

RESEARCH ARTICLE

A global analysis of elevational gradients in leaf herbivory and its underlying drivers: Effects of plant growth form, leaf habit and climatic correlates

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Abstract

1. Research on elevational gradients in species interactions holds that herbivore pressure increases towards warmer and more stable climates found at lower elevations. However, the generality of this expectation has been challenged by recent studies reporting no evidence of expected trends or even positive associations between elevation and herbivory, presumably due to uncontrolled biotic and abiotic factors influencing such relationships.
2. Using a world-wide dataset of insect leaf herbivory including 1,027 plant species and spanning an elevation gradient of 2,755 m, we tested if elevational gradients in herbivory were contingent on whether species were found at tropical vs. temperate latitudes, plant growth form (non-woody vs. woody species), and leaf habit (deciduous vs. evergreen woody species). In addition, we tested the influence of climatic correlates of elevation presumably underlying such elevational gradients.
3. Although there was no evidence of an overall relationship between elevation and damage, we found that elevational gradients in herbivory were contingent on species growth form whereby herbivory increased towards lower elevations for woody species, but no gradient was observed for non-woody species. We further found that elevational gradients in herbivory were contingent on leaf habit as herbivory increased towards lower elevations for deciduous species, but no gradient was present for evergreen species. Elevational variation in damage was not contingent upon latitudinal region. Finally, analyses of climatic factors indicated that although a significant association between temperature and herbivory for woody species was detected, the elevational gradient in leaf herbivory remained largely unchanged after accounting for temperature and precipitation, suggesting that climate does not fully account for the gradient.
4. *Synthesis.* This study delivers the first global assessment of elevational gradients in leaf herbivory and emphasizes the role of plant (e.g. life-history or defensive) traits and climatic factors in shaping elevational gradients in herbivory.

KEYWORDS

deciduous, elevation, evergreen, herbivory, non-woody species, precipitation, temperate regions, temperature, tropical regions, woody species

1 | INTRODUCTION

Biotic (e.g. herbivory and predation) and abiotic (e.g. climate and soil conditions) factors often covary in predictable ways along environmental gradients, and this variation in turn shapes concomitant clines in species abundance, traits and diversity (Linhart & Grant, 1996; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009; Woods, Hastings, Turley, Heard, & Agrawal, 2012). Environmental gradients occurring along latitude or elevation have been especially useful for understanding spatial variation in the global imbalance of plant and herbivore species richness and plant–herbivore interactions. Theory predicts that higher rates of herbivory under warmer and more stable climates, found at low latitudes or low elevations, have led to selection for more potent levels of plant defences (Johnson & Rasmann, 2011; Moles, Bonser, Poore, Wallis, & Foley, 2011; Rasmann, Pellissier, & Alvarez, 2014), and ultimately higher rates of plant (and herbivore) diversification (Coley & Kursar, 2014; Schemske et al., 2009).

Although elevational gradients in species interactions have historically received less attention by ecologists relative to latitudinal gradients, recent work has shown that elevation is a good proxy of clinal variation in species interactions and community attributes (Pellissier et al., 2012, 2016; Pellissier, Roger, Bilat, & Rasmann, 2014; Rasmann, Pellissier, & Alvarez, 2014; Rodríguez-Castañeda et al., 2010). Furthermore, the study of elevational gradients provides several advantages over latitudinal gradients. For instance, elevational gradients occur over much smaller spatial scales and are thus less prone to confounding effects in broad-scale latitudinal studies such as dispersal limitation and species turnover (Körner, 2007; Rasmann, Pellissier, & Alvarez, 2014). In addition, climatic variation found along elevational gradients occurs separately from variation in day length, and regional inter-annual variation in climate affects the whole gradient simultaneously. Elevational gradients therefore provide an ideal opportunity for understanding how clinal variation in abiotic factors drives variation in species interactions.

Studies conducted thus far have reported inconsistent associations between elevation and herbivory, ranging from the expected negative relationship (higher herbivory at lower elevations), to no association or even positive relationships (reviewed by Rasmann, Pellissier, Defosse, Jactel, & Kunstler, 2014). The variability in sign and magnitude of such associations can be explained by several factors (see Anstett, Nunes, Baskett, & Kotanen, 2016 for latitudinal gradients). One of these is the often cited, but seldom evaluated, influence of abiotic forcing, particularly climate, which may influence elevational gradients in herbivory in at least two ways. First, broad-scale differences in climatic conditions between tropical and temperate latitudes may condition the outcome of elevational gradients in herbivory because, for a similar elevational range, the magnitude of change in climatic conditions

