

High elevation insect communities face shifting ecological and evolutionary landscapes

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Climate change is proceeding rapidly in high mountain regions worldwide. Rising temperatures will impact insect physiology and associated fitness and will shift populations in space and time, thereby altering community interactions and composition. Shifts in space are expected as insects move upslope to escape warming temperatures and shifts in time will occur with changes in phenology of resident high-elevation insects. Clearly, spatiotemporal shifts will not affect all species equally. Terrestrial insects may have more opportunities than aquatic insects to exploit microhabitats, potentially buffering them from warming. Such responses of insects to warming may also fuel evolutionary change, including hitchhiking of maladaptive alleles and genetic rescue. Together, these considerations suggest a striking restructuring of high-elevation insect communities that remains largely unstudied.

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Rapid change in high mountains

Around the world, high-mountain regions are changing at an unprecedented rate [1]. In these regions, which are typically above tree line between 2000–4000 m, the hallmark of change is rapidly rising air temperature, with strong impacts on glacial cover [2], streamflow [3], and dissolved oxygen levels [4••], among other factors. Together, these changes pose a grave risk for small ectotherms, especially insects [5•]. To understand this risk, most studies have focused solely on abiotic factors, particularly temperature [6–9]. However, the best

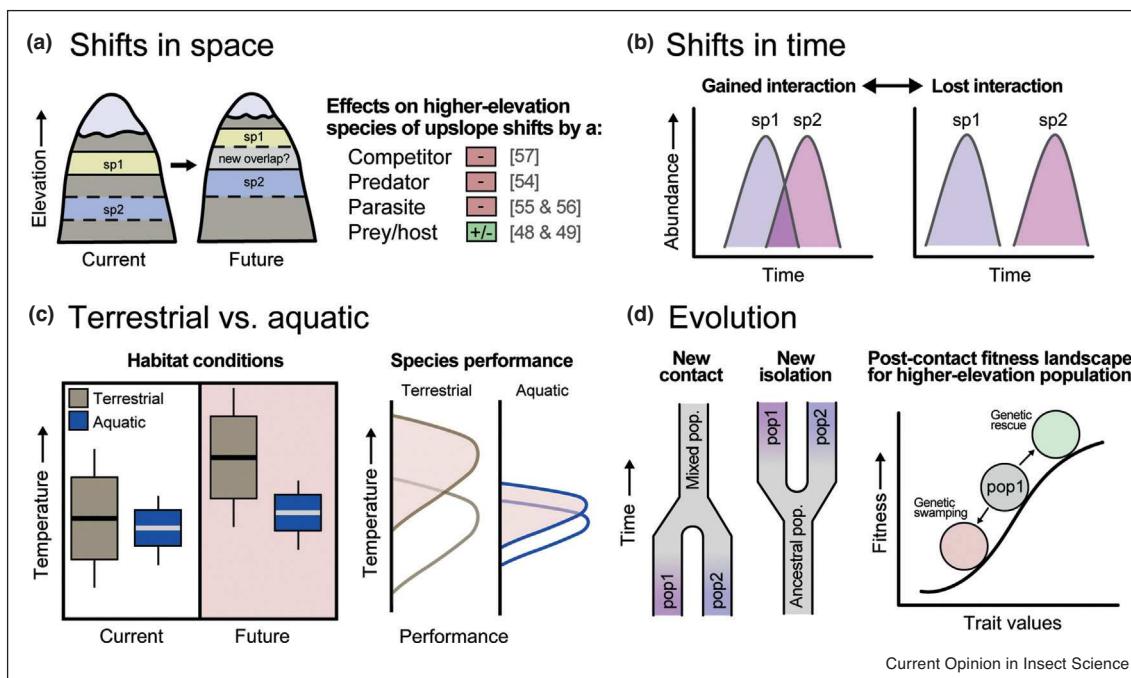
documented organismal responses to rising temperature – physical migration in space, often uphill, and phenological shifts in time for spatially co-occurring taxa [10,11] – will alter interactions and potentially restructure insect communities [12•]. Although this idea has been discussed in other contexts [13–15], it has not been considered for high-elevation insect communities, a key research gap given the rapid, ongoing climate change threats to mountain ecosystems [1]. Here, we outline how climate change may reassemble high-elevation communities through shifts in space and time, how patterns of community (dis)assembly across elevation may differ between terrestrial and aquatic insect species, and how these ecological changes may translate to evolutionary change (Figure 1).

