

# Demographic trade-offs in a neutral model explain death-rate–abundance–rank relationship

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**Abstract.** The neutral theory of biodiversity has been criticized for its neglect of species differences. Yet it is much less heeded that S. P. Hubbell's definition of neutrality allows species to differ in their birth and death rates as long as they have an equal per capita fitness. Using the lottery model of competition we find that fitness equalization through birth–death trade-offs can make species coexist longer than expected for demographically identical species, whereas the probability of monodominance for a species under zero-sum neutral dynamics is equal to its initial relative abundance. Furthermore, if newly arising species in a community survive preferentially they are more likely to slip through the quagmire of rareness, thus creating a strong selective bias favoring their community membership. On the other hand, high-mortality species, once having gained a footing in the community, are more likely to become abundant due to their compensatory high birth rates. This unexpected result explains why a positive association between species abundance and per capita death rate can be seen in tropical-forest communities. An explicit incorporation of interspecific trade-offs between birth and death into the neutral theory increases the theory's realism as well as its predictive power.

**Key words:** ecological equivalence; fitness invariance; life-history trade-offs; lottery model; neutral theory; species coexistence; time of coexistence.

## INTRODUCTION

Hubbell's (2001) neutral theory of biodiversity has been the focus of much recent interest and debate (Bell 2001, Chave 2004, Gaston and Chown 2005, Alonso et al. 2006, Holyoak et al. 2006, Etienne and Alonso 2007, Leigh 2007). The criticism has been predominantly directed at its fundamental assumption of neutrality that all species are ecologically equivalent on a per capita basis. Almost all neutral models have assumed identical per capita birth and death rates across species, presumably for the sake of mathematical simplicity and symmetry. However, species co-occurring within a community often reveal a wide variation in vital rates, as demonstrated by long-term community-dynamic studies in permanent tropical-forest plots (e.g., Swaine et al. 1987, Nascimento et al. 2005). Can neutral theory be reconciled with this observation of apparent differences between species? Hubbell (2001, 2005, 2006) argued that the stability of most communities through time suggests that all persistent species in a community have essentially identical per capita relative fitnesses. If this were not true so that one or another species had a persistently higher fitness, then that species would

eventually displace all of its competitors in the community. Such fitness invariance occurs in spite of species differences in vital rates because of interspecific trade-offs that equalize their fitness. In other words, neutrality need not require species to be identical in every aspect because differences in life-history traits do not necessarily lead to differences in their fitness. Unfortunately, this important facet of the neutral theory has not received as much attention as is its due (although alluded to in Etienne et al. [2007]), and neutral theory is still widely characterized as free of interspecific trade-offs (Chase and Leibold 2003, Kneitel and Chase 2004, Tilman 2004) and the presence of any trade-off is viewed as evidence against the role of ecological drift in structuring communities (e.g., Turnbull et al. 2005).

Zhang and Lin (1997) and Yu et al. (1998) both proposed a modification of Hubbell's model where either the fecundity or the mortality, but not both, was allowed to vary across species (and consequently the assumption of neutrality was violated). However, it is well known that a species' fitness or competitive ability is determined by both. As Chave (2004) pointed out, a proper estimate of the fitness for plant populations is the lifetime reproductive success, the number of new individuals produced over an individual's life span, which may be measured as the ratio of per capita birth to death rates. As a result, fitness equivalence can be realized by producing few offspring with high survival

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potential or by producing lots of offspring with low survivorship. It is worth emphasizing that this definition of fitness (and hence neutrality) is appropriate only when the community size is stationary (Charlesworth 1994), which the standard neutral model of Hubbell (2001) has already assumed. In communities where species play the zero-sum game and satisfy strict trade-offs between birth and death, the species identity of an individual does not matter or individual-level symmetry is maintained (Chesson and Rees 2007), since all individuals in the community have the same expected lifetime production of offspring. However, the zero-sum assumption is not always satisfied even though the community is regulated through density dependence (Parsons and Quince 2007). In such cases the lifetime reproductive success is no longer a suitable measure of fitness; as a consequence, finding a rigorous definition of neutrality that still allows species differences will become a challenge (Chesson and Rees 2007, Parsons and Quince 2007; but see Haegeman and Etienne 2008).

