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EVOLUTIONARY ECOLOGY OF PLANT DEFENCES

Assessing the evidence for latitudinal gradients in plant defence and herbivory

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Summary

1. The idea that biotic interactions, including herbivory, predation and competition are more intense at lower latitudes is widely accepted and underpins several dominant theories on the latitudinal gradient in biodiversity. Current theory also predicts that the intense biotic interactions at low latitudes will select plants for greater defence against herbivores. We reviewed the literature to provide an assessment of the evidence for and against the hypothesis that herbivory is more intense at lower latitudes, and that plants from low latitudes are better defended than are plants from high latitudes.

2. Only 37% of the 38 latitudinal comparisons of herbivory showed higher herbivory at lower latitudes, and the average effect size in a meta-analysis was not significantly different from zero. Thus, the available data do not support the idea that herbivory is generally more intense in the tropics.

3. Only nine of 56 comparisons found higher chemical defences at lower latitudes, and a meta-analysis showed that overall, chemical defences were significantly higher in plants from higher latitudes. This result is counter to the predictions of much of the literature.

4. A meta-analysis showed no significant effect of latitude on physical defence.

5. A review of the literature on feeding trials and common garden experiments showed that herbivores tend to prefer tissue from high latitudes. This trend could stem from differences in overall defence that were not captured by the metrics used in the literature, but could also result from differences in nutritional quality.

6. The empirical data do not support the widespread view that herbivory is generally more intense at lower latitudes, or that plants from low latitudes are generally better defended than are plants from higher latitudes. These results are counter to the prevailing thought on this topic, and suggest that this field may be ripe for the development of new theory.

Key-words: alkaloid, biogeography, biotic interactions, chemical defence, feeding trials, leaf toughness, palatability, phenolic, physical defence, temperate, tropical

Introduction

The idea that biotic interactions, including herbivory, predation and competition are more intense at low latitudes has a long history in ecology (Dobzhansky 1950; MacArthur 1972; Pennings & Silliman 2005). It is widely accepted that more herbivory occurs at lower latitudes, and this idea underpins several dominant theories in biogeography, including theory on the latitudinal gradient in biodiversity (Janzen 1970; Connell 1971; Gurevitch, Scheiner & Fox 2002), and the idea that plants from low latitudes will be better defended than will plants from higher latitudes (Dobzhansky 1950; MacArthur 1972; Coley & Aide 1991; Van Alstyne, Dethier & Duggins 2001).

The most widely cited evidence for a latitudinal gradient in herbivory comes from two studies that synthesized data from

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the literature. Coley & Aide (1991) compiled estimates of herbivory from 23 forests, and found that the annual rate of herbivory was significantly higher in tropical forests (10·9%) than in temperate forests (7·5%). Coley & Barone (1996) compiled data from 42 studies, and concluded that annual rates of damage to leaves were greater in the wet tropics (11·1% for shade-tolerant species; 48% in gap specialists) and in tropical dry forests (14·2%) than in temperate broad-leaved forests (7·1%). These excellent compilations laid the foundation for much work on latitudinal gradients in plant–animal interactions, and became widely accepted as proof of the existence of a latitudinal gradient in herbivory. However, the authors cautioned that their data came from studies with very different (and often imperfect) methods, and suggested that ecologists treat their results as a working hypothesis rather than a definitive demonstration that herbivory is greater in the tropics.

Since Coley & Aide (1991) and Coley & Barone's (1996) seminal work, many studies have used consistent methods to compare the amount of foliage lost to herbivores at sites from different latitudes. While some of these studies show higher herbivory at lower latitudes (e.g. Morrow & Fox 1989; Pennings *et al.* 2007, 2009), many show no relationship between herbivory and latitude (e.g. Andrew & Hughes 2005; Sinclair & Hughes 2008; Adams *et al.* 2009a, 2010), and others suggest higher herbivory at high latitudes (e.g. Gaston *et al.* 2004; Adams & Zhang 2009b; del-Val & Armesto 2010). We believe it is time for a formal assessment of the evidence for the hypothesis that rates of herbivory are higher at lower latitudes. This is the first goal of our review.

