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Demographic trade-offs determine species abundance and diversity

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Abstract

Aims

Much recent theory has focused on the role of neutral processes in assembling communities, but the basic assumption that all species are demographically identical has found little empirical support. Here, we show that the framework of the current neutral theory can easily be generalized to incorporate species differences so long as fitness equivalence among individuals is maintained through trade-offs between birth and death.

Methods

Our theory development is based on a careful reformulation of the Moran model of metacommunity dynamics in terms of a non-linear one-step stochastic process, which is described by a master equation.

Important Findings

We demonstrate how fitness equalization through demographic trade-offs can generate significant macroecological diversity patterns, leading to a very different interpretation of the relation between Fisher's α and Hubbell's fundamental biodiversity number. Our model shows that equal fitness (not equal demographics) significantly promotes species diversity through strong selective sieving of community membership against high-mortality species, resulting in a positive association between species abundance and per capita death rate. An important implication of demographic trade-off is that it can partly explain the excessively high speciation rates predicted by the neutral theory of the stronger symmetry. Fitness equalization through demographic trade-offs generalizes neutral theory by considering heterospecific demographic difference, thus representing a significant step toward integrating the neutral and niche paradigms of biodiversity.

Keywords: birth–death trade-off • ecological drift • fitness equivalence • neutral theory • species coexistence

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INTRODUCTION

The question central to the debate on biodiversity maintenance is no longer whether species coexistence is maintained by niche or neutral mechanism, but how coexistence is maintained by niche and neutral mechanisms. Recent theoretical and empirical studies have shown that niche and neutral theory do not have to diametrically oppose each other; they instead form a continuum defined by stabilizing mechanisms on the one end and equalizing mechanisms on the other (Adler *et al.* 2007; Cadotte 2007; Chase 2005; Chesson 2000; Gravel *et al.* 2006; Leibold and McPeek 2006). The equalizing endpoint of the continuum defines the neutral symmetry—species in a community are functionally equivalent in such a way that organisms, regardless of their identity, have identical demographics on a per capita basis. This is the stronger

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form of symmetry that is originally given by Hubbell (1997, 2001) and is the foundation on which almost all neutral models have so far been derived (Alonso and McKane 2004; Alonso *et al.* 2006; Bell 2001; Chave 2004; Chave *et al.* 2002; Etienne 2005; Etienne and Olff 2004; Hubbell 2001; McKane *et al.* 2004; Vallade and Houchmandzadeh 2003; Volkov *et al.* 2003). This strict version of neutral theory has shown to successfully predict several macroecological patterns involving abundance, diversity and distribution. In spite of this success, the basic assumption of neutrality that all the species have the same birth and death rates has found little empirical support (Chave 2004; Ostling 2004). It has increasingly been recognized that the assumption of identical birth and death rates in general is not essential to the neutral theory; what matters is fitness as defined by the demographic trade-offs between birth and death (Allouche and Kadmon 2009; Etienne *et al.* 2007; Holyoak and Loreau 2006; Hubbell 2005; Lin *et al.* 2009; Ostling 2004).

Different from the stronger symmetry, equal fitness relaxes the assumption of identical vital rates of birth and death. In this case, species can differ in birth and death rates; equal fitness is achieved as long as species fall on the same manifold of the birth and death trade-off (Hubbell 2001; Ostling 2004). In other words, species are considered of the same fitness if the ratio of per capita birth and death rates is the same: a species with high birth and high death is equivalent in fitness to a species of low birth and low death (Chave 2004; Hubbell 2005; Ostling 2004). Despite that it has been widely recognized that demographic trade-off is an important equalizing mechanism maintaining species diversity (Adler *et al.* 2007; Cadotte 2007; Chesson 2000; Gravel *et al.* 2006; Hubbell 2005, 2006; Leibold and McPeek 2006; Turnbull *et al.* 2008) and that there are a number of exceptional attempts to consider fitness equivalence (Allouche and Kadmon 2009; Etienne *et al.* 2007; Lin *et al.* 2009; Ostling 2004), no formal theory of biodiversity of the weaker symmetry has yet been derived. It is still widely accepted that trade-offs which balance the advantages of species that differ in demographic traits should not change the predictions of the original neutral model (Hubbell 2001).