Following Hubbell (2001), we aim to explore the effects of ecological drift due to birth–death trade-off on their own, uncluttered by other processes that may affect species coexistence. For this purpose we will make use of a particular finite-population version of Chesson and Warner's (1981) lottery model of interspecific competition. A striking and entirely unexpected property of this model is how greatly neutral coexistence of equivalent competitors is prolonged if rare species survive preferentially, inducing the excessive accumulation of low-mortality species within a community. On the other hand, persistent species with relatively high death rates are more likely to become very abundant due to their compensatory high birth rates, and consequently a positive association between species abundance and per capita death rate arises. In the discussion we use these theoretical results to address some major criticisms of the neutral theory.

#### THE LOTTERY MODEL OF TRADE-OFF-BASED DRIFT

The lottery model was originally proposed and intensively investigated by Peter Chesson and colleagues (Chesson and Warner 1981, Chesson 1982, 1984, Chesson and Huntly 1997). The model assumes that space is allocated to juvenile organisms by chance, with some possible bias to one species or another. Having the same zero-sum dynamics, unbiased forms of Chesson and Warner's lottery model are closely related to Hubbell's (1979, 2001) ecological-drift model, but they differ in how species' recruitment rates are modeled (Etienne and Alonso 2007). In the lottery model the individuals that die can still contribute to the pool of offspring competing for the sites left vacant by the dying individuals. In Hubbell's model, by contrast, the dying individuals cannot contribute, and the expected fraction of available sites allocated to the offspring of species  $i$  is given by the proportional abundance of the species after death events (Hubbell 2001:76). We consider the lottery

model more realistic than Hubbell's model in describing population dynamics, because a perennial adult is generally able to leave offspring before it dies. At the very least, Hubbell's model does not apply to annual plants where all adults die in one time step, leading to immediate extinction. Moreover, in Hubbell's model the lifetime reproductive success is not a suitable fitness measure. In this sense it is incorrect to assert that Hubbell's model corresponds to the finite version of the lottery model (e.g., Chesson and Huntly 1997, Hubbell 2001). Species living in a constant, finite, lottery system will experience the sort of random walk to extinction suggested by Hubbell (1979, 2001), with no stabilizing tendencies at all.

Let  $N_i(t)$  be the population of adults of the  $i$ th species at year  $t$  in the community. Then the number of the  $i$ th species present next year is given by

$$N_i(t+1) = (1 - d_i)N_i(t) + R_i(t)N_i(t) \quad (1)$$

where  $d_i$  is the adult death rate and  $R_i(t)$  is the per capita recruitment rate of new adults into the population. The relative recruitment rate for species  $i$  at year  $t$  is simply the number of sites vacated by deaths at year  $t$  multiplied by the fraction of all births of species  $i$  in the community. The total number of deaths in the community at year  $t$  is

$$\sum_j d_j N_j(t)$$

where the summation is taken over all existing species within the community. If  $b_i$  is the per capita birth rate of species  $i$  at year  $t$ , then  $R_i(t)$  is

$$R_i(t) = \frac{\sum_j d_j N_j(t) b_i}{\sum_j b_j N_j(t)}. \quad (2)$$

In this model  $d_i$  and  $b_i$  are constants, so stable coexistence is not possible: the species with higher  $b_i/d_i$  will drive the other species to extinction (Chesson and Warner 1981).

In order to test how demographic stochasticity affects species coexistence in a lottery model, we have to resort to simulations because analytical solutions of the finite version of the lottery model are extremely difficult to derive. For two-species cases we simulated a community with  $K = 500$  individuals due to the expense of computation. In the simulation every individual has a species-specific risk to die, with death probability being  $d_i$  per year. Then each death is replaced with a new individual, which is species  $i$  with the following probability:

$$\frac{b_i N_i(t)}{b_1 N_1(t) + b_2 N_2(t)}.$$

Here for simplicity we do not consider demographic stochasticity in births (but see Chesson (1982) for a modification), which is nonetheless unlikely to be very

important if the population size is not very small (causing little variation in total offspring production). After all available sites left vacated by death process are recruited, we count the number of sites occupied by species  $i$  and denote this as the population size at next year,  $t + 1$ . Repeat this death-replacement cycle again and again until one species goes extinct. The number of cycles is counted as the absolute time of coexistence. Also, the number of deaths in each year is counted and summed up across all years to give the so-called “relative time of coexistence,” a measure of coexistence time used in most previous studies (Hubbell 2001).

