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Species abundances and lifetimes: From neutral to niche-stabilized communities

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HIGHLIGHTS

- A model interpolating neutral and niche mechanisms is studied.
- An analytical prediction for species abundance distribution (SAD) is obtained.
- A mode in SAD emerges when intraspecific competition becomes stronger.
- Species lifetime distribution is modified by niche stabilization.
- Niche-stabilized communities sustain a larger diversity of longer-lived species.

ARTICLE INFO

ABSTRACT

We study a stochastic community model able to interpolate from a neutral regime to a niche partitioned regime upon varying a single parameter tuning the intensity of niche stabilization, namely the difference between intraspecific and interspecific competition. By means of a self-consistent approach, we obtain an analytical expression for the species abundance distribution, in excellent agreement with stochastic simulations of the model. In the neutral limit, the Fisher log-series is recovered, while upon increasing the stabilization strength the species abundance distribution develops a maximum for species at intermediate abundances, corresponding to the emergence of a carrying capacity. Numerical studies of species extinction-time distribution show that niche-stabilization strongly affects also the dynamical properties of the system by increasing the average species lifetimes, while suppressing their fluctuations. The results are discussed in view of the niche-neutral debate and of their potential relevance to field data.

1. Introduction

Understanding the forces shaping ecological communities and promoting species coexistence is a key longstanding issue in theoretical ecology. Niche theory (MacArthur and Levins, 1967; Chesson, 2000; Chase and Leibold, 2003) and neutral theory (Caswell, 1976; Bell, 2001; Hubbell, 2001) propose two alternative mechanisms for explaining long-term coexistence of species communities.

Many observational studies have highlighted the importance of specificities in resource exploitation and thus of niche differentiation for long-term coexistence (see Wright, 2002 and Silvertown, 2004 for two recent reviews). From a theoretical point of view, niche partitioning enhances competition with conspecific individuals. As a consequence, species limit their own populations more

than those of other species, providing a stabilization mechanism which promotes coexistence (Chesson, 2000). A simple mathematical formalization of this idea is provided by the Lotka–Volterra competition model (MacArthur and Levins, 1967), where coexistence emerges whenever intraspecific interactions overtake interspecific ones.

Conversely, ecological neutral theory (Hubbell, 2001) completely disregards species differences and assumes functional equivalence at the individual level. Within this theoretical approach, stochasticity is the leading ecological force, and species coexistence is the result of a dynamical balance between immigration/speciation processes and extinction. The drastic assumptions of neutral theory favour mathematical tractability leading to analytical predictions for ecological patterns such as species abundance distribution (see,e.g., Rosindell et al., 2011, and references therein). Such predictions, depending on few parameters, fit surprisingly well field data from tropical forests (see, e.g., Hubbell, 2001; Volkov et al., 2003, 2005).

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Due to its strong departure from traditional theoretical approaches, the neutral theory elicited a heated debate in community ecology about its validity and interpretation. A complication is that, in many cases, niche-based and neutral models yield similar fits of biodiversity patterns (see, e.g., Chave et al., 2002; McGill, 2003; Mouquet and Loreau, 2003; Tilman, 2004; McGill et al., 2006).

Here, we do not enter this debate, but embrace the view that "niche and neutral models are in reality two ends of a continuum with the truth most likely in the middle" (Chase and Leibold, 2003). Indeed, the ecological forces underlying niche and neutral models are not mutually exclusive. Following a similar view, different authors have proposed models synthesizing niche-based and neutral mechanisms (Tilman, 2004; Leibold and McPeek, 2006; Gravel et al., 2006; Adler et al., 2007; Kadmon and Allouche, 2007; Pigolotti and Cencini, 2010; Haegeman and Loreau, 2011; Noble et al., 2011a, 2011b). A desired property of these models is the possibility to recover pure neutrality as a limiting case (Alonso et al., 2006), allowing for studying the transition from niche-dominated to neutral regime when one (or more) ecological parameter is varied. A related issue concerns the robustness of the neutral theory. In particular, a general understanding of whether small non-neutral effects can undermine neutral predictions is still lacking. Finally, niche-neutral models could help our understanding of the dynamical features and long time behavior of ecosystems. Indeed, while neutral theory in principle allows for extrapolating ecosystem behavior at long time-scales (Pigolotti et al., 2005; Azaele et al., 2006; Bertuzzo et al., 2011), an open issue is that predicted species lifetimes tend to be too short compared to fossil records estimates (see, e.g. Lande et al., 2003; Ricklefs, 2003, 2006; Nee, 2005; Allen and Savage, 2007)

A difficulty with the above program is that usually such mixed models are very hard to analyze mathematically (see, e.g., Tilman, 2004). In this respect, surely, one of the reasons of success of the neutral theory has been its mathematical tractability, i.e. the fact that closed expression for distribution such as species abundance distributions (SAD) can be obtained and easily compared with data (Volkov et al., 2003, 2005). This is usually not possible in models where the neutral hypothesis is broken. Moreover, breaking the neutral hypothesis often leads to a proliferation of parameters, making general comparisons problematic.

As discussed by Adler et al. (2007), neutrality can be violated both at the level of fitness inequalities among the species and/or by the presence of stabilizing processes causing species to limit themselves more than they limit others. These are the two main mechanisms for coexistence identified by Chesson (2000). As for the former kind of violation, Zhang and Lin (1997) and Zhou and Zhang (2008) have shown that even small differences in fitness in an otherwise neutral model cause strong reduction of biodiversity. This result is not unexpected as fitness differences, in the absence of stabilizing effects, clearly lead to competitive exclusion. As for the second kind of violation of neutrality, quite interesting is the approach followed by Haegeman and Loreau (2011) who added demographic stochasticity and immigration to classical competitive Lotka–Volterra dynamics with symmetric interactions. A more general model, introduced in Noble et al. (2011a, 2011b) and Noble and Fagan (2011), incorporates both fitness inequalities and stabilizing mechanisms. In a nutshell, Noble et al. added a frequency-dependent birth rate to the Moran model in a such a way that it reduces to Hubbell's neutral model in an appropriate limit and recovers standard Lotka–Volterra phenomenology in the deterministic limit. They mostly explored ecosystems with few species, aiming at understanding niche stabilization effects at intermediate time scales.