Our second goal is to assess the evidence for a latitudinal gradient in plant defences. The dominant theory is that because species at lower latitudes experience more intense biotic interactions than do species at higher latitudes, they will have been under selective pressure to evolve more effective defences (Dobzhansky 1950; MacArthur 1972; Coley & Aide 1991; Van Alstyne, Dethier & Duggins 2001). Early studies tended to support the hypothesis that plants from low latitudes have stronger defences than do plants from high latitudes (e.g. Levin 1976; Coley & Aide 1991; Coley & Barone 1996). However, the recent body of literature compels a review of the evidence (e.g. Lesage *et al.* 2000; Azevedo *et al.* 2002; O'Neill *et al.* 2002; Gaston *et al.* 2004; Van Alstyne & Puglisi 2007; Stark *et al.* 2008; Adams *et al.* 2009a; Ardon, Pringle & Eggert 2009; Martz *et al.* 2009; Graca & Cressa 2010; Steinbauer 2010).

Our third goal is to assess the evidence that leaves from lower-latitude sites are less palatable than are leaves from higher latitudes. We compiled evidence from common garden experiments (in which plants from different geographical areas are exposed to a common suite of herbivores), and evidence from feeding trials (in which animals are offered foliage from different regions). These trials give information about the relative palatability of plants from different latitudes without confounding from differences in herbivore abundance, diversity or per-capita influence. This information will help us understand the factors that underlie any latitudinal gradient in herbivory.

Materials and methods

We searched ISI Web of Science in May 2010 using the terms (latitude and herbiv*), and (latitude and defen*). We also carried out specific searches for latitude and the main defence groups (e.g. tannins and phenolics), searched for additional studies from references in papers and searched for studies on specific types of herbivory (e.g. latitude and 'seed predation'). Most articles described studies of herbivory on leaves, but we also included studies of florivory, seed predation and twig browsing. We did not search for studies on gradients in productivity or temperature, because elevation and distance inland often dissociate these variables from latitude. Studies that made claims about latitudinal gradients based on data from a single site were excluded. Work on selectively bred cultivars and crops was also excluded.

Because the literature ranges from single species studies to cross-species studies, our units of replication differ between studies. Where studies compared the same species at different latitudes, we treated species as the units of replication. Where studies presented contrasts between congeners or confamilials from high and low latitudes, the taxonomic unit of study (e.g. genus or family) was the unit of replication. Where a study presented a cross species analysis of a latitudinal gradient, the study was the unit of replication. We refer to these replicates as 'comparisons' throughout the article. We performed regressions in PASW (formerly SPSS) 18 to determine whether the different types of replicates yielded different results.

The quality of studies of latitudinal trends in herbivory and defence varies greatly, not only in the number of replicate plants/leaves, but also in the number of sites and species compared, the range of latitudes, the methods used, and the ecosystems in which the studies were conducted. We have therefore presented summary information about each comparison in appendices (see Appendix S1, S2, S3 and S4 in Supporting Information). These appendices also show our decisions about what constitutes a replicate. In cases where a paper reported data for multiple traits (e.g. tannins and alkaloids), we counted each result separately. Leaf toughness assessed by ripping and penetrometer were treated as the same trait, but total phenols and condensed tannins were treated as separate traits. Where a paper reported results for multiple herbivores (e.g. vertebrates and invertebrates), different material (e.g. juvenile vs. mature foliage/twigs), or different sites (except where these sites are on different continents), we report a summary of the results in the tables, and use an average effect size in the meta-analysis.

To quantify the differences between values recorded from low and high latitudes, we used the log of the response ratio, $\ln(R) = \ln(\overline{X}_L/\overline{X}_H)$, where $\overline{X}_L$ is the mean value at low latitudes and $\overline{X}_H$ is the mean value at high latitudes (Hedges, Gurevitch & Curtis 1999). The log response ratio measures the proportional difference between measurements from either end of the latitudinal range such that $\ln(R)$ is greater than zero when the measurements are higher at low latitudes (i.e. higher concentrations of chemical defences, greater expression of physical defences, or higher rates of damage by herbivores), less than zero when measurements are higher at high latitudes, and equal to zero when the measurements does not differ between either end of the latitudinal range.

We used the software package MetaWin (Rosenberg, Adams & Gurevitch 2000) to calculate bootstrapped 95% confidence intervals (CI) around the mean effect sizes for each type of effect size, and separately for each of three habitats (terrestrial, marine and intertidal saltmarsh). Differences between measurements at each end of the latitudinal range are evident when these CI do not overlap zero. We used unweighted effect sizes due to the low proportion of studies that reported variances associated with their estimates of mean values. To account for possible non-independence in cases where more than one trait was recorded from a single plant species, analyses were repeated with a reduced data set that included only one effect size randomly selected from each species. The random selection process was repeated 10 times, and results were consistent with analyses on the full data set.

