NEUTRAL THEORY AND THE EVOLUTION OF ECOLOGICAL EQUIVALENCE

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Abstract. Since the publication of the unified neutral theory in 2001, there has been much discussion of the theory, pro and con. The hypothesis of ecological equivalence is the fundamental yet controversial idea behind neutral theory. Assuming trophically similar species are demographically alike (symmetric) on a per capita basis is only an approximation, but it is equivalent to asking: How many of the patterns of ecological communities are the result of species similarities, rather than of species differences? The strategy behind neutral theory is to see how far one can get with the simplification of assuming ecological equivalence before introducing more complexity. In another paper, I review the empirical evidence that led me to hypothesize ecological equivalence among many of the tree species in the species-rich tropical forest on Barro Colorado Island (BCI). In this paper, I develop a simple model for the evolution of ecological equivalence or niche convergence, using as an example evolution of the suite of life history traits characteristic of shade tolerant tropical tree species. Although the model is simple, the conclusions from it seem likely to be robust. I conclude that ecological equivalence for resource use are likely to evolve easily and often, especially in species-rich communities that are dispersal and recruitment limited. In the case of the BCI forest, tree species are strongly dispersal- and recruitment-limited, not only because of restricted seed dispersal, but also because of low recruitment success due to heavy losses of the seedling stages to predators and pathogens and other abiotic stresses such as drought. These factors and the high species richness of the community strongly reduce the potential for competitive exclusion of functionally equivalent or nearly equivalent species.

Key words: Barro Colorado Island; ecological equivalence; neutral theory; niche differentiation; shade tolerance; tropical tree communities.

INTRODUCTION

The unified neutral theory of biodiversity and biogeography (UNT) asks the following question (Hubbell 2001): What community-level patterns result from the simplifying assumption that all species in a community exhibit the same demographic stochasticity (ecological drift) on a per capita basis, and ecological drift is the only process occurring besides random dispersal and speciation? How similar are the community-level patterns predicted by the UNT on local to biogeographic scales to those observed in nature? The idea that all populations and communities are subject to demographic stochasticity is not particularly challenging for most ecologists. However, the assumption that trophically similar species in communities might be ecologically equivalent, at least to a first approximation, is more difficult to accept. Perhaps it becomes a bit more palatable when it is realized that the assumption is equivalent to asking what communities assembly would be like if species all strictly followed the mean. The value

of posing this question rigorously is that we obtain a quantitative null hypothesis against which to test when, to what extent, and for which species demographic differences among species are necessary to explain observed community patterns. The UNT is a non traditional approach because it does not postulate differences among species as the point of departure, but only adds them when necessary to explain the observed data.

Bell (2001) observed that there are two possibilities, a strong and a weak version of neutral theory. In the strong version, the UNT captures the true underlying mechanisms, whereas in the weak version, the theory is capable of generating patterns that resemble empirical patterns, without acknowledging that it correctly identifies the underlying mechanisms responsible for generating them. A number of papers critical of current neutral theory have made the point that neutral patterns do not necessarily imply underlying neutral processes (e.g., Chave et al. 2002, McGill 2003, Sugihara et al 2003, Tilman 2004, Purves and Pacala 2005). I agree, but obtaining acceptable fits from neutral models shifts the burden of proof to those who would assert that more complex theory is required to explain nature and with what level of detail and generality. In my opinion, the deepest puzzle raised by neutral theory is why it does as
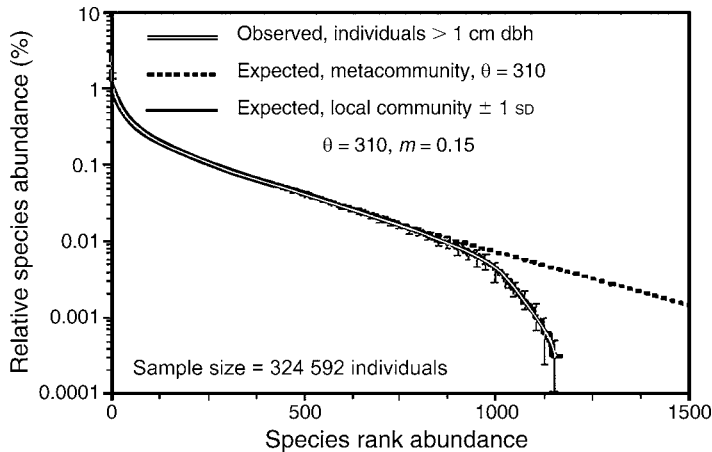
FIG. 1. The fit of the unified neutral theory of biodiversity and biogeography (UNT) to the dominance–diversity curve for the tropical tree community in Lambir Hills National Park, Sarawak, Borneo. The dotted line extending diagonally down to the right is the best-fit metacommunity curve for θ = 310, assuming no dispersal limitation (probability of immigration m = 1). The parameter θ is the fundamental biodiversity number of neutral theory, which is a composite of the speciation rate and the size of the metacommunity source area. The distribution of relative tree species abundance for the 52-ha plot was best fit with θ = 310 and m = 0.15. The heavy solid line is the observed dominance–diversity curve. The agreement between the fitted line and the observed line for 1197 species is excellent (r^2 = 0.996). Error bars represent ± SE. Note the log scale of the y-axis.

well as it does, despite its radical assumptions. For example, consider the fit of the UNT to the relative abundance data for the tree community in the 52-ha plot in Lambir Hills National Park, Sarawak (Fig. 1), which has an r^2 of 0.996 for over 1100 tree species. A similar level of fitting precision is obtained with a single free parameter for many of the other tree communities in the pantropical network of large forest plots managed by the Center for Tropical Forest Science (CTFS) (Volkov et al. 2005). This precision cannot be easily explained away, even if qualitatively similar-shaped curves can be produced by niche theory (Chave et al 2002, Tilman 2004). In my entire academic career, I have rarely if ever obtained such high quality fits. Even in its weak manifestation, why should the UNT ever get an acceptable answer—even approximately—for the wrong reason? I believe that the theory simply could not do so unless it accurately captures some fundamental statistical-mechanical characteristic of the behavior of biodiversity in aggregate and at large spatial and temporal scales.