In this paper we investigate a variant of the model introduced by Noble et al. (2011b) (see also Noble and Fagan, 2011), with stochastic death and reproduction events where fitness inequalities are disregarded while stabilizing mechanisms are retained via symmetric

interactions, similarly to Haegeman and Loreau (2011). Unlike Noble et al. (2011b) and Haegeman and Loreau (2011) we focus on large metacommunities with possibly many species subject to extinction and speciation, allowing us to probe the effect of niche-stabilization both on static patterns, such as the species abundance distribution, and dynamical ones, such as the species extinction time distribution. A similar study aimed at testing the role of niche-stabilization was undertaken in Adler et al. (2010), where a suitable individual based model was tuned by fitting the parameters of the dataset of a sagebrush steppe community. There, only four species were present and speciation was not considered. It is however remarkable that the sagebrush community investigated was not too far from our model assumptions, namely equal fitness and symmetric competition. Furthermore, other field-data studies (see. e.g., Volkov et al., 2009, for a recent study in this direction) support the idea that the most relevant deviation from neutrality consists in differences between intraspecific and interspecific competition. Such differences are usually explained in terms of species-specific resource consumption or more sophisticated mechanisms like Janzen–Connell effects (Janzen, 1970; Connell, 1971). Therefore, considering, as done here, equal fitness and intraspecific interaction larger than interspecific one is not too restrictive. The symmetric assumption may instead be stronger but has, at least, some relevance to field data.

One of our main result here is to derive a closed analytical expression for the SAD for the model we study. As this model is more complex than its neutral counterpart, our calculations rely on some assumptions and approximations. However, the obtained analytical species abundance curves are nearly indistinguishable from individual-based simulations of the model in a wide parameter range, supporting the validity of our approach. In the neutral limit, the classical Fisher log-series is recovered (Fisher et al., 1943; Hubbell, 2001). Departing from the neutral limit, the effect of niche stabilization is essentially reabsorbed into a single self-consistently derived parameter, which also modifies Hubbell's fundamental biodiversity parameter. As discussed before, most existing datasets satisfying our hypothesis are either made up of few species, or simply well fitted by neutral theory. Nevertheless, the availability of an explicit closed formula can be useful for fitting SAD in future field studies of diverse communities, where one believes that the impact of niche stabilization cannot be neglected.

We also quantify the effect of stabilization on species extinction times. Here, the extinction time — sometimes also dubbed species persistence time (Bertuzzo et al., 2011) — is defined as the time from appearance of the first individual entering the system via speciation to the extinction of the last individual of such species. In the neutral case, the probability distribution of such extinction time can be analytically computed (Pigolotti et al., 2005). In the presence of niche stabilization, we could not obtain an analogous closed expression, so that we resorted to stochastic simulations at varying the niche-stabilization parameter.

Model details are summarized in Section 2. Section 3 presents the main results: the analytical derivation of the SAD with numerical validation, and a numerical study of the species extinction times distribution as a function of the deviation from neutrality. Section 4 is devoted to discussing the results. The Appendix contains some technical details of the self-consistent derivation presented in Section 3.

2. Model

For the sake of simplicity, we start by introducing the neutral version of the model, which is the standard Moran model for a community with a fixed number J of individuals. At each timestep an individual, randomly chosen among the J composing the community, is killed. With probability ν, it is replaced with an

individual belonging to a new species, not present in the system (speciation). With probability $(1-\nu)$, it is replaced with a copy of one of the $J-1$ individuals already present in the community (reproduction). Denoting with n_i the number of individuals of species $i=1,\dots,S$ (S being the number of species currently in the system) present at time t, the death of an individual of species j followed by the birth of one of species i happens at rate

$$(1-\nu)\frac{n_j}{J}\frac{n_i}{J-1},\tag{1}$$

with $n_i,\ n_j \geq 1$.

We now move to the general non-neutral case. Similar to Noble et al. (2011b), non-neutrality is introduced by biasing reproduction. We introduce the frequency-dependent weights

$$w_i = r_i e^{-\sum_{j=1}^{S} a_{ij} n_j},\tag{2}$$

and substitute the term $n_i/(J-1)$ of Eq. (1) with

$$\frac{w_i n_i}{\sum_{k=1}^{S} w_k n_k},\tag{3}$$

where r_i models the intrinsic fitness advantage of species i and a_{ij} the competition among the species present in the community. With equal fitness $r_i = r$ and uniform competition $a_{ij} = a_j$, Eq. (3) reduces to the neutral value $n_i/(J-1)$ (by definition $\sum_{k=1}^{S} n_k = J-1$ as the dead individual does not participate to reproduction). In a different limit, one can draw a correspondence with the Lotka–Volterra competitive model by expanding (3) for small a_{ij} and neglecting fluctuations (Noble et al., 2011b; Noble and Fagan, 2011).

Specifically, we consider a simplified variant of the model by imposing equal fitness $r_i = r$ while retaining niche-stabilization (Adler et al., 2007) through a fully symmetric competition matrix $a_{ij} = a\delta_{ij} + b(1-\delta_{ij})$, as in Haegeman and Loreau (2011). With these simplifications, Eq. (3) reduces to

$$\frac{n_i e^{-an_i - b\sum_{j\neq i} n_j}}{\sum_{k=1}^{S} n_k e^{-an_k - b\sum_{j\neq k} n_j}} = \frac{n_i e^{-(a-b)n_i}}{\sum_{k=1}^{S} n_k e^{-(a-b)n_k}},\tag{4}$$

where we used $\sum_{j\neq i} n_j = (J-1) - n_i$. Parameters a and b tune the weights of intraspecific and interspecific competition, respectively. Finally, by defining $c = a-b$, the frequency-dependent rates can be written as

$$\omega^{(i)}(n_i) = \frac{n_i e^{-cn_i}}{\sum_{k=1}^{S} n_k e^{-cn_k}},\tag{5}$$

where c quantifies the deviation from the neutral case, $c=0$. We focus on the case niche stabilization $c>0$, meaning intraspecific competition being stronger than interspecific one (i.e. $a>b$), as observed in real data (Volkov et al., 2009).

3. Results

In this section we present the main results. First, we show that the species abundance distribution (SAD) of the model can be analytically computed by means of an approach similar to that used in Volkov et al. (2003) for the neutral model, complemented with a self-consistent ansatz for the treatment of non-neutral interactions. Second, we study the dynamical properties of the model by numerically investigating the species extinction times statistics.

