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Climate change and elevational range shifts in insects

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On mountains, unique in their steep and rapid climatic gradients, many insects are shifting their elevational range limits to track recent temperature change. In a review of the range shift literature to date, most of the 1478 montane insect populations tested so far are shifting to higher elevations, but there is conspicuous variation in the responses. We discuss the impact of study methodology as well as potential abiotic and biotic factors that may underlie this variation in climate change response. We encourage more empirical studies spanning greater insect biodiversity and directly testing how variation in species' traits, biogeography, and abiotic–biotic context shapes variation in range shift responses.

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Introduction

Human-induced climate change is occurring at a pace unprecedented in earth's history [1] and organisms are responding [2,3,4•]. The measured responses to climate change in insects (like all organisms) are shifts in latitudinal and elevational range limits [4•], population declines [5••], local extirpations [6], and phenological [7•,8,9•], morphological [10], and evolutionary changes [11•,12,13]. Despite empirical studies accumulating since the 1990's, empirical studies are still far outweighed by predictive, modeling, and theoretical work. Furthermore, the tempo of publishing empirical studies appears to be slowing. Should we continue collecting empirical data on insect responses to climate change or just focus on the higher-profile modeling and predictions, and put those model results toward conservation aims?

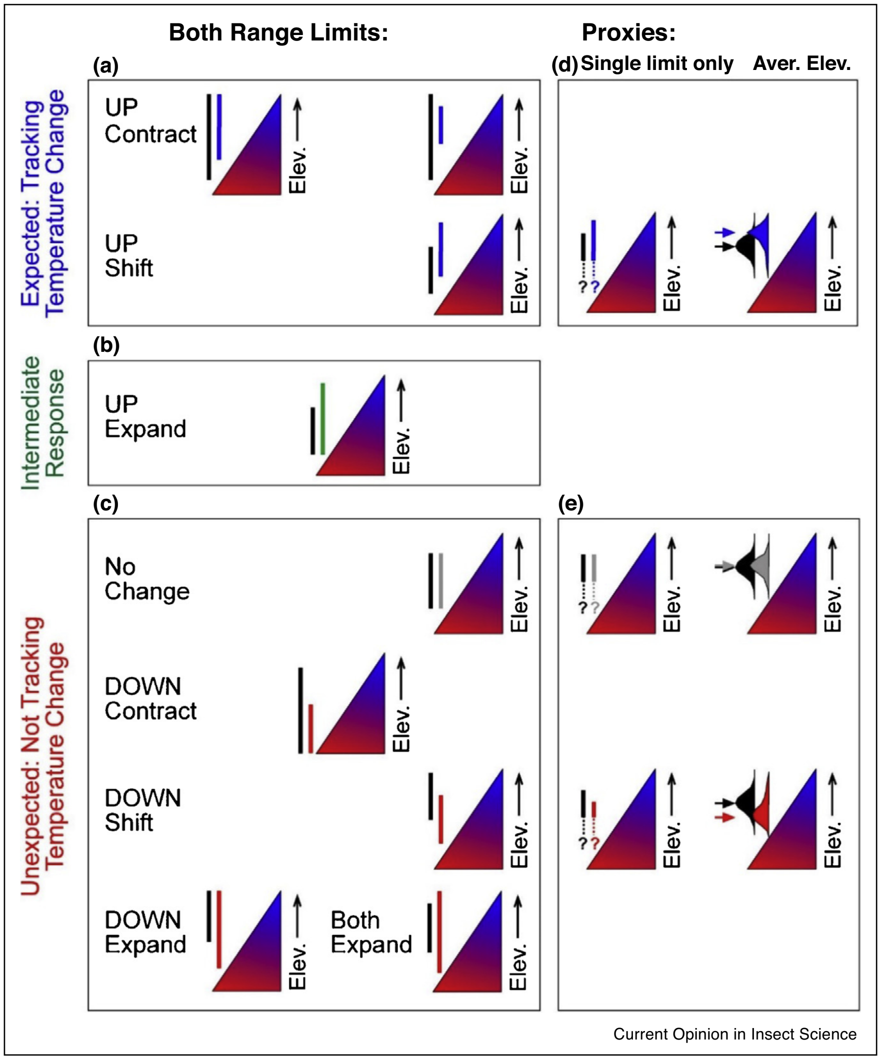
We argue that more empirical data on insect responses to climate change are of critical importance. Firstly, existing datasets are of restricted taxonomic and geographic scope (e.g. mostly lepidopterans and European: 33% and 72% of studied species, respectively) compared to the vast diversity of insects [14,15]. Secondly, most empirical studies only focus on responses to temperature change. While insects are ectothermic and critically depend on environmental temperature throughout all aspects of their life history, other niche aspects are also changing—precipitation, humidity, cloud cover, weather extremes, biotic interactions—with potentially dramatic impacts [16–18,19••]. Thirdly, not all species within a study or across a taxon are responding similarly to change [4•,15]. To date, researchers have focused on the species exhibiting expected responses to climate change (e.g. upward range shifts). But if we aim to predict organismal responses for critical conservation measures, then understanding response complexity is the key to valid understanding of climate change impacts. Finally, not all studies provide strong inference. Many are based on partial data or proxies (approximation substitutes for actual measurements) [20–22], and others are composites of community responses [23–26] not individual species' or population responses. If we are to assess factors underlying response variability, species-level data are necessary, not average responses across a clade.

