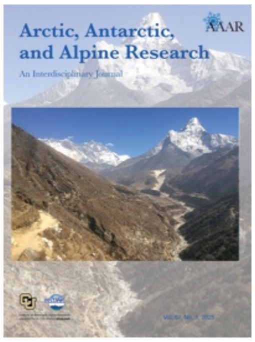

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Climate change impacts and adaptation in U.S. Rocky Mountain high-elevation ecosystems

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ABSTRACT

From a resource management perspective, climate change is considered to be one of the main threats to high-elevation ecosystems. However, these valuable ecosystems present unique challenges to climate change adaptation (actions in response to environmental change and its effects in a way that seeks to reduce harm) due to their rugged and remote characteristics. Within this context, we summarized literature on climate change impacts and adaptation actions across U.S. Rocky Mountain high-elevation ecosystems to address the important question: What are the knowledge gaps for climate change responses within this ecosystem that limit the ability of natural resource managers to perform successful climate change adaptation? In addressing this question, we focus specifically on the U.S. Rocky Mountains but also place regional conclusions for climate change adaptation in high-elevation ecosystems into a broader context. Overall, we found that the complex topography and temporally variable climate of mountains promote potential refugia that may buffer alpine obligate species in the near-term but also challenge resource managers to consider biological lags within this ecosystem.

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High-elevation ecosystems; climate change adaptation; management; climate change; microclimate

Introduction

High-elevation ecosystems—here defined as including the alpine vegetation, alpine lakes, glaciers, and the upper limit of trees (tree line)—are valuable both for the ecosystem services they provide and for the biodiversity they hold (Körner 2003). These landscapes provide ecosystem services including water resources for communities near and far (Immerzeel et al. 2020; Livneh and Badger 2020), ample recreation opportunities (Archie 2014), and habitat for a highly diverse and unique variety of flora and fauna (Antonelli et al. 2018). High-elevation ecosystems may be vulnerable to climate change due to higher rates of regional warming (Pepin et al. 2015), loss of snowpack (Musselman et al. 2021), lack of opportunities for upslope shifts at the highest elevations (Loik 2024), and general sensitivity of alpine species to climate (Körner 2003). However, these landscapes are also spatially heterogeneous, potentially allowing for resilience to climate change (Scherrer and Körner 2011). High-elevation ecosystems are characterized by complex topography, high spatial and temporal climate variability, and extreme climate events. Therefore, despite their relatively limited geographic coverage even in mountainous areas like the Rocky Mountain region of the United States (hereafter U.S. Rocky Mountains; Figure 1), these ecosystems may play an outsized role as an indicator of change or a refuge for species under a changing climate (Elsen, Monahan, and Merenlender 2020; Morelli et al. 2020).

Assessment of how high-elevation ecosystems overall may respond to changing climate and the role of management in shaping that process will facilitate a better understanding of what successful climate change adaptation may look like in this valuable ecosystem. Climate change adaptation is the process of adjusting to an actual or expected environmental change and its effects in a way that seeks to moderate harm or exploit beneficial opportunities (U.S. Global Change Research Program 2023). Effective and efficient climate change adaptation requires an understanding of (1) the regional climate