Whatever the fate of the current versions of neutral theory, the fundamental ideas underlying the UNT are likely to have long-term staying power in community ecology, just as parallel neutral ideas have had in population genetics. Current neutral theory in community ecology is still in its infancy and very much a work in progress (Nee and Stone 2003, Chave 2004), and there are a number of interesting comparisons with neutral theory in population genetics that remain to be drawn (Hu et al. 2006). Improvements and generalizations of the theory are also in development that increase its realism and analytical power (Houchmandzadeh and Vallade 2003, Vallade and Houchmandzadeh 2003, Volkov et al. 2003, McKane et al. 2004, Etienne and Olff 2004, Volkov et al. 2005). In the new framework, the stochastic equations of population growth are more analytically tractable and general than the approach taken in my book (Hubbell 2001). The new framework

will be especially useful for developing mixed models that incorporate both stochastic and deterministic processes—models presumably closer to the way nature really works. Such mixed models are already beginning to appear (e.g., Tilman 2004), but much work still needs to be done.

At the very least, neutral theory will remain a rich source of quantitative null hypotheses about the dynamics of ecological communities across multiple spatial and temporal scales. Perhaps the UNT's most significant and lasting contribution will be its explicit incorporation of linkages between the ecological processes of community assembly on local scales and evolutionary and biogeographic processes on large scales, such as speciation and phylogeography. I share Ricklefs' view (2004) that explaining patterns of biodiversity, even on quite local scales, requires a far deeper understanding of the large-scale biogeographic history of biotas. However, I am more optimistic than is Ricklefs that statistical mechanical approaches to characterizing and understanding these large-scale patterns will prove to be a predictive and powerful theoretical tool, perhaps more so than the small-scale reductionist approaches that currently pervade the field of ecology.

My ideas about neutral theory and the ecological equivalence of trophically similar species have developed over a quarter century from my research and that of my colleagues on the tropical moist forest on Barro Colorado Island (BCI). Panama (Hubbell and Foster 1983). Although the evidence on these questions is mostly nonexperimental, it is derived from a long-term observational study of spatial and temporal patterns in the dynamics of biomass and diversity in the BCI plot, and many hypotheses are simply not consistent with observed patterns. Moreover, since we began the study, new statistical methods have been developed for spatial processes that allow us to incorporate the spatial autocorrelation of demographic processes directly into

the models (Hubbell et al. 1999, Ahumada et al. 2004, Uriarte et al. 2004, 2005), along with improved methods for model comparisons. The data set also gives great analytical power because of its enormous size. Between 213 000 and 242 000 (depending on the census) free-standing woody plants with a stem diameter of 1 cm at breast height (dbh) of 300+ species have been tagged, measured, identified, and mapped. Since 1980, we have recensused the plot at 5-yr intervals, to record the growth, survival, and recruitment of every individual plant. The BCI plot is the flagship plot of the CTFS network of large forest plots; because the BCI plot is the oldest and best known, I restrict myself to the BCI findings.

There is considerable evidence for niche differentiation in the BCI tree community when one looks across all species in the community (Hubbell and Foster 1986b). This said, however, a majority of BCI tree species, particularly shade tolerant species, are not at all clearly niche differentiated, and resource-based niche theory has difficulty explaining the plethora of such species (Hubbell 2005a). The dominant axis of differentiation affecting vital rates is along a single, relatively narrow life history manifold, reflecting the well known tradeoff between good-competitor, shade-stress tolerat-ers and good colonizer, high-light demanding pioneer species. The trade-offs manifested by this relationship are not easily embodied in neutral theory, although I made an argument for how this might be reconciled with neutrality in my book (cf. Hubbell 2001: Chapter 10). But what about the demographically similar shade-tolerant species, which constitute more than three quarters of the BCI tree species?

It is immediately obvious that species are not uniformly distributed along this life history manifold, but that most species are concentrated at the shade-tolerant end. Growth and survival are parameters summarizing key demographic responses to light as a resource. If BCI tree species partition light as a resource (e.g., Ricklefs 1977), then these data are challenging because one must somehow explain why low-light conditions are more finely partitioned than high-light conditions (Hubbell 2005a). In contrast, recent models of limiting similarity predict relatively uniform spacing of species in resource space (Tilman 2004). The term niche partitioning is also problematic and unfortunate because it already prejudges species differences to be due to character displacement from interspecific competition.

I believe there is a much more parsimonious hypothesis for the large number and demographic similarity of shade-tolerant species. The hypothesis is simply that shady habitats have been much more abundant than sunny ones over the evolutionary history of these species, and therefore most species have evolved life histories adapted for survival and growth in the shade, irrespective of how many other species have taken the same evolutionary path. This hypothesis requires an explanation for how such ecologically equivalent species can coexist.

COEXISTENCE AND THE HYPOTHESIS OF ECOLOGICAL EQUIVALENCE

The hypothesis of ecological equivalence or functional redundancy is the cornerstone of neutral theory. I present a simple argument here for why I expect that ecological equivalence can evolve easily and naturally, and should be especially commonplace in species-rich communities of strongly dispersal- and recruitment-limited species, such as sessile plants. Zhang and Lin (1997) claimed that coexistence among functionally equivalent species is a fragile result, namely, that the long-term non-equilibrium coexistence of such species depends on perfect equality. However, this conclusion is not generally correct in spatial ecology under dispersal and recruitment limitation (Hurtt and Pacala 1995, Hubbell 2001).

Ecological equivalence is not a particularly new idea (Hubbell 1979, Goldberg and Werner 1983, Shmida and Ellner 1984), and it is the foundation for ideas about functional groups in ecosystem science (Hubbell 2005a). Loreau (2004) has challenged the importance of ecolog-ical equivalence in ecology. In some plant communities, there is some evidence that functional diversity promotes productivity (biomass) and stability (persistence of a set of species) (Kinzig et al. 2002, Loreau et al. 2002, and references therein). However, the weight of evidence is still equivocal, in my opinion, and the proportion of variance explained by functional diversity is generally fairly small (Naeem and Wright 2003, Hooper and Dukes 2004). I know of no ecologist who seriously questions that species differences promote coexistence, which logically implies some stabilizing effects at the commun-ity level (Chesson 1991, Tilman and Pacala 1993, Kneitel and Chase 2004). However, there is much less agreement on which differences are actually important to coex-istence, or even whether species differences are indeed essential for coexistence. The uncritical acceptance of any and all species differences as ipso facto evidence for niche differentiation is still all too common in ecology. It must also be demonstrated that these differences have emergent effects at the community level, such as patterns of species composition and relative species abundance. As far as the UNT is concerned, species differences that do not differentiate their vital rates on a per capita basis are irrelevant.

