COMMENTARY

Is the Notion that Species Interactions are Stronger and more Specialized in the Tropics a Zombie Idea?

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A zombie idea is an idea that is dead (because it has been killed by data and/or theory), but which still wanders the world feasting on scientists' brains (Fox 2011).

THE IDEA THAT BIOTIC INTERACTIONS ARE MORE INTENSE AND SPECIALIZED AT LOW LATITUDES IS A VENERABLE IDEA THAT IS EXTREMELY WIDELY ACCEPTED.

A range of factors have been proposed to contribute to this gradient, including the greater time since glaciation, the lack of freezing winters and a generally 'benign' climate, as well as the high species diversity of tropical habitats, and the subsequent narrower niches in tropical species due to greater 'species packing' in those communities (Dobzhansky 1950, MacArthur 1972, Schemske et al. 2009, Salazar & Marquis 2012, Coley & Kursar 2014). These ideas can be traced back to at least the second half of the 19th century; for example Wallace (1878), comparing tropical versus temperate vegetation, wrote that: "In the equable equatorial zone there is no such struggle against climate. Every form of vegetation has become alike adapted to its genial heat and ample moisture, which has probably changed little even throughout geological periods; and the never-ceasing struggle for existence between the various species in the same area has resulted in a nice balance of organic forces. . . The same general causes have led to the filling up of every place in nature with some specially adapted form."

The idea that biotic interactions are more intense in the tropics underpins much of our current thinking about global patterns in ecology. For instance, the higher rates of herbivory, predation, and parasitism on species at low latitudes are thought to have selected for higher levels of defense in tropical species (Dobzhansky 1950, MacArthur 1972, Coley & Aide 1991, Van Alstyne et al. 2001, Pennings & Silliman 2005, Salazar & Marquis 2012). The intensity of biotic interactions in the tropics is also thought to contribute to the high levels of biodiversity in the tropics, through mechanisms such as the Janzen-Connell effect (Janzen 1970, Connell 1971), and through evolutionary arms races (Coley & Kursar 2014). Linked to this is the idea that interactions between species (including both antagonistic and mutualistic relationships) are typically more specialized in the tropics compared to their temperate counterparts. The prevailing argument has been that the ecological niches of species, and therefore the range of other species with which they interact, should be more narrow in tropical communities because they are densely packed with other species (MacArthur 1972, Janzen 1973). However, recent large-scale empirical studies and meta-analyses have tended not to support the traditional understanding of latitudinal gradients in species interactions. In this commentary, we ask whether the notions that species interactions are stronger and more specialized in the tropics are actually supported by empirical evidence.

THE LATITUDINAL GRADIENT IN THE INTENSITY OF BIOTIC INTERACTIONS

We define the intensity of biotic interactions broadly, as the rate (or level) of damage or mortality. Evidence for latitudinal gradients in the intensity of biotic interactions therefore include measures of daily rates of herbivory, predation and parasitism, and snapshot measures that record the standing crop of damage or parasitism at a given point in time.

Early reviews tended to support the idea that rates of herbivory were higher in the tropics (Coley & Aide 1991, Coley & Barone 1996). These excellent studies set the stage for subsequent work on latitudinal gradients in biotic interactions, and have become citation classics. However, several studies have pointed out serious shortcomings of these early compilations (overview in del-Val & Armesto 2010), and the authors themselves warned that: “Although this latitudinal difference is statistically significant, it is not enormous, and given the paucity of accurate measures, it should be regarded as a working hypothesis” (Coley & Barone 1996).

Empirical studies on the latitudinal gradient in biotic interactions have yielded mixed results. Many studies have supported the idea that levels of predation, herbivory, and parasitism are higher at low latitudes (Morrow & Fox 1989, Pennings et al. 2007, 2009, Thieltges et al. 2009, Freestone et al. 2011, Garibaldi et al. 2011, Reme s et al. 2012, Becerra 2015). However, many studies have found the opposite (Gaston et al. 2004, Adams & Zhang 2009, del-Val & Armesto 2010, Anderson et al. 2013). One of the most frequent findings is no significant latitudinal gradient in the strength of biotic interactions (Garcia et al. 2000, Andrew & Hughes 2005, Sinclair & Hughes 2008, Adams et al. 2009, Studer et al. 2013). Mixed results are also common. For example, Peco et al. (2014) found that rates of seed predation by vertebrates increased with latitude, whereas rates of seed predation by invertebrates decreased with latitude. Similarly, Moreira et al. (2015) found a positive latitudinal gradient in seed predation, but a negative latitudinal gradient in herbivory. The mixed evidence in the literature makes it possible for researchers to cherry pick examples to support, or refute, the existence of latitudinal gradients in biotic interactions, so the next step is to assess the combined weight of the evidence.