The latitudinal gradient in herbivory

We found 38 comparisons of herbivory across latitudinal gradients (Appendix S1). Fourteen of these comparisons showed higher herbivory at lower latitudes, 14 showed no significant relationship between herbivory and latitude, two showed mixed results, and eight showed higher herbivory at higher latitudes (Fig. 1a). That is, only 37% of the published comparisons show higher rates of herbivory at lower latitudes. Thus, the evidence for higher rates of herbivory at lower latitudes is not nearly as clear as it is often made out to be (e.g. Schemske *et al.* 2009).

A meta-analysis of the data from the 36 comparisons for which effect sizes could be extracted showed that the average effect size was not significantly different from zero (average log response ratio = 0·16; 95% bootstrapped confidence interval (CI) = −0·31 to 0·59; Fig. 2). That is, the available data do not support the idea that herbivory is more intense at lower latitudes.

There were strong differences among habitats. In saltmarshes, herbivory is clearly more intense at low latitudes. Nine of the 10 comparisons of herbivory in saltmarshes showed higher herbivory at lower latitudes, and the average effect size (1·79) was significantly greater than zero (95% CI = 1·17 to 2·33). By contrast, only five of the 28 comparisons in terrestrial ecosystems show higher herbivory at lower latitudes, and the average effect size is not significantly different from zero (average effect size in terrestrial systems = −0·16; 95% CI = −0·62 to 0·25).

Ours is not the first study to cast doubt on the idea that biotic interactions are stronger at lower latitudes. Gruner *et al.* (2008) performed a meta-analysis of the results of herbivore exclusion studies. They found no relationship between latitude and the effect of herbivore exclusion, except in freshwater ecosystems. Similarly, Hillebrand (2009) performed a meta-analysis of experiments that quantified grazer effects on periphyton biomass, and found no effect of latitude. HilleRisLambers, Clark & Beckage (2002) found that the frequency of density dependent mortality (such as that caused by host-specific predators or pathogens) did not differ significantly between temperate and tropical regions. Finally, Cornell & Hawkins (1995) compiled life table data for 124 species of herbivorous insects, and found no evidence that competition and predation pressures were higher in the tropics than in the temperate zone, or that weather-induced mortality was more pervasive in the temperate zone. Overall, the evidence for stronger biotic interactions in the tropics is substantially less conclusive than has often been assumed.

