

What, if anything, can studies of adaptation to altitude reveal about responses to climate change?

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Abstract

Understanding the impacts of global climate change on biodiversity is critical to its conservation. Existing frameworks within evolutionary biology can help us predict whether, and under what conditions, adaptation may be a sufficient means for population persistence in a changing environment. Here, we consider the relevance of mountain ranges as natural systems for studying this process. Mountains compress environmental variation into short geographic distances, allowing adaptation across divergent environments to be studied at tractable spatial scales and, importantly, often in the presence of ongoing gene flow between markedly different habitats. We review empirical evidence for local adaptation across elevational gradients and argue that systems of migration-selection balance provide a particularly useful framework for connecting altitude adaptation to rapid climate adaptation. However, the analogy between altitude adaptation and climate adaptation is conditional. Elevation is a composite of temperature, oxygen availability, precipitation, radiation, and other environmental variables, only some of which are relevant to anthropogenic climate change. Moreover, inferring temporal evolutionary responses from spatial differentiation relies on a space-for-time substitution that may not always be valid. We argue that the greatest value of mountain systems therefore lies in using elevational gradients to explore whether responses to spatially varying selection can translate into evolutionary rescue. Integrating genomic and phenotypic approaches with experimental validation will be particularly important for determining when existing local adaptation provides populations with the capacity to keep pace with climate change.

1 Introduction

Habitats change across latitude and altitude, and in recent decades, altitude adaptation has become an increasingly popular area of enquiry (Gamba et al., 2024; Montejo-Kovacevich et al., 2019; Montejo-Kovacevich et al., 2022; Projecto-Garcia et al., 2013; Storz et al., 2007; Storz & Cheviron, 2021). Altitude adaptation can occur both within and between species. Here we focus primarily on within-species adaptation to altitude, which is a form of local adaptation to a multifaceted set of biotic and abiotic conditions (Klepsatel et al., 2014). This review is motivated by the observation that research on altitude adaptation increasingly also makes a connection to adaptation to climate change (Figure 1). Adaptation to climate change is a form of evolutionary rescue — a scenario in which population extinction is prevented through the process of adaptation (Bell, 2013; Gomulkiewicz & Holt, 1995). But what exactly is the relationship between local adaptation to altitude and evolutionary rescue in the context of climate change? We focus on two distinct aspects of this relationship: (i) the extent to which research on altitude adaptation can provide insight into climate change adaptation, i.e. a space-for-time substitution; (ii) the extent to which local adaptation to altitude on mountain ranges might facilitate evolutionary rescue through climate change adaptation.

Specifically, we briefly outline how local adaptation is measured for the benefit of readers new to this field (Box 1). We then link this to studies of altitude adaptation (Section 2), and summarise the approaches and challenges involved in demonstrating altitude adaptation (Section 3). We next discuss the relationship between adaptation to altitude and climate change, arguing that understanding the evolution of altitude adaptation can shed light on

the potential for adaptation to sudden climate shifts (Section 4). In the same section, we use a simple verbal model to discuss the conditions under which local adaptation with gene flow (i.e., many cases of altitude adaptation) can lead to evolutionary rescue (e.g., adaptation to climate change). We then set about challenging the simplifying assumptions of this model, exploring the ways in which selection pressures relevant to altitudinal adaptation are not relevant to climate change, and arguing that disentangling these factors is essential for understanding the possibility of evolutionary rescue (Sections 5, 6, and 7). Throughout, we also highlight the differences in local adaptation to altitude at different latitudes (Box 2) and the role of physiological constraints across different taxa in forming altitude adaptation (Box 3).