Climate-driven shifts in space and time

Warming in mountain ecosystems is promoting upslope movement of insects [16,17] and the organisms with which they interact [18,19] (Figure 1a). Patterns of movement, however, can be complicated. For example, over the past century, bumble bees from southern latitudes shifted to higher elevations by up to several hundred meters whereas species from northern latitudes moved to lower elevations [20]. Although cooler temperatures at high elevation may generally favor upslope migration, a number of other factors associated with higher elevation may constrain this movement, including shorter growing seasons [21], altered snow cover patterns [22], and linked effects of changing temperatures and other abiotic factors [4••]. For instance, populations of the leaf beetle in the Sierra Nevada Mountains may be prevented from uphill migration by hypoxia, which depresses larval performance and magnifies the effects of other factors like low temperature [23••]. Low-elevation species that successfully colonize high elevations will likely be those for which all life-cycle stages are able to cope with new high-elevation conditions [24].

Upslope movement may not be possible for species residing at the highest elevations. These species might be effectively 'trapped' because either they have reached the top of the mountain or there may not be suitable habitat beyond their current range edge [25]. This may result in the local extinction of many high-elevation endemics. However, a recent study has shown that a high-elevation aquatic insect community presumed to be imperiled by glacier loss has persisted despite widespread deglaciation in the highest elevations of Glacier

Figure 1



(a) Warming is causing upslope shifts of lowland species ('shifts in space') resulting in new species interactions that may be positive or negative, depending on the functional group of the shifting species (table at right: numbers indicate studies that have documented the general impact of shifting functional groups on native species). **(b)** Phenological shifts in insect abundance ('shifts in time'), can lead both to new species interactions and losses of previous ones. **(c)** Aquatic and terrestrial insects may be differentially impacted. Water temperatures tend to be cooler and less variable than nearby terrestrial temperatures, which are also projected to increase more drastically in the future. Terrestrial insects may therefore require large shifts in thermal performance curves (TPCs) or move greater distances to keep pace with changing temperatures. Aquatic species and life stages, however, may be buffered for longer despite narrower TPCs. **(d)** Novel ecological interactions may ultimately result in evolutionary change in high-elevation communities. Movement of populations (or species) across elevation could result in hybridization or isolation; and alleles from the lowlands may have a negative (maladaptive) or positive (rescue) effect on high-elevation insects.

National Park, USA [26]. Indeed, for some species, the need to escape may not arise if they have the physiological tolerance to cope with changing temperature [27–29]. For example, high-elevation aquatic insects have surprisingly wide thermal breadths compared to low elevation counterparts, which may have evolved as a result of the greater climatic variation typical of some high-mountain areas [8]. Thus, responses to changing conditions may largely depend on species' physiological ecology. Nevertheless, empirical studies indicate that many lower elevation species have already begun migrating upslope as their native habitats become increasingly unsuitable [30].

In addition to driving uphill migration, rising temperatures may alter the timing of life-history events, changing the extent of temporal overlap among species in high-elevation communities [31,32]. Such phenological shifts could eventually lead to changes in community structure and dynamics. Restructuring of communities could arise if winter and spring warming together with earlier spring snowmelt alter physiology and development during winter dormancy [22]. Ultimately, this will affect overwinter

survival and spring emergence timing. These and related temporal shifts will have two general outcomes: generation of new interactions or decoupling of existing ones (Figure 1b). When researchers experimentally warmed an alpine meadow, for example, an important interaction was lost because pollinating moth larvae emerged later, but the host plant for the moth flowered and senesced earlier [33]. The complexity of responses such as these suggests that understanding how phenology will change with rising temperatures will require both experimental approaches and long-term observations of high-elevation insect communities.

Varying responses in terrestrial and aquatic taxa

A number of considerations indicate that expected shifts in space and time will differ for aquatic and terrestrial insects. The high specific heat capacity of water relative to air underlies two predictions. First, aquatic habitats will be more buffered from future warming. Aquatic insects will therefore experience smaller average increases in temperature and be required to make smaller behavioral

or physiological adjustments than terrestrial insects (Figure 1c). Second, temperature variability in space and time is generally much lower in aquatic relative to terrestrial habitats. Although thermal heterogeneity can develop in still water (including ponds, lakes, and river and stream pools [34]), it is less likely to do so in swiftly moving mountain streams and is generally less pronounced than thermal heterogeneity on land. So, although terrestrial insects may have to cope with larger changes in mean temperatures, they will also have more opportunities to exploit microhabitat variation to select appropriate microclimates [35,36]. Further, aquatic insects may struggle to take advantage of thermal variation due to the greater difficulty of locomotion in water compared to air [37].

