

The merits of neutral theory

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Hubbell's neutral theory of biodiversity has challenged the classic niche-based view of ecological community structure. Although there have been many attempts to falsify Hubbell's theory, we argue that falsification should not lead to rejection, because there is more to the theory than neutrality alone. Much of the criticism has focused on the neutrality assumption without full appreciation of other relevant aspects of the theory. Here, we emphasize that neutral theory is also a stochastic theory, a sampling theory and a dispersal-limited theory. These important additional features should be retained in future theoretical developments of community ecology.

The entangled bank

'When we look at the plants and bushes clothing an entangled bank, we are tempted to attribute their proportional numbers and kinds to what we call chance. But how false a view is this!'. In this statement, Darwin clearly summarized his philosophical position: there is no place for stochasticity in population biology [1]. In 2001, Stephen Hubbell [2], after more than 25 years working on population and community ecology of tree species in tropical forests, presented an explanatory theory that is formulated entirely in terms of chance. Given that *On the Origin of Species by means of Natural Selection* [1] is one of the most influential scientific books ever written, it is no wonder that Hubbell's ideas have generated so much controversy among ecologists [3–10].

Here, we do not enter into a philosophical discussion of the nature and origins of randomness in the world around us, but instead take an operational approach and argue why chance should be taken into account in any attempt to gain insight in the structure and functioning of ecological communities [11,12]. We discuss the ability of neutral theory to generate new insights in community ecology, which, in the end, might not support neutrality. We also discuss the limitations and potential application of neutral ideas to biodiversity assessment in empirical settings.

Neutral theory is an ideal theory

Most previous articles on neutral theory highlight its failure to capture the complexity of ecological communities [5,13–15]. However, here, we emphasize its merits and argue that neutral theory in ecology is a first approximation to reality. Ideal gases do not exist, neither do neutral communities. Similar to the kinetic theory of ideal gases in physics, neutral theory is a basic theory that provides the

essential ingredients to further explore theories that involve more complex assumptions [16,17].

What are the essential ingredients of neutral theory? First, and foremost, it is a neutral theory in that the

Glossary

Beta-diversity: the component of biodiversity that is due to the spatial nature of ecological communities. It measures the extent to which species composition changes along the spatial dimension.

Binomial sampling: see dispersal-assembled communities.

Competitive hierarchy: a community ordered by competitive strength. Communities are called 'egalitarian' when such an ordering does not exist.

Dispersal-assembled communities: communities where it is assumed that species are present mainly or solely owing to dispersal (immigration), rather than because they adapted to the habitat (this yields niche-assembled communities). In a dispersal-limited community, immigrants cannot freely enter the community and the probability that an empty site will be occupied by an immigrant is <1 . According to recent theory, such a dispersal-limited community can be regarded as a dispersal-limited sample from the metacommunity, in contrast to a binomial (drawing with replacement) or hypergeometric (drawing without replacement) sample, which are random samples and apply to nondispersal-limited communities.

Dispersal limitation: see dispersal-assembled communities.

Ecological equivalence: when differences among individuals belonging to different species do not translate into differences in their probabilities of being, and persisting, in the present and future community.

Etienne sampling formula: see Box 3.

Ewens sampling formula: see Box 3.

Fundamental biodiversity number: a measure of regional diversity in neutral theory. It is a composite parameter, comprising the speciation rate and the metacommunity size (number of individuals). It is asymptotically equal to the alpha parameter introduced by Fisher, and can be estimated from species abundance data (Boxes 1 and 3).

Fundamental dispersal number: a measure of the amount of dispersal limitation of a given community in neutral theory. It is a composite parameter, comprising the immigration rate and the local community size. It is indicated by I and can be estimated from species abundance data.

Hypergeometric sampling: see dispersal-assembled communities.

Neutral drift: when the abundances of different species differ owing only to stochasticity in birth, death and dispersal. This causes neutral or ecological drift; a random walk of the abundance of a species.

Niche-assembled communities: see dispersal-assembled communities.

Sampling formula: multivariate probability distribution that gives the probability of obtaining n_1 individuals of species 1, n_2 individuals of species 2, and so on, when a given sampling process is applied. Sampling formulae are true likelihood functions to be used in parameter estimation and model comparison.

Species abundance distribution: a measure describing how abundances are distributed over species in a community. A species abundance data set contains the abundances of each species empirically observed in a sample. It can be summarized by giving the number of species that have the same abundance. When abundances are grouped in, usually logarithmic, abundance classes, the data can be plotted in a species abundance histogram and also by ordering the abundances by decreasing magnitude and then plotting them against their number in this order. This yields a rank-abundance curve, also known as a dominance-diversity curve (Box 3).

Species-area relation: how the number of species increases with the area sampled. At a very small scale, the number of species increases rapidly owing to sampling effects. At an intermediate scale, the number of species appears to increase as a power of the sampled area.