An equally problematic issue concerns the concept of coexistence itself, particularly in spatial ecology. Over the last decade, ecologists have discovered that including space explicitly in theoretical models of communities changes virtually everything (Tilman and Kareiva 2000). In the classical niche-assembly theory based on Lokta-Volterra equations, identical species cannot stably coexist (Loreau 2004, Hubbell 2005a). However, in spatial ecology, the competitive exclusion principle is considerably weakened if there is dispersal limitation (Hubbell 2005b). Tilman (1994) showed in a nonspatial model that, if species exhibited a strict transitive tradeoff between dispersal ability and competitive ability (site

tenacity), then in principle any number of competitors could coexist. Shortly thereafter, however, in a spatially explicit model, Hurtt and Pacala (1995) showed that, even in the absence of a competition-colonization tradeoff, arbitrarily large numbers of species could coexist for indefinite periods if they were sufficiently dispersal and recruitment limited. In the case of sessile seed-bearing plants, dispersal limitation is defined as the failure of a species to disperse seeds to all sites suitable for their germination, survival, and growth, and recruitment limitation is the failure to recruit seedlings, and ultimately reproductive adults, in all such sites. Under dispersal limitation, many sites are won by default by an inferior competitor because the best competitor for the site did not disperse or recruit to the site. Although the mathematical equilibrium is still competitive exclusion, the times to reach competitive exclusion of inferior competitors become essentially indefinitely delayed (hundreds of thousands of generations or longer) under ecologically reasonable dispersal and recruitment limitation, times commensurate with evolutionary timescales. Exclusion takes so long, in fact, that under the UNT, a very slow rate of speciation is all that is required to balance species extinction on regional scales. This conclusion arises from a theorem about the stochastic steady-state distribution of relative species abundance that arises in the metacommunity at the speciation-extinction equilibrium (Hubbell 2001).

EVOLUTION OF FUNCTIONAL EQUIVALENCE IN A SIMPLE MODEL COMMUNITY

Hurtt and Pacala (1995) did not examine the consequences of dispersal limitation for the evolution of niches in their model communities, however. The evolutionary implications of dispersal limitation should be profound because dispersal limitation, when sufficiently strong, can largely, or even completely, decouple competition from controlling the assembly of ecological communities. Persistent dispersal limitation over evolutionary time means that functionally equivalent species should be able to evolve, converging on similar life history strategies adapted to the most frequently encountered environments. These converging species should coexist for arbitrarily long time periods, and not be subject to competitive exclusion by other species evolving under the same selective regime. In such cases, the limits to local species richness in functional groups or communities, subject to a zero-sum rule in a defined area (Hubbell 2001), should be set by the balance between the rate of species loss as more species are added (reducing mean population size and making each species more prone to local extinction through demographic stochasticity), and the rate of re-immigration from the regional source pool.

Nearly 20 years ago, Robin Foster and I suggested that diffuse coevolution in species-rich communities might result in niche convergence toward generalist strategies rather than divergence to specialist strategies

(Hubbell and Foster 1986a). Our idea was an elaboration of an earlier suggestion made by Connell (1980). In species-rich communities, different individuals of a given species are often exposed to very different biotic neighborhoods. In the BCI forest, for example, there are an average of 14 different tree species among the 20 nearest neighbors of a given tree. Two individuals of the same species share an average of only four tree species in common among their 20 nearest neighbors (Hubbell and Foster 1986a). We argued that these different biotic neighborhoods in species-rich communities would not drive directional selection in any consistent direction for niche differentiation (character displacement). Instead, we expected species to converge on similar generalist life history strategies adapted to the long-term temporal and spatial average of the environments encountered over their evolutionary life spans.

We can capture this idea in a simple cartoon in which the direction of selection experienced by the locally dispersed offspring of each reproductive individual is represented by a small vector (Fig. 2). The top panel is a simple community of just two species, a community in which each species encounters the other on a chronic basis through evolutionary time. In this case, there is a strong and consistent trend in the direction of selection on progeny of each species. However, in the species-rich community (bottom panel), there is no consistency in the direction of selection within or between species, changing as a function of local biotic neighborhood both spatially and temporally. This directional inconsistency in selection from one individual to the next is different from, and in addition to, the dilution in the strength of pair-wise competition between species that will accompany increases in community species richness. Thus, selection for directional character displacement becomes ever weaker between pairs of any two species as species are added.

When we published our hypothesis of diffuse coevolution of functionally similar species (Hubbell and Foster 1986a), the importance of dispersal limitation was not yet apparent. Also our idea was presented only in a verbal model, and therefore it still remained to be shown that ecologically equivalent species could indeed evolve and persist in model communities. The details of this model will be published in a paper devoted to fully to its findings, but several important conclusions can be highlighted here. I adopted Hurtt and Pacala's (1995) framework but added genetics. With no loss of spatial generality, construct the model community as a one-dimensional circle (no edges) with a specified number of sites or cells, each occupied by a single adult individual of one of the species in the community. As in Hurtt and Pacala, there is a best competitor for each site. Unlike Hurtt and Pacala, however, the competitive ability for sites evolves and is controlled by a metric trait. Each individual of each species has a genotypic value for this metric trait, controlled by a set of genes of small additive effect. In the numerical experiments reported here, I used a 20-locus, two-allele model, each allele of which
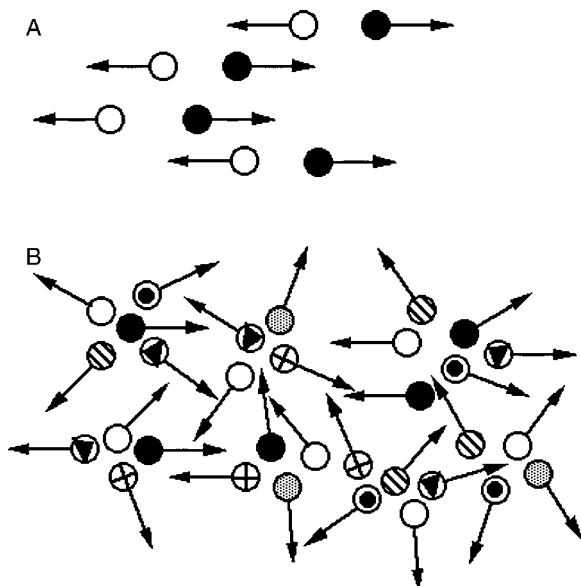
FIG. 2. Cartoon representing diffuse coevolution of species in (A) a species-poor community and (B) a species-rich community. Each symbol is an individual, and different symbol types represent different species. Character displacement evolves in the simple community because pairwise species encounters are chronic and predictable (A), but does not evolve, or evolves much more slowly, in the complex community due to low pairwise encounter frequencies between any two species (B).

