

# ECOGRAPHY

## Review

### Elevational gradients in plant defences and insect herbivory: recent advances in the field and prospects for future research

Xoaquín Moreira, William K. Petry, Kailen A. Mooney, Sergio Rasmann and Luis Abdala-Roberts

*X. Moreira* (<http://orcid.org/0000-0003-0166-838X>)([xmoreira1@gmail.com](mailto:xmoreira1@gmail.com)), *Biological Mission of Galicia (MBG-CSIC), Apartado de Correos 28, ES-36080 Pontevedra, Galicia, Spain.* – *W. K. Petry, Inst. of Integrative Biology, Eidgenössische Technische Hochschule (ETH) Zürich, Zurich, Switzerland.* – *K. A. Mooney, Dept of Ecology and Evolutionary Biology, Univ. of California, Irvine, CA, USA.* – *S. Rasmann, Inst. of Biology, Laboratory of Functional Ecology, Univ. of Neuchâtel, Neuchâtel, Switzerland.* – *L. Abdala-Roberts, Dept of Tropical Ecology, Autonomous Univ. of Yucatan, Merida, Yucatan, Mexico.*

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Classic research on elevational gradients in plant–herbivore interactions holds that insect herbivore pressure is stronger under warmer, less seasonal climates characteristic of low elevations, and that this in turn selects for increased defence in low- (relative to high-) elevation plants. However, recent work has questioned this paradigm, arguing that it overly simplifies the ecological complexity in which plant–insect herbivore interactions are embedded along elevational gradients. Numerous biotic and abiotic factors vary with elevation, and their simultaneous influences are the focus of current work on elevational gradients in insect herbivory and plant defences. The present review 1) synthesizes current knowledge on elevational gradients in plant–insect herbivore interactions; 2) critically analyses research gaps and highlights recent advances that contribute to filling these gaps; and 3) outlines new research opportunities to uncover underlying mechanisms and build towards a unified theory on elevational gradients. We conclude that the next generation of studies should embrace community complexity – including multi-trophic dynamics and the multivariate nature of plant defence – and to do so by combining observational data, manipulative experiments and emerging analytical tools.

Keywords: abiotic factors, climate change, community ecology, diversity, ecological gradients, insect herbivory, plant defences, tritrophic interactions

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#### Introduction

Environmental gradients are powerful tools for understanding how the abiotic environment shapes biodiversity, species interactions and trait evolution (Dobzhansky 1950, Schemske et al. 2009, Pratt and Mooney 2013, Rasmann et al. 2014a, b). Suites of ecologically important factors often co-vary along environmental gradients, making geographic distance (e.g. in latitude: Pennings and Silliman 2005, or elevation: Pellissier et al. 2012) effective proxies for multi-dimensional environmental variation. Environmental gradients thus serve as natural experiments that can reveal the



causes of spatial variation in traits within species (Linhart and Grant 1996).

Ecological gradients have been especially useful in the study of plant–insect herbivore interactions (Schemske et al. 2009). For example, theory holds that spatial variation in the strength of plant–insect herbivore interactions, mediated by abiotic factors, plays a central role in shaping the latitudinal gradient in biodiversity. Within this context, a long-standing paradigm holds that stronger herbivore pressure under less seasonal climates near the equator results in stronger biotic selection on plant defence traits (Moles et al. 2011), promoting plant coexistence through the diversification of defence niches (Kursar et al. 2009) and the co-diversification of plants and insect herbivores over evolutionary timescales (Futuyma and Agrawal 2009). However, recent syntheses of such latitudinal studies show patterns that are variable and that often fail to follow predicted patterns (Moles et al. 2011). In light of these inconsistencies, it is clear that there is a need to not only critically re-evaluate the evidence for geographic gradients in plant–insect herbivore interactions, but also to develop a new mechanistic framework for predicting the patterns that do exist.

Here we seek to achieve these goals by evaluating the responses of plant–insect herbivore traits and interactions to environmental variation over elevation. Unlike relatively well-studied latitudinal gradients, elevational gradients avoid several confounding effects that occur over the larger spatial scales of latitude. For example, studies of species interactions at broad spatial scales are often more strongly affected by dispersal limitation, which complicates testing for the effects of ecological filters (Stein et al. 2008). Similarly, species replacement along large-scale gradients that span multiple biogeographic zones changes insect herbivore and plant community composition, precluding comparisons of intra- and inter-specific patterns at the same scale and within the same climatic ranges (Johnson and Rasmann 2011, Anstett et al. 2016). Additionally, elevational gradients are largely independent of regional variation in other factors such as day length and inter-annual climatic variation. Finally, elevational gradients can be replicated both within and among regions, avoiding idiosyncrasies associated with any single latitudinal transect, and allowing for increased inference when replicate gradients differ in hypothesized drivers (e.g. soil fertility, growing season length, precipitation, etc.) of the ecological pattern. By recapitulating much of the latitudinal variation in abiotic conditions over much smaller geographical scales, elevational gradients thus provide a window for understanding the mechanisms by which abiotic variation drives variation in species composition, traits and interactions.

Our synthesis centers on plant–insect herbivore interactions because they are the basis for interactions at higher trophic levels and thus drive community-level dynamics, and as such, they are among the most studied interaction type across elevational gradients. Specifically, 1) we review the theoretical background for predicted patterns on elevational gradients in plant–insect herbivore interactions, 2) we critically analyse research gaps and highlight how recent advances contrib-

ute to filling them, and 3) we outline new research frontiers for understanding the mechanisms that underlie elevational gradients in plant–herbivore interactions and build towards a unified synthesis. In addressing these points, we provide an exemplar of a process-based paradigm for organizing our understanding of how species are shaped by interactions along ecological gradients, and ultimately, how such processes generate and maintain biodiversity.

