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ECOLOGICAL SOUNDING

Assessing the latitudinal gradient in herbivory

Jun Ying Lim[1]*, Paul V. A. Fine[1]* and Gary G. Mittelbach[2]

[1]*Department of Integrative Biology, University of California, Berkeley, CA 94720, USA,* [2]*W.K. Kellogg Biological Station and Department of Integrative Biology, Michigan State University, Hickory Corners, MI 49060, USA*

*Correspondence: Paul V. A. Fine, Department of Integrative Biology, University of California, Berkeley, CA 94720, USA.
E-mail: paulfine@berkeley.edu
Jun Ying Lim, Department of Integrative Biology, University of California, Berkeley, CA 94720, USA.
E-mail: junyinglim@berkeley.edu

ABSTRACT

Plant–herbivore interactions occur in all ecosystems and provide a major avenue for energy flow to higher trophic levels. A long-standing hypothesis to explain the latitudinal gradient in species diversity proposes that the relatively stable and frost-free climate of the tropics should lead to more intense biotic interactions in tropical compared with temperate environments, giving rise to a greater diversity of plants and herbivores. Herbivory rates have been compared across latitudes to test this biotic interactions hypothesis, with herbivory typically being measured from observable leaf damage. However, we argue that a measure of percentage leaf damage alone does not straightforwardly reflect the cost of herbivory to the plant, and on its own does not constitute an appropriate test of the biotic interactions hypothesis. For a given amount of herbivory, the impact of herbivory is dependent upon many factors, such as the construction cost of the leaf, the growth and replacement rates and leaf life span. We investigate the latitudinal gradient in herbivory by analysing a large dataset of herbivory rates for 452 tree species and separating the species into those with short and long leaf life spans. We show that annual herbivory rates tend to be greater at lower latitudes for evergreen species (which have long-lived leaves), but no trend in herbivory rate with latitude was found for species with short leaf life spans. Phylogenetic least squares regression assuming Ornstein-Uhlenbeck processes also showed a negative effect of latitude on herbivory rate for evergreen trees, but we caution that viewing herbivory as a species trait is problematic. An integrative approach that incorporates leaf life span, as well as the costs of investment in growth and potential costs of losing leaf tissue, is needed to further our understanding of the ecological and evolutionary dynamics of herbivory.

Keywords

Biotic interactions, leaf economic spectrum, leaf lifetime, tropical–temperate comparison.

INTRODUCTION

Biologists have long sought an explanation for the nearly universal biogeographic pattern that species richness increases from high to low latitudes (Willig *et al*., 2003; Hillebrand, 2004; Mittelbach *et al*., 2007). The ‘biotic interactions hypothesis’ is one of many proposed to explain the latitudinal diversity gradient. It focuses on relative differences in selective pressures between tropical and temperate environments (reviewed in Mittelbach *et al*., 2007). The harsher physical conditions of the environment at northern latitudes have been proposed to favour adaptation to abiotic factors, while the relatively benign and stable climate of the tropics is thought to favour adaptation and speciation in response to biotic interactions (Dobzhansky, 1950; Schemske, 2009; Schemske *et al*., 2009). Indeed, many biotic interactions have been found to be stronger or more prevalent at lower latitudes (Schemske *et al*., 2009).

Herbivory has featured prominently in comparative studies of the strength of biotic interactions, but determining the importance of herbivory across latitudes has been controversial. In two seminal papers in the 1990s, Coley and colleagues reviewed published herbivory rates in tropical and temperate forests and found that tropical trees experienced significantly higher annual herbivory rates, consistent with the biotic interactions hypothesis (Coley & Aide, 1991; Coley & Barone, 1996). In contrast, a recent meta-analysis of 38 latitudinal studies found no effect of latitude on herbivory rates (Moles *et al*., 2011a). However, we note that 35 of the 38 studies included by

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Moles *et al*. (2011a) were extra-tropical, and the mean low latitude of included studies was greater than 30°, far enough from the equator that freezing temperatures present a significant abiotic challenge. A strong test of the biotic interactions hypothesis requires a thorough sampling of tropical sites. In addition, comparisons of the importance of herbivory across latitude require careful consideration of the fitness costs of leaf loss. Evolutionary history may also influence herbivory rates across latitudes, as suggested by a recent global analysis of herbivory rates showing strong patterns of phylogenetic signal among plant clades (Turcotte *et al*., 2014a). We discuss below the challenges of comparing herbivory rates across latitude as a test of the biotic interactions hypothesis, focusing on the fitness costs of herbivory under different strategies of leaf investment and on the roles of leaf economics and evolutionary history on the global distribution of plants.

