

Commentary

The latitudinal herbivory-defence hypothesis takes a detour on the map

Evidence for and against the latitudinal herbivory-defence hypothesis

The impressive diversity of species in the tropics, contrasted against comparatively depauperate temperate and arctic ecosystems, is among nature's most striking biogeographic patterns (Dobzhansky, 1950). It is hypothesized that this gradient in diversity is in part explained by the ecological and evolutionary consequences of increasingly intense biotic interactions with decreasing latitude (Schemske *et al.*, 2009). Plant–herbivore interactions are cited as a quintessential example in support of this hypothesis. Specifically, experiments and reviews have convincingly shown that herbivory and its effects on plant biomass increase at lower latitudes (Coley & Aide, 1991; Coley & Barone, 1996; Dyer & Coley, 2002; Pennings *et al.*, 2009). These differences in the pattern and effects of herbivory are thought to have caused adaptive evolution, consistent with the observed increases in levels of defence with decreasing latitude (Levin, 1976; Coley & Aide, 1991; Rasmann & Agrawal, 2011). Here, we highlight the implications of a paper by Moles and colleagues in this issue of *New Phytologist* (Moles *et al.*, 2011b, pp. 777–788), as well as a second recent paper by members of this group (Moles *et al.*, 2011a), which contradict the latitudinal herbivory-defence hypothesis (LHDH).

'The results from Moles and colleagues ... largely contradict six decades of research into the biogeography of plant–herbivore interactions. We anticipate that these papers will be controversial for this fact alone.'

Angela Moles and colleagues re-examined the hypothesis that herbivory and plant defences increase with decreasing latitude. In their first paper (Moles *et al.*, 2011a), they use a meta-analysis to review whether the literature shows the

predicted latitudinal pattern for herbivory and resistance traits. Consistent with previous studies (Coley & Aide, 1991), they find that the frequency of species with extra-floral nectaries, and thus indirect defences provided by ants, are higher at lower latitudes. They also find that in some ecosystems, plants do indeed incur greater herbivory at lower latitudes, but these results on herbivory are only evident in salt marsh habitats. There were no clear latitudinal relationships with herbivory in other habitats. For example, only 18% of comparisons in terrestrial habitats showed higher herbivory at lower latitudes; remaining studies showed no trend or the opposite relationship. Similarly, chemical resistance traits such as tannins and phenolics showed higher concentrations at lower latitudes in only 11% of comparisons. Physical resistance traits showed a stronger association with latitude, but these results were again driven by data from salt marshes. On the whole, the meta-analysis pointedly contradicts previous reviews that document evidence in favour of pervasive latitudinal patterns of herbivory and resistance (Coley & Aide, 1991; Coley & Barone, 1996; Schemske *et al.*, 2009). Unfortunately however, these reviews all differ in the extent and location of the geographic ranges considered and the methods used for selecting studies. Moreover, none of these studies rigorously accounts for phylogenetic nonindependence inherent to their datasets, which could confound results. As noted by Schemske *et al.* (2009), the solution to this problem requires new large-scale investigations that test for latitudinal patterns across broad geographic areas using consistent methods.

In this issue of *New Phytologist*, Moles *et al.* (2011b) answer Schemske *et al.*'s 'call to arms' by examining global patterns of variation in plant resistance traits. In a single empirical study, the 48 authors collected trait data for 301 plant species across 75 sites in both hemispheres, and on all continents except Antarctica. Stunningly, this study finds very little evidence for increased expression of putative resistance traits towards lower latitudes. None of the specialized chemical or physical resistance traits (i.e. cyanogenesis, latex, spines, and extra-floral nectaries) – which have undisputed roles in defence against herbivores – showed a relationship with latitude. Protein binding capacity of tannins was weakly related to latitude, but in the opposite direction predicted by LHDH, with tannin activity increasing with latitude. Other traits (e.g. leaf area, leaf toughness, lipid concentrations) were also correlated with latitude, but these traits either increased with latitude (e.g. lipids), showed inconsistent patterns between hemi-

spheres (e.g. leaf toughness), or are difficult to ascribe a direct role in defence (e.g. leaf area). The only result that showed clear support for the predicted pattern was delayed greening of leaves during leaf expansion (Coley & Barone, 1996), which was most frequent at lower latitudes. Importantly, the authors also performed phylogenetic independent contrasts, which generally supported their nonphylogenetic analyses.