## **General background on plant–insect herbivore interactions along elevational gradients**

Plant–insect herbivore interactions are simultaneously shaped by biotic and abiotic factors. These factors may act at different scales and levels of biological organization and frequently vary along environmental gradients (Rasmann et al. 2014a). For example, variation in abiotic factors such as nutrient availability, sunlight and climatic factors (e.g. temperature, precipitation) may affect plant–insect herbivore interactions directly by influencing plant and herbivore traits or abundance. In addition, they may have indirect effects by altering the biotic (e.g. community) context within which plants and insect herbivores are embedded (Fig. 1A). In both cases, abiotic variation provides a template that drives interactions that in turn shape species abundance, diversity and distribution (Mooney et al. 2016).

Variation in abiotic factors along elevational gradients has been well documented, revealing both general and gradient-specific patterns (Körner 2007). Increasing elevation is typically associated with reduced temperature, reduced growing season (except in the tropics where season length does not change with elevation), increased variability in climatic conditions, increased sunlight exposure and wind and, in some cases, reduced water availability and soil fertility (Fig. 1A) (Körner 2007, Pellissier et al. 2014, Rasmann et al. 2014a, De Long et al. 2016).

Elevation has been proposed to be associated with inter- and intra-specific variation in traits driven by genetics and/or phenotypic plasticity, and this in turn may influence species interactions (Fig. 1B–C). With respect to plants, this includes variation in chemical and physical traits associated with resistance or food quality to insect herbivores (Pellissier et al. 2016). With respect to herbivores, this includes traits such as foraging patterns, feeding behaviour, and diet breadth (Pellissier et al. 2012, Rasmann et al. 2014a). However, the evidence for such patterns is somewhat limited and is biased toward temperate mountain ecosystems (76% of the cases). A number of these studies report a decrease in plant defences and herbivore pressure with elevation (Supplementary material Appendix 1 Table A1, Fig. A1), and a recent global analysis supports this decreasing pattern (Galmán et al. 2018) (Fig. 1A–B). However, other studies report elevation to be positively associated with increases in direct and indirect plant defences (34% of cases), damage sustained by plants (22%), and the abundance and species richness of insect herbivores (19%). Still others report ‘hump-shaped’ patterns where plant defences (4%)

