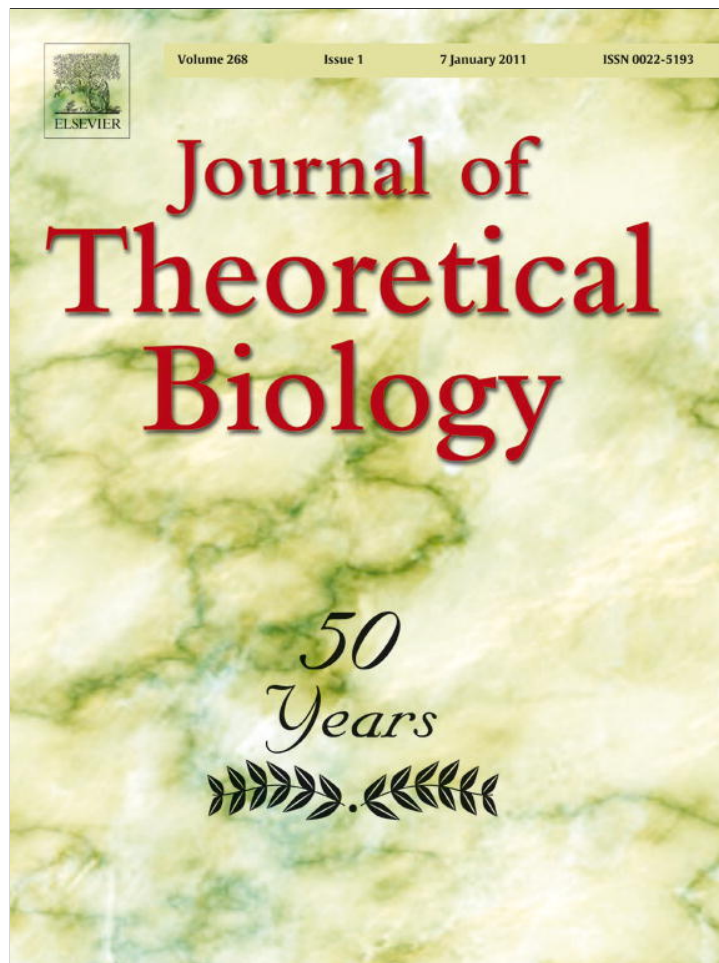


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Negative density dependence can offset the effect of species competitive asymmetry: A niche-based mechanism for neutral-like patterns

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ABSTRACT

The debate on the role of species differences in shaping biodiversity patterns, with its two extremes of pure niche theory and neutral theory, is still ongoing. It has been demonstrated that a slight difference in competitive ability of species severely affects the predictions of the neutral model. At the same time, neutral patterns seem to be ubiquitous. Here, we model both negative density dependence (NDD) and competitive asymmetry (CA) simultaneously. Our simulation results show that an appropriate intensity of NDD can offset the negative effect of CA (modeled as fecundity difference) on species coexistence and produce a neutral-like species abundance distribution. Therefore, our model provides a plausible mechanistic explanation of neutral-like patterns, but contrary to the neutral model, a species' relative abundance is positively related to its competitive ability in our model.

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1. Introduction

The debate on the role of species differences in shaping biodiversity patterns, with its two extremes of pure niche theory and neutral theory, is still ongoing (Kraft et al., 2008; Leibold and McPeck, 2006). Niche theory states that no ecologically equivalent species can coexist; only species with sufficiently differentiated niches may coexist within the same ecological community (Chase, 2005; Chesson, 2000; Leibold and McPeck, 2006; Vandermeer, 1972). Niche theory also assumes that species traits represent evolutionary adaptations to the environment, that species face unavoidable trade-offs, and that such trade-offs are essential mechanisms allowing interacting species to coexist and determine the relative species abundance and diversity patterns (Harpole and Tilman, 2006).