Even a simple vote-count shows that the evidence in favor of the traditional idea that biotic interactions are more intense in the tropics is not clear cut. For instance, a recent review of the literature on herbivory showed that only 37 percent of the 38 published latitudinal comparisons of herbivory found higher herbivory at lower latitudes (Moles et al. 2011). Of course, we have better tools available than vote counting. Syntheses and meta-analyses have been performed to bring together the available evidence on latitudinal gradients in several biotic interactions. These studies have not supported the idea that terrestrial herbivory (Moles et al. 2011), marine herbivory (Poore et al. 2012), distance or density dependent mortality in plants (HilleRisLambers et al. 2002, Comita et al. 2014), or seed predation (Moles & Westoby 2003) are more intense at lower latitudes. The only recent suggestions that there are general latitudinal gradients in the intensity of biotic interactions have been based on the citation of select examples rather than on quantitative assessment of the available evidence (Schemske et al. 2009, Coley & Kursar 2014).

THE LATITUDINAL GRADIENT IN SPECIALIZATION

The evidence for greater specificity of interactions such as mutualisms, host-parasite, plant-herbivore, and predator-prey relationships in the tropics is likewise mixed, and certainly does not support the idea that the tropics are always, or even often, more specialized (Ollerton 2012). For example, Scriber (1973) studied temperate versus tropical specialization in larval host plant use in papilionid butterflies and showed that a higher proportion of temperate species were generalist, defined as: ". . .species feeding on more than one taxonomic family of plants. . .", perhaps a rather broad definition but one that is used in more recent studies too. In contrast, Price (1980) found that tropical butterflies tended to be no more host specific than temperate species. Beaver's (1979) study of bark and ambrosia beetles demonstrated that these taxa are actually more host specific in temperate communities compared to the tropics, which he suggested was due to lower host tree density in the tropics, an interesting counter-argument to those earlier hypotheses suggested by MacArthur (1972) and Janzen (1973). A study of the parasitoids of plant-feeding insects by Hawkins (1990) found that those parasitizing insects that were exposed on the plant were typically more host specific in the tropics, but no trend was found for the parasitoids of herbivores concealed within the plant tissue.

Marine studies have been few and far between, but include early work by Rohde (1978) who found that tropical marine fish parasites in one group (Digenea) but not a second (Monogenea) were more host specific than temperate taxa.

A comprehensive meta-analysis of both mutualistic and antagonistic interactions in marine and terrestrial environments by V azquez and Stevens (2004) came to the conclusion that: "there is little evidence for a general effect of latitude on niche breadth" and that tropical interactions were therefore not more frequently specialized. However, the most recent large-scale assessment of herbivore specialization by Forister et al. (2015) concluded that their results were "consistent with a higher frequency of specialized insects in tropical regions", though this was certainly not the case for all insect guilds (see their Figure 3). In addition, their conclusions were based on a dataset from 17 sites that had no representation of tropical Africa and Asia, and indeed contained only one tropical site outside of Central and South America. The question of how representative temperatetropical comparison studies are is an important one; for example, Novotny et al. (2006) compared just one tropical (Australasia) and one temperate (Europe) site and concluded that there was no difference in the specificity of Lepidoptera caterpillars feeding on tree leaves between those sites. In contrast Dyer et al. (2007) compared seven sites (all in the New World) to conclude that: "larval diets of tropical Lepidoptera are more specialized than those of their temperate forest counterparts."