Mountains offer valuable insight for climate change studies because of their dramatic gradients in climate across elevation, their replication across space from tropical to temperate climates and islands to mainland, and the historical interest in documentation of montane organismal diversity [27–29]. Mountains thus serve as natural laboratories to study responses to climate and climate change. Montane gradients are already a source of important climate change studies for insects, including phenological shifts [7•,8,9•], host–plant interactions [30,31,32•], abundance declines [26], morphological impacts [33•], and richness changes [23,34]. Herein, we critically review how insect elevational range limits are altered with changing climate. We assess the impact of several methodological concerns, the role of proxies, and how inference can be improved. Lastly, we discuss the variability in responses and suggest key aspects that may differentiate responses. Our overarching aim is to foster new avenues of empirical work on insect elevational range shifts.

Measuring elevational range shifts

The aim of empirical climate change studies examining insect distributions on mountains is to assess if historical data gathered before climate change was detected globally (pre-1980s) is significantly different from contemporary data gathered during climate change. Because average annual temperatures decrease naturally with increasing elevation, species are expected to move to higher elevations as temperature warm. The strongest inferences about impacts of climate change on species' elevational ranges include tests of both lower and upper range limits [Figure 1a; 5••,25,30,35,36–42]. Such studies (or data included therein) can elucidate nine different responses in elevational ranges (Figure 1a–c). The expected responses to warming temperatures include upward shifts in both upper and lower range limits or upward contractions due to an upward shift in just the lower limit or changes in both limits (blue; Figure 1a). A species may expand their upper range limit with no shift in the lower limit (green; Figure 1b). This is considered an intermediate response in that the upper limit is shifting as expected by tracking temperature, but equivocally the lower limit is not yet tracking temperature change.

