkowska-Zuk & Ciurzycki, 2000). Both of these concerns are relevant to similar interaction at ROMO, and joint ventures focusing on these similarities could provide increased knowledge for land managers.

Response to disturbance: animal and insect ecology

Three main types of disturbance have been targeted in studies examining the influence on animals and insects in the Tatra Mountains, included physical disturbance, chemical disturbance associated with pollution, and biotic disturbance that may be argued as a natural cycle periodically wreaking havoc on the ecosystem. The effect of physical disturbance on soil nematodes was examined after windfall, log extraction, and fire in the High Tatra Mountains of Slovakia where areas of removed logs harbored the highest nematode species richness and areas of fire contained the greatest nematode abundance (Čerevková & Renčo, 2009). Chemical disturbance was associated with a contamination of water bodies by aerially deposited PCBs that negatively impacted the toxicity of lake fish such that colder lake temperatures were associated with higher concentrations of contaminants in fish tissues (Gallego et al., 2007).

Studies on biotic disturbance in the Tatras that are associated with animal or insect ecology have focused on the main disturbance vector itself- the bark beetle. One study highlighted differences in management strategies associated with a severe bark beetle outbreak and how to prevent massive damage to forests, finding that despite investments in active removal there was no difference in severity as compared to areas with no management plan in place (Grodzki et al., 2006). Prior to that study others had focused on developing barriers for bark beetles such as pheromone traps and using satellite imagery to predict and follow the infestation across the High Tatra Mountains (Jakuš, 1998b; Netherer & Noppmayr, 2005).

Response to disturbance: hydrology

The main disturbance for water throughout the Tatra Mountain Range has been chemical in origin, from industrial pollution and air-borne deposition from sources far away from the lakes, ponds and streams affected. Due to the importance of snow for mountain watershed hydrology it is no surprise that the chemical composition of the snowpack can have cascading effects for water bodies down slope, highlighting the impact to alpine and subalpine ecosystems from pollution. A study examining the chemical composition of the snowpack of the Slovakian Tatra Mountains found long-range atmospheric pollutants, including persistent organic compounds (poly cyclic hydrocarbons, PCBs, and organohalogens) increasing in concentration with altitude (Arellano et al., 2011). After melting out of the snowpack with spring thaw, these chemical compounds are transported lower in elevation through streams, where some amount of

assimilation and uptake specifically targets biologically reactive compounds such as nitrate and ammonium. A study focusing on the uptake of ammonium in alpine streams of the High Tatra Mountains in Slovakia found that the length of the river required to assimilate ammonium decreased with decreasing stream flow (Kopáček & Blažžka, 1994). Additionally the amount of ammonium released through nitrification was associated with the acidification level of the stream, accounting for 50% of the added nitrogen in non-acidified streams (Kopáček & Blažžka, 1994).

Some amount of nitrogen from pollution deposition makes its way to lakes and ponds in the alpine and subalpine environments, and there can have cascading effects on the processes within the water column and sediments. Many studies have examined the influence of seasonal inputs associated with spring melt and how this may alter water chemistry and nutrient status, finding that concentrations of ammonium decreased while nitrate increased in lakes of the High Tatra Mountains of Slovakia between July and October (Kopáček & Stuchlík, 1994; Kopáček et al., 1996). Another factor influencing the chemical composition and nutrient status of these high elevation lakes is the altitude in which they are found, as nitrate has been measured as the highest contributor to total nitrogen in lakes above the treeline, while organic nitrogen is most common in forest lakes (Kopáček et al., 1996). Local environmental conditions can influence composition of nutrients also, with differences in watershed cover linked to variation in ratios of total nitrogen to total phosphorus such that lakes with rocky watersheds had higher total N: total P values (Kopáček et al., 1995, 1996). A study targeting the variability in nitrate leaching from alpine catchments determined that leaching was negatively influenced by increased land cover by meadows, as well as soil depth and was enhanced by sleeper slopes, annual precipitation and elevation (Kopáček et al., 2005).

The effects of increased inputs for nitrogen, sulfur, and other pollutants can be long lasting and alter physical, chemical and biological processes within the lakes or ponds. Many studies have highlighted the consequences of deposition by using changes in native flora and fauna to approximate the amount of input. One study in the Slovakian High Tatra Mountains used changes in zooplankton communities to group high elevation lakes by historic levels of acidification (Fott et al., 1994). Another examined seasonal changes in benthic communities associated with precipitation and snowmelt and how these may be controlled by changes in pH (Kownacki et al., 2006). The impact of historic acidification associated with deposition has been highlighted in a number of studies examining changes in benthic communities and on hydrofauna, in many cases observing complete change in community type or loss of native species in lakes of the Slovakian West Tatra Mountains (Sacherová et al., 2006; Vranovský et al., 1994). Acidification alters not only the types and abundance of organisms living within the lakes, but also can have an effect on the contributions of those organisms to the chemical composition of the lake itself. A study conducted in the High Tatra Mountains of Slovakia found that total phosphorus and chlorophyll A (a byproduct of photosynthesizing algae) varied between lakes dependent upon the level of pH in that lake (Vyhnálek et al., 1994).