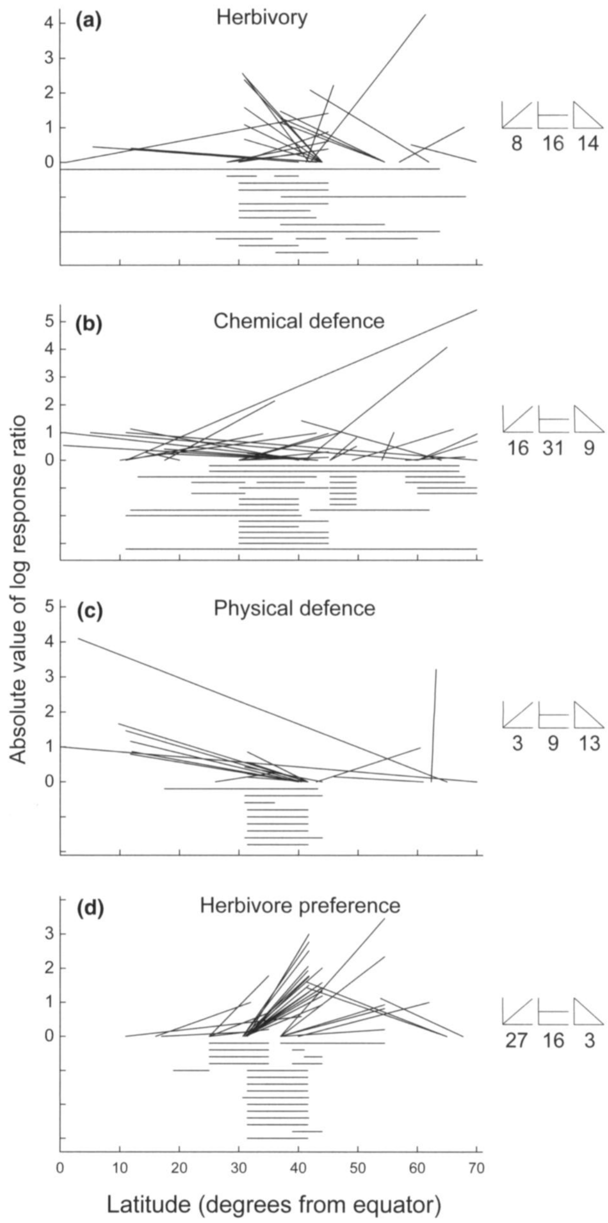

Fig. 1. Compilation of results from studies on the latitudinal gradient in: (a) Herbivory at high vs. low latitude sites in the field. (b) Chemical defences. (c) Physical defences. (d) Herbivore preferences in common gardens and feeding trials, where herbivores choose between plant materials from high and low latitudes. Each result is represented by a single line, stretching from the highest to lowest latitude of the study sites. Significant results are plotted so the line extends from zero to the absolute value of the log response ratio [ln(value at low latitude/value at high latitude)] with the slope indicating the direction of the response, while nonsignificant results are shown as horizontal lines. Results from the northern and southern hemispheres have been pooled. Where studies did not report the latitudes for which data were collected (e.g. 'temperate' vs. 'tropical') we have assigned appropriate latitudes for display purposes. Numbers to the right of each panel indicate the number of positive, nonsignificant and negative relationships.

Future directions

There is an urgent need for large-scale studies that apply consistent methods across a large number of sites spanning a wide

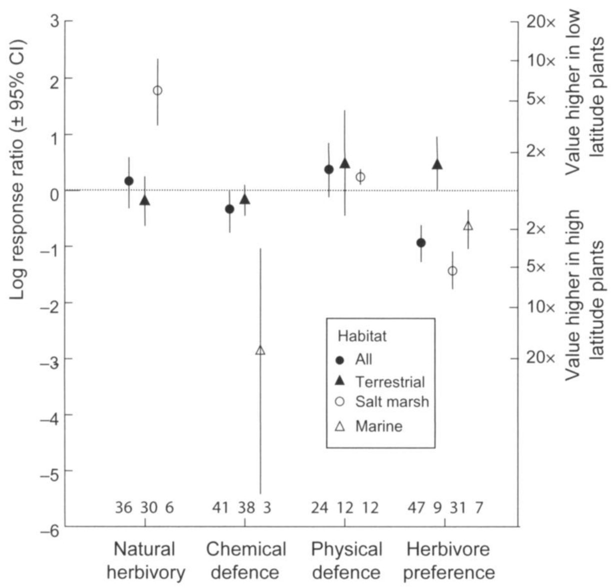

Fig. 2. Quantitative meta-analysis of the difference between high and low latitude plants in the published comparisons. The effect size is quantified by the log response ratio, ln(R) = ln(value at low latitude/value at high latitude). Error bars are the bootstrapped 95% confidence intervals around each mean effect size. For the natural herbivory comparisons, a positive ln(R) indicates that plants in low latitudes were consumed at higher rates than plants in high latitude plants, and a negative ln(R) indicates higher herbivory on high latitude plants. For the chemical and physical defence comparisons, a positive ln(R) indicates higher levels of defensive traits in low latitude plants, and a negative ln(R) indicates that high latitude plants were more defended. For the feeding preference trials, a positive ln(R) indicates that plants sourced from low latitudes were consumed at greater rates than plants from low latitudes, and a negative ln(R) indicates that high latitude plants were more palatable. For all comparisons, if the error bars overlap zero there was no significant difference between high and low latitude plants. The axis on the right indicates the proportional change between values from each end of the latitudinal range. The numbers above the x-axis indicate the sample size associated with each mean effect size.

range of latitudes. These studies need to be performed in a range of different ecosystems if we are to get results that can be applied broadly. These studies will also need to apply methods that give a fair comparison of herbivory across the latitudinal gradient. Many current studies of latitudinal gradients in herbivory use snapshot assessments of herbivory rather than measuring the accumulated damage over a set time. Because leaves tend to live longer in warmer places (Wright *et al.* 2004), there is probably a latitudinal gradient of leaf life span. If this were the case, then if the longer-lived leaves at lower latitudes accumulated damage at the same rate as did leaves from higher latitudes, they would appear to have more herbivore damage in snapshot studies. Thus, future work on the latitudinal gradient in herbivory needs to quantify the rate at which damage accumulates.

Quantifying global patterns in the relative importance of herbivory by vertebrate and invertebrate herbivores are also an important goal. There is so little known about the relative effects of these clades that we do not even know which group is responsible for the most herbivory. Since vertebrates and invertebrates have widely differing physiologies and feeding methods, this information would help us to understand the relative importance of different types of plant defences, both within and across ecosystems. For example, herbivory by marine mesograzers (amphipods, polychaetes and ascoglossans) is often unaffected or even stimulated by compounds that deter fish or urchins (Hay & Fenical 1988).

