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# Challenges and advances in the study of latitudinal gradients in multitrophic interactions, with a focus on consumer specialization

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Increases in data availability and geographic ranges of studies have allowed for more thorough tests of latitudinal gradients in trophic interactions, with numerous recent studies testing hypotheses that strength of interactions, herbivory, plant chemical defense, and dietary specialization all increase with decreasing latitude. We review the issues surrounding these latitudinal gradients, discuss some methodological challenges, and provide some caveats relevant to inferences from existing approaches. To examine some potential issues with studies on latitudinal gradients in dietary specialization, we simulate a latitudinal gradient of communities that increase in diversity and specialization towards the equator then test the power of different sampling designs for detecting the gradient. Based on this simple simulation, as well as apparent incongruities in the literature, we conclude that subtle differences in sampling design can be responsible for failure to detect existing gradients. Despite calls for rejecting some latitudinal gradient hypotheses, it is clear that a great deal of careful research remains to determine important correlates of the well-established latitudinal gradient in diversity. In particular, future studies should focus on replicated gradients, greater emphasis on continuous sampling, and use of taxonomic controls that allow for meaningful analyses across latitudes.

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## Latitudinal gradients in multitrophic interactions

The latitudinal diversity gradient is one of the strongest and most conspicuous large-scale ecological patterns. Numerous ecological, evolutionary, and statistical studies have attempted to elucidate the causes and consequences of diversity changes with latitude [1–5,6•]. These studies are putatively related to an actual large-scale gradient, but most are focused on comparisons of tropical versus temperate ecosystems rather than characterizing latitudinal gradients *per se* [7]. This is probably justified in some cases because the latitudinal gradient is not necessarily linear—for example, it could exhibit more extreme changes at around 24° latitude [8]. For plants and insects involved in multitrophic interactions, one relevant mechanistic hypothesis driving the diversity pattern is that higher levels of ecological specialization (for both producers and consumers) in the tropics have allowed for greater numbers of species [2,3,9], thus a number of empirical studies have attempted to document the latitudinal gradient in consumer specialization [10–12,13•]. Correlated with these increased levels of ecological specialization are hypothesized latitudinal changes in plant chemical defense, predation, parasitism on animal tissue, and herbivory, all of which contribute to maintaining increased diversity (as well as the higher levels of ecological specialization) in the tropics [14]. Indeed, there is excellent evidence that the strength of some biotic interactions is stronger at lower latitudes (e.g. herbivory and arthropod predation; [14,15••]). While attack rates and overall mortality from parasitoids might not be higher in the tropics [16,17], most empirical studies, including meta-analyses, indicate that herbivory and predation are more intense in tropical versus temperate ecosystems. Again, the majority of these studies related to interaction strength are simply tropical-temperate comparisons, not gradients. In some cases, studies that address latitudinal gradients in biotic interactions might indeed be gradients (with continuous sampling across some large geographic extent), but with sampling focused on temperate regions and thus not necessarily informative with respect to issues of global diversity [18••,19••,20,21]. One major challenge for understanding latitudinal gradients in trophic interactions is that standardized empirical data on predation [15••,22], parasitism [17], herbivory [18••,19••,23], chemistry [7,24,25,26•] and dietary specialization [12,14,27,28] are either limited or are characterized by methodological shortcomings or disagreements about the best approach.

## Problems with common approaches to studying latitudinal gradients in multitrophic interactions

There are four effective approaches to addressing macroecological questions about multitrophic interactions

across large gradients: first, simulation and analytical models relevant to assumptions and predictions of mechanisms that putatively generate diversity gradients; second, exhaustive meta-analyses or other quantitative summaries that use all available studies rather than subsets of published studies [13•,29,30]; third, collection of samples with comparable phylogenetic distributions [11] using standardized methods; and fourth, broad sampling across large numbers of taxa [31,32] using standardized methods. Some syntheses of the latitudinal gradient literature have criticized existing methods and provide direction for overcoming inconsistent methods or poorly framed hypotheses [20]. Clearly each approach has strengths and weaknesses, but continuing to combine these methods will lead to rapid progress in understanding biodiversity. These approaches could also be combined with network science, but currently most networks are unrealistic because they are based on scales that are irrelevant to the assembly and function of communities, poor natural history, or a mix of literature-based data of variable quality [33–35]. Thus, it may not be surprising that tests of latitudinal gradients using network parameters [27] produce different conclusions than those derived from other community data [36], as the use of networks may address peculiar hypotheses about unrealistic systems [5].

