

REVIEW

Neutral theory and community ecology

J. Chave

Laboratoire Evolution et
Diversité Biologique, CNRS and
Université Paul Sabatier,
bâtiment 4R3, 118 route de
Narbonne, F-31062 Toulouse,
France

Correspondence: E-mail:
chave@cict.fr

Abstract

I review the mathematical and biological aspects of Hubbell's (2001) neutral theory of species abundance for ecological communities, and clarify its historical connections with closely related approaches in population genetics. A selective overview of the empirical evidence for and against this theory is provided, with a special emphasis on tropical plant communities. The neutral theory predicts many of the basic patterns of biodiversity, confirming its heuristic power. The strict assumption of equivalence that defines neutrality, equivalence among individuals, finds little empirical support in general. However, a weaker assumption holds for stable communities, the equivalence of average fitness among species. One reason for the surprising success of the neutral theory is that all the theories of species coexistence satisfying the fitness equivalence assumption, including many theories of niche differentiation, generate exactly the same patterns as the neutral theory. Hubbell's neutral theory represents an important synthesis and a much needed demonstration of the pivotal role of intraspecific variability in ecology. Further improvements should lead to an explicit linking to niche-based processes. This research programme will depend crucially on forthcoming theoretical and empirical achievements.

Keywords

Community ecology, intraspecific variability, neutral theory, theoretical ecology.

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INTRODUCTION

A major goal of community ecology is to find synthetic explanations for the observed patterns of species abundance in space and time, and across scales (Ricklefs & Schluter 1993; Brown 1995). Over the past two decades, Hubbell (1979, 1997, 2001) has developed an original theory that seeks to predict these patterns. Hubbell's theory contends that drastic simplifications on the manifold processes that shape ecological communities can be made. This theory is *neutral* because it assumes that all individuals in a community are strictly equivalent regarding their prospects of reproduction and death. Although elaborate niche theories of species coexistence (Chesson 2000; Chase & Leibold 2003) are ignored, Hubbell (2001) has shown that his theory is capable of summarizing a surprising array of empirical patterns of species abundance. In a world where environmental issues and threats to biodiversity are urgent matters, a simple theory such as this one is in principle, highly desirable.

The neutral theory is considered by many ecologists as a radical shift from established niche theories. However, niche and neutral theories are complementary, not conflicting. Theories of coexistence by niche differentiation are mostly

concerned with purely deterministic processes, and a small number of species that interact through fixed rules, as prescribed in the Lotka-Volterra equations. By contrast, the neutral theory is primarily concerned with species-rich communities (tropical forests, coral reefs) with many rare species, where the role of stochasticity at the individual scale becomes unavoidable. Attempts to unify these two theories is currently not only hampered by mathematical problems but also by psychological biases, and a critical review is in need for both of them (Chase & Leibold 2003). My goal here is to review some of the prominent aspects of the neutral theory in community ecology and, hopefully, pave the road for a synthetic theory.

The premise of this review is that Hubbell's (2001) book represents an outstanding attempt to promote the neutral theory as an operational theory in community ecology. There is much to be learned from such approaches, provided that they are continuously exposed both to empirical knowledge and to theoretical advances. A number of Hubbell's (2001) critiques however deal with the difficulties of its mathematical developments and the poor linkage with existing theories of population genetics (Brown 2001). Although Bell (2001), in a review of what he refers to as the field of 'neutral

macroecology', clarified this connection with population genetics, it seems serviceable to be more specific about these relationships, some of which are explicit in Watterson (1974) and in Caswell (1976). I shall provide a brief historical account of the emergence of neutrality.

The second difficulty relates to the already large literature on tests of the neutral theory. As of December 2003, 2 years after the publication of Hubbell (2001), ISI's Web of Science reports 178 scientific articles citing this work. The impact of Hubbell's neutral theory can be evaluated in the light of empirical evidence. As we shall see, it turns out that tests of the neutral theory fail to invalidate its most recent versions, although they have been critical to emphasize the deficiencies of earlier versions. Much of this research has focused on tropical rainforest plants, and the present review reflects this bias. It would be important to extend this testing procedure to other communities.

A third, and fundamental, problem in the neutral theory concerns the assumption of equivalence among individuals. Bell (2001) commented on this point that 'perhaps ecologists find it difficult to accept that the differences they so clearly recognize among their study species have no functional significance, whereas geneticists, dealing with spots on a gel, are more inclined to neutralism'. While the natural 'inclination' of geneticists for neutralism is a highly debatable fact (Gillespie 1991; Kreitman 1996), it is certainly true that there is a strong psychological bias against this assumption amongst ecologists. I shall address the following questions: a) what does the assumption of equivalence imply?, b) is this assumption supported empirically?, c) if not, shall we decide that this theory is definitely falsified hence it should be rejected, or shall we salvage it?

Finally, I discuss the philosophical implications of the neutral theory, and conclude that we need to bridge the gap between niche-based and neutral theories, and develop both niche models that include stochasticity and quasi-neutral models that allow for interspecific differences.

PATTERNS OF ABUNDANCE AND THE EMERGENCE OF NEUTRAL MODELS

The emergence of the concept of neutrality in population genetics, and subsequently in community ecology, has been a long process. The successes of deterministic mathematical theories of species coexistence, where the essential role of intraspecific variability is largely ignored, may partly explain this difficult emergence.

Statistical models of abundance

Over the past century, ecologists have produced graphics to illustrate patterns of diversity (Whittaker 1972). Species-area, species abundance, and rank-abundance curves, and indices

of diversity have become standard tools. One of the most consistent findings of these studies is that in a sample, a small fraction of the species represent most of the organisms, while many species are represented by very few individuals, quite often singletons. In this section, I shall mostly focus on patterns of local species abundance (Whittaker 1972). Patterns of spatial species turnover (or beta-diversity) have been discussed in recent papers (Nekola & White 1999; Hubbell 2001; Chave & Leigh 2002; Condit *et al.* 2002; Mouquet & Loreau 2003) and will here be only mentioned in passing.

In the 1940s, statistical models were proposed to describe patterns of species abundance (Fisher *et al.* 1943; Preston 1948), and they still motivate a great deal of interest today (Magurran & Henderson 2003; McGill 2003). In a joint paper (Fisher *et al.* 1943), the great statistician Sir Ronald Fisher proposed an elegant method for modelling the observed species abundance in ecological studies. As this model turns out to be tightly connected with the topic of this review, a concise reminder of its mathematical formulation is provided below.