Our finding that the literature does not support the traditional idea that levels of herbivory are higher at lower latitudes has important ramifications. This idea underpins several theories on the latitudinal gradient in biodiversity, including the Janzen–Connell hypothesis (Janzen 1970; Connell 1971), and the hypothesis that herbivory can enhance diversity by preventing competitive exclusion (Gurevitch, Scheiner & Fox 2002). These theories will need to be reassessed if there is no latitudinal gradient in herbivory. The hypothesis that higher rates of herbivory might have led to selection for more strongly defended plants at low latitudes may also require reconsideration.

The latitudinal gradient in chemical defences

Plants are defended by a range of very different compounds. Rather than assuming that all these groups respond similarly across the latitudinal gradient, we present the results for five broad groups of defences (tannins and phenols, flavonoids, alkaloids, resins/oils and other), before presenting an overview across chemical defences.

There were 36 latitudinal comparisons of tannins or phenolics (Appendix S2). Four comparisons showed higher phenolic concentrations at lower latitudes, 25 showed no significant relationship, and seven showed higher phenolic concentration or activity at higher latitudes. Thus, the evidence for a latitudinal gradient in total phenolics and tannins is mixed, but by far the most common result is for no latitudinal gradient.

There were four latitudinal comparisons of flavonoids (Appendix S2). One of these showed a positive relationship between flavonoids and latitude, one showed a negative relationship, and two showed no significant relationship. That is, the available evidence is highly mixed, and does not provide strong support for the idea that flavonoid concentrations are higher at lower latitudes.

There were three latitudinal comparisons of alkaloids (Appendix S2). Two broad-ranging studies supported the idea that alkaloids are present in a greater proportion of plants at lower latitudes, and that alkaloids from tropical genera tend to be more toxic (Levin 1976; Levin & York 1978), while one more specific study showed higher concentrations of dauricine at higher latitudes (Zhou, Qu & Nan 2007). Overall, the balance of evidence suggests that alkaloids are more common and more toxic at lower latitudes, but further detailed studies would certainly be valuable.

There were nine latitudinal comparisons of resins or oils (Appendix S2). Five of these comparisons showed higher concentrations of resins/oils at higher latitudes, one showed higher concentrations of resin in twigs from lower latitudes, two showed no significant relationship between latitude and resin concentration, and one showed mixed results. Thus, the most common pattern is for higher concentrations of resins/oils at higher latitudes.

The remaining three latitudinal comparisons of chemical defences were of dimethylsulfoniopropionate concentration in macroalgae (Appendix S2). One comparison showed a positive relationship with latitude, one was negative, and the other showed no significant relationship.

Overall, we have 56 latitudinal comparisons of chemical defence. Sixteen of these show higher levels of chemical defence at higher latitudes, nine show higher levels of chemical defence at low latitudes, and 31 show no significant relationship or mixed results (Fig. 1b). Thus, only 16% of the comparisons showed the increased chemical defences at low latitudes that we would expect if high levels of herbivory in low latitude systems had selected for higher levels of defence.

A meta-analysis of the 41 comparisons for which effect sizes could be extracted showed an average effect size of −0·34, and the 95% confidence intervals did not overlap zero (95% CI = −0·74 to −0·01; Fig. 2). That is, chemical defences are, on average, about 40% higher at the higher latitude end of comparisons. This result is counter to the predictions of much of the literature.

There were important differences in the results between habitats. In terrestrial ecosystems, the average effect size indicated a nonsignificant trend towards a positive relationship between latitude and chemical defence (average log response ratio for terrestrial systems = −0·14; 95% CI = −0·44 to 0·10). However, in marine systems, our analysis suggested that high latitude algae were significantly more strongly defended (average log response ratio for terrestrial systems = −2·86; 95% CI = −5·41 to −1·04), although this result comes from just three comparisons, so the sample size is too small to be conclusive.