Zero-sum assumption: that the available resources in a community are saturated at all times. If, owing to the death of an individual in the community or to seasonal fluctuations, a resource becomes available, it will immediately be used by a new individual. When the amount of resources is constant, it implies that so too is the community size.

interactions among species are assumed to be equivalent on an individual ‘per capita’ basis [2]. Second, it is a stochastic theory, based on mechanistic assumptions about the processes controlling the origin and interaction of biological populations at the individual level (i.e. speciation, birth, death and migration). Because interactions are assumed to operate at the individual level, but the regularities that we would like to explain are truly macroscopic, this feature is reminiscent of the statistical thermodynamics approach in physics [2,18,19]. Third, it is a sampling theory: because it is built upon the sampling theory of selectively neutral alleles in population genetics [20], the sampling nature of the theory is guaranteed. In this way, we interact with the system under study through the sampling process and obtain measures in our sampling that are related to those in the real system in a particular way clearly specified by the theory. Fourth, and most innovatively, it is a dispersal-assembled theory [2]. This means that dispersal is assumed to have a leading role in structuring ecological communities. However, dispersal and sampling are intertwined and a nonrandom way of sampling can be formulated that incorporates dispersal limitation [17] (see Glossary).

The originality of Hubbell’s neutral theory lies in the combination of the fact that it (i) assumes equivalence among interacting species; (ii) is an individual-based stochastic theory; and (iii) can be formulated as a dispersal-limited sampling theory. Previous formulations of neutral theory lacked some of these aspects and no niche-based dynamical theory for ecological communities has been formulated as a sampling theory from scratch. Here, we discuss the relevance and limitations of each of these features.

Neutrality assumption

At the beginning of the 20th century, communities were viewed as a superorganism that develops in a particular and fixed way to form a well-established climax community [21]. A community is then a group of species whose competitive interaction strengths are determined by their niche overlaps, and new species originate through adaptation to new niches. This view was challenged by MacArthur and Wilson with their equilibrium theory of island biogeography [22], which was extended by Hubbell [2].

The importance of random mutations and genetic drift was formalized as the neutral theory in population genetics by Kimura and Crow [23]. As reviewed elsewhere [24], these ideas readily found an ecological interpretation (Box 1). Although Watterson [25], Caswell [26] and Leigh and co-workers [27] had already translated neutral models from population genetics into community ecology, Hubbell’s [2] original intuition was that, in addition to neutral drift, random dispersal is the main factor controlling the assembly of ecological communities. Migration had also been studied in population genetics, but had never taken such a prominent role as in Hubbell’s theory.

Hubbell’s unifying approach gives quantitative insights into the origin, maintenance and loss of biodiversity in a biogeographical context. The beauty of neutral theory is that it can be formulated by making only a few, albeit fundamental assumptions (Boxes 2 and 3). Hubbell’s original

Box 1. Community ecology and population genetics

Ideas of neutrality in population genetics were quickly acknowledged to also be valuable in ecology. In population genetics, a set of different alleles encoding the same protein is referred to as a genetic polymorphism. When the different protein variants encoded by each allele do not confer a selective advantage on the individuals carrying them, the different proteins are said to be functionally equivalent and the collection of such alleles is called a neutral polymorphism. Similarly, when the differences between any pair of species in a species community do not translate into an ecologically competitive advantage for either of them, the ecological community is said to be neutral. By analogy, we can also say that such species are ‘functionally equivalent’.

In Table I, we display various aspects of this analogy, in which the fundamental biodiversity number, θ , has a central role. The fundamental dispersal number, l , also has an analog in population genetics where it is confusingly also called θ [71]. The relative abundance, x , is defined as abundance divided by system size. For a very large metacommunity, or population, this can be regarded as a continuous variable ($0 < x < 1$) and the relative abundance distribution $\Phi(x)$, can be introduced. $\Phi(x)dx$ is then the number of species, or alleles, with a relative abundance x within the interval $(x, x + dx)$.

Table I. Analogies between community ecology and population genetics

Property	Community ecology	Population genetics
System (size)	Metacommunity (J_M)	Population (N)
Subsystem	Local community	Deme
Neutral system unit	Individual organism	Individual gene
Diversity unit	Species	Allele
Stochastic process	Ecological drift	Genetic drift
Generator of diversity	Speciation (at rate ν)	Mutation (at rate μ)
Fundamental diversity number	$\theta \approx 2J_M\nu$	$\theta \approx 4N\mu$
Fundamental dispersal number	$l \approx 2J_Lm$	$\theta \approx 4Nm$
Relative abundance distribution, $\Phi(x)$	$\theta x^{-1} (1-x)^{\theta-1}$	$\theta x^{-1} (1-x)^{\theta-1}$
Time to common ancestor (in small θ approximation)	$-J_M x (1-x)^{-1} \log(x)$	$-N x (1-x)^{-1} \log(x)$
Dispersal	Immigration	Migration

formulation [2] relies on two basic principles, which, in turn, are based upon two biological observations. The first is that different individuals from different species belonging to the same functionally uniform ecological community appear to be controlled by similar birth, death and dispersal rates. This leads to the so-called neutrality, equivalence, or symmetry [28,29] assumption, which includes neutral speciation. The second observation, that ecological systems are saturated, leads to what Hubbell [2] calls the ‘zero-sum dynamics’ assumption [30].