Many empirical studies in community ecology consist of sampling an assemblage of trophically equivalent co-occurring species, or community. Such samples can be permanent plots for plants, traps for insects, and counting protocols for vertebrates. Let us consider a sample containing N individuals. The abundance curve $F(n)$ is defined as the number of species in the sample represented by exactly n individuals. Fisher assumed that, if none of the species is very abundant, the expected number of individuals sampled in any of the species could be modelled by a Poisson sampling process for any given species $P_m(n) = e^{-m} m^n / n!$, where m is the expected abundance of this species and n , its observed abundance. He then hypothesized that the probability that a randomly chosen species has an expected abundance m , follows a gamma distribution $p_{k,\alpha}(m) = \alpha^k m^{k-1} e^{-\alpha m} / \Gamma(k)$, with no correlation among the expected abundances (throughout this paper, $\Gamma(k)$ represents the usual gamma function, such that $\Gamma(k) = (k-1)!$ for any integer $k > 0$). Fisher did not originally justify this hypothesis. The number of species with n individuals is obtained by the formula (see e.g. Fisher *et al.* 1943; Anscombe 1950; Engen 1978)

$$F_{k,\alpha}(n) = \frac{\Gamma(k+n)}{\Gamma(k)n!} x^n (1-x)^k, \quad \text{for } n \geq 0, \quad (1)$$

with $x = 1/(1 + \alpha)$. This is the negative binomial distribution. The species absent from the sample are not observable, and a proper normalization should be $S = \sum_{n=1} F_{k,\alpha}(n)$, giving rise to the 'zero-truncated' negative binomial. Fisher then went on to assume the parameter k close to zero and he found

$$F_{\alpha}(n) = \alpha \frac{x^n}{n}, \quad \text{for } n > 0. \quad (2)$$

This is the famous log-series distribution. In this formalism, $N = \sum_{n=1}^{\infty} n F_{\alpha}(n)$. Inserting eqn 1 in the expressions for S and N , the relationship between species number and sample size (species–individual curve) is

$$S \simeq \alpha \ln \left(1 + \frac{N}{\alpha} \right). \quad (3)$$

The single fitting parameter of this sampling curve is Fisher's α . Parameter inference for the log-series and the negative binomial sampling models is discussed in Anscombe (1950).

Fisher's model is certainly not the only possible sampling model of species abundance. Preston (1948) challenged it early. He lumped the species numbers into logarithmic abundance classes (species of abundance 1, 2–3, 4–7, 8–15, and so forth), and claimed that empirical evidence was supporting a Gaussian shape for this modified distribution. Hence, the species abundance distribution should be best fit by a log-normal distribution, rather than the log-series distribution. Although this claim is indeed supported in many cases (Tokeshi 1990), this is not universally valid. Figure 1 compares the log-transformed species abundance distribution for a tree census in the 50-ha permanent sampling plot in the moist tropical forest of Barro Colorado

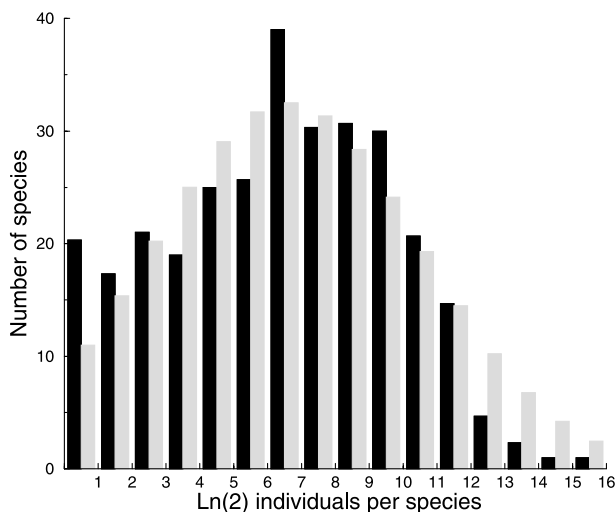


Figure 1 Species abundance distribution for the 50-ha permanent sampling plot in the moist tropical forest of Barro Colorado Island, Panama. All free-standing trees above 1 cm in diameter at breast height were included in the census ($\approx 230\,000$ individuals in each census). Black bars are species numbers averaged over three censuses (1985, 1990 and 1995). Grey bars correspond to the prediction of the log-normal species abundance distribution. Data from the Center for Tropical Forest Science.

Island (BCI), Central Panama, to the prediction of the log-normal species abundance distribution. The log-normal distribution typically predicts too few rare species (less than two individuals), and too many very abundant species (over 4096 individuals).

MacArthur (1957) proposed another model, known as the 'broken-stick' model, that assumes community assembly rules of sequential niche apportionment (Tokeshi 1990). In this model, the resource is in fixed supply and is represented by a segment of unit length. A first species settles and occupies a randomly drawn fraction of this resource. The second species then upholds a random fraction of the leftover resource, and so forth. The community relative abundance distribution can be derived from this construction (MacArthur 1957). I mention this model here, because it has an interesting history: after years of heated debates over its ecological pertinence, Cohen (1968) showed that it was mathematically equivalent to Fisher's model where the parameter k tends to one rather than to zero as in the log-series model (see also Engen 1978). Hence, the broken-stick model is a particular case of Fisher's sampling theory (with $k = 1$ in eqn 1).

From statistical models to neutral community models

Fisher's model does not rely upon demographic processes. The sole assumption is that the expected abundances of randomly chosen species are independently drawn from a gamma distribution. The first attempt to link this statistical theory to demographic population models was tackled by Kendall (1948). He proposed a simple model of population growth by a birth–death process, where the birth term exactly balances the death term. In such a model, the species abundance is undergoing an unbiased random walk, and the expectation that the species has n individuals at time t is given by the log-series distribution, with $x = t/(1 + t)$. This model does not assume a saturated community, as the expected number of individuals N is unbounded, and grows as $N \approx \alpha t$ (Kendall 1948; Caswell 1976). This model has been influential in theoretical population genetics, but in our context, the prediction that the community size is unbounded is unrealistic.

Following an important theoretical paper by Moran (1958); Karlin & McGregor (1967) proposed a model for the maintenance of polymorphism in natural populations. Contrary to Kendall (1948), their model assumes fixed-sized populations. Their model was originally described in the context of population genetics, but it readily translates into community ecology if the words 'species', 'speciation and immigration' and 'community' replace the words 'type', 'mutation' and 'population', respectively. In this model, the community consists of a fixed number of N individuals, each capable of speciating with probability v into a new

species at each generation. Hence, new species enter the system as a Poisson process through speciation or immigration at rate v . A finite number r of species can exist in a community, and the abundances n_i for species $i \in \{1, \dots, r\}$ can change only by one unit at a time.