3.1. Species abundance distribution

The empirical Species Abundance Distribution (SAD) $\phi(k)$ counts, among all species S present in a specific sample ecosystem, those having k individuals. In formulas, this can be expressed as $\phi(k) = \sum_{i=1}^{S} \delta_{k,n_i}$, with the Kroneker symbol $\delta_{km} = 1$ if $k=m$ and

zero otherwise. We are interested in the average SAD, $\Phi(k) = \langle \phi(k) \rangle$, where the brackets $\langle [\cdots] \rangle$ denote an average over time or, equivalently, over different realizations of the metacommunity dynamics.

In the following, we assume that species can be treated as independent,[1] so that the average can be performed over single-species abundance distributions. Furthermore, we assume that such probabilities do not depend on the species label as a consequence of species symmetry. Then, upon defining the probability $P_k \equiv \langle \delta_{k,n_i} \rangle$ of a species having k individuals, the mean SAD can be expressed as

$$\Phi(k) = \langle \phi(k) \rangle = \left\langle \sum_{i=1}^{S} \delta_{k,n_i} \right\rangle = \langle S \rangle P_k,\tag{6}$$

where $\langle S \rangle$ is the average number of species present in the system. The probabilities P_k are normalized to one, $\sum_{k=1}^{\infty} P_k = 1$, while the SAD sums up to the average number of species, $\sum_{k=1}^{\infty} \Phi(k) = \langle S \rangle$. We also remark that in the original model the total number of individuals is fixed and equal to J. This constraint is lost due to the independent-species assumption, but we will reintroduce it at the end of the calculation by imposing $\sum_{k=1}^{\infty} k\Phi(k) = J$.

Typical SAD $\Phi(n)$ generated by the considered model are shown in Fig. 1A for a system of $J=10^4$ individuals with speciation rate $\nu = 10^{-3}$ and different values of c. Increasing the stabilization parameter c, we observe a transition from a neutral-like SAD, given by the Fisher-log series (Fisher et al., 1943), to curves characterized by a maximum at intermediate abundances. The remainder of this section is dedicated to the derivation of an analytical expression for $\Phi(n)$.

As it will be used later, we introduce the Laplace transform of the SAD:

$$\tilde{\Phi}(z) = \sum_{k=1}^{\infty} \Phi(k) e^{-zk},\tag{7}$$

in terms of which the normalization to a prescribed number of individuals can be rewritten as

$$\tilde{\Phi}'(0) = \sum_{k=1}^{\infty} k\Phi(k) = J,\tag{8}$$

the prime denoting the derivative with respect to z.

In order to find an explicit analytical expression for $\Phi(k)$ using Eq. (6) we need the equilibrium probabilities P_k. To derive an expression for such probabilities we now consider a slightly simplified version of the model introduced in Section 2. We focus on a single species, labeled i, and write the master equation,

$$\frac{d}{dt}p_n^{(i)}(t) = b_{n-1}^{(i)}p_{n-1}^{(i)} + d_{n+1}^{(i)}p_{n+1}^{(i)} - (b_n^{(i)} + d_n^{(i)})p_n^{(i)},\tag{9}$$

ruling the evolution of the probability $p_n^{(i)}(t)$ of species i to have $n_i = n$ individuals at time t. The death and birth rates, $d_n^{(i)}$ and $b_n^{(i)}$, respectively, can be expressed as follows. The former is completely neutral and determined by the frequency of species i,

$$d_n^{(i)} = \frac{n_i}{J}.\tag{10}$$

The latter, instead, explicitly accounts for competition with the

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[1] It is important to stress that the assumption of independence does not necessarily amount to neglecting interactions. Indeed, this approach is commonly (and successfully) adopted in physics and chemistry to tackle complex many-body problems, such as in the so-called Hartree–Fock method or other mean-field approximations: instead of trying to include interactions exactly, one formally describes each particle as independent, but feeling an averaged effect of the interactions with the other particles. This will be the idea underlying the crucial step of our derivation.
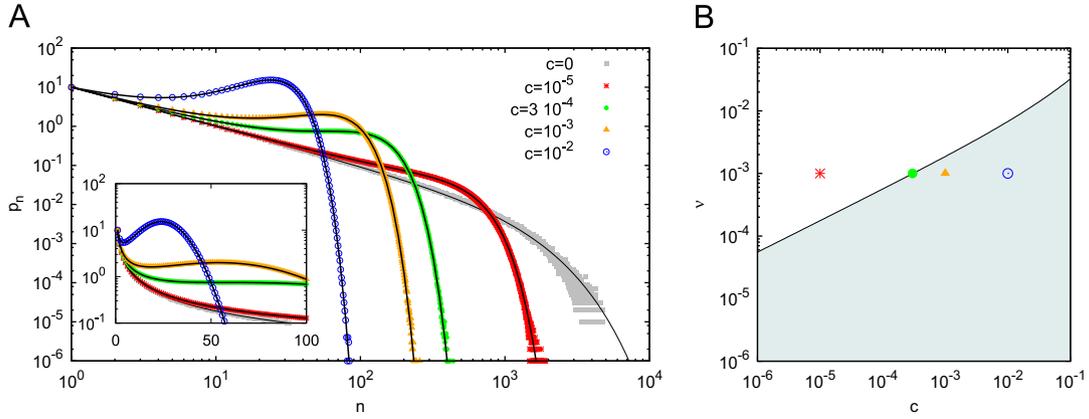
Fig. 1. (A) Species abundance distribution at varying the stabilization parameter c as in the legend. Inset: zoom of the same curves in log–lin scale to highlight the emergence of a mode. Symbols refer to simulations and solid curves to the prediction (16). (B) The (c, ν) parameter plane. The grey region corresponds to parameter values for which the condition (20) is fulfilled, i.e. where a peak in the SAD is present. The symbols correspond to parameters as in the simulations shown in (A) but for the neutral value $c=0$ here not represented.

other species

$$b_n^{(i)} = (1-\nu)\omega^{(i)}(n_i) = (1-\nu)\frac{n_i e^{-cn_i}}{\sum_{k=1}^{S} n_k e^{-cn_k}}. \tag{11}$$

As species are interacting, this probability depends parametrically on the populations of all the other species. The main difference between this simplified dynamics and the original model encoded in Eqs. (1)–(3) is that we are not taking into account that birth and death events are simultaneous at the community level. Consequently, the constraint on the total number of individuals is lost. As already discussed above, this constraint will be reintroduced with a suitable normalization of the SAD. In Eq. (11), the birth probability $\omega^{(i)}(n)$ is decreased by the factor $(1-\nu)$ to account for speciation, which from the point of view of the focal species corresponds to the possibility to give birth to an individual of a new species. Following Volkov et al. (2003) we set $b_0^{(i)} = \nu$. Notice that imposing $b_0^{(i)} > 0$ is necessary to achieve a proper stationary solution (see Azaele, 2006 for mathematical details), while its actual value is irrelevant as it can be reabsorbed into the normalization condition.