when moving from low to high elevation is greater in tropical than in temperate regions, leading to more pronounced concomitant clines in herbivore pressure in the tropics (Janzen, 1967). Therefore, the lower end of elevational gradients is under greater pressure in the tropics than in temperate regions such that not only mean herbivory is greater in the tropics but the gradient in herbivore pressure (and selection on defences) may also be steeper when moving from high to low elevations. However, thus far studies on elevational gradients in herbivory have been restricted to either tropical or temperate regions (Rasmann, Pellissier, Defosse, et al., 2014; Schemske et al., 2009), which could explain some of the inconsistency in the magnitude of these relationships. Second, and independently of latitudinal variation in climate, elevation per se has traditionally been used as a proxy for multiple covarying abiotic factors whose independent effects have not been explicitly measured or teased apart (Körner, 2007). Recent studies have demonstrated that addressing the simultaneous effects of these abiotic correlates (e.g. temperature and precipitation) is necessary to understand how local climate conditions set the template for how plant–herbivore interactions unfold along elevational gradients (Abdala-Roberts et al., 2016; De Long, Sundqvist, Gundale, Giesler, & Wardle, 2016; Moreira et al., 2014; Pellissier et al., 2014, 2016).

Another important aspect which could explain inconsistencies in elevational gradients in herbivory is that most studies have not considered whether such gradients are contingent upon plant life-history strategies. For instance, differences in growth form (e.g. woody vs. herbaceous) might influence the strength of elevational patterns considering that woody species are larger and longer lived and this presumably makes them easier to detect by herbivores as well as more predictable resources relative to smaller and ephemeral non-woody species (Feeny, 1976; Strauss, Cacho, Schwartz, Schwartz, & Burns, 2015). In accordance with these expectations, recent work has shown that woody plants suffer higher amounts of herbivory globally compared to non-woody species (Turcotte, Davies, Thomsen, & Johnson, 2014). Under an elevational context, woody plants would not only suffer from greater mean herbivory across the entire gradient but would presumably also be more attacked on the lower end of the gradient, therefore leading to a steeper increase in herbivory with decreasing elevation relative to herbaceous species. Likewise, differences in life-history strategies associated with resource use and acquisition might also influence plant defence investment and herbivory along elevational gradients (Lim, Fine, & Mittelbach, 2015; Moreira & Pearse, 2017). In the case of woody species, leaf habit is an important predictor of differences in resource use; evergreen species typically exhibit a more conservative resource-use strategy and this translates into slower growth rates (Givnish, 2002; Wright et al., 2004), whereas deciduous species exhibit an exploitative resource-use strategy and higher growth rates (Poorter & Garnier, 2007; Reich, Ellsworth,

& Walters, 1998). Assuming that growth and defences trade off, as they often do across many plant taxonomic groups (Coley, Bryant, & Chapin, 1985; Endara & Coley, 2011), evergreen species should grow less and be more highly defended, whereas faster growing deciduous species should be less defended. Under an elevational context, deciduous species would not only exhibit greater mean herbivory across the entire gradient but would also be more attacked on the lower end of the gradient than evergreen species leading to a steeper increase in herbivory with decreasing elevation.

To test the above predictions on latitudinal variation in the steepness of elevational gradients in herbivory and the contingency of such gradients on plant life-history traits, we analysed published data on leaf herbivory recorded for 1,027 plant species spanning an elevation gradient of 2,755 m (from 40°S to 64°N in latitude). Specifically, we asked the following: (i) is there an overall elevational gradient in leaf herbivory? (ii) Is any such elevational gradient dependent upon latitudinal region (tropical vs. temperate), growth form or leaf habit? and (iii) are elevational gradients in leaf herbivory associated with climatic factors, namely temperature and precipitation? By addressing these questions, this study delivers a novel global assessment of elevational clines in plant–herbivore interactions and sheds light into biotic and abiotic controls over such associations.

2 | MATERIALS AND METHODS

2.1 | Literature search, selection criteria and data acquisition

Herbivory data were obtained from two published datasets (Kozlov, Lanta, Zverev, & Zvereva, 2015; Turcotte, Thomsen, et al., 2014), as well as by searching the Web of Science and Google Scholar using the keywords “herbivory,” “leaf area loss,” “leaf damage,” “defoliation,” “folivory” and “plant-herbivory interaction” (Zhang, Zhang, & Ma, 2016). The access dates for this literature search spanned from 1952 to 30 November 2014. Following Zhang et al. (2016), the criteria used for data acquisition were as follows: (i) In order to be coherent with the two original datasets (Kozlov et al., 2015; Turcotte, Thomsen, et al., 2014), studies used were restricted to those where herbivory was measured as the percentage of leaf area consumed; (ii) only data representing most of the damage experienced during leaf lifetime was used, i.e. herbivory in mature leaves, herbivory at the end of the growing season and data summed damage of individual leaves over one or more months; (iii) in the case of experimental studies, only data from control treatments were considered; (iv) if herbivory was measured in a time series, the mean value of the time points was used; and (v) only data from studies performed under field conditions were considered. We previously analysed latitudinal gradients in leaf herbivory based upon this dataset and these results are reported in Zhang et al. (2016).