Karlin & McGregor (1967) studied $F(n)$, the expected number of species i for which $n_i = n$, equivalent to our species abundance distribution. The tipping point of their derivation lies in the fact that the r -species model is equivalent to a model with just two species, one of abundance n (the 'focal' species), and one of abundance $N - n$. Thus the growth rate λ_n and death rate μ_n for the focal species are, respectively (for large r and N):

$$\lambda_n = \frac{N-n}{N} \left(\frac{vN-n}{r} + (1-v) \frac{n}{N-1} \right),$$

$$\mu_n = \frac{n}{N} \left(v \frac{n}{N} + \left(1 - \frac{v}{r} \right) \frac{N-n}{N-1} \right). \quad (4)$$

These formulas have simple interpretations: for instance λ_n is the probability that a species of abundance n increases by one unit. This is possible only if an individual of another species is picked [probability $(N-n)/N$] and is replaced by an individual of the focal species, either by recruitment [probability $(1-v)/(N-1)$] or by speciation [probability $v(N-n)/(Nr)$]. This two-species model was solved by Moran (1958) who showed that the abundance distribution $F(n)$ reads (Moran 1958, eqn 10; Karlin & McGregor 1967, eqn 4.11):

$$F(n) = r \frac{\lambda_0 \dots \lambda_{n-1}}{\mu_1 \dots \mu_n} \quad (5)$$

In the case of very many distinct species ($r \rightarrow \infty$), this formula can be simplified:

$$F(n) = \frac{1}{n} \frac{Nv}{1-v} \frac{N!}{(N-n)!} \frac{\Gamma\left(\frac{N}{1-v} - n\right)}{\Gamma\left(\frac{N}{1-v}\right)}. \quad (6)$$

If the abundance of all the species is small, then $\lambda_n \approx \lambda_n/N$, $\mu_n \approx \mu_n/N$, and $\lambda_0 = v$, hence, from eqn 5, the abundance distribution takes on the form of a log-series distribution:

$$F(n) = vN \frac{(\lambda/\mu)^n}{n} \quad (7)$$

Comparing with eqn 2, vN is equivalent to Fisher's α (and to Hubbell's 1997 θ parameter), while $\lambda/\mu = x$. Hence, Karlin & McGregor's (1967) model predicts Fisher's sampling model.

Watterson (1974) and Caswell (1976) first made the connection between these population genetics and community ecology. Watterson (1974) provided a detailed (but technical) report of the implications of population genetics

theory when applied to ecology, with a particular emphasis on species-area curves. Caswell (1976) also made a notable attempt to promote this theory in community ecology. Both Watterson (1974) and Caswell (1976) explicitly discussed models with fixed communities (their model II is Karlin & McGregor's 1967 model). However, two limitations were encountered by Caswell: all of his models predicted an unrealistic species abundance distribution (formula 6, when plotted as a log-linear histogram does not show a mode), and they lacked empirical support.

These issues were realized by Hubbell (1979), who readdressed the role of neutral models in predicting patterns of abundance in a dry forest of Costa Rica. He simulated a forest with K individual trees, D of which are killed by natural disturbances every time step, irrespective of their species. The results were based on numerical simulations of a forest model, rather than on mathematical results. In fact, Hubbell's (1979) is formally equivalent to Karlin and McGregor's (1967) model described above (but $D > 1$ individuals are killed each time step, see Leigh *et al.* 1993), and the log-normal-like pattern is only observed for a few time steps in Hubbell's simulations, after which it converges to a species abundance distribution without a mode. Hubbell & Foster (1983) subsequently evaluated the neutral theory over larger spatial and temporal scales in the BCI plot.

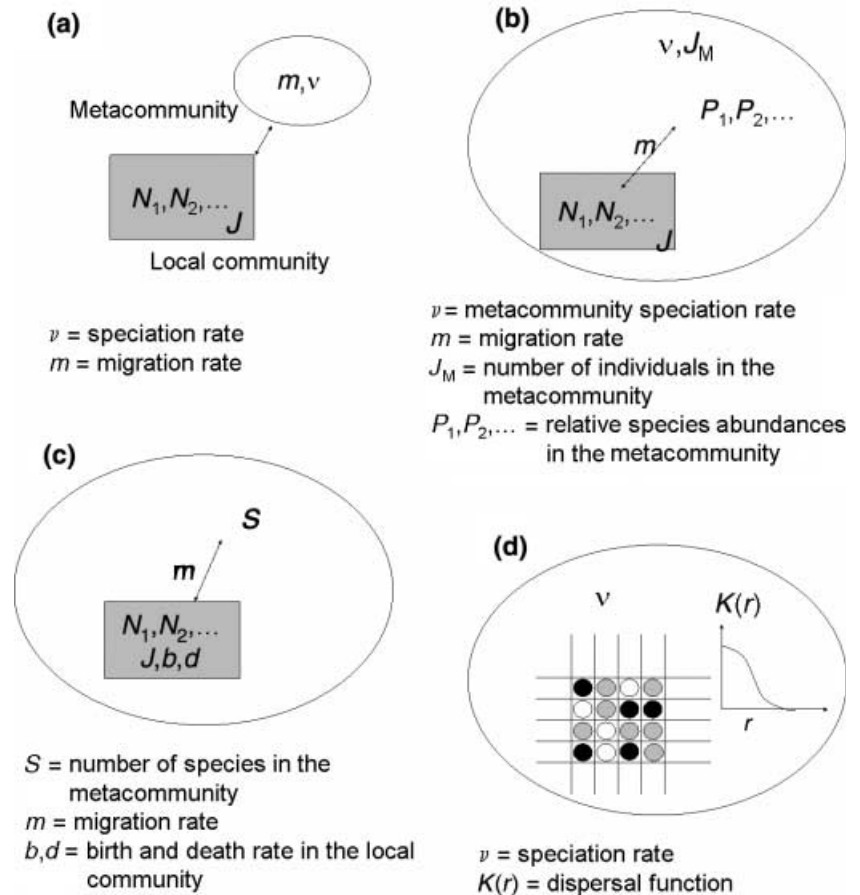
Over the 60 years since the publication of Fisher *et al.* (1943), neutralism has grown from a mere technical assumption in a statistical model to a mathematically consistent and testable theory, with Karlin and McGregor's (1967) work being probably among the most important theoretical work of all. Yet, the neutral theory needed to be taken one step further to explain larger scale patterns of species abundance.