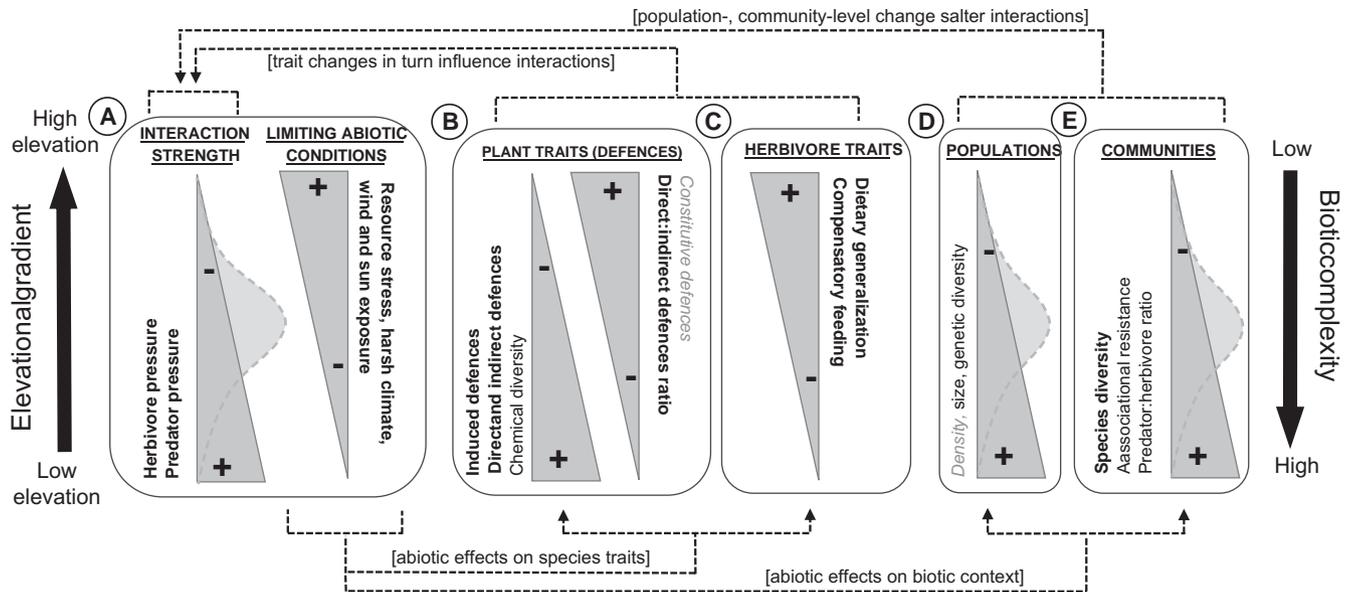


Figure 1. Conceptual model for biotic and abiotic drivers of elevational gradients in plant–insect herbivore interactions, and reported patterns for elevational gradients in biotic and abiotic components of the environment. The strength of biotic interactions (e.g. measured as per capita effects of species X on species Y; Abdala-Roberts and Mooney 2015), is expected to be greatest at lower elevations, whereas resource limitation, wind and sun exposure, as well as climatic variability is expected to increase with elevation (A). Note that interaction strength has also been reported to peak at intermediate elevations, represented here as a hump-shaped, dashed curve. Elevational changes in abiotic conditions may influence interactions by directly altering species traits (arrows linking abiotic factors to (B) and (C) and from these panels back to interactions in (A)), or indirectly by altering the biotic context in which focal interactions are embedded (arrows from abiotic factors to (D) and (E) and from these panels back to interactions in (A)). Changes in species interactions (mediated by the abiotic environment) may also influence traits, populations, and communities (effects of the latter three biotic components may influence each other, but these arrows are not depicted for sake of simplicity). Patterns in the empirical evidence depicted within (B–E) are as follows: plant induced defences, traits associated with indirect defences, and chemical diversity are expected to decline with increasing elevation, whereas constitutive defences and investment in direct relative to indirect defence are expected to increase at high elevations (B). Insect herbivore diet breadth and compensatory feeding (due to lower plant nutritional value) are expected to increase with elevation (C). Population size, density and genetic diversity are expected to decrease with elevation (D), whereas community attributes such as species diversity, associational effects, and the ratio of predator to insect herbivore abundance are expected to decrease towards higher elevations (E). Peaks in species abundance and diversity at intermediate elevations have been reported in some systems (Supplementary material Appendix 1 Table A1) and are depicted by a hump-shaped dashed curve. Bold, black font indicates that >60% of the study cases (listed in Supplementary material Appendix 1 Table A1) supported the predicted pattern, whereas grey, italic font indicates <60% of study cases supported the predicted pattern. Plain-faced black font shows hypothesized patterns that – to our knowledge – are untested.

and herbivory (8%) are highest at intermediate elevations (Fig. 1A–B, Supplementary material Appendix 1 Table A1). Accordingly, broad generalizations are not yet possible, and understanding the factors that control the functional form of the relationship between elevation and plant traits or herbivory is an outstanding problem.

Community-level attributes of both plants and insect herbivores are also shaped by abiotic conditions, and these attributes may in turn influence plant–herbivore interactions (Fig. 1E). Elevational changes in community attributes of both plants and insect herbivores may influence the amount of insect herbivory in different ways. For example, changes in plant species composition may be important when a damaging insect herbivore is sensitive to changes in elevation. Responses by this insect herbivore may influence overall (plant community-level) patterns of herbivory. Moreover, changes in the abundance or diversity of predators (natural enemies of insect herbivores; that is, the third trophic level) along elevational gradients

may result in concomitant changes in top–down control of insect herbivore populations and reduced pressure on plants (Hodkinson 2005).

The diversity and abundance of plants, insect herbivores, and predators have generally been found to decline with increasing elevation (Fig. 1E) (Hodkinson 2005, Pellissier et al. 2012). However, different species, functional groups, or biogeographic zones (e.g. temperate versus tropical; Galmán et al. 2018) may show variation in the functional form (linear versus non-linear, e.g. humped-shaped; Grytnes 2003, Rasmann et al. 2014a, Callis-Duehl et al. 2017) and sign (positive versus negative) of the association between elevation and population or community-level variables (Rasmann et al. 2014b) (Fig. 1E). In addition, alternative patterns may occur due to shifts in vegetation type (e.g. treeline), mid-domain effects, or more limiting conditions (e.g. drought) at low compared to high elevation (Rasmann et al. 2014a). Therefore, caution is needed in interpreting gradient patterns because,

in some cases, such deviations from the elevation-only prediction may in fact provide the exceptions that prove the rule.

While the above examples represent cases where abiotic factors directly and indirectly mediate species interactions along environmental gradients, the resulting changes in interactions may in turn feed back to shape the biotic components of the environment. Studies have generally found greater strength of species interactions (e.g. predation, insect herbivory, diseases, pollination) at lower elevations (Fig. 1A, Supplementary material Appendix 1 Table A1), possibly because warmer and less variable (i.e. low diurnal range and moderate seasonality) climatic conditions promote larger population sizes and higher species richness of consumers (Rasmann et al. 2014a). Accordingly, current evidence suggests that increased insect herbivore pressure at low elevations favours greater investment in plant defences (Scheidel and Bruelheide 2001, Zehnder et al. 2009, Rodríguez-Castañeda et al. 2010, Garibaldi et al. 2011, Pellissier et al. 2012, Rasmann et al. 2014a, b) (Fig. 1A–B, Supplementary material Appendix 1 Table A1). Unfortunately, the community-level attributes (e.g. changes in species abundance, diversity, or traits) underlying such elevation patterns have not been adequately characterized.

Finally, elevational dynamics are typically characterized at local scales without explicitly considering the influence of larger-scale biogeographical context, including mountain geological age, and historical events influencing species composition and diversity (Nagy and Grabherr 2009). For instance, the geological age of a mountain range influences communities along elevational gradients as older mountains allow for more species colonization and diversification (Schemske and Mittelbach 2017). In addition, local diversity at different elevations is shaped by the regional species pool and the species available to populate a given mountain range (Ricklefs and He 2016). Likewise, some mountain ranges have served as species refugia during glacial periods (Schönswetter et al. 2005), and such historical contingencies may shape variation in biotic communities among mountain ranges.

In summary, research on plant–insect herbivore interactions across elevational gradients has been strongly focused on describing associations between these groups and variation in the biotic and abiotic factors along the elevational gradient (Rasmann et al. 2014a). There has far less attention to the mechanisms behind these observed patterns and thus the causes of variation in both the sign and functional form of elevational gradients in plant–insect herbivore interactions remain unclear (Galmán et al. 2018). To help guide future work, we next define key research gaps, as well as recent progress towards addressing them. We then propose avenues for future research and integration to overcome the limitations of past work and build a more holistic, process-based understanding of gradients in plant–insect herbivore interactions.

