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REVIEW

Effects of climate change on alpine plants and their pollinators

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Alpine environments are among the habitats most strongly affected by climate change, and consequently their unique plants and pollinators are faced with the challenge of adapting or going extinct. Changes in temperature and precipitation affect snowpack and snowmelt, resulting in changes in the growing season in this environment where plant growth and pollinator activity are constrained to the snow-free season, which can vary significantly across the landscape if there is significant topographic complexity. As in other ecosystems, the resulting changes in phenology are not uniform among species, creating the potential for altered and new interspecific interactions. New plant and animal species are arriving as lower altitude species move up with warming temperatures, introducing new competitors and generating changes in plant–pollinator interactions. Repeating historical surveys, taking advantage of museum collections, and using new technology will facilitate our understanding of how plants and pollinators are responding to the changing alpine environment.

Keywords: alpine; climate change; pollinator; pollination; phenology

The changing alpine plant ecosystem

Alpine environments cover about 15% of the total land surface, in high-latitude and high-altitude parts of the world,[1] and are among the habitats that are being influenced most strongly by the effects of climate change, including the increased variability in climate.[2] This review is based primarily on the 90% of alpine areas that occur in the temperate zone, as that is where the preponderance of research has occurred. Alpine plant communities are relatively simple structurally, comprised primarily of long-lived perennial herbaceous plants and have a relatively low plant diversity. Trees are absent by definition, but striking changes have been found in some alpine areas as taller shrub communities have been expanding and subalpine plants have been migrating up,[3] to the detriment of smaller shrubs.[4] Thus, one of the major consequences of climate change for alpine environments may be that they are shrinking as shrubs and trees begin to encroach.[5] A more subtle change was observed in a 23-year study of alpine areas in the Adirondack Mountains, where there was an overall decrease in bryophytes/lichens and an increase in vascular plants, particularly in areas not disturbed by hikers.[6] Alpine plant community responses to climate change are reviewed in Grabherr *et al.*,[7] and Rammig *et al.*[8] present some projections of future changes, which may include taller and larger plants in response to the longer growing season. The strong regional variation that has been observed in warming experiments makes it problematic to make generalizations or conclusions appropriate to all alpine areas.[9]

Alpine habitats are at greater risk than lower altitudes for habitat loss as the climate warms; one estimate for European mountains is that 36–55% of alpine species, 31–51% of subalpine species, and 19–46% of montane species will lose more than 80% of their suitable habitat by 2070–2100, although different patterns of temperature and precipitation across different mountain ranges will generate variation in these changes.[10] Alpine areas are diverse enough

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that it is difficult to generalize about their future climate; for example, predictions of future precipitation patterns are different for northern and southern mountain areas in Europe, although downscaled regional projections are likely to be more accurate than global climate models.[11]

The topographically complex (rough and patchy) landscapes that characterize alpine ecosystems should be both more resistant and more resilient to climate change than those of topographically simple (flat and homogeneous) landscapes, which do not provide diverse microhabitats and refugia from the changing climate.[12] Warming of current alpine areas in the tropics may result in drastic declines in the geographic range and genetic diversity of some of the signature plants of those areas,[13] which have a variety of adaptations facilitating life in those extreme environments.[14]

To a limited extent, the loss of alpine habitats as the climate warms may be compensated for by the melting of glaciers, revealing ground that can then be colonized by alpine plants. For example, the loss of tropical glaciers is occurring at a rapid rate.[15] Plants that are visited by pollinators can appear within a few years of the disappearance of a glacier,[16] and the succession of plants in the path of glacial retreats has been studied extensively (e.g., see Refs. 17 and 18).

Alpine plant communities appear to be somewhat resistant to invasion by non-native species. Although the highest elevations are relatively free of non-native species due to constraints on seed dispersal, environmental effects of low temperature on population growth, and biotic interactions,[19] at least 200 species of such invaders have been reported worldwide. Most of these invasives are not adapted to extreme cold and there seem to have been relatively few impacts from them so far;[20] the relatively short growing season may also play a role. As the alpine climate warms, there will undoubtedly be increased pressure on resident species as thermophilic species from lower altitudes move up.