Recent developments: spatially structured neutral models

I shall now describe three recently published neutral models: the 'two-scale' model first published by Hubbell (1997) and extended in Hubbell (2001), the neutral model of Bell (2000), and the spatially structured model of Chave *et al.* (2002). These models are compared and contrasted to Hubbell (1979) in Fig. 2.

The most popular neutral model to date is without doubt that of Hubbell (1997, 2001). He proposed a two-scale neutral theory that accounts not only for the dynamics in local communities, but also for migration across these local communities. Species i can immigrate at rate m from a 'regional' pool (Ricklefs 1987), or metacommunity of J_M individuals, whose dynamics is itself governed by a neutral speciation-extinction process, and where it has a relative abundance P_i . Metacommunity species abundances are governed by Karlin & McGregor's (1967) model, but they

Figure 2 Four different neutral models of community ecology. In all these models, N_i represents the abundance of species i in the local community, and J the total abundance in the local community ($J = \sum_{i=1}^S N_i$). (a) Hubbell's (1979) neutral model. Local community dynamics is saturated: each death is immediately replaced with a new individual. Speciation (or, equivalently, immigration) enables diversity to be maintained in the metacommunity. (b) Hubbell's (2001) neutral model. Same as Hubbell's (1979) model, but the local community now interacts with the metacommunity through a migration process. (c) Bell's (2000) neutral model. Like in Hubbell (1979), the metacommunity is modelled implicitly. At each time step, each species of the metacommunity has a chance m of recruiting a single individual into the local community. In the local community, each individual gives birth to one offspring with probability b and dies with probability d . If the community size exceeds K individuals, the excess is removed at random. (d) Chave *et al.* (2002) neutral model. The whole metacommunity is modelled, and species richness is maintained by speciation within the metacommunity. Dispersal limitation is modelled through a dispersal function $K(r)$.



are not observable, only the species abundances in the local community are. Now, the local and regional scales are coupled through the migration rate m : if m is very small, the role of immigration at the local scale parallels that of speciation at the regional scale, except that immigration is a correlated process (a regionally abundant species is more likely to immigrate into any local community than a regionally rare one). This adds a further complication to the derivation of the species abundance distribution in this model, and it is only recently that Volkov *et al.* (2003) provided an ingenious solution of this puzzle. Their main result is a generalization of eqn 6.

Bell (2000) described a simple neutral model: he simulated a community where all individuals have the same birth rate b and the same death rate d , but where $b \geq d$. If the community exceeds the specified ceiling of K individuals, excess individuals are removed at random. A metacommunity is implicitly defined by fixing a maximal number S of species (N , in Bell's notations) (Bell 2000). Any of the S species can migrate into the community irrespective of their local abundance. These two assumptions differ from other neutral models (Karlin & McGregor 1967; Hubbell 2001), and his rule of community saturation yields mathematical complications, as it does not

allow a straightforward interpretation in term of transition probabilities. In addition, the assumption that any species can immigrate yield, for m large, a peak of species with abundance 1 (see his fig. 1A). Nonetheless, this model is an original and computationally simple alternative to other neutral models.

The next stage is to develop spatially structured neutral models, where the offspring are dispersed in a limited neighbourhood around their parent (Levin *et al.* 2003). In the presence of dispersal limitation, remote locales are expected to be more dissimilar in species composition than in a panmictic model. Durrett & Levin (1996) found that dispersal-limited models yield steeper species-area curves than panmictic models, illustrating the higher spatial turnover of species composition in the presence of dispersal limitation (for rigorous results, see also Bramson *et al.* 1996, 1998). In simulations, space can be modelled as a regular grid in which a cell represents either a local community like in Kimura's stepping stone model (Hubbell 2001, chapter 7), or a single individual (Durrett & Levin 1996; Chave *et al.* 2002). In the latter case, the distinction between local community and metacommunity becomes superfluous. Dispersal limitation can be modelled by assuming that individuals can only disperse onto nearest neighbouring

communities or sites, or by simulating a variety of more realistic dispersal curves, for instance a Gaussian or a Lévy-like dispersal curve (Chave & Leigh 2002; Chave *et al.* 2002; Levin *et al.* 2003). Such spatially structured neutral models are flexible but they are also difficult to simulate, and to study mathematically.

TESTING THE PREDICTIONS OF THE NEUTRAL THEORY

Tropical forests currently cover *c.* 17 millions sq. km, with roughly a thousand billion (10^{12}) trees above 10 cm diameter at breast height (dbh) that may belong to over 10 000 (10^4) different tree species, which in turn shelter a majority of the Earth's biodiversity (Novotny *et al.* 2002). Given these figures, it should come to no surprise that tropical forests are an important testing ground for hypotheses on biodiversity. Here, I also report results for other ecosystems (temperate plants, coral reefs, fish communities), though those represent a minority of the published tests on the neutral theory.

The neutral theory is difficult to test. Chave *et al.* (2002) contrasted the predicted species abundance patterns of both neutral and non-neutral simulated models, and they found that they predicted similar patterns. More precisely, Chave *et al.* (2002) carried out extensive simulations of spatially structured neutral models both with and without dispersal limitation, and six non-neutral models (models including density-dependence and/or tradeoffs among species, with

and without dispersal limitation). These results concerning the species abundance distribution are summarized in Fig. 3. The species abundance distribution was modified by the presence of dispersal limitation, and to a lesser extent by density-dependent processes, but not so much by the presence of other diversity-maintaining mechanisms. More recently, other studies have confirmed that non-neutral models predict patterns that are difficult to distinguish from neutral ones (Mouquet & Loreau 2003; D. Purves & S. Pacala, unpublished data). However, testing the predictions of the neutral theory can be useful and this process has have already led to important improvements.

Tests of Hubbell's 1979 model

Hubbell's (1979) model has been influential during a decade and a half in community ecology, and tests of this model are still being published. If Hubbell's (1979) model is correct, there should not be any concerted pattern of commonness across communities. Two neutral communities far apart (in time or in space) should share only a modest fraction of their species, because of their limited similarity.