Competitively equivalent species, by definition, have the same fitness, if the ratio  $b_i/d_i$  is a constant across all species. In other words, no matter how the per capita birth and death rates vary, species are considered equivalent as long as their ratios (fitness) remain the same. Letting  $C = b_i/d_i$ , we can easily see that  $R_i = d_i$  according to Eq. 2, and thus the expected abundance of each species at time  $t + 1$  will be the same as at time  $t$  according to Eq. 1. In other words, for a neutral community of fitness-equivalent species the recruitment rate of any species must equal its mortality rate and there is no deterministic trend in population dynamics. Without loss of generality, we can let  $C = 1$ . In simulations  $d_1$  and  $d_2$  are independently varied, with all possible combinations. To evaluate the effect of initial abundance on the coexistence time, we considered three initial abundances of 495, 450, and 250 (corresponding to 99%, 90%, and 50% of  $K$ ) from which the focal species 1 starts. For each parameter set, we ran 1000 independent simulations and found the median of the time to fixation (extinction or complete dominance) among 1000 replicates. The reason for using the median rather than the arithmetic mean is that the distribution of the time to fixation is strongly skewed rather than normal (see also Hubbell 2001). In all simulations the number of times the focal species wins the competition trial is also recorded to give an estimate of the focal species’ fixation probability.

#### *Neutral community dynamics in the presence of birth–death trade-offs*

To investigate the influence of differential fecundities and mortalities on species richness and relative abundances in a neutral community, we follow the above lottery model of birth and death and a point-mutation model of speciation described in Hubbell (2001) to form a metacommunity consisting of  $J_M = 200\,000$  individuals, with the fundamental biodiversity number  $\theta = J_M\mu = 20$ , where  $\mu$  is the rate of species input. Different from Hubbell’s model but following Chave et al. (2002), when a new species enters the metacommunity, we select its per capita death rate from the uniform distribution on  $(0, 1)$ . The uniform distribution of death rates for new species is used only for its convenience. A more realistic approach is to regard the mortality rates of new species as “mutations” on those of existing species in the system,

with the result that a “memory effect” will be present in the model. It is worth noting 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 (Bell 2001, Chave et al. 2002, Etienne et al. 2007).

In the simulation deaths in a year occur together and precede all births. For each death, the new recruit will be a new species with probability  $\mu$  and be one of the existing species with probability  $1 - \mu$ . In the latter case, the probability of recruitment of species  $i$  is

$$\frac{b_i N_i(t)}{\sum_j b_j N_j(t)}$$

Simulation is started with a single species with a death rate of 0.5 occupying all sites, and is continued until the metacommunity reaches a stochastic equilibrium, after 100 000 cycles (years). A set of 100 simulation runs is performed, and the mean of the abundance and the median of the death rate of  $r$ th ranked species are computed over the ensemble of 100 runs.

## RESULTS

### *Time of two species coexistence in a finite system*

When species have equal fitness but differential birth and death rates, the coexistence time can vary greatly, by more than an order of magnitude in a community as small as 500 individuals, regardless of what time unit, absolute or relative, is used (Fig. 1). In the case of equal initial abundances (first row in Fig. 1), the more differentiated with respect to vital rates, the longer the fitness-invariant species can coexist. But when species are started with unequal abundances (second and third rows in Fig. 1), the rarer species (i.e., species 2) has to survive better to achieve long-term coexistence. To put it another way, a rare-species advantage in survival (and meanwhile disadvantage in birth) is particularly favorable to transient coexistence of equivalent species.

The time unit matters to the coexistence result. It is trivially true that when both species have low death rates they can coexist for a long absolute time, as evidenced in Fig. 1. But this is not the case when coexistence is gauged from relative time. In this case, how many deaths are needed for one species to ultimately displace the other becomes fairly independent of the number of deaths in each year. What really counts from the viewpoint of relative time is the total number of deaths, which allows stochastic drift to take effect. In fact, fewer deaths are needed when both species have low death rates although the absolute time is longer (Fig. 1). However, the probability of monodominance (fixation) for the focal species remains constant, equal to its initial relative abundance (right-hand column in Fig. 1). This is a well-known result in the neutral theory of molecular evolution (Kimura 1983), and here shown to be preserved for neutral systems under fitness invariance and zero-sum dynamics. If community size is not held

