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REVIEW

Neutral theory in community ecology

Shurong ZHOU[1,2], **Dayong ZHANG** (✉)[1]

1 MOE Key Lab for Biodiversity Science & Ecological Engineering, Beijing Normal University, Beijing 100875, China
2 Laboratory of Arid Agroecology, Lanzhou University, Lanzhou 730000, China

Abstract One of the central goals of community ecology is to understand the forces that maintain species diversity within communities. The traditional niche-assembly theory asserts that species live together in a community only when they differ from one another in resource uses. But this theory has some difficulties in explaining the diversity often observed in specie-rich communities such as tropical forests. As an alternative to the niche theory, Hubbell and other ecologists introduced a neutral model. Hubbell argues that the number of species in a community is controlled by species extinction and immigration or speciation of new species. Assuming that all individuals of all species in a trophically similar community are ecologically equivalent, Hubbell's neutral theory predicts two important statistical distributions. One is the asymptotic log-series distribution for the metacommunities under point mutation speciation, and the other is the zero-sum multinomial distribution for both local communities under dispersal limitation and metacommunities under random fission speciation. Unlike the niche-assembly theory, the neutral theory takes similarity in species and individuals as a starting point for investigating species diversity. Based on the fundamental processes of birth, death, dispersal and speciation, the neutral theory provided the first mechanistic explanation of species abundance distribution commonly observed in natural communities. Since the publication of the neutral theory, there has been much discussion about it, pro and con. In this paper, we summarize recent progress in the assumption, prediction and speciation mode of the neutral theory, including progress in the theory itself, tests about the assumption of the theory, prediction and speciation mode at the metacommunity level. We also suggest that the most important task in the future is to bridge the niche-assembly theory and the neutral theory, and to add species differences to the neutral theory and more stochasticity to the niche theory.

Keywords community, neutral theory, niche theory, species diversity

1 Introduction

One of the central concerns in community ecology is to explain species distribution at different spatio-temporal scales. The most important issue here is how species coexist as they do (Tokeshi, 1990; Tilman and Pacala, 1993; Chesson, 2000; Hubbell, 2001). In the long history of pursuing the mechanisms of species coexistence, studies have mainly been focused on various mechanisms for niche differentiation. In view of the traditional coexistence theory based on niche differentiation, ecologically equivalent species cannot stably coexist for a long period (Zhang et al., 2000).

However, the niche differentiation theory cannot explain the species diversity distribution of tropical rain forests. There are so many species in such a community, and there cannot be so many niches for these species. For example, most of the tree species are shade tolerant species in the BCI tree community (Barro Colorado Island) that are not clearly niche differentiated, and the resource-based niche theory has difficulty in explaining the plethora of such species (Hubbell, 2005a; 2005b; 2006). American ecologist Stephen Hubbell and other ecologists put forward an explanation analogous to the neutral theory in population genetics (Hubbell, 1979; Hubbell and Foster, 1983; 1986; Hubbell, 2001; 2005a; 2005b; 2006)—ecologically equivalent species can coexist. The basic assumption in this so called neutral theory in community ecology is ecological equivalence among species. That is to say, all the individuals of all the species in the community have the same probability of birth, death, migration and speciation. The abundance of each species increases or decreases randomly, and the number of species in the community depends on the dynamic equilibrium between speciation (or immigration) and extinction.

In fact, the neutral theory dates back to the island biogeography theory first put forward by MacArthur and Wilson (1967). According to this theory, the number of species on an

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E-mail: zhangdy@bnu.edu.cn

island depends on the speed of immigration from outside and the extinction of extant species, as well as the area of the island and the distance from the mainland. Neither difference among species nor niche differentiation is considered in this theory. The neutral theory extends the theory of biogeography and takes population dynamics, the number of coexistent species as well as speciation into account for the species distribution both in a local community at the ecological scale and in a metacommunity at the evolutionary scale. A local community is the aggregate of species in a local area competing for the same or similar resources. A metacommunity is the collection of local communities mediated by gene flow between them. Species diversity in a metacommunity depends on the dynamic equilibrium between birth and death, stable species extinction and speciation. A local community is connected with the metacommunity via migration, and its species distribution is determined by individual birth, death and immigration from the metacommunity. The metacommunity is assumed to be relative to a local community when the focus is on the dynamic of the local community which occurs at a much larger spatio-temporal scale just as the metacommunity process. However, the concept of a local community is not clearly defined in the neutral theory, and it is also difficult to distinguish a local community from a metacommunity in nature.