One of the early such test came from landscape-scale studies of the tree species composition in the western Amazon (Terborgh *et al.* 1996; Pitman *et al.* 2001, 2002). Dozens of permanent sampling plots, one to a few hectares in size each, were laid out, and each tree stem over 10 cm in diameter was recorded and identified to the species. One of the most consistent finding of these studies is the ubiquity

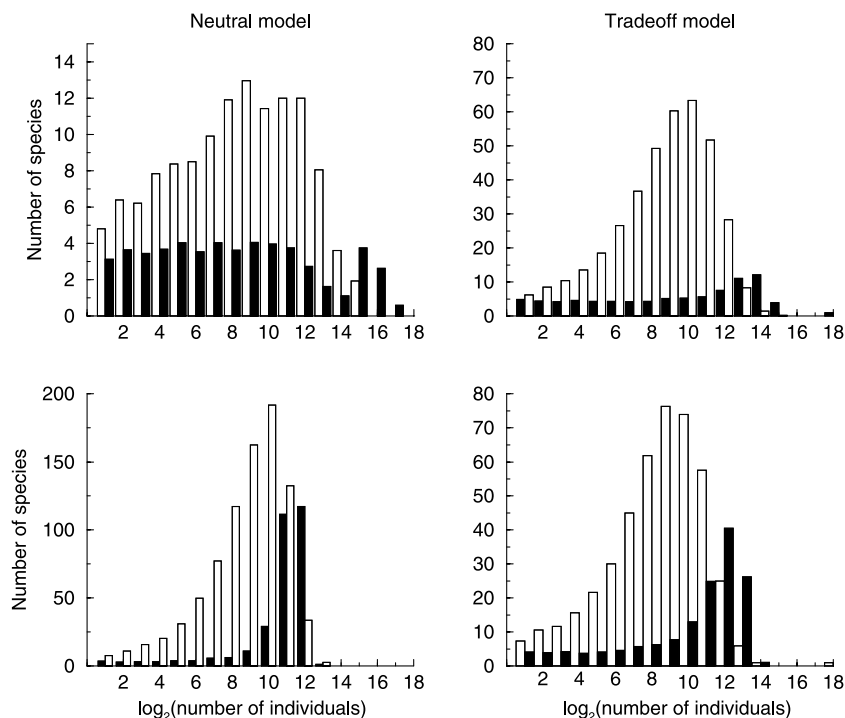


Figure 3 Equilibrium species abundance distributions in simulated ecological communities: neutral model without density-dependence (top left), tradeoff model without density-dependence (top right), neutral model with density-dependence (bottom left), and tradeoff model with density-dependence (bottom right). Light bars correspond to the model with nearest neighbour dispersal, while dark bars correspond to global dispersal. Only in the neutral model without density dependence and dispersal limitation does the abundance distribution have a flat shape. From Chave *et al.* (2002), fig. 7. Reprinted with permission from the University of Chicago Press.

of common species, that is, species that are both abundant locally, and frequently encountered across the landscape (Pitman *et al.*'s 2001 oligarchic species, with ≥ 1 stem per ha on average in the total data set). The most striking example of such species is the large palm *Iriartea deltoidea*, the most abundant species in two-third of the plots across Peru and Ecuador, that represented about 8% of the total sample. This palm has a broad biogeographic distribution, from Costa Rica to Bolivia. Pitman *et al.* (2001) report that 63% of the stems belong to common species in Ecuador, and 73% in Peru. See also Potts *et al.* (2002) for similar patterns of tree species composition in Borneo. Empirical support for oligarchic species runs against the predictions of Hubbell's (1979) model.

Other researchers have used chronosequences to test the temporal patterns of species abundance as predicted by Hubbell's model. Pandolfi (1996) used a paleo-reconstruction of coral reef assemblages in Papua, New Guinea over a period of 95 000 years, and he observed that the commonest species were consistently the same despite repeated climatic disturbances, suggesting that the most abundant species are also the best equipped to withstand environmental shifts (Pandolfi 1996, 2002). Clark & MacLachlan (2003) went one step further by combining spatial and temporal scales. They analysed the palynological record of tree taxa in an area 400 km on a side of southern Ontario, Canada, over 10 000 years. They showed that the abundance of selected tree taxa did not increase in variance among sites as would have been predicted by a neutral model much similar to Hubbell's (1979), and concluded that ecological communities are more homogeneous and persistent than predicted by this theory.

These arguments were strong incentives to include larger-scale processes in the neutral theory, and this resulted in Hubbell's (1997) unified model, where patterns of commonness are controlled by the metacommunity, not solely by the local community. Armed with this improved theory, Hubbell (2001), p 331 rejected as 'premature' Terborgh *et al.*'s (1996) and Pandolfi's (1996) conclusions. A different reading suggests that it is empirical findings themselves that led to the rejection, or rather the improvement, of the 1979 model. This is a nice example of 'theory maturation' (Lakatos 1970, see 'Synthesis'). Abundant species can have very large persistence times and broad ranges but these facts could not be predicted by Hubbell's (1979) model, which had no description of the regional pool.

Testing spatially structured neutral models

I now explore tests of spatially structured neutral models described in 'Recent developments: spatially structured neutral models'. These models are more complex, hence more difficult to test.

One recent attempt to test Hubbell's (2001) model is due to McGill (2003). He constructed species abundance distributions using the North American Bird Breeding Survey (BBS) and BCI's 50-ha plot. In both cases, he concluded that the log-normal species abundance distribution provided a better fit than Hubbell's (2001) distribution. However, the value of the BBS data in testing this theory is debatable, as neutral theory is explicitly concerned with communities of resident organisms (like plants, corals, or non-migratory animals). Also, Fig. 1 shows that the BCI species abundance distribution for all trees ≥ 1 cm dbh during the five censuses carried out so far is apparently non-normal. Yet, it may well be that Hubbell's (2001) model does an even poorer job at predicting this pattern than the log-normal distribution. The algorithmic procedure to construct the species abundance distribution described by Hubbell (2001) and used by McGill (2003) is complicated, but fortunately we can now use the results provided by Volkov *et al.* (2003). They derived a closed-form solution of the species abundance distribution for Hubbell's (2001) model. In response to McGill (2003), Volkov *et al.* (2003) concluded that the prediction of Hubbell's (2001) model did provide a better fit than the log-normal distribution for the BCI data. However, the differences between these two models are subtle and it would be unfair to use this test alone to reject one theory or the other.