Figure 1

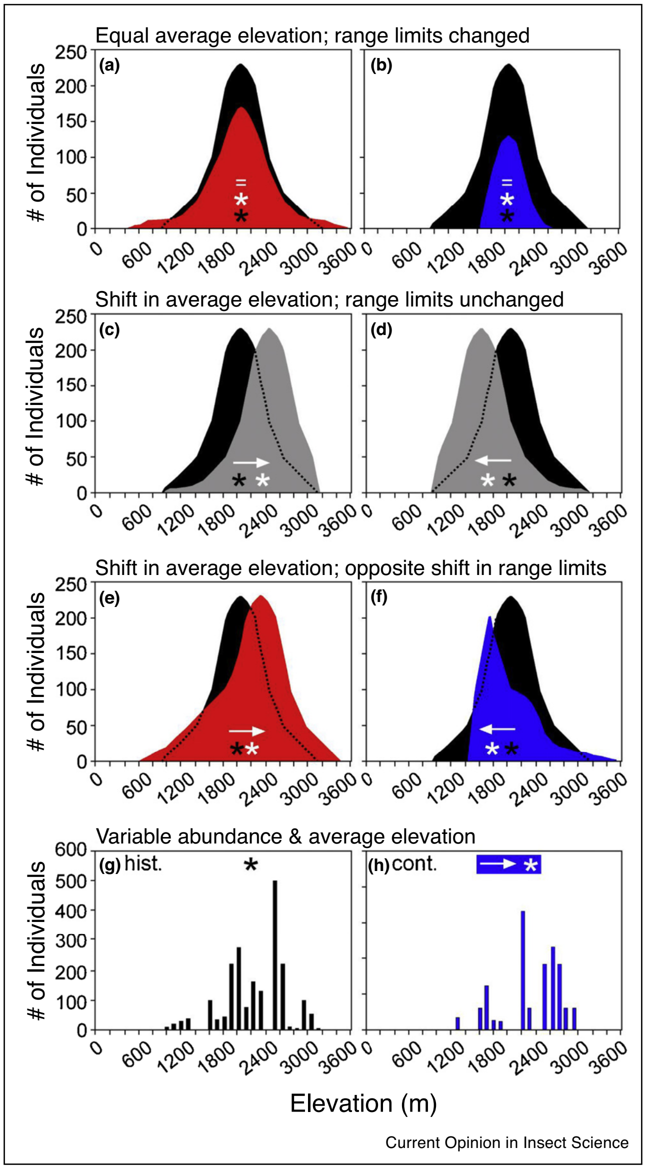


Potential climate change responses for insect elevational ranges measured for both range limits **(a)**–**(c)** or with proxies of a single range limit (shown here for upper limit) or an average elevation **(d)**–**(e)**. For both limits, three expected (a), an intermediate (b), and five unexpected (c) responses are possible, whereas proxies only include upward, downward and no change responses. (a) Expected: upward elevational range contractions and shifts based on changes in the lower range limit or both range limits. (b) Intermediate: upward shift in upper range limit but unchanged lower limit. (c) Unexpected: lack of change, downward elevational range contractions and shifts based on changes in one or both range limits, or expansion of both limits or the lower limit. (d) Expected upward shift of single range limit or average elevation (arrows). (e) Unexpected: lack of change or downward shift of single range limit or average elevation. Triangle depicts montane temperature variation from warm (red) to cool (blue). Black lines = historical ranges; blue lines = contemporary upward responses; green lines = contemporary upward expansion; red lines = contemporary downward and/or expansion responses; and grey lines = no contemporary change. For single limits, '?' and dashes indicate that one range limit is unmeasured and unknown. For average elevations, abundance is depicted as a shaded, unimodal curve for simplicity, but empirical data is likely more variable elevationally.

Unexpected responses to warming include no significant change to either limit (gray; Figure 1c), a downward contraction in the upper limit, a downward shift in both limits, or an expansion of the lower limit or both limits (red; Figure 1c). Alternatively, if the historical data are only available for the upper or lower limits, then only single limit changes are assessed as a proxy for overall elevational responses to climate change [left column of Figure 1d,e; 21,22,43••]. But with incomplete range data, the responses are limited to upward, downward, or no change. Similarly, many studies examine an average elevation as a single point of comparison historically and contemporarily (arrows; right column of Figure 1d, e) as a proxy for range shifts. This is measured several ways in the literature—most commonly as an abundance-weighted average elevation [20,31,36,44] or an occupancy-weighted average elevation [5••], although sometimes as an elevational mid-point or an average elevation of extirpations [6], map-occupancy or atlas-occupancy [45–47]. Such proxies were utilized because authors (a) detected large sampling differences among sites, elevational span, or time periods, (b) used data with broad elevational resolutions (e.g. 10 × 10 km map pixels), or (c) had more confidence in abundance trends. These average elevational change proxies are still limited to upward, downward, and no change responses.

