REVIEW

Diversity of Interactions: A Metric for Studies of Biodiversity

Lee A. Dyer[1,6], **Thomas R. Walla**[2], **Harold F. Greeney**[1,3], **John O. Stireman III**[4], and **Rebecca F. Hazen**[5]

[1] Biology Department 0314, University of Nevada Reno, 1664 North Virginia Street, Reno, Nevada 89557, U.S.A.

[2] Department of Biology, Mesa State College, 1100 North Avenue, Grand Junction, Colorado 81501, U.S.A.

[3] Yanayacu Biological Station & Center for Creative Studies, c/o Foch 721 y Amazonas, Quito, Ecuador

[4] Department of Biological Sciences, Wright State University, Dayton, Ohio 45435, U.S.A.

[5] Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana 70118, U.S.A.

ABSTRACT

Multitrophic interactions play key roles in the origin and maintenance of species diversity, and the study of these interactions has contributed to important theoretical advances in ecology and evolutionary biology. Nevertheless, most biodiversity inventories focus on static species lists, and prominent theories of diversity still ignore trophic interactions. The lack of a simple interaction metric that is analogous to species richness is one reason why diversity of interactions is not examined as a response or predictor variable in diversity studies. Using plant–herbivore–enemy trophic chains as an example, we develop a simple metric of diversity in which richness, diversity indices (*e.g.*, Simpson's 1/D), and rarefaction diversity are calculated with links as the basic unit rather than species. Interactions include all two-link (herbivore–plant and enemy–herbivore) and three-link (enemy–herbivore–plant) chains found in a study unit. This metric is different from other indices, such as traditional diversity measures, connectivity and interaction diversity in food-web studies, and the diversity of interaction index in behavioral studies, and it is easier to compute. Using this approach to studying diversity provides novel insight into debates about neutrality and correlations between diversity, stability, productivity, and ecosystem services.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: community structure; ecosystem function; food webs; multitrophic interactions; plant–insect interactions.

UNDERSTANDING THE ORIGIN AND MAINTENANCE OF TROPICAL DIVERSITY has always been one of the major goals of tropical ecology. Considerable progress has been made toward integrating the many feasible and well-tested hypotheses for why there is such a strong latitudinal gradient in diversity for most taxa (Willig *et al.* 2003, Mittelbach *et al.* 2007, Arita & Vazquez-Dominguez 2008). Nevertheless, there are important unanswered questions about how patterns of diversity should be measured, catalogued, monitored, and conserved (Reiss *et al.* 2009). In diverse tropical habitats, efforts to document species richness are naturally stymied by overwhelming biodiversity and rapid anthropogenic degradation of habitat. Tropical areas suffer disproportionate losses in biodiversity, at a rate measured in weeks rather than years, and there is an urgent need to develop and implement novel approaches to understanding tropical ecosystem structure.

Predictable patterns of diversity have been demonstrated within the tropics (Wake 1970, Connell 1978, Hubbell 1979, Gentry 1982, Terborgh *et al.* 1990, Colwell *et al.* 2008) and studies of tropical diversity have generated numerous testable hypotheses (Hutchinson 1959, Lewinsohn & Roslin 2008), or null models against which alternative models or hypotheses can be tested (Hubbell 1999, Arita & Vazquez-Dominguez 2008). To test these hypotheses, advances in field methods have allowed for accurate

measures of the number of species in communities for some taxonomic groups and some habitats (Longino & Colwell 1997). Furthermore, many novel analytical methods for evaluating and comparing diversity have been developed in recent years (*i.e.*, rarefaction techniques, partitioning α and β, multivariate analysis, and sampling distributions), and access to these analytical methods has been greatly improved (*e.g.*, Colwell & Coddington 1994, Gotelli & Colwell 2001, Alonso & McKane 2004). Recent tropical studies have suggested that another fruitful approach to documenting biodiversity is to compile quantitative inventories of interaction webs (Lewis *et al.* 2002, Janzen *et al.* 2005, Dyer *et al.* 2007, Novotny *et al.* 2007, Tylianakis *et al.* 2007, Bascompte 2009). These inventories have provided empirical data for testing hypotheses about relationships between diversity, the structure of communities, and the dynamics of community interactions. Here we propose a simple variable to quantify interaction diversity analogous to methods used to document and study biodiversity, and we identify the most important questions for which this variable may provide insight.

INTERACTION DIVERSITY

A rich literature exists for interaction diversity, which was loosely defined by Janzen (1974) and then by Thompson (1996) as the number of interactions linking species together into dynamic biotic communities. Janzen lamented the loss of interactions as a hidden consequence of extinction and Thompson (1996, 1997) pointed

out that most of the earth's diversity is in the interaction diversity found in the tropics (also see Ohgushi *et al.* 2007). Numerous studies have acknowledged that major theoretical and applied issues in ecology and conservation must go beyond documenting species diversity and take into account interaction diversity (Cohen & Briand 1984, Price 2002, Del-Claro 2004, Burslem *et al.* 2005, Ohgushi *et al.* 2007, Tylianakis *et al.* 2007, Del-Claro & Torezan-Silingardi 2009). All these studies acknowledge that interactions among species are important because they affect all ecosystem attributes, from primary productivity to population dynamics and the survival and reproduction of individuals. Nevertheless, there has been little effort to quantify interaction diversity in the same way that species diversity has been catalogued, mapped, highlighted, and used as a predictor or response variable in ecological studies (Ollerton & Cranmer 2002).

There are a number of methods available for measuring interaction diversity. The most prominent are found in literature on food webs and in behavioral studies (Slater 2000, Bersier *et al.* 2002). Quantitative food webs are an improvement over qualitative (binary) food webs because predators and prey are measured in the same units of density, allowing the relative differences in the number of linkages observed for each species to be proportional to their actual frequency in the community. In a quantitative food web, the abundance of each species is measured as a density such that the observed species abundances are assumed to be a representation of the populations of each species and their corresponding linkages in the community. In these studies, sampling variance, which affects the number of individuals of each species and thus the number of observed linkages, is the major source of unexplained variance and may be accounted for using a variety of subsampling and data exclusion methods.