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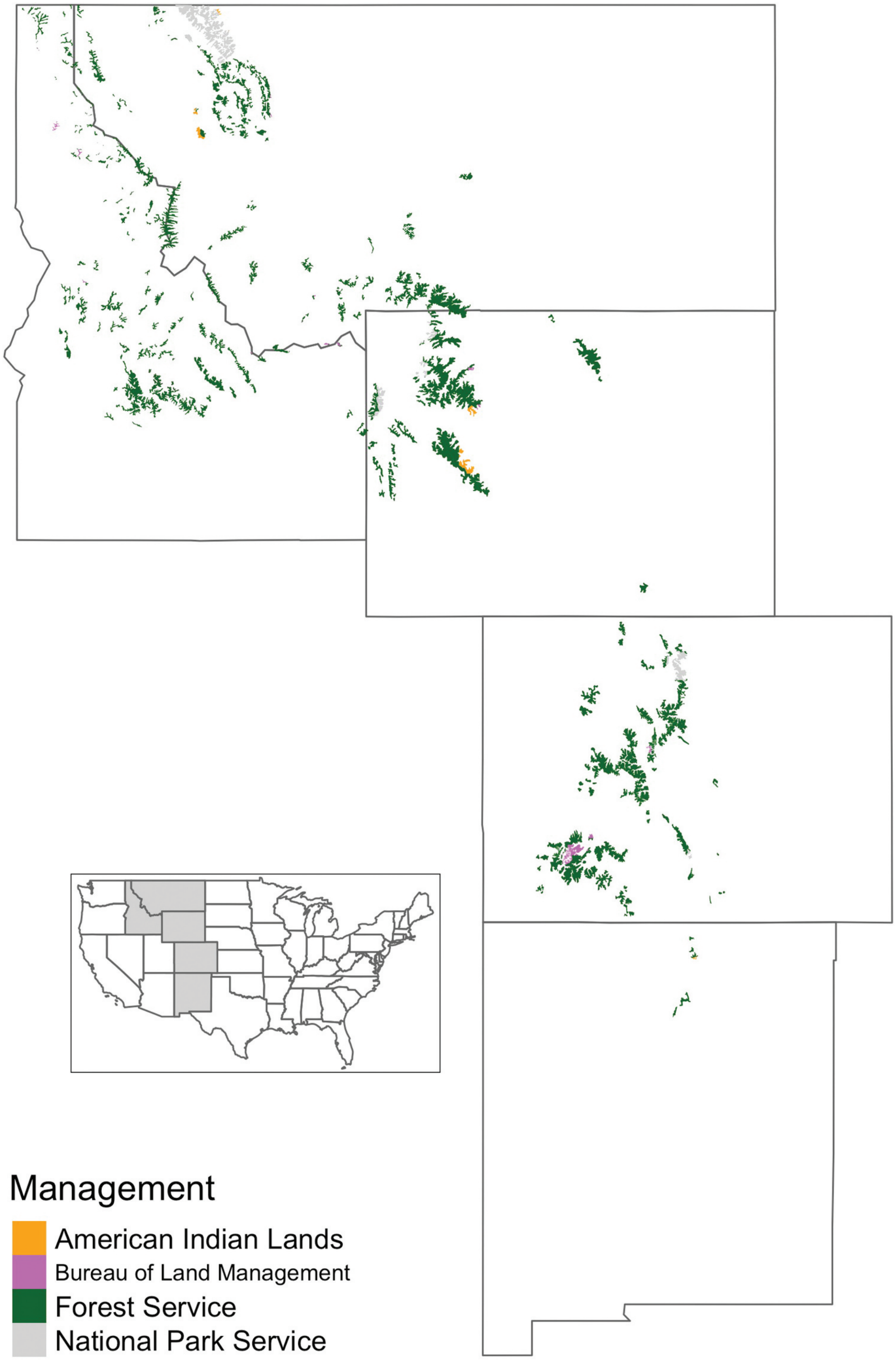

Figure 1. Map of areas considered high-elevation ecosystem in the U.S. Rocky Mountains. Colors indicate management agencies of these areas as determined by Protected Areas Database of the United States (U.S. Geological Survey Gap Analysis Project 2023). Alpine/tree line designation based on the following Ecoregion IV categories: Alpine Zone (21a) in Southern Rockies (NM, CO, WY), Alpine Zone (17h) in Central Rockies (WY, MT, ID), High Northern Rockies (15h) in Northern Rockies (MT, ID), Crestal Alpine-Subalpine Zone (41b) in Canadian Rockies, and High Idaho Batholith (16h) in the Idaho Batholith (MT, ID).

change trends and associated impacts, (2) the management levers that may mediate these impacts, and (3) the short- and long-term consequences of an action. High-elevation ecosystems present unique challenges for all three of these components of climate change adaptation; these systems are remote, making them harder to both measure and manage, and have topographic and biological characteristics that lead to spatially diverse and temporally lagged climate change impacts (Alexander et al. 2018; Graae et al. 2018). Within this context, we summarized literature on climate change impacts and adaptation actions in the alpine to address an important question: What are the knowledge gaps for climate change responses within this ecosystem that limit the ability of natural resource managers to perform successful climate change adaptation? For this work, we focus specifically on the U.S. Rocky Mountains (Figure 1) but also discuss how the patterns observed regionally may provide insight into the challenges and opportunities for climate change adaptation in high-elevation ecosystems systems more broadly.

Within the U.S. Rocky Mountains, most of the high-elevation ecosystems land is managed by the U.S. Forest Service (Figure 1). The National Park Service also manages some of these landscapes (e.g., Rocky Mountain National Park, Glacier National Park), as does the Bureau of Land Management in the Gunnison River Basin of southwestern Colorado. A small component of high-elevation landscapes in this region is managed by tribal entities, including on the Wind River Reservation and Blackfeet Indian Reservation (Figure 1). The various management entities for these landscapes often have different management objectives, as well as differing capacities to implement climate change adaptation actions. Further, many of these landscapes fall within wilderness designation. Although the Wilderness Act may be perceived to limit climate change adaptation, many types of passive actions (like protection of refugia or connectivity) and even more active action(s) (such as pest or invasive species management) may be permissible under the Wilderness Act (Long and Biber 2014). However, the Wilderness Act may be a strong deterrent for introductions of species outside their native range, which may complicate management of species shifting distributions as climate change reshapes habitat suitability (Long and Biber 2024).