The results from Moles and colleagues' meta-analysis (Moles *et al.*, 2011a) and empirical study (Moles *et al.*, 2011b), largely contradict six decades of research into the biogeography of plant–herbivore interactions. We anticipate that these papers will be controversial for this fact alone. However, it cannot be denied that these studies represent the largest and most rigorous tests of the LHDH. Therefore, one might feel justified in tentatively rejecting the hypothesis altogether – but not so fast! Despite their strengths, these studies are not free from criticism and we need to ask ourselves: Why might their conclusions contradict previous empirical reviews? First, one possible explanation is that identifying resistance traits is not as straightforward as is often portrayed. Classical chemical and physical resistance traits often show no clear association with susceptibility to herbivores (Carmona *et al.*, 2011). Therefore the traits selected in these papers may not play a direct role in defence, or they might provide only crude descriptions of complex resistance traits (e.g. tannins; Salminen & Karonen, 2011). Second, other reviews have focused on comparing tropical and temperate species with similar life-history forms or from roughly comparable habitats (Coley & Aide, 1991). By contrast, Moles *et al.* (2011b) examined species from a wide diversity of plant growth forms, habitats, and along a continuous latitudinal gradient – not just temperate vs tropical ecosystems. In this context, it is noteworthy that Moles *et al.* (2011a) did detect a consistent signature of increasing herbivory and defence with decreasing latitude in salt marsh habitats, a habitat that is relatively continuous and similar in community structure over a large latitudinal gradient. The approaches taken by Moles *et al.* (2011b) vs their predecessors are related but they do address slightly different questions that could account for the observed discrepancies. So at this juncture, how might we move forward?

Re-assessing assumptions and conditions for latitudinal gradients in herbivory and defence

In trying to formulate evidence for and against the LHDH, we need to revisit the assumptions and necessary conditions underlying the predicted latitudinal gradient in defensive plant traits. Classically, Coley & Barone (1996) suggested that tropical plants experience higher levels of herbivory, and this greater herbivory causes the evolution of increased resistance against herbivores in the tropics (Coley & Aide,

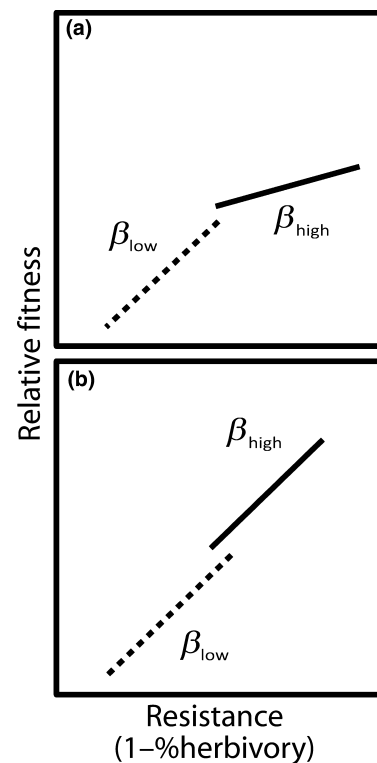


Fig. 1 Hypothetical strengths of natural selection on resistance against herbivores at low and high latitudes. Each line depicts the selection gradient (β) acting on resistance as the line of best fit between relative fitness in a population and the resistance trait or 1-%herbivory. Consider two populations of the same species: one at high latitude (solid line) and one at low latitudes (dashed line). In scenario (a), the evolutionary outcome of this interaction (assuming all else to be equal) is affected by the difference in the level of herbivory because there is a nonlinear relationship between relative fitness and the strength of selection on resistance (1-%herbivory), such that $\beta_{\text{high latitude}} < \beta_{\text{low latitude}}$. Thus, all else being equal, the rate of evolution will be faster at lower latitudes. In scenario (b), plants on average have higher fitness at high latitudes and lower percentage herbivory, and plants at low latitudes had higher overall fitness and greater herbivory. The evolutionary outcome of this interaction is unaffected by the difference in the level of herbivory because the strength of selection acting at high and low latitude populations is identical ($\beta_{\text{high latitude}} = \beta_{\text{low latitude}}$). Thus, all else being equal in (b), the direction, rate and long-term consequence of evolution by natural selection will be the same at high and low latitudes, regardless of the intercept of the line at each latitude.

1991; Schemske *et al.*, 2009). This will indeed be the case when increased herbivory causes stronger natural selection on resistance traits, where selection is measured as the slope of the line (β , the selection gradient) between relative plant fitness and resistance (e.g. 1-%herbivory) within a population ($\beta_{\text{high latitude}} < \beta_{\text{low latitude}}$, Fig. 1a) (Lande & Arnold, 1983). However, assuming all else to be equal, variation in herbivory itself does not necessarily translate to stronger selection on plant defence, such as when selection gradients between high and low latitude plants are identical ($\beta_{\text{high latitude}} = \beta_{\text{low latitude}}$), even if levels of herbivory differ

(Fig. 1b) – which Moles *et al.* (2011a) claim is not the case. This highly simplified example illustrates that to understand the conditions that might lead to biogeographic patterns in defence, we need to study the evolutionary processes thought to cause predicted patterns, and thus we require direct measures of genetic variation and natural selection on resistance along broad latitudinal gradients, as well as variation in ecological interactions and plant traits. This represents an important avenue for future research.