Recent prominent latitudinal gradient studies that did not utilize networks [7,12,13•,18••,24,28,32,37,38] are also not without flaws and have been characterized by opportunistic and haphazard selection of sites, study organisms, methods, and assumptions, such that there is no phylogenetic control or no broad representation of the most influential species from a majority of feeding guilds within an ecosystem. Standardized effect sizes and clear measures of interaction strength have also often been lacking in these studies, with an associated lack of understanding of the ecological relevance or natural history of the estimated statistics. For many studies, sites and taxa are not selected to test hypotheses about latitudinal gradients, rather they are haphazard collections of datasets from well-studied field stations or university-associated study sites [28,32]. The location of field sites is often (and necessarily) a matter of logistic or political convenience, while an ideal latitudinal gradient would be designed to control for a number of confounding variables—for example, only including lowland forests across South America. It would be far more powerful to have a continuous gradient across specific longitudinal bands or within biogeographic regions. It is difficult to determine how many sites should be added to achieve a full, informative gradient. Certainly one could only use 2 or 3 sites to generate a parameter estimate and to see if it is different from zero, but the real question is how many sites are needed for adequate statistical power, and for that question a few sensible guidelines should be considered. First, actual power analyses are essential for considering selection of sites, whether they be formal statistical analyses or simple considerations of tradeoffs between breadth and depth of data across the gradient. Second, to really get at the issues associated with the latitudinal species diversity gradient, it is important to sample right at the points where the greatest rates of change are expected—the transitions from subtropical to tropical, rather than samples within temperate or tropical latitudes. Third, if there are good theoretical reasons to expect other nonlinear responses, the areas where nonlinearity are expected should be better sampled, otherwise latitude still reverts to a nominal variable (tropical versus temperate) and the statistical power of a continuous or ordinal variable is potentially squandered. This approach may clarify issues associated with the fact that latitudinal gradient studies have found different results depending on where the gradient was situated and which ecosystems were or were not included. Such issues related to globally distributed field sites have hidden complexity and pitfalls which we address further below using a simulation approach. Although we focus largely on sampling schemes involving site-specific community data, it is worth noting that latitudinal gradients in interactions can also be studied from a phylogenetic perspective in which species (and the latitudinal position of their ranges) are the unit of replication, which shifts the emphasis to questions of evolutionary history. Egan *et al.* [39], for example, found that transitions to herbivory in clupeoid fishes were more common at lower latitudes.

In contrast to dietary specialization, which has been the subject of frequent study over the past decade [28,36,37], there is a dearth of thorough studies on latitudinal gradients in predation and plant chemistry. Many of the studies that do exist (predation/parasitism [14,16], chemistry [18••,19••,20,24,38,40]) are affected by the methodological issues mentioned above or by a restricted focus on individual enemy taxa or broad classes of defensive compounds that are not meaningful (see Ref. [41] for a review of the chemical ecology of individual compounds versus mixtures). When modern metabolomics methods are not available, a productive alternative is the use of bioassays, for example where plants are sourced across a latitudinal gradient and exposed to a single herbivore [19••] or seeds are experimentally placed in the field to study predation [42•]. One particularly appealing approach would be to examine latitudinal gradients in the phytochemical landscape [43], which would focus on variation in plant defenses and multitrophic consumer densities across study sites. Gradients in the phytochemical landscape could be examined by focusing on the same genus across a carefully designed gradient, or at least a focus on species in the same plant family, and by quantifying one or a small number of well characterized defenses (rather than classes of putative defenses, such as tannins). A rigorous, scaled-up version of that approach would be to select a group of plants at each site in the gradient that are separated by similar phylogenetic

distances [11]. Alternatively, one could attempt broader, ecosystem-level measures of defense. This would require either large scale bioassays [31] or metabolomics approaches [25] that include carefully selected taxa from ecosystems across a full latitudinal gradient. The selection of taxa is challenging and current approaches include focusing on a single taxon that spans a broad latitudinal gradient, or the phylogenetic pairing of species at different sites. Neither approach is perfect: in the former, broad distribution of a taxon does not necessarily imply useful distribution of species and potentially ignores the role of taxa with restricted ranges; the latter option (taxonomic pairing of species) is more difficult to implement in a design with continuous latitudinal sampling. The approach utilized by Miller and Hanson [31] was strong because they examined the effects of hundreds of tropical versus temperate plant species on a dietary generalist caterpillar, but this was unreplicated at the consumer level and was not a true gradient. The metabolomics approach [25], comparing one tropical and temperate site, also suffered from these issues.

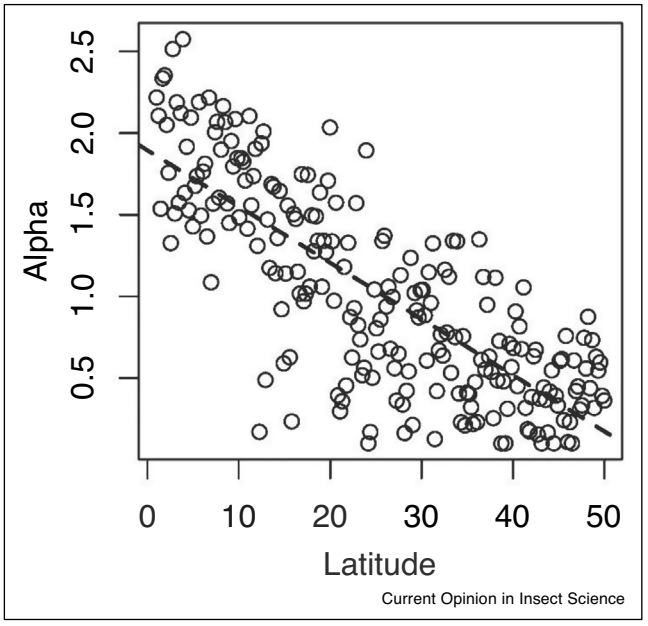
## Issues in the design of latitudinal studies, with a focus on ecological specialization

In contrast to the phytochemical landscape, consumer specialization is a parameter that suffers less from a lack of empirical data and more from an overabundance of definitions that differ in assumptions and interpretation, as well as in complex associations with other parameters, such as abundance and sampling intensity [44]. Because consumer specialization is relatively well studied, and global gradients in dietary specialization have been reported numerous times [28,32,36,45,46], it also provides a useful context for more rigorous examination of issues in the design of latitudinal studies. As mentioned above, many if not all of the largest studies to date have utilized data from field sites selected for reasons other than the careful sampling of global gradients. Given the importance to the field of ecology of the latitudinal gradient in diversity and related patterns, it is noteworthy that the consequences of relevant sampling designs have received little attention.