Quantitative food-web studies typically assess food-web structure using measures of connectance and compartmentalization. Connectance statistics assess the degree of species-level specialization between trophic levels by comparing the number of observed linkages to the number of potential linkages in a completely connected (generalist) food web. Low measures of connectance indicate communities with highly specialized consumers (Bersier *et al.* 2002). Graphic representations of food webs include visual representations of the relative abundance of species and linkages, but the information in these figures is not easily summarized statistically. Compartmentalization statistics measure the equivalent number of species within each independent group of interacting species. Here p_i is measured as the fraction of total species observed in a single compartment and species abundance is ignored. This measure is useful for determining the degree to which interacting species are divided into independent ecological units, and is valuable for designing experimental approaches to communities or community subsets. The number and evenness of compartments, however, assess a narrow aspect of trophic interactions that is maximized only when compartments are equivalent in their number of species. There remains no generalized analytical approach to measuring the structure of species interactions that includes information regarding the richness and abundance of individuals and linkages in a community.

A new focus in food-web studies and interaction diversity is to examine nestedness (Bascompte *et al.* 2003) and this is an effective method for examining interaction diversity. Qualitative mutualistic webs (*e.g.*, pollination, seed dispersal, and protection; Bascompte *et al.* 2003, Burns 2007, Ollerton *et al.* 2007, Rezende *et al.* 2007) have been examined for the degree of nestedness. One interesting pattern emerging from this work is that these mutualistic networks are cohesive in that the generalists in these systems create a dense core of interactions that provides a foundation for the rest of the community (Bascompte *et al.* 2003). This approach allows for insight about the consequences of losses of specific interactions or species from a community.

Unfortunately, these food web and network approaches involve extensive knowledge of natural history, which is not completely available for any ecosystem (Godfray *et al.* 1999, Novotny & Basset 2005), especially in the tropics. Although some well-resolved food webs exist (Kelly & Southwood 1999, Memmott *et al.* 2000, Brandle & Brandl 2001), these are merely slices embedded in more complex webs of interaction. This is true for even ubiquitous, cosmopolitan, and well-studied systems such as alfalfa monocultures, where species interactions are still not fully resolved (Dyer & Stireman 2003, Pearson *et al.* 2008). This lack of actual food-web data illuminates a major problem facing current diversity research: accumulation of relevant empirical data lags far behind the plethora of mathematical, graphical, and verbal models in ecology (Dyer 2008). Thus, we cannot test hypothesized correlations between tropical diversity and variables such as specialization, predation, and competition because the growing literature on ecological theory relies on a large number of untested assumptions, such as the concept that tropical organisms are more specialized.

In the tropics, our knowledge of the basic life histories for plants and animals (*e.g.*, Singer *et al.* 1982, Fortey 2008, Stork 2008) remains in its infancy. Rapidly accumulating species lists provide a blurry glimpse of community assemblages, but their lack of information on community structure provides only weak suggestions for conservationists and those attempting to preserve them or counter the effects of habitat fragmentation and its disruption of ecological processes. The current devaluation of natural history studies has been lamented by many modern biologists and their importance touted by many others (Futuyma 1998, Dayton 2003), but a demand for novel theoretical advances seems to have eclipsed any coordinated efforts for basic descriptions of ecological communities. We suggest that using subsamples of life-history strategies (*i.e.*, interactions) will allow for quantification of natural history observations and can provide unique insight into the understanding of patterns of biodiversity.

For tropical ecosystems, the lack of a simple interaction diversity metric or approach is exacerbated by the fact that most empirical and many theoretical studies of diversity are potentially irrelevant to tropical ecosystems given the limited range of diversity studied. For example, the classic studies of Tilman (*e.g.*, Tilman *et al.* 2006) examine effects of 1–24 species of plants on primary productivity or ecosystem stability, whereas changes in plant richness from temperate to tropical ecosystems or from low to high elevation can be two to three orders of magnitude (Kreft & Jetz

2007). Similarly, food-web studies that range from 3 to 33 species (Cohen & Briand 1984) or mathematical models that compare two-predator systems to three-predator systems (*e.g.*, Begon *et al.* 1996) are of limited utility when trying to understand causes and consequences of enemy diversity gradients that cross orders of magnitude. Thus, it is not clear how variables such as community stability and ecosystem function are affected when a forest patch has 1000 vs. 10 species of parasitoids or when a forest has 20 vs. 200 species of vascular plants.

A SAMPLING APPROACH TO MEASURING INTERACTION DIVERSITY

Ideally, a quantitative approach to measuring the properties of food webs should include quantified information on trophic interactions for all trophic levels and involves all species in a community, but such an approach is impractical for most reasonably diverse communities (Lewis *et al.* 2002). Quantifying diversity of interactions is similar to the measurement of species diversity and the numerous problems associated with measuring tropical diversity (discussed or reviewed by Heck *et al.* 1975; Lande 1996; DeVries *et al.* 1999, 2001; Magurran 2004; Jost 2006, 2007) apply to measures of interaction diversity (Cohen & Briand 1984). Because interactions are defined by the species observed interacting, distributions are likely to behave similarly to the number of species in having an effectively infinite number of unique units, even though many of those units are likely to be very rare or infrequent in samples. In addition, the number of interactions observed in a given sample is likely to be correlated with sampling effort.

The quantitative investigation of food webs therefore requires the development of sampling schemes designed to infer the properties of the complete community food web from samples that in practice represent only a portion of the community. Current quantitative food-web investigations solve this problem by intensively sampling a restricted food web, focused on guilds or subsets of interacting species (Memmott & Godfray 1994). This approach gains precise quantitative characterization of trophic interactions in terms of the numerical importance of interactions within the guild, but sacrifices inference to the other species in the community that were not sampled. An alternative approach is to sample interactions at random from the total community pool of interactions with the intent of estimating the properties of the total community food web. A clear advantage of this approach is that it allows inferences about the total community food web to be made directly from the information in samples because the experimental unit of interest is the total community as opposed to a single family or guild of organisms. By design this approach sacrifices the precision and within-guild resolution of interactions provided by exhaustive sampling of focal groups to gain greater insight for the entire community. The random sample approach to the study of food webs takes advantage of the well-established methods used in the study of species diversity to estimate the properties of the total community from a limited number of samples.