The quantitative nature of neutral theory has fostered empirical evaluation with species abundance data [3–7,9,16,29,31]. In a review of tests of neutral theory, McGill [32] found that most studies overwhelmingly reject its predictions. However, McGill also summarized good statistical practices to test the theory and concluded that all published empirical tests violate at least one of those practices. Furthermore, concerning the species abundance distribution, which is one of the most accurate quantitative predictions of the neutral theory, only two of the 13 tests reported in [32] were performed using the dispersal-limited sampling formula [33] and other related

Box 2. Hubbell's mainland–island model

Including dispersal as a leading mechanism controlling species abundances makes neutral theory a spatial theory. The particular model discussed here is only one of those studied by Hubbell [2], and is a spatially implicit model where either dispersal or migration is the mechanism linking the biogeographical area (the metacommunity) with the local community (Figure 1).

The metacommunity

Metacommunity dynamics is controlled by two quantities: a probability for an individual to undergo speciation, ν , and to reproduce, β , per unit time. The neutrality assumption implies that these are the same for all species. The zero-sum assumption means that the total number of individuals is fixed (J_M), and so a new individual can only be introduced at the expense of one being eliminated (i.e. dying). We can formulate the dynamics as a one-step stochastic process in continuous time [40] by focusing on one species i , and writing down a set of equations telling us how the probability that there are n individuals of species i in the community at time t , $P(n,t)$, changes with time. This set of equations is called the 'master equation'. After a long enough period of time, the system reaches a dynamical equilibrium that is characterized by a stationary probability distribution, $P_s(n)$. Because all species are equivalent, $P_s(n)$ is the probability that any species is represented by abundance n at equilibrium. Thus, this distribution corresponds to the classic definition of a species abundance distribution.

The local community

The diversity of the local community is maintained by immigration from the metacommunity; no speciation is assumed to take place within it. We denote the number of individuals in the local community as J . The dispersal parameter m measures the probability that any dying individual is replaced by an immigrant from the metacommunity, rather than by offspring of a local individual. The dynamics can be formulated in the same way as for the metacommunity: a master equation can be constructed and be solved for stationarity [57].

The time evolution of the meta- or local community can be determined by either solving the master equation analytically or numerically, or more directly by simulating the original process.

Hubbell originally relied mostly on simulations, but remarkably many of the most interesting quantities can be calculated exactly or with good accuracy within approximation schemes [57].

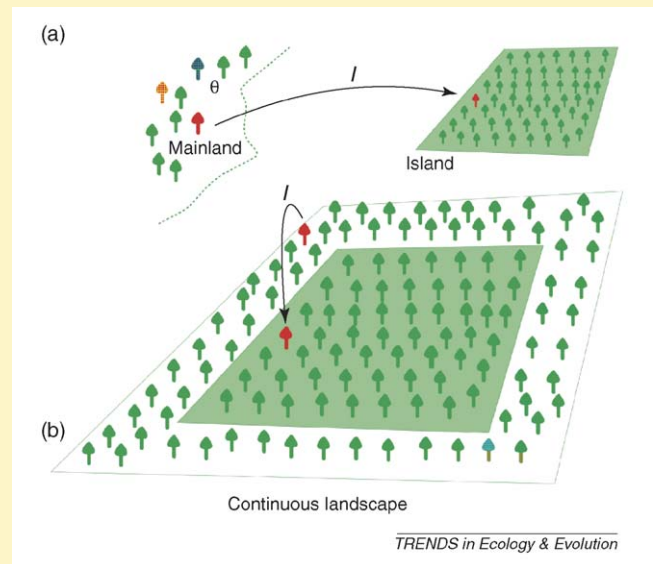


Figure 1. Hubbell's mainland–island model and its relation to a sample from a continuous landscape. When we sample a locality, represented here by a rectangular area shaded in green in (b), within a continuous region (or metacommunity), and obtain estimates of the fundamental biodiversity and dispersal numbers, we are calculating the effective neutral mainland–island model (a), that best approximates the empirical distribution of species abundances observed. The fundamental numbers of the theory do not depend on sample size. The fundamental biodiversity number (θ) is a measure of the effective regional (or metacommunity) diversity, while the fundamental dispersal number (I) is a measure of the effective degree of isolation of the local community.

recent theoretical advances [17,29], mainly because, at that time, such tools were not yet available. But, most importantly, the main common limitation to all tests was that the alternative model was poorly and loosely defined; therefore, the rejection of neutral theory does not imply that a particular alternative niche-based theory holds [32]. Unlike neutral theory, current niche-based theory is not a sampling theory and, thus, lacks the important property of falsifiability. Finally, testing neutral theory has encountered the problem of the diversity of theory formulations and model versions (Box 3) [24].