There are two fundamental assumptions in the neutral theory. One is the assumption of the constant size of a community. In such a community, an increase in one species' abundance will definitely accompanied by a decrease of the same extent in other species' abundance. The second assumption is the ecological equivalence among all the individuals of all the species in the community. Based on these assumptions, the neutral theory predicts that species abundance distribution in a local community is the zero-sum multinomial distribution rather than the log-normal distribution. Compared to the log-normal distribution, the zero-sum multinomial distribution has a long tail at the end of rare species, and its length depends on the community size and migration from the metacommunity. This theory is very successful in recreating the relative species abundance distribution and the species-area relationship in tropical rain forests, despite that most of the species may have different fecundity rates, death rates and migration rates. In fact, Hubbell accepted that there are significant difference in the growth rate and the ability of shade tolerance among tropical tree species, but he claimed that such difference is not important to the community structure (Hubbell, 2001; Bell, 2000; 2001), and species diversity mainly depends on the demographic stochasticity at the individual level.

The earliest theories of relative species abundance were based on statistical distributions without considering the underlying ecological process (Fisher et al., 1943; Preston, 1948). Later deductive theories of relative species abundance also failed to derive from the fundamental biological processes in population dynamics. The neutral theory includes some factors that are normally neglected in the niche theory, such as migration, speciation and community size. It provides a theoretical framework for investigating the community structure from the viewpoint of individuals. This theory has brought about deep discussion and related studies in ecology. Hubbell's book *The Unified Neutral Theory of Biodiversity and Biogeography* was also reviewed and widely appreciated.

In this paper, we summarize theoretical and experimental researches on the neutral theory. We also highlight the possible progress that can be made in the near future.

2 Species abundance distribution and neutral theory of biodiversity

In the 1940s, statistical models were used to investigate species abundance distribution in a community (Fisher et al., 1943; Preston, 1948). Fisher et al. defined the number of species consisting of n individuals in a sample of J individuals as

$$F_\alpha(n) = \alpha \frac{x^n}{n} \quad n > 0 \tag{1}$$

where $\alpha > 0$ (Fisher's α) and $0 < x < 1$. Because $F_\alpha(n)$ is proportional to the items in the following Taylor formula

$$-\ln(1-x) = x + \frac{x^2}{2} + \frac{x^3}{3} + \frac{x^4}{4} + \ldots (-1 \leqslant x < 1)$$

this distribution is called log-series distribution. It is clear that $x = \frac{J}{\alpha + J}$, and

$$S = \sum_{n=1}^{\infty} F_\alpha(n) = \sum_{n=1}^{\infty} \alpha \frac{x^n}{n} = -\alpha \ln(1-x)$$
$$= -\alpha \ln(1 - \frac{J}{J+\alpha}) = \alpha \ln\left(1 + \frac{J}{\alpha}\right)$$

because of

$$J = \sum_{n=1}^{\infty} n F_\alpha(n) = \alpha \sum_{n=1}^{\infty} n \frac{x^n}{n} = \alpha \sum_{n=1}^{\infty} x^n = \frac{\alpha x}{1-x}$$

Fisher's α is usually used to fit datasets from insect and animal communities with large numbers of individuals. But it often underestimates number of species when it is applied to tropical forests.

Despite of Fisher's model, Preston put forward another famous model for species abundance distribution (Preston, 1948). Preston transformed the number of individuals into log2 abundance categories (species of abundance 1, 2–3, 4–7 and so on), and found that species abundance distribution is log-normal rather than log-series. Log-normal distribution fits well in many real communities (Tokeshi, 1990), but not always. For example, log-normal distribution predicts too many abundant species and too few rare species for the BCI rainforest (Chave, 2004).