AN EXAMPLE: TRITROPHIC INTERACTIONS, DIVERSITY, AND SPECIALIZATION

Plants, phytophagous insects, and enemies make up well over half of global terrestrial biodiversity (Price 2002) and interactions between these trophic levels have generated important theoretical advances in ecology and evolutionary biology (Hairston *et al.* 1960, Ehrlich & Raven 1964, Lawton & McNeill 1979, Price *et al.* 1980, Novotny *et al.* 2006), but complete quantitative food webs including these guilds are scarce (Godfray *et al.* 1999). In fact, detailed information will never be available for all of the terrestrial food webs on earth, nor will any complete food web be constructed for a tropical ecosystem. Tritrophic chains are exemplary systems for creating food web metrics that broadly capture interacting species in a community but do not require documenting all the existing interactions. Using plant–herbivore–enemy trophic chains as an example, we recommend that tropical community ecologists utilize a simple metric of diversity in which richness, diversity indices, and rarefaction diversity are calculated with links as the basic unit rather than species. Interactions can include all two-link (herbivore–plant and enemy–herbivore), and three-link (enemy–herbivore–plant) chains found in a reasonable study unit, such as a 100-m^2 plot or a 200-m transect (Fig. 1). The simplest measure is the total number of these interactions per unit area.

This sampling method depends on certain assumptions when analyzing interaction diversity as a response variable in models that compare effects between different habitats, elevations, and latitudes. If one samples a plot or transect for caterpillars, rears them out to yield an adult moth or parasitoid, and then counts up the interactions (Fig. 1), the distribution of unique interaction links can be analyzed using methods applied to traditional species diversity. For such an approach, we make four basic assumptions: (1) interactions are sampled at random, (2) interactions are homogenously distributed within a plot, (3) any distribution of abundance among interactions is possible, and (4) interactions are equally likely to be encountered at all locations compared.

We are currently utilizing this method to document interaction diversity at a number of tropical sites, including Yanayacu Biological Station Ecuador and La Selva Biological Station, Costa Rica, as well as temperate sites in the Sierra Nevada (California), Great Basin (Nevada), Arizona, and Louisiana. Plants and associated lepidopteran larvae and their parasitoids are quantified at all sites in 10-m diam. plots (methods described in Dyer *et al.* 2007). Preliminary analyses of plot data from the Ecuador and Louisiana sites, for which we have sufficient number of plots for initial analyses, indicate that interaction richness and diversity are significantly higher at the Ecuador vs. Louisiana site (for interaction richness, $t = 8.8$, $df = 650$, $P < 0.0001$; Table 1), while species richness per unit area is higher at the Louisiana site. This is consistent with the hypothesis that interaction richness asymptotes more quickly than species richness (Fig. 1G), much like diversity indices asymptote more quickly than richness (Lande 1996). Although unique interactions are likely to be characterized by a lognormal distribution, this distribution should be hyperkurtotic, with a few
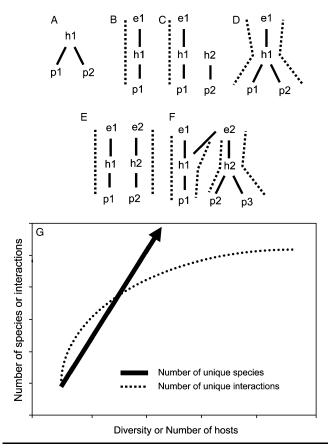
FIGURE 1. Simple examples of interaction diversity in subsamples of communities; interaction richness for each subsample is (A) 2, (B) 3, (C) 4, (D) 5, (E) 6, and (F) 10. Generalist herbivores and enemies in the subsamples are linked to more than one host; specialists are linked to only one host. Solid lines are two-link interactions and dashed lines are three-link interactions; numbers refer to unique species; e = enemy, h = herbivore, and p = plant. (G) Interaction diversity measured using this method should generate an accumulation curve that asymptotes faster than a species accumulation curve, given that interactions are dominated by selected (and typically more generalized) interactions (Bascompte et al. 2003). Many extremely rare interactions exist but are not detected (due to a hyperkurtotic, positively skewed distribution), thus the apparent asymptote. In addition, focusing on particular interactions combined with the fact that tourists are a significant component of any sample of organisms, the number of interactions per plot will usually be lower than the number of species.

common interactions dominating and most other interactions being extremely rare (Bascompte et al. 2003).

Measures of specialization are wrought with pitfalls (Novotny & Basset 2000, Ødegaard 2000, Novotny et al. 2006), but interaction diversity per unit area may be less susceptible to methodological flaws for measuring diet breadth as long as samples are random and well replicated (Fig. 2A). Thus, it is interesting to contemplate how interaction diversity per unit area, as well as beta diversity of interactions, would vary across a gradient from Europe to Papua New Guinea (Novotny et al. 2006) or across the Americas (Dyer et al. 2007; Figs. 2B, C, and E). The beta diversity, or spatial turnover, of species in tropical forests has recently become a focal point

TABLE 1. *Preliminary data comparing tropical (Ecuador) and temperate (Louisiana) interaction diversity in 10-m diam. circular plots. Means are reported ($\pm$ SE).*

	Ecuador	Louisiana
Sample size (number of plots)	429	222
Mean species richness per plot	20.5 (0.8)	20.8 (0.8)
Mean interaction richness per plot	10.2 (0.3)	5.7 (0.2)
Mean interaction diversity (1/D) per plot	5.6 (0.3)	3.3 (0.3)

of analysis in the field of tropical ecology (Condit et al. 2002, Ødegaard 2006, Novotny et al. 2007, Lewinsohn & Roslin 2008). This concept of beta diversity or turnover could be expanded to examine how the diversity of interactions varies over space. Examination of interaction beta diversity could be used to determine whether species interact with the same set of consumers or hosts over their range and how rapidly these interactions undergo spatial turnover. Recent progress has been made by Novotny (2009) in developing a conceptual and analytical framework to quantify how diversity of interactions varies in space using a beta-diversity partitioning approach. In addition to the usefulness of such analyses in understanding patterns of community structure in a spatial context, they could aid in understanding important evolutionary phenomena, such as coevolutionary processes occurring over a geographic mosaic of interactions (Gomulkiewicz et al. 2000, Thompson 2005).