As an alternative to niche theory, neutral theory (Bell, 2001; Hubbell, 1997, 2001) asserts that ecologically equivalent species can coexist. Although the ecological equivalence assumption seems unrealistic (Whitfield, 2002), neutral theory provides a new stochastic, dispersal-limited sampling theory for ecological communities (Alonso et al., 2006; Etienne and Alonso, 2005) and offers a surprisingly accurate quantitative prediction of macroecological patterns such as the species abundance distribution (SAD) (Etienne, 2005) and the species-area relationship

(Rosindell and Cornell, 2007) for realistic values of the speciation rate (Rosindell and Cornell, 2009; Rosindell et al., 2010), suggesting a simple mechanistic explanation of community assembly, in particular tropical forest and coral reef communities (Volkov et al., 2003, 2007; Whitfield, 2002). Hubbell (2005) argued that ecological equivalence can easily be the result of evolution, especially in species-rich communities: inter-specific differences – which evidently do exist – are just not sufficient to make the per capita vital rates differ substantially between species. However, many studies have indicated that a slight difference in the birth rate (Zhang and Lin, 1997), mortality rate (Yu et al., 1998) or non-exactly fulfilled trade-offs (Purves and Turnbull, 2010) can dramatically reduce the time of species coexistence and hence decrease the biodiversity of ecological communities. Thus the ecological equivalence hypothesis, which is essential to neutral theory does not seem to be robust. The question then arises: why are neutral patterns observed?

One possibility is that a neutral-like pattern can emerge if species in a trophically homogeneous community are nearly neutral. Analogous to the nearly neutral theory of molecular biology, Zhou and Zhang (2008) proposed a nearly neutral model of community ecology that allows asymmetry among species in their per capita competitive ability and investigated the effects of this asymmetry on species coexistence time and community structure. They found that, although species asymmetry can speed up competitive exclusion, the SAD pattern can often still be fitted well by a neutral model. However, other mechanisms may also be possible. For instance, some studies have demonstrated that niche differentiation and neutral drift both can

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contribute to species coexistence (Chase, 2007; Levine and HilleRisLambers, 2009; Rominger et al., 2009). It has been shown that a neutral pattern does not imply neutral process – there can be non-neutral processes yielding neutral-like patterns (Lin et al., 2009; Purves and Pacala, 2005; Walker, 2007; Wootton, 2005; Zhou and Zhang, 2008) or neutral patterns are special cases where species have equivalent fitness without stabilizing mechanisms (Adler et al., 2007). These studies suggest that, if species asymmetry plays a role in community assembly, then other mechanisms must exist to counteract its effect.

As an important stabilizing process in population ecology, NDD can affect per capita rates of birth, death and migration or any combination of these rates (Chave et al., 2002; Chesson, 1998; Hubbell et al., 1990; Volkov et al., 2005). Increasing evidence shows that natural enemies (Mitchell and Power, 2003; Torchin et al., 2003) or limiting resources (Tilman et al., 1982) are responsible for these negative conspecific effects. Strong negative conspecific effects have been reported in particular for very common species implying that NDD prevents the most common species from competitive dominance (Amarasekare, 2004; Hubbell et al., 1990; Wright, 2002). Volkov et al. (2005) also demonstrated that, as an alternative explanation to dispersal limitation, a special form of density dependence can account for the observed relative species abundance (RSA) in rainforests. Although SADs without additional information often cannot be used to discriminate among different underlying mechanisms (Chave et al., 2006; Volkov et al., 2006), NDD could maintain the species coexistence and shape the species abundance patterns in tree communities (Comita et al., 2010; Harms et al., 2000; Packer and Clay, 2000).

In this paper, we combine NDD and competitive asymmetry (CA) in the context of general lottery models of competition (Chesson and Warner, 1981). Our hypothesis is that strong NDD offsets species asymmetry in competitive ability, providing a potential mechanism of neutral-like patterns observed in nature.