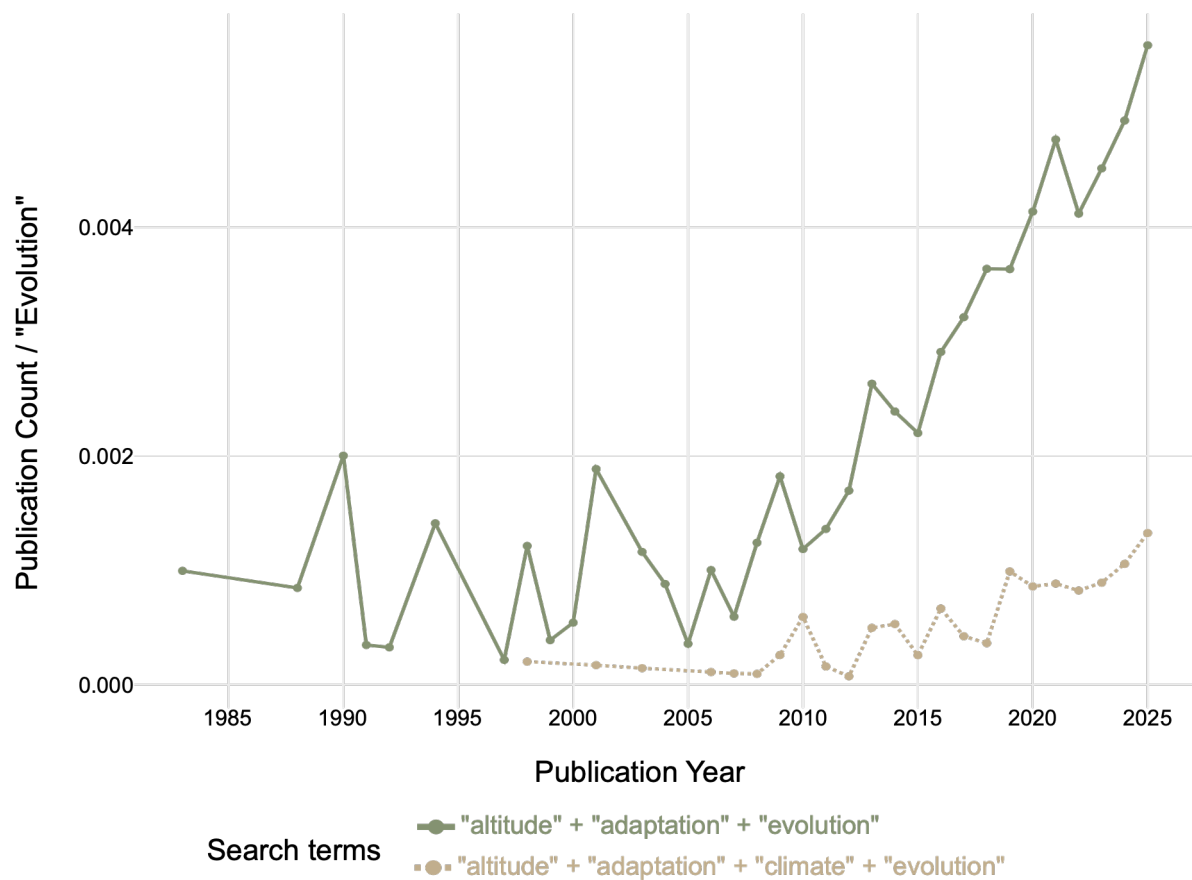


Figure 1 | Studies of local adaptation to altitude have increased in prevalence in recent decades. A Web of Science search for papers published on altitude adaptation (green, solid) and climate change (brown, dotted) between 1800 and 2025 showed an upward trend in rate of publications. We controlled for inflation in the scientific literature by dividing the counts for each search term by the search term "Evolution".

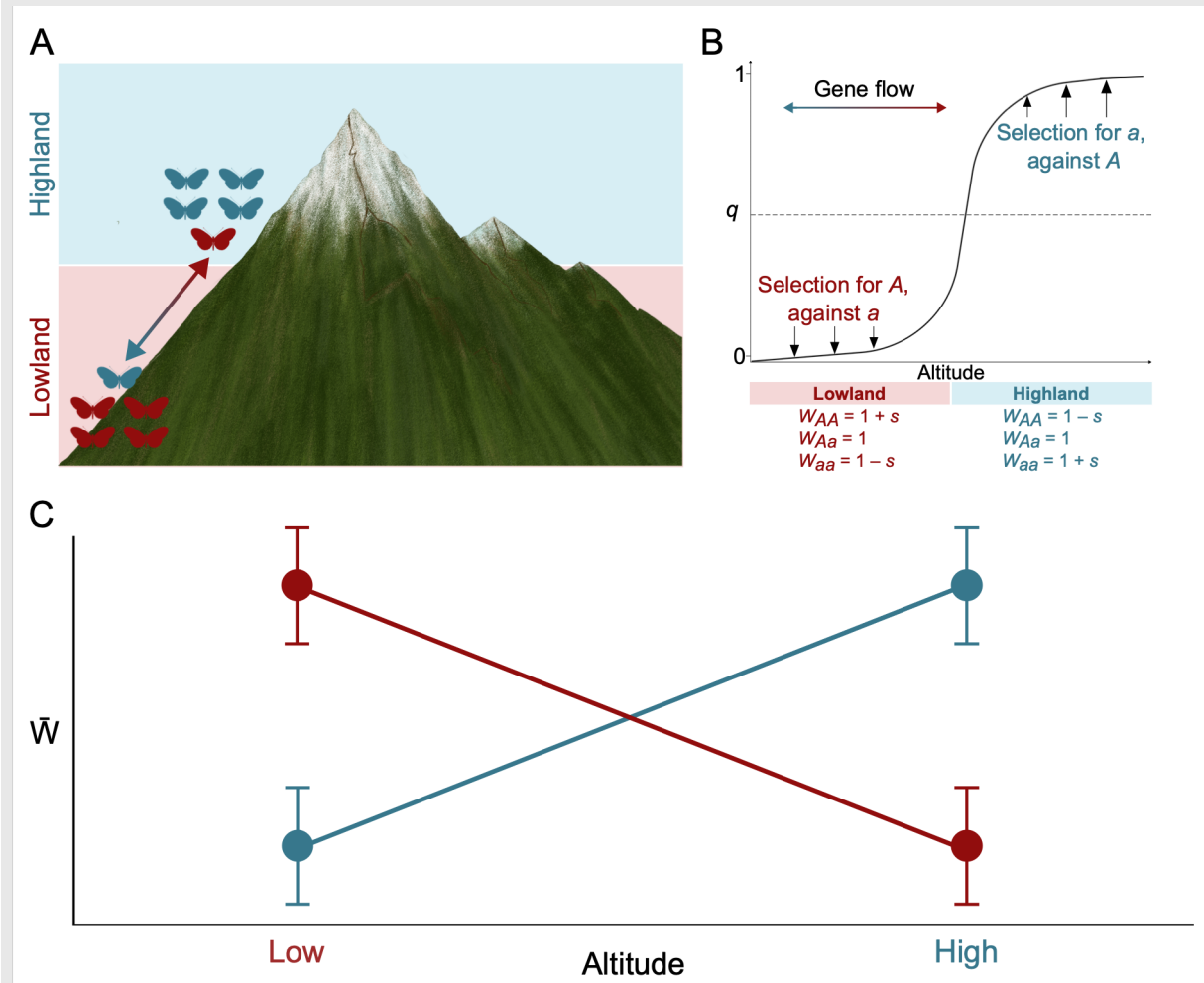
Box 1: How is local adaptation measured?

Local adaptation occurs when the fitness of a population at its native site is greater than the fitness of any other population introduced to that site (Kawecki & Ebert, 2004). This can only occur when the strength of natural selection outweighs the countervailing force of gene flow from maladapted populations, including in situations where there is no gene flow (i.e., local adaptation in allopatry). This is modelled as migration-selection balance, the equilibrium that results from the opposing forces of divergent selection (causing differentiation) and

gene flow (causing homogenisation) between environments (Burger & Hofbauer, 1994; Haldane, 1930; Wright, 1931; Yeaman & Whitlock, 2011). Direct evidence for local adaptation comes from measurements of higher fitness in a focal population's local environment relative to counterparts drawn from other environments (Kawecki & Ebert, 2004). These genotype-environment interactions can be detected using reciprocal transplant experiments and common garden studies (Blanquart et al., 2013).

Data-driven genomic approaches, such as genomic scans for outlier summary statistics, can also be used to detect genomic signatures of local adaptation (Haas & Payseur, 2016; Martin & Jiggins, 2013). However spatially structured genetic differentiation can also arise through drift and population structure (Tigano & Friesen, 2016), through globally beneficial mutations spreading across structured populations (Booker et al., 2021) or through loci linked to reproductive isolation independently of divergent selection on locally adapted genes. Genomic approaches are most powerful when gene flow occurs frequently enough to homogenise between-environment genetic differentiation resulting from drift. Hence, hybrid zones along environmental gradients, where genetically distinct populations (which may or may not be different species) meet and hybridise, provide natural laboratories for studying local adaptation (Barton & Hewitt, 1985; Gompert et al., 2017). Geographic cline analysis represents a particularly useful set of tools for describing the genetic architecture of local adaptation in this context (Szymura & Barton, 1986; Taylor et al., 2015). This requires sampling allele frequencies in populations along a transect (e.g. from low to high altitude) such that the change in allele frequency across space can be measured. Loci with steep allele

frequency changes that are coincident with an environmental transition are those expected to be subject to divergent selection in a model of migration-selection balance.