WHY PLANT STRATEGY INFLUENCES THE COST OF HERBIVORY

The direct costs of herbivory to a plant depend on the construction cost of the leaf and the opportunity cost in loss of photosynthate (Lamarre *et al*., 2012), which in turn are dependent on plant growth strategies and resource availability (Coley *et al*., 1985; Fine *et al*., 2004; Endara & Coley, 2011; Wieski & Pennings, 2014). At the extremes, some plants have large numbers of cheaply produced leaves and may be able to outpace herbivory with high growth rates, while others produce a few expensive, well-defended leaves and grow slowly. Leaves of deciduous and pioneer species tend to have low leaf mass per area (LMA) and a short leaf life span. On the other hand, evergreen species tend to have longer-lived leaves and leaves with a higher LMA (Wright *et al*., 2004). Thus, species at opposite ends of the leaf economic spectrum may experience very different costs of herbivory for the same areal loss of leaf.

Lamarre *et al*. (2012) attempted to account for differences in plant growth strategy by introducing the concept of 'herbivory impact' (HI), which divides herbivory rates by leaf production rates to produce a unitless measure. By scaling herbivory rates by rates of leaf production, HI gives a more accurate estimate of the potential cost of herbivory to the plant and allows for interspecific comparison of plants across different resource availabilities and/or latitudes (Lamarre *et al*., 2012). Unfortunately, there is still very little information on leaf production rates. However, some evidence suggests that a high leaf production rate is negatively correlated with expensive leaves (i.e. a low specific leaf area; Lamarre *et al*., 2012), and leaves that are costly to produce tend to have longer life spans (Reich *et al*., 1999; Wright *et al*., 2004). Thus, as a first approximation, leaf lifetime can be used as a proxy for leaf economic strategy.

We predict a strong latitudinal gradient in herbivory rates for species with long leaf lifetimes (e.g. evergreen trees), because evergreen species will experience little or no attack from invertebrates during the winter in the temperate zone but will experience many months of damage from herbivores in the tropics. Conversely, we hypothesize that species with short leaf lifetimes may or may not exhibit a latitudinal gradient in herbivory rates, because these species are likely to be employing a strategy to maximize leaf growth during optimal conditions (temperate summers, tropical wet seasons and/or in the presence of a canopy gap) that simultaneously promote large herbivore and third trophic level abundances at all latitudes. Latitudinal gradients in herbivory would be muted if greater herbivory in the tropics also drives selection for better plant defences. However, due to coevolving interactions between plants and their enemies driving the evolution of counter-defences (Ehrlich & Raven, 1964), even more highly defended leaves of tropical evergreens may still experience greater herbivory rates than temperate zone evergreens – see Wieski & Pennings (2014) for such a case in a species with long-lived leaves, *Iva frutescens*, across a latitudinal gradient from Maine to Florida.

HERBIVORY RATE AND LEAF LIFETIME

To examine the above predictions, we analysed herbivory data from a recently published dataset reporting 2641 population-level annual and/or daily rates of leaf herbivory for 1145 species of vascular plants collected from 189 studies (Turcotte *et al*., 2014b). This dataset presents the largest compilation to date of herbivory rates and its world-wide distribution includes many tropical and temperate species and sites (Fig. 1), allowing for a comparison of herbivory rates across all latitudes. Although the dataset of Turcotte *et al*. includes several growth forms (trees, grasses, forbs, shrubs and vines), we do not compare herbivory rates across different plant growth forms because this would introduce confounding factors to the test of the biotic interactions hypothesis – for example, woody species exhibit higher rates of leaf herbivory than non-woody species (Turcotte *et al*., 2014a). Only trees are reasonably well represented across all latitudes, so we limit our analysis to that of 898 population-level measured herbivory rates for 452 tree species in the dataset. Only wild populations and populations identified to the species level were included. Population herbivory estimates for which latitude was unspecified were excluded.