Almost simultaneously, species abundance patterns were discussed by Magurran & Henderson (2003) who analysed a fish community in the Bristol Channel, UK, over a 21-year period, with monthly sampling. They did not directly test Hubbell's (2001) model, but they found that the species composition could be partitioned into persistent species, staying over 10 years in the record, and occasional species, staying less than 10 years and encountered in low abundances. They moreover showed that the species abundance distribution differed between the two groups, persistent species following a log-normal distribution, while occasional species followed a log-series distribution. Hence, only the rare species may be neutral, not common species. However, this could mean that the neutral model still works for the rare species, which are virtually impossible to study empirically, and for which predictive models are utterly needed. Also, one could argue that if the neutral model is disproved for the most abundant species, there is no reason to believe that it should be valid for the rare species either. Bell's (2000) simulations of his neutral model (see above) provide an interesting insight to this problem. He partitioned species into 'immigrant' species (those that appeared in the last 100 time steps) and 'long-resident' species. Constructing distinct species abundance distributions for these two species pools (see his fig. 2), he found exactly the pattern observed by Magurran & Henderson (2003). Hence, these results are compatible with the predictions of Bell's (2000) model.

The decrease of species similarity between communities as distance increases, or beta-diversity, is also predicted by the neutral theory (Chave & Leigh 2002). Condit *et al.* (2002) tested these predictions in three forests in Panama, Ecuador and Peru. The fit they obtained was good, showing that dispersal limitation alone predicts a substantial fraction of the beta-diversity, and providing a support for the neutral theory. A similar result was recently obtained in the Cameroonian rainforest (Hardy & Sonké in press). At small scales (<100 m), the quality of this fit was poorer, but this may be because of the practical choice of a Gaussian dispersal curve, rather than to a failure of the neutral model, as was also found in population genetics studies (Hardy & Vekemans 1999). Beta-diversity differed between Panama, Ecuador and Peru (Condit *et al.* 2002), and also Cameroon (Hardy & Sonké in press), reflecting expected historical differences among these biogeographic units.

An alternative interpretation is that environmental factors such as rainfall and geology of the substrate explain a large fraction of the variance in beta-diversity (Ashton & Hall 1992). Tuomisto *et al.* (2003) developed a similar thesis, basing their analysis on an impressive sampling of two groups of neotropical understory plants (Melastomataceae and pteridophytes). They evidenced a strong association with soil characteristics at the landscape scale (soil pH, content in exchangeable cations, moisture). However, if species show a strong habitat specialization, the community-wide species abundance distribution are the sum of within-habitat distributions, and if communities are neutral within each habitat, then the abundance distribution should be indistinguishable from the neutral prediction (D. Purves & S.W. Pacala, unpublished data). Hence, it is difficult to detect even a strong habitat specialization on patterns of species abundance. Empirical studies on habitat association, although extremely important for understanding the biology and the functioning of species, are not of great help to unravel non-neutral patterns of species abundance at the community scale.

Speciation and the evolutionary context

So far, I have largely ignored the evolutionary implications of the neutral theory. A comprehensive discussion of these aspects is beyond the scope of the present review, as they have recently been discussed by Ricklefs (2003). Important hypotheses on plant species diversification have been put forth decades ago, but are only being tested now with the help of molecular approaches (Richardson *et al.* 2001). Hubbell (2001) evaluated two modes by which species may arise in a metacommunity: the 'point mutation' mode and the 'fission' mode. In his point mutation mode, speciation is summarized into a probability for one individual to create a whole new species, like in polyploid isolation. He also explored models of allopatric speciation, his 'fission' mode,

where the members of one species are suddenly split into two species, for example by the uplift of a mountain.

Ricklefs (2003) first considered the predictions of the neutral theory under a point mutation mode with speciation rate v . This theory predicts that the average species lifetime T is $T \sim 2 \ln(1/(2v))$. Taking the above mentioned figure of 10^{12} trees and 10^4 different tree species across the tropics, we get an estimate of θ around 10^2 , or a speciation rate around $v \approx \theta/N = 10^{-10}$. Hence, the above formula yields an average species lifetime of 44 generations, or 4400 years (assuming 100 years per generation). Ricklefs (2003) remarked that this model would yield 25 new species every 100 years on the BCI plot. The point mutation model, he therefore argued, would lead to an astounding number of 'cryptic' species, that would be difficult to recognize by classic taxonomic methods. However, the 'fission' model of speciation would be consistent with the typically inferred species lifespan, but it would yield too many abundant species, leaving too little room for rare species. Ricklefs (2003) therefore concludes that a re-thinking of the basic mechanisms of species production is needed in Hubbell's (2001) neutral theory.

Hubbell (2003) replied that only old and abundant lineages qualify as species for taxonomists. The opportunities for introgression and hybridization even in what taxonomists recognize as different species suggests that a conservative definition of species is wise (Stacy 2001). Hence, Ricklefs's cryptic species may correspond to intraspecific variation, commonly observed in population genetics studies. Nonetheless, many tropical plant species have been described from unique specimens, and taxonomists generally have no indication of age. Furthermore, relatively few variants are described in tropical trees; indeed the tendency has been to elevate variants to full species in many cases. A 'neutral' solution of the too long species persistence in the fission model would be to acknowledge the importance of environmental shifts and catastrophic extinctions over long time scales (Morley 2000). In such a situation, the whole community would be periodically reduced to a much smaller size so that extinction rates would increase significantly even for the abundant species. The most sensible argument in favour of Hubbell's (2001) approach is that these two models, though unrealistic as such, represent the two extremes of a 'speciation continuum' (Hubbell 2003). Much more complex models of speciation could alternatively be included in this theory (Gavrilets 2003) but it is not clear that such elaborations would really add much at this point.

One way of testing the evolutionary predictions of the neutral theory consists in seeking regularities in phylogenies, and looking for relationships between species abundance and richness in higher order taxa, like the classic species/genus ratio. Webb *et al.* (2002) provided a thoughtful review of the

relationships between phylogenetic approaches and community ecology.