Box 1 Figure Legend | [A] Lowland (red) and highland (blue) populations remain connected by gene flow (arrow), introducing a migration load into the resident population. [B] Migration-selection balance. For a string of subpopulations along an altitudinal gradient, allele A (with frequency $1-q$) is selected against in the highlands and selected for in the lowlands, and vice versa for allele a (with frequency q). Gene flow continuously reintroduces alleles from the alternate environment. Panel adapted from Mallet (2001) [C] Local adaptation to altitude. The average fitness ($\bar{W}$) of lowland individuals (red circle) is greater in the lowland than it is for any other population, and vice versa for highland individuals (blue circle).

2 Mountains as natural laboratories for studying local adaptation

Mountains — characterised by a ruggedness and ecological gradient that host diverse habitats (Körner et al., 2007, 2011) — present ideal biogeographic contexts in which to study local adaptation. This is due to the extreme and repeated environmental changes that occur over relatively short distances. Elevational gradients compress contrasts in abiotic and biotic conditions observed across tens of degrees of latitude into a matter of kilometres. For example, the same change in mean annual temperature over 1 km of altitude (5°C) occurs over 1,000 km of latitude (Jump et al., 2009). Ambient air temperature changes predictably with elevation, while a suite of other abiotic variables — including atmospheric pressure, ultraviolet exposure and precipitation — also covary with altitude (Ghil & Lucarini, 2020). Altitude adaptation recurs across a broad range of taxa exposed to similar selective pressures, including low temperatures, hypoxia, and elevated UV radiation, providing replicated opportunities to ask whether similar environments produce similar adaptive responses (but see Box 2).

Hypoxia provides perhaps the clearest example. Human populations native to the Tibetan Himalayas and Peruvian Andes have independently evolved distinct genetic solutions to chronic oxygen limitation despite occupying broadly comparable high-altitude environments. Genome-wide scans in Tibetan highlanders identify positively selected haplotypes at *EGLN1* associated with decreased haemoglobin concentration (Simonson et al., 2010; Yi et al., 2010), whereas Peruvian Andean highlanders show a largely independent genomic signature for the same phenotype (Zhu et al., 2026). Convergent physiological adaptation can therefore arise through different molecular routes. A similar pattern occurs in deer mice,

where high-altitude populations have evolved haemoglobin with increased O₂-binding affinity, enhancing pulmonary O₂ loading under hypoxia (Storz et al., 2007). The unusually high oxygen affinity of haemoglobin in the Andean frog *Telmatobius peruvianus* provides a further example of physiological adaptation to hypoxia (Weber et al., 2002).

Thermal tolerance is also a recurrent target of selection in montane populations given the predictable altitude-associated changes in temperature. For example, high-altitude populations of deer mice, in addition to their increased O₂ affinity, have evolved enhanced aerobic thermogenesis via increased capacity to oxidise lipids, as well as changes in regulation of genes involved in oxidative phosphorylation (Cheviron et al., 2012). Elevation also interacts with plasticity in thermal tolerance. For example, tropical insects at higher elevations display greater plasticity in thermal tolerance compared to lowland tropical insects (Holzmann et al., 2026).

Pigmentation is also repeatedly associated with altitude, though the mechanism of selection favouring pigmentation is not always consistent. In *Drosophila melanogaster*, more melanised variants are observed in sub-Saharan mountain ranges, peaking highland Ethiopia (1,600 to 3,100 m). Here, UV intensity is identified as a variable controlling pigmentation in a manner consistent with the prediction that animal colouration varies with climatic variation, also known as Gloger's rule (Bastide et al., 2014; Delhey, 2017). Colourations may also respond to thermal pressures. For instance, the thermal melanism hypothesis predicts that darker individuals and species heat faster than lighter ones and should therefore be found in colder habitats (Clusella Trullas et al., 2007). Such a pattern is observed in relation with

climate variables in lizards (Clusella-Trullas et al., 2008), and across a latitudinal gradient in butterflies (Kang et al., 2021), and is particularly strong in the near infrared range. Similarly, highland alpine butterfly species absorb more near-infrared radiation (Ashe-Jepson, 2026). However, a positive association between pigmentation and altitude is not observed universally. For example, transparent species of tropical clearwing butterflies (Ithomiini) dominate high elevations despite their reduced ability to absorb solar radiation and thermoregulate (Ossola et al., 2025).

Convergent altitudinal adaptation can also be studied using a ‘reverse genetics’ approach: comparing replicate highland and lowland populations to identify alleles consistently associated with altitude. For example, in two tropical *Heliconius* butterfly species, replicated comparisons across elevational gradients in independent populations on both sides of the Andes identified convergent altitude-associated genetic differentiation, including shared regions of the genome implicated across independently evolving populations (Montejo-Kovacevich et al., 2022). This result suggests that standing genetic variation can facilitate local adaptation to similar elevational gradients.

Box 2: Are all mountains made equal?