We used a recently published simulation framework [35] to generate an artificial world of plants and herbivores with qualitatively realistic latitudinal gradients in species richness and diet breadth (Figure 1). The gradient in diet breadth among simulated communities was created by varying alpha, the shape parameter from the discrete, truncated Pareto power law, which we have used elsewhere [28] to quantify variation among communities in consumer specialization and generalization (higher values of the shape parameter indicate assemblages of more specialized herbivores). In the simulation of communities, alpha was linked to the diversity of plants and herbivores such that high levels of diversity were associated with high levels of specialization—a pattern that has been documented empirically by numerous studies (Figure 1). To investigate how the design of latitudinal studies impacts the discovery and quantification of such patterns, we separately generated thousands of sampling schemes that differ in the number of sites studied, the specific location of sites studied, and the depth of sampling at each site. We then took those simulated sampling schemes and returned to the simulated world to ask if a particular combination of sampling sites would better discover the true latitudinal gradient (the 'true' gradient in this case is the slope from our simulated world). We also used network parameters from these same simulated communities to examine how networks, especially those at the broader scales that are reported in the literature, produce different inferences about gradients.

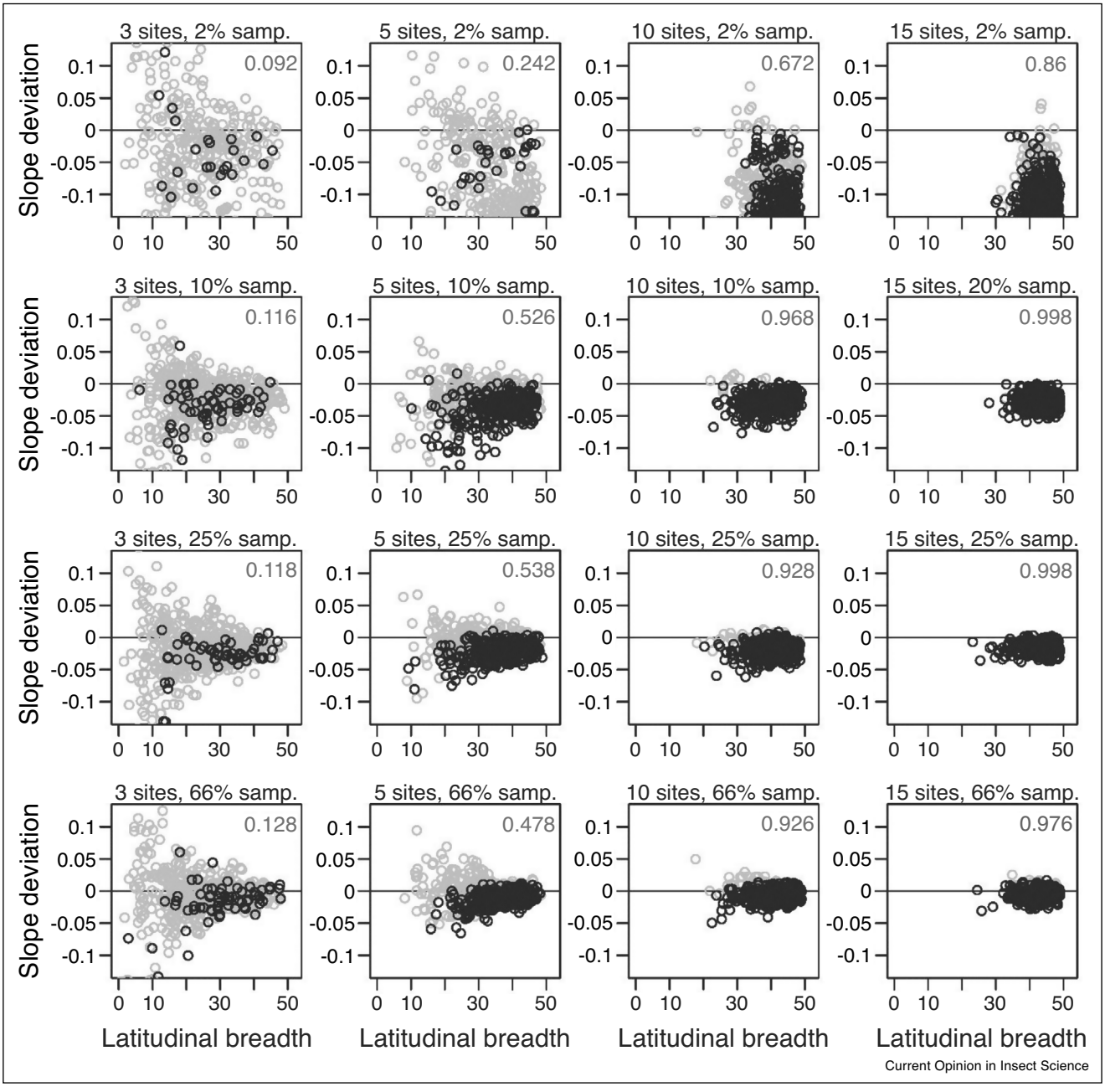
Results from the re-sampling of the simulated world show clear effects of sampling design on inferences about gradients (Figure 2). For example, when we examined the difference between the observed and true latitudinal