A study of latitudinal specialization of biotic pollination in plants by Ollerton & Cranmer (2002) used two independent datasets, the first comprising 35 plant communities, the second 103 species from the Apocynaceae subfamily Asclepiadoideae, though there were still geographical gaps within the coverage of the data. Nonetheless a clear signal emerged, that these interactions are not more specialized in the tropics compared to extra-tropical regions once sampling effort is taken into account, suggesting that assemblages of interacting species in the tropics tend to be undersampled. However, network-level studies of subsets of flower visitors are finding rather different results, suggesting that there may be some differences between taxa. For example, Dalsgaard et al. (2011) showed that hummingbird–flower networks are significantly more specialized in the tropics, and that this is correlated with species richness, current precipitation, and climate-change velocity during the Quaternary, suggesting a range of possible determinants of that specialization. In contrast, a more recent analysis of mutualistic interaction networks (pollination and frugivory) has shown that in the tropics, these networks tend to be less specialized (Schleuning et al. 2012), a result that is both controversial and that highlights the need for further, dedicated research in this area, particualrly focused on the responses of different groups of flower visitors rather than assuming that all pollinators show the same trends with latitude (Ollerton 2012).

Future progress in understanding latitudinal gradients in specialization will require researchers to more clearly define both their hypotheses (perhaps moving from conceptual to formal

mathematical models) and their definitions. At least some of the disagreements in the literature stem from different definitions of terms such as ‘specialized’ and ‘generalized’ (Ollerton et al. 2007). This is clear when we consider that tropical communities, on average, certainly contain a higher number of functionally specialized pollination systems (e.g., bee, bird, beetle, fly, cockroach, etc.) and temperate systems have more plants that are functionally generalized (mixed bee/fly/butterfly, etc., Ollerton et al. 2006). However, tropical plants are not more ecologically specialized, in terms of the number of pollinating animal species servicing each plant (Ollerton & Cranmer 2002). So, depending upon whether we are referring to functional or ecological specialization of plants in tropical communities, we could come to very different conclusions (see also Armbruster 2006).

CONCLUSION

There is still scope for more studies of latitudinal gradients in biotic interactions. For instance, there are types of interactions that have not yet been satisfactorily quantified across broad gradients (such as belowground interactions and insect bacterial parasites).

Meta-analyses of levels of parasitism and predation on animals would also be extremely valuable contributions to the debate. However, it will take something quite substantial at this stage to overturn the mass of accumulated evidence against the idea that species interactions are generally stronger and more specialized in the tropics. In fact, if there has been publication bias against results contrary to the traditional idea in the past (either through the file-drawer effect [Rosenthal 1979,], or from reviewers being harsher on studies they perceived as getting the 'wrong' answer), then the publication of syntheses and meta-analyses showing that the traditional ideas are not nearly as strongly supported as we thought (e.g., V azquez & Stevens 2004, Moles et al. 2011, Ollerton 2012, Poore et al. 2012) might actually lead to an accumulation of evidence contrary to the traditional ideas over the next few years. At present, the combined weight of empirical evidence does not support the idea that interactions are generally stronger or more specialized in the tropics. There is no longer any excuse for simply assuming that the traditional ideas in this field are correct. Despite this, high profile papers are still published that selectively cite evidence in favor of the traditional idea that interactions are more intense at lower latitudes (Schemske et al. 2009, Coley & Kursar 2014). These are not isolated incidents: papers that report higher rates of herbivory at lower latitudes are cited six times more often than papers showing results contrary to traditional ideas (Moles 2013).

Moving past the idea that species interactions are stronger and more specialized in the tropics will allow us to generate new and improved theories about the factors that shape macroecological gradients in plant–animal interactions. Any inclusive theory of latitudinal trends in strength and specialization must take into account the marine as well as terrestrial realm, and should apply to the full suite of global ecosystems including seasonal tropical forests, rainforests and savannas, and higher latitude grasslands, herbfields, shrublands, and forests (deciduous and evergreen). As in many areas of macroecology, studies that bring together data to determine whether observed patterns are consistent across continents and different ecosystem types will be valuable. Improving our understanding the factors that drive global scale patterns in ecosystem function is likely to become increasingly important as we attempt to predict (and mitigate) the effects of global climate change.

Studies showing that species interactions are not stronger or more specialized in the tropics do not change the fact that tropical ecosystems are beautiful and amazing places. The observation that some aspects of ecology work in similar ways in tropical and temperate ecosystems is not actually all that surprising, and it means that tropical biologists and ecologists from other parts of the world can work together to advance our understanding of the ways that species interact.

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