Neutral theory in community ecology and the hypothesis of functional equivalence

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Introduction

Probably no ecologist in the world with even a modicum of field experience would seriously question the existence of niche differences among competing species on the same trophic level. The real question, however, is how did these niche differences evolve, how are they maintained ecologically, and what niche differences, if any, matter to the assembly of ecological communities? By *ecological community* I refer to co-occurring assemblages of trophically similar species. By *assembly* I mean which species, having which niche traits, and how many species, co-occur in a given community. In my judgement, despite a long and rich tradition of research on these questions in community ecology (Chase & Leibold 2003), we are still far from having definitive answers.

Several years ago, in an attempt to provide a fresh approach for tackling these questions, I introduced a formal neutral theory for ecology (Hubbell 1997, 2001). The traditional strategy has been to assume that ecological communities are inherently high-dimensional *sensu* Hutchinson's (1957) niche hypervolume for each species, and then to build rather complex models from the outset, incorporating as many of the details of the growth and interactions of each and every species and with their physical environment as possible. Neutral theory, however, adopts a fundamentally different strategy, taking virtually the opposite tack. It begins with the simplest possible hypothesis one can think of – for example, the functional equivalence of species – and then adds complexity back into the theory only as absolutely required to obtain satisfactory agreement with the data. In this approach, one does not assume from the start that ecological communities are high-dimensional. Indeed, the fundamental question now becomes: What *is* the minimum necessary dimensionality of the theory required to characterize a given ecological community to a desired level of realism and precision?

The hypothesis of *functional equivalence* is the cornerstone of neutral theory. It states that trophically similar species are, at least to a first approximation, demographically identical on a per capita basis in terms of their vital rates, of birth, death, dispersal – and even speciation. Elsewhere I have also used the term *symmetry* to describe such species (Hubbell 2005). Under the

hypothesis of functional equivalence, species can still differ in a great many ways – including characters that enable taxonomists to recognize them as good species – so long as species do not differ in their per capita vital rates. All species in all trophically defined communities violate this assumption to some degree, but the question is, how good an approximation is it?

In ecology, there are often multiple, sufficient explanations for the same phenomenon (Chave, Muller-Landau & Levin 2002; Purves & Pacala 2005), and this is especially true of approximate explanations. The strategy of neutral theory relies heavily on Occam's Razor; but whether the assembly rules of ecological communities in nature obey this maxim – to always choose the most parsimonious explanation – is not yet clear. However, as Harte (2003) pointed out, one doesn't necessarily discard theories just because they are just approximations. Physicists still use Boyle's Law, $PV = nRT$ (pressure P times volume V is a linear function of absolute temperature T), even though there are no perfect gases that follow this relationship exactly. Similarly, we continue to teach the Lotka–Volterra equations in ecology, even though no ecologist today would defend them as precise or mechanistic descriptions of nature.

Much has been written about the unified neutral theory (UNT) since my book appeared (Hubbell 2001), some of it critical, and there have been several major technical and conceptual advances in the theory since then (e.g. Volkov *et al.* 2003; Vallade & Houchmandzadeh 2003; Houchmandzadeh & Vallade 2003; McKane, Alonso & Sole 2004; Etienne & Olff 2004). However, my main focus for this forum on neutral theory will not be on the new developments in the theory or on the criticisms. Rather, I wish to highlight the empirical observations that led me to question my own long-held beliefs about the assembly rules for ecological communities in the first place, particularly in plant communities. Before discussing these observations, however, I should sketch out a few of the major milestones in the intellectual history of the classical paradigm of competitive niche assembly theory.

