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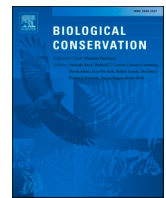
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Press, pulse, and squeeze: Is climatic equilibrium ever possible on mountains?

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ABSTRACT

Mountains present challenging habitats for biological conservation assessment and intervention. Atmospheric warming is pressuring populations, communities and ecosystems to move toward higher elevations, but increasingly variable precipitation patterns could enhance or reverse the upward trend. The effects of warming pressure from lower elevations combined with irregular annual precipitation pulses will be complicated by the squeeze cause by decreasing habitat area at higher elevations. Given the evidence to date this raises the question, can species' distributions on mountains ever be in climatic equilibrium?

Snowfall is a critical driver of patterns and processes in mountain ecosystems, and snowpack provides water storage for billions of people around the world (Figs. 1A, B, S1) (Immerzeel et al., 2020). Snow cover, depth, duration and extent have globally declined, particularly at the lower elevation limit of snowlines (Hock et al., 2019), a trend that is likely to continue (Notarnicola, 2022; Zou et al., 2022). The conservation of biological populations will be affected by the presence and persistence of snow and the loss of montane snowpack (Williams et al., 2007; Barnett et al., 2008). Snow is more widespread in the Northern Hemisphere, and snowline elevations are lower in temperate regions above about 35° latitude (Fig. 1B). Multiple critical impacts will result from climate change-induced snowpack loss (Fig. 1C), including reduced water and carbon storage by ecosystems (Siirila-Woodburn et al., 2021; Albrich et al., 2023). The highly variable timing and magnitude of snow (Fig. 1D) will likely drive changes in species distributions on mountains (Lenoir and Svenning, 2015), largely toward higher elevations (Inouye et al., 2000; Callaghan et al., 2004). The expected reduction of mountain snowpack will affect local and regional climate through lower albedo, increased local temperatures, and reduced evaporated and sublimated water (Schulz and de Jong, 2004). Less snow would result in a decrease in spring stream flow timing and amount, affecting wildlife habitat (Hammond and Kampf, 2020), and confounding downstream commerce (Sturm et al., 2017). The impacts on biological communities will profoundly affect the economic well-being of those who rely on seasonal recreation (Huss et al., 2017). The importance of species movements toward higher elevations in response to climate change has been recognized for some time (Peters and

Lovejoy, 1992), but how will climate and the shape of mountains interact to affect biodiversity?

Montane species that are reliant on snowpack are being challenged by the ways that mountain climates are changing. In fact, the combination of warming temperatures, spatial and temporal snowpack variability, and the tapered shape of mountains could result in “climate disequilibrium” (Svenning and Sandel, 2013), whereby species range limits do not keep up with the environmental filters that are moving due to climate change (Fig. 2). Mountain air temperatures decrease with increasing altitude due to the adiabatic lapse rate (Fig. 2A). However, climate change is warming the atmosphere, accelerating snow melt and reducing snowpack, thereby causing the lower elevation of the snowline to move upward to higher elevations in many regions (Fig. 2B). These changes, which can be characterized as a chronic press, will continue to compel upslope movements for some species. Yet climate change is also causing snowfall to be more variable, as wetter-than-average years have more snowfall and lower snowlines. Thus, there will be both increases and decreases in snowpack depth in some places and in some years (Fig. 2B). Interannual snowpack cover and depth are also highly variable in many mountain regions. The spatial and temporal variability of snow produces pulses of soil water and other resources at multiple scales (Loik et al., 2004) that are potentially important for species ability to disperse and successfully establish in new locations (Fig. 2C). Complicating matters for species that are pressed toward higher elevations is that most mountains have a more-or-less tapered shape, meaning that some species may be squeezed into smaller areas of potential habitat. The reduction in habitat area along with a general decrease in spatially

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important resources (food, nest sites, burrows, hibernacula) could result in increased intensity or frequency of stressful or negative biotic interactions (Fig. 2D). Some species have always migrated in response to past climate changes (Millar et al., 2019), whereas other species stayed in place, adapted to the altered climate, faced dispersal barriers, or were extirpated (Holt, 1990; Alexander et al., 2018), highlighting a diversity of responses to climate change on mountains. Nevertheless, it is not clear how important ecological and evolutionary processes will be affected by the unprecedented press of warming temperatures in combination with highly pulsed precipitation and squeezed habitat availability.