2. Models

We start with Chesson and Warner's lottery model (Chesson and Warner, 1981) and the probability of vacant cells occupied by species i at time $t+1$ is:

$$P_i(t+1) = [1 - \delta_i(t)]P_i(t) + \left[\sum_{j=1}^S \delta_j(t)P_j(t) \right] \left[\frac{w_i^*(t)P_i(t)}{\sum_{j=1}^S w_j^*(t)P_j(t)} \right] \quad (1)$$

where $\delta_i(t)$ is proportion of adults of species i dying during $(t, t+1)$, S denotes total number of species and $w_i^*(t) = c_i w_i(t)$ denotes the CA between species i and $w_i(t)$ denote the relative competitive abilities of different species and per capita net reproduction of species i during $(t, t+1)$, respectively.

Based on this model, we developed several stochastic local and metacommunity models incorporating NDD and CA to study biodiversity patterns and species coexistence mechanisms in a community. Reproductive ability (e.g. number of seeds) and survival probability (e.g. of seeds, seedlings and adults) are very important demographic traits (Leibold and McPeck, 2006) that differ between species and also determine the probability of successful recruitment to vacant cells. Here we assume that CA implies that the per capita fecundity rate w_i differs among different species (w_i should be positive) and incorporate NDD in the survival probability $v_i(t)$ (Bell et al., 2006; Freckleton and Lewis, 2006). As in the neutral model, death is assumed to occur randomly irrespective of species labels, i.e. $\delta_i(t) \equiv \delta$, which we call the turnover rate in our models and the total number of deaths

can be obtained by multiplying turnover rate δ with community size J .

2.1. Coexistence time (time to fixation) in a spatially explicit two-species metacommunity without speciation

We first explored the effect of inter-specific differences in fecundity and conspecific NDD in survival on the time to fixation (monodominance) in a two-species metacommunity without speciation. We used the absolute time to measure the median time to fixation to avoid the influence of community size (Yu et al., 1998; Zhou and Zhang, 2008). We assumed the landscape to be a torus, that is, cells on the right edge are neighbors of those on the left and cells on the bottom are neighbors of those on the top. In order to simulate efficiently, we only considered small metacommunity sizes (Zhou and Zhang, 2006, 2008), because the extremely efficient coalescent-based approaches (Rosindell et al., 2008) can no longer be used in asymmetric models. Let L be the square root of metacommunity size. For this model we use the values of $L=16$ and 32 , so the metacommunity size J is 256 and 1024 , respectively. We also performed several simulations for larger metacommunity sizes but found that the fundamental relationship between species competitive asymmetry, NDD, and the coexistence time did not change with community size.

In the simulations, we used a value for turnover rate of 1.7% per year as reported for tropical forests (Swaine et al., 1987). The death-recruitment cycle was modeled as follows. At the beginning of each simulation, both species have the same abundance i.e. $P_1(t) = P_2(t) = 0.5$. First, an individual dies at random. A new individual is recruited immediately (zero-sum assumption) by a local birth. The recruitment probability of each existing species is determined by each species' per capita fecundity, dispersal ability and density dependent survival rate of seeds and seedlings. For simplicity, we only considered two extreme cases of dispersal strategies: nearest neighbor dispersal (the total number of possible dispersal cells $A=8$) and global dispersal ($A=J-1$). For each recruitment event, we calculated the total probability of each species within the dispersal distance of the vacant cell and denoted them as $\sum_{k=1}^A P_{i,k}(t)$. $P_{i,k}(t)$ denotes the probability of occupying the specific cell k by species i during $(t, t+1)$. The vacant site is then colonized by a seed of species i with probability $\frac{\sum_{k=1}^A P_{i,k}(t)w_i}{\sum_{i=1}^S \sum_{k=1}^A P_{i,k}(t)w_i}$. The probability of recruitment by species i is the product of this colonization (immigration) probability and the survival (establishment) probability (Jabot et al., 2008). Following Chave et al.'s (2002) simulation methods for density dependence, the probability of an offspring successfully surviving to adulthood (i.e. establishing) decreases in proportion to the number of neighboring sites occupied by conspecifics. We incorporated such effects by calculating the proportion $q_i(t)$ of the eight nearest-neighbor cells that are occupied by species i and set the (relative) survival probability of an offspring of species i equal to $v_i(t) = 1 - \alpha q_i(t)$, where α is the density dependent factor.