Means, standard errors/deviations and sample sizes were extracted from texts, tables or figures (Zhang et al., 2016). For data expressed in figures, the UTHSCSA Image Tool (University of Texas, USA) was used to obtain exact values (Zhang et al., 2016). Elevation values (m above sea level) were obtained based on information on the

latitude and longitude coordinates of each site (Zhang et al., 2016). We excluded studies with unclear or imprecise information on the coordinates of the sampling site. The dataset also included information on the mean annual temperature (°C) and mean annual precipitation (mm). These climatic variables were taken from original literature or from web searches of the study sites. In cases where this information was not available, climatic data were extracted from the CRU CL 2.0 dataset which is a set of global climate grids with 10-min spatial resolution (New, Hulme, & Jones, 1999). In addition, we also categorized the plant species as temperate or tropical based on geographic coordinates of sampling points, as well as by growth form (non-woody or woody species) and by leaf habit (evergreen vs. deciduous) in the case of woody species. In the first case, we adopted the commonly accepted latitudinal boundaries of climate zones, defining tropical regions as those below 23.5° (north and south, i.e. between the tropics of Cancer and Capricorn) and temperate regions as those from 23.5° to 66.5° (north and south, i.e. between the tropics and the polar circles). We excluded a few data points corresponding to polar regions (above 66.5°N) that were included in Zhang et al. (2016). Overall, the dataset included 1,847 leaf herbivory data points for a total of 1,027 plant species distributed from 0 to 2,755 m of elevation above sea level. These plant species were divided into 484 species growing in temperate regions and 543 species growing in tropical regions. Likewise, 353 species were non-woody and 674 were woody, and in the latter case 294 were deciduous and 380 were evergreen.

2.2 | Data analyses

For all statistical analyses, we logit-transformed leaf herbivory data and in those cases where a species was sampled at multiple space or time points, we used species-level means for herbivory as well as the mean value of elevation, temperature and precipitation across the sampling points (Lim et al., 2015). We also conducted analyses at the population level (using species as a random factor) and found similar results compared with analyses at the species level (Table S1). We note, however, that a high number of plant species in the dataset had a single data point and in those cases where there were multiple data points per species, these were strongly skewed towards a handful of species with high population-level replication. Because this may introduce potential biases in the results (i.e. some species contributing much more to the overall pattern), we opted for the species-level over the population-level analyses.

We analysed elevational gradients in leaf herbivory in the following way. First, to test for an overall elevational gradient in leaf herbivory, we performed an ordinary least squares linear regression using the full dataset where elevation predicted leaf herbivory. Second, to analyse differences in elevational gradients depending on latitudinal region and plant life-history traits, we performed an ANCOVA model using the full dataset where leaf herbivory was predicted by elevation, latitudinal region (tropical vs. temperate), plant growth form (non-woody vs. woody), and all two- and three-way interactions among these factors. The two-way interactions between elevation and latitudinal region and elevation and growth form tested for differences in the magnitude

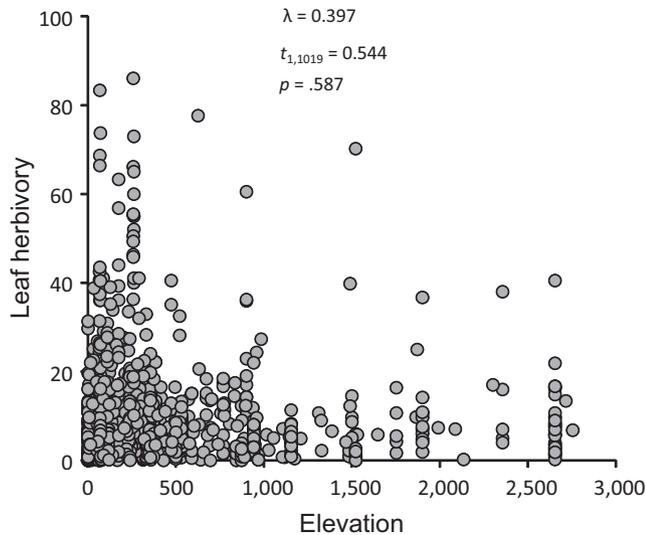


FIGURE 1 Elevation as a predictor of leaf herbivory (measured as the percentage of leaf area consumed) in 674 woody and 353 non-woody species. Shown are Student's *t*-test values (*t*) with associated degrees of freedom and *p*-values based upon logit-transformed data after controlling for phylogeny using a phylogenetic least squares regression (PGLS) are shown. Phylogenetic correlation parameter (λ) was estimated using maximum likelihood. Circles represent plant species means