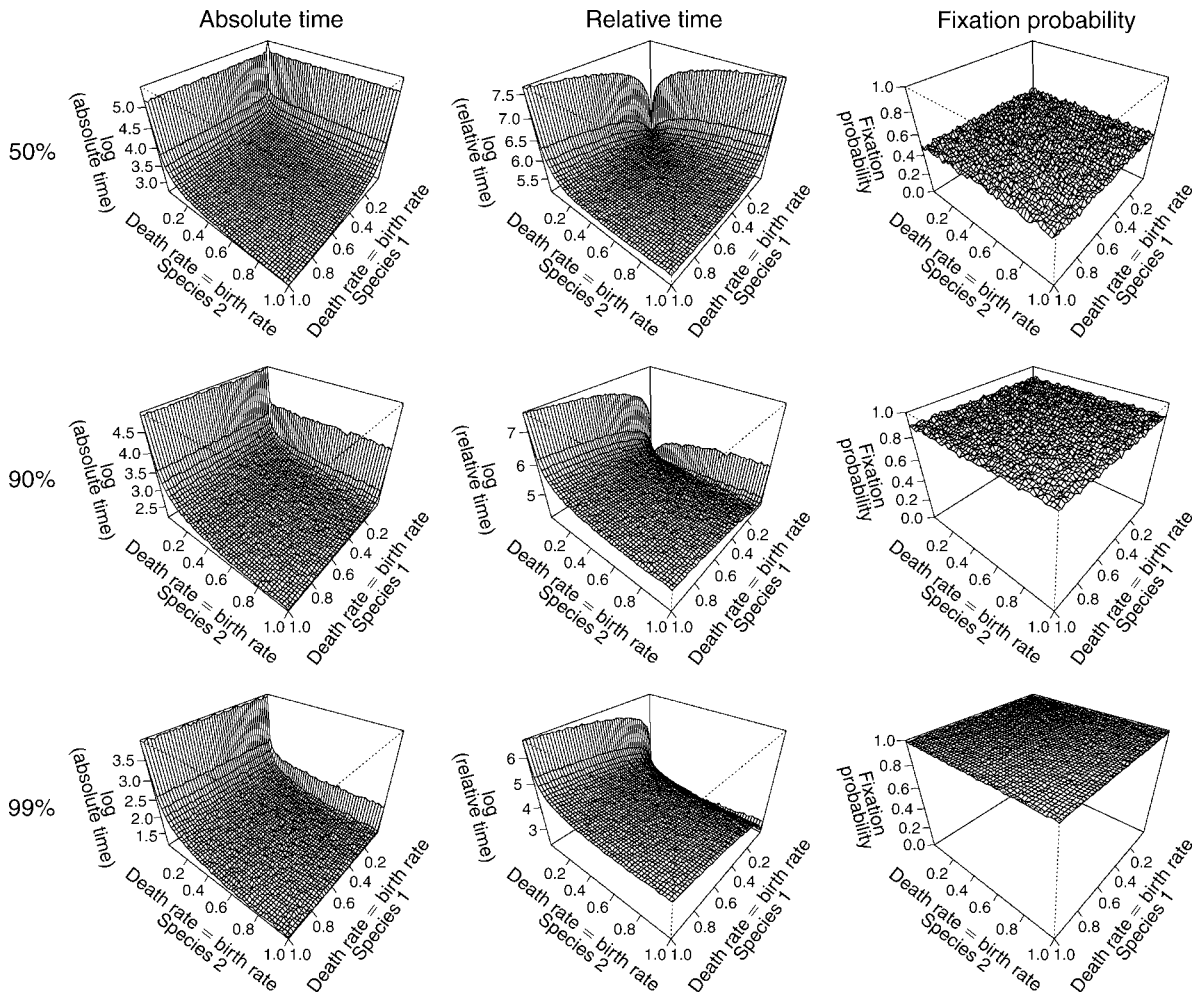


FIG. 1. Absolute time (left-hand column) and relative time (middle column) of two-species coexistence and fixation probability (right-hand column) of species 1 under its various initial relative abundances of 50% (first row), 90% (second row), and 99% (third row) in a community of 500 individuals. Species are assumed to have equivalent fitness, i.e.,  $b_1/d_1 = b_2/d_2$ , where  $b_i$  is the per capita birth rate of species  $i$  and  $d_i$  is the per capita death rate.