Here, we develop an analytical framework for the dynamics of species with equivalent fitness at the metacommunity scale. We demonstrate how such a weaker form of neutral symmetry can lead to not only the same log-series species abundance distribution as before but also several novel consequences for community structure and biodiversity, including a strong selective sieving of community membership against high-mortality species and a positive association between species abundance and per capita death rate. Therefore, even under neutrality, life history traits affecting the relative fitness of species can play an important role in determining their abundance and persistence in the community. More significantly, incorporating a trade-off between birth and death rates leads to a different interpretation of the relation between Fisher's α and Hubbell's fundamental biodiversity number, partially explaining the overestimates of speciation rates in neutral theory without demographic trade-offs. This weaker symmetric model, along with previous similar attempts for local communities (Allouche and Kadmon 2009; Etienne *et al.* 2007), generalizes neutral theory by considering heterospecific demographic difference and thus represents a significant step toward integrating the neutral and niche paradigms of biodiversity.

MODEL AND RESULTS

To accommodate species differences within a neutral framework, individuals belonging to species with different vital rates must have equal per capita fitness (Hubbell 2001; Turnbull *et al.* 2008), which for most purposes can be measured by the lifetime reproductive success or the ratio of per capita birth to death rate (Chave 2004). We start with a careful reformulation of the Moran (1958) model of metacommunity dynamics in terms of a non-linear one-step stochastic process. Apart from the introduction of a birth–death trade-off, there is only one other difference (Etienne and Alonso 2007) between our model and Hubbell's original model; i.e. individuals that will die in the next time step are allowed to leave offspring before they die in our model but not in Hubbell's.

We assume that there are n_i individuals of species i in the community, with the total number of individuals of all species being J, i.e. $J=\sum_{i=1}^{S} n_i$, where S is the total number of species that could ever arise due to speciation. Strictly speaking, S must be infinitely great and as a result, $n_i = 0$ is necessarily a common occurrence; in other words, $S \gg J$. The probability for a given individual of species i to die in the time interval $(t, t + \Delta t)$ is $d_i\Delta t$, where d_i is a species-specific per capita death rate. From this assumption, it follows that the probability of one death occurring in $(t, t + \Delta t)$ in the whole population of species i is $n_i d_i \Delta t + o(\Delta t)$, where $o(\Delta t)$ denotes quantities such that $\lim_{\Delta t \to 0} \frac{o(\Delta t)}{\Delta t} = 0$. Therefore, assuming that Δt is infinitesimally small, we can disregard the term $o(\Delta t)$ and write the above probability directly as $n_i d_i \Delta t$.

We follow Hubbell (Hubbell 2001) by assuming a point mutation model of speciation such that each new recruit speciates with probability v into a new species; the new recruit will be one of the existing species with probability $1 - v$. Note, here, we treat speciation as immigration from a species pool containing S species, as did in Karlin and McGregor (1967), McKane *et al.* (2000, 2004) and Volkov *et al.* (2003, 2007). Obviously, this approach is only realistic in the limit of an infinite species pool so that $S \gg J$ is a reasonable assumption.

Let $W_i(n_i, n_i{+}1)$ be the probability that the number of species i increases from n_i to $n_i + 1$ during an infinitesimal time interval $(t, t + \Delta t)$. This is possible only if an individual of another species dies (with probability $\sum_{l \neq i}^{S} n_l d_l \Delta t$) and is replaced by an individual of the focal species, either by recruitment (probability $\frac{n_i b_i}{\sum_{l=1}^{S} n_l b_l}(1 - v)$) or by speciation (probability $\frac{\sum_{l \neq i} n_l b_l}{\sum_{l=1}^{S} n_l b_l}(v/(S-1))$, where b_i is the per capita birth rate of species i. The transition probability, $W_i(n_i, n_i{+}1)$, can now be written as (see also McKane *et al.* 2000, 2004).