An abrupt change in national and regional policy toward emission of pollutants, specifically targeting sulfur and nitrogen, in the 1980s has also provided researchers with a natural system in which to evaluate rates of recovery across the Tatra Mountains, and indeed throughout much of Central Europe. Initial studies suggested that the emissions reduction, on the order of 30-40%, prompted reduction in the concentration of sulfate and nitrate in mountain lakes across the Central European region (Kopáček et al., 1998, 2002). Future and past recovery associated with the decline in emissions was modeled to determine potential long lasting effects,

for Slovakia and Poland, showing an increase in concentration of strong acid anions and base cations, but a decrease in HCO_3^- that was predicted to re-establish in the 2000s and a recovery of soil pool exchangeable base cations was predicted after 2010 (Kopáček et al., 2003). An updated version of this model focused on the recovery of lake ion exchange capacity, and the authors determined that current levels of emissions were still high enough that full recovery was not possible by 2020 and therefore lake acidification will continue without further measures taken (Kopáček et al., 2004). Field measurements collected during the 15 years post onset of the reduction in acid deposition found that the acid neutralizing capacity has shown signs of recovery (Kopáček et al., 2006). Other field work localized to particular watersheds in the Tatra mountains of Poland have examined the impact of catchment and local processes on contributing to the recovery of lakes from acidification, and determined that the precipitation chemistry showed a reduction in sulfate and hydrogen ions, but no change in nitrate, ammonium or total N (Rzychoń & Worsztynowicz, 2008).

Response to disturbance: soil

Studies reporting disturbances that influence soil properties in the Tatra Mountains have been limited to those associated with physical (windthrow, fire) and chemical (pollution) disturbance, leaving room for future work examining interactions including the impact of herbivores, climate or other disturbances in general. A large windthrow event in the Slovak TNP allowed comparison of soil microbial characteristics associated with respiration, N mineralization, biomass and functional diversity between areas impacted by the windthrow and reference plots (Gömöryová et al., 2011). This study additionally was able to examine the impact of management strategies associated with removing fallen trees, finding that microbial biomass reflected the different management regimes in the disturbed areas (Gömöryová et al., 2011). Fire on a portion of the forest already affected by windthrow and differing management practices allowed a further examination of changes in the soil, where the highest microbial activity was associated with fire (Gömöryová et al., 2008).

Soil response to chemical disturbance, particularly associated with pollution and the deposition of nitrogen and sulfur, was examined in a manipulation experiment that found the alpine soils of the Slovakian TNP are so depleted in base cations that soil chemistry is equivalent to acid mine drainage soils (Bowman et al., 2008). This extreme change in soil chemistry resulted in not only depletion of elements required by plants (calcium and magnesium) but also aluminum, leaving iron cations to be released into the soil water (Bowman et al., 2008). A long-term study using records as far back as the 1970s found directional movement of plant communities in alpine ecotones associated with decreased area and transitions between ecosystem types in the High Tatra Mountains of Slovakia, driven by changes in industrial air pollution (Rusek, 1993).

Larger compounds associated with industrial pollution have also been monitored through the Tatra Mountains, with a measured persistence of organochlorine compounds in the sediments of high altitude lakes, frequently associated with cold water temperatures (Grimalt et al., 2004). There is also continued monitoring of atmospheric pyrolytic pollution with deposition of hydrocarbons into remote high altitude lakes, where the age of deposited compounds has been placed as far back as the 1830s and into the present (Fernández et al., 2000). Both of these studies contribute to the idea of global connectivity, and emphasize the impact of political and industrial decisions far beyond the borders of the national park.

Response to disturbance: physical processes- climate and geology

Many physical processes associated with geology may be considered as a disturbance, as they are infrequent, difficult to predict and can impart lasting changes to the environment around them. Geological processes associated with this kind of physical disturbance have been well studied throughout the Tatra Mountains, although climate related processes are less represented in the literature relative to ROMO. Debris flow of rocks, gravel, etc. can have a drastic disturbance effect in the surrounding environment. An initial survey was conducted in the 1980s to identify locations of rockfall as well as other types of talus slopes allowed later research on how and when such formations were created (Kotarba et al., 1984). Of these later studies many have used the growth of lichen on debris deposits to estimate the age, and therefore approximate frequency, of such debris flows in the High Tatra Mountains of Poland (Jonasson et al., 1991; Kotarba, 1992b). These records, also based upon geomorphological mapping, determined that historic debris flow activity was much higher during the Little Age than present, related to both climatic factors and higher earthquake occurrence during that time (Kotarba, 1992b, 1997). Modern disturbances associated with debris flows and rockfalls appear to be focused between the upper timberline (1500 m) and 1950 m, and are associated with higher than average rainfall events (Kotarba, 1992a, 1997).

Visitor-park interactions: effect of land-use changes and/or changes of pulse disturbances

The number of park visitations across the Tatra Mountains, and knowing where guests are spending time is of particular importance for providing necessary resources both to the guests themselves but also for preventing damage to the park in heavily used areas. A recent study in the Slovakian Tatra National Park aimed to improve visitor monitoring using counting devices on hiking trails to examine temporal trends associated with daily to weekly use between May and November (Švajda, 2009). These results will be used to determine impacts on the environment and to provide data for management decisions.

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