Neither Fisher's model nor Preston's model directly relies on actual demographic processes. It is Karlin and McGregor's neutral model in population genetics that combines the stochastic theory and demographic population models (Karlin and McGregor, 1967). It is easy to translate this model into community ecology by replacing 'type', 'mutation' and 'population' with 'species', 'speciation and immigration' and 'community', respectively. In this model, the community is assumed to be of constant size with J individuals and v probability for speciation. Hence, new species enter the community as a Poisson process through speciation or immigration at rate v in each generation. There are totally S species that coexist in the community n_i, which is the abundance of species I and will increase or decrease by one within one time interval. If the abundance of all the species is small, and there are many distant species, Karlin and McGregor deduced $F(n)$, which is equivalent to the abundance of species i in community ecology when $n_i = n$ as

$$F(n) = vJ\frac{(\lambda/\mu)^n}{n} \tag{2}$$

where λ and μ is per capita birth and death rate, respectively. Compared with model (1), vJ is equivalent to Fisher's α with $\lambda/\mu = x$

The first realistic neutral model in ecology was proposed by Hubbell (1979; 2001). Hubbell extended MacArthur and Wilson's dispersal assembly theory (MacArthur and Wilson, 1963; 1967) and proposed the neutral theory of biodiversity at the individual level. Hubbell made the first attempt to explain species abundance in a community based on fundamental biological processes. Based on the assumption that a community consists of a constant of J individuals that share the same probability of birth, death and migration, and there is just one birth following one death at one time interval, then the probability that there is one birth in species i and one death in species j is

$$\Pr\{N_i+1, N_j-1, N_k, \dots, N_S \mid N_i, N_j, N_k, \dots, N_S\} = \frac{N_j}{J}\left[mP_i + (1-m)\left(\frac{N_i}{J-1}\right)\right]$$

The probability that there is no change in each species' abundance is

$$\Pr\{N_i, N_j, N_k, \dots, N_S \mid N_i, N_j, N_k, \dots, N_S\} = \sum_{i=1}^{S}\frac{N_i}{J}\left[mP_i + (1-m)\left(\frac{N_i-1}{J-1}\right)\right]$$

where m is per capita migration rate, and P_i is the relative abundance of species i in the metacommunity. This matrix gives the probability of the transformation from one state to another. Its eigenvector gives the equilibrium probabilities of each relative abundance combination in the local community.

Denote the probability of the kth combination as $\varphi(k)$, then the expected abundance of the ranked species in a local community of size J is given by

$$E_{local}\{r_i \mid J\} = \sum_{k=1}^{C} r_i(k)\cdot\varphi(k) \tag{3}$$

where C is the total number of combinations, $r_i(k)$ is the abundance of the ith ranked species in the kth configuration. Such a species abundance distribution in a local community is named the zero-sum multinomial distribution, and its shape depends on the fundamental biodiversity number θ, the size of the local community J, and the immigration rate m (Fig. 1).

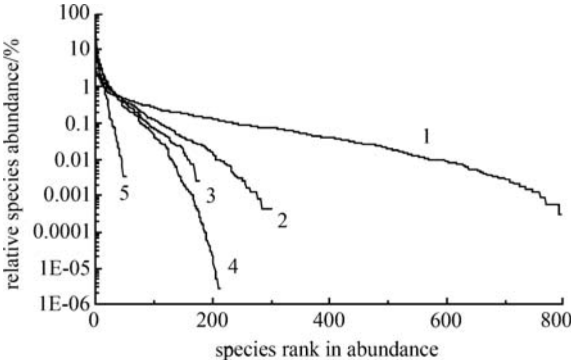

Fig. 1 Patterns of relative species abundance in a diverse array of ecological communities. Note: Species in each community are ranked in percent relative abundance from the commonest (left) to the rarest (right). The percent relative abundance is log transformed on the y-axis. 1. Tropical wet forest in Amazonia; 2. tropical dry deciduous forest in Costa Rica; 3. marine planktonic copepod community from the North Pacific gyre; 4. terrestrical breeding birds of Britian; 5. tropical bat community from Panama (revised from Hubbell, 2001).

For a metacommunity, Hubbell used Karlin and McGregor's (1972) method and gives the probability that there are S species consisting of n_1, n_2, …, n_S individuals respectively in a sample of J individuals from a metacommunity undergoing the point mutation mode of speciation as

$$P_r\{S, n_1, n_2, \dots, n_S\} = \frac{J!\theta^S}{1^{\phi_1}2^{\phi_2}\dots J^{\phi_J}\phi_1!\phi_2!\dots\phi_J!\prod_{k=1}^{J}(\theta+k-1)}$$

Where $\theta = 2J_M v$, J_M is the size of the metacommunity, v is the speciation rate, and φ_i is the number of species consisting of i individuals in a sample of J individuals. Hence, the rank-abundance distribution in a metacommunity of size J is

$$E\{r_i \mid J\} = \sum_{k=1}^{C} r_i(k)\cdot P_r\{S, r_1, r_2, \dots, r_S\}_k \tag{4}$$

where $r_i(k)$ is the expected abundance of the ith ranked species in the kth configuration, and C is the total number of configuration, and $P_r\{S, r_1, r_2, \dots, r_S\}_k$ is the probability of the *k*th configuration. The fundamental diversity number θ, which is equal to twice the speciation rate times the metacommunity size, is dimensionless and is equivalent to α in the log-series distribution. It controls species richness and relative species abundance in a metacommunity at equilibrium between speciation and extinction. This parameter appears throughout the neutral theory at all the spatio-temporal scales.