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$$W_i(n_i, n_i+1) = \left\{\sum_{l\neq i} n_l d_l \Delta t\right\}\left\{\frac{n_i b_i}{\sum_{l=1}^{S} n_l b_l}(1-v) + \frac{\sum_{l\neq i} n_l b_l}{\sum_{l=1}^{S} n_l b_l}\frac{v}{(S-1)}\right\}. \tag{1}$$

Following similar logic, we can write the probability that the number of this species decreases from n_i to $n_i - 1$ as

$$W_i(n_i, n_i-1) = \{n_i d_i \Delta t\}\left\{\frac{n_i b_i}{\sum_{l=1}^{S} n_l b_l} v + \frac{\sum_{l\neq i} n_l b_l}{\sum_{l=1}^{S} n_l b_l}\left(1-\frac{v}{S-1}\right)\right\}. \tag{2}$$

Define $g_i(n_i)$ and $r_i(n_i)$ as the rates at which the species i increases or decreases in abundance such that $W_i(n_i, n_i{+}1){=}g_i(n_i)\Delta t$ and $W_i(n_i, n_i-1){=}r_i(n_i)\Delta t$. Now let's invoke the weaker form of ecological symmetry by assuming fitness equivalence so that the ratio of the per capita birth rate to the per capita death rate is invariant across species, i.e. $b_i/d_i = C$ for any species i. The plausibility of fitness invariance across species relies on the fact that bad competitors have been eliminated by Darwinian selection and consequently all persistent species must be equalized in fitness or competitive ability. We hasten to add that in a niche model species also achieve ecological equivalence at their coexistence equilibrium and thus fitness equalization by itself does not necessarily imply neutral dynamics (Chave 2004; Doncaster 2009; Holyoak and Loreau 2006). Furthermore, if the abundance of individual species is very small compared to the community size, or $n_i \ll J$, and recalling that $S \gg J$, then we have the following approximation (Alonso and McKane 2004; Chave 2004):

$$g_i(n_i) \approx n_i b_i \frac{\sum_l n_l d_l}{\sum_l n_l b_l}\left(1-v\right) = d_i n_i\left(1-v\right), \tag{3a}$$

and

$$r_i(n_i) \approx n_i d_i. \tag{3b}$$

This linear representation for $g_i(n_i)$ and $r_i(n_i)$ is precisely the starting point chosen by Volkov *et al.* (2003, 2007) in order to derive the stationary abundance distribution at the speciation–extinction equilibrium. Under this linear approximation, species are independent and we can write down a master equation describing the aforementioned one-step stochastic process as follows.

Let $P_i(n_i, t)$ is the probability that the ith species contains n_i individuals at time t. Equations (3a) and (3b) suggest that the transition rates of species i are independent of other species. Thus, the rate of change in $P_i(n_i, t)$ from time t to $t + \Delta t$ can be written as

$$\frac{\Delta P_i(n_i,t)}{\Delta t} = g_i(n_i-1)P_i(n_i-1,t) + r_i(n_i+1)P_i(n_i+1,t) - \left[g_i(n_i)+r_i(n_i)\right]P_i(n_i,t),$$

which leads to the steady-state or equilibrium solution (McKane *et al.* 2000, 2004; van Kampen 1981; Volkov *et al.* 2003), denoted by $P_i^e(n_i)$:

$$P_i^e\left(n_i\right) = \frac{g_i(n_i-1)g_i(n_i-2)\ldots g_i(0)}{r_i(n_i)r_i(n_i-1)\ldots r_i(1)}P_i^e\left(0\right), \tag{4}$$

for $n_i > 0$ and where $P_i^e(0)$ can be deduced from the normalization condition $\sum_{n_i=0}^{J} P_i^e(n_i){=}1$, leading to

$$P_i^e(0) = \frac{1}{1+\sum_{n_i=1}^{J}\frac{g_i(n_i-1g_i(n-2)\ldots g_i(0)}{r_i(n_i)r_i(n_i-1)\ldots r_i(1)}} = \frac{1}{1+\frac{g_i(0)}{d_i}\sum_{n_i=1}^{j}\frac{(1-v)^{n_i-1}}{n_i}} \approx \frac{1}{1+\frac{g_i(0)\ln\left(\frac{1}{v}\right)}{d_i\ (1-v)}}, \tag{5}$$

where we have used $\sum_{n_i=1}^{j}\frac{(1-v)^{n_i}}{n_i} \approx -\ln v$ for large J.

Over-representation of low-mortality species

According to Equation (1),

$$g_i\left(0\right) = \frac{v}{S-1}\sum_{l=1}^{S} n_l d_l = \frac{vJ\bar{d}}{S-1}, \tag{6}$$

where $\bar{d}{=}\sum_{l=1}^{S}\left(\frac{n_l}{J}\right)d_l$ is community average death rate. $g_i(0)$ is the rate of appearance of the species under consideration and must be infinitesimally small under the condition of an infinite species pool, i.e. $g_i(0)\rightarrow 0$. Therefore, we have the following approximation:

$$P_i^e\left(0\right) \approx 1 - \frac{vJ\bar{d}}{d_i S}\frac{\ln\left(\frac{1}{v}\right)}{(1-v)}. \tag{7}$$

The probability for species i to persist in the community is $1 - P_i^e(0)$, and from Equation (7) it follows that $\frac{1-P_i^e(0)}{1-P_j^e(0)}{=}\frac{d_j}{d_i}$, meaning that species with higher death rates are less likely to persist in the community.