Thus Eq. (1) can be written as:

$$P_i(t+1) = (1 - \delta)P_i(t) + \delta \frac{\sum_{k=1}^A P_{i,k}(t)w_i(1 - \alpha q_i(t))}{\sum_{j=1}^S \sum_{k=1}^A P_{j,k}(t)w_j(1 - \alpha q_j(t))} \quad (2)$$

For convenience we denoted the per capita fecundity factor of the focal species 1 relative to the non-focal species 2 by w (i.e. $w_1 = w$ and $w_2 = 1$) and selected values of w of 1.0 (the neutral case where there is no difference in per capita fecundity), 1.01 and 1.1. Also for simulating efficiently and because we were interested in small deviations from the neutral model, we only assumed the following small values for α : 0 (neutral case where

there is no NDD), 0.01, 0.05 and 0.1. The death-recruitment cycle was repeated until one species became mono-dominant (fixation) in the community. Then we recorded the absolute time to fixation. For each parameter combination, we calculated the median fixation time over 100 replicate simulations.

For the two-species case and global dispersal, Eq. (2) reduces to the following equation if NDD occurs globally (i.e. $q_i(t) = p_i(t)$):

$$P_1(t+1) = (1-\delta)P_1(t) + \delta \frac{w_1 P_1(t)(1-\alpha P_1(t))}{w_1 P_1(t)(1-\alpha P_1(t))_1 + w_2 P_2(t)(1-\alpha P_2(t))} \\ = P_1(t) \left[1 - \delta + \delta \frac{w_1(1-\alpha P_1(t))}{w_1 P_1(t)(1-\alpha P_1(t))_1 + w_2 P_2(t)(1-\alpha P_2(t))} \right] \quad (3)$$

and therefore

$$\lim_{P_1(t) \rightarrow 0} \frac{P_1(t+1)}{P_1(t)} \approx 1 + \delta \left(\frac{w_1 - w_2(1-\alpha)}{w_2(1-\alpha)} \right) \\ \lim_{P_2(t) \rightarrow 0} \frac{P_2(t+1)}{P_2(t)} \approx 1 + \delta \left(\frac{w_2 - w_1(1-\alpha)}{w_1(1-\alpha)} \right) \quad (4)$$

Both species can stably coexist if the signs of $((w_1 - w_2(1-\alpha))/w_2(1-\alpha))$ and $((w_2 - w_1(1-\alpha))/w_1(1-\alpha))$ are both positive, i.e. $1-\alpha < (w_1/w_2) < (1/(1-\alpha))$ when $0 < \alpha < 1$ and $(1/(1-\alpha)) < (w_1/w_2) < 1-\alpha$ when $\alpha > 1$. The blue area in Supplementary Fig. A1 shows when these two species can stably coexist.

2.2. Species abundance distribution in a spatially implicit metacommunity with speciation

We then explored the joint influences of species CA and NDD on the SAD in a multiple-species metacommunity with speciation but without explicit spatial structure.

For metacommunities, we introduced stochastic speciation to our model. We used the algorithm described by Hubbell (2001) to construct the initial metacommunity containing $J_M = 10^5$ individuals with a fundamental biodiversity number $\theta = 100$. Again, individuals were assumed to die at random, immediately followed by recruitment of one new individual. The probability of recruitment by a new species is $v = \theta / (\theta + J_M - 1)$ (Etienne, 2005), otherwise the recruitment is the birth of an existing species with probability $1 - v$ which also depends on its fecundity and density. We followed the method in Zhou and Zhang (2008) to select each species' per capita fecundity factor w_i from the normal distribution $N(1, \sigma^2)$, where σ is the standard deviation. Here we considered five cases for σ : $\sigma = 0$ (neutral case), $\sigma = 0.001$, $\sigma = 0.003$ (the largest standard deviation in Zhou and Zhang, 2008), and $\sigma = 0.005$. As in the previous model, we incorporated NDD in the survival probability: $v_i(t) = 1 - \alpha q_i(t)$. Because this model assumes global dispersal and globally occurred density dependence, the proportion q_i is the relative abundance of species i in the metacommunity ($q_i = Q_i$). But here we introduced stochastic speciation to our model, so the dynamics of species is not simply deterministic and cannot easily be put in a form similar to Eq. (1).