Statistical regularities resembling neutral patterns have been observed [2,29,34–37] (Box 3, Figure 1) and thus call for a convincing explanation. Although it is now generally accepted that neutral theory works as a null model of community structure with which to study when empirical data are consistent with neutrality, two central questions remain. First, to what extent is the neutral assumption a good operational first approximation to describe ecological communities and, second, which mechanisms are responsible for any observed departures from neutrality? We also need to be aware that non-neutral processes can also generate neutral patterns [38,39]. In Box 4, we summarize different mechanisms that, although strictly violating the equivalence assumption, can generate patterns resembling neutrality.

An individual-based stochastic dynamical theory

There is a long tradition of stochastic modelling in ecology [12,40]. Most classical stochastic approaches are population-level descriptions and deal with one- or two-species systems. However, controversial and important topics in community ecology, such as community assembly, invasion resistance, food-web structure and function, or the diversity–stability debate, all involve a large number of interacting species. Whenever this is the case, a population-level deterministic approach has been taken, owing to its simplicity. More recently, it has been recognized that stochastic, discrete and spatial approaches are important to gain insight into ecological processes [41]. Individual-based approaches have been even envisioned as a paradigm shift in ecology [42]. As a consequence, these issues have been explicitly addressed by taking into account demographic and environmental stochasticity and by trying to understand individual-based stochastic dynamics of species-rich ecological communities [12,38,43–47].

Any theoretical attempt to explain the distribution, abundance and diversity of species in a biogeographical context requires at least three ingredients. First, it must define the stochastic dynamics of species from their origins to their extinction. Second, it must have an (implicit and explicit) spatial formulation. Third, it must consider the dynamics of discrete individuals, which enables a more

Box 3. Theoretical formulations, sampling formulae and abundance curves

Theoretical formulations

Essentially, there are only two different formulations of current neutral theory: with [2] or without zero-sum dynamics [31]. The latter maintains the ‘equivalence’ assumption, but assumes instead of the ‘zero-sum’ assumption that species grow, die and disperse independently from each other, performing a stochastic process governed by density-independent birth-death rates in the metacommunity. For ecological communities that are extraordinary large and species-rich, these two formulations are similar [35]. For the zero-sum formulation [2], an exact sampling formula is available [33], whereas there is currently no sampling formula for the non-zero-sum formulation [31].

Sampling formulae

Different sampling processes produce different sampling formulae. We can sample individuals until we have observed S species, or we can sample a fixed number of individuals J regardless of the number of species that we finally obtain [29]. An example of the latter is the Ewens sampling formula [20], which describes the probability of observing species abundance data in a neutral community without dispersal limitation. The Etienne sampling formula is a generalization of this formula, allowing for dispersal limitation [33]. The estimate of the parameter θ and the corresponding likelihood inform us about the importance of dispersal limitation in a particular situation (Figure 1).

Abundance curves

The number (or fraction) of species with abundance n is called the (relative) species abundance distribution or abundance curve (RSA) [24] (Figure 1). These curves are traditionally used to represent commonness and rarity in community composition empirically.

The abundance curve has frequently been used for model fitting [7,16,31,37], but this is not strictly correct, because it ignores the fact that a particular sampling process can introduce correlations between species abundances encountered in the sample. Sampling formulae correctly account for this [33]. Current theory relates sampling formulae to abundance curves as follows [17,25] (Equation 1):

$$E[S_n|\theta, J] = \sum_{\{D\}} \Phi_n[D] P[D|\theta, J] \quad [\text{Eqn 1}]$$

$E[S_n|\theta, J]$ is the expected number of species with abundance n in sample of size J , that is, the theoretical prediction for the abundance curve under a model with parameters θ (θ and l in the neutral model). $P[D|\theta, J]$ is the probability of a sample $D = (n_1, \dots, n_S)$, that is, the sampling formula for D . $\Phi_n[D]$ denotes the number of species with abundance n in the sample D . The sum is over all samples of size J .