If the populations of the other species, n_j for $j \neq i$, were constant, the equilibrium distribution $p_k^{eq(i)}$ for species i would simply be obtained by imposing detailed balance

$$p_k^{eq(i)} = \mathcal{N} \prod_{j=1}^{k} \frac{b_{j-1}^{(i)}}{d_j^{(i)}} = \mathcal{N}\frac{\nu}{1-\nu}\frac{J^k(1-\nu)^k e^{-c/2(k(k-1))}}{k\prod_{j=1}^{k}\sum_{l=1;n_i=j}^{S} n_l e^{-cn_l}} \tag{12}$$

where the constant $\mathcal{N}$ has to be fixed by the normalization condition, $\sum_{k=1}^{\infty} p_k^{eq(i)} = 1$. We stress that, strictly speaking, (12) represents just a formal expression for the equilibrium probability of species i, $p_k^{eq(i)}$, valid for given values of the populations of the other species n_l (with $l \neq i$).

Now we make the ansatz − whose validity will be justified a posteriori by comparing the result of the calculation with numerical data − that Eq. (12) can be used to express the equilibrium probabilities, i.e. $p_k^{eq(i)} = P_k^{(i)}$, of the considered model by replacing the denominator with a suitable average over the probabilities to be determined. Doing so we will obtain a self-consistent expression for the SAD.

We exploit again species symmetry by dropping any explicit dependence on the species label i. Then, consistently, we relax the constraint $n_i = j$ in the sum appearing in the denominator of (12) and rewrite it as an average expressed in terms of the

(yet unknown) SAD

$$\left\langle \sum_{j=1}^{S} n_j e^{-cn_j} \right\rangle = \left\langle \sum_{j=1}^{S}\sum_{k=1}^{\infty} \delta_{k,n_j} n_j e^{-cn_j} \right\rangle$$
$$= \sum_{k=1}^{\infty} k e^{-ck}\left\langle \sum_{j=1}^{S} \delta_{k,n_j} \right\rangle = \sum_{k=1}^{\infty} k\Phi(k) e^{-ck} = -\tilde{\Phi}'(c), \tag{13}$$

where we used (6) in the third equality and (7) in the last one. Now, using Eqs. (6), (12), and (13), we can write

$$\Phi(k) = \theta\frac{J^k(1-\nu)^k e^{-c/2(k(k-1))}}{k(\sum_{j=1}^{\infty} j\Phi(k)e^{-cj})^k} \tag{14}$$

where the constant θ will be fixed by imposing $\sum_{k=1}^{\infty} k\Phi(k) = J$, similarly to Hubbell's biodiversity number in the neutral case (Volkov et al., 2003). Notice that (14) is a self-consistent equation expressing Φ as a function of Φ itself. Finally, using (8) to re-express J, the last equality in (13), and introducing the constant

$$g = \tilde{\Phi}'(0)/\tilde{\Phi}'(c) \tag{15}$$

we obtain our central result

$$\Phi(k) = \theta\frac{[(1-\nu)g]^k e^{-c/2(k(k-1))}}{k}. \tag{16}$$

The above equation provides an analytical prediction for the SAD in terms of the unknown constant g which needs to be determined self-consistently. From the definition (15) we obtain the self-consistent condition

$$g = g(c,\nu) = \frac{\tilde{\Phi}'(0)}{\tilde{\Phi}'(c)} = \frac{\sum_{k=1}^{\infty}(1-\nu)^k g^k e^{-(c/2)(k(k-1))}}{\sum_{k=1}^{\infty}(1-\nu)^k g^k e^{-(c/2)(k(k+1))}}. \tag{17}$$

As shown in the Appendix, the above equation can be approximated in the continuum limit and g can be obtained as the solution of the transcendental equation

$$\frac{1-\nu}{\nu} = \sqrt{\frac{\pi}{2c}}\,\text{erfc}\left(\frac{3c-2\ln(g(1-\nu))}{2\sqrt{2c}}\right)e^{[c-2\ln((1-\nu)g)]^2/8c}. \tag{18}$$

Further, imposing the normalization $\sum_{k=1}^{\infty} k\Phi(k) = -\Phi'(0) = J$ leads to (see Appendix)

$$\theta = \frac{J\nu}{g(1-\nu)}. \tag{19}$$

In the neutral limit, $c=0$, we have $g=1$ so that θ is equal to the neutral biodiversity number $J\nu/(1-\nu)$ and the SAD (16) reduces to the Fisher log-series (Hubbell, 2001; Volkov

et al., 2003). Conversely, in the general case $c \neq 0$, $g > 1$ so that the shape of the SAD will vary and the biodiversity number is reduced with respect to the neutral case. However, as shown below, such reduction does not imply lower diversity, as the average number of species always increases with niche-stabilization.

In Fig. 1A, SADs from the model at different values of ν and c (as indicated by symbols in the c, ν plane shown in Fig. 1B), are compared with the analytical prediction of Eq. (16), represented in solid lines. In all cases, numerical data (symbols) are in excellent agreement with the theory, validating the assumptions underlying the self-consistent approach.

For small values of c, the SAD is monotonically decreasing with n, similarly to the (neutral) Fisher log-series but for a faster (Gaussian) fall-off for large populations. Interestingly, for larger values of c, SAD curves develop a maximum at a finite number of individuals, as emphasized in the inset of Fig. 1A. A study of the function (16) reveals that the condition for developing a maximum at $n > 1$ is

$$\frac{c}{2} + \ln(g(1-\nu)) - 2\sqrt{c} > 0, \tag{20}$$

corresponding to the shaded area in Fig. 1B.