The following values for the parameter of NDD α were chosen for simulation in order to produce neutral-like patterns: 0, 0.01, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 and 1. The above death-recruitment cycle was continued for 10,000 community turnovers, which is long enough for the metacommunity to reach dynamical equilibrium. We repeated this simulation 100 times and obtained the average distributions of relative species abundances. We also recorded the mean fecundity factor of species with the same abundance.

We used the bootstrap Kolmogorov–Smirnov (bootstrap ks) to test the significance of differences between the relative SADs, which are produced by the pure neutral and our non-neutral model SADs. The bootstrap ks test is an improved Kolmogorov–

Smirnov test (which is valid even when the distributions being compared are not entirely continuous) of the equality of two distributions (Præstgaard, 1995).

2.3. Species abundance distribution in a spatially implicit local community

For local communities, we integrated the joint effects of NDD, CA (here we only consider the case: $\sigma = 0.003$) and limited dispersal from a metacommunity on the SAD in a local community. For each metacommunity constructed above, we constructed a local community of size $J_L = 2000$ by dispersal-limited sampling from the metacommunity. Death is assumed to occur randomly as in the metacommunity. However, the process of recruitment is somewhat different from that of the metacommunity. After a random death, the vacant site is either replaced by a migrant from the metacommunity (with probability m), or a local birth (with probability $1 - m$), where m is the immigration probability or dispersal probability from the metacommunity. When immigration occurs, the probability of species i being recruited is proportional to its relative abundance in the metacommunity. Similar to the simulation method for the metacommunity outlined above, the probability of local recruitment is determined by the combination of colonization probability and density-dependent survival probability. Thus Eq. (1) becomes

$$P_i(t+1) = (1-\delta)P_i(t) + \delta \left[mQ_i + (1-m) \frac{w_i(t)P_i(t)(1-\alpha P_i(t))}{\sum_{j=1}^K w_j(t)P_j(t)(1-\alpha P_j(t))} \right] \quad (5)$$

where Q_i is the relative abundance of species i in the metacommunity.

We chose the following values for m : 0.002, 0.01, 0.05 and 0.25. The simulation was continued until a stochastic equilibrium was reached (approximately 20,000 turnover events). This simulation was repeated 100 times and the final SAD is the mean of these replicate local communities drawn from the same metacommunity.

3. Results

NDD promotes species coexistence with or without dispersal limit (Figs. 1 and 2). Although small differences in species' per capita fecundity can largely decrease the coexistence time of two species (Zhang and Lin, 1997; Zhou and Zhang, 2008) which is also shown in Fig. 1, NDD can delay competitive exclusion and offset the negative effect of CA on species coexistence (Fig. 1). Species coexistence time increases dramatically with the strength of NDD, especially when species differences in per capita fecundity are small and there is no dispersal limitation (global dispersal strategy). Comparing Fig. 1a with b, we can see that the effect of NDD on species coexistence becomes more prominent when community size increases.

Dispersal limitation is generally thought to be advantageous for species coexistence (Yu et al., 2004). Dispersal limitation has also been invoked to reconcile competitive exclusion and neutral coexistence in a community (Hubbell, 2001, 2006). Indeed, dispersal limitation can also increase species coexistence time but this effect is rather weak (Fig. 1, and see Zhou and Zhang, 2008). In fact, CA may dominate community dynamics even under strong dispersal limitation where an individual disperses its seeds only to its neighboring sites. As shown in Fig. 1, when the intensity of NDD becomes stronger, the effect of dispersal limitation on species coexistence may be even reversed. NDD can substantially