## Recent advances: adding complexity and realism to elevational gradient studies

### *Plants deploy multiple defensive strategies across elevational gradients*

Traditionally, theory on elevational gradients in plant defence and insect herbivory holds that intra- and inter-specific variation in constitutive chemical and physical plant defences are strongly associated with elevational variation in herbivore pressure. However, other strategies such as tolerance (e.g. re-growth capacity or overcompensation in reproduction; Carmona et al. 2011), induced defences (Karban 2011), and indirect defences (i.e. plant traits that facilitate the recruitment of natural enemies of insect herbivores; Kessler and Heil 2011) are also central to plant defence and may exhibit elevational gradients (see Box 1 for definitions). Further, these axes of plant defence are not independent of each other, but can show positive correlations (defence syndromes) or negative correlations (defence tradeoffs) depending on their relative costs and benefits under different ecological contexts (Agrawal et al. 2010). In these instances, two or more defensive traits or strategies may positively or negatively co-vary along an elevational gradient, precluding an accurate assessment of plant defence based upon analyses of individual traits. For example, constitutive and induced defences frequently trade off both within- and among-species (Koricheva et al. 2004). Shifts in the relative allocation of defences between these strategies may influence the deployment of the other along environmental gradients. More limiting environments (e.g. cool temperatures, low nutrients,

#### Box 1. Definition of plant defensive strategies

- **Direct defences:** plant chemical traits (e.g. carbon- and nitrogen-based compounds) and physical traits (e.g. spines, thorns, hairs) that deter herbivores, reduce their consumption or decrease their survival (Agrawal 2007).
- **Indirect defences:** plant chemical traits (e.g. extrafloral nectar, volatiles) and physical traits (e.g. domatia) that provide shelter, rewards, or information about the presence of herbivore prey to natural enemies (predators and parasitoids) that suppress herbivores and, in turn, indirectly increase plant biomass and reproduction (Heil 2008).
- **Constitutive defences:** plant direct and indirect defences that are always expressed in plants (Núñez-Farfán et al. 2007, Schemske et al. 2009).
- **Induced defences:** plant direct and indirect defences produced and expressed in response to perceived pathogen- or herbivore-damage (Karban 2011).
- **Defence syndrome:** suites of defensive traits that positively co-vary at the species or population level across environments (Agrawal and Fishbein 2006).
- **Tolerance:** plant capacity to maintain fitness despite damage inflicted by herbivores. Tolerance mechanisms include compensatory growth and reproduction, increased photosynthetic rates, and changes in nutrient allocation and uptake rates (Strauss and Agrawal 1999, Pratt and Mooney 2013).

high wind at higher elevations) are commonly associated with slow-growing species which experience higher costs of tissue replacement and thus bear higher fitness costs when attacked. Consequently, plant species adapted to environments with limiting abiotic conditions are predicted to increase allocation to expensive constitutive defences (relative to induced defences), as the energy demand of replacing tissues consumed by insect herbivores is higher under such stressful conditions (Moreira et al. 2014, Pellissier et al. 2016) (Fig. 1B). In support of this hypothesis, Moreira et al. (2014) found that constitutive and induced levels of defensive resins traded off among pine species, and an elevational gradient among species was observed for constitutive (but not induced) resins, with these defences increasing with elevation. Similarly, tradeoffs between tolerance and resistance have also been reported in other temperate plant–insect herbivore interactions (Fineblum and Rausher 1995, Agrawal et al. 1999) and are thus expected to tradeoff along elevational gradients. However, we know of no such test of this prediction.

Plant defence strategies are also expected to respond to changes in plant-associated multi-trophic communities along elevational gradients. For example, changes in the ratios of insect herbivores to predators may underlie shifts in plant allocation to traits associated to direct versus indirect defence (Rasmann et al. 2011, Pellissier et al. 2016, Rodríguez-Castañeda et al. 2016). Predator diversity and abundance are generally higher at low elevations (Hodkinson 2005, Rasmann et al. 2014a), such that low-elevation plants are expected to invest more in traits that attract predators (i.e. indirect defences) than their high-elevation counterparts (Fig. 1B). In support of this hypothesis, Pellissier et al. (2016) found tradeoffs between direct and indirect defences among *Cardamine* species; they reported that species growing at lower elevations invested more in indirect defences (by increasing volatiles that attract predators) whereas species growing at higher elevations invested more in direct defences (by increasing glucosinolate concentrations). However, Dostálek et al. (2016) reported that direct (phenolic compounds) and indirect (volatile organic compounds that recruit predators) defences of the herbaceous plant *Salvia nubicola* did not trade off, and that populations growing at lower elevations invested more in both direct and indirect defences. Patterns may therefore change depending on the system studied, presumably driven in part by the presence and strength of allocation tradeoffs in the plant and the community context.

Plants can also simultaneously deploy an arsenal of defensive traits that act synergistically against multiple insect herbivore species, resulting in positive (rather than negative) co-variation between defences (Agrawal and Fishbein 2006), including plant chemical and physical defences, indirect defences and tolerance. These so-called ‘defence syndromes’ can vary both among and within plant species depending on the ecological context (Callis-Duehl et al. 2017). To our knowledge, only two studies to date have looked at the

influence of elevation on plant defensive syndromes (Dostálek et al. 2016, Pellissier et al. 2016). In one of these, Pellissier et al. (2016) found a positive correlation between inducibility of direct and inducibility of indirect defences among herbaceous species, and that the simultaneous expression of these two strategies was stronger at lower elevations. The authors speculated that higher insect herbivore abundance and species richness at lower elevations selects for multiple defences that act synergistically to provide the most effective means of resistance (Pellissier et al. 2016).