We now discuss how the average number of species $\langle S \rangle = \sum_k \Phi(k)$ changes upon varying the stabilization parameter. As the number of species is proportional to the number of individuals J, in Fig. 2A we plot the fraction $\langle S \rangle / J$ as a function of the speciation rate ν and the intensity of stabilization c. For any fixed value of the speciation rate ν, the average number of species grows upon increasing c, meaning that the system is able to sustain a larger diversity with respect to the neutral case thanks to the stabilizing effect of niches. In Fig. 2B, we compare the prediction obtained by summing the terms of Eq. (16) with numerical simulation of the model, again showing an excellent agreement between theoretical prediction and simulation of the stochastic model.

3.2. Species extinction times

We now focus on dynamical, rather than static, patterns which provide useful information on the differences between neutral and non-neutral theories (Pigolotti et al., 2005; Azaele et al., 2006; Allen and Savage, 2007; Bertuzzo et al., 2011). In particular, it is interesting to compare features of the dynamical balance between appearance and extinction of species as a function of the stabilization parameter c. As in the model species originate from a single individual, we are interested in the statistics of the time it takes for a new species (introduced via a single individual) to become extinct. The results are presented in unit of generations, meaning that $t=1$ corresponds to J iteration steps of the model of Section 2.

In the neutral case $c=0$, by applying ideas from the theory of branching processes (Harris, 1989), it is possible to derive an analytical expression for the probability of a species to survive a time t (from the time of its introduction in the system), which is given by (Pigolotti et al., 2005)

$$p_e(t) = \left(\frac{\nu}{e^{\nu t} - 1 + \nu}\right)^2 e^{\nu t}. \tag{21}$$

For $\nu \ll 1$, such distribution displays a power-law tail t^{-2}, followed by an exponential cutoff set by ν. Notice that the power-law t^{-2} can be modified by dispersal properties different from the global one here considered (Bertuzzo et al., 2011). For $c > 0$, no closed expression for the extinction-time distribution is available. Indeed, also a simple quadratic nonlinearity in the birth (or death) rates for a single species makes the problem analytically intractable, but for clever approximations as discussed in a series of works (see, e.g. Norden, 2001; Newman et al., 2004; Doering et al., 2008; Parsons et al., 2008). For this reason, we limit ourselves to a numerical study. In Fig. 3, we show the extinction-time distribution, $p_e(t)$, for different values of c fixing ν. Increasing c has a non-trivial effect on the shape of the extinction-time distribution.

Qualitatively, one can identify three regimes. At short times, the distribution is only weakly dependent on c, i.e. by the presence of stabilization, and essentially reproduces the neutral result. At intermediate times, the extinction-time probability increases with c. Finally, at large extinction times it decreases with c by developing an exponential cutoff, $p_e(t) \sim \exp(-\alpha t)$, much steeper than predicted by formula (21), i.e. with $\alpha(c) > \nu$. The exponential rate of decrease, α, as a function of the stabilization parameter c (shown in the inset of Fig. 3) suggests, at least for not too large c, a logarithmic dependence of extinction probability, namely $\alpha = a \ln c + b$, which would imply of the form $p_e(t) \sim c^{-at} e^{-bt}$.

As suggested by niche-stabilization arguments, the net effect of these different regimes on the average extinction time is always positive: the average lifetime of a species in our model is a growing function of c (see Fig. 4), which can exceed up to 2 or 3 order of magnitude (depending on ν) the neutral value

$$\langle t \rangle = \frac{\ln(1/\nu)}{1-\nu}, \tag{22}$$

derived from Eq. (21). It is interesting to notice that, while enhancing stabilization (larger c) increases the average extinction time, it decreases its relative fluctuations as confirmed by the
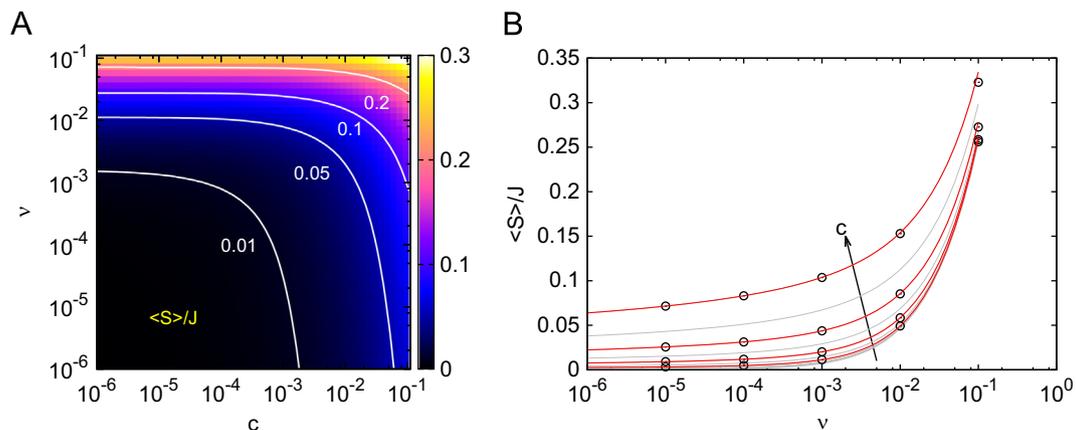
Fig. 2. (A) Average number of species normalized by the community size, $\langle S \rangle / J$, in the (c, ν) parameter space, as predicted by summing the terms of Eq. (16). (B) Same quantity as a function of ν for different values of c, increasing in the arrow direction. Symbols are results from simulations, in excellent agreement with the prediction in red lines. Grey lines correspond to values of c different from those of the simulations. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)
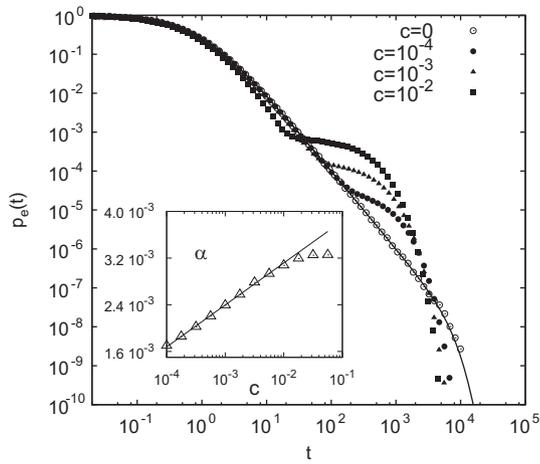
Fig. 3. Probability density function, $p_e(t)$, of the extinction times for $J = 10^4$, $\nu = 5 \times 10^{-4}$ and different values of the stabilization parameter c, as in the legend. For $c = 0$ the prediction of (21) is perfectly verified. Inset: behavior of the exponential rate of decrease α of the pdf tail, where $p_e(t) \sim \exp(-\alpha t)$, as a function of c. Notice that the graph is in log–lin scale. The solid line displays the fit $\alpha = a \ln(c) + b$ with $a = 0.000312$ and $b = 0.00455$.
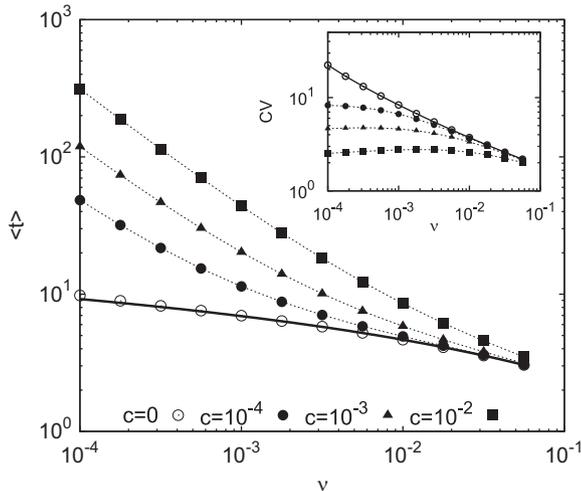
Fig. 4. Average extinction time as a function ν for different values of c, as in the legend. For $c = 0$, the prediction of Eq. (22) perfectly agrees with the data. Inset: coefficient of variation of the extinction time, defined as $CV = (\langle t^2 \rangle - \langle t \rangle^2)^{1/2} / \langle t \rangle$, as a function of ν for the same values of c.