Here, we derive Equation (7) under the linear approximations of $g_i(n_i)$ and $r_i(n_i)$, but the qualitative conclusion of over-representation of low-mortality species seems unlikely to change in the more general setting, as shown by our numerical example (Fig. 1a).

The distribution of relative species abundances

Obviously, every species will inevitably disappear as time goes by or $P_i^e(0) \approx 1$. As a consequence, the steady-state solution for species i (Eq. 4) is given by

$$P_i^e\left(n_i\right) \approx \frac{vJ\bar{d}}{(1-v)(S-1)d_i}\frac{(1-v)^{n_i}}{n_i} \approx \frac{\theta\bar{d}(1-v)^{n_i}}{Sd_i\quad n_i}, \tag{8}$$

where $\theta = \frac{Jv}{(1-v)} \approx Jv$ (if $v \ll 1$), in conformity with standard notation in neutral theory.

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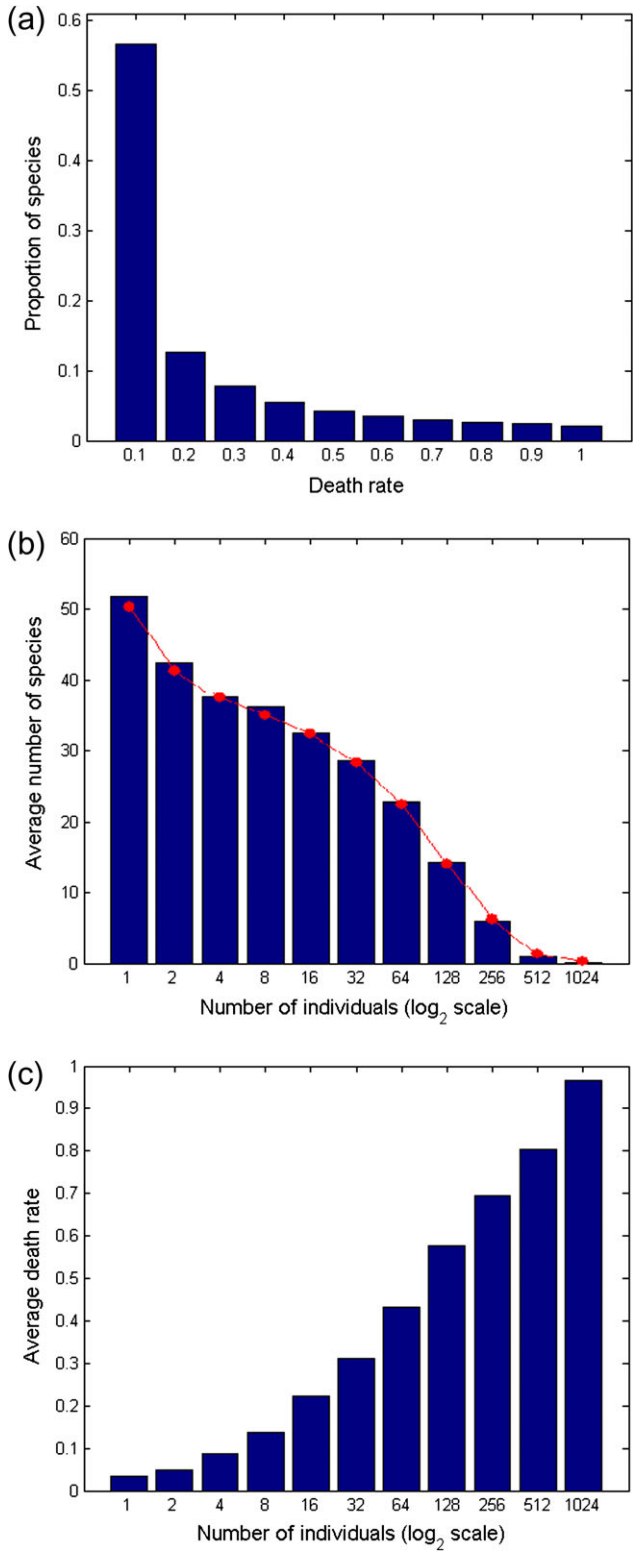