Competition and the classical niche paradigm

Since Grinnell (1917), and more formally since Hutchinson (1957, 1959), ecologists have sought a theoretical framework for the ecological niche concept that would be both necessary and sufficient to explain the coexistence

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of species having particular suites of traits in ecological communities. Early on, Gause (1934) put forth the central tenet of niche theory in his competitive exclusion principle, which states, paraphrased, that no two species with identical niches can coexist indefinitely. Gause tested this idea by fitting the celebrated Lotka–Volterra equations of two-species competition to the dynamics of competitive exclusion in laboratory populations of *Paramecium*. From Gause's day onward, the discussion of coexistence and community assembly rules has been framed almost exclusively in terms of competition, despite numerous but largely unsuccessful attempts to broaden the discussion to include additional mechanisms. Gause's principle implied that there must be a maximum tolerable overlap in the use of shared resources for two species to coexist or, in other words, there should be some limiting similarity between the niches of coexisting species (Hutchinson 1959; MacArthur & Levins 1967; MacArthur 1970). The principle also implied that competitive exclusion should be a commonplace observation in nature, or at the very least, that there should be widespread evidence of character displacement in resource use when very similar species co-occur. The empirical evidence, in general, has not borne out these predictions (Grant 1972, 1975), particularly in plant communities. There are only a few well documented examples of character displacement, all of which are in animals; for example, the evolution of beak size in competing Darwin's finches (Grant 1986), similar niche separation in seed-eating sparrows (Pulliam 1975) or in body size in desert rodents (Brown 1975). Most of these cases involve low-dimensional resource competition. However, I know of few examples of proven character displacement in plants, and the list of species whose actual disappearance from a community can be attributed to competitive exclusion is vanishingly short.

Hutchinson's (1957) niche hypervolume was a more general concept of niche than one defined solely by limiting resources, and included, for example, the tolerance ranges for physical variables of the environment. His ideas about the fundamental and realized niches invoked competition to explain why species only occupy a subset of the niche space that would be suitable for them in the absence of competitors. However, if niches evolve, and if species are always restricted to smaller, realized niches in equilibrium communities, then how do we explain the persistence of adaptations for parts of fundamental niche space that are never occupied? I will return to this question shortly.

The theory for community assembly based on the competitive niche paradigm became highly developed, first with multispecies community matrix theory (Levins 1968), which was developed on the foundation of the Lotka–Volterra equations, and then with more mechanistic theory, which explicitly incorporated the dynamics of resource supply and consumption along with the dynamics of the resource-dependent consumer species (Tilman 1982, 1987). This resource-based theory gave new impetus to testing community assembly rules through direct experimental manipulations of resource availability, most notably in plant community ecology. Perhaps the most significant conceptual spin-off of resource-based theory, however, was broader recognition of the fundamental importance of physiological and life history trade-offs (e.g. Tilman 1982, 1988; Kneitel & Chase 2004). In resource-based, or so-called R* theory, trade-offs occur everywhere because they are essential for coexistence. For example, in two-species competition for two limiting resources, stable coexistence happens only when each species has a higher break-even (R*) requirement for that resource which most limits its own growth, which represents a trade-off in the ability to exploit the two resources.

The importance of trade-offs in resource use led Tilman (1994) to consider trade-offs in other life-history characteristics besides those involving resource exploitation, and here additional problems with the classical paradigm began to surface. In particular, Tilman revisited the old fugitive species concept of Hutchinson, and showed theoretically that if there was a strict transitive trade-off between competitive ability (site tenacity) and dispersal ability then, in principle, any arbitrary number of species could coexist. However, soon thereafter, Hurtt & Pacala (1995) showed that Tilman's trade-off assumption could be relaxed and that species of arbitrary competitive and dispersal abilities could coexist if dispersal and recruitment limitation were sufficiently strong. Hurtt and Pacala defined *dispersal and recruitment limitation* as the failure of species to reach and/or establish in all sites favourable for their growth and survival. When dispersal was infinite, such that all species reached all sites, then the best competitor won each site for which it was superior, the equilibrium solution expected from the classical theory. However, when dispersal and recruitment limitation were strong, many sites were won by default by competitively inferior species because the best competitor for the sites failed to reach them. Although the coexistence produced by this mechanism is non-equilibrium, Hurtt and Pacala showed that competitive exclusion could be essentially infinitely delayed. This result meant that Gause's competitive exclusion principle was not generally true in spatial ecology. The slowness to reach equilibrium also depended on species richness. The more species there were in the community, the stronger dispersal limitation became, and the slower the approach to equilibrium. The elimination of species by competitive exclusion is so slow, in fact, that all it takes to balance species loss and achieve a true long-term equilibrium in species richness and relative species abundance is to incorporate a very slow rate of introduction of new species (i.e. speciation) (Hubbell 2001).