**Figure 1**



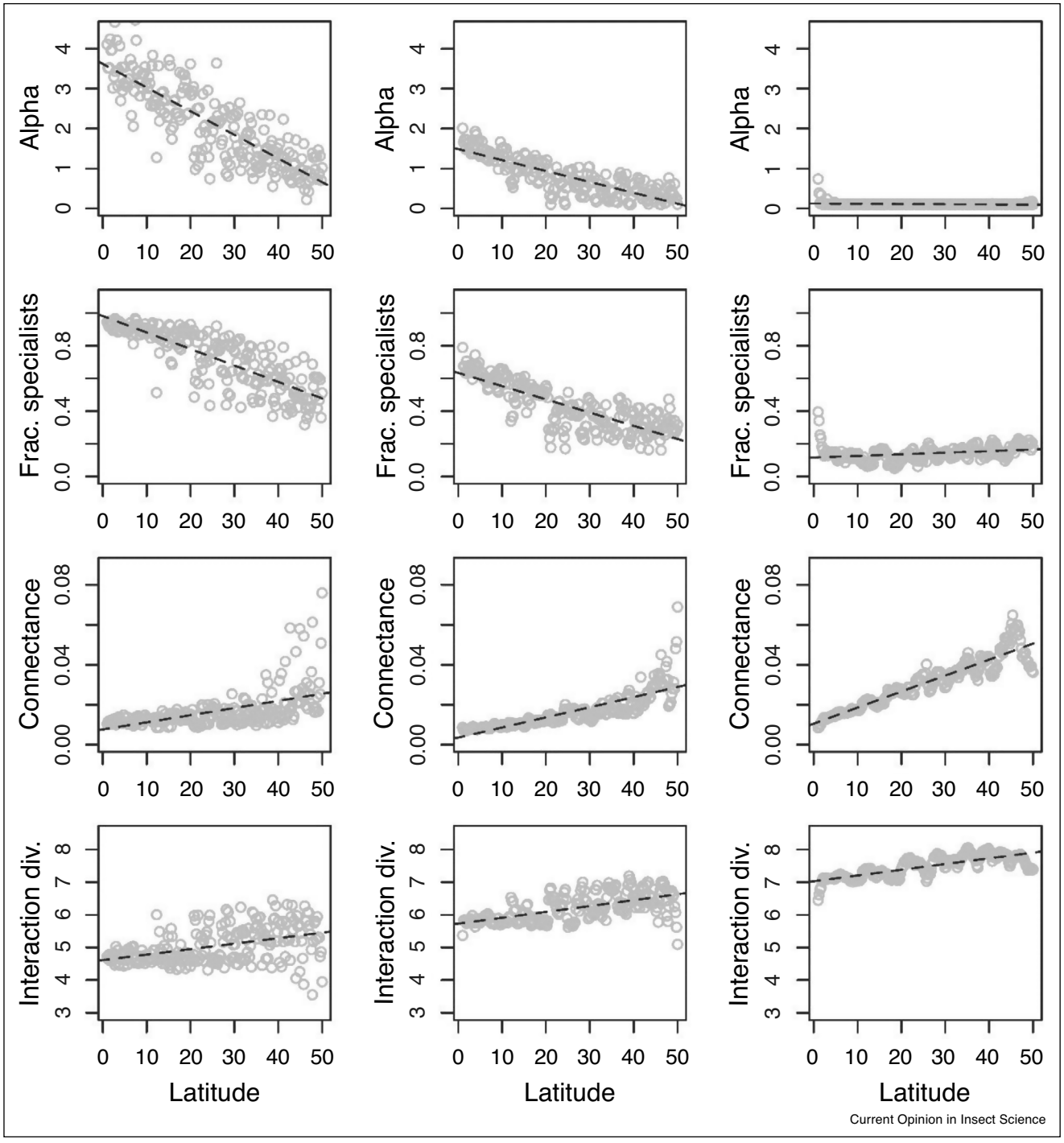

Simulated latitudinal gradient, utilizing the multitrophic model described by Pardikes *et al*. [35]. Individual points are simulated communities characterized by plants and associated herbivores. For each community, we fit a discrete, truncated Pareto power law [50], and extracted alpha, the shape parameter. Higher values of alpha correspond to communities more dominated by specialist consumers. The relationship (shown as the dotted line) between alpha and latitude was estimated with a simple linear regression, and the slope of this regression is taken as the point of comparison for simulated resampling of the latitudinal gradient, as shown in Figure 2. The latitudinal gradient shown here is qualitatively similar to the empirical gradient reported in Forister *et al*. [28], in which alpha ranges from approximately 2 to less than 0.5 across 50° of latitude.

**Figure 2**




Results from 8000 simulated latitudinal gradient studies in which different artificial sampling schemes were applied to the simulated world. Each panel shows the difference between the true latitudinal pattern (the slope from Figure 1) and the slope estimated by resampling the simulated world. Note that here (in contrast to Figure 1), each point is not an individual community or geographic location, rather each point is the outcome of a single, multi-location latitudinal study. Results from 500 simulated studies are shown in each panel, which are organized by the number of sites studied (from 3 on the left to 15 on the right) and the depth of local sampling (from 2% to 66% of local plant–herbivore interactions observed, from top to bottom). In each panel, the gray circles are individual studies that fail to reject the null of no latitudinal pattern, while black circles indicate studies that detect the pattern ($P < 0.05$); the fraction of statistically significant studies is shown in the upper right of each panel. The x axis for all panels is the latitudinal spread (or breadth) of each simulated study. With greater numbers of sites sampled (from 3 to 15), the latitudinal spread necessarily compresses towards the high end.