Figure 1: a hypothetical community of $J = 10^4$, $v = 10^{-3}$ and $S = 10^4$ based on Monte Carlo simulations. We run the simulation 100 times, each with 10^7 time steps. The death rates of species are $d_i = i * 10^{-4}$ for $i = 1, \ldots, 10^4$. At the start of simulation, all species from the species pool are present, each with one individual. At the end of simulation, about 270 species remain in the community. (**a**) Distribution of death rates for all the species that still persist by the end of simulation. The death rate for the first bar ranges from 0 to 0.1, the second from 0.1 to 0.2 and so on. Clearly, species having low death rates are more likely to persist in the community. (**b**) Relative species abundance of the simulated community. The bars are observed mean numbers of species binned into $\log_2$ abundance categories over an ensemble of 100 simulation runs. The first histogram bar represents $\langle\phi_1\rangle$, the second $\langle\phi_2\rangle + \langle\phi_3\rangle$, the third $\langle\phi_4\rangle + \ldots + \langle\phi_7\rangle$ and so on. The curve is the prediction of the log-series distribution of Equation (9), where $\hat{d} \approx 0.102$, $\bar{d} \approx 0.52$ and $\alpha \approx 51$. Note that the community average death rate $\bar{d}$ turns out to be very close to the arithmetic mean, 0.5, and that Hubbell's $\theta = Jv = 10$. (**c**) The positive correlation between death rate and species abundance. The first histogram represents the average death rate for species with 1 individual, the second for species with 2 to $2^2 - 1$ individuals, the third with 2^2 to $2^3 - 1$ individuals and so on. That is, high-mortality species, if having gained a footing in the community, are likely to become more abundant.

Following Volkov *et al.* (2003), the mean number of species containing n individuals is given by

$$\langle\phi_n\rangle = \sum_{i=1}^{S} P_i^e(n) = \alpha\frac{(1-v)^n}{n}, \tag{9}$$

It is obvious that the species abundance distribution of the weaker form of symmetry also follows a log-series distribution (see Fig. 1b) but has a very different parameterization from the classic neutral log-series distribution (Volkov *et al.* 2003). Under the assumption of fitness equivalence, combining Equations (8) and (9), we see that

$$\alpha = \theta\frac{\bar{d}}{\hat{d}}, \tag{10}$$

where θ is Hubbell's fundamental biodiversity parameter and $\hat{d} = \left(\frac{1}{S}\sum_{i=1}^{S}\frac{1}{d_i}\right)^{-1}$ is the harmonic mean of the death rates. Clearly, $d = \hat{d}$ if all species have the same death rate, leading to the classic log-series model under identical vital rates (Alonso and McKane 2004; Vallade and Houchmandzadeh 2003).

Correlation between species abundance and death rate

It has been shown through Monte Carlo simulations (Lin *et al.* 2009; Ostling 2004) that the abundances of persistent species are positively correlated with their respective death rates, although an analytical proof of this claim is mathematically difficult. In other words, existing species with higher death rates are expected to have a greater population size than low-mortality species (Fig. 1c).

However, if we made use of the linear approximations for g_i and r_i, then the expected abundance of species i conditional on its persistence in the community, $\langle n_i\rangle_{n_i>0}$, would be essentially the same for all persisting species in the community. This can be seen by combining Equations (7) and (8) to obtain the approximation:

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$$\langle n_i \rangle_{n_i>0} = \sum_{k=1}^{J} \frac{kP_i^e(k)}{1 - P_i^e(0)} = \sum_{k=1}^{J} \frac{(1-v)^k}{\ln\left(\frac{1}{v}\right)} \approx \frac{(1-v)}{v\ln\left(\frac{1}{v}\right)}, \qquad (11)$$

which is independent of species' vital rates. This must be so since the linear approximation requires species to have much smaller population sizes than the total community size (Alonso and McKane 2004; Chave 2004). But for species that are not so rare, especially for those few species among the most common in the community, the linear approximation may break down.