From a management perspective, climate change (e.g., warming temperatures, decreased snowpack, and changing snow conditions) is considered the main threat to high-elevation ecosystems in the U.S. Rocky Mountains (Colorado State Wildlife Action Plan 2015; Wyoming State Wildlife Action Plan 2017; Idaho Department of Fish and Game 2024). High-elevation areas in this region may also be impacted by other stressors—including human disturbance through recreation and infrastructure (e.g., roads), grazing, and atmospheric nitrogen deposition—all of which likely will interact with direct climate change impacts (Colorado State Wildlife Action Plan 2015; Wyoming State Wildlife Action Plan 2017; Idaho Department of Fish and Game 2024). For example, climate change may greatly exacerbate the impacts of fire and invasive species on high-elevation environments relative to the limited impacts these types of disturbances had on these ecosystems historically (Alexander et al. 2016; Lembrechts et al. 2017; Higuera, Shuman, and Wolf 2021). Within this context, climate change adaptation actions to mitigate biodiversity and ecosystem services loss in high-elevation ecosystems that have been considered or implemented include preservation of species refugia and migratory pathways (Dobrowski and Parks 2016; Morelli et al. 2020), recreation management (Chardon et al. 2019), fish removal (Moser et al. 2019), seed preservation (Mondoni et al. 2011; Seglias 2022), restoration actions (Risberget, Hagen, and Aschehoug 2024), pest or invasive species management, and snow seeding (French et al. 2018). However, there has been very limited testing of the efficacy of climate adaptation actions even if considering actions across multiple ecosystem types (Hansen, Braddock, and Rudnick 2023), and the coauthors know of no efficacy tests of climate adaptation in high-elevation ecosystems in our focal region. To strengthen the link between threat and adaptation actions, our synthesis of known climate change impacts reveals scientific gaps and specific challenges for effective climate change adaptation in this ecosystem.

Climate change trends and ecological responses in the Rocky Mountain alpine

To assess trends and research gaps for climate adaptation in the U.S Rocky Mountain high-elevation ecosystems, we synthesized more than ninety-five papers representing empirical climate change impacts on tree line, alpine lakes, and alpine vegetation in the region. We compiled this literature through Web of Science with the following keywords: “climate change response” AND “alpine” AND “rocky mountains”; “pika” AND “climate change” AND “alpine”; “elk” AND “climate change” AND “alpine”; “ptarmigan” AND “climate change” AND “alpine”; “bighorn sheep” AND “climate change” AND “alpine”; “rocky mountains” AND “climate change” AND “treeline”; “mountain goat” AND “climate change” AND “alpine”; “wolverine” AND “climate change” AND “alpine”; “rocky mountains” AND “climate change” AND “glacier”; “rocky mountains” AND “climate change” AND “microclimate”; “rocky mountains AND “climate change” AND “plants. We only included empirical papers that focused at least in part on the focal region and focal ecosystems and had explicit relationships between the abiotic or biotic patterns and changing climate; this led to a larger focus on papers containing temporal data sets, as opposed to spatial data sets where the link between climate change