or direction of elevational patterns in herbivory between tropical vs. temperate regions and between non-woody vs. woody species respectively. In those cases where the two-way interactions were significant, we ran univariate regressions with elevation as predictor separately for each level of the factor (growth form or latitudinal region) that interacted with elevation. We did not include latitude per se as a continuous predictor in this ANCOVA model because a previous study using a subset of our dataset (Zhang et al., 2016) treated latitude in such a way and we preferred not to repeat the same analysis. In addition, our hypothesis was based on differences across broad latitudinal zones, and treating this predictor as a categorical predictor provided an explicit test of this latitudinal effect. Similarly, although previous results by Zhang et al. (2016) indicated contrasting latitudinal patterns in herbivory between hemispheres, we did not include hemisphere in the statistical model because we had no a priori expectation or candidate mechanisms to explain the effects of hemisphere on elevational variation in leaf herbivory. Third, the previous ANCOVA indicated a significant elevational gradient only for woody species (significant growth form by elevation interaction; see Results section) and to investigate the mechanistic underpinning this finding, we ran a model using only woody species where herbivory was predicted by elevation, leaf habit and their interaction. The interaction term tested for differences in elevational gradients between evergreen vs. deciduous woody species. Likewise, if the interaction was significant, we ran univariate regressions between herbivory and elevation separately for deciduous and evergreen species.

If the overall elevational gradient was significant in the univariate regression model using the full dataset, we assessed whether such gradient was underlain by climatic factors by running a multiple regression

that included elevation, mean annual temperature, and annual precipitation. Similarly, in those cases where elevation interacted significantly with a given factor (from ANCOVA models described above), after running univariate regressions between elevation and herbivory separately for each level of the factor we ran multiple regressions for each level of that factor including elevation, temperature, and precipitation as predictors. If the effect of elevation in the univariate regression turned non-significant after accounting for climatic variables in the multiple regression, we interpreted this as evidence that climate underlies the elevational gradient in herbivory. Because collinearity between predictors may influence this analysis, we previously explored the associations between elevation and climatic variables. Results from univariate regressions indicated that associations for elevation vs. temperature and elevation vs. precipitation were weak ($R^2 = 0.05$ and 0.02 respectively). Although this suggested a moderate influence of collinearity, we nonetheless decided to explore a more conservative approach where the residuals from a model where temperature and precipitation predicted herbivory were regressed onto elevation. Findings from this analysis did not change the interpretation of the results relative to the multiple regression with climatic predictors. Based on these findings, and considering that the multiple regression has the advantage over the model using residuals of providing an explicit evaluation of the individual effects of climatic variables underlying the elevational gradient, we opted for the multiple regression approach.

In all of the above statistical models, we conducted phylogenetic least squares regressions (PGLS) to account for the influence of evolutionary relationships among species (Martins & Hansen, 1997). The species-level phylogeny was obtained from a super tree using Phylomatic (v.3.0, stored tree "20120829"; Webb & Donoghue, 2005). Divergence times were calculated in the trees with the BLADJ algorithm in Phylocom (Webb, Ackerly, & Kembel, 2008). We ran all the statistical analyses in R (version 3.1.1; R Core Team, 2014) and the PGLS analyses were conducted using the *PHYLOLM* package (Ho & Ane, 2014) and the phylogenetic models for the error term were selected based on the Akaike information criterion values.

It is important to note that the dataset analysed by Turcotte, Thomsen, et al. (2014) included information about the method used to quantify leaf herbivory (single time point measurements vs. multiple measurements on single leaves to measure rates or cumulative damage). However, we lacked this information for species from the other datasets (e.g. Kozlov et al., 2015), so we were not able to account for this factor in our statistical analyses.

3 | RESULTS

3.1 | Elevational gradients in leaf herbivory

Using the full dataset (all species included), we found no significant association between leaf herbivory and elevation (Figure 1). Results from the ANCOVA using the full dataset including categorical factors (latitudinal region, growth form) and their interactions with elevation indicated a significant effect of growth form (percentage of leaf area consumed: 10.74 ± 0.46 for woody species vs. 8.20 ± 0.67

TABLE 1 Effects of elevation, latitudinal region (tropical vs. temperate), growth form (non-woody vs. woody) and their interactions on leaf herbivory (measured as the percentage of leaf area consumed) in 353 non-woody and 674 woody species. Degrees of freedom, Student's *t*-tests (*t*) and *p*-values for an analysis based upon logit-transformed data after controlling for phylogeny using a phylogenetic least squares regression are shown. Significant ($p < .05$) *p*-values are typed in bold