We separated tree species into two categories: 'short leaf lifetimes' and 'long leaf lifetimes (or evergreen)'. Short leaf lifetime species are defined as plants with leaf lifetimes of less than 1 year (often much less) and included temperate and tropical deciduous species and tropical pioneer species, whereas evergreens have leaf lifetimes of greater than 1 year (Wright *et al*., 2005; van Ommen Kloeke *et al*., 2012; Kikuzawa *et al*., 2013). We looked up each species to see if it was described as evergreen, deciduous or pioneer from the original papers cited in Turcotte *et al*. (2014b), supplemented by searches of the literature.

It is worth noting that the Turcotte *et al*. (2014b) dataset includes annual herbivory rates measured on both marked and standing leaves (standing damage was assumed to directly translate to the annual herbivory rate). Herbivory rates measured on marked leaves are generally more accurate (Coley & Barone, 1996). Standing rates, although more common, are probable underestimates as they represent 'snapshots' of missing tissue on

Figure 1 Localities of the 898 population-level herbivory studies for the 452 tree species analysed in this paper. Data from Turcotte *et al.* (2014b).

mature leaves, and may thus miss leaves that have been completely eaten (Coley & Barone, 1996).

We analysed logit-transformed herbivory rates in two ways. We first analysed the influence of latitude on species-level herbivory rates using ordinary least-squares linear regression. We excluded three species with zero values due to the difficulty of including zero values in a regression of logit-transformed rates. Species-level herbivory rates and latitude were obtained by calculating species-level means from all population estimates for a given species. We also analysed logit-transformed population-level herbivory rates within a linear mixed effects model framework due to the aforementioned issues associated with different techniques for quantifying herbivory. Latitude and leaf lifetime were fitted as fixed effects, whereas species identity and herbivory measurement type (standing versus marked) were fitted as random effects on the intercept to take into account intraspecific variation in herbivory rates. We also fitted a nested random effect of species identity and herbivory measurement type to account for variation in herbivory rates for species that were measured by different methods (standing versus marked). We report both marginal R^2 (the proportion of variance explained by fixed effects) and conditional R^2 (the proportion of variance explained by both fixed and random factors), calculated following Nakagawa & Schielzeth (2013).

To account for evolutionary relationships among species, we performed a phylogenetic least squares regression (PGLS) (Grafen, 1989; Martins & Hansen, 1997) of herbivory rate against absolute latitude on all species, under three different models for the expected covariance of residuals: a Brownian motion (BM) model (Felsenstein, 1985), an Ornstein–Uhlenbeck (OU) model (Martins & Hansen, 1997) and a model that accommodates for phylogenetic signal (PS) in traits using a measure of phylogenetic correlation, λ (Pagel, 1999). We repeated this analysis restricting the sample to only evergreen and only short leaf liftetime species. We generated the species-level phylogeny from a supertree using PHYLOMATIC (version 3.0, stored tree '20120829'; Webb & Donoghue, 2005). Divergence times in our tree were estimated using the BLADJ algorithm in PHYLOCOM (Webb *et al.*, 2008), calibrated with a range of node ages from Wikström *et al.* (2001).

All statistical analyses were performed in R (version 3.1.1; R Core Team, 2014), with mixed effect models implemented using the 'lme4' (Bates & Maechler, 2013). We used the 'lmerTest' (Kuznetsova *et al.*, 2013) package to calculate *P*-values using Satterthwaite approximations to determine degrees of freedom. PGLS analysis was performed using the 'phylolm' (Ho & Ane, 2014) package.