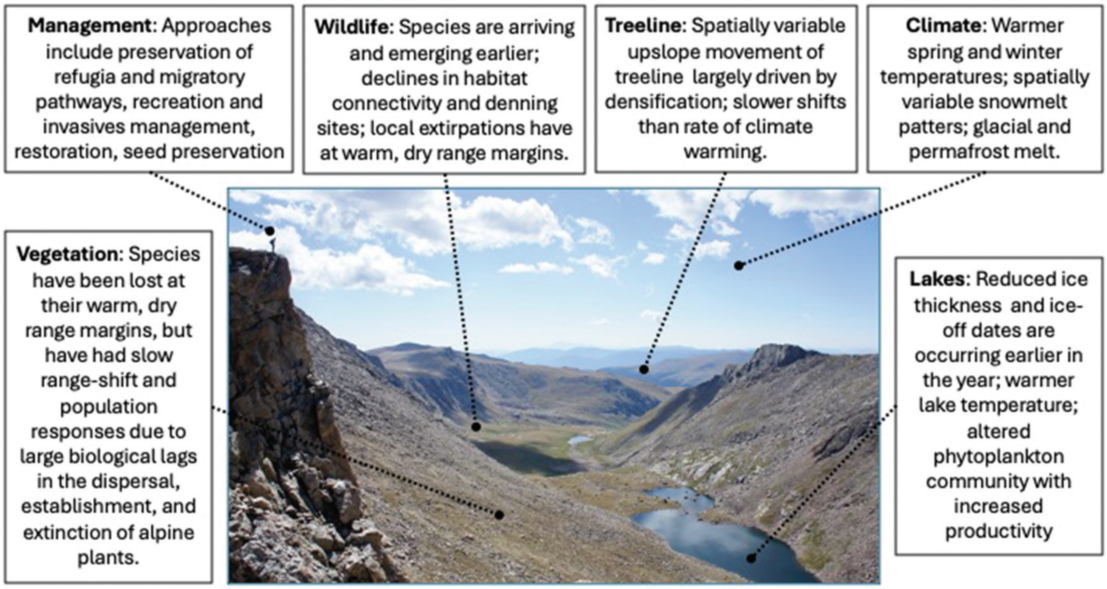

Figure 2. Succinct summary of documented climate change trends, empirical climate change responses, and potential management actions in response to changing climate in the high-elevation ecosystems in the U.S. Rocky Mountains.

and biotic responses is usually more implicit (and assumes a space–time substitution). Papers that only stated that there were implications for a changing climate or extrapolated findings from other regions to the U.S. Rocky Mountains were not included. Common emergent patterns are summarized in Figure 2 and discussed in more detail below.

Observed climate change trends

The spatial resolutions of climatic trends in the literature are usually coarse relative to the scale of high-elevation ecosystems. At broad spatial scales (>10 km^2), the U.S Rocky Mountains have experienced rising temperatures (Rangwala and Miller 2010; Oyler et al. 2015) that are potentially amplified at higher elevations (Rangwala and Miller 2012; Minder, Letcher, and Liu 2018; Palazzi et al. 2019) and an increasing accumulation of annual growing degree days during the growing season (Oldfather et al. 2023). There have also been dramatic decreases in snowpack (Mote et al. 2018) in part due to earlier snowmelt, more rainfall rather than snowfall in spring months, and declines in winter precipitation (Pederson et al. 2011; Musselman et al. 2021; Hale et al. 2023). Further, earlier snowmelt trends have contributed to changes in runoff and stream discharge (Clow 2010; Fritze, Stewart, and Pebesma 2011). However, these precipitation patterns are highly spatially variable. For example, despite a regional trend of less snow, the long-term precipitation data at the Niwot Ridge Long Term Ecological Research Network site in the Front Range, Colorado Rocky Mountains, has shown a 60 mm per decade increase in precipitation at the highest elevation site between 1952 and 2010 (Kittel et al. 2015). Overall, all of these observed changes in climate have occurred against a backdrop of spatially heterogeneous and temporally variable mountain climate, at both the intra- and interannual scales (Dettinger, Udall, and Georgakakos 2015).

Rapid glacier retreat and permafrost loss have been documented in multiple locations in this region, including in Yellowstone and Glacier National Parks (Hall and Fagre 2003; Bosson, Huss, and Osipova 2019). Only smaller glaciers in Rocky Mountain National Park have shown more moderate loss over the last century (Hoffman, Fountain, and Achuff 2007). Glacier loss will have large consequences on water storage in the Rocky Mountains (Martin-Mikle and Fagre 2019) and could imperil stream insects and microbes that rely on cool water (Muhlfeld et al. 2011; Giersch et al. 2017) and lead to novel lake communities (Vanderwall et al. 2024). In contrast to ice glaciers, rock glaciers are common in the U.S. Rocky Mountains and may respond more slowly to changing climate (Johnson, Thackray, and Van Kirk 2007; Anderson et al. 2018; Brighenti et al. 2021). Rock glaciers may therefore act as key refugia for cold water–dependent mountain biodiversity as ice glacier loss continues at a rapid rate (Seligman, Klene, and Nelson 2019; Brighenti et al. 2021).

Alpine lakes in the region have generally become warmer (Roberts et al. 2017), with earlier annual ice loss (Preston et al. 2016). However, there has been no change in ice phenology at Yellowstone Lake (North America's largest high-elevation lake in Yellowstone National Park; Tronstad et al. 2024). With climate change, the productivity of alpine lakes and the rates of community turnover have increased (Porinchu, Haskett, and Reinemann 2017). Droughts have caused changes in water quality in alpine lakes and also transformed the phytoplankton community (Flanagan et al. 2009). Further, drought and warming in combination with enrichment of nitrogen, and other pollutants, may lead to alpine lakes with increased algal biomass (Wolfe, Van Gorp, and Baron 2003; Oleksy et al. 2020; Oleksy, Baron, and Beck 2021).