Snow is a major component of weather in alpine ecosystems and can have major consequences for the flora and fauna. Snow is a good insulator and can help protect the soil and its biota from extreme cold winter temperatures. The disappearance of the snowpack is usually considered to delimit the growing season, although some species may begin to grow when a few centimeters of snow remains and poke up through the remaining cover; with that little snow some light can reach ground level. For example, *Claytonia lanceolata* and *Erythronium grandiflorum*, the first two species to bloom after snowmelt in my montane study site at the Rocky Mountain Biological Laboratory, can both be found protruding above the last of the melting snow.

Snowmelt also provides a major source of water at the beginning of the growing season. As more precipitation falls as rain rather than snow because of the changing climate, there will be earlier and perhaps longer growing seasons, and possibly increased summer drought.[5] The rapid warming of the ground once the insulating snow cover is gone is undoubtedly also a cue for plant growth. Some alpine species respond positively to increased temperature and reduced snow cover, although as a group they do not respond uniformly to such changes.[21] Even within species, there can be genetically determined variation in responses to snowmelt timing.[22]

As winter snowfall declines in some alpine areas, and snowpack melts more quickly due to warmer spring temperatures and more frequent dust-on-snow events in the Colorado Rocky Mountains,[23–25] one consequence is that there can be more frequent frost damage to high-altitude wildflowers,[26,27] including in the alpine. Reproductive structures were found to be more sensitive to frost effects than vegetative parts in alpine Europe.[28] In the alpine of New Zealand, however, the relationship of frost resistance with daylength rather than snowmelt date may confer some protection.[29] At 3750 m in the Colorado Rocky Mountains, there was an unusually late and light snowpack in the winter of 2017–2018, and in some areas there was significant damage to krummholz trees and to ericaceous ground cover (personal observation). A study in the Swiss Alps, however, found that the time of snowmelt and the last spring frost date have advanced at similar rates, so that the frequency and intensity of frost during the vulnerable period for plants remained unchanged.[30]

Although there are many similarities between alpine and arctic tundra communities, in the future they may diverge in their responses to climate change. Both areas are experiencing warming temperatures and alterations in precipitation patterns, and potentially longer growing seasons, but alpine tundra plants are more commonly responsive to daylength, which will limit the extent to which they can respond plastically to changes in the growing season; the earlier snowmelt that can result in decreased water availability can lead to earlier senescence, also limiting responses to the longer growing season.[31] Loss of the historical temporal relationship among daylength, beginning of the growing season, and frost resistance may thus constrain adaptation via plastic responses and require evolutionary change before such plants can take advantage of the longer season.

Alpine pollinators

Alpine pollinators have been studied since the 1800s, when the German biologist Herman Müller published about them in both English[32] and German.[33] Interest by pollination biologists has continued until the present, progressing beyond descriptive studies, and work on alpine pollinators now includes network analyses applying niche theory and optimal foraging theory.[34,35] For some alpine plant species, anemophily (wind pollination) supplants or complements a need for pollinators.[36,37] It is hypothesized that self-fertilization should increase with increasing altitude as a result of pollinator limitation at higher altitudes, but a study of the alpine cushion plant *Eritrichium nanum*, sampled along an altitudinal gradient in the Swiss Alps, found that selfing decreased with increasing altitude and the authors called for additional study of the mating systems of alpine species.[38]