DISCUSSION

Life history trade-offs are widely acknowledged to be a prerequisite for species coexistence in the context of niche models (Chesson 2000; Tilman 2004). However, it is much less appreciated that they are also essential to Hubbell's neutral theory when species apparently differ in their vital rates. For the first time, we have shown that neutral theory can easily incorporate this demographic variation without changing the mathematical framework of the theory. The weaker form of symmetry is still a neutral model by definition, but it departs from the neutral endpoint on the neutral–niche continuum, making the model more realistic than the symmetric model and leading to several novel predictions for community structure that the previous neutral models fail to predict, which we discuss in the following.

Firstly, there is a general tendency for the community to discriminately accumulate low-mortality species. This has also been shown by simulations based on the finite-population version of the lottery model (Lin *et al.* 2009; Ostling 2004). In our model, new species enters the community through speciation, hence starting with the smallest possible population of single individuals. At this moment, it is self-evident that the species are quite vulnerable to extinction due to demographic stochasticity. What our model demonstrates, and confirmed by previous simulations (Lin *et al.* 2009; Ostling 2004), is that low mortality is favorable to species persistence (Fig. 1a). On reflection, it is easy to understand qualitatively why actual community membership is biased against high-mortality species. In a drifting community, high-mortality species will tend to fluctuate more in abundance simply because they undergo absolutely more births and deaths per unit time than low-mortality species, and more fluctuations in abundance would in turn give rise to higher risk of extinction.

Secondly, a positive correlation between species abundance and mortality occurs under the weaker form of symmetry, as present (Fig. 1c) and previous (Lin *et al.* 2009; Ostling 2004) simulations have repeatedly suggested. Why this is so? In a fitness-equivalent community, species continuously undergo stochastic fluctuations in abundance and the mean is determined by both low and high excursions of the population. But low excursions of the population lead to extinction, and so there is a bias to high excursions in mean abundance of a species that persists. These high excursions are higher for species with high death and birth rates, resulting in a positive correlation between species abundance and death rate, which was also found in two previous simulations of the lottery model (Lin *et al.* 2009; Ostling 2004).

However, we have to bear in mind that this positive correlation is vulnerable to be obscured by a number of factors. As shown by Equation (11), if the zero-sum assumption is violated such that species independence becomes a good approximation, the death or birth rate of a species will be indifferent to its abundance, which is a function of the speciation rate only. Furthermore, it has been shown that even a slight relaxation in fitness equivalence can lead to very different patterns (Fuentes 2004; Zhang and Lin 1997; Zhou and Zhang 2008). In a nearly neutral community, species abundance is largely determined by the ratio of per capita birth to death rate (fitness) rather than by the individual absolute rates. As noted before (Chave 2004), all species in the Barro Colorado Island (BCI) plot are not equivalent in fitness, and this may explain the lack of a positive correlation between species abundance and death rate in BCI (Condit *et al.* 1995).

Thirdly, although weaker symmetry can lead to the same log-series distribution of species abundance as the strict symmetry (Eq. 9), there is a big difference in the interpretation of the parameters (Eq. 10). Our results show that Hubbell's θ is equal to Fisher's α only in the special case when all species have identical demography on a per capita basis but not in more general neutral cases of equalized fitness due to demographic trade-offs. A famous inequality from mathematics is that the harmonic mean is always less than or equal to the arithmetic mean. To the extent that the arithmetic mean can be reasonably approximated by $\bar{d}$, we have $\bar{d} \geqslant \hat{d}$. In general, we expect Fisher's α to be much larger than Hubbell's θ, as confirmed by our numerical example (see Fig. 1b).

The fitness equivalence model can explain, at least partly, why previous estimates of speciation rates from neutral theory appear to be too high (Nee 2005; Ricklefs 2003, 2006). For demographically asymmetric species with different per capita birth and death rates, considerable bias might be introduced by ignoring the ratio of community average death rate to the harmonic mean death rate. In our numerical example, it can lead to an overestimate of the speciation rate five times larger than the true speciation rate used in the simulation. Although this increase seems not big enough to fully account for the problem of time (Nee 2005; Ricklefs 2003, 2006), trade-offs-based neutral theory coupling with other processes (e.g. division of a large system into smaller homogeneous neutral communities, repeated historical reductions in community size, occasional occurrence of superior competitors or protracted speciation; see Rosindell *et al.* 2010) can offer a promising solution to the problem of time. It is also important to bear in mind that the dynamical introduction of species in neutral models includes not only speciation in the usual (genetic) sense but also immigration from outside the community.