Tree line dynamics with changing climate

Upslope advancement of tree line has been linked to changing climate in this region. Tree line has advanced at ~0.5 m per year from the 1700s to 2000s, with tree establishment increasing after 1850 and peaking in the early 1900s at Glacier National Park (Bekker 2005). However these patterns are temporally and spatially variable, and that variability is expected to continue under future warming (Elliott 2011; Bourgeron et al. 2015). For example, in the Rocky Mountains—specifically demonstrated by studies in Idaho (Elliott and Petruccelli 2018), New Mexico, Colorado, and Wyoming (Elliott and Kipfmueller 2010; Elliott and Cowell 2015)—tree line advance has been observed largely on cooler north-facing slopes, especially in years with more springtime precipitation. Generally, it is likely that rates of tree line advancement will fluctuate with the decadal-scale modes of variability (e.g., Pacific Decadal Oscillation), where time periods with more moisture may facilitate upslope establishment (Alftine, Malanson, and Fagre 2003). Tree line advancement is also often facilitated by a positive feedback where existing trees create microclimates that increase the likelihood of future establishment (Bekker 2005; Elliott 2012a). Bekker's (2005) analysis of 494 tree cores from Glacier National Park described this feedback; he observed a "windward to leeward pattern of successively younger trees" (1), illustrating the importance of microenvironment establishment in new seedlings. Another analysis of tree lines in Glacier National Park corroborated this finding (Elliot 2012a).

Densification of tree line is a more spatially consistent trend than advancement across this region—including Colorado's western slope (Sakulich 2015) and Glacier National Park in Montana (Klasner and Fagre 2002)—especially for spruce and fir and in wetter parts of the landscape (Daly and Shankman 1985; Baker and Weisberg 1997). This pattern is likely associated with warmer springtime, which can facilitate establishment (Elliott 2012b) if drought does not impact seedling survival (Kummel et al. 2021). Though landscape-scale patterns of densification have been observed, densification patterns in individual stands vary based on stochastic patterns, microtopography, presence of *krummholz* or nurse trees, seedling suppression by shrub encroachment, and more (Bourgeron et al. 2015). For example, though Bourgeron et al. (2015) predicted that tree density would decrease based on tree age and life stage due to density-dependent mortality, they instead found that saplings occurred in higher densities than seedlings or trees. Aridification may become an important influence for all life stages as warming continues, particularly in less mesic areas in the southern Rocky Mountains (Andrus et al. 2018), leading to shifts in the species dominant at tree line. For example, in the Front Range of Colorado, limber pine (Pinus flexilis) establishment has been found to be less sensitive to the aridification effects of warming, potentially leading to a shift to pine-dominated tree line in the future (Kueppers et al. 2017). Densification of tree line may also facilitate the risk of disease prevalence (e.g., blister rust) at higher elevations, as well fire spread (Resler and Tomback 2008). Fire is occurring more often at higher elevations with climate change (Alizadeh et al. 2021; Higuera, Shuman, and Wolf 2021), which may have a major impact on future tree line across the western United States. More frequent fire at tree line could cause an increase in the area and structural complexity of tree line ecotone (Cansler, McKenzie, and Halpern 2018).

Alpine vegetation responses to changing climate

The warming trend in the western United States is expected to reduce the area of alpine vegetation. Based on a gridded climate data at 4-km resolution, Diaz and Eischeid (2007) estimated a 73 percent reduction in the suitable climate area for alpine vegetation in western United States between 1987 and 2006. However, such estimations must be considered with caution because of limited climate observations at high elevations and inhomogeneities found in high-elevation observations (Rangwala and Miller 2012; Oyler et al. 2015). Gridded climate products therefore are unlikely be able to adequately represent the topographic and microclimate conditions experienced by small, stationary organisms such as alpine plants and therefore may over or underestimate climate change exposure (Scherrer and Körner 2011; Graae et al. 2018; Kemppinen et al. 2024).