behavior of the coefficient of variation, $CV = \sqrt{\langle t^2 \rangle - \langle t \rangle^2} / \langle t \rangle$, shown in the inset of Fig. 4. This means that, while in the neutral case when $\nu \ll 1$ extinction times can vary greatly around the average value, niche stabilization has also the effect of making the average time a better prediction for the lifetime of a randomly chosen species.

4. Discussions

We studied a community model incorporating neutral demographic stochasticity with niche stabilization. The model belongs to a general class of niche-neutral models discussed in the recent literature (Gravel et al., 2006; Adler et al., 2007) and, in particular, is built upon two specific models originally proposed by Noble et al. (2011b) and Haegeman and Loreau (2011) to which we added speciation. We assumed that violation of neutrality is controlled by a single parameter, c, tuning the intensity of niche stabilization. For the sake of simplicity, similarly to Haegeman and Loreau (2011), we assumed that, even in non-neutral cases, species are

symmetric and with no intrinsic fitness advantages, as also observed in some field data (Adler et al., 2010). The model depends also on rate ν of introduction of new species by speciation or immigration.

We proposed a self-consistent calculation which allowed us to derive an analytical expression for the species abundance distribution, Eq. (16). The assumptions and approximations at the basis of the self-consistent calculation seem to be well verified and the analytical formula does not show significant deviations from simulations of the individual based model. While we focused here on one specific source of non-neutrality, possibly other non-neutral (symmetric) models may be approached using similar ideas. Indeed, species permutation symmetry is the crucial assumption to compute the SADs. However, we remark that even in the presence of species permutation symmetry, the self-consistent ansatz may not lead to the correct result when this symmetry is spontaneously broken (Borile et al., 2012).

Interestingly, in a large portion of the parameter space (c, ν), the relative abundance distribution curves show a maximum for intermediate abundance classes. Specifically, such mode appears when the stabilization parameter c exceeds a critical value (predicted by Eq. (20)) depending on the rate ν of introduction of new species. This feature of the distributions we obtain is reminiscent of many instances of SAD curves measured on the field (Hubbell, 2001), although one should keep in mind that when plotting in log abundances, as in a Preston plot, the mode will emerge at a quantitatively different value of c than predicted from Eq. (20). We remind that spatially implicit implementations of the neutral model, which effectively include a form of dispersal limitation by coupling a community and a metacommunity, provide very good fits of such field-measured SAD curves (Hubbell, 2001; Volkov et al., 2003). Without dispersal limitation, good fits have been obtained by combining neutral community models with specific forms of density-dependent reproduction rates (Volkov et al., 2005).

Within the model here investigated, the presence of a peak in SAD curves corresponds to the natural emergence of an effective carrying capacity for each niche, so that the population of each species fluctuates around a well defined average value. It should be remarked, however, that the tail of the SAD distribution, i.e. the probability of encountering a very abundant species, falls off in a much sharper way for large n than in Hubbell's spatially implicit neutral model, due to the presence of a term proportional to $\exp(-cn^2)$ in Eq. (16). Typical datasets well fitted by the neutral theory (Hubbell, 2001; Volkov et al., 2003) support the presence of a fatter log-normal-like tail. As a consequence, best fits of those datasets with formula (16) (not shown) are biased by such long tails and are thus realized close or at the neutral limit (i.e. for $c \to 0$), where the peak disappears.

The emergence of this Gaussian cutoff, conflicting with classic datasets, is likely due to the fact that the niche-stabilization mechanisms incorporated in our model are particularly strong in the absence of dispersal limitation. It is indeed reasonable to expect that the sharp fall-off should be a quite general feature for global dispersal models in which an effective carrying capacity for any single species emerges and should not depend too much on model details. We conjecture that including some form of dispersal limitation with competition acting on a finite range may lead to fatter tails. Similar features were observed in Chave et al. (2002) while comparing global and limited dispersal models with density dependence or other stabilizing mechanisms, such as tradeoffs. In this perspective, it would be interesting to extend the model to incorporate, even in a spatially implicit form, some degree of dispersal limitation. Unfortunately, this extension makes the analytical treatment much harder and it is left for future investigations. Another way fatter tails may arise would be to

break the symmetric hypothesis and letting different species having different carrying capacity.