IMPORTANT QUESTIONS FOR INTERACTION DIVERSITY IN THE TROPICS

Biodiversity research has not been focused exclusively on tropical ecosystems, but most of the major theoretical and applied issues in biodiversity research are important for understanding tropical diversity. These issues include: (1) the latitudinal gradient in diversity (reviewed by Rohde 1992, Willig et al. 2003, Arita & Vazquez-Dominguez 2008), (2) neutral theory (Hubbell 2001, Chave 2004, Chave & Norden 2007), (3) diversity–stability relationships (reviewed by McCann 2000, Tilman et al. 2006), (4) biodiversity and ecosystem function (Duffy 2003, Thebault & Loreau 2003, Srivastava & Vellend 2005, Long et al. 2007, Bastian et al. 2008), (5) specialization (reviewed by Irschick et al. 2005, Lewinsohn et al. 2005), (6) latitudinal and elevational range size (Rapoport 1975, Stevens 1992, reviewed by Ribas & Schoereder 2006, Ruggiero & Werenkraut 2007), and (7) effects of climate change on biodiversity (Colwell et al. 2008, Berggren et al. 2009). Hypotheses relevant to these issues have generated a considerable number of empirical and theoretical studies, but reviews of this literature acknowledge that there are substantive questions that remain unresolved for all of these diversity patterns and hypotheses. For example, the latitudinal gradient in diversity, first formally described by Darwin (1859) and Wallace (1878), still generates considerable research without consensus on which mechanisms are most important for generating diversity gradients in any given taxa or communities.
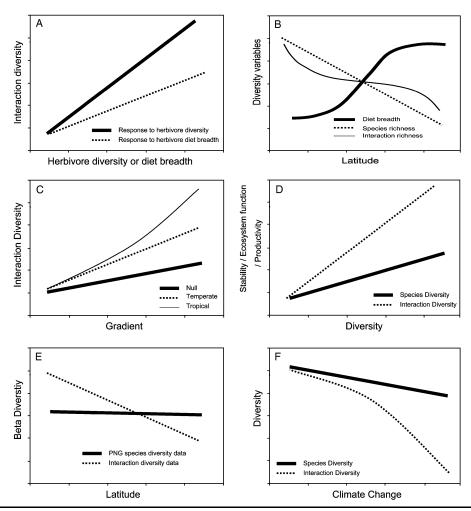
FIGURE 2. Predictions of how interaction diversity should behave in phytophagous insect systems. (A) Species diversity of herbivores increases interaction diversity more than number of hosts per herbivore (*i.e.*, diet breadth). For each extra plant host for an herbivore, only one new interaction is added, whereas for each extra herbivore per host plant, there is at least one new interaction and potentially more (via multiple parasitoids). (B) Interaction richness should reach its lowest levels at high latitudes due to the low species richness, despite appreciable diet breadth. It will increase rapidly with decreasing latitude as species richness increases, but as diet breadth drops the rate of increase will flatten out or even decline. Finally, at some latitude, the increase in species richness will be great enough to result in a strong upswing in interaction diversity, despite the continued increase in specialization. (Diversity of interactions across altitudinal gradients should be similar.) (C) Interaction diversity will vary with environmental gradients (latitudinal, species richness, disturbance, etc.). A null model would predict random assemblages of interactions drawn from the (usually lognormal) distribution of plants, herbivores, and enemies, increasing with diversity. 'Interaction' models would also predict increases in interaction diversity across gradients but the slope will be more pronounced for coevolved species assemblages because of a more kurtotic distribution of interactions that is shifted to the right. (D) Interaction diversity should have a stronger effect on response variables such as stability and ecosystem function since it is a better measure of the mechanisms that create the correlations with diversity. (E) Novotny *et al.* (2007) found that beta diversity was low in a tropical ecosystem, which generates the beta-diversity prediction depicted here. Interaction diversity, which should asymptote more quickly, might be a better metric for assessing beta diversity, which should be greater in the tropics based on a number of factors, including the narrow consumption niches of tropical organisms (Janzen 1974). (F) Effects of climate change on diversity. Interactions are likely to decline at a greater rate than species, given that climate-driven changes in phenologies of plants and herbivores can affect multiple consumers (*e.g.*, Stireman *et al.* 2005).

How is interaction diversity related to the important questions in biodiversity research? For many relationships, such as correlations between biodiversity, stability, and ecosystem function, interaction diversity is a more intuitive variable for understanding mechanistic relationships (Reiss *et al.* 2009). Thus, when Terborgh *et al.* (2001) showed that losing predator–prey interactions led to 'ecological meltdown' in islands, changes in the total number of species did not explain what happened to the island communities. It was clear that the response was due to losing important predator–prey–plant interactions—or a decline in interaction diversity. Stability can be understood in the same way—it is easier to explain or model the consequences of loss of interaction diversity than it is to understand the loss of species diversity (Fig. 2D). Much of the historical and current debate concerning the relationship between

diversity and stability of ecological communities is concerned with the number of trophic links (*i.e.*, connectance) and their relative strength (MacArthur 1955, May 1973, McCann 2000). For example, recent generalized modeling analyses of vast numbers of simulated food webs by Gross *et al.* (2009) have concluded that stability is enhanced by oligophagy in top predators and high diversity of intermediate trophic levels, and it is decreased by high variation in link (interaction) strengths. In addition, it has been argued that diverse weak interactions ('the weak interaction effect'; McCann *et al.* 1998, McCann 2000) and trophic complexity (Jiang *et al.* 2009) both play pivotal roles in community stability. These relationships can readily be explored by examining interaction diversities between component trophic levels, even when complete food-web information is unavailable. Such interaction diversities and associated metrics can be compared among ecological communities or across gradients to make predictions concerning patterns of stability and resilience.