Environmental variables that vary strongly with altitude are also shaped by latitude. Hence, equivalent elevational gradients may capture different environmental conditions. Janzen argued that low seasonal temperature variation in tropical environments favours narrower thermal tolerances (Janzen, 1967). Moving between elevations may consequently expose tropical organisms to temperatures lying outside those normally experienced within their

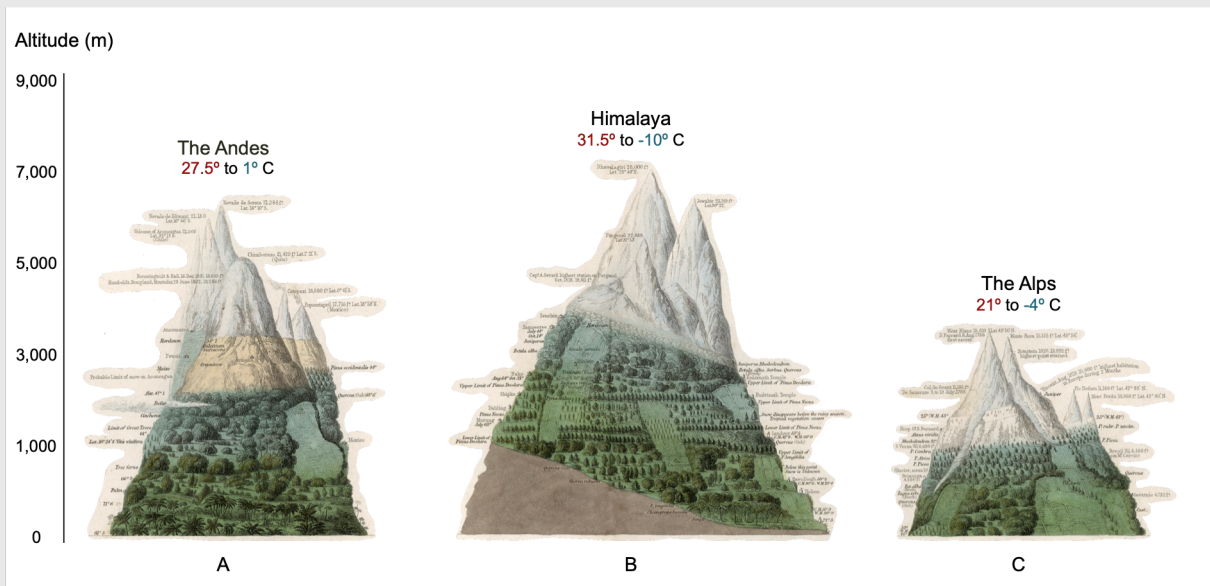
home range. This makes a given tropical elevational distance a stronger physiological and dispersal barrier than it would be in a seasonal temperate environment (Ghalambor, 2006). Consistent with this prediction, elevational ranges generally expand with latitude across several vertebrate groups (McCain, 2009). Additional empirical studies further support this — tropical montane insects have narrower thermal tolerances, lower dispersal and greater population differentiation than related temperate taxa (Polato et al., 2018).

However, Janzen's prediction is not a law. For example, comparisons of tropical and temperate alpine plants have not shown the expected broader thermal tolerances at higher latitudes (Sklénář et al., 2023). Further, temperate mountains are themselves environmentally heterogeneous. Lowland and montane populations experience pronounced seasonal temperature variation, whereas populations above the treeline occupy alpine environments characterised by short growing seasons, recurrent freezing and strong fine-scale climatic heterogeneity (Hagedorn et al., 2019).

Greater seasonality can increase thermal overlap among elevations, as predicted by Janzen. However, alpine environments can still impose strong local selection and restrict suitable habitat to fragmented high-elevation “islands” — at least in plants (Marx et al., 2017).

Climatic history further complicates this comparison. Repeated glacial expansion and contraction has connected, fragmented and displaced temperate alpine populations, leaving contemporary patterns of diversity and gene flow partly shaped by historical range dynamics rather than present elevational gradients (Smyčka et al., 2022).

Hence, mountain systems should not be treated as interchangeable elevational replicates. Their ecological structure emerges from interactions among latitude, seasonality, topographic heterogeneity, climatic history and position relative to major ecological boundaries such as the treeline (Rahbek et al., 2019). Consequently, the same geographic or elevational gradient can represent very different environmental and evolutionary distances among mountain systems.



Box 2 Figure Legend | The differences in plant distribution in mountain ranges of different latitudes was first described by Humboldt (1807). Figure adapted from “The Distribution of Plants in a Perpendicular Direction”, created by Alexander Keith Johnston in collaboration with Alexander von Humboldt in 1850, showcasing the differences in vegetation and habitat composition at similar elevations in [A] the Andes, [B] Himalaya, and [C] the Alps. Temperatures in red show that of lowland and blue that of highland. These values are means recorded by Humboldt converted from Fahrenheit to Celsius. The altitudes on the vertical axis were converted from ‘English feet’ to metres.

3 Linking phenotypes, genotypes, fitness, and elevation

Common garden experiments provide strong evidence for local adaptation to altitude (see Box 1). For example, Montejó-Kovacevich et al. (2020) measured heat tolerance in wild *Heliconius* butterflies along the Eastern and Western slopes of the Andes, recording how

221 long individuals could withstand temperatures of 39-41°C before losing locomotor function.
222 Across ten species, highland individuals (~1,400 m) tolerated heat for about 5 minutes on
223 average, compared with about 16 minutes for lowland individuals (~500 m). To test the
224 degree to which this difference was plastic, they reared offspring of *Heliconius erato* females
225 collected from both sites under common-garden conditions at 600 m. The difference in heat
226 tolerance between lowland- and highland-derived broods fell to about 1.4 minutes,
227 indicating that much of the variation observed in the wild reflects plasticity rather than fixed
228 genetic differences. However, experiments such as these are not always possible. Other
229 trait-based approaches, such as measuring morphological, physiological or behavioural traits
230 across elevational gradients and relating their variation to survival or reproductive success,
231 can also provide insight into local adaptation (Kingsolver et al., 2001). In bees, traits such as
232 thoracic hair length and relative wing length have been shown to predict both individual
233 thermal performance and species altitudinal distributions (Peters et al., 2016). Additionally,
234 Jones et al. (2026) recently showed body size, itself a strong predictor of thermal
235 performance and reproductive output (Kalinkat et al., 2015), responds to elevation and the
236 timing of snowmelt in subalpine solitary bees. This suggests that climate effects on body size
237 along altitudinal gradients is partly mediated through phenology and food availability.
238 However, given developmental plasticity can lead to differences in phenotype, a fitness-
239 associated phenotypic cline is not, on its own, evidence of adaptation. A systematic survey of
240 common-garden, reciprocal transplant and molecular studies across animals found recurrent
241 phenotypic divergence between high- and low-elevation populations in traits including body
242 mass, wing morphology, thermal tolerance and melanisation (Keller et al., 2013). The

relationship between temperature, phenotype, and fitness, however, is further complicated by differences in how organisms produce heat and regulate temperature (see Box 3).