Future directions in testing the latitudinal herbivory-defence hypothesis

There are many reasons why variation in herbivory along latitudinal gradients might not directly translate to stronger selection for plant defences. For example, low latitude plants often have access to higher levels of resources, which can reduce the fitness effects of herbivory (i.e. higher tolerance; Coley *et al.*, 1985). Indeed, tropical sites characterized by high soil fertility, rainfall, and temperature, can favour the evolution of fast growth (Coley & Barone, 1996; Fine *et al.*, 2004). This might therefore lead to selection for lower resistance and higher tolerance to herbivory in seasonally stable tropical habitats, vs plants that occur in temperate or tropical areas that experience greater fluctuations in temperature, water or nutrients. However, the roles of herbivores' natural enemies along latitudinal gradients, which received only partial attention by Moles *et al.* (2011b) when measuring extrafloral nectaries, have been shown to vary with latitude (Hawkins *et al.*, 1997; Dyer & Coley, 2002). For example, when studying food web dynamics at high and low latitude eastern North American salt marshes, Marczak *et al.* (2011) found that although high latitude *Iva frutescens* plants are less defended, these benefits for herbivores were mostly swamped out by much stronger predator effects, which dampened effects of herbivores on plants across latitudes. Such latitudinal variation in the strength of trophic cascades appear to be common, with top-down effects of predators on herbivores being generally but not universally more prevalent in the tropics and subtropics than in temperate and arctic ecosystems (Hawkins *et al.*, 1997; Dyer & Coley, 2002).

Taking resource variation and tritrophic interactions into account might be done with the implementation of controlled sampling strategies and manipulative experiments. Specifically, measuring resources such as soil fertility, temperature, rainfall and light, and including these variables as covariates in models, might increase a study's explanatory power. Likewise, effects of the third trophic-level on herbivores and plants could be incorporated with the use of cage experiments that manipulate access by natural enemies and examine the survival and performance of herbivores. This would give an estimate of plant quality effects and predator pressure in the area. An alternative method would be to

experimentally study the disappearance rate of herbivores in a range of study sites (Hawkins *et al.*, 1997).

Phylogenetically controlled samplings of related taxa and more precise measurements of the concentrations and diversity of resistance traits are also likely to have important consequences for testing the LHDH. The effects of latitude on plant defences might be most apparent when we compare a group of closely related plant species (e.g. species in the same genus or family) that have diversified along a latitudinal gradient (Rasmann & Agrawal, 2011), or communities from comparable habitats along the gradients (Pennings *et al.*, 2009). Moreover, the use of phylogenetically explicit comparative methods, such as those employed by Moles *et al.* (2011b), will continue to be important in accounting for phylogenetic nonindependence. Finally, future studies need to more comprehensively characterize the many defences used by plants (Agrawal, 2011), including tolerance and the induction of resistance traits, which are too often neglected in studies of latitudinal gradients. The importance of such defences are apparent in the > 50 milkweed species endemic to the Americas, where recent phylogenetically explicit analyses showed that species from lower latitudes induce higher levels of toxic cardiac glycosides than species from higher latitudes (Rasmann & Agrawal, 2011).

Summary

The recent papers by Moles *et al.* (2011a,b) provide the most rigorous test of the LHDH. Their results suggest that the explanatory power of the hypothesis is less general than previously believed. However, this conclusion is far from certain and we hope the forecasted controversy that comes with these papers will spur on renewed interest into the processes and patterns underlying the biogeography of plant–herbivore interactions. Meeting this challenge will require further intercontinental collaborations among plant ecologists, entomologists, chemical and evolutionary biologists.

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Where are all the undocumented fungal species? A study of *Mortierella* demonstrates the need for sequence-based classification

How many different kinds of fungi inhabit the earth? Hawksworth's (2001) estimate of 1.5 million extant species is widely cited, but many other figures have been proposed, from a 'lower limit' of 712 000 species (Schmit & Mueller, 2007) to over 5 million species (O'Brien *et al.*, 2005). While there is great disparity among these estimates, they all suggest that the *c.* 100 000 species that have been described (Kirk *et al.*, 2008) represent just a small part of the actual diversity of fungi. It follows that most unidentifiable environmental sequences probably represent new species, which has led to proposals for sequence-based taxonomy (Hibbett *et al.*, 2011). In this issue of *New Phytologist*, Nagy *et al.* (pp. 789–794) assess the gap between the described and sequenced dimensions of fungal diversity, focusing on the zygomycete genus *Mortierella* (and the related mitosporic taxa *Umbelopsis*, *Gamsiella* and *Dissophora*).

'As long as the locality and substrate data are consistent, these modern sequences could be applied to older names. Doing so would honour past authors and forge a link to the literature ...'

Nagy *et al.* downloaded 832 mortierelloid internal transcribed spacer (ITS) sequences from GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) and combined them with a newly constructed reference dataset of 102 sequences from type or authentic strains, representing 78 described species (including synonyms). Using a 97% sequence similarity cut-off, they grouped the sequences into 92 molecular operational taxonomic units (MOTUs). Fifty-two MOTUs contained one or more sequences from the reference dataset, but 40 MOTUs could not be identified. Observing a roughly linear relationship between the number of reference