The hypothesis of functional equivalence

The idea of assuming functional equivalence as a theoretical point of departure in community ecology is

not particularly new, particularly in plant ecology (Hubbell 1979; Goldberg & Werner 1983; Shmida & Ellner 1984). Neutral theory assumes functional equivalence at the entire community level, but this is much broader than is typically assumed by ecophysiologists and ecosystem ecologists when they aggregate similar species into functional groups (e.g. Reich, Walters & Ellsworth 1997). Recognizing functional groups implies that niche differences among these groups are believed to matter to the assembly, stability and resilience of communities to disturbance (e.g. Loreau, Naeem & Inchausti 2002), although their quantitative importance remains controversial (Hubbell 2005). However, the literature on functional groups has been remarkably silent about the assumption of species equivalence *within* functional groups, which flies squarely in the face of classical niche theory. Perhaps this silence is because the idea of functional groups largely emerged from the ecosystem perspective, which traditionally has not been focused on species-level questions. There has also been very little discussion about the selective regimes that would lead to the evolution of functional equivalence within functional groups (Hubbell & Foster 1986b; Hubbell 2005). As a result, there is not much development of theory in community ecology for the assembly of functional groups. Does a limiting niche similarity for species in functional groups exist? How many coexisting species can be packed into a functional group? I believe that the answer to the first question is *no* (at least in plants), and the answer to the second question is essentially *arbitrary* (again, at least in plants). Loreau (2004) has recently argued that functional equivalence does not really exist. However, in a companion paper (Hubbell 2005), I demonstrate that functional equivalence can evolve easily and often, under selective circumstances that should be commonplace in nature, especially in species-rich communities.

My ideas on functional equivalence have developed slowly over the past quarter century. Since 1980 my colleagues and I have been studying the dynamics of a large (50 ha) mapped plot of old-growth tropical forest on Barro Colorado Island (BCI), Panama, attempting to understand the assembly rules of the BCI tree community (Hubbell & Foster 1983). The BCI Forest Dynamics plot contains a little over 300 tree and shrub species and 230–240 thousand stems, depending on the census, with a stem diameter of at least 1 cm at breast height (d.b.h). Details of the BCI plot and the dataset are now well known, and the research design has now been replicated in a pantropical network of plots (Condit 1998). However, I will confine my discussion to the BCI findings because the BCI dataset is the oldest, having now been censused five times.

The first observation about the BCI tree community is that there appears to be single dominating axis of niche differentiation, organized by variation in light and its distribution in the forest, that can be well characterized by a trade-off between survival under shade stress and maximum growth rate in full sun (Fig. 1)
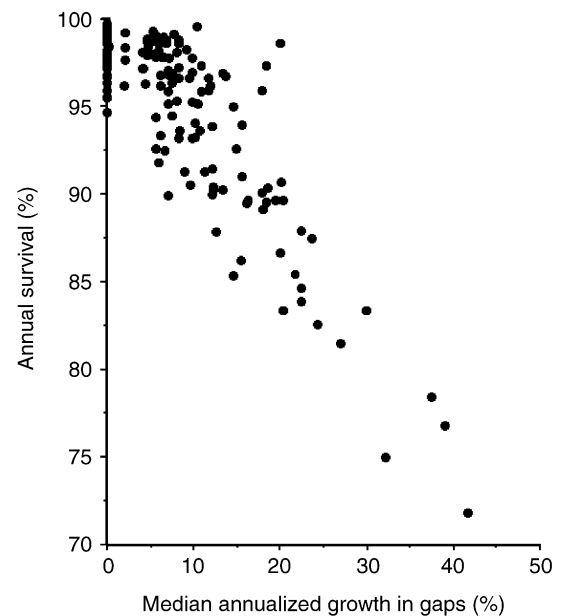