has a value of either 0 or 1. The range of possible genotypes for this metric trait is 0 to 40 for an individual (the sum of the allele values at all 20 loci). All loci independently assort. For simplicity, I assumed that there is a one-to-one match between genotype and phenotype. This assumption maximizes the rate of response to selection; reducing the heritability simply slows the response, but the equilibrium outcomes are unaffected. In the version of the model discussed here, there is a single metric trait; in the fuller discussion of the model, I include multiple traits, which opens the possibility for tradeoffs among traits to evolve.

For the sake of discussion, suppose we are considering a tree community and the metric trait is a proxy for phenotypic position along the dominant axis of life history differentiation, the shade-tolerant to shade-intolerant life history manifold. Further suppose that each cell of the community has a characteristic light environment, and let the best competitor for that light environment be the individual that has the closest matching genotype. So, in this example, there are 41 possible light environments (0–40), and there are 41 possible best (matching) quantitative states of the metric character (0–40). Let relative fitness for a given light environment be linearly related to the difference between the genotypic score and the light environment, such that an individual with a smaller difference has the higher fitness, irrespective of species.

In the numerical experiments reported here, the size of the community was 1000, occupied by 10 species. For initial conditions (except in experiment 2), I randomly populated the sites in the community with equally abundant species, whose initial genotype were identically distributed random binomial distributions with equally probable alleles. As in Hurtt and Pacala, I slowed competitive exclusion to a near standstill by imposing strong dispersal and recruitment limitation. In the model, offspring dispersed random-uniformly over a distance of five cells in either direction from the natal site. Mating distance (pollen movement) was limited as well (nearest conspecific within five cells), and there was a constant fecundity resulting from each mating (set to 10 in these experiments). If no conspecific was present within a distance of five cells, then the tree selfed with recombination. I replaced each death by the offspring having the most closely matched genotype to the environmental state of the site (the best competitor among all offspring that reached the site regardless of species).

Here, I highlight the results of three replicated numerical experiments with the model to illustrate my main points. In the first experiment, light environments were "fine grained" sensu Levins (1968) and all species were randomly distributed across all light environments. In the second experiment, light environments were "coarse grained," and species were clustered with exposure only to a limited range of light environments. In the third experiment, light environments were again "coarse grained," but species nevertheless had exposure to the full range of light environments. It should be noted that "light environment" is a simplified representative device for modeling a complex of selective environments. Greater model complexity and realism will need to be added in later versions of the model. However, I expect that the main qualitative conclusions from the simple model will remain intact even after greater realism is added.

The first experiment explored the possibility of convergent trait evolution among the set of 10 species. The selective environment consisted of light environment values sampled from a beta distribution [$\beta(\nu, \omega) = \beta(2,10)$]. These parameters produce a beta distribution with most of the probability at low values of the beta variate. I chose this distribution to represent the frequency distribution of light levels in the understory of a closed-canopy forest, most of which will be low and distributed is in a left-skewed fashion. In the first experiment, there was no spatial autocorrelation of the light environments apart from that produced by a random draw of the beta distribution. This meant that in experiment 1, the variation in the light environment was fine grained with respect to the distribution of each species.

Now I let the dispersal-limited species evolve. What happened? All species rapidly converged on genotypes for the most prevalent light conditions in the forest, namely, shade conditions (Fig. 3). After just 20
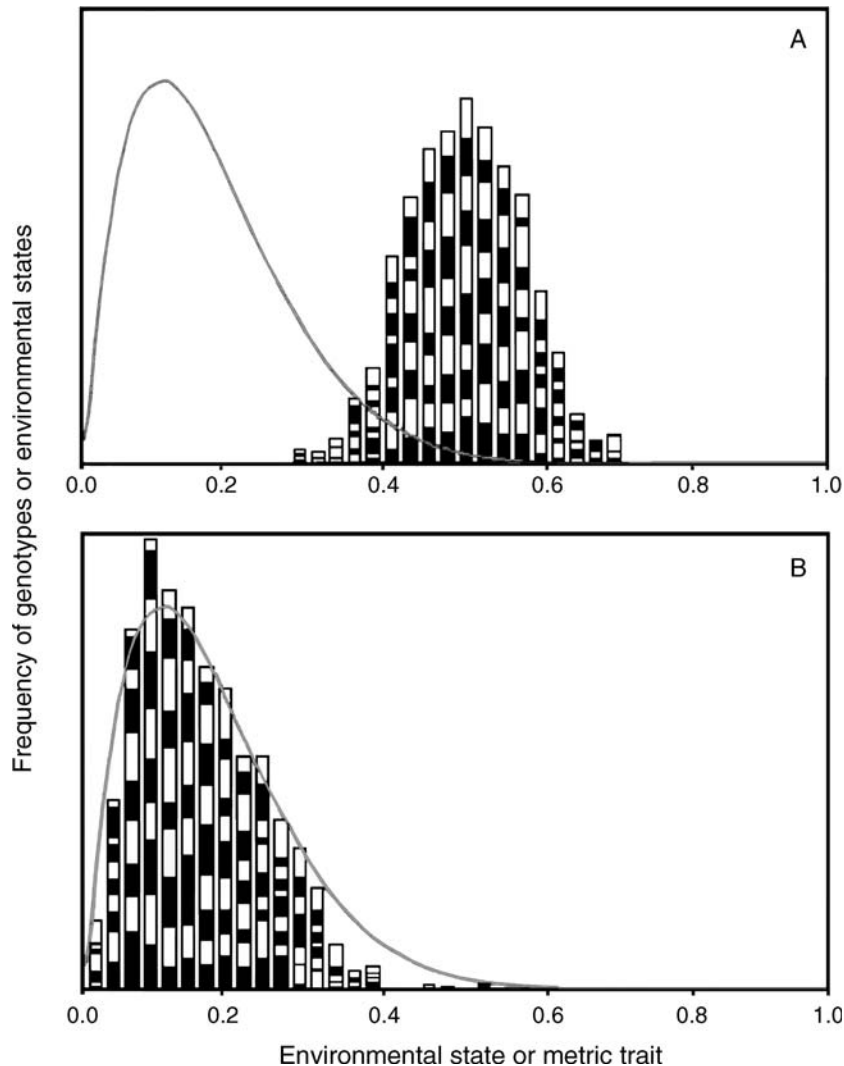
FIG. 3. Results of numerical experiment 1. Convergent coevolution of functionally equivalent species in a dispersal- and recruitment-limited model tree community. The frequency of states of the light environment (thin line) is given by a beta distribution β(2,10), skewed to reflect the low light levels found in the understory of a closed-canopy tropical forest. The beta distribution is a two-parameter probability density function over the interval [0–1] that can take many shapes, depending on the values of its parameters. (A) The initial genotype frequencies of the 10 species were binomially distributed for the metric character (stacked histogram; alternate black and white bars represent different species) and were distributed spatially randomly in the community. (B) The genotype frequencies of the 10 species after 20 generations of complete community turnover. The genotype distributions have largely equilibrated, and the combined frequencies of all species approximate the abundances of environmental states.