Understanding mechanistic relationships due to interaction diversity is also important for applied issues, such as determining the effects of climate change on biodiversity. Stireman *et al.* (2005) found that parasitoid abundance declines with increasing climatic variability. The mechanism proposed for this connection is related to interaction diversity. Extreme weather events may decrease interaction diversity via disrupting associations between parasitoids and their herbivorous hosts, thus decreasing the number of potential tritrophic interactions. In this case, it was the more specialized hymenopteran parasitoids that were most affected by increased climatic variability, suggesting that parasitoid–host interaction richness, as well as abundance, was reduced. Climate change and climatic variability have also been shown to influence diversity and trophic interactions in other systems, such as vertebrate–insect interactions (Spiller & Schoener 2008, Mazia *et al.* 2009) and invertebrate marine communities (Przeslawski *et al.* 2008). Extending analyses of these effects beyond species diversity and abundances by examining interaction diversity (Fig. 2F) may provide considerable insight into both the community consequences of climate change as well as the mechanisms involved.

Perhaps the most exciting change in biodiversity research for tropical ecology is the explosion of empirical and theoretical advances spurred by the development of the neutral theory (Hubbell 2001, Chave & Norden 2007, Zhou & Zhang 2008, Ellwood *et al.* 2009). Although neutral theory is relevant and useful for studying tropical diversity in theoretical frameworks by providing appropriate null hypotheses, it is primarily focused on single trophic levels. The majority of studies seeking to test if community structure can be explained by purely neutral processes have examined abundance distributions and diversity of plant species without regard to their interactions with consumers (Hubbell 2001, Chave 2004). Indeed, one problem with neutral theory as an explanatory model (rather than just a null model) is that it assumes that interactions among trophic levels are inconsequential in shaping species abundance distributions, despite extensive empirical data to the contrary (*e.g.*, Paine 1969, Terborgh *et al.* 2001). Nevertheless, a similar 'neutral' approach can be used to develop models of interaction diversity based on the richness and abundance of trophically interacting

communities. Such models can be used to assess empirical deviations from expected neutral 'interaction distributions' to understand how community structures differ from neutrality and provide some insight into why they may differ. This general approach of using neutral models to examine species interactions has proven profitable in recent studies on the asymmetry (Vazquez *et al.* 2007) and nestedness (Krishna *et al.* 2008) of mutualistic interactions. There is much room, however, for the development of null models that explain the structure of other types of trophic interactions, other properties of interaction diversity, and higher-order (*e.g.*, tritrophic) interactions.

Finally, the latitudinal gradient in diversity is a robust and fascinating pattern of diversity that may be better understood by examining interactions. Novotny *et al.* (2006) utilized an indirect measure of interaction diversity to address a difficult question related to the diversity gradient: why are there so many species of tropical insects? These authors compared the number of herbivore species collected in standardized samples of tree species in tropical and temperate forests. They found that herbivore richness per tree species did not differ significantly across sites and that dietary specialization of herbivores (relative to the set of host species examined) was also similar for the two sites. Furthermore, they found that beta diversity across the lowlands of Papua New Guinea was relatively low (Novotny *et al.* 2007). Although they concluded that the latitudinal gradient in herbivorous insect diversity can be explained as a simple function of greater host plant richness in the tropics, a similar study indirectly examining interaction diversity across eight New World sites (Dyer *et al.* 2007) demonstrated that Lepidoptera are more specialized in the tropics than at temperate latitudes. Dyer and colleagues argue that between-plant species beta diversity in tropical lepidopteran herbivore communities is greater than in temperate communities, and that this may play an important role in shaping the latitudinal diversity gradient of insects. In both of these alternative views, the basic precept that 'diversity begets diversity' (Janz *et al.* 2006) is implicit; they differ rather in the form of that relationship—whether it is linear or nonlinear and how strongly it is influenced by other factors. More explicit and thorough analyses of interaction diversity across latitudinal gradients could help to determine more precisely how community structure varies latitudinally, how this variation contributes to patterns of species diversity, and help to reconcile these seemingly contradictory patterns (Figs. 2A–E).

CONCLUSIONS

It is clear that multitrophic interactions play key roles in the origin and maintenance of species diversity (*e.g.*, Singer & Stireman 2005), thus it is relevant to utilize a biodiversity metric that quantifies these interactions. Current experiments that manipulate diversity via changing number of species, number of guilds/functional groups, identity of species, or other traditional diversity metrics should be supplemented with experiments that randomly assign different levels of interaction diversity to plots and examine the responses of productivity, mortality, temporal variance of species diversity, and other relevant response variables. Conservation issues

cannot wait for a complete understanding of tropical life histories and community assemblages. Our proposed interaction diversity metric should form a basis for developing more realistic pictures of community structure for comparative purposes applicable to a broad array of ecological, evolutionary, and conservation issues. Marrying natural history, ecology, and conservation through the quantified sampling of interaction diversity is one-way forward to understanding the evolution, maintenance, and preservation of rapidly dwindling biodiversity.

ACKNOWLEDGMENTS

LITERATURE CITED

ALONSO, D., AND A. J. MCKANE. 2004. Sampling Hubbell's neutral theory of biodiversity. Ecol. Lett. 7: 901–910.

ARITA, H. T., AND E. VAZQUEZ-DOMINGUEZ. 2008. The tropics: Cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. Ecol. Lett. 11: 653–663.

BASCOMPTE, J. 2009. Disentangling the web of life. Science 325: 416–419.

BASCOMPTE, J., P. JORDANO, C. J. MELIAN, AND J. M. OLESEN. 2003. The nested assembly of plant–animal mutualistic networks. Proc. Natl. Acad. Sci. 100: 9383–9387.

BASTIAN, M., R. G. PEARSON, AND L. BOYERO. 2008. Effects of diversity loss on ecosystem function across trophic levels and ecosystems: A test in a detritus-based tropical food web. Aust. Ecol. 33: 301–306.

BEGON, M., S. M. SAIT, AND D. J. THOMPSON. 1996. Predator-prey cycles with period shifts between two- and three-species systems. Nature 381: 311–315.

BERGGREN, A., C. BJORKMAN, H. BYLUND, AND M. P. AYRES. 2009. The distribution and abundance of animal populations in a climate of uncertainty. Oikos 118: 1121–1126.