Variable	<i>df</i> _{num,den}	<i>t</i> -value	<i>p</i> -value
Elevation	1, 1,013	1.31	.191
Latitudinal region	1, 1,013	-1.88	.060
Growth form	1, 1,013	3.86	<.001
Elevation × latitudinal region	1, 1,013	1.58	.114
Elevation × growth form	1, 1,013	-1.97	.049
Elevation × latitudinal region × growth form	1, 1,013	-0.65	.513

for non-woody species), and a marginally significant effect of latitudinal region (percentage of leaf area consumed: 9.61 ± 0.62 for tropical regions vs. 9.33 ± 0.52 for temperate regions; Table 1). More importantly, there was a significant elevation × growth form interaction indicating that elevational gradients in herbivory were contingent on whether species were non-woody or woody (Table 1). Subsidiary univariate regressions indicated an elevational gradient in leaf herbivory for woody species, in which herbivory increased towards lower elevations (Figure 2b), but not for non-woody species (Figure 2a). In contrast, the elevation × latitudinal region interaction was not significant, indicating that the effects of elevation on herbivory were not contingent upon latitude (Table 1). In fact, we found no evidence of elevational gradients in herbivory for either temperate (Figure 2c) or tropical (Figure 2d) species. Results from this model indicated that the three-way elevation × latitudinal region × growth form interaction on leaf herbivory was not significant (Table 1). Finally, the ANCOVA for woody species indicated a non-significant effect of leaf habit but a significant elevation × leaf habit interaction on leaf herbivory (Table 2). Univariate regressions for each category of leaf habit showed a significant elevational gradient for deciduous species where herbivory increased towards lower elevations (Figure 3a), but no significant pattern for evergreen species (Figure 3b).

3.2 | Climatic correlates of elevational gradients in leaf herbivory

After accounting for both climatic variables (i.e. temperature and precipitation), the multiple regression model for woody species indicated that mean annual temperature (but not precipitation) was significantly and positively associated with leaf herbivory (i.e. species growing in warmer sites exhibited higher rates of leaf herbivore damage Table 3a). However, the effect of elevation on herbivory remained significant after including climatic predictors (Table 3a), suggesting that temperature did not fully account for the elevational gradient in woody species.

In the case of deciduous woody species, for which a significant elevational gradient was also observed, the multiple regression with climatic variables indicated that mean annual temperature and annual precipitation were not significantly associated with leaf herbivory (Table 3b). In addition, the effect of elevation on herbivory remained significant after including climatic predictors (Table 3b), suggesting that these climatic correlates of elevation did not explain the observed gradient for deciduous species.

4 | DISCUSSION

This study represents the first global assessment of elevational gradients in leaf herbivory across tropical and temperate regions, and further explores the mechanistic underpinnings of such gradients by evaluating the influence of plant life-history traits and climatic factors. Following predictions, we found that elevational gradients in leaf herbivory were contingent on species growth form whereby herbivory on woody species increased towards lower elevations, but no gradient was observed for non-woody species. Furthermore, elevational gradients within woody species were contingent on leaf habit whereby herbivory increased towards lower elevations for deciduous woody species, but no gradient was observed for evergreen woody species. However, contrary to expectations, elevational variation in herbivory was not contingent on latitudinal region (i.e. tropical vs. temperate), and although an association between temperature and herbivory was detected (in the case of woody species), the elevational gradient in leaf herbivory remained largely unchanged after accounting for temperature and precipitation, suggesting that climate does not fully account for the gradient.

With respect to latitudinal region, our expectation was that the magnitude of change in climatic conditions from low- to high-elevation sites would be greater in tropical relative to temperate regions, and that this would set the template for steeper elevational gradients in herbivory in the tropics. Supporting this prediction, Fernandes and Price (1988) reported a steeper elevational gradient in the number of galling species feeding on plants in the tropics in comparison with their temperate counterparts. Counter to this study, we found that the elevational gradient in leaf herbivory was not steeper in tropical relative to temperate zones. Despite the null influence of latitudinal region on elevational gradients in herbivory, we consider that examining the interactive effects of latitude and elevation on geographic variation in herbivory represents an important consideration for future research. Controlled experiments using groups of related species where herbivory is measured on "phytometer" plants or common gardens planted at low and high elevations, and with this design being replicated at different latitudes (and at the same elevational range), would advance our understanding of ecological and evolutionary patterns of herbivory.