The alpine climate is not conducive to some groups of lower altitude pollinators, including mammalian and reptilian pollinators, but some species of insects such as bumble bees, flies, and moths are commonly found at high altitudes. Within these groups, certain species specialize in life at the higher altitudes. For example, among bumble bees, only some species are typically found in the alpine, a subset of the broader community found along altitudinal transects.[39–41] Similarly, certain species of butterflies and moths are characteristic of alpine habitats, with life histories that allow them to tolerate the relatively harsh environment. Some species may only occur there seasonally, such as the bogong moth (*Agrotis infusa*), an Australian species notable for its biannual long-distance seasonal migrations, which bring them to the tundra to aestivate over the summer, but they do occasionally visit flowers.[42] Ants have also been found to pollinate some alpine species.[43–45]

In parts of the world where bumble bees (*Bombus* sp.) occur, some species are common in alpine habitats. In areas where these social bees are not found, flies are typically the most important high-altitude pollinators, and even where the bees do occur, flies may constitute a higher proportion of the pollinator flora than at lower altitudes.[46–49] At least in Norwegian mountains, however, this has not resulted in a significant change in flower color to match the increased importance of flies at higher altitudes.[50] The unusually high preponderance of white flowers in the New Zealand alpine does not seem to reflect the prevalence of fly pollinators; syrphid flies preferred yellow, while solitary bees preferred white, so floral traits other than color may be more important at the community level.[51] Other studies have also documented a preference for yellow by some fly species.[49] Studies of flower color in the alpine appear to be restricted so far to temperate areas.

Common families of flies found visiting temperate alpine flowers include Syrphidae,[52–54] Muscidae,[55] and Empididae.[46] Butterflies, beetles, and moths have been recorded as alpine flower visitors in Australia, where there are no bumble bees,[56] but in Swedish Lapland bumble bees were found to be much more important than butterflies,[57] being active at temperatures too cold for butterflies and visiting flowers more often. In alpine New Zealand, where there are no bumble bees, syrphid flies and short-tongued solitary bees are common flower visitors, with the bees typically contributing most of the pollination service.[53] In alpine Switzerland, over 95% of pollinators were Diptera.[58] There do not appear to have been comparable studies yet of tropical alpine pollinators.

As alpine areas shrink because they are invaded by shrubs and trees, the connectivity of pollinator populations can be affected. For example, the rising tree line in the Canadian Rocky Mountains has been shown to isolate populations of the alpine butterfly *Parnassius smintheus*, decoupling the population dynamics of its subpopulations. The resulting smaller, independent populations are therefore placed at greater risk of local extinction, although the risk of regional extinction might be lowered.[59] Similarly, *Boloria acrocnema*, a monophagous butterfly that only uses *Salix reticulata* (snow willow) as a larval host, has very small alpine populations at risk[60] from the spatial and phenological mismatches that may occur in the future (https://ecos.fws.gov/ecp0/profile/speciesProfile?spcode=I01Q), although its populations seem to have recovered some from low numbers recorded in the 1980s.[61] Although other alpine species of butterflies may face similar problems, they have not been studied in this context.

Alpine environments are the coldest habitats where pollinators occur. Given the responses of plants and ectothermic insects to higher temperatures, which can speed up metabolic processes, it is not too surprising that plants have evolved mechanisms such as heliotropism[62–65] or other mechanisms to warm flowers,[66] and that pollinating insects are attracted to warmer flowers.[65,67] As ambient temperatures increase, it is possible that the selection for mechanisms to increase flower temperature may relax. A strategy to mitigate potential damage from alpine precipitation is found in a species of alpine gentian (*Gentiana algida*), which closes its flowers within minutes of an approaching thunderstorm and reopens them once direct sunlight returns.[68] Flowers that were experimentally prevented from closing during rain had substantial losses of pollen as a result, with consequent detriments to female fitness (seed size and mass, number of ovules and seeds produced, and seed germination).