generations of intense selection (20 complete community replacements), the combined frequency distribution of genotypes across all 10 species almost perfectly matches the frequency distribution of environmental states. The genotype distributions of each of the 10 species are represented by the stacked, alternating black and while bars in the genotype histograms. They are statistically indistinguishable. All 10 species remained at these positions in life history space, without any sign of competitive exclusion, for 1000 generations, at which point the experiment was terminated. However, relative abundances differentiated under ecological drift, and some species became more abundant than others. The

results of this numerical experiment were representative of a general result under dispersal limitation in fine-grained environments, namely, each species evolved to adapt to the most frequently encountered conditions in its environment, irrespective of what other species were doing—which happened to be the same thing. This adaptive convergence is obtained despite the fact that there is continuous and intense intra- and interspecific competition among genotypes in this model, among the offspring of all species that managed to reach a given site. This clustering of species at the shade-tolerant end of the life history manifold for model species is qualitatively what is observed among BCI tree species
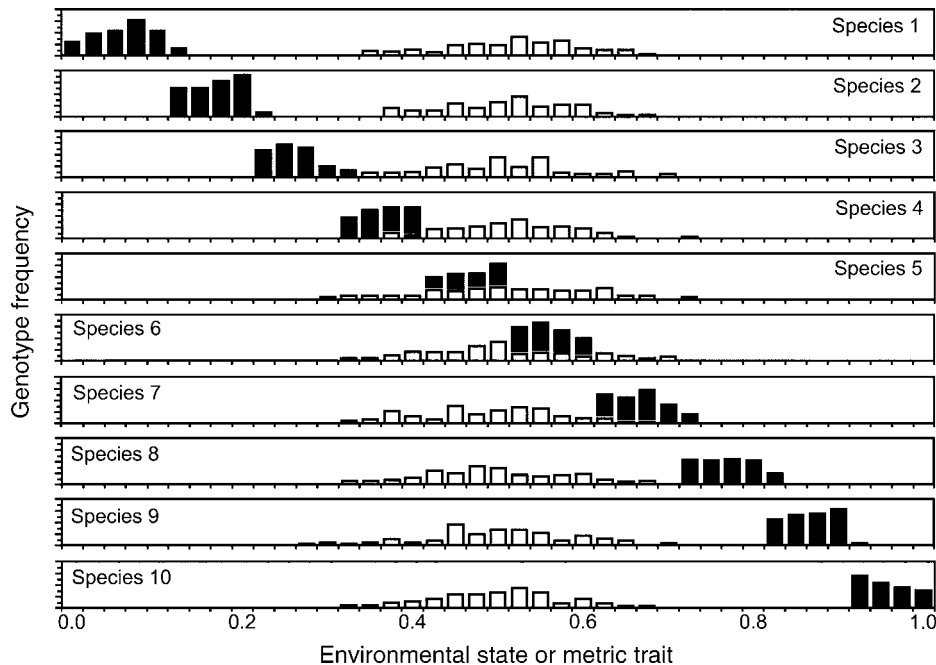
Fig. 4. Results of numerical experiment 2: evolution of niche specialists via classical niche differentiation in a dispersal- and recruitment-limited model community. In experiment 2, the light environment is spatially autocorrelated, and each species is initially distributed in clumps at particular spatial positions in the community, so they are not initially exposed to all light environments. In this case, species rapidly specialize on the light environments to which they are exposed, and this results in a stable, niche-differentiated community. Open-bar histograms are initial genotype frequencies, and solid-bar histograms are genotype frequencies after 1000 generations.

(Hubbell 2001, 2005a). In the model, there is no limit to the number of coexisting, functionally equivalent species beyond that imposed by community size, species rarity, and the immigration–extinction equilibrium.