Changes in single limits or average elevation proxies are ambiguous as to the true response of the species' elevational range to warming temperatures. This is particularly important in estimation of risk. For studies of single limits (e.g. upper limits), if a downward shift of an upper range limit is detected, we assume a species at low risk from climate change. But if the lower limit had simultaneously shifted up dramatically, this would indicate an upward range contraction and a species of high risk. However, differentiating between the two risk conclusions is impossible based on a single limit shift. Similarly, for studies of average elevation, the change to the range limits can have a minor impact on calculation of the average elevation (Figure 2). In six of the seven examples in Figure 2(a–f) the directional shift for the abundance-weighted average elevation is different than the directional shift assessed using the upper and lower range limits. For example, in Figure 2e,f, imagine two beetles with same historical range limits and abundance-weighted average elevation, but contemporarily, one (e) expanded both its range limits, but the average elevation shifted up, whereas the other (f) shifted both range limits upward but the average elevation shifted down. Thus, the proxy and the range limits would conclude opposite indications of risk. At the minimum this uncertainty needs to be acknowledged in these studies and in meta-analyses. Importantly, studies measuring average elevation change are asking a different question: 'Is the overall elevational trend in population density shifting in response to climate change?' Thus, they should be scientifically framed as such, and not as estimates of range shifts.

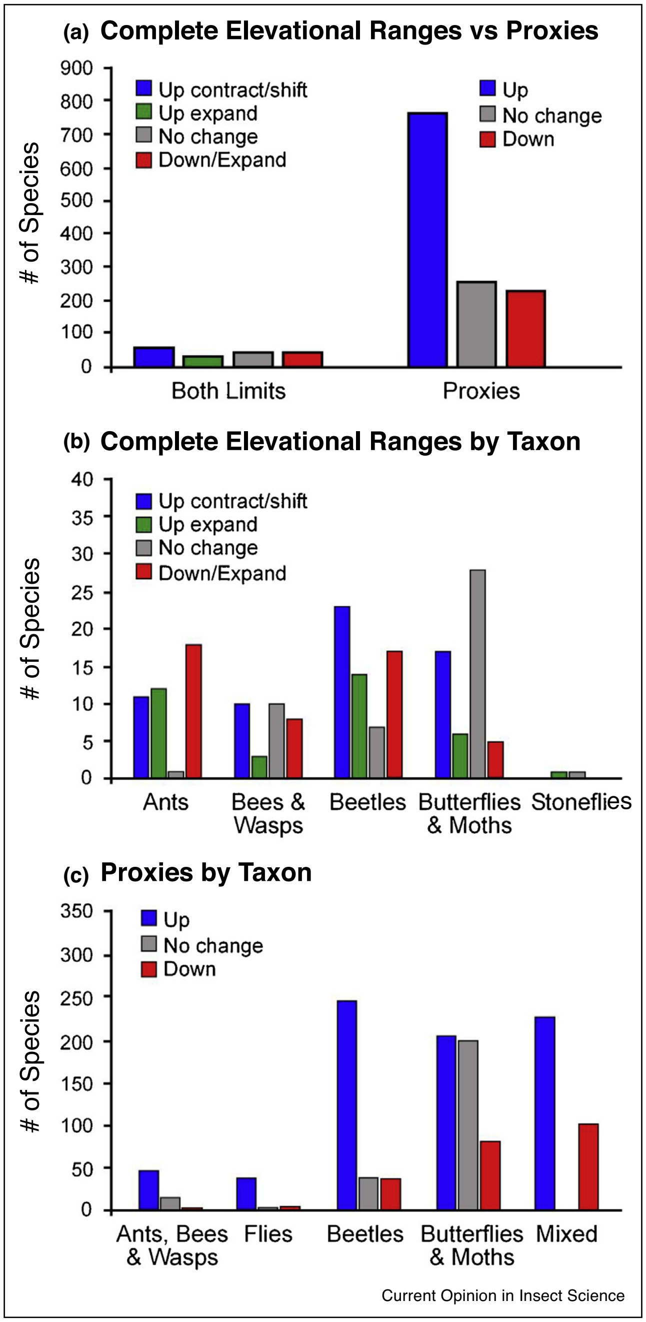
Figure 2



Comparison of range shift conclusions based on the average abundance-weighted elevation proxy (AE) and both range limits (RL). **(a)–(f)** show examples in which the AE proxy differs from the change in RL. **(g)–(h)** show how much empirical data on abundance varies elevationally and between time periods (unlike idealized smooth curves). (g)–(h) is the only comparison where AE and RL change is consistent: both shift upward. Historical data are in black for elevational distributions and AE values (*). Contemporary data are colored for RL change (blue for expected upward changes; gray for no change; red for unexpected downward or expanding limits) and white stars for AE values. Arrows indicate directional change of AE proxy.