constant by density-dependent processes, but fluctuates around the equilibrium (see Parsons and Quince [2007] for an example), the fixation probability of a species will deviate from the simple neutral prediction, even though the ratio of per capita birth to death rate is the same for both species (Parsons and Quince 2007). Additionally, it is interesting to note that strictly neutral species (i.e., those having exactly the same birth and death rates) in general do not constitute maximum coexistence, particularly when viewed from relative time in the case of equal initial abundances (Fig. 1). When species start with vastly different initial abundances, so that one species (species 2 in Fig. 1) is very rare in the beginning, the time of coexistence effectively consistently increases with decreasing death rate of the rarer species 2, conditional on a fixed death rate of the common species 1. For strictly neutral species the absolute time of coexistence decreases dramatically, whereas the relative

time increases slightly, with the increase of death rate (Fig. 2).

#### *Neutral communities due to strict trade-offs between birth and death*

Speciation–extinction dynamics depend only on how many turnovers take place in the community, which probably explains why species richness of strictly neutral communities increases with death rate. Fig. 3 illustrates the influence of interspecific trade-off between birth and death on species richness and relative abundances in a neutral metacommunity. As expected, the species abundance distribution is close to log-series, but the equilibrium species number differs between strictly neutral and trade-off-based neutral communities. Further supporting evidence can be found in Etienne et al. (2007) and Haegeman and Etienne (2008) who showed that the abundance distribution of species subject to strict trade-offs only depends on the ratio of per capita

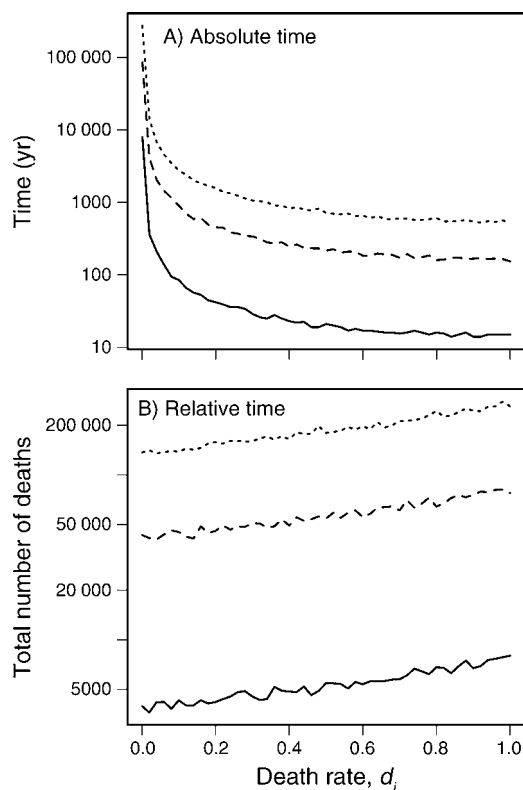


FIG. 2. (A) Absolute time and (B) relative time of coexistence for demographically identical species. Results are shown for three initial relative abundances of species 1: 50% (dotted line), 90% (dashed line), and 99% (solid line).

birth to death rate, not on the individual absolute rates. However, they do not look into how species abundances are related to the individual birth and death rates as we do here (see Fig. 4). As shown in Fig. 1, if species are differentiated along the birth–death trade-offs, coexistence is prolonged to a considerable extent when rare species survive preferentially, and this explains why diversity equilibrium maintained by drift and speciation is higher in the presence of trade-offs.

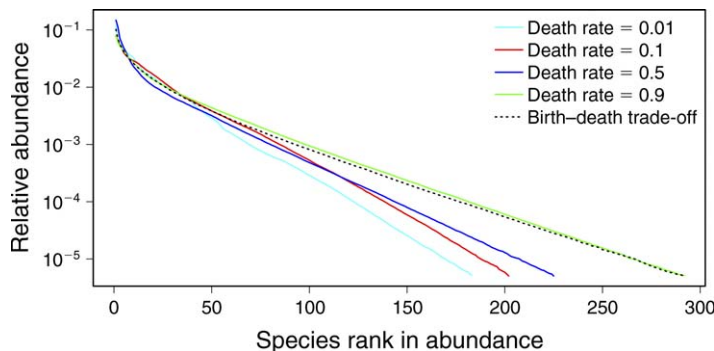
With interspecific trade-offs between birth and death included in the neutral model, there is a general tendency for the community to discriminately accumulate low-mortality species (Fig. 4A). It is clear from Fig. 1 that

rare species must survive preferentially to avoid quick extinction. This result reveals that only those new species that have low per capita death rates will likely survive the quagmire of rareness when first entering the community, thus creating a strong selective bias favoring their community membership. In other words, demographic stochasticity alone is sufficient to induce the excessive accumulation of rare low-mortality species within a community. On the other hand, high-mortality species, once having gained a footing in the community, are more likely to become very abundant due to their compensatory high birth rates. Consequently, a positive association between species abundance and per capita death rate arises from this effect (Fig. 4B).