The study of individual plant defence traits is common, and has been a practical solution to the challenges of characterizing complex, multivariate phenotypes in general, and specifically to the lack of analytical methods for some classes of chemical defences (particularly in tropical species). Yet this reductionist approach has limited our understanding of how multiple defensive traits are simultaneously shaped by extrinsic biotic and abiotic pressures, and how responses to those pressures are limited by plant intrinsic constraints. Advances in the application of multivariate statistics to ecology and evolution have made detecting such patterns in complex phenotypes more feasible. Although an exhaustive review of these techniques is not feasible here, several tools are particularly useful when working with multivariate plant defence and herbivore community data. Unconstrained ordination techniques (e.g. principal component analysis) have been widely used in ecology – including for the analysis of plant defences (Moreira et al. 2014) – to reduce the dimensionality of datasets for analysis with common univariate statistical tests. Many types of plant defence and herbivore community data are also well suited for constrained ordination techniques (e.g. distance-based redundancy analysis, canonical correspondence analysis; Kazemi-Dinan et al. 2015) and dissimilarity analyses (e.g. Mantel tests; Pratt et al. 2014). Future work that simultaneously addresses different defensive strategies (e.g. induced and constitutive defences), defensive traits (e.g. physical and chemical), and their association with different guilds of insect herbivores is necessary to better understand how elevation shapes the deployment and evolution of the plant’s defensive phenotype as a whole (e.g. in the form of syndromes).

#### ***Plants are under attack by multiple species of phytophagous insects, and herbivore traits and communities vary with elevation***

Throughout their distribution range, plant species are frequently attacked by multiple species of insect herbivores. However, these herbivores may vary in their susceptibility to changing conditions and therefore exhibit differences in abundance and damage on focal host plants along environmental gradients (Pennings et al. 2009, Pratt et al. 2017). For example, elevation is often associated with decreases in the abundance of leaf-chewing and sap-feeding insect herbivores, and increases in the abundance of grazing insect herbivores that respond to increasing representation of grasslands at high elevation (Hodkinson 2005).

Elevational gradients also lead to changes in insect herbivore communities, and such changes can influence the outcome of plant–insect herbivore interactions. Elevational changes in insect herbivore species composition result in different insect herbivore species selecting upon different plant defensive traits along the gradient (Rasmann et al. 2014a). In addition, changes in species composition may be accompanied by elevational changes in the prevalence of traits within the insect herbivore community. For example, insect herbivore diet breadth has been shown to increase with elevation (Pellissier et al. 2012, Rasmann et al. 2014a) (Fig. 1C), with potential consequences for selection on plant traits because specialist herbivores typically select for different plant defensive traits or strategies than generalists (Ali and Agrawal 2012). Insect herbivore species richness can also decrease with elevation (Fig. 1A), due to both reductions in plant diversity and to the combined increases in climatic variability and decreases in productivity with elevation that tend to reduce insect herbivore population sizes (Körner 2007, Pellissier et al. 2012, Rasmann et al. 2014a). In this sense, recent work poses that higher insect herbivore richness at lower elevations selects for simultaneous expression of multiple defences (i.e. defence syndromes) or increased chemical diversity, where each of several insect herbivore species selects for a particular defensive trait or combination of traits (Dostálek et al. 2016, Pellissier et al. 2016). In addition, although untested, it can be predicted that co-evolutionary dynamics may be stronger and less likely to be contingent upon varying abiotic factors at low elevations, allowing for stronger escalation of plant (and insect herbivore) defences.

In summary, recent studies have revealed the important role of the insect herbivore community context within which plant species are embedded for structuring elevational patterns in plant–insect herbivore interactions. This interaction complexity suggests that a deeper understanding of elevational patterns will require confronting non-additive dynamics that stem from multi-species insect herbivore effects. A key prerequisite for this is a critical evaluation of how herbivore diversity and abundance relates to actual herbivory experienced by plants, as herbivore abundance was commonly taken as a proxy for herbivory in our literature review (65% of cases; Supplementary material Appendix 1 Table A1). Although this clearly presents a substantial empirical challenge to ecologists, it would add realism and increased understanding of ecological gradients in plant–insect herbivore interactions.

#### ***Plant–plant interactions influence plant traits and insect herbivores along elevational gradients***

Most studies of plant defence and insect herbivory have focused exclusively on trophic interactions. Nevertheless, recent evidence has emerged that ‘horizontal’ interactions within a trophic level – conspecific or heterospecific – may indirectly influence the amount of damage received (and defences produced) by focal plants. Competition with neighbouring plants can alter focal plant growth and quality for insect herbivores (Kim and Underwood 2015), and theory

on these associational effects offers avenues to disentangle the neighbourhood effects mediated by conspecific density and focal species’ frequency relative to that of heterospecific neighbours (Underwood et al. 2014). Although it is not known whether these effects operate over elevational gradients, conspecific densities (and thus their frequency relative to heterospecifics) are known to respond to abiotic factors that change with elevation (Fig. 1D) and at (elevational) range centres versus range margins (Angert 2009). For example, a recent study using data from 16 alpine experiments found evidence for positive plant–plant interactions at high elevations (facilitation) versus negative plant–plant interactions (competition) at low elevation, where both of these dynamics were driven by environmental stress and neighbour trait effects (Michalet et al. 2014).