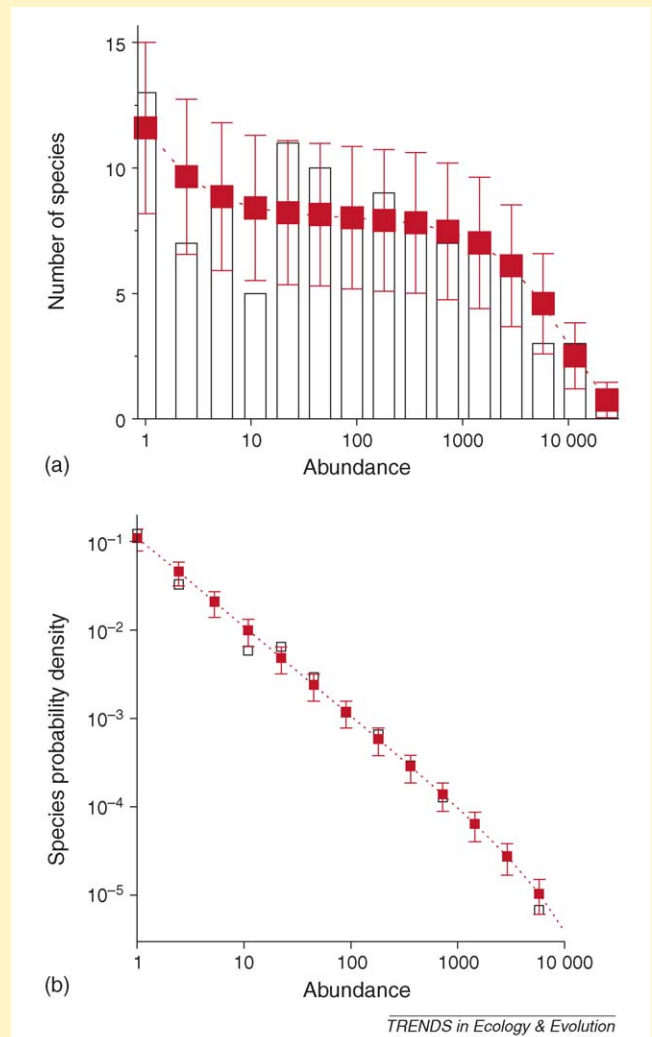


Figure 1. A large data set of marine *Diatomea* (112 352 individuals representing 107 species, [66,37]), presented as abundance curves in the form of a Preston-like histogram (a) and a log-log plot (b); in both cases, actual data are presented by open bars or squares, the predictions of the neutral model for the expected abundance curve, based on these parameter estimates, are shown by red squares. The Etienne sampling formula yields maximum likelihood estimates of $\theta = 11.6$ and $l = \infty$ ($m = 1$), suggesting that this is a nondispersal-limited sample of *Diatomea* from the metacommunity. (For details of the exact interpretation of the species probability density, see [35,37]).

straightforward testing of the theory by using empirical data. The three features together enable quantitative predictions to be made regarding very general patterns, such as the abundance distribution of species, the spatial and temporal turnover of species, the distribution of species ranges, the species–area relation, and the relation between species range and abundance. Neutral theory is the first example of such a theory. Its dynamical formulation is purely stochastic, individual based, and spatial (Box 2), and it provides a unifying explanation and quantitative predictions for all these general macroecological patterns [2,48]. The degree of generality, and the ability to furnish quantitative insights (which relies on the confluence of the three key features mentioned above) are rarely

encountered in other stochastic dynamical theories for ecological communities [12,43,47].

A dispersal-limited sampling theory

Hubbell’s neutral theory is designed to apply to samples from a community, not just to the community as a whole. This is an important property, because it facilitates confrontation of the neutral model to data (Box 3); the theory is thus tailor-made for the empiricist. Other community models, such as the lognormal model of species abundances, do not apply to samples. Furthermore, the classic lognormal model is not an abundance distribution based on individual-level mechanistic processes such as migration, reproduction, speciation, species interactions, or the way

Box 4. Non-neutral mechanisms causing neutral patterns

Patterns do not uniquely imply process and this also holds for neutral patterns [38,39]. In Darwin's entangled bank, any change in the abundance of a species can be caused by various factors. However, communities are assemblages of many individuals and it is through a process of statistical mechanical averaging that most factors balance out [2,18,19,37]. As a result, neutral patterns can arise through non-neutral ecological processes within communities where the 'equivalence' assumption is violated.

Tradeoffs

As Hubbell [2] stated: 'Life history trade-offs equalize the per capita relative fitness of species in the community, which set the stage for ecological drift'. For instance, the hierarchical competitive model analyzed by Tilman [62,67] shows a log-series abundance distribution that is mediated by a specific trade off between colonization ability and persistence. At the other extreme, for a totally egalitarian community where there is only competition for empty space, it can be shown, by using the same modelling approach [68], that coexistence is also mediated by a similar tradeoff and the community is also represented by a log-series distribution at equilibrium. Similar tradeoffs have been reported in spatially extended model communities [38].

Invariance under assemblage

In the absence of dispersal limitation, the expected neutral abundance curve is essentially a power law of exponent -1 [37]. The factor multiplying this power law depends on the particular model formulation used. Power law distributions are invariant under aggregation, which enables us to pool noninteracting, but not ecologically equivalent, neutral subguilds into a nonuniform total guild that will still show the same neutral pattern [37].

The complexity of ecological interactions and the 'melting' of competitive hierarchies

If we take two species from a functionally uniform ecological community, it is easy to test, under controlled experimental conditions, which species outcompetes the other. These experiments appear to point to the existence of competitive hierarchies in nature [69,70]. However, complex coexistence mechanisms, environmental variability, perturbations and specific natural enemies are always present. Under these changing conditions, rigid competitive hierarchies fail to control competitive interactions. The complexity of such interactions enhanced by variable natural conditions might prevent real competitive differences between species from always resulting in the same predictable output. In the long term, this unpredictability might cause nonequivalent species to behave effectively almost neutrally, giving rise to neutral patterns at at least some temporal or spatial scales.

individuals react to environmental heterogeneity and physical disturbances [49,50]. In spite of these limitations, it has been extensively used as an alternative model to neutrality [7,29,31]. To apply the lognormal and other models, which are defined at the community level, to community samples, we must perform an additional operation. Preston [51] already noted that there is a substantial sampling effect at low abundances in that rare species are likely to be unobserved. He accounted for this effect by simply truncating the lognormal distribution with the so-called 'veil line' at some low abundance. Pielou [52] and Bulmer [53] and, more recently, Dewdney [54] and Diserud and Engen [49] argued that this crude truncation should be replaced by Poisson sampling or, even more accurately, by hypergeometric sampling [54]. Finally, as zero abundances cannot be observed, the resulting distribution must be renormalized [29]. In the neutral model, all these additional operations are incorporated in the theory [25].