Finally, equal fitness (not equal demographics) significantly increases species diversity as evident from the relative species

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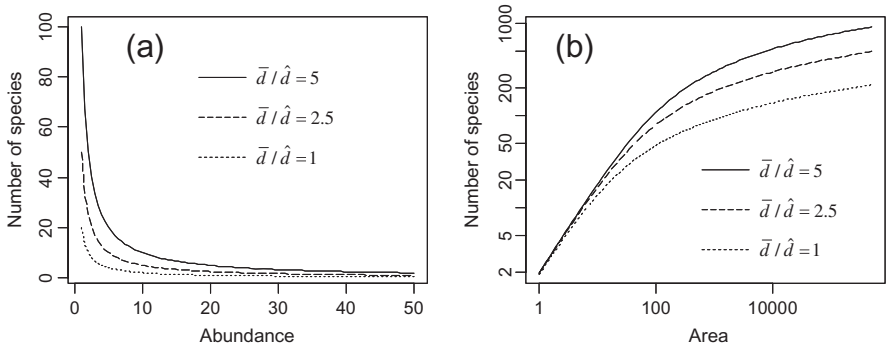

Figure 2: (**a**) Effect of fitness equivalence on the relative species abundance distribution (Eq. 9) with $\theta = 20$, $J = 2 \times 10^4$ and $\bar{d}/\hat{d}$ varying from 5, 2.5 to 1. $\bar{d}/\hat{d}$=1 describes Volkov *et al.*'s (2003) log-series model for the stronger form of symmetry with equal demographics. (**b**) Species-area curves derived from Equation (9), of form: $s_n=\theta\frac{\bar{d}}{\hat{d}}\log\left(1+\frac{n\hat{d}}{\theta\bar{d}}\right)$. Here, n is a proxy for area. Larger $\bar{d}/\hat{d}$ ratios indicate stronger trade-offs of fitness equivalence.

abundance distribution and the corresponding species-area curves shown in Fig. 2. Compared with the strict neutral model (i.e. $\bar{d}/\hat{d}$=1), the number of species in fitness-equivalent communities increases with the $\bar{d}/\hat{d}$ ratio, indicating that demographic trade-off promotes species diversity, and the stronger the trade-offs, the higher the diversity (See also He et al. 2012).

We do not want to leave readers with an impression that the neutral theory ignores trade-offs at all. Although there is a propensity to suggest that trade-offs do not change the predictions of the neutral model, our results together with two previous simulation studies (Lin *et al.* 2009; Ostling 2004) find this is not the case. Trade-offs do change the predictions, as detailed above. The focus of our study on metacommunity differs from previous analyses on local communities (Allouche and Kadmon 2009; Etienne *et al.* 2007; Haegeman and Etienne 2008). The fitness equivalence log-series species abundance distribution derived from this study gives a very different interpretation of the model. This study together with the previous works (Allouche and Kadmon 2009; Etienne *et al.* 2007; Haegeman and Etienne 2008) provides a trade-offs-based neutral theory for community assembly.

In summary, the finding that the same macroecological patterns can arise from fitness equivalence greatly generalizes neutral theory and highlights the importance of demographic trade-offs to species coexistence and diversity (Fig. 2). Evidence has increasingly shown that such trade-offs can make species equalized in fitness (Adler *et al.* 2007; Hubbell 2005, 2006; Leibold and McPeek 2006). Although stabilizing mechanisms are essential to stable coexistence of species, equalizing mechanisms can significantly promote coexistence (Adler *et al.* 2007; Chesson 2000; Leibold and McPeek 2006). Under equalizing mechanisms, species can either coexist long enough in the ecological time scale for significant diversity patterns to arise or for stable coexistence to be maintained even under the operation of very weak stabilizing forces which can be readily met in a varying environment (Adler *et al.* 2007; Cadotte 2007; Chesson 2000; Leibold and McPeek 2006; Turnbull *et al.* 2008). That said, we urge caution in assuming perfect fitness equalization in any neutral models. Incorporating small fitness asymmetries from a nearly neutral perspective (Chase 2005; Fuentes 2004; He et al. 2012; Peng et al. 2012; Zhang and Lin 1997; Zhou and Zhang 2008) is an obvious next step for theory development so as to push the theory farther down the neutral–niche continuum.

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