Many of the compounds reviewed here have roles other than defence. For example, flavonoids may protect plants from photodamage (Close & McArthur 2002), and phenolics in general can have a role in frost-tolerance (Teklemariam & Blake 2004). Although there are few demonstrations of plant alkaloids playing a role other than in plant defence (Manson, Otterstatter & Thomson 2010), the rapid turnover of alkaloids in a plant suggests that this may be more common than realised. Furthermore, some compounds, such as tannins, have mixed effects on herbivores (e.g. Min *et al.* 2003; Barbehenn *et al.* 2009). Thus, the presence of a compound or a group of compounds does not prove defence against herbivores, nor are their concentrations necessarily good predictors of herbivore deterrence (Carmona, Lajeunesse & Johnson 2011). Also, many of the chemical data are crude. Despite these deficiencies, ecologists have long accepted latitudinal gradients in presence or concentration of chemical groups such as phenolics and alkaloids as evidence that plants are better defended at lower latitudes. Changing the criteria for accepting evidence about latitudinal gradients in chemical defence just because the results no longer support traditional thought on the topic would be disingenuous.

Leaves from lower latitudes may still be better defended than are leaves from higher latitudes, either through possessing a greater range of defences, or through possessing unstudied, taxon-specific defences. There is insufficient literature to make conclusions about either of these possibilities. For now, we must conclude that the evidence does not support the hypothesis that plants from lower latitudes are better defended chemically than are plants from higher latitudes. In fact, the balance of evidence suggests that plants from higher latitudes actually have higher levels of chemical defence than do plants from lower latitudes.

The latitudinal gradient in physical defences

We found 25 latitudinal comparisons of physical defences (Appendix S3). Thirteen of these (52%) showed higher physical defences at lower latitudes, nine (36%) showed no relationship or mixed relationships between latitude and physical defence, and three (12%) showed higher physical defences towards the poles (Fig. 1c).

A meta-analysis of the 24 comparisons for which effect sizes could be extracted showed an average effect size of 0·37, but the 95% confidence intervals overlapped zero (95% CI = −0·10 to 0·85; Fig. 2). That is, there is no overall effect of latitude on physical defences. Looking at the results within habitats, we see no significant effect of latitude in terrestrial ecosystems (average effect size = 0·50; 95% CI = −0·43 to 1·43), but we do see evidence for higher physical defences towards lower latitudes in saltmarshes (average effect size = 0·24; 95% CI = 0·12 to 0·39).

Most comparisons of physical defences were of physical toughness [mostly leaf or phyllode toughness, but one study measured the percentage of lignin in bark (Wainhouse & Ashburner 1996), and one measured the proportion of calcified algae (Gaines & Lubchenco 1982)]. Eight comparisons (44%) showed higher physical toughness at lower latitudes, two (11%) showed higher physical toughness at high latitudes, and eight comparisons (44%) showed no significant trend or mixed results. It seems likely that this latitudinal trend in leaf toughness is associated with the longer leaf lifespan of plants in warmer environments (Wright *et al.* 2004).

All three comparisons of extra floral nectaries, an indirect defence that attracts predators, suggested that extra floral nectaries were more prevalent in the tropics (Appendix S3). This is in line with a recent meta-analysis that showed that the effects of experimentally excluding ants were generally stronger in tropical than in temperate regions (Rosumek *et al.* 2009).

The literature on latitudinal gradients in physical defences is much sparser than the literature on latitudinal gradients in herbivory or chemical defences. This would be a fruitful area for research, given the diversity of physical defences (e.g. spines, thorns, hairs, trichomes, sclerites and silica), their importance in deterring herbivores, and the ease with which many of these traits can be measured.

Combining the results for chemical and physical defences, we have 22 comparisons that show higher defence at lower latitudes, 40 comparisons showing no relationship or mixed results, and 19 comparisons showing higher defences at higher latitudes. A meta-analysis combining results for physical and chemical defence gives us an average effect size of −0·0769 with the 95% confidence intervals overlapping zero (−0·3976 to 0·2099). Thus, the evidence does not support the hypothesis that plants from lower latitudes will be generally better defended than are plants from high latitudes. Many ecologists have predicted a latitudinal gradient in defence because they assume that the increased pressure from herbivores at low latitudes will select for increased defences. Under this theory, the lack of a latitudinal gradient in defence is consistent with the lack of a latitudinal gradient in herbivory.

Herbivore preferences for plant material from high vs. low latitudes

We found 48 latitudinal comparisons of herbivore preferences (Appendix S4). In these comparisons, higher consumption of plant material from higher latitudes would suggest that plants from higher latitudes are more palatable to herbivores. Thus, if plants from lower latitudes were better defended, we would expect to see most herbivores favouring plant material from higher latitudes.