Nonetheless, both experimental and long-term observational data sets have found that alpine vegetation in this region is largely responding to warming conditions through changes in abundance (Seastedt and Oldfather 2021). For example, dominant grasses have increased in abundance with warming growing seasons (Oldfather et al. 2023). There is less evidence for local colonization or extirpations with a changing climate; only in the driest southern edges of species ranges have mountaintop extirpations been observed with warming (Lesica and McCune 2004; Lesica 2014; Lesica and Crone 2017). Further, these species-specific abundance patterns are greatly mediated by topographic or microclimate conditions (Spasojevic et al. 2013; Suding et al. 2015). Specifically, there is variation in the species that are increasing or decreasing across fine-scale snowpack gradients across the landscape (Walker et al. 1999; Bowman 2000; Seastedt and Oldfather 2021), with recent warming driving shifts to warmer-adapted species in snowier parts of the landscape but shifts to more cool-adapted and drought-adapted species in exposed landscape positions (Oldfather et al. 2023). Related, soil moisture dynamics strongly mediate the impacts of climate change in these systems (Winkler, Chapin, and Kueppers 2016), and overall community responses to warming are mediated by snowpack and nitrogen dynamics (Farrer et al. 2015; Winkler et al. 2018). In addition to abundance changes among alpine plants, shrubs have been quickly advancing into the alpine and transforming the alpine community. However, fine-scale spatial variation was also observed for shrub colonization, with transformation to shrub dominance largely occurring in meadows as opposed to rocky areas or snowbeds (Formica et al. 2014; Bueno de Mesquita et al. 2018).

Notably, the climate responses of the flora in the Rocky Mountain alpine are largely inconsistent with the much more extensively studied alpine vegetation in European mountain landscapes. It is worth noting that most work cited in this section is from work at the Niwot Ridge Long Term Ecological Research Network site in the eastern Colorado and therefore does not adequately represent the vegetation responses across this entire region. Globally, the general vegetation responses to changing climate for alpine ecosystems include increases in richness and abundance of thermophilic, faster-growing vegetation associated with lower elevations of mountain ecosystems (Pauli et al. 2012; Rumpf et al. 2018; Steinbauer et al. 2018). This contrasts with the above findings that have indicated largely only community turnover within the alpine vegetation communities or loss of richness as observed in western Colorado (Zorio, Williams, and Aho 2016). However, it may be difficult to resolve short-term versus long-term trends in these systems (Malanson and Fagre 2013). The one qualitatively similar pattern between regional and global alpine ecosystems is in the phenological advances in vegetative and reproductive timing with changing climate (Jabis, Winkler, and Kueppers 2020; Collins et al. 2021).

Climate change impacts on wildlife

There are a large number of wildlife species important to land managers that are or are predicted to be directly impacted by climate change within the U.S. Rocky Mountains. Wolverine (*Gulo gulo*) are projected to experience reduced den site suitability with decreasing springtime snowpack in low-elevation and low-latitude sites both across Colorado and Montana (Barsugli et al. 2020), as well as across the entire western United States (McKelvey et al. 2011). However, north-facing slopes may act as refugia for wolverine, decreasing the loss of overall area and snow connectivity for wolverine populations (McKelvey et al. 2011; Barsugli et al. 2020). Climate change may also negatively impact mountain goats (*Oreamnos americanus*) and bighorn sheep (*Ovis canadensis*) due to range declines and habitat loss, although these climate impacts may not be as crucial for management as disease (Gude et al. 2022; Renaud, Festa-Bianchet, and Pelletier 2022; Whiting et al. 2023). Populations of white-tailed ptarmigan (*Lagopus leucura*) have also shown to have limited demographic responses to changing climate conditions, with no observed local extirpation observed in the Mount Evans Wilderness Area in Colorado (Wann, Aldridge, and Braun 2014, 2016). According to studies in Glacier National Park, the ability of pika (*Ochotona princeps*) to move uphill in response to demographically detrimental warmer temperatures may be limited, because their geomorphic habitat requirements are less available at higher elevations (Butler 2012). Habitat availability, type, and connectivity may greatly shape this species' response to climate change (Schwalm et al. 2016; Smith et al. 2019). In addition to direct negative effects of temperature on pika demography (Galbreath, Hafner, and Zamudio 2009), lower-latitude pika populations may face a future nutrient deficiency due to graminoid increases with warming temperature (Bhattacharyya and Ray 2015; Yandow, Chalfoun, and Doak 2015).

Indirectly, fauna will also be impacted by climate change through vegetation responses. The "green wave," which is important for migrating mammals, is correlated with mountain snowmelt phenology (O'Leary et al. 2020), so migration dynamics of species that rely on high-elevation ecosystems for summer forage (e.g., elk [*Cervus canadensis*]) likely will be indirectly altered by earlier higher-elevation snowmelt (Rickbeil et al. 2019). In terms of phenology, fauna—such as hibernators (*Marmota flaviventris*) and migrators (*Turdis migratorius*)—are showing evidence of earlier activity in the spring with changing climate at high elevations in the Colorado Rocky Mountains (Inouye et al. 2000). However, phenological mismatches between food resources and reproductive events may impact survival and coexistence mechanisms. Lower chick survival was observed for *L. leucura* females with larger phenological mismatches (Wann et al. 2019). Further, a recent Colorado study showed that both resident alpine bees and lower-elevation bees have increasingly mismatched phenology with floral resources, potentially allowing the lower-elevation generalist bees to eventually outcompete alpine obligate bees (Miller-Struttmann, Miller, and Galen 2022). Alpine butterflies have shown species-specific changes in egg viability and flight time with climate change; for many species, the benefit of more flight time due to increasing temperatures may outweigh the cost in egg viability (Buckley and Kingsolver 2012). Further, evolutionary responses and phenotypic plasticity of butterflies shape this balance and may be impacted by the climate variability both within and across seasons (Kingsolver and Buckley 2015; MacLean, Kingsolver, and Buckley 2016).