**Figure 3**




Changes in network parameters resulting from pooling adjacent sites that were simulated across a latitudinal gradient. Four commonly used indices are examined, two that are related to dietary specialization (Pareto alpha and fraction of extreme specialists) and two that are related to edge diversity in a network (interaction diversity and connectance). Alpha is the shape parameter from the discrete, truncated Pareto power law, and it provides a useful estimate of dietary specialization. Fraction of extreme specialists is simply the proportion of all individuals that utilize only one host. Interaction diversity is the Shannon entropy of all sampled edges in a network. Connectance is the fraction of all possible links that actually exist in a network. The first column is based on site specific sampling. In the middle column, networks were assembled by pooling sets of three consecutive sites (a focal site, and one on either side). For the right column, we pooled eleven sites—five sites on either side of a focal site. Pooling of data in this context means that if a particular herbivore is found in association with one host plant at one site and a second host at another site, the pooled data would have the herbivore associated with two hosts (even though it only ever attacks one host locally). In all cases, communities were sampled to a depth of 10% (similar to the second row of panels in Figure 2). The latitudinal gradient for alpha and fraction of

pattern for studies that each contained three sites and sampled local communities to a depth of 2% (i.e. that fraction of local interactions was recorded; Figure 2, top graph on the left), the vast majority of studies suffered from type 2 error, failing to reject the null of no relationship between consumer specialization and latitude. Of the studies that correctly recovered a latitudinal pattern, most tended to slightly overestimate the strength of the latitudinal relationship, although a few studies found, by chance, a latitudinal pattern that was significant and more positive than the true slope. As the number of sites sampled increases (along the columns from left to right in Figure 2), the type 2 error decreases; as sampling intensity within each site increases (from top to bottom among the panels), accuracy increases with the recovered slopes converging on the true slope.

However artificial they may be, these results are potentially sobering for certain real world designs. With only 3 sites sampled (the left column of Figure 2), an increase in local sampling intensity (from 2% to 66% of interactions recovered) results in a negligible increase in power to reject the null of no latitudinal relationship (never rising above 13% of studies detecting a pattern). The depth of local sampling for most researchers will be related to years of effort, thus one conclusion from our power analyses is that when years are limiting, the importance of having more sites is elevated. It is also interesting to note that the influence of geographic breadth (the latitudinal span covered, as shown on the X-axes of Figure 2) is not as pronounced as one might expect: with only 3 or 5 sites samples, greater latitudinal breadth brings the average estimated slope only a bit closer to the true slope. Of course, a more realistic biotic gradient may not be linear, especially as one shifts from temperate to tropical ecosystems, and in that case, a greater latitudinal breadth could be considerably more important. Another positive note from these results, provided that model assumptions are realistic, is that complete local sampling is not necessary for recovery of a latitudinal gradient in dietary specialization. Consider studies with 10 sites and 10% of local interactions observed: 96.8% of those studies detect the latitudinal gradient with only slight overestimation of the negative strength of the pattern.

This approach also gives a glimpse into issues with curation of data based on assumptions about the abundance of particular interactions, such as rare specialized feeders, and how those assumptions can have substantive consequences for inferences. For example, singletons (in which a particular herbivore is observed exactly once) are frequently excluded from community data. This is typically presented as a conservative measure, since the confidence in that observation of a plant–insect interaction link might be low and these singletons could be transient species [47]. However, the exclusion of singletons from the simulated world that we have analyzed here could have substantive consequences. For our simulated networks, without singletons, the fraction of studies recovering the true latitudinal gradient never rises above 34% even under the most rigorous conditions (15 sites and 66% of interactions observed; results not shown). It can also be noted that the inclusion of singletons is inherently related to an issue of type two error in studies of latitudinal gradients. In datasets from the most diverse communities, the numbers of individuals observed for all species (including the most rare) are lower than in less diverse communities (for a given level of sampling effort). One consequence could be that the discovery of generalists becomes more difficult at higher levels of diversity, thus producing a latitudinal gradient of specialization. This possibility highlights the value of high quality data and the need for long years of study at any diverse location; although, as we find in our simulation results, the value of sampling depth might (counter-intuitively) be less important than the value of dense geographic sampling. A second issue potentially giving rise to an erroneous inference of a latitudinal gradient is taxonomic uncertainty. Where uncertainty is high (i.e. fewer formally described species) it could be more difficult to link occurrence records, such that a particular herbivore is observed on two different host plants but recorded as a unique morphospecies in both cases. Beyond these issues, false discovery rates within a frequentist framework are well understood, and we would only expect 5% of studies to report a correlation between latitude and ecological specialization if, in fact, the actual slope relating latitude and ecological specialization is zero. Considering meta-analyses and qualitative reviews, we are not aware of any authors who have suggested that 5% or fewer of published studies have reported a latitudinal gradient.