Fig. 1. Principal axis of life history differentiation among BCI tree species is in relation to light availability. Each dot represents the mean phenotype of a single species. Species at the upper left are shade-tolerant species with high annual percentage survival in understorey shade but low annual relative growth rate in full sun, measured as a percentage of initial stem diameter. Species at the lower right are light-demanding, gap-dependent species that exhibit high mean relative growth rates in full sun, but low mean annual survival rates in understorey shade. Note the concentration of species at the shade-tolerant end of the manifold. Data such as this are usually interpreted as evidence for a trade-off between survival and growth rate. However, these mean phenotype points mask significant within-species variation in survival and growth performance (see Fig. 4). After Hubbell & Foster (1992).

(Hubbell & Foster 1992). The ends of this axis, or life history manifold, are occupied on one end by species that have high survival in deep shade but low maximal growth rate in full sun, and on the other end, by species that have low survival in the shade, but have very high relative growth rates in full sun. Looking only at species at the extremes of the life history manifold, one can clearly identify different functional syndromes of traits. At some risk of caricature, one end of the manifold is the colonizer (pioneer) functional group and the other end is occupied by the competitive (stress tolerater) functional group. Species exhibiting the colonizer syndrome generally have good dispersal ability, are light-demanding and fast-growing, but also have relatively short life spans, low wood density, and low resistance to predators, herbivores, and pathogens. Species exhibiting the competitive syndrome, on the other hand, typically have variably poorer dispersal ability, and are tolerant of low light levels, but are generally slower growing in full sun, and they have longer life spans correlated with high wood density and with generally higher resistance to predators, herbivores, and pathogens.

Having made this generalization, however, we note that the numbers of species exhibiting these syndromes are very different. There are very many more shade-tolerant

species in the BCI forest than pioneer species. Note also that that there is no clear life history dichotomy separating these two syndromes into functional groups. In fact, there is a complete continuum of intermediate species between the extremes. There is also a complete continuum in the demographic characteristics of BCI tree species in terms of population sizes, skewing of stem size class distributions, and wood density (Wright *et al.* 2003). In general, the mean abundance of species also declines with an increase in the degree of 'gappiness'.

These results might be reconciled with classic niche theory, but it is not easy to do so. First of all, in the densely populated shade-tolerant end of the life history manifold, there are many species that are virtually indistinguishable in their shade tolerance and relative growth rates. If this clustering of species at the shade end is to be explained by niche theory, then one must come up with a plausible argument for why niches are more finely partitioned under low-light conditions than under high-light conditions. If there is a limiting niche similarity in these basic functional traits, then it is not at all obvious.

To my way of thinking, these data are more simply explained by an alternative hypothesis. I believe that species are selected to exhibit the syndrome of traits that adapt them for growth and survival under the commonest environmental conditions, regardless of how many other species are doing the same thing. This evolutionary process has the incidental effect of causing species to converge on similar trait syndromes, given whatever constraints are imposed by their different phylogenetic histories (Chazdon *et al.* 2003). Functional convergence provides one possible evolutionary mechanism to explain the 'environmental filtering' hypothesis of Weiher & Keddy (1995, 1999), which says that species with similar niche requirements are sorted into similar habitats.