Genome scans provide a complementary approach by identifying genotype-environment associations without requiring prior knowledge of the phenotype under selection (Rellstab et al., 2015). However, disentangling signals of adaptation from population structure is a challenge. Patterns resembling local adaptation can arise from a shared demographic history or a globally advantageous mutation spreading through a subdivided population (Lotterhos & Whitlock, 2015). Even so, various approaches can strengthen this inference. Population branch statistics, for instance, use a third population to identify excess allele frequency change along a focal population branch (Shpak et al., 2025). For example, both Montejó-Kovacevich et al. (2022) and Yi et al. (2010) used population branch statistics to distinguish population-specific altitude adaptation from differentiation between low- and high-altitude populations due to drift. Another approach to parse out the effects of demography is to focus on convergent altitudinal adaptation. In general, genome scans are particularly informative in systems where populations under divergent selection regimes are connected by gene flow (e.g., along elevational gradients) where dispersal occurs between populations experiencing different selective environments maintaining a migration-selection balance (see Box 1 and Section 4).

Box 3: Thermal adaptation manifests differently across taxa

The same change in temperature across elevations does not impose equivalent selective pressures across taxa due to physiological and life-history traits. Animals occur across a

metabolic regulatory continuum (ecto- versus endotherms) and a temperature variability spectrum (poikilo- versus homeotherms) (Kardong, 2019). In ectotherms, like insects, body temperature and physiological performance are relatively tightly coupled to environmental temperature, making temperature an important constraint on activity and geographic distributions (Buckley et al., 2012). However, behaviour can mitigate this link. Access to shade, burrows and active thermoregulation, like basking or flying, allows many ectotherms to maintain body temperatures different to those predicted by ambient air temperature (Sunday et al., 2014). Homeothermic endotherms like mammals, on the other hand, maintain comparatively stable internal temperatures through metabolic thermoregulation, buffering environmental temperature variation at a substantial energetic cost (Buckley et al., 2012). Altitude-associated thermal selection may therefore act directly through thermal performance and activity in ectotherms, while in endotherms it may operate by changing the energetic demands of maintaining body temperature. The sessile nature of plants presents a different problem. Individuals cannot behaviourally relocate or actively seek thermal refugia. However, morphology, transpiration and other physiological processes can help buffer tissue temperature from ambient air temperature (González et al., 2025; Zhou et al., 2023).

Comparisons of altitude adaptation across taxa should ideally distinguish ambient temperature from biologically experienced temperature and identify the mechanisms through which thermal exposure ultimately affects fitness (Montejo-Kovacevich et al., 2020). Nonetheless, the different ways in which organisms respond to temperature gradients on mountains likely offers insights into how those same organisms will respond to changing temperatures more broadly.

4 Migration-selection balance across elevational gradients and its relationship to evolutionary rescue

Elevational gradients can provide a means of observing how selection and gene flow jointly determine evolutionary responses to contemporary climate change (Yeaman & Otto, 2011; Yeaman & Whitlock, 2011). This is because mountain ranges represent case studies in which substantial environmental change occurs over short geographic distances, such that dispersal and subsequent gene flow can connect populations experiencing markedly different selective pressures. In cases where connectivity is sufficiently high, this results in migration load: gene flow from maladapted populations (Bachmann et al., 2020; Bolnick & Nosil, 2007; López-Goldar & Agrawal, 2021). While gene flow reduces differentiation caused by drift across much of the genome at selectively neutral loci, loci experiencing sufficiently strong divergent selection can remain differentiated between environments. This increases their contrast against the genomic background in genomic scans. Therefore, mountains represent powerful systems of migration-selection with which to distinguish local adaptation from population structure generated by demographic history. For instance, in the speckled teal duck (*Anas flavirostris*), genes associated with high-altitude physiological function remain differentiated between elevations despite extensive gene flow (Graham et al., 2018). Similarly, rufous-collared sparrows show sharp, environmentally associated mitochondrial clines against a background of much greater nuclear gene flow (Cheviron & Brumfield, 2009). Andean hummingbirds also exhibit altitude-associated allele-frequency clines across remarkably steep elevational ranges despite the homogenising effects of gene flow (Lim et al., 2019). Similar dynamics occur across elevational boundaries between closely related taxa. In *Syma* kingfishers selection appears to maintain lowland and highland species

boundaries despite post-divergence gene flow (Linck et al., 2020). Further, the Andean leaf-eared mouse (*Phyllotis vaccarum*) occupies an elevational range extending from sea level to volcanic summits above 6,700 m, yet shows unexpectedly little genome-wide population structure, implying substantial gene flow across elevation. Despite this connectivity, common-garden experiments simulating elevations up to 7,000 m found that highland mice maintained thermogenic capacity under hypoxia better than lowland conspecifics, associated with greater mitochondrial respiratory capacity in skeletal muscle (Liphardt et al., 2026). If it is the case that these altitude-adapted traits are relevant to climate adaptation (Section 5), these systems provide useful insight into evolutionary responses in the Anthropocene.

As well as presenting useful models of climate adaptation, mountain systems may also be predisposed to rapid evolutionary responses to climate change under some conditions. Montane systems 'compress' extreme environmental variation into spatial scales over which dispersal is more likely to occur. In common frogs (*Rana temporaria*), for example, dispersal was estimated to extend 30% farther geographically along a latitudinal (1,550 km) than an elevational gradient (2 km), yet dispersal relative to the underlying environmental gradient was 3.9 times greater across elevation (Bachmann et al., 2020). This suggests gene flow on the mountain slope connected much more environmentally dissimilar populations. A recent comparison of replicated spruce hybrid zones provides a genomic example of this spatial compression. Here, similar changes in ancestry occur over ~500 km along a broad latitudinal transect but over <10 km within parts of an elevational transect (Nocchi et al., 2026). The elevational transect also contained longer introgressed ancestry tracts, which the authors

335 attribute to steep environmental gradients over short distances reducing mixing by
336 migration and recombination relative to drift and selection. Given this high degree of gene
337 flow in montane systems, we might expect the standing levels of genetic and phenotypic
338 diversity to be enhanced while mean fitness is reduced, compared to a counter-factual
339 scenario of lower gene flow (e.g. latitudinal adaptation). Building on this assumption, we can
340 ask how such a system would respond to an adaptive challenge as sudden as climatic
341 change.