Studying dynamic patterns of species lifetimes (Section 3.2) revealed that the main effect of violating neutrality via niche-stabilization is to suppress the large fluctuations of lifetimes, typical of neutral dynamics (Pigolotti et al., 2005). On the one hand, stabilization prevents the possibility of a species to achieve a very large population size and thus lifetimes much longer than the average, which are exponentially suppressed. Similar exponential distributions of lifetimes have been observed in fossil data, a fact often explained in terms of the Red Queen effect in a changing environment (Van Valen, 1973). On the other hand, a species is favored when rare making it less prone to extinction by demographic stochasticity when its population is small (see also Adler et al., 2010). These effects are weighted by the stabilization parameter, as a result the average species lifetime results increased with respect to the neutral expectation (22).

As observed by many authors (see, e.g. Lande et al., 2003; Ricklefs, 2003, 2006; Nee, 2005; Allen and Savage, 2007), one of the problems with the neutral theory relies on the fact that average species lifetimes are typically too short, up to some order of magnitude, compared to those estimated from fossil records. The origin of such discrepancy is likely due to the point speciation mode, typically implemented in neutral models (Hubbell, 2003). As suggested by Allen and Savage (2007), a possible way-out for overcoming this problem is to allow for larger incipient-species abundances. Moreover, the same authors have also shown that allowing for some environmental stochasticity can decrease the lifetime of very abundant species, which is another issue with the neutral prediction for the species lifetimes distribution.

Furthermore, our model shows that niche-stabilization induced by intraspecific interactions larger than interspecific ones, for a given value of ν, both increases the average lifetime (up to 2 or 3 order of magnitudes depending on ν and c) and suppresses large fluctuations. In particular, the smaller the value of ν, the larger is the effect of stabilization. This allows the system for sustaining a larger diversity (Fig. 2) of longer-lived (Fig. 4) species with respect to a purely neutral community and, at the same time, suppressing the probability of species with exceedingly large lifespan with respect to the average.

Acknowledgments

Appendix A. Computation of g and θ

Here, we derive the expression for the normalization θ presented in Eq. (19), and discuss a semi-analytical method to estimate the parameter g, which is self-consistently defined as

$$g = g(c, \nu) = \frac{\tilde{\Phi}'(0)}{\tilde{\Phi}'(c)} = \frac{\sum_{k=1}^{\infty}(1-\nu)^k g^k e^{-(c/2)k(k-1)}}{\sum_{k=1}^{\infty}(1-\nu)^k g^k e^{-(c/2)k(k+1)}}. \quad (A.1)$$

For the sake of notation simplicity we denote with N and D, respectively, the numerator and denominator in the right hand side of expression (A.1). By rearranging the indices in the
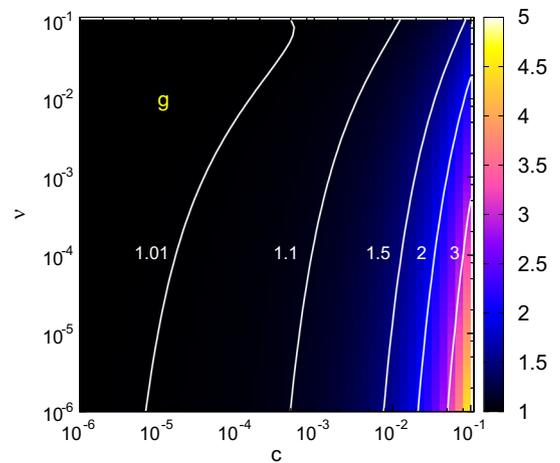

Fig. A1. Contour plot of the quantity g in the (c, ν)−plane, as computed by solving Eq. (18) semi-analytically.

summations, one can show that they satisfy

$$D = \frac{N - g(1-\nu)}{g(1-\nu)}. \quad (A.2)$$

Substituting (A.2) into (A.1) yields an expression for D:

$$D = \sum_{k=1}^{\infty}(1-\nu)^k g^k e^{-ck(k+1)/2} = \frac{1-\nu}{\nu}. \quad (A.3)$$

The normalization θ can be then derived by imposing the condition $\sum_k k\Phi(k) = J$. By direct substitution, one obtains $\sum_k k\Phi(k) = \theta N$. Then, using the fact that $N = gD = g(1-\nu)/\nu$ yields the result (19).

Let us now discuss how estimating g in the relevant parameter range of $c \ll 1$ and $\nu \ll 1$. In such limit, one can approximate very closely the series in (A.3) with an integral

$$\frac{1-\nu}{\nu} \approx \int_1^{\infty} dk (1-\nu)^k g^k e^{-(c/2)k(k+1)}$$
$$= \sqrt{\frac{\pi}{2c}} \mathrm{erfc}\left(\frac{3c - 2\ln(g(1-\nu))}{2\sqrt{2c}}\right) \exp\left\{\frac{[c - 2\ln((1-\nu)g)]^2}{8c}\right\} \quad (A.4)$$

Equating the first and the last term in the above expression leads to Eq. (18), that can be solved for g semi-analytically by standard methods. The dependence of g on ν and c is shown in Fig. A1.

We conclude by discussing possible analytical expressions for g. In the neutral limit of $c = 0$, one has $g = 1$, it is thus tempting to build up an expansion to obtain a closed expression for g at least in the limit $c \ll 1$. However, such expansion in Eq. (A.4) requires additional assumptions on the relative magnitude of the two small parameters c and ν. For example, the argument of the error function is very small when $\nu \ll c \ll 1$, but very large when $c \ll \nu \ll 1$, so that in the first case a Taylor expansion is appropriate, while in the second one has to perform an asymptotic expansion. More formally, one can show that the function $g(\nu, c)$ is not analytic at the point $\nu = c = 0$, so that one cannot perform a Taylor expansion in the two small parameters. This also suggests that, more in general, other near-neutral models can be hard (or impossible) to treat with perturbative methods due to the interplay between the two small parameters.

References

Adler, P., Hillerislambers, J., Levine, J., 2007. A niche for neutrality. Ecology Letters 10, 95–104.
Adler, P., Ellner, S.P., Levine, J.M., 2010. Coexistence of perennial plants: an embarrassment of niches. Ecology Letters 13, 1019–1029.
Alonso, D., Etienne, R.S., McKane, A.J., 2006. The merits of neutral theory. Trends in Ecology and Evolution 21, 451–457.

Allen, A.P., Savage, V.M., 2007. Setting the absolute tempo of biodiversity dynamics. Ecology Letters 10, 637–646.