Pollinators could respond in multiple ways to the challenges posed by climate change. Some responses could be plastic, such as changing their altitudinal distributions (see below). Another category of responses would involve evolution, and in most cases the time scale of such changes is long enough that they are not likely to be observed in the timespan of most research projects. These responses might be behavioral, physiological, or morphological in nature. An example of the latter was described for two bumble bee species, which have evolved shorter tongue lengths over a 40-year period.[69] The authors argue that the change was a consequence of warmer summers that have resulted in declining floral resources, requiring bees to be more generalist in their foraging.

Alpine flowering phenology

Alpine flowering phenology has been described from many parts of the world, including the high Andean Cordillera of central Chile,[70] Norway,[47] Japan,[71–73] Greece,[54] China,[74–76] Switzerland,[77] India,[78,79] Australia,[56,80] the High Arctic,[81] and North America.[82–85] In addition to direct observation, herbarium specimens have been useful for understanding alpine flowering phenology.[86] A general conclusion is that because snowmelt dates are advancing, growing seasons are getting longer and flowering phenology is getting earlier.[87] But in one study, warmer temperatures are leading to shorter community-level flowering seasons in tundra ecosystems due to a greater advancement in the flowering times of late-flowering species than early-flowering species.[88]

Snowmelt date is probably a major determinant of flowering phenology in the alpine environment, as the growing season typically cannot begin, at least for herbaceous species, until the snow melts. In subalpine environments, a few species may begin to grow before all the snow is gone, so that they may emerge through the final few centimeters of snow; *C. lanceolata* and *E. grandiflorum* do this in subalpine areas of the Colorado Rocky Mountains (personal observation). If there is significant topographical variation, as may be common over short spatial scales in montane alpine regions, differences in aspect, wind direction, or altitude can generate variation in snowpack, snowmelt, and hence phenology, on small spatial scales.[73,82,89–92]

Flowering phenology can determine which pollinator species, or which castes in social bees, can interact with particular flowers and can also influence visitation rates,[47] outcrossing rate and seed production,[71] and pollen limitation.[93] Possibly, as a consequence of a relatively low frequency of pollinator visits in the alpine, flowers in this habitat are generally long-lived,[94,95] and in one study alpine flowers tended to bloom early in the growing season.[54] This greater longevity can compensate for lower visitation rates so that pollination (as measured by a combination of pollinator abundance, visitation rates, pollen deposition, and duration of stigma longevity) of *Campanula rotundifolia* may be similar in both alpine and lower altitudes.[96] Another study found that multiple aspects of the floral biology of this species differed between alpine and montane populations, raising the point that it is not always possible to generalize about the pollination of alpine species from studies in other environments.[97]

There are some predictions of how alpine phenology will change under various projected scenarios of climate change. For example, drawing upon almost a decade of data from 17 meteorological stations in different alpine regions along the Swiss Alps, regression analyses revealed "highly significant correlations between mean air temperature in May/June and snow melt out, onset of plant growth, and plant height."[8] These correlations were then used to project plant growth phenology for future climate conditions; melt out and onset of growth were projected to occur on average 17 days earlier by the end of the century than in the control period from 1971 to 2000. Plant height and biomass production were projected to increase by 77% and 45%, respectively.[8] Another study in the Alps found that there has been an earlier onset of spring in recent years, mainly since 1988, when a clear shift in spring appearance occurred; "the mean overall trend of 1.5 days per decade was clearly driven by winter and spring temperatures whereas precipitation showed no significant influence."[77]

One of the consequences of changing phenologies is that although they may all be advancing, they are not doing so at the same rate, creating the potential for future phenological mismatches in historically synchronized events, such as the emergence or arrival of pollinators, and the availability of their floral resources. For example, in a comparison of years with an average and an abnormally warm spring, there were significant differences in the phenology of bees and flowers, and even differences among bumble bee species in how they responded.[98] Bee frequencies were highest at the end of the flowering season of the warm year, but the flowering season ended 2 weeks earlier that year. Some alpine areas comprise significant topographical variation, such that snowmelt may vary significantly over short distances.[91] At one of my alpine study sites, a late-lying snowbank is often found in the same spot almost every year, and it may melt a few months after a meadow 10 m away. In such circumstances, the potential for phenological mismatch may be buffered to some degree, although another consequence may be that the plant species differ as a result of the consistent differences in snowpack.[91]