Plants also shape the amount of insect herbivory that their neighbours experience by influencing herbivore foraging behaviour and recruiting or repelling shared herbivores (‘associational susceptibility’ sensu Barbosa et al. 2009, or ‘plant apparent competition’ sensu Connell 1990). At the community level, insect herbivore-mediated apparent competition among plants is suspected to underlie overdispersion in plant defence traits (i.e. greater divergence in chemical profiles between species or genotypes than expected by chance) (Becerra 2007, Kursar et al. 2009). Changes in the relative frequency of conspecific or heterospecific plant neighbours along elevational gradients may thus set the stage for strong bottom–up effects of plants on associated faunas and for feedbacks to the plants themselves (i.e. increasing dispersion of plant defensive traits) in high-herbivory locations along elevational gradients.

#### ***Tritrophic interactions influence plant–insect herbivore elevational gradients***

A growing number of studies have considered the role of elevational variation in tri-trophic (e.g. plant–insect herbivore–predator) interactions (Koptur 1985, Hodkinson 2005, Rasmann et al. 2014c). There is ample opportunity for tri-trophic interactions to vary along elevational gradients both above- and belowground (Kergunteuil et al. 2016). Predators and parasitoids are highly sensitive to changes in abiotic conditions, often more so than are plants and insect herbivores (Voigt et al. 2003, Preisser and Strong 2004, Stireman et al. 2005). Natural enemy abundance and diversity frequently decrease with increasing elevation (Fig. 1A). As a result, predator and parasitoid attack rates are expected to decrease with elevation (Roslin et al. 2017). Elevational differences in enemy diversity and abundance may thus lead to variation in enemy top–down pressure, in turn shaping variation in plant–insect herbivore interactions (Rodríguez-Castañeda et al. 2010, Rasmann et al. 2014a). Differences in abiotic conditions along elevational gradients also control clines in plant intra- and inter-specific trait variation (Rasmann et al. 2014a), and this variation influences (and is influenced by) insect herbivores and their associated enemies (Mooney and Singer 2012). Finally, insect herbivore abundance and traits (e.g. diet breadth) can vary along elevational gradients

(Rasmann et al. 2014a), potentially influencing variation in predator and parasitoid effects on plants (Singer et al. 2014). Elevational variation in insect herbivore traits could therefore shape concomitant variation in trophic cascades.

Studies on elevational variation in tri-trophic dynamics have commonly focused on predator effects on plant–insect herbivore interactions (Hodkinson 2005, Rodríguez-Castañeda et al. 2016). For example, studies in both tropical and temperate mountains have found increasing elevation to be associated with lower insect herbivore attack by parasitoids (Preszler and Boecklen 1996, Maunsell et al. 2015), predatory arthropods (Koptur 1985, Rodríguez-Castañeda et al. 2011, Rasmann et al. 2014c, Sam et al. 2015, Roslin et al. 2017), and insectivorous birds (Sam et al. 2015) (Fig. 1A). However, several other studies assessing changes in both enemy abundance and pressure have found no elevational patterns (McMillin and Wagner 1998, Roininen et al. 2006), and other authors that have reported expected decreases in parasitoid diversity or predator abundance with elevation have not found concomitant elevational gradients in parasitism or predation (Straw et al. 2009, Tantowijoyo and Hoffmann 2010, Zehnder et al. 2010). In these latter studies, elevational gradients in insect herbivore abundance and plant damage were presumably influenced by abiotic factors that directly (or indirectly via effects on host plants) influence herbivores rather than via indirect defence. Recent work has also pointed at the importance of considering changes in predator species or guild composition (e.g. increasing bird predation but decreasing ant predation with elevation; Sam et al. 2015), which may lead to contrasting elevational gradients in plant traits mediating indirect defence assuming that different predators select upon different traits.

Current theory poses that increasing climatic variability and reduced plant availability at high elevations favours broader niches for insect herbivores (Rasmann et al. 2014a). In addition, plant defences (e.g. concentration, variety of compound types) generally decrease with elevation and this could also broaden diet breadth (Rasmann et al. 2014a). Accordingly, under a tri-trophic context, decreasing enemy pressure with increasing elevation should favour broader insect herbivore niches. For example, the benefit of escaping predation having a narrow diet breadth becomes less important with decreasing predation at higher elevations. However, this hypothesis remains to be tested, and such a test would ideally control for other mechanisms that influence insect herbivore diet breadth (e.g. plant density, plant chemistry, climate).

Elevational variation in tri-trophic interactions may also arise from insect herbivore mediation of plant–predator interactions, and such effects may in turn lead to top–down feedbacks through changes in insect herbivory or predation. For instance, Sam et al. (2015) recently found that artificially damaging leaves of tropical trees increased ant and bird predation on insect herbivores and that the effect of leaf damage on predation was stronger at lower elevations. Although predators were presumed to be attracted by volatile emissions or visual cues, the authors did not test these hypotheses or

measure other plant traits. More recently, Pellissier et al. (2016) and Dostálek et al. (2016) measured plant volatile emissions and reported higher levels of induction of indirect defences in low- than high-elevation-adapted herbaceous species (*Cardamine* spp. and a species of *Salvia*, respectively). Similar studies on plant traits mediating ant attraction (e.g. rewards, volatile emission) have also found greater ant predation at lower elevations (Koptur 1985, Rasmann et al. 2014c, Rodríguez-Castañeda et al. 2016), and such dynamics might be particularly important in tropical systems where ants constitute a dominant carnivore group (Rodríguez-Castañeda et al. 2016).