Given decreased thermal variation in water, aquatic insects may have evolved narrower thermal tolerances [28] and live closer to their thermal limits, potentially making them *more* susceptible to warming conditions than terrestrial species (but see Ref. [38]). However, recent work with a common mayfly revealed that plasticity in thermal tolerance through development can facilitate population persistence across highly variable thermal conditions [39*]. Rising temperatures may also increase an aquatic insect's oxygen demand relative to stream oxygen availability, and in some cases could cause insects to succumb to oxygen limitation at warm temperatures [40]. By contrast, upper thermal limits for terrestrial insects appear to be unrelated to oxygen levels, at least at biologically realistic oxygen partial pressures [41].

Because aquatic insects have a limited ability to capitalize on microclimates, and have narrower thermal tolerances, they may be more likely than terrestrial insects to move upslope to escape warming temperatures. Moving upstream will be especially challenging for aquatic insects, given the confined paths for movement of immature stages (but see Ref. [42]). At the highest elevations, the harsh conditions of glacial runoff (e.g. low temperature and high conductivity) have historically acted like a barrier to upstream dispersal of lower elevation aquatic insects [43]. But as glacial runoff decreases with rising temperature, such abiotic barriers may be lifted, thus facilitating upstream migration. Most aquatic insects have a winged terrestrial adult phase, the primary life stage capable of upslope dispersal. Temperatures experienced by aquatic larvae can influence morphology of terrestrial adults and alter dispersal ability [44*]. Given that juveniles and adults occupy divergent thermal conditions, they likely also differ in thermal tolerance and in capacity to thermoregulate, which together may drive them to respond asynchronously to a warming climate.

Novel interactions arising from shifts in space and time

Insect communities are structured mainly by predation, disease loads, competition, and the quantity and quality

of available resources [45]. Climate change at high elevations will alter the strengths of existing interactions – particularly when interacting species have different thermal performance curves such that shifts in temperature lead to differential changes in performance among the interactors [46]. In addition, species and population shifts in space and time will generate many qualitatively new kinds of interactions [13]. Because plants are important resources for many insects, most studies have focused on spatial and phenological shifts involving plant-herbivore interactions, but few of these focus on high-elevation regions [47]. Insects that can switch hosts may benefit from the immigration of new host species. For example, after its distribution shifted in response to warming, the comma butterfly altered its host preference from a native plant to two nonnative species and subsequently grew and survived better [48]. Other insects may be negatively impacted as immigrating plants outcompete native plants or adapt to high elevation and produce tougher new leaves with reduced nutrients and increased levels of secondary compounds, making them unsuitable for supporting growth [49]. Insects that rely on new leaves in the spring may also be negatively impacted if warming causes asynchrony in the timing of insect emergence and leaf-out in the spring. Elevation differences in the timing of leaf-out dates for tree species in the European Alps, for instance, advanced strikingly from 1960 to 2016 [50] (but see Ref. [51]), reflecting stronger warming at higher elevations [52]. If these results hold more generally across geographic regions and plant taxa, then widespread mismatches between leaf-out and the appearance of spring insect herbivores are expected.

Empirical studies on the formation of new predator-prey or competitive interactions following climate change are rare. Nevertheless, these interactions are likely to have a strong impact on insect communities as new parasitoids, predators [53], and competitors [32] appear in high-elevation regions. High-elevation insects may be especially imperiled if predators invading from low elevations are generalists, as was found in an experimental transplant of lowland carnivorous stoneflies into an alpine stream [54]. Similarly, when the Brown Argus butterfly expanded its latitudinal range northward to track cooler temperatures, it encountered novel, generalist parasitoids, which quickly adopted the butterfly as a new host [55]. Whether most parasitoids moving upslope will be able to switch to endemic high-elevation hosts is presently unknown [56].