The point mutation mode implies that a family represented by many individuals is likely to be more diverse than a rare family. Moreover, more abundant species will have a higher probability of speciation. As we shall see now, the few studies that have addressed this issue failed to find a convincing disagreement between the neutral model and observed patterns. Enquist *et al.* (2002) used a collection of 0.1-ha plots collected by Alwyn Gentry in tropical South America, and showed that species number in these plots was strongly correlated to both family and genus numbers. Pooling all these datasets they constructed a 'South American species pool', and concluded that the species/genus ratio of samples randomly drawn from this pool departed significantly from the observations in real plots. Hence, tree communities are not random samples of the surrounding community. However, Enquist *et al.* (2002) may have improperly constructed the regional pool: in the network of 0.1-ha plots, genera and families are much better sampled than species (N.C.A. Pitman, pers. comm.). When this bias is accounted for, tree plots do not significantly depart from a random sampling of the regional species pool. Webb & Pitman (2002) tested that species and individuals in tree census plots of two tropical forests were randomly distributed across the angiosperm phylogeny, in agreement with the neutral theory. They also found that more diverse families tended to have more abundant species. However, this finding conflicts with the pattern found by Schwartz & Simberloff (2001) at a global scale and even with the pattern found in a different analysis of the same South American dataset used by Webb & Pitman (see Pitman *et al.* 2001). Possible causes of this discrepancy are discussed by Webb & Pitman (2002), and it is difficult to interpret this pattern as clear evidence for or against the neutral theory.

STATUS OF THE EQUIVALENCE ASSUMPTION

The previous section has demonstrated that the neutral theory can be considerably extended to predict previously unforeseen patterns of species abundance. It is possible to include a description of metacommunity processes, of dispersal limitation, and of various speciation modes. Yet, possible extensions are not unlimited. I now explore the assumption common to all neutral models, and discuss its biological pertinence.

Definition of the equivalence assumption

In a neutral community, all individuals within and across species are equivalent, that is, they have the same prospects of reproduction or mortality. In Hubbell's (2001, p 6) words, 'neutrality is defined at the *individual* level, not at the

species level [...] I use *neutral* to describe the assumption of per capita ecological equivalence of all individuals of all species in a trophically defined community.' The local community saturates the resource, assumed to be in fixed supply: each dying individual may be immediately replaced by the progeny of one of the surviving individuals.

This implies that species are ecologically equivalent, and that interspecific competition must be symmetrical. However, equivalence among individuals is a much stronger statement. Indeed, life-history interspecific variation is impossible, as it would not be equivalent to exchange an adult of species A for a juvenile of species B. Density-dependence or other stabilizing effects also are impossible. For instance, imagine the following stabilizing mechanism: the death rate could increase proportionally to each species' abundance, so that rare species are at an advantage over common species (Armstrong 1989; Chave *et al.* 2002). Hubbell (2003) suggested that such models can be called neutral so long as the intensity of the density-dependent effect is equal across species. However, an individual of a rare species would then have lower prospects of death than an individual of a common species. Thus, density-dependent models are incompatible with the assumption of equivalence among individuals (Chave *et al.* 2002).

Testing the equivalence assumption

The assumption of equivalence among individuals is difficult to assess: although the *prospects* of reproduction and death are assumed equal across individuals, the *actual* birth and death events are determined by stochastic processes. Hence, one can only test the assumption that all the species should have the same birth and death rates, bearing in mind that equivalence across species is a necessary, but not a sufficient condition for equivalence among individuals. Zhang & Lin (1997) and Yu *et al.* (1998) both proposed a modification of Hubbell's (1979) model where the mortality or the fecundity were allowed to vary across species. The species persistence time decreased dramatically, and the best 'competitor' (i.e. the species with the largest lifetime reproductive success) quickly took over the simulated community. Wright (2002) showed that such models should yield species persistence times intermediate between the prediction of Hubbell's (1979) model and that of Yu *et al.* (1998). This confirms that this equivalence assumption is crucial, and that the model's predictions are not robust to slight uncorrelated departures from it.

Does field evidence confirm the species-equivalence assumption? To address this question, I rely on the BCI data set. In 1990–1995, mortality rates of tree species varied from 0.44 to 16.4% per year and recruitment rates varied from 0.34 to 12.0% per year for the 63 species with over 50 individuals ≥ 10 cm dbh (see also Condit *et al.* 1995; Sheil

et al. 2000). To test how many species departed from the mean community recruitment and death rates, I also computed a standard error (assuming that both processes are Poisson), and performed a *t*-test on each species. I found that for only 26 species of 63 (41%) the null hypothesis (neutrality) could not be excluded. Hence, the majority of species are non-neutral, even with this permissive test. This clearly runs against the equivalence of demographic parameters among species.

Fitness equivalence

Faced to this result, we are left in the uncomfortable position of justifying why a model whose principal assumption looks so evidently false still deserves consideration. Hubbell (2001, p 327) writes: '[a]ccording to the neutral theory, mostly what mechanisms remain once per capita relative fitnesses are equalized are processes of ecological drift'. In other words, the invariance of per capita relative fitness explains why the neutral theory is so successful, despite this apparent falsity (see also Hubbell 2001 pp 320–322). In fact, the neutral theory says nothing about such processes of fitness equalization. A rough estimate of the fitness for plant populations is the lifetime reproductive success, the number of new individuals produced during the lifetime of an individual, which may be measured as the ratio of birth rate over death rate ($R_0 = b/d$). A community where all the species have exactly the same fitness (that is $R_0 = 1$ for all species) is at demographic equilibrium: it shows no consistent trend of change in species abundance. This definition is closely related to Chase & Leibold's (2003, p 26) definition of a species's zero net growth isocline (ZNGI).

Is the assumption of fitness equivalence valid, for example in the BCI plot? I computed R_0 together with a standard error for the same 63 species as above. R_0 varied between 0.20 and 4.36. A total of 53 species (84%) showed no marked increase or decrease over the 1990–1995-period ($P > 0.05$). The remaining 10 species were non-neutral during this period. Condit *et al.* (1999) reported additional information on the rapidly changing populations in both BCI and the Pasoh 50-ha plot (peninsular Malaysia). Arguably, 5 years is a very limited period for studying the dynamics of tropical trees. The rare studies that have investigated long-term trends of forest composition however confirm the remarkable permanence of species abundances over half a century (Manokaran & Swaine 1994 for peninsular Malaysia 1947–1985; Sheil *et al.* 2000 for Uganda 1933–1993). Leigh *et al.* (1993) arrived at a different conclusion by studying six islands created in 1913 by the formation of Gatun Lake, Central Panama. However, only a few non-neutral species may have confused their analysis. It would be important to reanalyse these data by looking at the species by species trends.

While much caution should be paid when interpreting these demographic and statistical analyses (for instance, birth and death are unlikely to be real Poisson processes, we are implicitly assuming that all trees ≥ 10 cm dbh have the same potential of reproduction, see e.g. Cam *et al.* 2002), it is tempting to conclude that many natural communities indeed verify the assumption of fitness equivalence. Together with the assumption of fixed total community size, this implies that the *expected* net growth is zero for each species (this does not mean that abundances themselves are fixed, as they are stochastic variables and therefore fluctuate in time).