How does the shape of mountains affect habitat area? Mountain surface area decreases with altitude, so the tapered shape of mountains could cause species to be squeezed into smaller habitat space as they move toward higher elevations in search of preferred conditions. For species that occur up to the mountaintop, the area available for occupation can be approximated as the lateral surface area of a cone. For species with mid-mountain elevation limits, the area available for occupation as habitat can be estimated as the surface area around the mountain, bounded by the upper and lower elevation limits of its populations (which describes a surface called a frustum.) Mount Morrison in eastern California, USA is a symmetrically-shaped mountain that illustrates the effect of elevation on habitat availability. It has an average slope of 60° , a base height on the Long Valley Caldera floor of 2134 m above sea level (7000'), and a peak elevation of 3731 m (12,241'). Considering a species with a lower elevation limit of 2743 m (9,000') and upper elevation boundary at the peak, the potential habitat would be the lateral surface area of the cone, and would have about 0.5 km^2 of mountain area to potentially occupy. The adiabatic lapse rate varies with vapor content, but at the midpoint (0.6° per 100 m), 1.0 degree of warming corresponds to a change in elevation of about 250 m. Such changes are comparable to transformations of trailing-edge forests

(Meigs et al., 2023). If the lower elevation margin was to rise by 250 m to almost 3000 m altitude (9843'), the area available as potential habitat would decrease by 46 %. This shows that small changes in upward elevation movement of range margins result in dramatic reductions in habitat space. This is a highly oversimplified illustration because mountains are overtly heterogeneous habitats and not right-angle cones. Latitude, elevation, aspect, slope, topographic variability (ridgelines, gullies) and forest cover would drive complex interactions with the impacts of press-squeeze-pulse on the presence/absence of habitat available for supporting species diversity (Coblentz and Riitters, 2004). Moreover, certain features might act as corridors or refugia that could facilitate species' movements or stasis, respectively (Chester et al., 2013; Alexander et al., 2018).

How might species respond to the combined effects of simultaneous warming press, habitat squeeze, and highly variable interannual precipitation pulses? Altered snow ablation (particularly earlier disappearance due to melting and sublimation) can cause a loss of synchrony between the timing of biological interactions, such as pollination or predator-prey relations. These "phenological mismatches" can have important consequences for population processes (Visser and Gienapp, 2019; Twining et al., 2022). The date of snowmelt is a key ecological trigger for the emergence and growth of many kinds of organisms in montane ecosystems. Earlier snowmelt and onset of development can cause plants to be damaged by freezing air temperatures, resulting in reduced flower abundance, suggesting reduced seed availability, recruitment and impacts on pollinators and herbivores (Inouye, 2000, 2008) For early-season plants, the loss of snowpack can lead to cold-induced photoinhibition for some plant species, in which processing of light energy by the photosynthetic apparatus is impaired due to combined light and temperature stresses (Germino and Smith, 2000; Loik et al., 2004). The loss of snow cover removes the thermal insulation