Herbivores showed a significant preference for plant material from higher latitudes in 27 of the 48 comparisons (59%). There was no significant difference in consumption of material from high vs. low latitudes or mixed results in 16 comparisons (35%), and herbivores preferentially consumed material from lower latitudes in just three comparisons (Fig. 1d).

A meta-analysis showed that herbivores have a significant preference for plants from higher latitudes (average effect size = −0·94, 95% CI = −1·27 to −0·62; Fig. 2). On average, herbivores consume plants from higher latitudes 2·5 times more than plants from lower latitudes. This result was driven by studies in saltmarshes (average effect size = −1·43, 95% CI = −1·75 to −1·09), with no significant trend in marine systems (average effect size = −0·62, 95% CI = −1·03 to 0·34) and a significant preference for plants from lower latitudes in terrestrial systems (average effect size = 0·49, 95% CI = 0·04 to 0·97). Our results for terrestrial systems are broadly consistent with those from a meta-analysis by Swihart & Bryant (2001). Using nine studies of mammalian feeding preferences, these authors found that herbivory was negatively related to latitude in 86% of studies, although the overall correlation between latitude and browsing was marginally nonsignificant.

The fact that 59% of comparisons showed herbivore preferences for material from low latitudes and the significant meta-analysis result for preference trials might initially seem at odds with our finding that only 26% of comparisons showed that plants from lower latitudes had more chemical or physical defences and the lack of an overall effect of latitude on defence in our meta-analyses. However, plant palatability depends not only on plant defences, but also on the herbivores' susceptibility to the defences and the nutritional quality of the leaves (Bryant & Kuropat 1980; Pennings, Siska & Bertness 2001). Herbivores may preferentially select nutritious but well-defended plant tissue, especially if the herbivores are somewhat resistant to the plant's defences.

Data considerations

We asked whether comparisons with small latitudinal ranges might have influenced our results. There were no significant relationships between the latitudinal range of a comparison and the log response ratio, ln(R), for herbivory (linear regression, in PASW 18; $P = 0{\cdot}58$, $n = 36$), chemical defences ($P = 0{\cdot}34$, $n = 56$), or herbivore preferences ($P = 0{\cdot}39$, $n = 46$). However, there was a positive relationship between ln(R) and latitudinal range for physical defences ($P < 0{\cdot}001$, $R^2 = 0{\cdot}70$; slope $= 0{\cdot}08$, $n = 25$). That is, comparisons with larger latitudinal ranges were more likely to find greater physical defences at lower latitudes. As only physical defences showed any relationship between latitudinal range and effect size, we can rule out the possibility that the lack of significant latitudinal trends in herbivory, the trend towards higher chemical defences at higher latitudes, or the preference of herbivores for material from low latitudes are due to the inclusion of studies with small latitudinal ranges. The positive relationship between effect size and latitudinal range in comparisons of physical defences suggests that if we had been able to include more studies with larger ranges, we would have seen a stronger trend for species at lower latitudes to have greater physical defences.

Next, we asked whether the direction of a comparison's results depended on its latitude. In other words, might different patterns at very high and very low latitudes obscure a latitudinal gradient? There were no significant relationships between ln(R) and either the highest latitude or the lowest latitude for chemical defence or herbivory (regressions all with $P > 0{\cdot}05$). These results rule out the possibility that the lack of a significant latitudinal gradient in herbivory and/or the trend towards higher levels of chemical defence at higher latitudes are due to the latitudinal position of the studies included in our review. There was a significant ($P = 0{\cdot}027$) positive relationship between ln(R) and the highest latitude, and a marginally significant ($P = 0{\cdot}05$) positive relationship between ln(R) and the lowest latitude in comparisons to herbivore preference. That is, studies that stretched to higher latitudes were more likely to show herbivore preferences for plant material from low latitudes. The difficulty of replacing lost leaf material in arctic environments may explain this result. For physical defence, there was no significant relationship between ln(R) and the highest latitude in the comparison ($P = 0{\cdot}72$), but there was a significant negative relationship between ln(R) and the lowest latitude in the comparison ($P < 0{\cdot}001$). That is, studies that stretch to lower latitudes are more likely to find stronger physical defences at low latitudes, but the likelihood of finding a relationship between physical defence and latitude is unrelated to the higher latitude end of the comparison. This result could reflect the fact that comparisons over wider ranges of latitude are more likely to show significant differences in physical defences, or it could be that there is a sudden step down in physical defence at some point in the latitudinal gradient. This possibility merits future investigation.