In general, the most problematic treatments of latitudinal gradients are those that examine network parameters across latitudes without consideration of network scale [36]. Even if the scales from which data are derived are somehow standardized (e.g. plot-based networks [8]), there is a tendency for researchers to choose a scale for network assembly that is larger than the scale at which meaningful interactions actually take place. This is an understandable bias, since a greater spatial scale allows for the accumulation of more data, but the consequence is that networks often span regions or ecosystems with clear barriers to dispersal and gene flow between them. We

**(Figure 3 Legend Continued)** specialists disappears with pooling. Connectance and interaction diversity retain the positive slope, but the magnitude of the slope and y-intercepts change considerably with pooling. Note that the upper left panel (site-specific sampling of the alpha parameter) overestimates the true slope as seen in Figure 1. This overestimation is consistent with a bias resulting from sampling 10% of possible interactions (Figure 2).

examined this issue in the context of detecting latitudinal gradients, by pooling the simulated communities described above (Figure 1) that are from neighboring latitudes and examining four network parameters across the global gradient: the alpha parameter from the discrete, truncated Pareto distribution of diet breadth, the fraction of extreme specialists (with a diet breadth of one host), network connectance, and interaction diversity (Shannon entropy). For all parameters, site-specific sampling provides a different picture than pooling sets of three or eleven consecutive sites (Figure 3), and this change is most severe for the alpha estimate of specialization and the fraction of specialists, for which the latitudinal gradient disappears with the modest pooling of eleven neighboring sites. The other network parameters, connectance and interaction diversity, retain the same type of relationship across the latitudinal gradient (i.e. a positive slope), but the parameter estimates (slope and y-intercept) also change in magnitude. Thus, network studies of latitudinal gradients should consider these scaling issues, especially if the associated inferences are that there is no latitudinal gradient in a specific parameter, such as specialization. This is especially true if the intent is to detect gradients in local interactions, as may be the case for ecological interactions that affect diversity.

## Conclusions

A recent paper [48] suggested that a latitudinal gradient in species interactions is a 'zombie idea' that refuses to die. Regardless of the details of individual studies, the complexity of the issue (a global ecological gradient) should make one suspicious, *a priori*, of any claims that our relatively young science is somehow done with this important issue. Such a suggestion would be analogous to a geneticist from years past evaluating a handful of studies and suggesting that the organization of genetic material in the nucleus is sufficiently understood; in fact, of course, the organization of genetic material is still an object of important study, and the complexity of genetics is ultimately embedded in the complexity of any large-scale organismal pattern. Thus there is no particular reason to think that the issue of global interaction gradients has been laid to rest, and we should expect (indeed, hope for) many more years of both controversy and progress. In our simple simulation, we have focused on a single measure of consumer diet breadth. However, there is no reason to think that similar conclusions would not be had for other indices studied at a global scale, perhaps even human consumption of natural resources [49••]. Ecologists have a long tradition of encouraging but rarely implementing power analyses, which can be useful both for experimental design and the interpretation of results. Given the expenses associated with generating latitudinal data, this is certainly an area of ecology that should pay closer attention to the value of Monte Carlo (resampling) perspectives on both real and simulated data [5]. Finally, there are a number of important approaches that should be especially fruitful for understanding large-scale gradients in coming years, including the use of metabolomics and detailed phytochemical landscape data, more studies of natural enemies, and better integration between community simulations and empirical results.

## Conflict of interest statement

Nothing declared.

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## References

1. Wallace AR: *Tropical nature and other essays*. Macmillan; 1878.
2. Dobzhansky T: **Evolution in the tropics**. *Am Sci* 1950, **38**:209-221.
3. Schemske DW, Mittelbach GG: **Latitudinal gradients in species diversity: reflections on Pianka's 1966 article and a look forward**. *Am Nat* 2017, **189**:599-603.
4. Araújo WS: **Global patterns in the structure and robustness of plant-herbivore networks**. *Front Biogeogr* 2016, **8**:e31053.
5. Pellissier L, Albouy C, Bascompte J, Farwig N, Graham C, Loreau M, Maglianesi MA, Melián CJ, Pitteloud C, Roslin T *et al.*: **Comparing species interaction networks along environmental gradients**. *Biol Rev* 2018, **93**:785-800.
6. • Stevens RD, Tello JS: **A latitudinal gradient in dimensionality of biodiversity**. *Ecography (Cop)* 2018, **41**:2016-2026 http://dx.doi.org/10.1111/ecog.03654.
This paper demonstrates that increases in bat species richness with decreasing latitude are accompanied by increases in dimensionality (low correlations between different dimensions of diversity) when examining other dimensions, including measures of phylogenetic, functional, and phenetic diversity.
7. Dyer LA, Coley PD: **Latitudinal gradients in tri-trophic interactions**. In *Multitrophic level interactions*. Edited by Tscharntke T, Hawkins BA. Cambridge University Press; 2001:67-88.
8. Dyer LA, Walla TR, Greeney HF, Stireman IIIJO, Hazen RF: **Diversity of interactions: a metric for studies of biodiversity**. *Biotropica* 2010, **42**:281-289.
9. Pianka ER: **Latitudinal gradients in species diversity: a review of concepts**. *Am Nat* 1966, **100**:33-46.
10. Fiedler K: **Diet breadth and host plant diversity of tropical- vs. temperate-zone herbivores: South-east Asian and west Palaearctic butterflies as a case study**. *Ecol Entomol* 1998, **23**:285-297.
11. Novotny V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y: **Why are there so many species of herbivorous insects in tropical rainforests**. *Science* 2006, **313**:1115-1118.
12. Gainsbury A, Meiri S: **The latitudinal diversity gradient and interspecific competition: no global relationship between lizard dietary niche breadth and species richness**. *Glob Ecol Biogeogr* 2017, **26**:563-572.
13. • Frank K, Krell F-T, Slade EM, Raine EH, Chiew LY, Schmitt T, Vairappan CS, Walter P, Blüthgen N: **Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient**. *Ecol Lett* 2018, **21**:1229-1236.
The authors utilize data from published studies across a full latitudinal gradient to demonstrate an increase in diversity with decreasing latitude for dung beetles but found that the diet breadth was very generalized across the gradient.

14. Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K: **Is there a latitudinal gradient in the importance of biotic interactions?** *Annu Rev Ecol Evol Syst* 2009, **40**:245-269.

15. •• Roslin T, Hardwick B, Novotny V, Petry WK, Andrew NR, Asmus A, Barrio IC, Basset Y, Boesing AL, Bonebrake TC *et al.*: **Higher predation risk for insect prey at low latitudes and elevations**. *Science* 2017, **356**:742-744.
This paper utilizes a simple approach with model caterpillars across multiple latitudinal gradients (i.e. six continents) to demonstrate that predation rates by arthropod predators are greater at lower latitudes.

16. Hawkins BA: *Pattern and process in host-parasitoid interactions*. Cambridge University Press; 1994.

17. Stireman JO, Dyer LA, Janzen DH, Singer MS, Lill JT, Marquis RJ, Ricklefs RE, Gentry GL, Hallwachs W, Coley PD *et al.*: **Climatic unpredictability and parasitism of caterpillars: implications of global warming**. *Proc Natl Acad Sci U S A* 2005, **102**:17384-17387 http://dx.doi.org/10.1073/pnas.0508839102.

18. •• Moreira X, Castagneyrol B, Abdala-Roberts L, Berny-Mier y Teran JC, Timmermans BGH, Bruun HH, Covelo F, Glauser G, Rasmann S, Tack AJM: **Latitudinal variation in plant chemical defences drives latitudinal patterns of leaf herbivory**. *Ecography (Cop)* 2018, **41**:1124-1134.
The authors document changes in herbivory, nutritional quality and phenolic content for the English oak,*Quercus robur*, along an 18° latitudinal gradient, reporting a decrease in herbivory and an increase in phenolic content with increasing latitude.

19. •• Baskett CA, Schemske DW: **Latitudinal patterns of herbivore pressure in a temperate herb support the biotic interactions hypothesis**. *Ecol Lett* 2018, **21**:578-587.
Using a combination of palatability assays in the lab and surveys of naturally occurring insects, the authors studied a continuous gradient of interaction strength in a focal herbaceous plant. Although restricted to temperate latitudes, the study is noteworthy for accounting for leaf phenology and for testing for step changes in a latitudinal pattern.

20. Anstett DN, Ahern JR, Johnson MTJ, Salminen J-P: **Testing for latitudinal gradients in defence at the macroevolutionary scale**. *Evolution* 2018, **72**:2129-2143 http://dx.doi.org/10.1111/evo.13579.

21. Elsberry LA, Fales RJ, Bracken MES: **Changes in biodiversity and species associations along a latitudinal gradient**. *Front Biogeogr* 2018, **10**:e37952 http://dx.doi.org/10.21425/F5101-237952.

22. Jeanne RL: **A latitudinal gradient in rates of ant predation**. *Ecology* 1979, **60**:1211-1224.

23. Kozlov MV, Lanta V, Zverev V, Zvereva EL: **Global patterns in background losses of woody plant foliage to insects**. *Glob Ecol Biogeogr* 2015, **24**:1126-1135.

24. Moles AT, Bonser SP, Poore AGB, Wallis IR, Foley WJ: **Assessing the evidence for latitudinal gradients in plant defence and herbivory**. *Funct Ecol* 2011, **25**:380-388.

25. Sedio BE, Parker JD, McMahon SM, Wright SJ: **Comparative metabolomics of forest communities: species differences in foliar chemistry are greater in the tropics**. *biorxiv.org*. 2018 http://dx.doi.org/10.1101/271361.

26. • Wang XF, Liu JF, Gao WQ, Deng YP, Ni YY, Xiao YH: **Defense pattern of Chinese cork oak across latitudinal gradients: influences of ontogeny, herbivory, climate and soil nutrients**. *Sci Rep* 2016, **6**:27269.
Chemical defenses and herbivore pressure increased at lower latitudes, although chemistry focused on broad classes of compounds (phenolics and tannins) and the latitude encompassed was only 14°. Of note is the simultaneous quantification of chemical and physical defenses (including lignin and cellulose).

27. Schleuning M, Fründ J, Klein A-M, Abrahamczyk S, Alarcón R, Albrecht M, Andersson GKS, Bazarian S, Böhning-Gaese K, Bommarco R *et al.*: **Specialization of mutualistic interaction networks decreases toward tropical latitudes**. *Curr Biol* 2012, **22**:1925-1931.

28. Forister ML, Novotny V, Panorska AK, Baje L, Basset Y, Butterill PT, Cizek L, Coley PD, Dem F, Diniz IR *et al.*: **The global distribution of diet breadth in insect herbivores**. *Proc Natl Acad Sci U S A* 2015, **112**:442-447.