342

343 A simple verbal model connecting local adaptation to altitude and climate change (Figure 2)
344 can be described as follows: sufficient gene flow between lowland and highland populations
345 can increase genetic variation, and therefore phenotypic variation in a polygenic trait, in
346 both populations. Climate change imposes an adaptive challenge — a gap between the new
347 contemporary optimal phenotype under a changed climate and the contemporary trait
348 mean in the population (which reflects a historical fitness optimum). The increased
349 phenotypic variance generated by moderate levels of gene flow means that, under some
350 conditions, lowland or highland populations are more likely to already contain individuals
351 with the contemporary best phenotype, increasing the likelihood of evolutionary rescue (e.g.
352 Figure 2B).

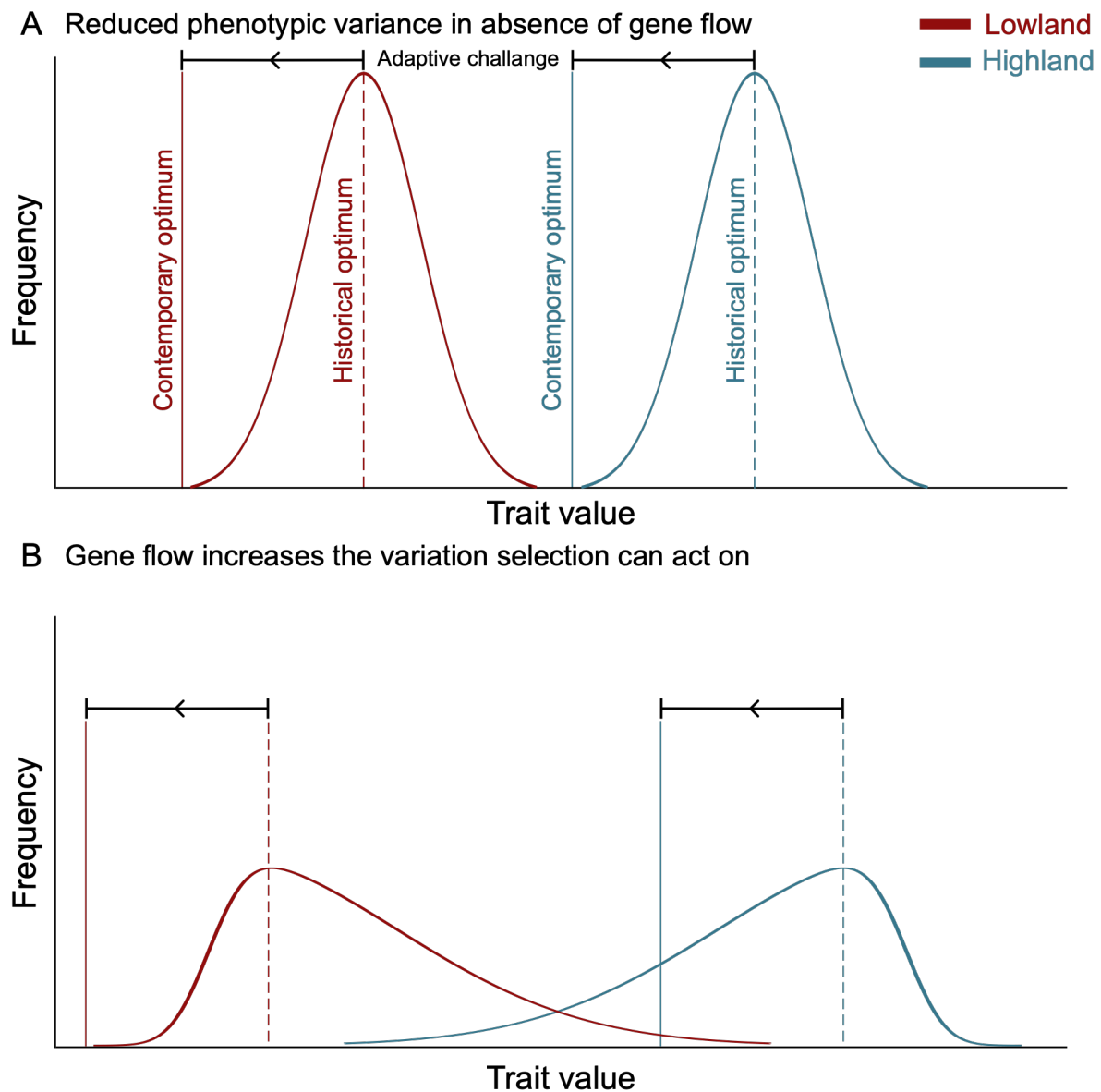


Figure 2 | Verbal model of local adaptation to altitude and climate change. [A] With limited gene flow, the mean of a polygenic trait under divergent selection in lowland (red) and highland (blue) populations reflects the long-term historical optimum in each population (dashed line). A new contemporary trait optimum imposed by a changed climate (solid line) sits beyond the contemporary phenotypic distribution of both populations. [B] As for [A] but with increased gene flow between lowland and highland populations, the phenotypic variance increases such that the new contemporary highland optimum sits within the range of contemporary highland traits, increasing the likelihood of evolutionary rescue through selection on standing variation in the highland population, but not the lowland population.

Therefore, a focus in future research should be quantifying the direction and magnitude of the adaptive challenges climate change imposes on montane species. This will help us understand (i) how genetic architecture or population connectivity constrain evolutionary rescue, and (ii) how plasticity might ‘dampen’ the severity of these challenges. Hybrid zone analyses can be particularly useful in this regard: as Taylor et al. (2015) argue, repeated sampling within hybrid zones can reveal changes in range boundaries, cline shape and position, species interactions, and adaptive introgression in real time.

5 Are all components of altitude adaptation relevant to climate change?

The verbal model described above, as well as the claim that altitudinal adaptation is a useful model of climate adaptation, imply a range of simplifying assumptions. The most significant of these assumptions is that the same selective pressures acting along elevational gradients are those that will differ through climate change. This is, in some cases, reasonable: mean temperature declines with increasing elevation, making elevational gradients an intuitive analogue for climatic warming. As temperatures rise, the thermal conditions experienced at lower elevations are expected to increasingly occur further upslope (Bässler et al., 2013; Freeman et al., 2018; Neate-Clegg et al., 2021; Ramírez-Barahona et al., 2025). However, climate change does not simply push the existing elevational temperature gradient upwards. Rates of warming can themselves vary with elevation, with evidence for elevation-dependent warming in many mountain systems but no globally consistent relationship (Mountain Research Initiative EDW Working Group, 2015; Pepin et al., 2022). Additionally, the biological significance of this gradient depends on organismal thermoregulatory capacity, as discussed in Box 3.