To examine the variability within and among clades and methods, we searched the literature for studies examining

Figure 3



Quantification of montane insect responses to climate change for studies assessing both elevational range limits (**(a)**, left) and proxies ((a) right), including single range limits or average elevation change. Responses varied conspicuously within and among taxonomic groups measured with both elevational range limits **(b)** and for proxies **(c)**. Taxonomic groups measured in (b) included ants (Formicidae), bees and wasps (Apocrita), beetles (Coleoptera), butterflies and moths (Lepidoptera), stoneflies (Plecoptera); and in (c) included ants, bees, and wasps (Hymenoptera), flies (Diptera), beetles (Coleoptera), butterflies and moths (Lepidoptera), and mixed (multiple undifferentiated arthropod clades plus other organisms) [47]. Named and colored responses correspond to those in Figures 1 and 2.

elevational range shifts for insects through online systematic searches (Web of Science, Google Scholar) as well as examining articles cited in meta-analyses and other climate change papers. Surprisingly, only 26 empirical papers studied (or included data for) species-level elevational range shifts in insects and only one was published in the past three years [5••]. These studies included montane populations of 1478 insect species. Most populations were from Europe (72%), followed by North America (13%), tropical Americas (8%), and Asia (7%).

The contrast of montane insects studied for complete range shift responses as compared to proxies (e.g. single limit or average elevational shift) is stark (13% versus 87%; Figure 3a). More species have shifted or contracted upward as expected with warming temperatures compared to no response, downward, or expanding responses, but the variability is conspicuous in both cases. The variability is even more striking when contrasted within and among insect clades for complete ranges (Figure 3b) as well as proxies (Figure 3c). For complete ranges, more montane ants (Formicids) displayed downward or expanding responses, whereas butterflies and moths (Lepidopterans) included more species with no detectable response to warming. Beetles (Coleopterans) appear to be tracking temperature change the most, particularly with upward shifts and contractions as well as upward expansions. In general, the proxies detected fewer cases of unexpected responses, which may reflect the fewer potential responses or could indicate a true bias where contemporary sampling is predisposed to an upward change (e.g. greater contemporary sampling at higher elevations) [21,38]. Comparing taxa between both limits and proxies, Hymenopteran (ants, bees, wasps) and Coleopteran proxies vastly underestimate downward movement and expansion, whereas Lepidopteran proxies underestimate species with little or no response to warming.

Methodological concerns

All responses to climate change need to be considered within the context of interannual population variability [48,49••,50]. This is true for studies of both range limits and proxies. But responses that depend heavily on abundance measures are more susceptible to measurement error, including abundance changes in snapshot historical-contemporary comparisons, population extirpations, and population density shifts across elevational ranges [48,49••]. Insects are quintessentially irruptive demographically, with large population increases and periods of low abundance, and therefore vary highly year to year [5••,50,51]. Recent simulations and analyses of long-term datasets detected alarming error levels for measured responses to climate change in organisms with high interannual population variability [48,49••]. For instance, short-term snapshot resurveys based on modeled populations detected a 50% probability of erroneously detecting the opposite trend in population abundance change and nearly zero probability of detecting no change. Similarly, under scenarios of moderate to high population variability across a species' range or at the range edges, there is a bias toward erroneous detection of range limit changes. This interannual variability is displayed empirically for two long-term insect studies in the California Sierras [5••,52•], where range limits fluctuated widely year to year. Any two chosen short-term snapshots for comparison would be strongly contingent on those particular year's dynamics, not the longer-term directional trend [5••,52•]. Studies that estimate range limits across a broader time scale of historical and contemporary data are more robust to effects of interannual variability [48]. In contrast, short-term (1 or 2 seasons of sampling) snapshot resurvey comparisons on abundance distributions (weighted average elevation) across an elevational range are highly prone to the influence of interannual variability [e.g. Refs. 20,31]. Those calculating occupancy statistics or integrating elevational abundance over more years (5+ years) are less prone to such error [5••,48,53].