Following predictions, our results showed that elevational gradients in leaf herbivory were only present for woody species. Our prediction was that woody species represent a resource with more predictable availability and are easier to locate by herbivores relative to short-lived,

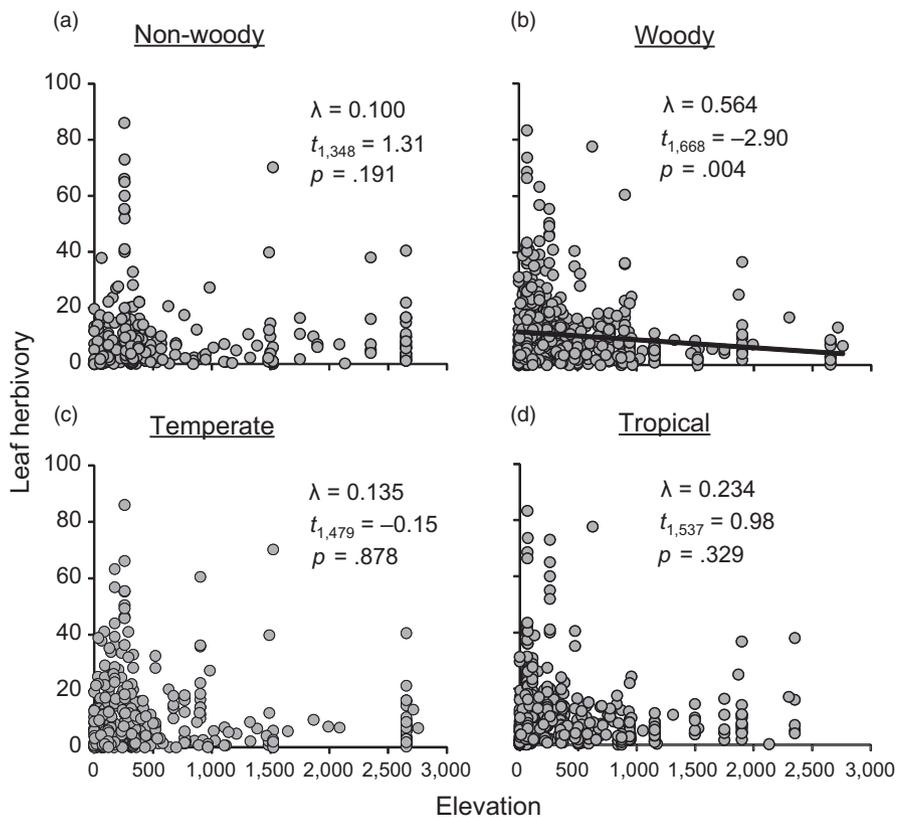


FIGURE 2 Elevation as a predictor of leaf herbivory (measured as the percentage of leaf area consumed) in (a) non-woody species ($n = 353$ species), (b) woody species ($n = 674$ species), (c) temperate regions (236 species) and (d) tropical regions ($n = 438$ species). Shown are Student's t -tests (t) with associated degrees of freedom and p -values based upon logit-transformed data after controlling for phylogeny using a phylogenetic least squares regression (PGLS) are shown. Phylogenetic correlation parameters (λ) were estimated using maximum likelihood. Circles represent plant species means

herbaceous species (Feeny, 1976; Strauss et al., 2015), and that this would presumably lead to a more pronounced elevational cline herbivory due to a steeper increase in damage towards lower elevations. In one of the few available studies, Fernandes and Price (1988) found partial support for our prediction as they reported an elevational gradient of a decreasing number of galling insects with elevation for shrubs, whereas no gradient was found for the number of galls on herbaceous species. Unfortunately, this study is to our knowledge one of the few (if not the only) previous study to test for effects of plant growth form on elevational gradients of herbivory, such that it is yet not possible to reach any type of generalization. Future work is needed to test for the influence of plant traits, population and community attributes along elevational gradients by integrating theoretical frameworks in community ecology (e.g. Resource Concentration Hypothesis, Plant Apparency Theory) and plant-centred evolutionary ecology (e.g. Resource Availability Hypothesis) to understand gradients in plant-herbivore interactions. In addition, testing for the individual effects of different plant traits while controlling for others (e.g. choosing pairs of species with contrasting traits or performing phylogenetically controlled experiments) will be key in order to achieve better understanding of the role of bottom-up variation in shaping elevational gradients in herbivory.

Our results further indicated heterogeneity in elevational gradients of herbivory within woody species, as only deciduous species exhibited a significant (negative) cline in leaf herbivory. Leaf habit is a powerful correlate of resource use and acquisition strategies in plants (e.g. Givnish, 2002; Wright et al., 2004), where evergreen species are often associated with slow growth and more conservative resource-use strategies, which, if growth and defences trade off, is expected to lead to