Beyond temperature, other elevation-associated variables are less translatable to climate change. Atmospheric oxygen declines predictably with elevation and imposes strong selection, as the hypoxia examples discussed in Section 2 illustrate, but oxygen availability is not itself undergoing an analogous spatial shift in terrestrial systems under climate change. Consequently, loci underlying hypoxia adaptation will not necessarily contribute to adaptation to climatic warming. Precipitation also varies with elevation in geographically complex and often non-monotonic ways (Celleri et al., 2007; Pepin et al., 2022). Elevation is therefore better understood as a composite environmental gradient, comprising multiple, partly correlated abiotic axes, rather than a direct proxy for climate (Körner et al., 2007). Identifying which components of altitude adaptation are transferable to adaptation under contemporary climate change is therefore central to adopting elevational gradients as study systems.

There is also an important distinction between observing adaptation across an existing environmental gradient and predicting adaptation as that environment changes rapidly through time. This concern reflects a broader limitation of space-for-time substitutions. For example, ecological chronosequence-based studies argue responses to environmental change through time can be inferred by studying the changes in sites formed from the same parent material (Walker et al., 2010). Such approaches assume some degree of space-time equivalence where the relationship between environment and phenotype, genotype, or distribution observed across space is transferable to the same environmental change occurring through time (Johnson & Miyanishi, 2008; Lovell et al., 2023). However, this assumption may not always hold. Spatially separated populations reflect different

demographic, ecological, and evolutionary histories. Contemporary differences among them may be a product of historical contingency, population structure, gene flow, biotic interactions, or adaptation to correlated environmental variables (Evans et al., 2025; Lovell et al., 2023). Consequently, a spatial association between temperature and an adaptive phenotype or allele does not necessarily imply that the same phenotype or allele will change in a predictable direction or rapidly enough as climate shifts.

Empirical studies of space-for-time substitutions have produced mixed results. On one hand, for instance, models of fish responses to hydrological change in the Florida Everglades performed comparably to, and sometimes better than, models (Banet & Trexler, 2013). On the other hand, spatial climate-vegetation relationships reconstructed from Late Quaternary pollen records predicted temporal compositional change at approximately 72% of the accuracy of models based directly on temporal relationships, with performance deteriorating when the magnitude of spatial and temporal climatic variation differed (Blois et al., 2013). This highlights the uncertainty over (i) causality of spatial relationships, and (ii) transferability of those relationships through time (Lovell et al., 2023). Therefore, translating spatial patterns into predictions of evolutionary responses to climate change requires identifying the selective axis involved and disentangling whether spatial differentiation predicts temporal evolutionary change.

6 Is low-altitude adaptation really analogous to climate adaptation?

A simple interpretation of the adaptive challenge depicted in Figure 2B would be that climate change makes high-altitude populations more like low-altitude populations, e.g. in

terms of temperature. However, selection pressures on low-altitude populations are not directly comparable to those imposed by a changing climate. For example, mountains are often a place of refuge for various species in response to land use and fragmentation in the lowlands (Guo et al., 2018). Therefore, although populations moving upslope might already be adapted to warmer environments, they will still need to adapt to other stressors that a higher elevation imposes on them.

The predictive value of an elevational gradient lies in testing what contemporary genotype-environment associations reveal about the direction and magnitude of evolutionary change under warming. A popular approach to achieving this is genomic offset methods, which are also a form of space-for-time substitution. These methods identify putatively adaptive loci based on genotype-phenotype correlations, estimate the optimal genomic composition given some environmental condition (e.g. a climate change scenario), and treat the gap between current and optimal genotypic constitution as a proxy of maladaptation (Rellstab et al., 2021). In principle, such approaches can bridge spatial studies of local adaptation and forecasts of climate vulnerability. However, they have a number of limitations. In addition to the challenges of distinguishing adaptive and nonadaptive genetic variation (see Box 1 and Section 3), genomic offset methods do not capture factors that are central to the process of adaption (e.g. the efficacy of selection, the genetic architecture of adaptive traits, population connectivity) and do not present an obvious measure of population vulnerability (Lotterhos, 2024).

7 Is there an escalator to extinction?

Looking at future implications of local adaptation to altitude, one could ask, if warming progressively shifts suitable thermal conditions upslope, will populations currently occupying the upper end of an elevational gradient be disproportionately prone to extinction? Unlike their lowland counterparts, the ability of high-altitude populations to track suitable climate is constrained by the finite height and area of a mountain. This constraint forms the basis of the “escalator to extinction” hypothesis (Urban, 2018). A resurvey of a Peruvian montane bird community after 30 years showed that following $\sim 0.42^{\circ}\text{C}$ of warming high-altitude species contracted in range and several highland species disappeared. Low-altitude species, by contrast, expanded their ranges upslope (Figure 3A) (Freeman et al., 2018). Even so, elevation level alone does not determine vulnerability. Chen et al. (2025) conducted a comprehensive test of the “escalator to extinction” hypothesis, covering more than 8,800 historical and contemporary elevational ranges across 440 and 1,629 animal and plant species, respectively. They reported limited evidence for range contractions in highland populations beyond what is expected from a null model that accounts for the geometric constraints in the bounded domain of a mountain range, which can produce negative correlations between range shift and elevation by chance (Figure 3B, see Chen et al. 2025 supplementary text and supplementary figure S1 for a detailed explanation). This result does not imply highland populations are secure, because delayed losses may generate an extinction debt as populations persist temporarily in increasingly unsuitable habitats (Kuussaari et al., 2009). However, it suggests vulnerability emerges from the interaction between geographic constraint and adaptive capacity, which makes it more difficult to predict.