29. Kinlock NL, Prowant L, Herstoff EM, Foley CM, Akin-Fajiye M, Bender N, Umarani M, Ryu HY, Şen B, Gurevitch J: **Explaining global variation in the latitudinal diversity gradient: meta-analysis confirms known patterns and uncovers new ones**. *Glob Ecol Biogeogr* 2018, **27**:125-141.

30. Gurevitch J, Koricheva J, Nakagawa S, Stewart G: **Meta-analysis and the science of research synthesis**. *Nature* 2018, **555**:175-182.

31. Miller JC, Hanson PE: **Laboratory feeding tests on the development of gypsy moth larvae with reference to plant taxa and allelochemicals**. *Bull Agric Exp Stn Oregon State Univ* 1989, **674**:1-63.

32. Dyer LA, Singer MS, Lill JT, Stireman JO, Gentry GL, Marquis RJ, Ricklefs RE, Greeney HF, Wagner DL, Morais HC *et al.*: **Host specificity of Lepidoptera in tropical and temperate forests**. *Nature* 2007, **448**:696-699.

33. Poisot T, Canard E, Mouillot D, Mouquet N, Gravel D: **The dissimilarity of species interaction networks**. *Ecol Lett* 2012, **15**:1353-1361.

34. Ballantyne G, Baldock KCR, Willmer PG: **Constructing more informative plant-pollinator networks: visitation and pollen deposition networks in a heathland plant community**. *Proc Biol Sci* 2015, **282** 20151130.

35. Pardikes NA, Lumpkin W, Hurtado PJ, Dyer LA: **Simulated tri-trophic networks reveal complex relationships between species diversity and interaction diversity**. *PLoS One* 2018, **13**:e0193822.

36. Dalsgaard B, Schleuning M, Maruyama PK, Dehling DM, Sonne J, Vizentin-Bugoni J, Zanata TB, Fjeldså J, Böhning-Gaese K, Rahbek C: **Opposed latitudinal patterns of network-derived and dietary specialization in avian plant-frugivore interaction systems**. *Ecography* 2017, **40**:1395-1401.

37. Novotny V, Basset Y, Miller SE, Weiblen GD, Bremer B, Cizek L: **Low host specificity of herbivorous insects in a tropical forest**. *Nature* 2002, **416**:841-844.

38. Moles AT, Wallis IR, Foley WJ, Warton DI, Stegen JC, Bisigato AJ, Cella-Pizarro L, Clark CJ, Cohen PS, Cornwell WK *et al.*: **Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes**. *New Phytol* 2011, **191**:777-788.

39. Egan JP, Bloom DD, Kuo C-H, Hammer MP, Tongnunui P, Iglésias SP, Sheaves M, Grudpan C, Simons AM: **Phylogenetic analysis of trophic niche evolution reveals a latitudinal herbivory gradient in Clupeoidei (herrings, anchovies, and allies)**. *Mol Phylogenet Evol* 2018, **124**:151-161.

40. Coley PD, Aide TM: **Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests**. In *Plant-animal interactions: evolutionary ecology in tropical and temperate regions.* Edited by Price PW, Lewinsohn TM, Fernandes GW, Benson WW. John Wiley & Sons; 1991:25-49.

41. Dyer LA, Philbin CS, Ochsenrider KM, Richards LA, Massad TJ, Smilanich AM, Forister ML, Parchman TL, Galland LM, Hurtado PJ *et al.*: **Modern approaches to study plant–insect interactions in chemical ecology**. *Nat Rev Chem* 2018, **2**:50-64.

42. • Chen S-C, Hemmings FA, Chen F, Moles AT: **Plants do not suffer greater losses to seed predation towards the tropics**. *Glob Ecol Biogeogr* 2017, **26**:1283-1291.
Seed predation was studied across 28° of latitude and hundreds of species: in among-species comparisons, the intensity of predation did not change with latitude, while among-species predation increased away from the equator.

43. Hunter MD: *The phytochemical landscape: linking trophic interactions and nutrient dynamics*. Princeton University Press; 2016.

44. Fründ J, McCann KS, Williams NM: **Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model**. *Oikos* 2016, **125**:502-513.

45. Peguero G, Bonal R, Sol D, Muñoz A, Sork VL, Espelta JM: **Tropical insect diversity: evidence of greater host**

**specialization in seed-feeding weevils**. *Ecology* 2017, **98**:2180-2190.

46. Trøjelsgaard K, Olesen JM: **Macroecology of pollination networks**. *Glob Ecol Biogeogr* 2013, **22**:149-162.

47. Novotny V, Basset Y: **Rare species in communities of tropical insect herbivores: pondering the mystery of singletons**. *Oikos* 2000, **89**:564-572.

48. Moles AT, Ollerton J: **Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea?** *Biotropica* 2016, **48**:141-145.

49. •• Chapron G, Levrel H, Meinard Y, Courchamp F: **A final warning to planet earth**. *Trends Ecol Evol* 2018, **33**:651-652.
The authors call for a new assessment of the future of the planet that includes, among other things, a call for businesses to create new markets that outcompete natural ecosystem services (by making, for example, artificial AI-powered pollinators 'which create many jobs and do not sting'). Although not explicitly concerned with global gradients, the implications are clear given historically positive relationships between business capital, consumption and latitude.

50. Kozubowski T, Panorska A, Forister M: **A discrete truncated Pareto distribution**. *Stat Methodol* 2015, **26**:135-150.