Let us now turn to the discussion of these results. It is essential to emphasize that in tightly regulated niche models, where the species abundance does not fluctuate at all but is strongly constrained by its environment, the same assumption of fitness equivalence holds. Thus this assumption does *not* define neutral models, but a much broader class of models, including many non-neutral ones. Chesson (2000) recently proposed two main types of diversity-maintaining mechanisms in models of species coexistence: *equalizing* mechanisms, that tend to minimize average fitness differences among species, and *stabilizing* mechanisms, if negative intraspecific interactions tend to be greater than interspecific interactions (Armstrong 1989; Chesson 2000). In this terminology, a precise hypothesis can be formulated: a large class of equalizing – but not stabilizing – models, predict exactly the same patterns as neutral models. That the neutral theory makes excellent predictions of species abundance patterns, despite the fact that its crucial assumption of equivalence is invalid, is therefore not a paradox.

This interpretation raises one problem. If the above is correct, then the presence of stabilizing effects should lead to patterns that differ from those predicted by the neutral theory. Indeed, simulations show that in a model with density-dependence, the species abundance distribution is more peaked than in the neutral model (Fig. 3). An important stabilizing effect in plant community ecology is the limitation of competitive exclusion because of negative density-dependence, possibly mediated by predators or by diseases (Janzen-Connell effect, reviewed in Givnish 1999; Wright 2002). Most tropical plant ecologists now agree that this process is at play in tropical plant communities. Such a process may not be incompatible with neutral-like patterns at the community level, if a different, *destabilizing* mechanism compensates for it. Recent simulations (J. Chave & H. Chaté, unpublished results) suggest that dispersal limitation, which typically leads to spatial clumping of species, could play the role of such a destabilizing mechanism (for a related discussion in a different system, see Neuhauser & Pacala 1999).

In sum, I here contend that neutral theories are useful, not because the real world is neutral (it is not) but because the functional differences we observe among species or among individuals are not essential to predict some of the

patterns observed at larger scales. This is an important lesson in community ecology, and a strong motivation for further explorations of the connections between neutral and non-neutral theories.

SYNTHESIS

The neutral theory has generated much controversy because it suggests a radically different view of ecological communities. This is reminiscent of the debate on null models that has been so decisive in shaping the contemporary thinking in ecology (Simberloff 1983; Diamond & Case 1986; Loehle 1987). At this time, one camp was declared against the strict hypothetico-deductive method allegedly espoused by Popper, while the other was against an anarchic proliferation of knowledge, mostly based on implicit hypotheses, rather than on precisely specified ones. Ironically, two decades later, some of the critics of the neutral theory have endorsed the dogmatic falsificationist approach. However, dogmatic falsificationism is no more acceptable in ecology than in other sciences. According to Lakatos (1970), 'insistence on testing predictions too early [...] may result in premature rejection of a partially correct theory', hence theories should be 'sheltered' before they are 'mature'. Moreover, 'theory tenacity', the unwillingness to give up an idea in the face of contradiction, is a necessary factor to enable theory maturation. However, a research programme should eventually be exposed to the facts of the real life, bearing in mind that 'no experiment, experimental report, observation statement [...] alone can lead to falsification. There is no falsification before the emergence of a better theory' (Lakatos 1970).

It is too early to speculate on the future of the neutral theory, but I largely endorse Brown (2001)'s opinion. In its most radical interpretation, the neutral theory is blind to all the biological mechanisms that may contribute to niche differentiation in real communities. This position is evidently wrong, as mechanisms of niche differentiation play an essential role in nature. As a result, a widely held conclusion is that the neutral theory is not a useful representation of nature. While I agree that mechanisms of niche differentiation are indeed essential, I disagree with this conclusion. Again, citing Lakatos (1970), p 137: 'we may appraise research programmes even after their elimination for their *heuristic power*: how many new facts did they produce, how great was their capacity to explain their refutations in the course of their growth? (we may also appraise them for the stimulus they gave to mathematics [...])'. With this criterion, the neutral theory emerges as a most valuable one. Ecology, just like any other science, needs not only predictive theories but also conceptual ones. Physical sciences abound of such examples: the kinetic theory of gases developed in the 19th century is not a useful representation of nature (except perhaps for interstellar

gases). However, the fundamental concepts of statistical physics (temperature, entropy, free energy) were first correctly defined within this theory. The neutral theory in its present formulation resembles the kinetic theory of gases: it may not be a pertinent description of nature, but it does contain important aspects that other theories are missing, or ignoring: it places a strong emphasis on stochasticity, deals with large assemblies of *individuals* of different kinds, and makes assumptions about the ways these *individuals* are interacting.

In conclusion, the neutral theory has been influential in developing quantitative models in molecular evolution and in population genetics. If it is to provide the same service in community ecology, it should (1) foster the acquisition and access to biodiversity data, (2) be tested using well-designed statistical methods, and (3) provide the basis for more developed theories that would include niche differentiation processes. This programme has already started, but much progress is ahead.

Development of databases

There is a persistent gap in the access to quantitative data in community ecology and in macroecology. This problem will be overcome by creating world-wide databases, comparable with the Global Pollen Database, or the Genome Database. Institutions and researchers are fortunately now addressing this issue by making available facilities to compile, synthesize and analyse macroecological data. Two remarkable examples of such an effort are provided by the Salvias project (<http://www.salvias.net/>) and the Centre for Tropical Forest Science (<http://www.ctfs.si.edu/>).

Tests of the neutral theory

The development of statistical methods to test ecological theories is also a key point. Such tests have already been developed in molecular ecology (Ford 2002), but they need to be adapted to ecological questions. I have here reviewed several empirical tests of the neutral theory. Broadly, these tests fall into two classes: tests of the theory assumptions and tests of the theory predictions. So far these tests have been more useful to improve on the theory than to falsify it. Because most of them have assumed a limiting formulation of this theory, their conclusions needed a critical reassessment.

Theoretical progress

The underlying mathematical theory for neutral models, the theory of Markov processes, is an extremely powerful tool. A theoretical derivation of species abundance distributions is now possible, and a better interpretation of the observed

species-area curves will hopefully follow. The next challenge ahead is to integrate niche and neutral theories, that is to add more processes in neutral theories and more stochasticity in niche theories. The crucial role of niche theories in this programme is to explain how and under which circumstances the conditions for the application of the neutral theory are fulfilled.

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