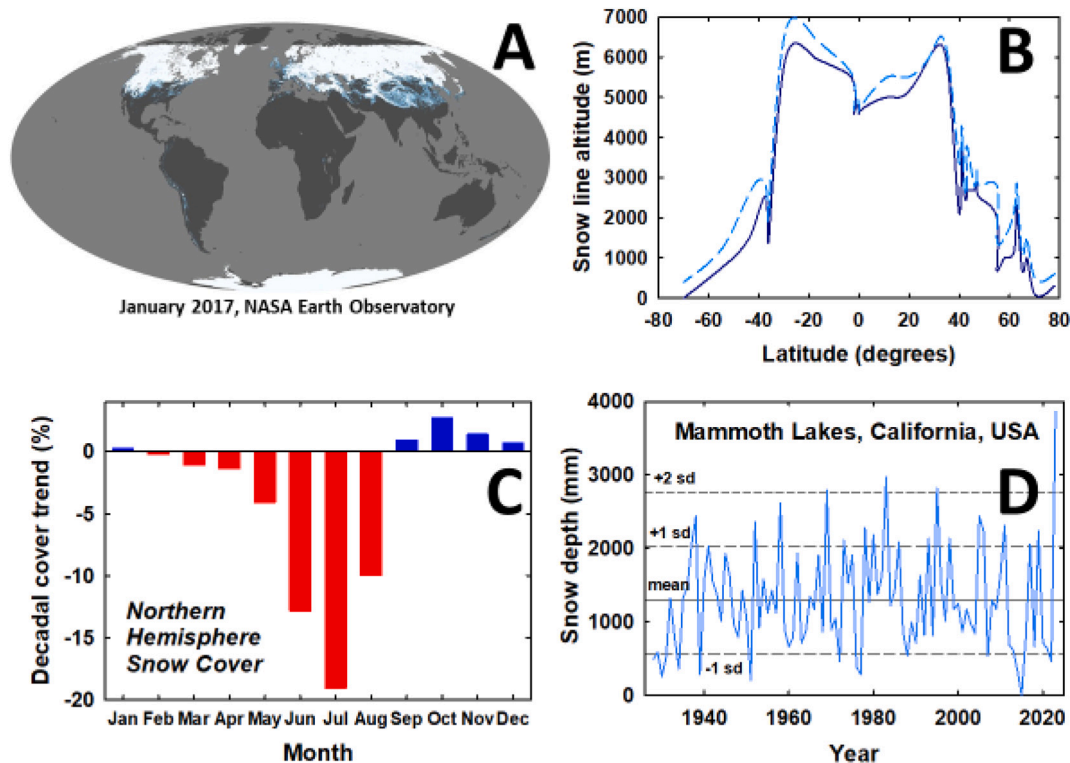


Fig. 1. Variation in snow cover and snow depth over time and space on mountain environments (A) Maximal annual Northern Hemisphere snow cover, January 2017; maximal Southern Hemisphere snow cover is shown in Fig. S1. Data are from the NASA Earth Observatory. (B) Minimum (solid line) and maximal (dashed line) snow line altitude as a function of latitude. Data are adapted from (Adam et al., 1997) and (Leonard and Fountain, 2003) (C) Decadal trends in Northern Hemisphere snow cover from 1967 to 2023. Data are from the National Centers for Environmental Information and the Rutgers University Global Snow Laboratory (GSL). (D) Decadal variation in 1 April snow depth at 2530 masl (8300') near Mammoth Lakes, California, USA, in the Sierra Nevada. Winter 2023 value exceeds 3 sd. Data are from the California Data Exchange Center.

effect, resulting in colder soils, altered nutrient transformations, and soil gas fluxes (Edwards et al., 2007). Warming temperatures and climate disequilibrium portend shifting distributions and widespread impacts on life-history evolution (Phillips et al., 2010) and biodiversity (Huntley et al., 2018). Some studies have found evidence for widespread climate disequilibrium among conifers, fish, and invasive insects (Early and Sax, 2014; Hill et al., 2017; Kirk and Rahel, 2022). The climate-sensitive mammal *Ochotona princeps* (American Pika) has limited dispersal ability, is reliant on snow for thermal insulation and to avoid predators, and requires thermal refugia in summer to stay cool. This species has attracted conservation attention because rapidly shifting environmental conditions may cause isolated alpine species to become locally extirpated (Wilkening et al., 2015; Waterhouse et al., 2018). Recent genetic evidence indicates population decreases throughout the range of pikas (Klingler et al., 2021). However, other studies indicate limited movements between elevations in some regions (Henry et al., 2012), increasing isolation in other places (Klingler et al., 2023), whereas other populations appear robust (Millar and Westfall, 2010). This indicates that responses to climate are not universal within high mountain species, and highlight differences in how pikas are responding across their distribution in North America (Schmidt et al., 2021). These studies suggest that for this sensitive snow-reliant species, any impacts of press, pulse and squeeze are geographically distinct. Moreover, they highlight the need for studies that explicitly test the effects of press, pulse and squeeze on species' ranges. (Rowe et al., 2010).