Furthermore, Etienne and Alonso [17] showed that, in a neutral community, a local sample can be equivalently viewed as a binomial sample from an infinite metacommunity or a hypergeometric sample from a finite metacommunity with or without dispersal limitation. The dispersal-limited distribution can be applied to transform community descriptions of nonsampling theories in the same way as the Poisson or hypergeometric distribution was applied before (e.g. for the lognormal). The result is a dispersal-limited description of the ecological community. The neutral theory has thus led to new ways of studying the effect of dispersal limitation even in non-neutral settings.

Recent developments and prospects

Most work on neutral theory to date has been concerned with investigating spatially implicit models [17,31,33,35,55–58]. In this context, the dispersal-limited sampling formula [33] has probably been one of the most relevant theoretical achievements since 2001. A few authors have also analyzed spatially explicit models [59–61]. The calculation of the probability, $P(x)$, that two individuals, which are separated by a certain distance x , belong to the same species is another important theoretical achievement [59]. When this prediction was tested by using spatial data from rainforests, an inconclusive result was obtained [4], which would imply that the ecological community behaves neutrally only at some spatial scales.

Future developments of the neutral theory will no doubt relax the neutrality assumption. This should be done in such a way that neutrality arises naturally as a limiting case. It is likely that ecological communities are often not neutral, but they are not strictly hierarchical competitive communities either [62]. Within a larger community, there might be neutral subcommunities related to each other through non-neutral processes [39,63]. Within a particular subcommunity, species are exchangeable and, thus, ecologically and functionally equivalent. Community structure and dynamics can be easily described with the community matrix by using an individual-based stochastic approach [45,46]. The number of different subcommunities is a measure of functional diversity, while the average number of species per neutral subcommunity in relation to the total number of species in the community is a measure of functional redundancy. Neutral communities are characterized by high functional redundancy, because the extinction of a few species has little effect on the functional integrity of the community as a whole. However, high functional redundancy might not result in community robustness, because community robustness to environmental hazards is linked to both functional diversity and functional redundancy. In fact, given that neutral species would react to extinction pressures in the same correlated fatal way, persistent disturbances would have a stronger effect on a functionally equivalent neutral community than on a functionally diverse non-neutral community with some degree of functional redundancy.

Hubbell's formulation of neutrality [2] has been criticized because of the poor linkage of the theory with current existing theories in population genetics. Since Ewens' sampling theory for selectively neutral alleles [20], much work has been done to understand the role of selection,

migration and neutrality in dynamically maintained genetic polymorphisms [64]. We believe that some of these genetic population models are also relevant in the context of community ecology and that advances in community ecology might find applications in population genetics.

Finally, after years of statistical diversity indices with practical use but difficult dynamical interpretation [65], the neutral theory has provided the fundamental biodiversity number, which has a solid interpretation in terms of the effectively ideal neutral community that best approximates the real sampled community that is being characterized. The same can be said about the fundamental dispersal number [17] as a measure of the average dispersal limitation of the local community under study and, hence, beta diversity. These measures might correlate well with the true quantities that they try to represent and can be used to compare diversity and the degree of isolation in different areas. Because there are methods available to estimate these quantities from abundance data, it will be worthwhile investigating this issue further.

Concluding remarks

We have emphasized here the three main features of neutral theory. Further work is needed to assess which communities, and in which situations, the neutrality assumption provides a first approximation in the description of ecological communities. However, we strongly believe that any useful theory of species diversity in a geographical context should be a dynamical individual-based (and spatial) stochastic theory that can be formulated as a sampling theory. Any further progress toward a better understanding of biodiversity dynamics should be based on a synthesis of neutral (or quasi-neutral) and niche-based community theories incorporating both demographic and environmental stochasticity [12] within the context of a sampling theory. Only this sampling feature will enable a straightforward and sound comparison to be made of theory predictions with empirical data.