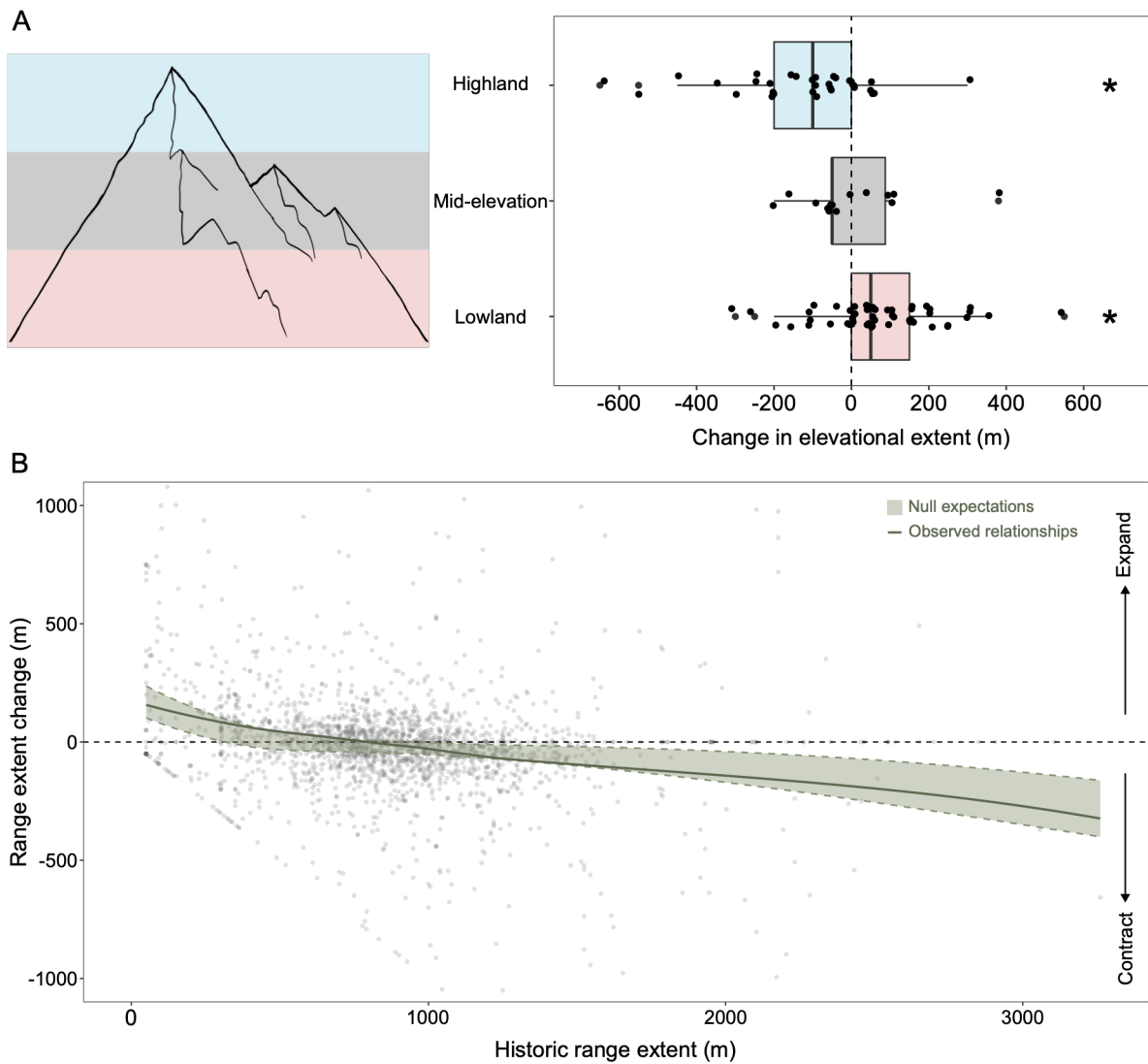


Figure 3 | Mixed evidence for an ‘escalator to extinction’ [A] Highland Peruvian bird species have significantly contracted in range between 1985 and 2017, whereas their lowland counterparts have expanded. This highlights the increased vulnerability of highland populations in the focal species. Reproduced from Freeman et al. (2018), Figure 3. [B] Highland species ranges have not contracted more than expected by chance. The green solid line shows the range shifts observed across datasets. The shaded area is a null distribution of randomised boundary shifts, which produces a negative correlation between range extent change and historical range extent simply due to the geometric constraint of bounded mountain ranges. Grey dots are observed range extent changes from 2,200 species' range records. The horizontal dashed line marks no change. Reproduced from Chen et al. (2025), Figures 3, panel G.

Thermal niches vary across latitude and altitude, and behavioural access to cooler microclimates can further buffer organisms in the face of warming (Montejo-Kovacevich et al., 2020; Sunday et al., 2014). Therefore, two populations occupying equally high elevations may not be equally vulnerable. Risk will, instead, depend on how close populations are to their thermal limit, the availability of thermal refugia, capacity for plasticity and thermoregulating behaviours, and ability to access warm-adapted genetic variation through gene flow or mutation. For instance, and contrary to the “escalator to extinction” hypothesis, a recent survey of upper and lower thermal tolerance limits of around 2,300 tropical insect species showed that while highland species can rely on plasticity as a coping mechanism, lowland species that are much closer to their thermal limits are at more risk (Holzmann et al., 2026). Rescue requires variants that are beneficial under the new conditions to be present or arise, and for selection on them to produce an adaptive response rapidly enough to outpace environmental deterioration. Predictions of vulnerability will, therefore, be strongest when both magnitude of the environmental stress and the capacity for plastic and adaptive responses are considered.

8 Concluding remarks

We argue that mountain ranges are powerful but conditional systems for studying climate change adaptation. Their value is twofold: they can be useful models of adaptation to climate change, and they can be opportunities for evolutionary rescue. In both cases, this is because of the compression of substantial environmental variation into short geographic distances, creating a setting in which repeated instances of divergent selection, gene flow and standing genetic variation can be studied simultaneously. This feature of altitude

systems is exploited in increasingly informative ways. For instance, through comparisons of high- and low-altitude populations and independently evolved high-altitude lineages, experimental transplants and climate manipulations, and genomic approaches. This has established elevational gradients as tractable natural systems for understanding generation and maintenance of adaptive traits (Kawecki & Ebert, 2004; Yeaman & Whitlock, 2011).

In order to be useful, no single study needs to establish the complete chain of causation from environmental variation to genetic architecture to fitness and future evolutionary response. Studies that isolate particular components of this process can each reveal important constraints on adaptive responses. However, stronger predictions about climate adaptation ultimately need these components to be connected. Under this framework, the question is “can the current adaptive variation distributed across an elevational gradient be redistributed, selected or generated rapidly enough to maintain population fitness as those gradients shift?”. Mountain ranges make each component of this process empirically accessible with their strongest contribution to climate change research being as systems in which we can test when, how, and under what conditions existing local adaptation translates into evolutionary capacity to keep pace with climate change.

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