Thus, according to this hypothesis, the low numbers of pioneer species in closed-canopy forests such as BCI is simply a reflection of the rarity of gap environments over evolutionary time relative to shady environments. From this evolutionary perspective, what really determines the species richness of shade-tolerant and gap species in a particular local tree community is the richness of the regional species pool and the abundance of shady and gap habitats in the metacommunity over long periods of time. This then has a trickle-down effect on α diversity in a local community such as BCI. A prediction of this perspective is that short-term changes in the disturbance regime may cause a short-term increase in the collective abundance of pioneer species, but it will have a relatively minor effect on the total number of pioneer species that are present.

Life history convergence of this sort in classical niche theory is expected to lead to a loss of species through competitive exclusion, but there is no evidence to suggest that this is happening among BCI species. I believe that two major factors are at work that prevent competitive exclusion. The most important factor is
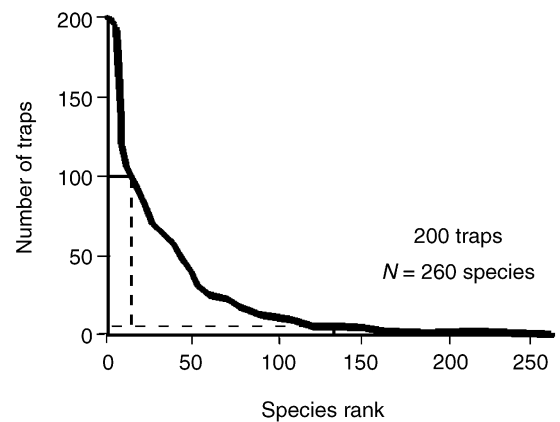

Fig. 2. Evidence for strong dispersal limitation among 260 species in the BCI forest, over a 10-year sampling period, during which seeds were collected and identified weekly from 200 traps across the BCI plot. Only 12 species managed to hit over 50% of the traps in a decade, and half of all species dispersed seeds into five or fewer traps during this 10-year period. After Hubbell *et al.* (1999).

the combination of dispersal and recruitment limitation. There is pervasive evidence of strong dispersal and recruitment limitation in the BCI tree community (Hubbell *et al.* 1999; Harms *et al.* 2000), and it is strong even in the best dispersers, with few exceptions (Dalling *et al.* 2002). The evidence for dispersal and recruitment limitation comes from a long-term study of seed rain into a network of 200 seed traps throughout the BCI 50 ha plot, with paired sets of seedling germination plots, a study now in its 18th consecutive year.

First, consider dispersal limitation. During the first decade of the study, only 12 of 260 species managed to disperse at least one seed to half or more of the traps, and more than half of the tree species were collected in five or fewer traps in 10 years (Fig. 2) (Hubbell *et al.* 1999). The only species in the BCI forest with a seed bank are the pioneers, but even these species have only limited seed dispersal in space and time. Most seeds land within 20 m of the parent tree, and seeds of most pioneer species remain viable for only 2–3 years. The one notable exception may be *Jacaranda copaia* (Bignoneaceae), an emergent gap-dependent species which, genetic markers reveal, manages to disperse a sizeable fraction of its seeds long distances (Jones *et al.* unpublished).

Next there is recruitment limitation, which is also very strong. Harms *et al.* (2000) analysed seedling germination in the plots immediately adjacent to each seed trap, and discovered pervasive density dependence in the seed to seedling transition in all species that had sufficient seed numbers to analyse. Harms *et al.* measured the strength of density dependence by the slope of the regression of the log number of seedlings germinating on the log number of seeds of the same species falling into the adjacent trap. A slope of unity would indicate density independence. All of the slopes were < 1, and many effects were so strong that the slopes were actually negative (more seeds in, absolutely fewer seedlings out) (Fig. 3).
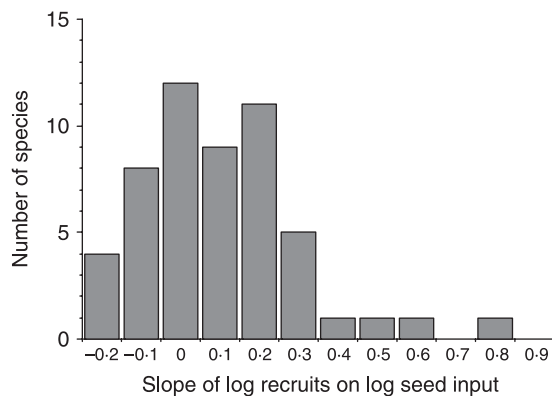
Fig. 3. Evidence for strong recruitment limitation. Histogram represents the binned slopes of the regression of log number of germinated seedlings (recruits) vs. log number of seeds of the same species collected in the adjacent trap, over all 200 traps in the BCI plot. Regression slopes of 1·0 would indicate no density dependence. However, the slopes for all species were < 1·0, indicating density-dependent mortality in the seed-to-seedling transition. Density dependence was so strong in nearly a third of the species that the slopes of the log–log relationship between seeds in to seedlings out were actually negative. Thus, these species actually recruited absolutely more poorly in sites where more seeds were deposited. After Harms *et al.* (2000).