In the first experiment, the environment was fine grained sensu Levins (1968), in that environmental states were uncorrelated spatially in the community, and species were initially randomly distributed with respect to these states. There was also strong dispersal limitation. The second experiment was designed to explore the opportunity for niche differentiation in dispersal limited species, but in a spatially autocorrelated (coarse-grained) environment. In this case, the light environment was sorted such that it went from low to high in a sinusoidal gradient around the circular community. Also in the second experiment, each species started out in clusters, already spatially aggregated at positions along the gradient. However, species were started with the same binomial genotypic distributions ($P = 0.5$ for either allele at each locus). The result of this experiment was rapid evolution of a stable assemblage of niche-differentiated species (Fig. 4). This experiment demonstrates that limited evolutionary exposure to the range of selective regimes in patchy environments can lead to specialization or niche differentiation. The history of which selective environments are experienced by a given species affects the direction and outcome of

niche differentiation. In this case, because of the initial clustering of species, interspecific competition sharpens the niche boundaries between species. In experiment 2, we thus obtain the traditionally expected outcome of competition leading to adaptive specialization and narrow niche breadths in heterogeneous environments.

The third and final experiment illustrated here was identical to the second experiment in that the selective environment was once again spatially autocorrelated. However, in this experiment, each species was not initially aggregated in a cluster at one point along the gradient, but was randomly scattered across the entire gradient. In this case, a completely different outcome was obtained: the species evolved to become generalists, with broadly overlapping niches, maintaining high genetic diversity within each species (Fig. 5). The time slice shown in Fig. 5 is at the end of the experiment after 1000 complete community turnovers. All 10 species were still present and show no sign of excluding one another. This experiment illustrates a different kind of convergence in life history from the outcome of experiment 1; in the first experiment, species converged on becoming nearly identical specialists. In contrast, in experiment 3, species became genetically polymorphic generalists, with broadly overlapping niches at the species level resulting from many locally adapted ecotypes. In this case, species are comprised of populations of individual niche
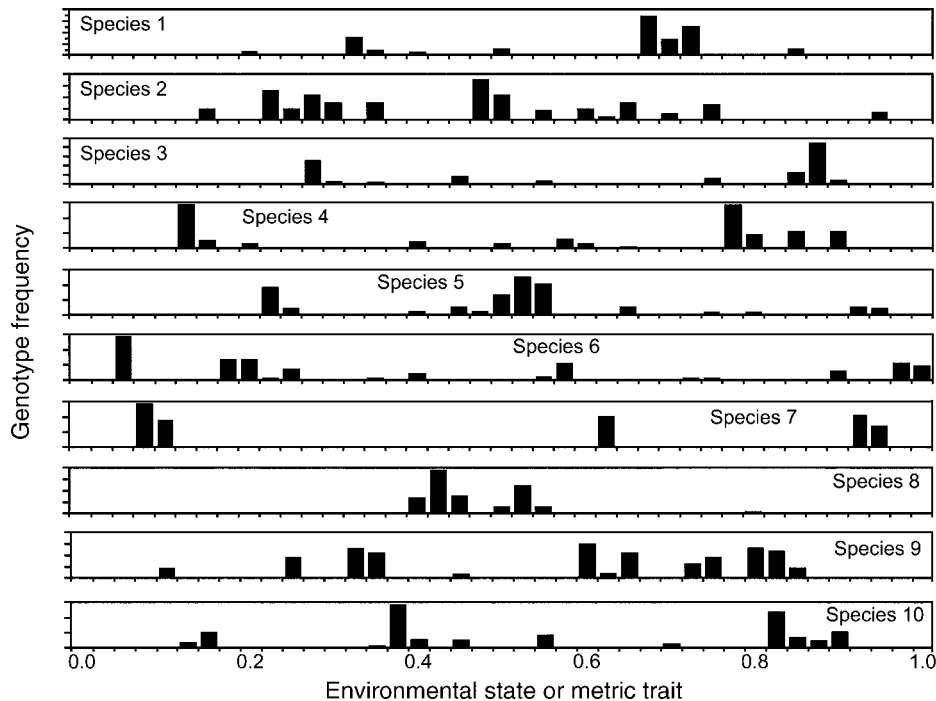
Fig. 5. Results of numerical experiment 3: diffuse coevolution of niche generalists, representing a different form of convergence (increasing niche overlap through the broadening of niche breadth). In experiment 3, individual species were not initially aggregated on the spatially autocorrelated environment, but were scattered randomly all across the environment. In this case, species evolve into generalists, maintaining high levels of genetic diversity and polymorphisms for multiple environmental states. Solid-bar histograms are genotype frequencies of each species after 1000 generations.

specialists, so one could argue that this is also a niche assembly case. However, it differs fundamentally from the classical niche argument in that if one goes looking for limiting similarity and/or character displacement at the species level, one will fail to find them. At the species level of aggregation, there is no limiting similarity. This may be an explanation for why so many BCI tree species seem to be habitat generalists (Hubbell and Foster 1986b, Harms et al. 2001), why the birth and death rate of most BCI tree species are insensitive to the species composition of their neighborhoods (except to the presence of conspecifics; Hubbell et al. 2001, Ahumada et al. 2004, Uriarte et al. 2004, 2005) and why tropical tree species maintain such high levels of genetic diversity (Hamrick 1992).

My point in describing this model is not to make excessive claims for its realism. Nevertheless, despite its simplicity, the model does capture the essential theoretical elements of the diffuse co-evolutionary process envisioned by Hubbell and Foster (1986a). The model makes my primary qualitative point, which seems unlikely to change even if more complexity and realism are included, namely, that ecologically equivalent species probably can evolve and be maintained indefinitely in ecological communities that are subject to dispersal and recruitment limitation.

FUNCTIONAL DIVERSITY, PRODUCTIVITY, AND STABILITY OF THE BCI TREE COMMUNITY

In Hubbell (2005a), I reviewed some of the evidence of the ecological equivalence or near equivalence of BCI tree species. I conclude this paper with some additional BCI evidence for an apparent lack of relationship between species richness and either stability or productivity. Condit et al. (2006) also report that the 16-fold variation in species richness among the plots in the pantropical CTFS network was not explained by functional diversity as measured by variation in demography among species. Working on tropical tree communities, we unfortunately do not have the luxury of economical and short-term experimental tests of the relationship between functional diversity, productivity, and stability. Moreover, we have only been studying the dynamics of the BCI tree community since 1982, which is less than a quarter of the life span of most BCI canopy tree species. These caveats aside, the BCI forest is remarkably dynamic: in 18 years, there has been nearly a 43% turnover of trees and their saplings in the 50-ha plot, so we have an opportunity to evaluate at least the short-term correlations among diversity, stability, and productivity.