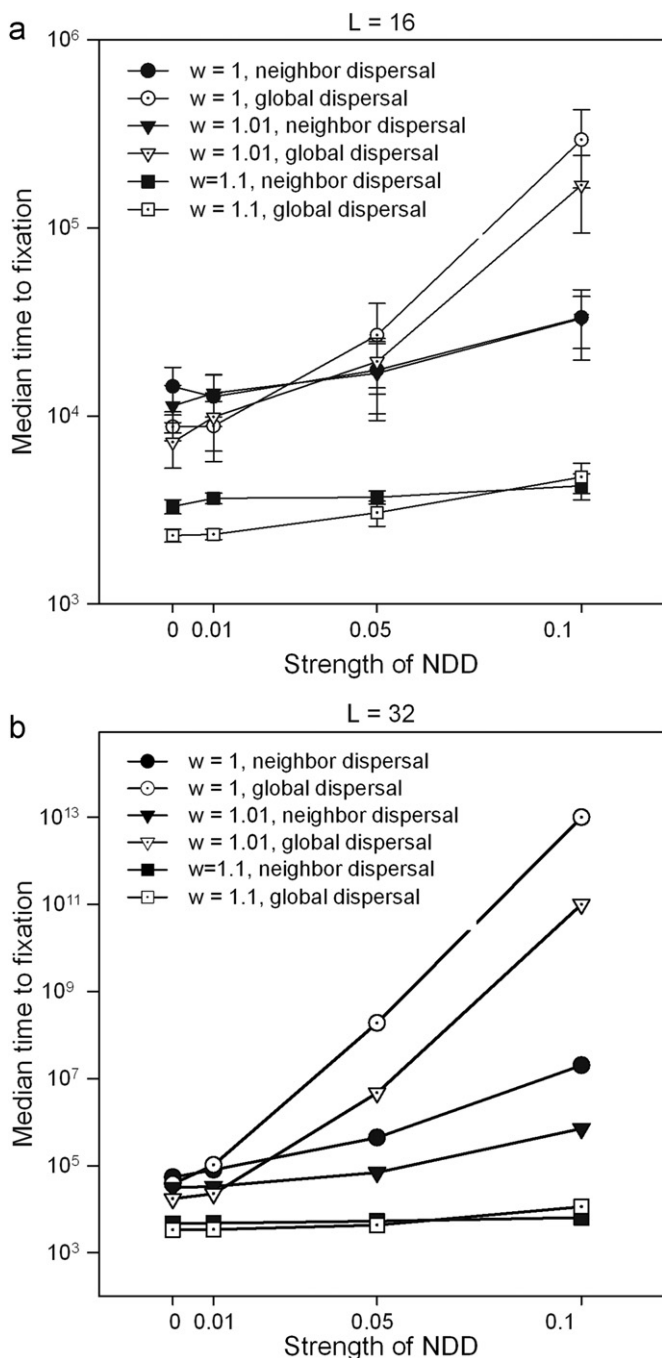


Fig. 1. Influence of inter-specific differences in fecundity and NDD on the median time to fixation in a two-species community of size 16×16 (a) and 32×32 (b). NDD can considerably increase species coexistence time, and this effect becomes more marked as community size increases.

delay competitive exclusion due to difference in per capita fecundity, if dispersal is only weakly limited.

For the multi-species metacommunity with speciation, small differences in species per capita fecundity ($\sigma=0.003$) can substantially decrease species richness and the SAD deviates much from that predicted by the neutral model (Fig. 2a, also see Zhou and Zhang, 2008). NDD can restore species richness by decreasing the abundance of common species and increasing the number of rare species regardless of with or without CA (Fig. 2 and Supplementary Fig. A2). In the presence of CA (species difference in fecundity, $\sigma=0.003$), an appropriately chosen intensity of NDD (e.g. $\alpha=0.6$) can produce an SAD that is indistinguishable from

the SAD predicted by the neutral model (see Fig. 3). The bootstrap tests indicate that neutral-like patterns can be produced with an appropriate intensity of NDD, which increases with the competitive asymmetry. However, in contrast to the neutral model, species differ in their competitive ability. As shown in Fig. 2b, species with higher per capita fecundity factor has higher abundance, while less common and rare species are nearly neutral. It is competitive ability that determines persistence of species and the commonness of species.