Evidence is growing that individuals, populations, communities and ecosystems are decoupled from environmental conditions, raising some questions about the role of press, pulse and squeeze on montane biodiversity. First, for the case where species are not in climate equilibrium, do wet years with low-elevation snowlines create conditions favorable for equilibration? If so, do species actually equilibrate, or are the pulses too short for an effective “catch up”? Several new and emerging methods could help identify whether a study system is out of equilibrium. For example, repeat drone-based hyperspectral mapping could be particularly helpful for identifying the shifting distribution of species in the challenging topography of mountain habitats (Kluczek et al., 2023). Hypotheses about the relative importance of precipitation vs. warming could be tested using drought shelters, overhead heaters, or snow manipulations (Dunne et al., 2003; Wahren et al., 2005; Moyes et al., 2013; Knapp et al., 2015), particularly in combination with transplanting across current distributional limits. Likewise, experiments that test effects of warming or precipitation in combination with habitat removal or biotic treatments (e.g. increased or decreased competition, herbivore or pollinator exclusion) could help evaluate the relative importance of press and pulse compared to squeeze. What if some species are more sensitive to the squeeze than the pulses or press, will that result in altered distributions that reflect the disproportionate influences (Hordley et al., 2023)? Assisted migration and reciprocal transplant experiments could help to test hypotheses about the relative importance of biotic interactions associated with habitat squeeze by comparison to