## Opportunities for future research

### *Disentangling the dynamic relationship between plant defences and insect herbivory*

Theory on elevational gradients in plant defence and insect herbivory has typically been proposed from a plant-centric view, in which plants at low elevations have adapted to higher insect herbivory by evolving higher levels of defences. However, the relationship between insect herbivory and plant defences is dynamic and likely involves ecological and evolutionary feedbacks such that the sign or direction of their association may shift over space and time (Thompson 2007, Massad et al. 2011). The fluctuating nature of co-evolutionary dynamics between plants and insect herbivores may thus result in either a positive relationship between damage by these herbivores and plant defences (suggesting insect herbivory drives defences) or a negative relationship (defence drives insect herbivory) depending on which stage of the co-evolutionary arms-race the interaction is found at (Abdala-Roberts et al. 2016). For example, Pellissier et al. (2016) found a negative association between insect herbivory and chemical defences (glucosinolates) in species of *Cardamine*, where constitutive defences increased with elevation and this gradient was associated with (and presumably drove) a decrease in insect herbivory with elevation. Having said this, a correlation between plant defences and insect herbivory does not always imply that they are causally linked along an environmental gradient. For example, Abdala-Roberts et al. (2016) found a negative association between insect herbivory and chemical defences (phenolic compounds) in *Quercus robur*, but both were positively associated with elevation suggesting that defences did not drive elevational variation in insect herbivory. It is also possible for insect herbivory and plant defences to co-vary due to a common third cause (e.g. an abiotic factor) such that co-variation cannot be taken as cause and effect. Therefore, accounting for the simultaneous effects of multiple abiotic factors may be necessary for understanding how abiotic forcing concurrently influences plant defences and insect herbivory along elevational gradients, as these third-party factors may complicate the assessment of causality (Abdala-Roberts et al. 2016).

Much of the work conducted so far has been correlative in nature, precluding a mechanistic assessment of the link

between insect herbivory and defences across elevations. Performing manipulative experiments across multiple trophic levels is a challenge, and there are a number of logistical constraints that may arise depending on the natural history and complexity of the interactions under study. However, it is these studies that are most needed to disentangle the potentially complex reasons for the simple patterns we observe across elevational gradients. We advocate for the integration of observational data with common garden or reciprocal transplant experiments to understand elevational patterns of plant traits and insect herbivory, a powerful approach that has already yielded key insights into similar patterns over latitudinal gradients (Pennings et al. 2009).

#### ***Addressing both within- and among-species variation in plant defences***

Both intra- and inter-specific elevational clines in insect herbivory and plant defences may feed back on one another (Hahn and Maron 2016). The majority of studies, however, have either studied these patterns among-species (34% of the cases) or within-species (63%), with very few studies (3%) considering both simultaneously (Supplementary material Appendix 1 Table A1, Fig. A1). Joint attention to intra- and inter-specific elevational clines would not only improve our understanding of the processes operating at each level, but would also enable tests for crossover effects and feedbacks between them. An important consideration of studies describing intra-specific patterns is to consider species' elevational ranges. Within each range there are regions of highest plant performance (e.g. the center of their elevational distribution or in lowlands), and elevations at which plant growth is slow or insect herbivory is too high to establish or reproduce. Addressing these range limit effects is necessary in order to understand the evolution of species elevational range limits (and underlying traits), intra-specific variation in species interactions along ecological gradients, and community-level effects based on the degree of overlap in species distributions.

Recent work simultaneously addressing intra- and inter-specific elevational gradients have reported that patterns may change depending on the level of organization studied (see Anstett et al. 2016 for latitudinal gradients). For example, Descombes et al. (2017) reported an overall increase in plant palatability with elevation based on plant community-weighted trait means, but at the individual species level, there was no effect of elevation on plant palatability in most cases. Similarly, Callis-Duehl et al. (2017) found an overall decline of physical and chemical defensive traits with elevation for most plants at the community level, but elevational patterns varied in strength and direction when analyses were conducted individually for each species. Studies such as these remain scarce, but are especially valuable for understanding how intra-specific variation contributes to community-level patterns, and vice versa: how whole communities can be decomposed into species-level clines and its underlying mechanisms. Within this context, an advantage of elevation over latitudinal gradients is that the climatic variation across a species elevation range is often far greater than the climatic

variation across its latitudinal range. This offers an opportunity to simultaneously test for intra- and inter-specific variation throughout most of the range of abiotic conditions present along these gradients (Abdala-Roberts et al. 2016).

#### ***A community ecology approach to elevational gradients that simultaneously considers bottom-up and top-down forcing***

Much of the work on elevational gradients in species interactions has represented a simplification of more complex ecological dynamics by focusing, for example, on pairwise, bi-trophic interactions rather than multi-species interactions across two or more trophic levels (Rasmann et al. 2014a). However, plants and insect herbivores are embedded in complex communities that require a multi-trophic perspective to deepen our understanding of environmental gradients in plant-animal communities.

Research on elevational gradients in multi-trophic interactions offers an opportunity to achieve a predictive understanding of the biotic and abiotic drivers responsible for shifts in bottom-up (i.e. resource) versus top-down (predator) control over populations and communities. Although the use of elevational gradients for these questions is rare, the few examples suggest that shifts between bottom-up and top-down control do occur. Preszler and Boecklen (1996) reported changes in the relative importance of bottom-up and top-down forcing along an elevational gradient for an insect herbivore, where effects of plant quality on herbivore mortality were stronger at high elevations but predator and parasitoid effects were more important at low elevations. Similarly, Rodríguez-Castañeda et al. (2016) reported that ant abundance and their protection of plants from herbivores decreased with increasing elevation, leading to a shift in the relative importance of plant indirect defences (i.e. rewards for ants) and direct defences. Because all species consume resources and most are themselves consumed, multitrophic community modules across ecological gradients are particularly well-suited for exploring how abiotic and biotic interactions jointly shape species distributions and diversity.