The relative abundance distribution in a metacommunity is a zero-sum multinomial distribution under random fission speciation (Hubbell, 2001).

Hubbell considered the neutral theory as a unified neutral theory of biodiversity and biogeography. This theory seems mediating the log-series and log-normal distributions. The unified theory predicts the existence of a new distribution of relative species abundance distribution called zero-sum multinomial distribution, which would be logseries-like, lognormal like, or geometric-like, depending on the degree of isolation from the metacommunity under the semi-log scale. This distribution fitted many species abundance distributions well in real communities. But Hubbell did not present an analytical expression of relative species abundance with dispersal limitation, and this makes it difficult to fit the datasets of the natural community (McGill, 2003).

Bell (2000; 2001) proposed another neutral model based on two assumptions that differed from Hubbell's models. The first one is constant migration. That is, the probability that a species can immigrate into the local community does not depend on whether the species is already present in the community. Bell also assumed equivalent per capita birth rate b and death rate d in his model, with $b \geqslant d$. If the number of individuals is more than the size of community J, excess individuals are removed at random, which is similar to the model developed by Ewens (1972). Bell's model predicts approximately log-normal species abundance distribution, skewed to the left by immigration.

Some neutral models also considered the spatial structure of a community (Durrett and Levin, 1996; Chave et al., 2002; Chave and Leigh, 2002; Levin et al., 2003), but this makes the models more complicated to simulate or analyze.

3 Recent developments and analytical expressions of the neutral theory

To obtain an analytical expression of the neutral model, two methods are used. The mean-field master equation approach with a Markovian description of states and transition probabilities deduces analytical expressions and approximations for the expected number of species with certain abundance in a dispersal-limited local community (Volkov et al., 2003; Alonso and Mckane, 2004). Volkov et al. started with a simple model describing the birth-death population process and obtained the species distribution both in a metacommunity and local community. They deduced the log-series distribution for a metacommunity with $x = b/d$, and $\theta = S_M P_0 v/b$, which is equal to Fisher's α, where P_0 is the extinction probability and S_M is the number of species in a metacommunity. For a local community, the expected number of species with n individuals is given as

$$\langle \phi_n \rangle = \theta \frac{J!}{n!(J-n)!} \frac{\Gamma(\gamma)}{\Gamma(J+\gamma)} \int_0^{\gamma} \frac{\Gamma(n+y)}{\Gamma(1+y)} \frac{\Gamma(J-n+\gamma-y)}{\Gamma(\gamma-y)} \exp(-y\theta/\gamma)dy \qquad (5)$$

where $\gamma = \dfrac{m(J-1)}{1-m}$.

For certain parameter values of J, θ, and m, the numerical solution of Eq. (5) is available. Volkov et al. fitted their analytical model to the BCI dataset and compared its merits with that of the log-normal model. They found the species abundance distribution is better fitted by the neutral model than the log-normal model. This advance in the time method can directly calculate the expected number of species with certain abundance, but it is constrained to practical application because it is difficult to estimate the unknown parameters.

The other method takes a coalescent-type approach in which individuals are traced back to the ancestors that once immigrated into the community. Such an effort results in the multivariate probability of observing a specific species abundance distribution in a sample of J individuals. The probability of such a sample consisting of S species with abundance n_1, n_2,…, n_S respectively is given by Etienne and Olff (2004a; 2004b), Etienne (2005) and Etienne and Alonso (2005)

$$P\left[\vec{D} \mid \theta, m, J\right] = \frac{J!}{\prod_{i=1}^{S} n_i \prod_{j=1}^{J} \Phi_j!} \frac{\theta^S}{(I)_J} \sum_{A=S}^{J} K(D,A) \frac{I^A}{(\theta)_A} \qquad (6)$$