#### DISCUSSION

Traditional niche theory treats coexistence of species as the result of both their similarities and differences, but has largely discounted the role of demographic stochasticity (Chesson 2000). Neutral theory, on the other hand, disregards differences among species when it comes to predicting community composition (Hubbell 2001). There is no question that species differ in many ways in nature. Different from the niche paradigm, neutral theory takes a radically simplified approach to perceive nature by assuming ecological equivalence, and complexity is only added when necessary. From this perspective, the framework of the neutral theory can be adapted to accommodate species differences as long as species' fitness is balanced by life-history trade-offs (Hubbell 2001). This point is critical for understanding the merit of neutral theory for explaining empirical systems, but it has surprisingly been ignored. All life-history trade-offs invariably lead to equalizing effects, but we are much less certain that they can also lead to stabilizing effects as required by traditional niche theory. In this context it seems rather eccentric that much more attention has been directed to the stabilizing effects while the equalizing role of trade-offs has been ignored in the literature. Here we have shown how the incorporation of interspecific trade-offs between birth and death into the neutral theory increases the theory's realism as well as its predictive power. More significantly, it creates a strong selective sieving of community membership (Fig. 4A) and a positive association

FIG. 3. Metacommunity species-abundance distribution in the presence of birth–death trade-offs (black dotted line) as compared to that of demographically identical species with four different death rates.



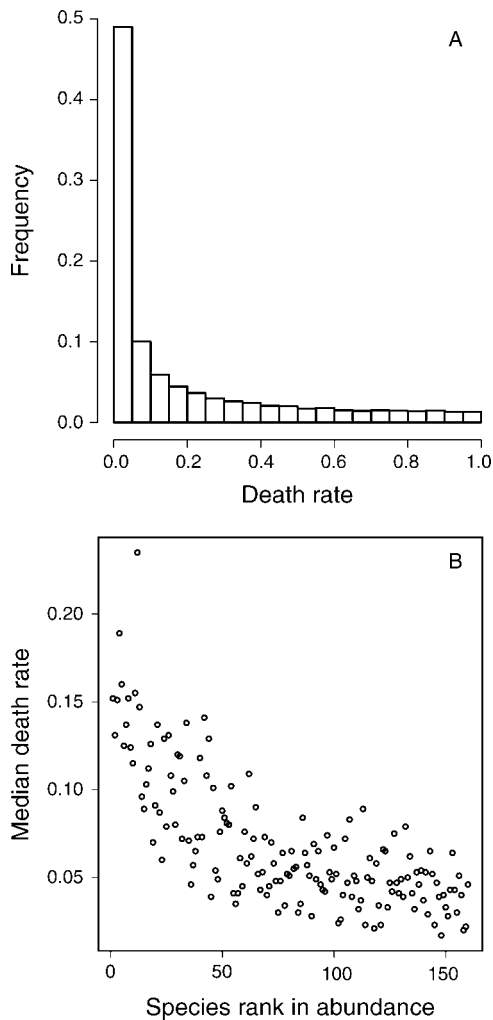


FIG. 4. Community-level consequences of demographic stochasticity in the presence of birth–death trade-offs. (A) Distribution of mortality rates for all species in an ensemble of 100 simulated communities ( $J_M$  [size of metacommunity] = 200 000 and  $\theta$  [fundamental biodiversity number,  $J_M\mu$ ] = 20). Each simulation run was started with a single species having mortality rate of 0.5, and the mortality rate of a new species entering the community is assigned by an independent random draw from a uniform distribution on (0, 1). (B) The apparently negative correlation between species' mortality rate and abundance rank. The mortality rate is obtained by computing the median in the mortality of each ranked species over an ensemble of 100 simulation runs, with the highest species rank being the smallest species number among 100 replicate communities.

between species abundance and per capita death rate (Fig. 4B), whereas relative species-abundance distribution is found to be log-series-like (Fig. 3), as the current neutral model predicts.