BERSIER, L. F., C. BANASEK-RICHTER, AND M. F. CATTIN. 2002. Quantitative descriptors of food-web matrices. Ecology 83: 2394–2407.

BRANDLE, M., AND R. BRANDL. 2001. Species richness of insects and mites on trees: Expanding southwood. J. Anim. Ecol. 70: 491–504.

BURNS, K. C. 2007. Network properties of an epiphyte metacommunity. J. Ecol. 95: 1142–1151.

BURSLEM, D. F. R. P., M. A. PINARD, AND S. E. HARTLEY. 2005. Biotic interactions in the tropics. Their role in the maintenance of species diversity. Cambridge University Press, Cambridge, UK.

CHAVE, J. 2004. Neutral theory and community ecology. Ecol. Lett. 7: 241–253.

CHAVE, J., AND N. NORDEN. 2007. Changes of species diversity in a simulated fragmented neutral landscape. Ecol. Model. 207: 3–10.

COHEN, J. E., AND F. BRIAND. 1984. Trophic links of community food webs. Proc. Natl. Acad. Sci. USA-Biol. Sci. 81: 4105–4109.

COLWELL, R. K., G. BREHM, C. L. CARDELUS, A. C. GILMAN, AND J. T. LONGINO. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322: 258–261.

COLWELL, R. K., AND J. A. CODDINGTON. 1994. Estimating terrestrial biodiversity through extrapolation. Philos. Trans. R. Soc. Lond., Ser. B 345: 101–118.

CONDIT, R., N. PITMAN, E. G. LEIGH, J. CHAVE, J. TERBORGH, R. B. FOSTER, P. NUNEZ, S. AGUILAR, R. VALENCIA, G. VILLA, H. C. MULLER-LANDAU, E. LOSOS, AND S. P. HUBBELL. 2002. Beta-diversity in tropical forest trees. Science 295: 666–669.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

DARWIN, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, UK.

DAYTON, P. K. 2003. The importance of natural sciences to conservation. Am. Nat. 162: 1–13.

DEL-CLARO, K. 2004. Multitrophic relationships, conditional mutualisms, and the study of interaction biodiversity in tropical savannas. Neotrop. Entomol. 33: 665–672.

DEL-CLARO, K., AND H. M. TOREZAN-SILINGARDI. 2009. Insect–plant interactions: New pathways to a better comprehension of ecological communities in neotropical savannas. Neotrop. Entomol. 38: 159–164.

DEVRIES, P. J., AND T. R. WALLA. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. Biol. J. Linn. Soc. 74: 1–15.

DEVRIES, P. J., T. R. WALLA, AND H. F. GREENEY. 1999. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. Biol. J. Linn. Soc. 68: 333–353.

DUFFY, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecol. Lett. 6: 680–687.

DYER, L. A. 2008. The ecology of tri-trophic interactions in the tropics. In W. P. Carson and S. A. Schnitzer (Eds.). Tropical forest community ecology, pp. 275–293. Blackwell Publishing, Oxford, UK.

DYER, L. A., M. S. SINGER, J. T. LILL, J. O. STIREMAN, G. L. GENTRY, R. J. MARQUIS, R. E. RICKLEFS, H. F. GREENEY, D. L. WAGNER, H. C. MORAIS, I. R. DINIZ, T. A. KURSAR, AND P. D. COLEY. 2007. Host specificity of Lepidoptera in tropical and temperate forests. Nature 448: 696–699.

DYER, L. A., AND J. O. STIREMAN. 2003. Community-wide trophic cascades and other indirect interactions in an agricultural community. Basic Appl. Ecol. 4: 423–432.

EHRLICH, P. R., AND P. H. RAVEN. 1964. Butterflies and plants: A study in coevolution. Evolution 18: 568–608.

ELLWOOD, M., A. MANICA, AND W. FOSTER. 2009. Stochastic and deterministic processes jointly structure tropical arthropod communities. Ecol. Lett. 12: 277–284.

FORTEY, R. 2008. Dry storeroom no. 1: The secret life of the natural history museum. Alfred A. Knopf, New York, New York.

FUTUYMA, D. J. 1998. Wherefore and wither the naturalist? Am. Nat. 151: 1–6.

GENTRY, A. H. 1982. Patterns of neotropical plant-species diversity. Evol. Biol. 15: 1–85.

GODFRAY, H. C. J., O. T. LEWIS, AND J. MEMMOTT. 1999. Investigating insect diversity in the tropics. Philos. Trans. R. Soc. Lond., Ser. B 354: 1811–1824.

GOMULKIEWICZ, R., J. N. THOMPSON, R. D. HOLT, S. L. NUISMER, AND M. E. HOCHBERG. 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. Am. Nat. 156: 156–174.

GOTELLI, N. J., AND R. K. COLWELL. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379–391.

GROSS, T., L. RUDOLF, S. A. LEVIN, AND U. DIECKMANN. 2009. Generalized models reveal stabilizing factors in food webs. Science 325: 747–750.

HAIRSTON, N. G., F. E SMITH, AND L. B. SLOBODKIN. 1960. Community structure, population control, and competition. Am. Nat. 94: 421–424.

HECK, K. L., G. VAN BELLE, AND D. SIMBERLOFF. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology 56: 1459–1461.

HUBBELL, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299–1309.

HUBBELL, S. P. 1999. The maintenance of diversity in a neotropical tree community: Conceptual issues, current evidence, and the challenges ahead In F. Dallmeier and J. A. Comiskey (Eds.). Forest biodiveristy, research, monitoring and modeling. Man and the Biosphere Series, Vol. 20, pp. 17–44. UNESCO and Parthenon Publishing, Paris, France.

HUBBELL, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? Am. Nat. 93: 145–159.

IRSCHICK, D., L. A. DYER, AND T. W. SHERRY. 2005. Phylogenetic methodologies for studying specialization. Oikos 110: 404–408.

JANZ, N., S. NYLIN, AND N. WAHLBERG. 2006. Diversity begets diversity: Host expansions and the diversification of plant-feeding insects. BMC Evol. Biol. 6: 4.

JANZEN, D. H. 1974. The deflowering of central America. Nat. Hist. 83: 49–53.