The importance of these findings for the present discussion is that dispersal and recruitment limitation are sufficiently strong to prevent competitive exclusion among species whose life history traits exhibit the same or very similar adaptations for the most common environments in the forest. We have not yet developed a full forest simulator for BCI that incorporates the measured effects, but simple models incorporating dispersal and recruitment limitation are fully capable of maintaining arbitrary levels of species diversity of arbitrarily competent competitors (Hurtt & Pacala 1995; Hubbell 2005). At this point, niche theorists may point out that, if host-specific density-dependent predation is included in the description of species characteristics, this is simply a broader definition of niche beyond competition that includes interactions with predators. Indeed, Chase & Leibold (2003) argue that predation risk is a legitimate component of niche. I have no problem with this, but this view of niche is not the classical paradigm. Moreover, it is not obvious how predation pressure could drive character displacement. The issue is further clouded by complexities such as the possibility of indirect competition via shared predators, *sensu* Holt (1977). In the case of BCI species, most of the mortality (> 95%) in the seed-to-seedling transition is actually density independent (cf. Harms *et al.* 2000). However, host specificity in agents of mortality, contrary to popular belief, is not required in order for recruitment limitation to be effective in promoting species coexistence. Any factor which limits seedling recruitment – even a randomly moving lawn-mower – will increase the tendency of species to win sites by default, irrespective of species specificity.

The second factor preventing competitive exclusion of species is the heterogeneity of the biotic and abiotic microenvironments experienced by individuals of each species. Nearly 20 years ago, we offered the hypothesis that in species-rich communities, the opportunities for directional character displacement among a large number of competing species would be low. Diffuse coevolution of many competing species would lead to convergence on the statistical average of biotic and abiotic neighbourhood conditions (Hubbell & Foster 1986b). We found in the BCI tree community that, on average, there were 14 species in the 20 nearest neighbours of each individual tree, and that conspecific trees shared, on average, only 20% of the species in their 20-individual neighbourhoods. This is related to the previous argument about life-history convergence on the most common environments. Back then, the concept of dispersal and recruitment limitation was not in the theoretical literature, but such limitation is one of the main reasons why biotic neighbourhoods are not completely mixed. If this hypothesis is true, then the long-term survival and growth performance of focal trees should be independent of the species composition of their neighbourhoods, with the exception of conspecific neighbours. We tested this hypothesis on 18 years of growth and survival data on BCI species. With few exceptions, the species identity of the focal plant's neighbours was neither quantitatively important or statistically significant (Hubbell *et al.* 2001; Ahumada *et al.* 2004; Uriarte *et al.* 2005).