We attempted to test for a diversity–stability connection by examining the temporal coefficient of variation in Fisher's α on a variety of spatial scales as
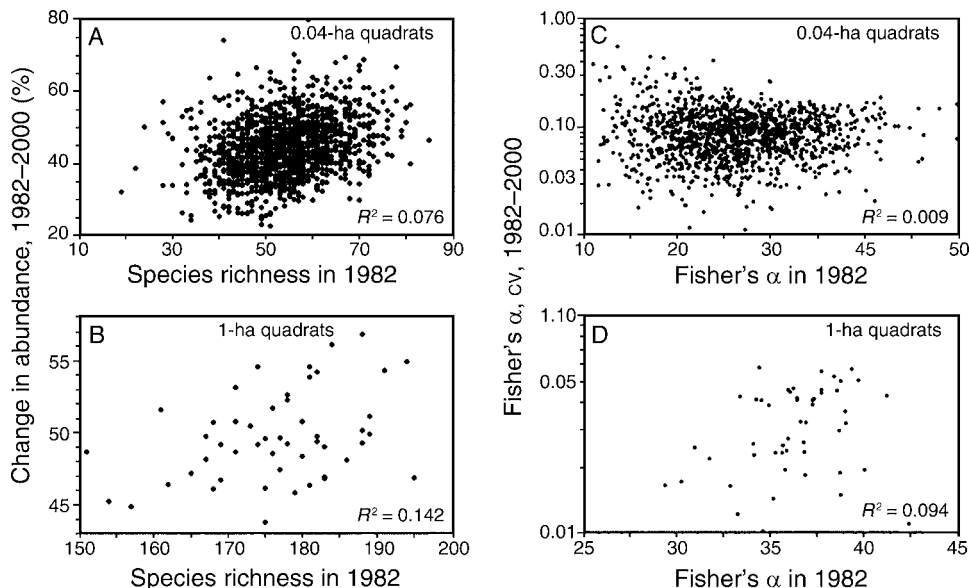
Fig. 6. Two measures of the weak correlation between diversity and stability in the BCI tree community in the 50-ha plot. (A, B) Mean per species absolute percentage of change in abundance over an 18-yr period (1982–2000) in relation to species richness in 1982. (C, D) The coefficient of variation in the diversity parameter, Fisher's α, measure over five censuses over an 18-yr period (1982–2000) in relation to diversity (Fisher's α) in 1982. Panels A and C represent 20×20 m quadrats (0.04 ha); panels B and D represent 100×100 m quadrats (1 ha).

a function of the initial value of Fisher's α in 1982. We chose to use Fisher's α (Fisher et al. 1943) because it is the oldest, most famous, and most stable measure of diversity in the face of variation in sample size (Magurran 1988). Fisher's α is also directly derivable from the UNT (Hubbell 2001, Volkov et al. 2003), and is proportional to the speciation rate at large landscape scales. If there is a diversity–stability connection, we would predict that areas having relatively higher diversity within the plot as measured by Fisher's α would exhibit smaller variation in α through time.

This prediction was not supported. Fig. 6 shows the lack of correlation between the temporal coefficient of variation in Fisher's α over the five censuses of the BCI plot and the value of Fisher's α in 1982. We checked for a correlation on several spatial scales. The top panel of Fig. 6 is the correlation for 20×20 m quadrats (0.04 ha), and the bottom panel is for 1-ha quadrats. The relationship is non significant on both spatial scales, and all other scales tested within the plot. It is also similarly non significant within habitat types defined by topography (Harms et al. 2001). This result was obtained despite the fact that there is considerable variation in tree species richness in the plot, varying by about 50% from one place to another at the scale of 400 m^2. Variation in species richness is strongly correlated with topography, but not with the history of gap disturbances at least since 1982 (Hubbell et al. 1999). If functional diversity is captured by species richness, then these combined results suggest that the diversity–stability connection is weak at best in the BCI forest.

If functional groups are exploiting different resources, then one would predict that greater functional diversity should lead to an "overyield" phenomenon (Hooper and Dukes 2004). As mentioned, we cannot address this question experimentally in the BCI tree community. However, we can make the reasonable prediction that biomass per unit area should be positively correlated with species richness per unit area. On a variety of spatial scales, and for two tree size class cutoffs, we found no such relationship in the BCI tree community. Fig. 7 shows the relationship between the biomass proxy, total basal area, and species richness on the spatial scales of 400 m^2 (0.025 ha), 2500 m^2 (0.25 ha), and 10 000 m^2 (1 ha), for all trees and saplings >1 cm dbh (left), and for larger trees >10 cm dbh (right). In no case was there any sign of over-yielding that would lead to a positive relationship between functional diversity (species richness) and biomass (proxy variable: total basal area). We also redid the analysis by clustering species into functional groups based on adult stature and position on the life history manifold. However, once again, there was no evidence of over-yielding. The failure to find a correlation at the species level means that a significant correlation at the level of functional groups is even more unlikely. This is because more functional diversity should be expected at the species level than when species are pooled into functional groups.