Migration dates of broad-tailed hummingbirds in the Rocky Mountains are advancing, but not at the same rate as flowering by the early subalpine wildflowers they typically visit.[99] At the same site, timing of snowmelt was the best predictor of phenology of syrphid flies at a subalpine study site, which are important pollinators, but flowering advanced at a faster rate than syrphid phenology. These rates of phenological advancements resulted in more days of temporal overlap between the flowers and syrphids in years of early snow melt because of extended activity periods. Thus, phenological synchrony for these flies at the community level is likely to be maintained for some time.[100]

What limits seed production in the alpine environment?

The process leading to successful seed production can be broken down into many components, with many of them related to the process of pollination.[101] A way to quantify the role of pollinators in this interaction is through studies of pollen limitation, looking at the degree to which insufficient pollen deposition limits reproduction. Totland[102] found that while lower altitude populations of *Ranunculus acris* were pollen limited (i.e., seed set increased with pollen addition), higher altitude populations were not; he concluded that seed production in the higher populations was temperature limited. Japanese alpine-snowbed shrubs can also be strongly pollen limited at some times of the season, although they may also be able to self.[103] Giblin[97] found that alpine populations of *C. rotundifolia* were pollen limited, in contrast to montane populations, and Fulkerson *et al.* found strong pollen limitation in *Parrya nudicaulis*.[104] In a comparison of alpine and lowland communities, Lázaro *et al.*[105] found low overall levels of pollen limitation that did not differ significantly between the two. Thus, it appears that the role of pollen limitation in the alpine is not universal across alpine habitats.

Some plant species may extend floral longevity in the absence of pollination, which could be interpreted as a response to pollen limitation, but a study of Chinese alpine gentians concluded that floral lifespan, pollinator frequency, and pollination limitation did not vary consistently with altitude.[106] A comparison of lowland and alpine communities found low overall levels of pollen limitation in both habitats, although in the alpine area pollinators were scarcer and species' visitation rates and selfing capability were negatively related to pollen limitation.[105] A meta-analysis of alpine pollen limitation concluded that pollen supplementation experiments do not always show high levels of limitation, but that in general alpine plants are pollen limited; the authors also suggested that additional research on this topic is warranted.[107] Given the longevity of many alpine species and the variation among years in pollinator populations, there could be significant pollen limitation in many years, but it may only take a few years of more successful seed production to maintain population size. Unfortunately, it is difficult to find grant support for very long-term studies to follow such variables.

Straka and Starzomski[108] concluded that seed production of flowering plants in the alpine may be mediated by a combination of flowering time, pollination syndrome, and susceptibility to seed predators (in the case of *Arnica latifolia*, larvae of tephritid flies that eat developing seeds). Predisperal seed predation by these flies occurs in some other species of subalpine and alpine Asteraceae (e.g., *Helianthella quinquenervis*[109]), and some tephritid species are moving up in altitude in the Colorado Rocky Mountains, where other species are already found in the alpine as predispersal seed predators of Asteraceae (D. Inouye, unpublished). Additional studies of seed predation in the alpine would be useful to understand its significance for plant reproduction.