JANZEN, D. H., M. HAJIBABAEI, J. M. BURNS, W. HALLWACHS, E. REMIGIO, AND P. D. N. HEBERT. 2005. Wedding biodiversity inventory of a large and complex Lepidoptera fauna with DNA barcoding. Philos. Trans. R. Soc. Lond., Ser. B 360: 1835–1845.

JIANG, L., H. JOSHI, AND S. PATEL. 2009. Predation alters relationships between biodiversity and temporal stability. Am. Nat. 173: 389–399.

JOST, L. 2006. Entropy and diversity. Oikos 133: 363–375.

JOST, L. 2007. Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439.

KELLY, C. K., AND T. R. E. SOUTHWOOD. 1999. Species richness and resource availability: A phylogenetic analysis of insects associated with trees. Proc. Natl. Acad. Sci. USA 96: 8013–8016.

KREFT, H., AND W. JETZ. 2007. Global patterns and determinants of vascular plant diversity. Proc. Natl. Acad. Sci. 104: 5925–5930.

KRISHNA, A., P. R. GUIMARAES, P. JORDANO, AND J. BASCOMPTE. 2008. A neutral-niche theory of nestedness in mutualistic networks. Oikos 117: 1609–1618.

LANDE, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 76: 5–13.

LAWTON, J. H., AND S. MCNEILL. 1979. Between the devil and the deep blue sea: On the problem of being a herbivore. Symp. Br. Ecol. Soc. 20: 223–244.

LEWINSOHN, T. M., V. NOVOTNY, AND Y. BASSET. 2005. Insects on plants: Diversity of herbivore assemblages revisited. Annu. Rev. Ecol. Evol. Syst. 36: 597–620.

LEWINSOHN, T. M., AND T. ROSLIN. 2008. Four ways towards tropical herbivore megadiversity. Ecol. Lett. 11: 398–416.

LEWIS, O. J., J. MEMMOTT, J. LASALLE, C. H. C. LYAL, C. WHITEFOORD, AND H. C. J. GODFRAY. 2002. Structure of a diverse tropical-forest insect-parasitoid community. J. Anim. Ecol. 71: 855–873.

LONG, Z. T., J. F. BRUNO, AND J. E. DUFFY. 2007. Biodiversity mediates productivity through different mechanisms at adjacent trophic levels. Ecology 88: 2821–2829.

LONGINO, J. T., AND R. K. COLWELL. 1997. Biodiversity assessment using structured inventory: Capturing the ant fauna of a tropical rain forest. Ecol. Appl. 7: 1263–1277.

MACARTHUR, R. H. 1955. Fluctuations of animal populations, and a measure of community stability. Ecology 36: 533–536.

MAGURRAN, A. E. 2004. Measuring biological diversity. Blackwell, Oxford, UK.

MAY, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey.

MAZIA, C. N., E. J. CHANETON, T. KITZBERGER, AND L. A. GARIBALDI. 2009. Variable strength of top-down effects in nothofagus forests: Bird predation and insect herbivory during an ENSO event. Aust. Ecol. 34: 359–367.

MCCANN, K., A. HASTINGS, AND G. R. HUXEL. 1998. Weak trophic interactions and the balance of nature. Nature 395: 794–798.

MCCANN, K. S. 2000. The diversity-stability debate. Nature 405: 228–233.

MEMMOTT, J., AND H. C. J. GODFRAY. 1994. The use and construction of parasitoid webs. Hawkins, B. A. and W. Sheehan (Eds.). Parasitoid community ecology, pp. 300–318. Oxford University Press, New York.

MEMMOTT, J., N. D. MARTINEZ, AND J. E. COHEN. 2000. Predators, parasitoids and pathogens: Species richness, trophic generality and body sizes in a natural food web. J. Anim. Ecol. 69: 1–15.

MITTELBACH, G. G., D. W. SCHEMSKE, H. V. CORNELL, A. P. ALLEN, J. M. BROWN, M. B. BUSH, S. P. HARRISON, A. H. HURLBERT, N. KNOWLTON, H. A. LESSIOS, C. M. MCCAIN, A. R. MCCUNE, L. A. MCDADE, M. A. MCPEEK, T. J. NEAR, T. D. PRICE, R. E. RICKLEFS, K. ROY, D. F. SAX, D. SCHLUTER, J. M. SOBEL, AND M. TURELLI. 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. Ecol. Lett. 10: 315–331.

NOVOTNY, V. 2009. Beta diversity of plant-insect food webs in tropical forests: A conceptual framework. Insect Conserv. Diversity 2: 5–9.

NOVOTNY, V., AND Y. BASSET. 2000. Rare species in communities of tropical insect herbivores: Pondering the mystery of singletons. Oikos 89: 564–572.

NOVOTNY, V., AND Y. BASSET. 2005. Review—Host specificity of insect herbivores in tropical forests. Proc. R. Soc. B 272: 1083–1090.

NOVOTNY, V., P. DROZD, S. E. MILLER, M. KULFAN, M. JANDA, Y. BASSET, AND G. D. WEIBLEN. 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science 313: 1115–1118.

NOVOTNY, V., S. E. MILLER, J. HULCR, R. A. I. DREW, Y. BASSET, M. JANDA, G. P. SETLIFF, K. DARROW, A. J. A. STEWART, J. AUGA, B. ISUA, K. MOLEM, M. MANUMBOR, E. TAMTIAI, M. MOGIA, AND G. D. WEIBLEN. 2007. Low beta diversity of herbivorous insects in tropical forests. Nature 448: 692–698.

ØDEGAARD, F. 2000. How many species of arthropods? Erwin's estimate revised. Biol. J. Linn. Soc. 71: 583–597.

ØDEGAARD, F. 2006. Host specificity, alpha- and beta-diversity of phytophagous beetles in two tropical forests in Panama. Biodiversity Conserv. 15: 83–105.

OHGUSHI, T., T. P. CRAIG, AND P. W. PRICE. 2007. Ecological communities. Cambridge University Press, Cambridge, UK.

OLLERTON, J., AND L. CRANMER. 2002. Latitudinal trends in plant–pollinator interactions: Are tropical plants more specialized? Oikos 98: 340–350.