Finally, we asked whether the different replicate types (single-species comparisons, taxonomic pairs and cross species comparisons) showed different results. There was no significant effect of replicate type on ln(R) for herbivory, chemical defence or herbivore preferences (all $P > 0{\cdot}1$). However, the average effect size for cross species comparisons of physical defences (1·7) was significantly different ($P < 0{\cdot}01$) to the average effect size for single-species comparisons (−0·1).

Conclusions and future directions

The data from the literature do not support the idea that herbivory is generally more intense at low latitudes, or the idea that plants from low latitudes will have greater levels of defence against herbivores.

Our findings on herbivory and defence are contrary to prevailing thought. However, the quality of the evidence ranges from good to poor, with most studies sampling only a small part of the possible latitudinal range. Before we can conclusively reject the traditional hypotheses on latitudinal gradients in herbivory and defence, we will need empirical studies that apply consistent, rigorous methods across many sites along broad latitudinal gradients. However, until these studies are performed, we should not assume that herbivory is more intense at low latitudes, or that plants from lower latitudes are more strongly defended against herbivores than are plants from higher latitudes. Our results also suggest that this is a field ripe for research.

Once we have data from studies with consistent methods that span a wide range of latitudes, we will be able to ask what shape any relationships between latitude and herbivory, or between latitude and chemical or physical defence take. Most studies test only for linear relationships, but a latitudinal gradient may be curvilinear or, if the tropics function differently to temperate ecosystems, then the relationship could be stepped. Knowing the shape of the relationship will refine our hypotheses about the mechanisms that drive patterns.

The responses in many of our analyses depended substantially on the type of ecosystem. There is clear evidence for a latitudinal gradient in herbivory and palatability in saltmarsh ecosystems, but the results were very different in terrestrial systems. An important goal for the future is to perform well-replicated, studies in a range of ecosystems, so that we can begin to understand the sorts of conditions that lead to positive, negative and null results.

Another obvious direction for the future is to move away from describing latitudinal gradients in herbivory and defence, to determining which environmental factors drive the patterns. It would be particularly interesting to quantify the global relationship between net primary productivity and herbivory and defence, to see whether the predictions of the resource availability hypothesis [as examined in Endara & Coley (2011)] hold true at the global scale. Determining which factors are most strongly correlated with herbivory and defence will sharpen our hypotheses about the causes of latitudinal gradients and allow us to move towards a mechanistic understanding of global patterns in herbivory and plant defence. These studies would also identify the ecosystems or conditions under which latitudinal gradients in herbivory and defence are likely.

Much of the data on latitudinal gradients in chemical defence relies on crude chemical assays and there are few latitudinal studies of known defensive compounds (Moore *et al.* 2004). Further, a recent review suggests that there is no significant relationship between the concentrations of plant secondary compounds and susceptibility to herbivores (Carmona, Lajeunesse and Johnson 2011). It would be good to begin quantifying variables of relevance to herbivores (such as protein binding capacity, for studies of vertebrate herbivory), and move away from quantifying concentrations of compounds that have unpredictable effects on herbivores.

Future studies of plant defences would also benefit from a pluralistic approach, considering several traits simultaneously, including a range of physical and/or chemical defence types, and considering how these defences relate to other aspects of the species' life history strategies (Carmona, Lajeunesse and Johnson 2011; Endara and Coley 2011). For instance, it would be interesting to investigate the diversity of chemical and physical defences within species from high and low latitudes. Possessing defences that require different detoxification mechanisms and/or different morphology for handling might slow the rate at which herbivores can evolve resistance to the compounds (Langenheim 1994). Thus, it might be more effective for plants to have a range of defences than a high concentration of any particular compound or a high level of one type of physical defence. A pluralistic approach would give a more complete picture, both of plants' strategies in investing in defences, and of the total deterrence that prospective herbivores encounter (Agrawal 2011).

In conclusion, the empirical data do not support the widespread view that herbivory is generally more intense at lower latitudes, or that plants from low latitudes are generally better defended than are those from higher latitudes. These findings are contrary to traditional thought on this topic, and highlight an urgent need for large-scale empirical studies with consistent methods. If new data also fail to support the hypothesis that defence and herbivory are greater at lower latitudes, then we will be in the exciting position of needing a new generation of theory for understanding global patterns in plant–animal interactions.

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Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1. Summary of the results of studies of herbivory in natural environments.

Appendix S2. Summary of the results of studies of latitudinal gradients in chemical defence.

Appendix S3. Summary of the results of studies of latitudinal gradients in physical defence.

Appendix S4. Summary of the results of studies of herbivore preferences across latitudinal gradients.

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