Changes in altitudinal distributions and their consequences

One response of relatively mobile organisms to the changing climate is to move to stay within the climate zone to which they are adapted. There are a growing number of studies documenting latitudinal and altitudinal range shifts as the climate warms. Many of them take advantage of distributional data collected decades ago, sometimes archived in museum or herbarium collections. For example, studies of the altitudinal distribution of bumble bee species in the vicinity of the Rocky Mountain Biological Laboratory in Colorado were conducted by graduate students in the 1970s and have since been repeated. Pyke[39,40,110] described results of conducting altitudinal transects in 1974 to sample bumble bees, and in a follow-up study in 2007 it was found that queens of some species had extended their altitudinal range up, although observed changes in elevation were often less than the upward shift of 317 m required to maintain average temperature over the 33-year period.[41] Although this altitudinal shift occurred in montane/subalpine habitats, a similar shift was seen in an alpine species (*Bombus alpinus*) in the Alps, where its lowest altitudinal limit has moved up 479 m since 1984.[111]

Latitudinal shifts in butterfly distributions have been attributed to climate change[112,113] and altitudinal responses have also been observed,[114–117] although range shifts may lag the spatial changes in climate,[118] creating continental-scale "climatic debts."[119] Given the shorter distances required for travel, it seems likely that altitudinal changes are more likely, or at least more likely to occur in shorter time spans, than latitudinal changes.

As different species of pollinators respond uniquely to the changing climate, for example, moving up in altitude at different rates, there are likely to be large-scale changes in community composition. Even within genera, species may differ in their changes in altitudinal distributions,[41,120] and bumble bees have species-specific responses to changes in floral resources.[121] New interactions between plants and pollinators may be created, while others go extinct. New competitive interactions will arise as lowland species move up in altitude and then overlap with the high-altitude species already present on mountain tops. We do not yet know whether resource partitioning will allow these newly enlarged communities to persist, or whether some species will be extirpated.

Network perspective on alpine pollination

In the past couple of decades, pollination biologists interested in community-level interactions have begun to adopt a network approach to such studies. The topology of these networks, similar to the food web perspective that has been around much longer, can provide information about patterns that might not otherwise be easily discerned. The relationships can be quantified through indices such as distributions of connectivity (the number of links per species of plant or pollinator).[122] Because they may be relatively sparse in terms of species, alpine pollination networks may not exhibit the modularity of more complex networks, where modules include "one or a few species groups with convergent trait sets that may be considered as coevolutionary units."[123] Ramos-Jiliberto *et al.*[124] found that network topology is strongly and systematically affected by elevation, as the number of potential pollinators per plant decreased with increasing altitude, and there were fewer and more strongly connected modules. In a repeat of a bumble bee survey from almost 50 years earlier, Miller-Struttmann and Galen[125] used a network perspective to look at altitudinal distributions of a montane-alpine bumble bee community. The alpine networks were more highly nested than either subalpine or montane networks due to increased asymmetric specialization, and alpine communities had higher niche overlap than subalpine bees. Their results imply that pollination of alpine plants will change dramatically as the subalpine species with different foraging strategies move up into the alpine.

Santamaría *et al.*[126] assessed the robustness to species extinction of two Spanish alpine pollination networks and found that they ranked intermediate to high compared to other networks. That robustness could be a function of the networks' connectance and asymmetry, as those two variables showed a positive relationship with robustness. They called for additional research on "(1) the order in which network species will get extinct, (2) how species rewire once they have lost their partners, and (3) how much species depend on their mutualistic interaction," to further our understanding of conservation needs of alpine systems.

Albrecht *et al.*[34] used quantitative network analysis to study the structure of plant–pollinator communities at seven sites along a chronosequence from 8 to 130 years since land was uncovered by glacial retreat, in a nice example of a space-for-time substitution. Species richness of plants and pollinators increased along the chronosequence at least for the first 80 years after deglaciation, as did measures of interaction diversity and evenness. At the two youngest sites, they found that bees dominated, whereas in the more mature communities flies were dominant. The network measure of nestedness—"a nested pattern of interactions leads to greater biodiversity in mutualistic systems such as plant–pollinator networks"—[127] increased along the temporal sequence, but specialization and the asymmetry of interaction strength declined in the first half of the sequence.