Consideration for anticipating future climate impacts in the alpine

By the nature of the general shape of mountains, as temperatures warm, high-elevation species that currently occupy the coldest parts of landscapes may have limited opportunities to move uphill to newly suitable areas (known as the "mountaintop squeeze hypothesis"; Loik 2024). However, this may depend on the specific shape of a given mountain, with some mountain ranges having the most limited amount of physical area at mid-elevations as opposed to the highest elevations (Elsen, Monahan, and Merenlender 2020). In the same vein, the overall topography of the mountain will also impact its ability to act as a refugium. Refugia, or "safe havens," are areas that are relatively buffered from changing climate and therefore may promote species persistence. However, the spatial scale and temporal scale matter, underscoring the importance of questions about for whom this is a refugium for and for how long (Morelli et al. 2020). Refugia for some species may cause the local extinction of others; for example, cooler and wetter high elevation landscapes may provide refugia for subalpine species (Morelli et al. 2016), which may displace higher elevation species (Alexander, Diez, and Levine 2015; Ackerly et al. 2020). The environmental variability of mountains also mean that specific environmental conditions may only exist within limited areas, suggesting an increase in the impact and importance of species interactions for mountain species' responses to climate change (Graae et al. 2018). Refugia that are not large enough for population stability will not be long-term solutions. Further, the effectiveness of refugia in buffering climatic change impacts may be limited in time. Refugia may therefore be best viewed as a stopgap measure or "holdout" while other biological mechanisms (e.g., evolutionary rescue) or management actions (e.g., restoration) take effect (Hannah et al. 2014; Morelli et al. 2020).

Beyond refugia, alpine species, expected responses to climate change may be "slow" or lagged for climatological, topographic, and biological reasons. First, the complex topography of mountains creates a wide range of habitats at the scale of meters. As such, the initial biogeographic responses of alpine and tree line species to climate change may be across local topographic gradients (e.g., slope, aspect) as opposed to broad altitudinal or latitudinal shifts (Graae et al. 2018; Oldfather et al. 2020; Antão et al. 2022), potentially allowing species to track suitable climate within the landscape and leading to slower overall ecosystem response. Second, the highly variable seasonal and interannual climate in the alpine may also dampen the speed at which climate change impacts occur, with the long-term biological impacts of mean changes in climate potentially being masked in the short term. The life histories of alpine plants (e.g., slow-growing, long-lived) interact with this climate variability and inherently lead to biological responses lagging behind climate change (Alexander et al., 2018). For example, many alpine plant species have evolved to rely heavily on adult survival as opposed to seedling germination success to cope with the high spatial and temporal variability in environmental conditions in the alpine (Körner 2003). With climate change, even if the conditions are no longer suitable for long-term population persistence, hardy adults may continue to survive in the short term with reproduction only occurring in increasingly rare climatically suitable years (Jackson et al. 2009). This lack of short-term ecosystem responses has led many to conclude that alpine systems are resilient to climate change. However, all of the processes discussed in this section may also lead to extinction debt —local extirpation of species due to past events. Lags in this system indicate that we could see sudden collapses in vegetation and wildlife communities due to extreme event, disturbance, or reaching a biological tipping point (Williams, Ordonez, and Svenning 2020; Nomoto and Alexander 2021).

Lastly, for climate change responses in the U.S Rocky Mountain high-elevation ecosystem specifically, the interaction between temperature and moisture dynamics (especially with snow) will be crucial for shaping climate change impacts (Chan et al. 2024). Within this drier (relative to mountainous areas globally) region, the high-elevation flora and fauna will be impacted by both regional warming and drying trends, further complicating the overall response of this ecosystem to changing climate (Seastedt and Oldfather 2021). It is not clear whether this interaction could lead to slower or more rapid responses to climate change, but it is worth noting that the changes observed in wetter alpine areas globally have shown increases in richness due to lower elevation species moving uphill (Pauli et al. 2012; Rumpf et al. 2018). These patterns have not been observed in more arid ranges, indicating potentially more lagged responses in U.S. Rocky Mountain high-elevation ecosystem relative to global patterns.