The arrival of new species seeking the same resources can create new competitive interactions. For instance, warming in an arctic pond induced major changes in the resident chironomid community, presumably through new competitive interactions with warm-adapted species [57]. In the Swiss Alps, alpine plant performance was significantly reduced through competition with novel competitors experimentally transplanted from the

lowlands [58]. If high-elevation species are cold-temperature specialists, then generalist competitors from lower elevations may be particularly problematic.

In addition to bringing about new ecological interactions, warming may alter the outcome of existing interactions due to differences in thermal sensitivities. We know of no study exploring such trophic changes in high-elevation insects, but elegant experiments have been conducted in other systems. When faced with warming, for example, predatory field spiders relocated to cooler habitats, altering spatial overlap with less sensitive grasshopper prey and shifting interactions in the food chain [59^{••}]. Research aimed at understanding the effects of differential thermal sensitivities will be key in predicting winners and losers among interacting species in warming habitats.

Evolutionary changes following novel ecological interactions

Not only will the arrival of new resources, predators, and competitors alter community composition and the dynamics of species interactions, but in the presence of adequate standing genetic variation, it could also drive rapid evolutionary change. For example, soapberry bugs native to African grasslands have rapidly evolved longer mouthparts to match and exploit fruits of an invasive balloon vine [60^{••}]. In other insects, such as nymphalid butterflies, high speciation rates are strongly associated with host-shifts, though empirical documentation of these radiations remains rare [61].

A less appreciated possibility is the rise of hybrids that are more adept at dealing with change [62]. Hybrid alpine butterflies, for example, persisted in extreme alpine conditions even though both parental species could not [63]. Unlike the parental species, hybrids did not attach eggs to the host plants, so that when the plants died in winter or blew away with strong winds, the eggs remained close to new plant growth in the following spring. Similarly, lab-reared hybrid copepods could tolerate much warmer temperatures than either parental species [64]. Hybridization among species, or even gene flow between locally adapted populations, may thus create novel combinations of alleles that are well-suited to new conditions, or that provide the necessary genetic background for rapid adaptation under novel selective regimes.

Increased tolerance to heat stress in hybrids (and also low-elevation immigrants) may not always be beneficial, especially if mechanisms for different types of stress responses lead to trade-offs. Individuals may derive greater heat tolerance from altered membrane compositions that are more stable at high temperatures – but which may also cause membranes to be too solid at low temperatures [65]. Increased heat tolerance may make hybrids more susceptible to cold snaps, thus driving the evolution of maladaptive winter physiologies.

Evolutionary change may also arise from the uphill movement of populations adapted to low elevations. Most simply, previously isolated populations may be reconnected with new gene flow, homogenizing their genetic differences. Alternatively, uphill movement of some, but not all, of a population (or shifts in reproductive timing [66]) could cause an existing population to diverge into two or more, perhaps eventually promoting climate-induced speciation (Figure 1d). If local adaptation exists, one potential consequence of an uphill shift is the introduction of maladaptive alleles that decrease the ability of resident populations to survive high-elevation conditions (Figure 1d). For example, introduced alleles from stick insects locally adapted to one host plant reduced the patch occupancy of stick insects locally adapted to another by disrupting their patterns of camouflage [67].

An alternative outcome is genetic rescue, in which an influx of low elevation alleles introduces new genetic variation into small, inbred, high-elevation populations in a way that potentiates evolutionary change (Figure 1d). Although no specific accounts of genetic rescue exist for montane insects, there are examples in other taxa. For instance, headwater populations of Trinidadian guppies experienced remarkable increases in population size owing to higher recruitment and survival following an experimental introduction of low elevation guppies from the same drainage [68].

Implications and a call to action

Insect communities in high-mountain regions are facing rapid change. Increasing temperatures are causing shifts in species distributions and phenologies that will lead to new ecological interactions and evolutionary change. Thus far, research on high-elevation insects has been limited, due in part to the difficulty of accessing alpine areas, with little known of their endemic communities and how they are being altered. We identify three areas of research that should be addressed. First, observational work is needed to establish current relationships among members of high-mountain communities. Second, long-term monitoring efforts are critical to understand how community composition and dynamics are changing over time. Third, experimental research is required to quantify key physiological traits and underlying genetic bases to predict current high-elevation insect sensitivities, evolutionary potentials, and response to encroaching lower elevation taxa. Together, these efforts will vastly improve our understanding of high-mountain insect communities and strengthen our ability to predict their responses to climate change.

Conflict of interest statement

Nothing declared.

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