Fang and Huang[35] looked at variation among 4 years of quantifying pollination networks in alpine meadows in China and found that "ranked positions and idiosyncratic temperatures (temperature is a measure of disorder of the network) of both plants and pollinators were more conservative between consecutive years than in non-consecutive years." Despite the high turnover in network composition among years, which highlights the need to conduct multiyear studies, the core groups (those that formed link nodes that were persistent across years) were found to be much more stable than peripheral groups. In their networks, "plants were relatively specialized, exhibiting less variability in pollinator composition at pollinator functional group level than at the species level." They speculated that the redundancy in these networks could help to buffer them against the intrinsic variability that characterizes alpine environments.

These examples demonstrate the utility of the network perspective for alpine pollination studies in order to compare them with other ecosystems and suggest that additional work along these lines is warranted. Long-term studies that encompass the temporal variability characteristic of alpine areas, studies of a variety of alpine study sites around the world, and studies that provide a baseline for future comparison will all be valuable contributions.

Needs for future research

Alpine research presents logistical constraints, as the growing season is short, weather can be extreme, and access can be difficult. Some of these constraints can be addressed now with remote sensing and data loggers, and in some cases the use of remote cameras. For example, remote automated cameras have proved useful both for documenting phenology[128] and visitation to flowers,[129] and ultrasonic snow sensors provide useful phenological information.[130] These tools will facilitate future research in the alpine, although careful observation will remain an essential component for studies of pollinators and pollination.

The value of historic surveys of altitudinal distributions and community composition of both plants and pollinators has been increasingly recognized, and a growing number of them have now been repeated in order to ascertain how species are changing ranges and interactions. Contemporary baseline surveys of the phenology and distribution of individual species, and of whole communities too, are valuable both for the insights they provide about current status and as the foundations for future surveys as species continue to respond to the changing climate. Studies in a variety of areas are beneficial, as climate change and habitat losses will not proceed uniformly.[10] Monitoring efforts have begun for alpine vegetation in California[131] and globally through the GLORIA network.[7,132]

Given the inherent variability, both spatial and temporal, that characterizes alpine ecosystems, there is limited value to studies that only include a single small plot or single field season. Multiyear studies with plots in a diversity of microhabitats will provide more reliable insights into how stable network interactions are, how much flowering phenology can vary across a landscape, and thus how the potential for phenological mismatch with pollinators could be affected as the climate changes.

Experimental approaches can provide valuable insights into responses of alpine communities to climate change. Snowmelt, a major driver of alpine phenology,[87] is relatively easy to manipulate to study effects on plant phenology, growth, and fecundity,[133–136] although this is probably not possible at large spatial scales. There have not yet been snowmelt manipulations to study the effects on pollinators, which in the alpine would mostly be overwintering underground. The International Tundra Experiment (ITEX Network) and the open-topped chambers it has recommended to raise ambient growing-season temperatures by ∼1 °C are likely to continue to provide insights into the consequences of warming in the alpine, although they focus on just the plants and not pollinators.[137] Modeling studies of snowpack and snowmelt[138] will also facilitate projections of changing phenology, given the tight link among those variables in the alpine environment.[31] Transplant experiments can also be a useful tool for investigating changes likely to result from climate change, effecting space-for-time substitutions[139] and providing insights into differences between low- and high-altitude populations.[140]

With regard to pollination, there has been a call for additional studies of pollen limitation in the alpine,[107] and additional network studies would be a valuable contribution, particularly in understudied alpine areas of the world. Regional differences that have already been identified suggest that additional studies will provide new insights as the geographical distribution of alpine studies increases.[10] For example, a study of alpine pollination in Greece found that in a number of cases, the phenological and flower visitor patterns deviated from those observed in other alpine environments, perhaps because of a Mediterranean influence.[54] There is a particular need for work on tropical alpine systems, which comprise about 10% of global alpine areas[141] but are likely changing more rapidly than temperate zone alpine areas in response to climate change. For example, tropical glaciers are disappearing rapidly[15] as are temperate ones too.[142]

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Competing interests

The author declares no competing interests.

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