Recent empirical findings on tropical-forest communities support these theoretical predictions of our trade-off-based neutral model. Using census data from seven New and Old World tropical-forest-dynamics plots, Wills et al. (2006) have shown that more trees of the common species died over time than did those of rarer

species, thus increasing the relative representation of rare species. These findings were initially interpreted as resulting from the operation of nonrandom processes of several competing frequency-dependent models in these forests, diametrically opposed to neutral theory. Supported by the result of Fig. 4B, we suggest that an alternative explanation be the neutral theory based on trade-offs and fitness equivalence. In this context, we also note that although rare species survive better, they recruit at a lower rate than common species (Wills et al. 2006). Thus trade-off-based neutral drift more convincingly and parsimoniously explains what appears to be an empirical rejection of the neutral theory. We hasten to emphasize that we are not claiming the hegemony of neutral explanations for tropical-forest diversity, but we do see a need for appreciating the role of equalizing life-history trade-offs in promoting species coexistence in the absence of stabilizing niche mechanisms. Furthermore, the present neutral explanation for the association between mortality and abundance does not incorporate large-scale disturbances (e.g., drought or hurricanes). If this effect is taken into consideration, then high-mortality and high-fecundity species would be even further favored because of an advantage to the species with higher birth rate in disturbed communities.

Although coexisting species are constrained to occupy a narrow life-history manifold as predicted by the effect of fitness invariance and also verified by the trees on Barro Colorado Island (Hubbell 2001), tropical tree species are not uniformly distributed along the manifold. Instead, most species are found to concentrate at the end of low mortality and shade tolerance (Hubbell 2001). This pattern is not easy to explain within the framework of the niche theory (Hubbell 2006), but is nicely predicted by the neutral model of demographic trade-offs, as shown by the excessive number of low-mortality species (Fig. 4A). This is a more parsimonious and coherent model than Hubbell's (2006) explanation by which the uneven distribution of species death rates is hypothesized to be determined by the degree of contrasting variation in environments (shady vs. sunny).

Wootton (2005) tested the neutral theory on a rocky-intertidal community from Tatoosh Island, Washington, USA. Although the observed species relative-abundance distribution follows that predicted by the neutral theory, the abundance of each species following the experimental removal of a dominant species is poorly fitted by a parameterized neutral model. However, this discrepancy can better be explained by our neutral model of birth–death trade-offs. If some variation in birth and death rates does exist across species in the intertidal community, the capturing of empty space freed from dominant species removal will depend not only on the relative species abundance but also on the birth rate of each species. It is necessary to take into account variation in species' vital traits to improve the predictive ability of the neutral-drift model.

Neutral theory is commonly considered of little use for explaining the biodiversity effects on ecosystem functioning (Chase 2005, Purves and Pacala 2005, Leigh 2007). However, the trade-off-based neutral model presented in this study does predict a role for particular species. As Loreau and Mouquet (1999) pointed out, community productivity in a lottery system can be measured approximately as

$$\bar{b} = \sum_j b_j N_j$$

i.e., community average seed production, on the assumption that a species' productivity is correlated with its birth rate. From this assumption it is almost self-evident that higher productivity is expected if more species are included in the biodiversity–ecosystem-functioning experiment. The trade-off-based neutral model may even explain why the biodiversity effects in these experiments become progressively stronger with time. As Fig. 4B illustrates, more productive species with higher mortality are, by chance, more likely to become abundant, increasing their representation in the experimental communities, which in turn leads to higher community productivity. If experimental communities are initially unsaturated, as is often the case in biodiversity experiments, more-productive species would become even more overrepresented with time.

Life-history trade-offs are widely acknowledged to be a prerequisite for species coexistence in traditional niche models, but it is much less heeded that neutral theory also needs to invoke trade-offs to explain why species with very different vital rates can co-occur within a community and undergo ecological drift. Future work should consider the interplay of unequal fitnesses among species and demographic stochasticity on species coexistence (Fuentes 2004, Zhou and Zhang 2008). After all, no one seriously argues for complete equivalence of species' fitnesses in any real ecological communities. It seems highly desirable to determine whether the neutral predictions depend on perfect equality and how the interplay of drift and selection influences species diversity. Finally, our analysis should also be applicable to understanding the mutation–extinction equilibrium of neutral or nearly neutral allele frequencies in population genetics, and to understanding the survival of small populations in invasion and conservation biology.

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