Azaele, S., Pigolotti, S., Banavar, J.R., Maritan, A., 2006. Dynamical evolution of ecosystems. Nature 444, 926–928.

Azaele, S., 2006. Linear one-step processes with artificial boundaries. Journal of Statistical Physics 125, 491–511.

Bell, G., 2001. Neutral Macroecology. Science 293, 2413–2418.

Bertuzzo, E., Suweis, S., Mari, L., Maritan, A., Rodríguez-Iturbe, I., Rinaldo, A., 2011. Spatial effects on species persistence and implications for biodiversity. Proceedings of the National Academy of Science 108, 4346–4351.

Borile, C., Muñoz, M.A., Azaele, S., Banavar, J., Maritan, A., 2012. Spontaneously broken neutral symmetry in an ecological system. Physical Review Letters 109, 038102.

Caswell, H., 1976. Community structure: a neutral model analysis. Ecological Monographs 46, 327–354.

Chase, J.M., Leibold, M.A., 2003. Ecological Niches: Linking Classical and Contemporary Approaches. The University of Chicago Press.

Chave, J., Muller-Landau, H.C., Levin, S.A., 2002. Comparing classical community models: theoretical consequences for patterns of diversity. American Naturalist 159, 1–23.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31, 343–366.

Connell, J.H., 1971. On the roles of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer, P.J., Gradwell, G.R. (Eds.), Dynamics of populations. Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeek, Netherlands. Pudoc, Wageningen, pp. 298–312.

Doering, C.R., Sargsyan, K.V., Sanders, L.M., 2008. Extinction times for birth-death processes: exact results, continuum asymptotics, and the failure of the Fokker–Planck approximation. Multiscale Modeling and Simulation 3, 283–299.

Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12 (1), 42–58.

Gravel, D., Canham, C.D., Beaudet, M., Messier, C., 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9, 399–409.

Haegeman, B., Loreau, M., 2011. A mathematical synthesis of niche and neutral theories in community ecology. Journal of Theoretical Biology 269, 150–165.

Harris, T.E., 1989. The Theory of Branching Processes. Dover University Press New York.

Hubbell, S.P., 2001. The Unified Neutral Theory of Biodiversity and Biogeografy. Princeton University Press, Princeton, NJ.

Hubbell, S.P., 2003. Modes of speciation and the lifespans of species under neutrality: a response to the comment of Robert E. Ricklefs. Oikos 100, 193–199.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104, 501–528.

Kadmon, R., Allouche, O., 2007. Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. American Naturalist 170, 443–454.

Lande, R., Engen, S., Saether, B.E., 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press, Oxford, UK.

Leibold, M.A., McPeek, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87, 1399–1410.

MacArthur, R., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101, 377–385.

McGill, B.J., 2003. Strong and weak tests of macroecological theory. Oikos 102, 679–685.

McGill, B.J., Maurer, B.A., Weiser, M.D., 2006. Empirical evaluation of neutral theory. Ecology 87, 1411–1423.

Mouquet, N., Loreau, M., 2003. Community patterns in source–sink metacommunities. American Naturalist 162, 544–557.

Nee, S., 2005. The neutral theory of biodiversity: do the numbers add up? Functional Ecology 19, 173–176.

Newman, T.J., Ferdy, J.-B., Quince, C., 2004. Extinction times and moment closure in the stochastic logistic process. Theoretical Population Biology 65, 115–126.

Noble, A.E., Temme, N.M., Fagan, W.F., Keitt, T.H., 2011a. A sampling theory for asymmetric communities. Journal of Theoretical Biology 273, 1–14.

Noble, A.E., Hastings, A., Fagan, W.F., 2011b. Multivariate Moran process with Lotka–Volterra phenomenology. Physical Review Letters 107, 228101.

Noble, A.E., Fagan, W.F., 2011. A Unification of Niche and Neutral Theories Quantifies the Impact of Competition on Extinction. arXiv preprint arxiv:1102.0052.

Norden, R.H., 2001. On the distribution of the time to extinction in stochastic logistic population model. Advances in Applied Probability 14, 687–708.

Parsons, T.L., Quince, C., Plotkin, J.B., 2008. Absorption and fixation times for neutral and quasi-neutral populations with density dependence. Theoretical Population Biology 74, 302–310.

Pigolotti, S., Flammini, A., Marsili, M., Maritan, A., 2005. Species lifetimes for simple models of ecologies. Proceedings of the National Academy of Science 102, 15747–15751.

Pigolotti, S., Cencini, M., 2010. Coexistence and invasibility in a two-species competition model with habitat preference. Journal of Theoretical Biology 265, 609–617.

Ricklefs, R.E., 2003. A comment on Hubbell's zero-sum ecological drift model. Oikos 100, 185–192.

Ricklefs, R.E., 2006. The unified neutral theory of biodiversity: do the numbers add up? Ecology 87, 1424–1431.

Rosindell, J., Hubbell, S.P., Etienne, R.S., 2011. The unified neutral theory of biodiversity and biogeography at age ten. Trends in Ecology and Evolution 26, 340–348.

Silvertown, J., 2004. Plant coexistence and the niche. Trends in Ecology and Evolution 19, 605–611.

Tilman, D., 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences 101, 10854–10861.

Van Valen, L., 1973. A new evolutionary law. Evolutionary Theory 1, 1–30.

Volkov, I., Banavar, J.R., Hubbell, S.P., Maritan, A., 2003. Neutral theory and relative species abundance in ecology. Nature 424, 1035–1037.

Volkov, I., Banavar, J.R., He, F., Hubbell, S.P., Volkov, A. Maritan, Igor, Banavar, Jayanth R., 2005. Density dependence explains tree species abundance and diversity in tropical forests. Nature 438, 658–661.

Volkov, I., Banavar, J.R., Hubbell, S.P., Maritan, A., 2009. Inferring species interactions in tropical forests. Proceedings of the National Academy of Science 106, 13854–13859.

Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130, 1–14.

Zhang, D.-Y., Lin, K., 1997. The effects of competitive asymmetry on the rate of competitive displacement: how robust is Hubbell–community drift model? Journal of Theoretical Biology 188, 361–367.

Zhou, S.R., Zhang, D.Y., 2008. A nearly neutral model of biodiversity. Ecology 89, 248–258.