#### ***Climate change offers challenges and opportunities for novel insights***

Elevational gradients have been effective tools for predicting the impacts of climate change on species ranges (Colwell et al. 2008, Chen et al. 2011, Telwala et al. 2013), species traits (Franks et al. 2014, Petry et al. 2016), and ecosystem processes (reviewed by Sundqvist et al. 2013). However, the use of elevational gradients for predicting changes in species interactions under climate change – including those shaping patterns of insect herbivory and plant defences – has been more difficult to generalize (Elmendorf et al. 2012, Alexander et al. 2015).

One of the barriers that limits the use of elevational gradients to infer the effects of changing abiotic factors on plant defences and insect herbivory is the dependence of nutrients and the population dynamics of plants, insect herbivores and predators on abiotic factors. This complicates the attribution to changes in plant defences and insect herbivory to specific factors. Although global temperatures are generally expected to increase under climate change (IPCC 2013), the predictions

for other abiotic factors (e.g. precipitation) are more uncertain and spatially variable (e.g. drought is projected to increase in some regions while others may see increases in precipitation or no change) (IPCC 2013). Still other abiotic factors that may influence plant–herbivore interactions such as UV radiation, barometric pressure and several physical properties of soils will remain unchanged. By monitoring how insect herbivory and plant defence along elevational gradients change over time, the list of candidate abiotic drivers can be narrowed substantially as novel climates decouple these factors. For example, Thompson and colleagues used multi-decadal elevational surveys of chemical defences (terpenes) in wild-growing thyme *Thymus vulgaris* to show that less palatable, freeze-intolerant chemical types have colonized higher elevations as climate change has changed the elevations where freezing occurs (Amiot et al. 2005, Thompson et al. 2013). However, researchers should be aware that climate change may affect other abiotic drivers of plant–insect herbivore interactions that may not vary over elevational gradients. For example, atmospheric CO<sub>2</sub>-concentrations generally do not change markedly with elevation, but experimentally-increased CO<sub>2</sub>-concentrations have been shown to affect both plants and their interactions with insect herbivores (Stiling and Cornelissen 2007, Robinson et al. 2012, Pincebourde et al. 2017).

Changing climate may also reshuffle plant and insect herbivore communities through asynchronous range and phenological shifts (Urban et al. 2012, CaraDonna et al. 2014, Alexander et al. 2015), enabling insight into the roles of trophic and competitive interactions in shaping plant defence and insect herbivory. For example, the elevation range of the oligophagous butterfly *Aporia crataegi* was historically limited by the range of its host plants. However, temperature increases over the past several decades have reduced larval survival due to changes in population density, phenology and habitat use at low elevation such that the butterfly is no longer found or attacks its host plant in the lower 300 m of its former range (Merrill et al. 2008). Range-shifted insect herbivores may also encounter novel host species (Buckley and Bridle 2014) or different defence levels (Rasmann et al. 2014a) than they experienced previously, catalysing new ecological and co-evolutionary dynamics (Raffa et al. 2013).

Predicting community and ecological and evolutionary responses to climate change from observed patterns alone will continue to be a fraught exercise without synergistic experimental climate and distribution manipulations. Moreover, climate change may be too rapid for plants and insect herbivores to reach equilibrium abundances, distributions, and trait values, inducing time lags that make it difficult to understand the underlying mechanisms. Given the state of our current understanding of elevational gradients in plant defence and insect herbivory, we expect that near-term climate change will be more useful as a tool for elucidating the mechanisms underlying patterns in defence and insect herbivory rather than as a target for predictions. Creative exploitation of the partial independence between elevational and temporal climate change is likely to be a fruitful approach to this challenge.

## Outlook

The simultaneous influences of biotic and abiotic factors described in this paper greatly complicate the study of elevational gradients in insect herbivory and plant defences. Still, these gradients have attracted and will likely continue to attract substantial interest due to the advantages of studying changes in species interactions along gradual changes in abiotic conditions offered by elevation. The lessons offered by existing studies of gradients in plant–insect herbivore interactions (including positive, negative, nonlinear or no associations with elevation) emphasize how challenging it is to connect pattern and process in ecology and evolutionary biology. At the same time, we believe that conflicting evidence (e.g. positive versus negative associations between insect herbivory and elevation), need not limit our understanding of plant–insect herbivore interactions, but instead offer an underappreciated opportunity to rigorously evaluate the mechanisms that cause species to interact. In capitalizing upon this opportunity, the next generation of studies needs to account for community complexity and multi-trophic dynamics. Such efforts will be greatly benefitted by addressing the multivariate nature of plant defence and by integrating observational data and manipulative experiments across trophic levels, perhaps initially on simplified ecosystems (i.e. managed agricultural or forested landscapes). Finally, elevational gradients in tropical systems deserve special attention given the bias toward temperate mountains and the lack of baseline natural history information for many tropical species (Supplementary material Appendix 1 Table A1, Fig. A1). There are still knowledge gaps and limitations to conducting comprehensive studies of elevational gradients in plant–insect herbivore studies. Nevertheless, we are encouraged by the advent of novel analytical tools in chemical ecology, metabolomics, systems ecology, spatial ecology, bioinformatics and remote sensing, each of which presents exciting opportunities for advancing the field of plant–insect herbivore interactions along elevational gradients.

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Supplementary material (online as Appendix ecog-03184 at <[www.ecography.org/appendix/ecog-03184](http://www.ecography.org/appendix/ecog-03184)>). Appendix 1.