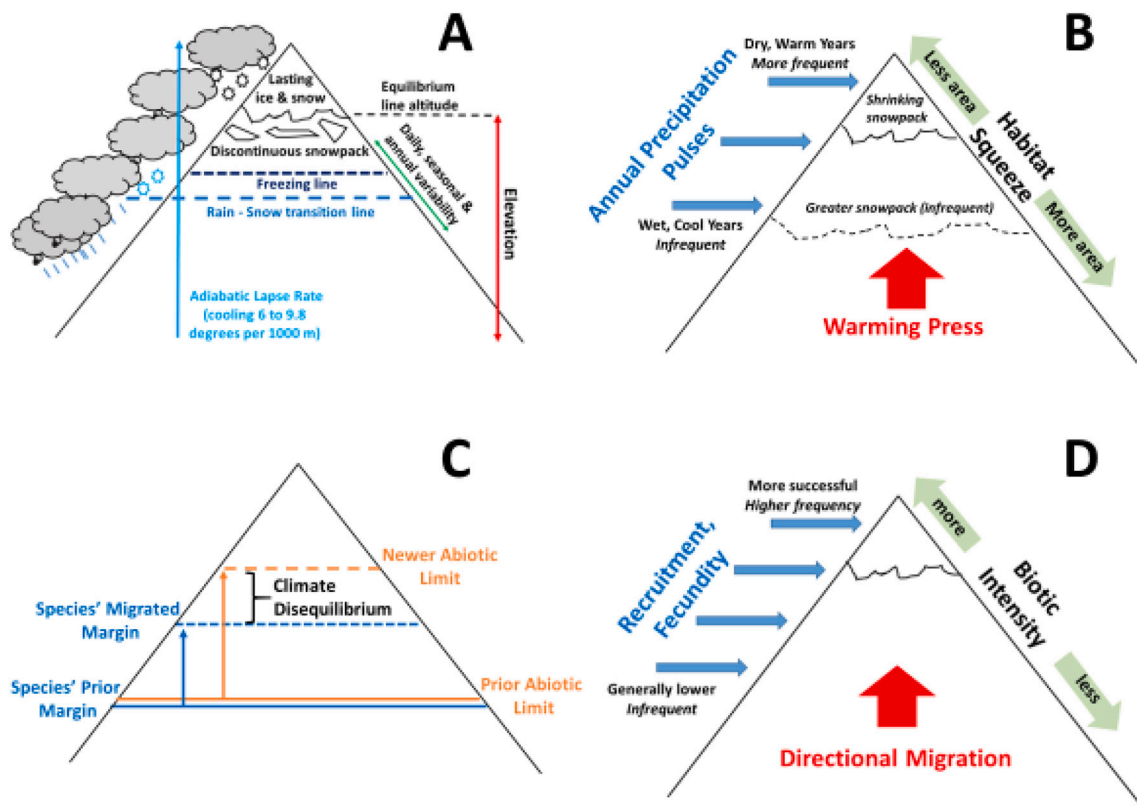


Fig. 2. Characteristics of mountain habitats that create press, pulse, and squeeze constraints. (A) The adiabatic lapse results in colder temperatures with elevation. The rain-snow transition and freezing lines, snowpack limits and continuous (glacial) snow cover occur at different elevations over daily, seasonal and annual time scales due to external meteorological forcings, and global warming. (B) Anthropogenic climate change is causing air temperatures to warm, creating a pressing trend from lower elevations. Variable snowfall means the snowline position varies from year to year, setting the stage for heterogeneous interannual water inputs and ecological outcomes. Depending on their slope, mountains tend to have less habitat availability with elevation; younger (steeper) mountains will have more pronounced reductions in area. (C) An abiotic factor (freezing, snow depth, soil moisture) may impose an upper limit on a species distribution. However, climate change is causing movements in the elevation at which abiotic limits occur. Species may be compelled to migrate to match the abiotic limit but mismatched movement rates can lead to climate disequilibrium, where the species has not kept up with the abiotic limit. (D) Some potential ecological outcomes of press, pulse, and squeeze influences. Warming temperatures may press species to migrate toward higher elevations that match their fundamental niche. Variability of precipitation (e.g. infrequent heavy snowfall years) could lead to pulses of high fecundity or recruitment for certain species in “suitable” years. And, the tapering shape of mountains may reduce habitat or other resource availability, leading to higher numbers or intensity of biotic interactions such as competition, herbivory/predation, or disease.

abiotic press and pulse influences (Wadgymar and Weis, 2017; Midolo and Wellstein, 2020; Charles and Stehlik, 2021). And, how do other kinds of meteorological episodes that rapidly melt snow (e.g., rain-on-snow events, spring heatwaves) affect climate disequilibrium and conservation outcomes for species of concern on mountains? Warm-water additions could test hypotheses about the seasonal timing and temperature of precipitation on key processes that affect species ability to track preferred conditions. Given their higher altitudes and isolated nature, how would press, pulse, and squeeze affect climate disequilibrium on tropical mountains (Veettil et al., 2017; Flantua et al., 2019)? We might hypothesize relatively less impact from the warming press due to the higher snowline altitudes, compared to pulses or the habitat squeeze, which could be tested by examining the impact of passive warming shelters (Hollister et al., 2022) vs. supplemental watering or planting density on species establishment.

What should conservation biologists and practitioners be most concerned about when it comes to press, pulse, and squeeze on mountains? For one thing, adapting conservation strategies for changing climates, such as when designing restoration plans, management of invasive species, or scoping for assisted migration efforts, is already challenging in an era of rapid climate and biotic change. Predicting how climates will change, whether soils will be suitable if species are translocated, what might be the impacts of an invasive species or pest outbreak, and whether key beneficial biotic interactions will be maintained are difficult enough on flat ground. In all likelihood, there will be additional costs, time, and special expertise required for monitoring, restoring species, or providing assisted migration in the complex topography of mountains. Testing hypotheses about the importance of abiotic press and pulse limitations vs. biotic interactions within squeezing habitat will help develop new theory about controls on montane biodiversity.

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CRedit authorship contribution statement

Michael E. Loik: Conceptualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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