higher investment in defences. In addition, evergreen species have to produce leaf defences against herbivores year round. In contrast, deciduous species tend to be faster growing and would be expected to invest less in defences if growth and defences trade off, and additionally do not require to invest in leaf defences against herbivory during winter after leaves are shed (e.g. Bai, He, Wan, & Jiang, 2015; Pearse & Karban, 2013; Poorter & Garnier, 2007; Pringle et al., 2011; Reich et al., 1998). Accordingly, we predicted that less defended deciduous species would exhibit a steeper increase in herbivory at low elevation relative to better-defended evergreen species. Supporting our findings, Rasmann, Pellissier, Defossez, et al. (2014) observed steeper elevational gradients in leaf damage for seedlings of deciduous tree seedlings in comparison with those of evergreen species (mainly conifers) along an elevation gradient in the French Alps. However, not all evidence is supportive, as a related study by Lim et al. (2015) found that leaf herbivory increased towards the equator for evergreen species, but no association between herbivory and latitude for deciduous species. These authors argue that steeper latitudinal gradients in herbivory are expected for evergreen species because insect damage on these species is low or close to absent during the winter months in temperate zones, whereas herbivory in the tropics remains more consistent throughout the year presumably leading to higher cumulative herbivory year round (Lim et al., 2015). In contrast, deciduous species are only attacked during the growing season and do not suffer herbivory during the winter in both temperate and tropical zones, which would lead to a weaker year round differences in herbivore pressure across tropical and temperate latitudes in these species. Likewise, longer leaf life span in evergreen species increases exposure to damage throughout the year, presumably leading

TABLE 2 Effects of elevation, leaf habit (evergreen vs. deciduous) and their interaction on leaf herbivory (measured as the percentage of leaf area consumed) in 674 woody species. Degrees of freedom, Student's *t*-tests (*t*) and *p*-values for an analysis based upon logit-transformed data after controlling for phylogeny using a phylogenetic least squares regression are shown. Significant ($p < .05$) *p*-values are typed in bold

Variable	<i>df</i> _{num,den}	<i>t</i> -value	<i>p</i> -value
Elevation	1, 666	-3.40	<.001
Leaf habit	1, 666	-1.23	.221
Elevation × Leaf habit	1, 666	1.97	.049

to greater investment in plant defences, and this would thus increase the chance of detecting latitudinal gradients relative to short-lived leaves in deciduous species. Although these arguments could also apply for explaining elevational gradients in herbivory for different plant life-forms, our results do not seem to fit these explanations. Further studies are necessary to test these competing hypotheses by measuring year round herbivory rates (total amount of herbivory throughout the year), as well as relate these herbivory patterns with measurements of plant growth rate, leaf senescence and defences.

Although climatic factors associated with elevation are considered important drivers of herbivore abundance, diversity and damage (e.g. Abdala-Roberts et al., 2016; Pellissier et al., 2014), our results indicated that they did not fully explain elevational gradients in leaf herbivory for woody species in general or woody deciduous species in particular. Particularly, we found a positive association between temperature and herbivory for woody species (the only growth form category for which herbivory was significantly associated with climatic variables) which is expected given that this variable exerts strong controls over herbivore abundance and feeding rates (Körner, 2007). However, including temperature in the statistical model did not eliminate the effect of elevation on herbivory, suggesting that other abiotic factors (e.g. other climatic variables or soil characteristics) should be

TABLE 3 Multiple regression showing the effects of elevation and climate (mean annual temperature and annual precipitation) on leaf herbivory (measured as the percentage of leaf area consumed) in (a) woody species ($n = 674$ species) and (b) deciduous woody species ($n = 294$ species). Degrees of freedom, Student's *t*-tests (*t*) and *p*-values for an analysis based upon logit-transformed data after controlling for phylogeny using a phylogenetic least squares regression are shown. Significant ($p < .05$) *p*-values are typed in bold

	<i>df</i> _{num,den}	<i>t</i> -value	<i>p</i> -value
(a) Woody species			
Elevation	1, 664	-2.21	.027
Temperature	1, 664	2.41	.016
Precipitation	1, 664	0.01	.995
(b) Deciduous woody species			
Elevation	1, 288	-3.22	.001
Temperature	1, 288	1.42	.157
Precipitation	1, 288	-1.53	.127

considered for better understanding abiotic control over elevational gradients in herbivory. For example, Abdala-Roberts et al. (2016) recently found that temperature-related climatic variables strongly influenced elevational gradients of insect herbivory in the widespread oak *Quercus robur*. Similarly, in a manipulative experiment, Pellissier et al. (2014) demonstrated that temperature partially accounted for elevational variation in herbivore pressure in the herbaceous plant *Plantago lanceolata*. At the same time, however, and in agreement with our results, evidence from other investigations has shown that elevational gradients in abiotic factors are not always associated with geographic patterns of herbivory. For example, Pellissier et al. (2016) found that neither temperature nor precipitation influenced herbivory in *Cardamine* species growing along an elevational gradient. Although correlative approaches have contributed to understanding the concurrent effects of abiotic factors on geographic variation in plant traits (Abdala-Roberts et al., 2016), experimental manipulations of candidate climatic drivers are ultimately needed to disentangle the effects