HERBIVORY RATE AND LATITUDE

The mean annual herbivory rate across all 452 tree species was 10.8%. The logit-transformed herbivory rate was significantly negatively correlated with latitude for evergreen tree species (Fig. 2a; slope = –0.02, $t = -3.6$, d.f. = 278, $R^2 = 0.045$, $P < 0.001$), but there was no effect of latitude on herbivory rate for deciduous trees (Fig. 2b; slope = 0.001, $t = 0.3$, d.f. = 154, $R^2 = 0.0004$, $P = 0.779$). For evergreen tree species, this corresponds to a difference of approximately 1.2-fold in herbivory rate for any 10° change in latitude. When analysed at the population level the results are qualitatively similar. Evergreen herbivory rate had a significantly negative interaction with latitude (Satterthwaite approximation d.f. = 538.2, $F = 4.97$, marginal $R^2 = 0.03$, conditional $R^2 = 0.66$, $P = 0.03$). Of the random effects, most of the variation in herbivory rate was within species

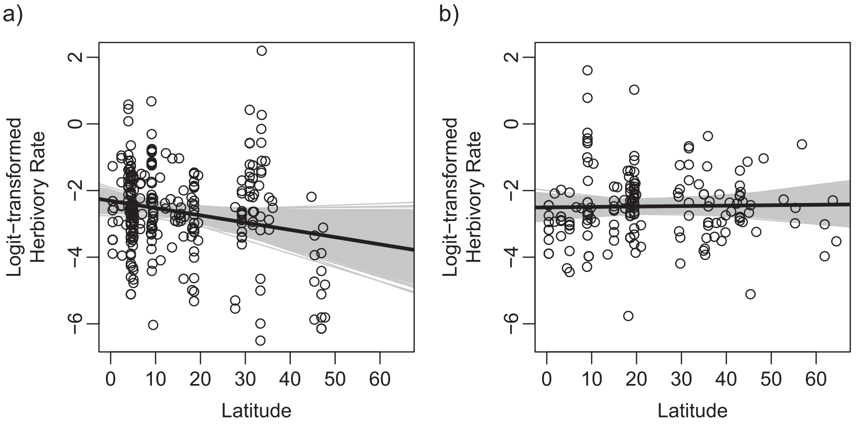

Figure 2 Logit-transformed annual herbivory rate against latitude for (a) evergreen species [$n = 280$, slope and 95% CI = –0.02 (–0.033, –0.007)], and (b) species with short leaf life spans [$n = 172$, slope and 95% CI = 0.001 (–0.006, 0.009)]. Confidence intervals were calculated from 1000 bootstrap replicates.

given herbivory measurement type (25%), followed by variation within herbivory measurement type (18%) and variation within species (27%).

Our results are consistent with a biotic interactions hypothesis that incorporates investment strategies and leaf traits: we found significantly higher herbivory rates for evergreen species occurring at low latitudes, but no latitudinal pattern for plants with short leaf life spans. The magnitude of the change in herbivory rate with latitude for evergreen trees, however, is relatively small. We suggest that the frost-free environment in moist tropical forests allows attack from herbivores during the entire year, which may result in greater herbivore pressure on long-lived leaves in the tropics than in the temperate zone (e.g. Salazar & Marquis, 2012). Species that invest in fast growth and short leaf life spans, however, may experience similar periods of vulnerability to herbivores irrespective of latitude. This could explain why evergreen trees show a latitudinal decrease in herbivory rate whereas deciduous trees do not.

Alternatively, temperate evergreen species may be better defended than tropical evergreen species, resulting in lower herbivory rates at higher latitudes. Empirical and theoretical models of leaf life span suggest that evergreen species at higher latitudes have longer leaf life spans as a response to compensate for a shorter photosynthetic period during the year (Kikuzawa *et al.*, 2013; Reich *et al.*, 2014). This response to a shorter growing period may concurrently lead to increased selective pressure to reduce herbivory. For example, a recent study found a positive relationship between constitutive defence allocation and latitude in a pine (Moreira *et al.*, 2014). However, reviews that have included a more global comparison and have considered all of the different defence strategies available to plants have shown that tropical plants in general contain a greater amount and diversity of chemical and physical defences than temperate plants (Coley & Aide, 1991; Coley & Barone, 1996; Schemske *et al.*, 2009; but see Moles *et al.*, 2011b; Onoda *et al.*, 2011).