The merits of the neutral theory are diverse. First, a philosophical merit: science should aim at finding the minimal set of processes that can satisfactorily explain observed phenomena. Neutral theory identifies the minimal but common set of mechanisms working in all functionally homogeneous ecological communities. This common set of mechanisms might be progressively obscured by a cascade of ever less important system-dependent ecological factors [37]. Put another way: good theory has more predictions per free parameter than does bad theory. By this yardstick, neutral theory fares fairly well. For this reason, it has been extensively and successfully used as a null model and it should continue to be used as such. Second, a practical merit: neutral theory provides a method to assess species diversity in a potentially better way than do previous diversity indices. Third, and most importantly, an intellectual merit: neutral theory has fostered a rich debate about community structure over the past few years, challenging niche-based approaches with a simple combination of neutrality, stochasticity, sampling and dispersal. It has inspired and will continue to inspire further developments in community ecology,

which, along with sound data analysis, should increase our understanding on the different mechanisms controlling species diversity from ecological to evolutionary spatio-temporal scales.

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References

- 1 Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*, John Murray
- 2 Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press
- 3 Yu, D.W. *et al.* (1998) Can high tree species richness be explained by Hubbell's null model. *Ecol. Lett.* 1, 193–199
- 4 Condit, R. *et al.* (2002) Beta-diversity in tropical forest trees. *Science* 295, 666–669
- 5 Clark, J.S. and McLachlan, J.S. (2003) Stability of forest biodiversity. *Nature* 423, 635–638
- 6 Magurran, A.E. and Henderson, P.A. (2003) Explaining the excess of rare species in natural species abundance distributions. *Nature* 422, 714–716
- 7 McGill, B.J. (2003) A test of the unified theory of biodiversity. *Nature* 422, 881–885
- 8 Fuentes, M. (2004) Slight differences among individuals and the unified neutral theory of biodiversity. *Theor. Popul. Biol.* 66, 199–203
- 9 Turnbull, L.A. *et al.* (2005) Niches, rather than neutrality, structure a grassland pioneer guild. *Proc. R. Soc. B* 272, 1357–1364
- 10 Harpole, W. and Tilman, D. (2006) Non-neutral patterns of species abundance in grassland communities. *Ecol. Lett.* 9, 15–23
- 11 Solé, R.V. *et al.* (2002) Self-organized instability in complex ecosystems. *Phil. Trans. R. Soc. B* 357, 667–681
- 12 Lande, R. *et al.* (2003) *Stochastic Population Dynamics in Ecology and Conservation*, Oxford University Press
- 13 Ricklefs, R.E. (2003) A comment on Hubbell's zero-sum ecological drift model. *Oikos* 100, 185–192
- 14 Adler, P.B. (2004) Neutral models fail to reproduce observed species-time and species-area relationships in Kansas grasslands. *Ecology* 85, 1265–1272
- 15 Wootton, J.T. (2005) Field parametrization and experimental test of the neutral theory of biodiversity. *Nature* 433, 309–312
- 16 Volkov, I. *et al.* (2005) Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438, 658–661
- 17 Etienne, R.S. and Alonso, D. (2005) A dispersal-limited sampling theory for species and alleles. *Ecol. Lett.* 8, 1147–1156. Etienne, R.S. and Alonso, D. (2006). Erratum. 9, 500
- 18 Maurer, B.A. (1999) *Untangling Ecological Complexity*, University of Chicago Press
- 19 Levin, S.A. (2003) Complex adaptive systems: exploring the known, the unknown, and the unknowable. *Bull. Am. Math. Soc.* 40, 3–19
- 20 Ewens, W.J. (1972) The sampling theory of selectively neutral alleles. *Theor. Popul. Biol.* 3, 87–112
- 21 Clements, F.E. (1916) *Plant Succession: Analysis of the Development of the Vegetation*, Carnegie Institution of Washington
- 22 MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*, Princeton University Press
- 23 Kimura, M. and Crow, J.F. (1964) The number of alleles that can be maintained in a finite population. *Genetics* 49, 725–738
- 24 Chave, J. (2004) Neutral theory and community ecology. *Ecol. Lett.* 7, 241–253
- 25 Watterson, G.A. (1974) Models for the logarithmic species abundance distribution. *Theor. Popul. Biol.* 6, 217–250
- 26 Caswell, H. (1976) Community structure: a neutral model analysis. *Ecol. Monogr.* 46, 327–354