where $\vec{D} = (n_1, n_2, \ldots, n_S)$,

$$K(D,A) = \sum_{\{a_1,\ldots,a_S \mid \sum_{i=1}^{S} a_i = A\}} \prod_{i=1}^{S} \frac{\overline{s}(n_i,a_i)\overline{s}(a_i,1)}{\overline{s}(n_i,1)},$$

$$m = I/(I+J-1),$$

Φ_j is the number of species with j individuals in a natural community and $\overline{s}(y,i)$ is the ith coefficient in the expression of $(x)_y = \prod_{i=1}^{y}(x+i-1)$. The model parameters can be estimated using likelihood maximization approach. Hence it is suitable for parameter estimation and model comparison, but the rank-abundance distribution is not straightforward. However, formulas from these two lines can be related to one another (Etienne and Alonso, 2005).

4 Fundamental assumption of the neutral theory

The assumption that all the individuals of all the species in a community are ecologically equivalent or symmetric is fundamental to the neutral theory of biodiversity, and it is also always questioned. According to this assumption, all of the individuals have the same probability of birth, death and migration and speciation. It also implies the symmetric competition among species. This assumption results in no difference in the life history among species, and stabilizing factors such as density dependence are also non-existent in such a community. For example, density dependence implies that the death rate will increase with the community size, which means the existence of rare species' advantages (Armstrong, 1989; Chave et al., 2002). Hubbell claimed that ecological equivalence stands as long as the intensity of density dependence is equal among species (Hubbell, 2003). But the birth rate of an individual of rare species should be higher than that of a common species if density dependence works. Hence, density dependence and ecological equivalence are virtually contradictive.

Zhang and Lin (1997) and Yu et al. (1998) relaxed the ecological equivalence of the neutral model by allowing the small differences in fecundity or mortality among species. They both found that the time of species coexistence decreases dramatically due to these small differences among species. The competitively superior species with higher fecundity rates or lower death rates becomes dominant in the community very quickly. This means that the assumption of ecological equivalence is fundamental to the neutral theory. It also should be pointed out that ecological equivalence automatically implies the equal competitive ability, but not the reverse.

Let us turn to natural communities. The mortality rates of tree species varied from 0.44% to 16.4% annually and the recruitment rates varied from 0.34% to 12.0% annually for 63 species with over 50 individuals bigger than 10 cm dbh during 1990–1995 (Condit et al., 1995; Sheil et al., 2000; Chave, 2004). Chave also calculated standard errors and performed a *t*-test on each species. He found only 26 of the 63 species (41%) are neutral. This seems running against the neutral assumption. What about individual relative fitness? Does ecological equivalence make sense with individual relative fitness? Chave calculated R_0, which is the ratio of per capita birth rate to per capita death rate for the 63 tree species and found they varied from 0.20 to 4.36 (Chave, 2004).

However, Hubbell supposed that niche differentiation will result in the equal relative fitness among species, and then the species abundance distribution will be structured by the ecological drift (Hubbell, 2001). But there is no mechanism in the neutral theory for such a process. To verify that ecological equivalence is a reasonable assumption, Hubbell (2006) developed a spatially explicit model to demonstrate that the ecological equivalence for resource use can evolve easily and often, especially in species-rich communities with limited dispersal and recruitment. He asserted that dispersal and recruitment limitation, as well as high species richness strongly reduce the potential for the competitive exclusion of functionally equivalent or nearly equivalent species, making it possible for slow speciation to compensate species extinction (Hubbell, 2006). In the BCI forest, two individuals of the same species share an average of only four tree species in common among their 20 nearest neighbours (Hubbell and Foster, 1986). He argued that such different biotic environments in species-rich communities will not result in any consistent direction for niche differentiation. Instead, he expected species to evolve similar strategies adapted to their common environments encountered over their evolutionary life spans. He also presented some evidence of ecological equivalence or near equivalence of BCI tree species, as well as evidence for the lack of relationships between species richness and stability or productivity (Hubbell, 2005a; 2006).

5 Testing predictions of the neutral theory

Experimental tests of the neutral theory are usually conducted in species-rich communities, such as tropical rain forests. Hubbell based the fitting of the neutral theory mainly on BCI datasets (Hubbell, 2001; 2005a; 2006). He also fit the neutral model to the relative abundance data from the tree community in the 52-ha plot in Lambir Hills National Park, Sarawak (Hubbell, 2006), and obtained a very high fitting precision ($r^2 = 0.996$) for over 1100 species (Fig. 2). However, controversy occurs even upon the same BCI dataset. McGill (2003) tested the prediction of the neutral theory using the North American Bird Breeding Survey (BBS) and the BCI's 50-ha plot. In both cases, he concluded that the log-normal species abundance distribution provided a better fitting than Hubbell's (2001) distribution. But Volkov et al. fitted the analytical version of the neutral model to BCI datasets and concluded that the analytical solution of the neutral model fitted BCI datasets better than the log-normal distribution (Volkov et al., 2003).