PGLS models assuming a Brownian covariance structure performed poorly (Table 1). However, PGLS models that assume a covariance structure consistent with OU processes showed a significant negative effect of latitude on herbivory rates for evergreen species and not for short leaf lifetime species, mirroring the results in Fig. 2. A recent study by Turcotte *et al.* (2014a) also found that OU models best described the distribution of herbivory rates across 1145 species in their data set, including the 452 tree species from this analysis. PGLS models that incorporate phylogenetic signal using λ Pagel (1999) had somewhat lower Akaike information criterion (AIC) values than the OU models (Table 1), and for evergreen trees these models showed no significant effect of latitude on herbivory rate.

Table 1 Phylogenetic generalized least squares (PGLS) regression models of species-level herbivory rate (logit-transformed) and latitude. PGLS was implemented with the full dataset (all tree species) or with either evergreen species or species with relatively short leaf life spans. Phylogenetic correlation parameters, α and λ, were estimated using maximum likelihood.

	Slope estimate	AIC	*t*, d.f.	*P*-value
All species				
BM	0.007	1513.9	1.1,450	0.257
OU ($\alpha = 0.02$)	−0.008	1436.7	−1.8,450	0.080
PS ($\lambda = 0.40$)	0.003	1418.0	0.7,450	0.506
Species with short leaf lifetimes				
BM	0.008	562.5	1.2,170	0.227
OU ($\alpha = 0.11$)	0.001	505.0	0.3,170	0.801
PS ($\lambda = 0$)	0.001	505.0	0.3,170	0.799
Evergreen species				
BM	−0.004	967.0	−0.4,278	0.720
OU ($\alpha = 0.02$)	−0.022	912.7	−3.1,278	0.002
PS ($\lambda = 0.43$)	−0.002	907.4	−0.3,278	0.792

BM = Brownian Motion model; OU = Ornstein-Uhlenbeck model; PS = phylogenetic signal model.

PHYLOGENETIC SIGNAL

Phylogenetically explicit tests of latitudinal rates of herbivory displayed mixed signals. On the one hand, assuming herbivory rate evolves as an OU process along the phylogeny (as Turcotte *et al.* 2014a showed for their data), we again found a significant negative correlation with latitude in evergreen species but not in short leaf lifetime species, consistent with our non-phylogenetic results. An OU model for trait evolution assumes that characters evolve as a random walk but tend to be drawn toward some median value (Martins & Hansen, 1997). On the other hand, a simpler phylogenetic signal model which had somewhat lower AIC scores showed no significant correlation in latitudinal herbivory rates. One reason for this result may be because latitudinal variation in evergreen tree herbivory rates is driven in part by the uneven geographical distribution of gymnosperms. Although gymnosperms occur in the tropics, they are much more abundant in high-latitude forests than low-latitude forests (Eckenwalder, 2009). In the full Turcotte *et al.* (2014b) data set, gymnosperms experience seven-fold lower herbivory rates than angiosperms (Turcotte *et al.*, 2014a). One possible explanation for the low ecological dominance of gymnosperms at lower latitudes could be the conservative growth strategy employed by most gymnosperms (including, but not limited to, large investment in anti-herbivore defences like resins), which precludes them from effectively competing in high-resource habitats at lower latitudes (Aerts, 1995).

We suggest that there are several reasons to be cautious in relying on phylogenetically explicit analyses to interpret correlations of herbivory rates with latitude. First, the biotic interactions hypothesis, which posits that herbivory of tropical regions should be stronger than extra-tropical regions, is a community-level not a clade-level hypothesis. The strongest test of this hypothesis would be to sample multiple sites across latitudes and measure herbivory rates of each species within a community, including relative abundance as well as a measure of leaf quality (or lifetime as argued above), and compare community-weighted means of herbivory rates across latitudes. Such a test would not require any sort of phylogenetic correction.

Second, the question about whether phylogenetic identity influences herbivory rates and whether this can explain latitudinal patterns is complicated. If there were pervasive differences in herbivore pressure across latitude, as predicted by the biotic interactions hypothesis, one would expect plant lineages to evolve in response and thus have higher investment in defence traits at lower latitudes. However, it is less clear what the prediction would be for herbivory rates because plant species do not inherit herbivory rates from their ancestors, they inherit resistance and/or tolerance traits. Moreover, the assumption that herbivory rates are a function of plant resistance traits is too simplistic, because herbivores respond to both the amount of defence as well as the type of defence. For example, some chemical defences are effective against insect herbivores but do not deter vertebrates, and vice versa (Barbehenn & Constabel, 2011). For these reasons, the strongest phylogenetically explicit tests of the biotic interactions hypothesis would be to compare the herbivory rates of tropical and extra-tropical sister species pairs, because recently diverged taxa would be most likely to share similar resistance traits.