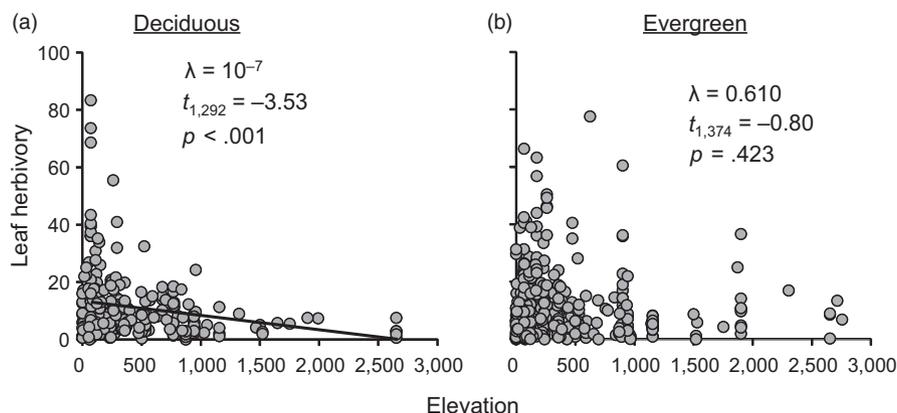


FIGURE 3 Elevation as a predictor of leaf herbivory (measured as the percentage of leaf area consumed) in (a) deciduous ($n = 294$ species) and (b) evergreen ($n = 380$ species) woody species. Shown are Student's *t*-tests (*t*) with associated degrees of freedom and *p*-values using logit-transformed data after controlling for phylogeny using a phylogenetic least squares regression (PGLS) are shown. Phylogenetic correlation parameters (λ) were estimated using maximum likelihood. Circles represent plant species means

of climatic factors on plant–herbivore systems across elevational gradients (Pellissier et al., 2014).

It is important to also note that soil characteristics may influence plant defences and herbivory, but their influence remains largely ignored in elevational studies, including our present work. Within this context, the Resource Availability Hypothesis predicts that plant species growing in nutrient-poor soils invest more in chemical defences relative to species growing in nutrient-rich soils (Coley et al., 1985; Endara & Coley, 2011). Shifts in soil resource availability along elevational clines could therefore influence plant defences and herbivory, and in some cases lead to unexpected outcomes depending on whether key nutrients decrease or increase with elevation (Abdala-Roberts et al., 2016; De Long et al., 2016; Pellissier et al., 2016). For example, in a recent study, De Long et al. (2016) reported that soil nitrogen availability drove elevational gradients in plant community-level chemical defences in a subarctic tundra heath, and that such effects presumably exert an important bottom-up control on herbivory. In addition, high resource availability is associated with faster life histories characterized by higher leaf nutrient concentrations and this may in turn result in high rates of herbivory. Further studies measuring and manipulating soil resources as well as climatic factors are needed to tease apart the direct and indirect effects of abiotic factors on plant defences and herbivory.

Overall, this study builds towards a better understanding of plant traits and climatic factors shaping elevational gradients in herbivory. However, a typical limitation of global datasets and purely correlative studies such as ours is that it is not possible to establish a strong link between pattern and process via presumed mechanisms without performing manipulative experiments. In addition, there are potentially important geographic and taxonomic biases in databases such as that used here. For example, certain taxonomic groups in some geographic regions may dominate the datasets (e.g. *Inga* spp. in tropical regions and *Quercus* or *Pinus* spp. in temperate regions), such that results are driven by certain taxonomic groups that are overrepresented. As sampling effort increases (both spatially and taxonomically), databases such as this will be less influenced by potential biases and we will gain a more complete understanding of elevational gradients in herbivory and its underlying drivers. At the same time, the robustness of individual studies would increase by including replicated designs across multiple sites at a given latitude or elevation, as well as sampling schemes that spanned both tropical and temperate zones. It would be particularly useful that such studies: (i) measure plant physical and chemical defences, (ii) compare patterns by specialist and generalist herbivores and associate these with plant traits, (iii) use pairs of plant species with contrasting traits under a phylogenetically controlled setting and (iv) manipulate climatic and soil variables. Addressing these aspects will bring a deeper understanding of the relative importance and interactive effects of plant traits, abiotic factors and variation in herbivore communities on elevational gradients in plant defence and herbivory.

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AUTHORS' CONTRIBUTIONS

X.M. formulated the idea of the manuscript; S.Z., X.M., J.C.B. and A.G. collected data; X.M. and S.Z. analysed the data; X.M. and A.G. wrote the first draft of the manuscript; L.A.R. and S.R. contributed critically to the writing.

DATA ACCESSIBILITY

The dataset used in this study is archived at Table S1 in Zhang et al. (2016).

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