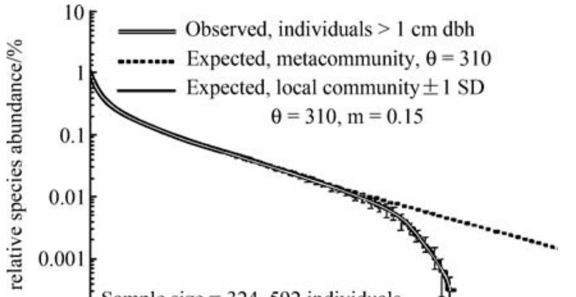

Fig. 2 Fit of the UNT to the dominance-diversity curve for the tropical tree community in Lambir Hills National Park, Sarawak (Borneo). Note: The dotted line extending diagonally down to the right is the best-fit metacommunity curve for $\theta = 310$, assuming no dispersal limitation (probability of immigration m = 1). The distribution of the relative tree species abundance for the 52-ha plot was best fit with $\theta = 310$ and $m = 0.15$. The error bars are ± one standard deviation. The heavy solid line is the observed dominance-diversity curve. The agreement between the fitted line and the observed line for 1197 species excellent ($r^2 = 0.996$) (revised from Hubbell 2006).

Tests of the neutral model have also been conducted in other communities. Pandolfi used a paleo-reconstruction of coral reef assemblages in Papua, New Guinea over a period of 95000 years, and he observed that the commonest species were consistently the same despite the repeated exposure to marked fluctuations of sea level and sea-surface temperatures (Pandolfi, 1996; 2002). This suggests that the most abundant species are also the best equipped to withstand environmental shifts, which works against the neutral drift model. Magurran and Henderson (2003) tested the neutral theory using a 21 years' dataset from an estuarine fish community at Hinkley Point in the Bristol Channel, UK, in which 80 species and 96,000 individuals were recorded. They showed that an ecological community could be separated into two components. Core species, which are persistent, abundant and biologically associated with estuarine habitats, are log normally distributed. Occasional species, which are typically low in abundance and have different habitat requirements, follow a log series distribution. The prediction of the neutral theory is also challenged by a continental-scale analysis of habitat and bird distribution in South America (Ostling, 2005). Recently, Walker and Cyr (2007) tested the neutral theory in 30 well-studied lake communities. Three different fit measures are used. They found all but two zooplankton communities (7 of 9) and three fish communities (9 of 12) were consistent with all the three fit measures. However, all the nine phytoplankton communities did not fit the neutral model by at least one measure.

Chave et al. (2002) contrasted the predicted species abundance patterns of both the neutral and non-neutral simulated models, and they found that they predicted similar patterns. They also carried out extensive simulations of spatially structured neutral models both with and without dispersal limitation, and six non-neutral models including density-dependence and/or tradeoffs among species, with and without dispersal limitation. The results showed that 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. Some other studies also confirmed that non-neutral models predict patterns that are difficult to be distinguished from neutral ones (McGill, 2003; Mouquet and Loreau, 2003; Sugihara et al., 2003).

Despite the debate on fitting natural communities, some studies found that species are quite different ecologically while the species abundance distributions are fitted well by the neutral model. Poulin (2004) investigated the patterns of relative species abundance in intestinal parasite communities of vertebrates and found the patterns qualitatively fit what is expected under the neutral theory. However, the parasite community deviate both assumptions of the neutral theory. With respect to individual helminths, host populations (i.e. parasite component communities) are not saturated with individual parasites. There are also huge inequalities in body size among and within helminth species. Harpole and Tilman (2006) studied grassland communities at Cedar Creek, US, where competition for nitrogen is a key factor in structuring communities. They measured in monoculture the species trait R^*, and the minimum level of nitrogen in the soil for the sustainable growth of the species, and showed that across a variety of gradients in nitrogen availability (experimental manipulation, successional, and large scale natural), species abundance was well predicted by R^*, even though the observed abundance distribution was qualitatively consistent with the neutral theory. These studies lead to the conclusion that the neutral pattern does not imply neutral processes (Purves and Pacala 2005).