Research gaps for climate change adaptation in the Rocky Mountain alpine

Limited climate observations, particularly for spatially variable precipitation and snow processes, reduce our ability to assess past climate change and project future trends within this region. Further, at spatial/temporal scales relevant to resource management, the patterns of biological responses to climate change are not yet generalizable. The transferability of findings from one study site may be limited to unknown due to differences in topography and therefore the geographic and ecological contexts in which climate change impacts may play out. Another major complication stems from the differences in the foci of studies across sites, which can be driven by either different organismal focus (e.g., alpine cushion plant versus marmot phenology) or different measurement types even for a single organism. Further complicating the generalization of climate change patterns is the overall dearth of observational and spatial data in this ecosystem. Because these systems are remote and extreme, they are difficult to reach and scientific instrumentation often fails, leading to less spatial resolution of climate and biological data relative to other ecosystems despite the known importance of spatial variation. This dearth of spatial data makes comparisons across latitude and elevation difficult, and therefore generalizing about trends even within a single region is difficult. As is a theme through this section, we found it difficult to discern the transferability of the climate and biological trends across study sites—more spatially resolved data collection is needed across mountains in this region.

These ecosystems have been characterized as both highly vulnerable and resilient to climate change. This apparent paradox of alpine vulnerability and resilience has implications for climate change adaptation. The resilience argument hinges largely on topographic complexity providing refugia. Regional alpine-specific empirical examples of transformation and refugial dynamics with climate change are lacking, although modeling studies offer some insights into these dynamics (Morelli et al. 2016). Further, it will be key to understand how the refugial properties interact with disturbances (e.g., fire) and whether there are refugia for all or just part of the alpine ecosystem and for how long. This temporal component also connects to the high likelihood of lags in response to climate change in this system. Determining where alpine communities are likely to be resilient to climate change over the long term, versus experiencing lagged responses, is needed. Without this understanding, the need for active intervention is unclear and therefore will not likely be supported logistically. Therefore, one key conclusion is the need for a better understanding of the efficacy of more passive management actions, such as conservation of likely refugia, for climate change in high-elevation ecosystems more generally.

The possibility of lagged responses in high-elevation ecosystems challenges management planning and actions (Svenning and Sandel 2013). Lagged responses can eventually lead to abrupt biological responses when a threshold has been reached (Dullinger et al. 2012), the early warning signs of which could be informative for management (Williams, Ordonez, and Svenning 2020). In lagged systems, especially in conjunction with limited data on localized species natural history and climate measures, habitat suitability models may give a false sense of understanding of how alpine species will respond to climate change and therefore can lead to misinformed decisions regarding the potential effects of future climate scenarios. Rather, moving past species presence/absence may be important for conservation of high-elevation ecosystems. Identifying indicators of change that may lead to abrupt loss (e.g., reproductive failure during droughts) could better support management decisions related to species or ecosystems that are subject to lags. Very broadly, this harkens to the idea of understanding the "rate of change" of a system (e.g., how fast it will change with climate change) to support monitoring and management that is climate adaptive (Williams, Ordonez, and Svenning 2020). By understanding the "rate" of this system, management may be more able to actively intervene to reduce the risk of abrupt community collapse.

Overall, our synthesis of climate trends, biological responses, and climate change adaptation in the alpine in the U.S Rocky Mountains led to the following questions for research that could support future climate change adaptation work in this ecosystem:

(1) How do we best identify and manage systems with substantial biological lags?
(2) How might different types of extreme events or disturbances impact high-elevation ecosystems in the future (e.g., fire above tree line)?
(3) Given lags, stochastic events, and spatiotemporal variability, can we anticipate areas of transformational change versus areas that may provide future refugia?
(4) What is the relationship between direct climate impacts on flora and fauna and indirect impacts, such as through forage quality?
(5) How much transferability is there in trends observed or lessons learned in one area to other high-elevation ecosystems?
(6) What are the implications of the observed and predicted climate change impacts on the valuable resources provided by the high-elevation ecosystem?

We also identified multiple important considerations for climate change adaptation in high-elevation ecosystems. These considerations include jurisdictional/policy issues that limit potential actions, challenges of accessing remote areas for management and research, lack of data to fully understand these heterogeneous ecosystems and their responses to climate change, and challenges of anticipating the rate of biological responses. Addressing these questions and complications will be crucial for assessing where and when management action should be taken to mitigate the impacts of climate change on the biodiversity and ecosystem services of alpine ecosystems.

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