Generally, in elevational range limit studies, the equality and robustness of sampling across the entirety of the elevational ranges are of utmost necessity for quality inference about climate change response. But in the case of historical and contemporary resurveys, the ineffectiveness of short-term sampling within a context of high interannual variability dictates the need for wider sampling windows and repeat sampling across broader temporal scales [48,50].

Probing variability in responses

Why are the responses to temperature warming on mountains so variable? The answer is the key to robust predictions of climate change responses within and among insect clades. Sampling, interannual population variability, and methodological error may underlie some of the variation in responses, but not all of it. And it would be naïve to suppose all species exhibiting no change or unexpected changes are just delayed in their negative responses to climate change, but undoubtedly that may be true in some cases. Nonetheless, there are potential abiotic and biotic factors other than temperature (e.g. precipitation, latitude, body size, foraging strategy) that may underlie variation in responses [14,30]. Similarly, variation in species' traits, evolution, and plasticity may lead to losers and winners with anthropogenic climate change [33•,52•,54••]. Abiotically, each species' niche is multidimensional and much more complex than temperature alone [55]. Those species with stronger non-temperature niche components (e.g. precipitation, humidity, vegetation and host–plant associations, food resources, oxygen availability) will track those dimensions, which are not necessarily colinear with temperature or temperature change [51,56–58,59••]. This can lead to tradeoffs in range shifts if changing precipitation necessitates downward shifts but warming necessitates upward shifts [17,60], for example. At biogeographic scales, populations measured on mountains at the warmer, drier trailing edge of their geographic range may respond more readily to temperature change than populations on mountains central to their range or at the leading edge [6,61]. Or alternatively, populations may respond more where warming is the greatest (e.g. high latitudes or particular elevations) and less so where warming is less detectable [8].

Mean air temperatures may not reflect the temperatures experienced by an individual insect. Microclimate and microhabitat scaled to the body size of the organism is of critical importance to a coupled response to actual temperature change as experienced by individual animals [14,62•,63,64]. The biotic and abiotic environment can dampen or accentuate small-scale temperatures [14]. The spatial distribution and duration of this microsite temperature variability can play an enormous role in whether animals can choose a particular temperature regime or must inevitability experience temperature change [14]. Species traits may also partition responses. For example, variation in thermal physiology [11•,12,62•,65], melanism [66•], stage or type of ontogeny [67], and sociality [68] are implicated in differential responses among and between insect species and clades. This biological complexity within and among insect clades based on abiotic and biotic context, biogeographic position, species traits, and potential for evolution or plasticity could separate species that shift their ranges to track temperature change and species that do not. Designing studies to probe this biological complexity simultaneously with range shifts will start building a foundation for better predictive ability.

Future directions

Improving our knowledge of empirical insect range shifts on mountains around the world is still imperative. Conducting new studies with robust sampling, testing both range limits, and compensating for interannual variability will improve inference and robustness. Directly examining how variation in traits, biogeography, and abiotic–biotic context shape variation in range shift responses is the next empirical frontier. Explicitly linking data on thermal tolerance and empirical range limits is rare [43••], but critical in determining if temperature changes are directly responsible for climate change-related range shifts. While empirical data on thermal tolerance is plentiful [69•], understanding its role in climate change responses requires that studies address the effects of age, stage of development, and senescence [70,71], microclimate refugia [62•], thermoregulatory behavior [72], and methodology [69•] on thermal limits. Unlike vertebrates, insect lab and field experiments are feasible to contrast species with expected and unexpected responses. Plant climate change studies benefit from common garden and reciprocal transplant experiments, which also may be possible for some insect systems [30,73]. Lastly, lack of historical datasets for resurveys is one impediment to more empirical range shift studies. Most studies in the review resurveyed data from a single study, whereas the abundant historical locality data in entomological collections is largely an untapped resource. Local or regional elevational ranges can be constructed based on specimen localities, and augmented with contemporary sampling. Statistical modelling techniques are available to build in occupancy statistics or Bayesian models to accommodate sampling variability and undersampling based on museum data [53,61]. We conclude that the relatively small number of species (192; 72% from Europe) tested for climate change impacts at both range limits necessitates more robust empirical studies that aim to understand the complexity of responses.

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Conflict of interest statement

Nothing declared.

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