Most of the studies aim at testing whether the rank-abundance distribution in natural communities are best fitted by the neutral model, which was classified as the weak test by Wootton (2005), because the predicted distributions are tuned by the fundamental diversity parameter θ and immigration rate m, permitting the predicted distributions to match a wide range of functional shapes. Wootton contended that a stronger test would be able to estimate model parameters from system dynamics, and then test the predictions of the parameterized model in an independent situation that varied in known ways, such as in a field experiment. He applied this method to a rocky intertidal community and found that the neutral theory recreated rank-abundance distribution of the system, but the neutral theory poorly predicted the results of the field experiment, indicating an essential role of variation in species interactions.

6 Speciation mode

Hubbell (2001) assumed two modes of speciation: point mutation and fission mutation. In the point mutation mode, one individual mutate into a new species with a certain probability; while with the fission mutation mode, the assemblage of one species split into two species. These two different mutation modes in a metapopulation result in two different species abundance distributions—the log-series distribution and the zero-multinomial distribution, respectively. Ricklefs (2003) investigated the predictions of the neutral theory under these two mutation modes. In the point mutation mode, new species arise with one individual, and they may likely go extinct soon because of the drift. Taking the BCI tropical forest as an example, the average species lifespan is $T\sim2\ln(1/2v)$ under the neutral assumption. This yields 25 new species every 100 years with a speciation rate of $v \approx 10^{-10}$, where v is the speciation rate. Ricklefs argued that this would result in a large number of species that are difficult to recognize by classic taxonomic methods. On the other hand, the fission mode of speciation would lead to too many abundant species and too few rare species. Hubbell (2003) responded to Ricklefs's arguments that only old and abundant lineages qualify as species for taxonomists. Hence, Ricklefs's cryptic species would be recognized as intraspecific variation, which is commonly observed in population genetics. Hubbell also argued that the point mutation mode and the fission model represent the two extremes of a ‘speciation continuum’. Hubbell proposed a new mutation mode as ‘peripheral isolate speciation’, which is in the middle of those two modes. In this mode, the species lifetime and initial size of new species would also be in the middle of those under the point mutation mode and the fission mode. Hubbell showed by simulation that the initial size of new species has an important effect on species abundance distribution.

7 Neutral versus niche theory and synthesis

The species abundance distribution and the underlying mechanism remain the main concern in community ecology. Among several classical improvements, the neutral theory has intrigued much interest as well as controversy because of its radically different view of ecological community. Although the neutral theory may not be able to exactly describe natural communities at this stage, it did include some important processes neglected by other community assembly theories. The neutral theory provided a novel view on the mechanism of community assembly and created species abundance distributions similar to those observed in natural communities. It at least put forward a numerical null model of community dynamics at different spatio-temporal scales. Its simplicity and elegance should also be appreciated. The niche theory is somewhat less elegant compared to the simplicity of the neutral theory, and the dispersal limitation and stochasticity makes it more complex. However, it is the niche theory rather than the neutral theory that helps us in understanding the role that species diversity and composition plays in the functioning of entire ecosystems. Perhaps what should be done is to bridge the neutral theory and the classical niche differentiation theory. Adding drift and dispersal limitation in niche models, as well as developing nearly neutral models and incorporating differences among species (Zhou and Zhang, 2007) may fill the gap. Several studies have made efforts to do this (Chase, 2005; Purves and Pacala, 2005; Volkov et al., 2005). The frame provided by Volkov et al. (2003) may be used to integrate both demographic processes and determinative processes (Volkov et al., 2005). A unified theory for species abundance distribution in communities consisting of key processes of both the neutral theory and the niche theory will definitely be a breakthrough in community ecology (Chase, 2005).

The neutral theory of biodiversity is still in its infancy. Progress on the neutral theory depends on both theoretical and experimental improvements. Efforts should be made to test the predictions of the neutral model in other communities except for tropical rain forests (Pandolfi, 2002; Magurran and Henderson, 2003; McGill, 2003; Poulin, 2004; Walker and Cyr, 2007). We should also pay much attention to the assumption of ecological equivalence and the speciation mode. The role dispersal limitation and recruitment limitation play in community assembly, and whether ecological equivalence can be easily evolved are still not well understood and verified. Important progress will also be made by constructing powerful stochastic models to test the predictions of the neutral model.

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