DISCUSSION AND CONCLUSIONS

In this paper, using a simple, spatially explicit model of community evolution, I show that ecologically equivalent species can evolve, and that, once they
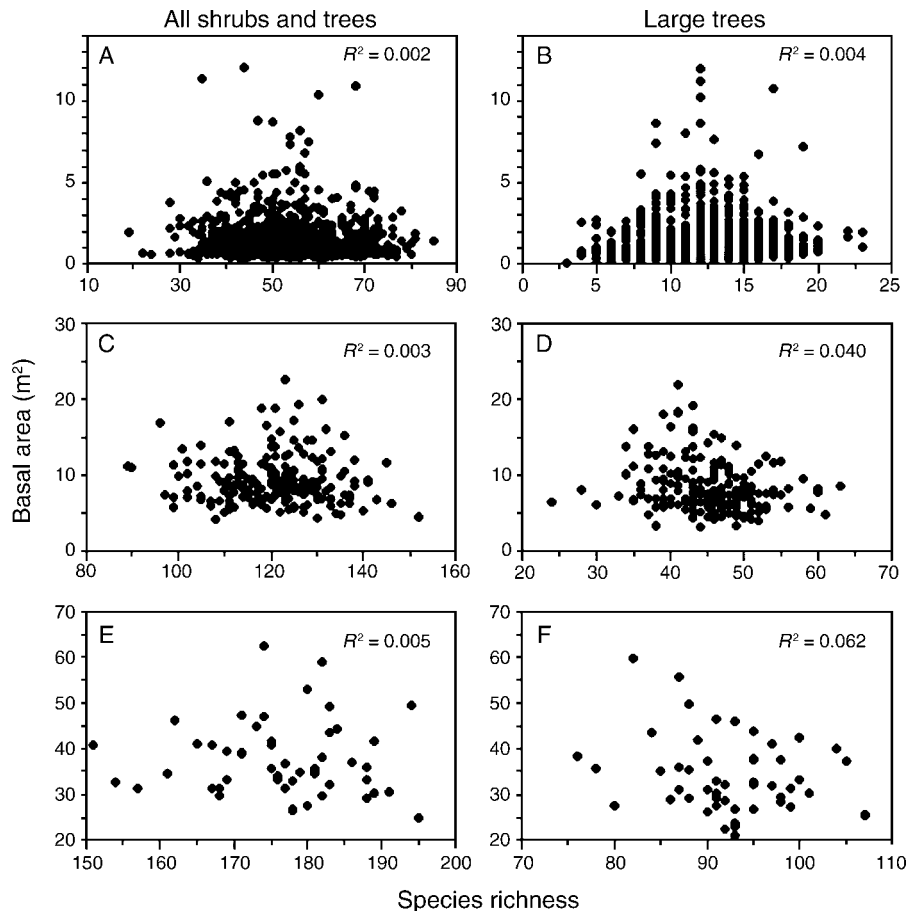
Fig. 7. Lack of evidence for an over-yielding phenomenon in the BCI forest. Total basal area is used as a proxy variable for biomass. Correlations were examined for all trees and shrubs >1 cm dbh (panels A, C, E), and for just large trees >10 cm dbh (panels B, D, F). Correlations were also examined at different spatial scales, 20×20 m quadrats (panels A, B), 50×50 m (0.25 ha) (panels C, D), and 1-ha quadrats (panels E, F). The apparent peak of biomass points in the middle of some plots is not significant, but is a sample-size artifact (there are a greater number quadrats containing an intermediate number of species).

evolve, they can coexist for arbitrarily long periods. Ecologically equivalent species are expected to arise frequently in fine-grained environments in communities that are strongly dispersal and recruitment limited. In this case, species evolve adaptations for the most abundant environmental conditions. Ecologically equivalent species can also evolve in coarse-grained environments under dispersal and recruitment limitation provided that individual species are distributed across the grain or patchiness of the environment. In this case, however, species achieve their equivalence not by specializing on the regionally most prevalent environments, but by becoming generalists with broad niche overlap at the species level, maintaining high levels of genetic polymorphism. Although these species are comprised of locally habitat-specialized individuals, at the species level, one does not observe limiting similarity or character displacement among these generalists.

The evolution and long-term coexistence of functionally equivalent or near-equivalent species requires factors that prevent competitive exclusion. I have

invoked strong dispersal and recruitment limitation as the most important of these factors. In my study system, there is abundant evidence that virtually all BCI tree species are strongly dispersal and recruitment limited (Hubbell et al. 1999, Harms et al. 2000, Dalling et al. 2002, Muller Landau et al. 2002). Much of this evidence comes from an 18-yr study of seed rain and seedling germination in the BCI plot.

Strong dispersal limitation of the BCI tree community is indicated by the fact that, in the first decade of the seed rain study, only five of 260 recorded species managed to disperse seeds to half of the 200 seed traps in the BCI plot, and half of all species hit five or fewer traps in the same 10-yr period (Hubbell et al. 1999). Dispersal kernels fit to the seed rain data strongly support this finding (Muller Landau et al. 2000, Dalling et al. 2002). Even if seeds reach a given site, however, there is very heavy subsequent mortality, leading to even stronger recruitment limitation. More than 95% of this mortality is density independent and due to factors such as drought-induced seedling death (Engelbrecht and

Kursar 2003, Tyree et al. 2003). However, there is also a significant density-dependent component (Harms et al. 2000). Tree species whose seeds are relatively more abundant in traps are less so in adjacent seedling germination plots.

Much has been made about the importance of spatial density dependence in the maintenance of the high species richness of tropical forests (Janzen 1970, Connell 1971), and the data from Harms et al. (2000), showing pervasive density dependence in the seed-to-seedling transition in the BCI tree community is strong support for a predator mediated coexistence of BCI tree species through limiting recruitment success. However, it should be noted that any factor that reduces recruitment success, regardless of whether it acts in a density-dependent or a density-independent manner, will promote coexistence of species that are equivalent in their use of limiting resources. Despite the discovery of density dependence in the seed-to-seedling transition, we still do not know whether the effects of this early mortality propagate long enough and strongly enough—through the extended juvenile stages and the overlapping generations—to regulate the populations of reproductive adults. However, we do know that whatever stabilizing Janzen-Connell effects there have been over the past quarter century, they have not been strong enough to prevent major compositional changes in relative species abundances in the BCI forest.

Many of my colleagues would argue that dispersal and recruitment limitation mediated by seed and seedling predators and pathogens, implies that niche differentiation is still required for coexistence. I have no problem with this, but simply point out that this hypothesis is very different from the classical niche paradigm, which focuses on competitive niche differentiation in the exploitation of limiting resources. At present, there is no neutral theory for trophic interactions, and niche theory for predator and pathogen effects is still relatively undeveloped (Chase and Leibod 2003). For example, it would be interesting to study whether predation can generate selection for limiting similarity or character displacement in the niches of prey species. It should be noted that neutral theory can be extended to communities whose species experience identical predator limitation, provided that these effects are symmetric and the same in all species. I would also note, however, that the evolution of ecologically equivalent species does not require predator (top down) control. Potentially any factor, abiotic or biotic, that limits community-wide dispersal and recruitment, can produce ecological conditions that are conducive to the evolution of functionally equivalent or near-equivalent species.

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