- 27 Leigh, E.G., Jr *et al.* (1993) The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evol. Ecol.* 7, 76–102
- 28 Hubbell, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* 19, 166–172
- 29 Etienne, R.S. and Olf, H. (2005) Bayesian analysis of species abundance data: assessing the relative importance of dispersal and niche-partitioning for the maintenance of biodiversity. *Ecol. Lett.* 8, 493–504
- 30 Hubbell, S.P. (1979) Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203, 1299–1309
- 31 Volkov, I. *et al.* (2003) Neutral theory and relative species abundance in ecology. *Nature* 424, 1035–1037
- 32 McGill, B.J. Empirical evaluation of neutral theory. *Ecology* (in press)
- 33 Etienne, R.S. (2005) A new sampling formula for neutral biodiversity. *Ecol. Lett.* 8, 253–260
- 34 Fisher, R.A. *et al.* (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12, 42–58
- 35 Alonso, D. and McKane, A.J. (2004) Sampling Hubbell's neutral theory of biodiversity. *Ecol. Lett.* 7, 901–910
- 36 Latimer, A.M. *et al.* (2005) Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. *Science* 309, 1722–1725
- 37 Pueyo, S. (2006) Diversity: between neutrality and structure. *Oikos* 112, 392–405
- 38 Chave, J. *et al.* (2002) Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.* 159, 1–23
- 39 Purves, D.W. and Pacala, S.W. (2006) Ecological drift in niche-structured communities: neutral pattern does not imply neutral process, In *Biotic Interactions in the Tropics* (Burslem, D. *et al.* eds), pp. 107–138, Cambridge University Press
- 40 Nisbet, R.M. and Gurney, W.S.C. (1982) *Modelling Fluctuating Populations*, John Wiley & Sons
- 41 Durrett, R. and Levin, S. (1994) The importance of being discrete (and spatial). *Theor. Popul. Biol.* 46, 363–394
- 42 De Roos, A.M. and Persson, L. (2005) Unstructured populations models: do population-level assumptions yield general theory? In *Ecological Paradigms Lost. Routes of Theory Change* (Cuddington, K. and Beisner, B., eds), pp. 31–62, Elsevier
- 43 Chesson, P.L. and Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117, 923–943
- 44 Engen, S. and Lande, R. (1996) Population dynamics models generating species abundance distributions of the gamma type. *J. Theor. Biol.* 178, 325–331
- 45 Solé, R.V. *et al.* (2000) Scaling in a network model of multispecies communities. *Physica A* 286, 337–344
- 46 McKane, A. *et al.* (2000) Mean-field stochastic theory for species rich assembled communities. *Phys. Rev. E* 62, 8466–8484
- 47 Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. U.S.A.* 101, 10854–10861
- 48 Bell, G. (2000) The distribution of abundance in neutral communities. *Am. Nat.* 155, 606–617
- 49 Diserud, O.H. and Engen, S. (2000) A general and dynamic species abundance model, embracing the lognormal and the gamma models. *Am. Nat.* 155, 497–511
- 50 Williamson, M. and Gaston, K. (2005) The lognormal distribution is not an appropriate null hypothesis for the species-abundance distribution. *J. Anim. Ecol.* 74, 409–422
- 51 Preston, F.W. (1948) The commonness and rarity of species. *Ecology* 29, 254–283
- 52 Pielou, E.C. (1969) *An Introduction to Mathematical Ecology*, John Wiley & Sons
- 53 Bulmer, M.G. (1974) On fitting the Poisson lognormal distribution to species abundance data. *Biometrics* 30, 101–110
- 54 Dewdney, A.K. (1998) A general theory of the sampling process with applications to the veil line. *Theor. Popul. Biol.* 54, 294–302
- 55 Vallade, M. and Houchmandzadeh, B. (2003) Analytic solution of a neutral model of biodiversity. *Phys. Rev. E* 68, 061902
- 56 Etienne, R.S. and Olf, H. (2004) A novel genealogical approach to neutral biodiversity theory. *Ecol. Lett.* 7, 170–175
- 57 McKane, A.J. *et al.* (2004) Analytical solution to Hubbell's neutral model of local community dynamics. *Theor. Popul. Biol.* 65, 67–73
- 58 He, F. (2005) Deriving a neutral model of species abundance from fundamental mechanisms of population dynamics. *Funct. Ecol.* 19, 187–193
- 59 Chave, J. and Leigh, E.G. (2002) A spatially explicit neutral model of β -diversity in tropical forests. *Theor. Popul. Biol.* 62, 153–168
- 60 Houchmandzadeh, B. and Vallade, M. (2003) Clustering in neutral ecology. *Phys. Rev. E* 68, 061912
- 61 He, F. and Hubbell, S.P. (2003) Percolation theory for the distribution and abundance of species. *Phys. Rev. Lett.* 91, 198103
- 62 Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75, 2–16
- 63 Etienne, R.S. and Olf, H. (2004) How dispersal limitation shapes species-body size distributions in local communities. *Am. Nat.* 163, 68–83
- 64 Wakeley, J. (2004) Recent trends in population genetics: more data! More math! Simple models? *J. Hered.* 95, 397–405
- 65 Magurran, A.E. (2004) *Measuring Biological Diversity*, Blackwell
- 66 Margalef, R. (1994) Through the looking glass: how marine phytoplankton appears through the microscope when graded by size and taxonomically sorted. *Sci. Mar.* 58, 87–101
- 67 Tilman, D. *et al.* (1994) Habitat destruction and extinction debt. *Nature* 371, 65–66
- 68 Solé, R.V. *et al.* (2004) Habitat fragmentation and biodiversity collapse in neutral communities. *Ecol. Complex.* 1, 65–75
- 69 Gause, G.F. (1934) *The Struggle for Existence*, Hafner Press
- 70 Tilman, D. (1982) *Resource Competition and Community Structure*, Princeton University Press
- 71 Rannala, B. (1996) The sampling theory of neutral alleles in an island population of fluctuating size. *Theor. Popul. Biol.* 50, 91–104



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