This result suggests that the direction of selection imposed by interspecific competition differs at the level of virtually every individual. There is little or no consistency in the direction of selection operating at the species level to drive character displacement in one direction or another, unlike the selection for beak shape in Darwin's finches. I suspect that this heterogeneous selection regime is a major reason that tropical trees maintain such high levels of genetic variation and heterozygosity (Hamrick & Loveless 1986). One would expect that most BCI species are habitat generalists, and this does seem to be the case (Hubbell & Foster 1986a; Harms *et al.* 2001). Even the pioneer species exhibit high levels of variability. For example, consider the huge variation in growth rates among individuals of the pioneer *Jacaranda coapia* (Fig. 4). The variation in growth rates in this single species spans virtually the entire spectrum of growth rates of both the pioneer and the shade-tolerant functional group extremes. At this stage we cannot interpret how much of this variation is adaptive, but it does indicate that there may be problems with simple species-level trade-off arguments between survival and growth rate that we outlined previously. Some ecologists have argued that such massive intraspecific and interspecific variability implies that ecological communities are very high dimensional (e.g. Clark *et al.* 2001). However, if species overlap broadly because the within-species variability is far greater than the between-species variability, then simple
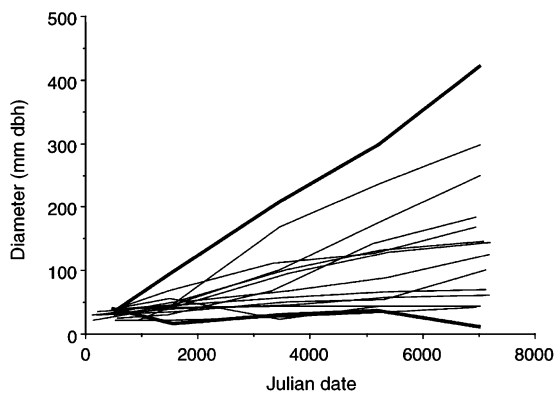
Fig. 4. Illustration of the enormous variability in growth rates of the pioneer species, *Jacaranda copia* (Bignoniaceaee). Graph represents a random sample of 15 *Jacaranda* individuals that were 1–4 cm d.b.h. saplings in 1982 that survived until the year 2000 census. The range of diameters after 18 years was from 1·0 cm d.b.h., a tree that hardly grew at all (lower heavy line), to a canopy-emergent adult of 43 cm d.b.h. (upper heavy line). This variability in just 15 Jacaranda trees spans the entire range of variation observed in growth rates across the entire BCI tree community, including shade-tolerant species. This variability is not atypical, and indicates that BCI trees overlap considerably in the distribution of their vital rates. It further indicates that the concept of limiting similarity has little applicability to demographic traits of BCI trees. Such variability also challenges the trade-off arguments applied to Fig. 1.

stochastic models, such as symmetric neutral theory, may not be such a bad approximation to reality after all.

Conclusion

The hypothesis of functional equivalence can only be taken so far, but the main point of this paper is that there are both empirical and theoretical grounds for taking the hypothesis seriously, at least in the tropical tree communities I have studied. It is almost certainly the case that the hypothesis will apply better to some communities and functional groups than others. I suspect it will be less often true in communities of mobile animals, but this question will be for the experts on those communities to answer. What continues to surprise me, however, is how far one can get with a neutral theory based on the strong assumption of functional equivalence. Although critics have rightly noted that non-neutral theories can also produce many of the same patterns, to me this is not the main point of neutral theory. More realistic – but also more complex – theories *ought* to fit the data better if the theorist knows what he or she is doing. To me the most interesting and challenging question of all is why neutral theory performs as well as it does, given the assumptions it makes. For me, neutral theory has been a welcome conceptual advance because it is a theory of diversity that derives naturally from fundamental demographic processes in population biology. For example, it is both amazing and encouraging that one can derive the most famous measure of species diversity, Fisher's α (Fisher

et al. 1943) very simply and directly from the theory (Volkov *et al.* 2003), and that this number turns out to be proportional to the speciation rate. It is results like this that fuel my belief that neutral theory is capturing something fundamentally true about the aggregate statistical behaviour of biodiversity on large, spatially structured landscapes. Only time will tell if my belief is correct.

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