OLLERTON, J. D., D. G. MCCOLLIN, FAUTIN, AND G. R. ALLEN. 2007. Finding NEMO: Nestedness engendered by mutualistic organization in anemonefish and their hosts. Proc. R. Soc. B-Biol. Sci. 274: 591–598.

PAINE, R. T. 1969. A note on trophic complexity and community stability. Am. Nat. 103: 91–93.

PEARSON, C. V., T. J. MASSAD, AND L. A. DYER. 2008. Diversity cascades in alfalfa fields: From plant quality to agroecosystem diversity. Environ. Entomol. 37: 947–955.

PRICE, P. W. 2002. Resource-driven terrestrial interaction webs. Ecol. Res. 17: 241–247.

PRICE, P. W., E. E. BOUTON, P. GROSS, B. A. MCPHERON, J. N. THOMPSON, AND A. E. WEISS. 1980. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. Annu. Rev. Ecol. Syst. 11: 41–65.

PRZESLAWSKI, R., S. AHYONG, M. BYRNE, G. WÖRHEIDE, AND P. HUTCHINGS. 2008. Beyond corals and fish: The effects of climate change on noncoral benthic invertebrates of tropical reefs. Global Change Biol. 14: 2773–2795.

RAPOPORT, E. H. 1975. Areografia: estrategias geograficas de las especies. Fondo De Cultura Economica.

REISS, J., J. R. BRIDLE, J. M. MONYOYA, AND G. WOODWARD. 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends Ecol. Evol. 24: 505–514.

REZENDE, E. L., J. E. LAVABRE, P. R. JR. GUIMARES, P. JORDANO, AND J. BAS-COMPTE. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. Nature 448: 925–928.

RIBAS, C. R., AND J. H. SCHOEREDER. 2006. Is the Rapoport effect widespread? Null models revisited. Global Ecol. Biogeogr. 15: 614–624.

ROHDE, K. 1992. Latitudinal gradients in species diversity: The search for the primary cause. Oikos 65: 514–527.

RUGGIERO, A., AND V. WERENKRAUT. 2007. One-dimensional analyses of rapoport's rule reviewed through meta-analysis. Global Ecol. Biogeogr. 16: 401–414.

SINGER, M. S., AND J. O. III. STIREMAN. 2005. The tri-trophic niche concept and adaptive radiation of phytophagous insects. Ecol. Lett. 8: 1247–1255.

SINGER, T. R. E, V. C. MORAN, AND C. E. J. KENNEDY. 1982. The richness, abundance and biomass of the arthropod communities on trees. J. Anim. Ecol. 51: 635–649.

SLATER, J. V. P. 2000. Advances in the study of behavior, Vol. 29. Academic Press, San Diego, California.

SPILLER, D. A., AND T. W. SCHOENER. 2008. Climatic control of trophic interaction strength: The effect of lizards on spiders. Oecologia 154: 763–771.

SRIVASTAVA, D. S., AND M. VELLEND. 2005. Biodiversity-ecosystem function research: Is it relevant to conservation? Annu. Rev. Ecol. Evol. Syst. 36: 267–294.

STEVENS, G. C. 1992. The elevational gradient in altitudinal range—an extension of rapoport latitudinal rule to altitude. Am. Nat. 140: 893–911.

STIREMAN, J. O. III, L. A. DYER, D. H. JANZEN, M. S. SINGER, J. T. LI, R. J. MARQUIS, R. E. RICKLEFS, G. L. GENTRY, W. HALLWACHS, P. D. COLEY, J. A. BARONE, H. F. GREENEY, H. CONNAHS, P. BARBOSA, H. C. MORAIS, AND I. R. DINIZ. 2005. Climatic unpredictability and parasitism of caterpillars: Implications of global warming. Proc. Natl. Acad. Sci. 102: 17384–17387.

STORK, N. E. 2008. Arthropod faunal similarity of bornean rain forest trees. Ecol. Entomol. 12: 219–226.

TERBORGH, J., L. LOPEZ, P. NUNEZ, M. RAO, G. SHAHABUDDIN, G. ORIHUELA, M. RIVEROS, R. ASCANIO, G. H. ADLER, T. D. LAMBERT, AND L. BALBAS. 2001. Ecological meltdown in predator-free forest fragments. Science 294: 1923–1926.

TERBORGH, J., S. K. ROBINSON, T. A. PARKER, C. A. MUNN, AND N. PIERPONT. 1990. Structure and organization of an Amazonian forest bird community. Ecol. Monogr. 60: 213–238.

THEBAULT, E., AND M. LOREAU. 2003. Food-web constraints on biodiversity-ecosystem functioning relationships. Proc. Natl. Acad. Sci. 100: 14949–14954.

THOMPSON, J. N. 1996. Evolutionary ecology and the conservation of biodiversity. Trends Ecol. Evol. 11: 300–303.

THOMPSON, J. N. 1997. Conserving interaction biodiversity. In S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens (Eds.). The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity, pp. 285–293. Chapman & Hall, New York, New York.

THOMPSON, J. N. 2005. The geographic mosaic of coevolution. University of Chicago Press, Chicago, Illinois.

TILMAN, D., P. B. REICH, AND J. M. H. KNOPS. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441: 629–632.

TYLIANAKIS, J. M., T. TSCHARNTKE, AND O. T. LEWIS. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. Nature 445: 202–205.

VAZQUEZ, D., C. J. MELIAN, N. M. WILLIAMS, N. BLUTHGEN, B. R. KRASNOV, AND R. POULIN. 2007. Species abundance and asymmetric interaction strength in ecological networks. Oikos 116: 1120–1127.

WAKE, D. B. 1970. Abundance and diversity of tropical salamanders. Am. Nat. 104: 211–213.

WALLACE, A. R. 1878. Tropical nature and other essays. Macmillan, New York, New York.

WILLIG, M. R., D. M. KAUFMAN, AND R. D. STEVENS. 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annu. Rev. Ecol. Evol. Syst. 34: 273–309.

ZHOU, S., AND D. ZHANG. 2008. A nearly neutral model of biodiversity. Ecology 89: 248–258.