Finally, while high herbivory rates may faithfully reflect a lack of resistance (but see above about qualitative differences in resistant traits), low herbivory rates can either mean high resistance or low discovery by herbivores, or low community-level herbivore abundance (or simply that herbivores were not present during the period of measurement). Furthermore, herbivory rates of any plant species within a community should also be related to the level of host specialization of locally common herbivores or the relative abundance of local generalist herbivores, which in turn are controlled by climate, resource availability and predator abundance, in addition to plant palatability and defences, meaning that there are many other factors besides plant resistance traits that will influence the measurement of herbivory in the field. Similarly, herbivory could vary among regions, above and beyond latitudinal gradients (i.e. the Eastern and Western Hemispheres have plant communities with different phylogenetic assemblages, and different herbivores).

CONCLUSIONS AND FUTURE DIRECTIONS

We show that the relationship between herbivory rates and latitude depends on leaf lifetime, and that annual herbivory rates increase with decreasing latitude for evergreen tree species but not for tree species with short leaf life spans. The Turcotte *et al.* (2014b) data set is the most comprehensive, world-wide collection of herbivory rates currently available. However, this compendium is very heterogeneous in terms of the types of studies included and their methodologies. Thus, our comparison of herbivory rates in evergreen trees and those with short leaf lifetimes across latitude is far from definitive. Still, we strongly caution that statements sounding the death knell for the biotic interactions hypothesis (Moles *et al.*, 2011a; Moles, 2013) are premature at best. Future studies that incorporate measures of leaf life span, production rate or construction cost (e.g. LMA), as well as multiple censuses of marked leaves to estimate herbivory rates are likely to provide the best test of the biotic interactions hypothesis because such studies will more closely quantify the impact of herbivores on plant fitness as well as provide better community-level estimates of the amount of trophic transfer across latitudes.

Moreover, rather than only considering latitude, researchers should quantify the climatic variables that are likely to influence plant–herbivore interactions. For example, different herbivore guilds are likely to respond idiosyncratically to gradients in temperature versus precipitation (Moreira *et al.*, 2015).

The advent of large datasets has allowed for global-scale studies that have led to rapid progress in various aspects of plant ecology (e.g. Wright *et al.*, 2004; Kattge *et al.* 2011; Onoda *et al.*, 2011). In particular, the leaf economic spectrum of ‘fast–slow’ strategies has introduced a new framework for thinking about plant carbon and nutrient balances (Reich, 2014). We propose that a productive way forward for testing latitudinal relationships with herbivory rates would be to integrate plant functional trait approaches (including physical and chemical defences) with hypotheses of plant–herbivore interactions. An integrated framework would better account for the costs of herbivory to a plant and better explain patterns of biotic interactions across evolutionary and ecological scales. In addition, testing large-scale phylogenetic patterns in species-level herbivory rates is challenging, and it is not straightforward to connect the results of phylogenetically controlled analyses to the hypothesis of stronger biotic interactions at lower latitudes. We recommend replicated, community-level studies across many sites and a large latitudinal extent spanning the tropics and temperate zones that: (1) measure the relative importance of specialist and generalist herbivores (Salazar & Marquis, 2012), (2) match defensive traits with herbivory rates (especially with regard to specialist and generalist herbivores), and (3) link defence traits with leaf economics and herbivory.

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BIOSKETCHES

Jun Ying Lim is a graduate student in the Department of Integrative Biology, University of California, Berkeley. His research focuses on understanding community assembly processes in space and time.

Paul Fine is also in the Department of Integrative Biology. His lab investigates tropical tree diversity and plant–herbivore interactions.

Gary Mittelbach is a community ecologist at the Kellogg Biological Station.

Author contributions: all authors conceived the main ideas and contributed to its development; J.Y.L. conducted all analyses; all authors wrote the paper.

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