Turning to the local community, dispersal limitation also plays an important role in structuring local communities. Our model can easily produce a neutral-like SAD particularly when immigration from the metacommunity is relatively high (Fig. 4a). Furthermore, for larger immigration rates (e.g. $m=0.05$ and 0.25) we find a better match between the predicted SADs and neutral-like SADs and a larger range of NDD where a good match is obtained (results not shown); also, the strength of NDD that produces neutral-like patterns increases with immigration rate. Strong dispersal limitation (small migration rate m) results in steeper rank-abundance distributions (more abundant species and smaller total number of species within the local community) whereas strong NDD causes flatter rank-abundance distributions (more rare species and larger total number of species within the local community) given a fixed CA ($\sigma=0.003$) or without any CA (Fig. 4a, Supplementary Figs. A2,A3). The positive relationship between species abundance and species competitive ability for common species still remains (Fig. 4b).

4. Discussion

Based on the assumption of functional equivalence, neutral theory successfully predicts SADs and species-area relationships in many species-rich communities. However, it has been demonstrated that a slight deviation from the equal fitness assumption can lead to a dramatic decrease in species coexistence time (Yu et al., 1998; Zhang and Lin, 1997; Zhou and Zhang, 2006, 2008). Although species can still coexist in such a nearly neutral case, species richness is substantially decreased and such coexistence is also unstable (Zhou and Zhang, 2008). In this paper, we emphasized the effect of NDD within species on community assembly and abundance distributions. We showed that an appropriately chosen strength of NDD can offset the negative effect of CA on species coexistence, producing SAD patterns that are indistinguishable from those predicted by the neutral model. NDD persistently promotes the community species richness, which is consistent with many previous empirical and theoretical findings (Amarasekare, 2004; Bell et al., 2006; Comita et al., 2010; Goldenheim et al., 2008; Hubbell et al., 1990; Volkov et al., 2005; Wills et al., 1997). Moreover, we can easily satisfy the conditions for stable coexistence of two species in metacommunities with global dispersal and NDD (as shown in Supplementary Fig. A1).

Some important ecological insights can be gained from our study. First, neutral pattern does not necessarily imply neutral mechanism. Our study further confirms this and puts forward another plausible mechanistic explanation of neutral-like patterns. We showed that NDD can offset the effect of species differences on biodiversity and abundance patterns, resulting in neutral-like patterns. Whether other macro-ecological patterns, such as the species-area relationship, remain unchanged under neutral and non-neutral mechanisms still remain to be investigated.

Second, the optimal dispersal strategy that prolongs species coexistence time, changes with the intensity of NDD. Although

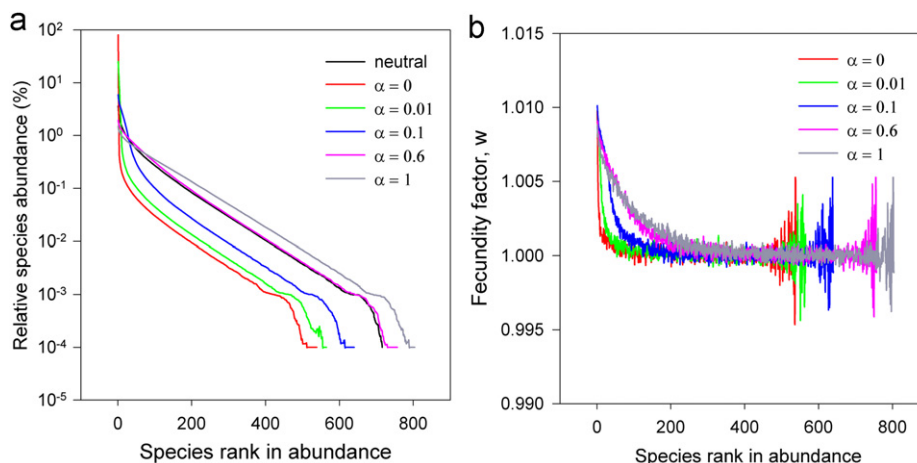


Fig. 2. (a) Metacommunity equilibrium rank-abundance curves for models with and without species CA or NDD and (b) relationship between species abundances and their fecundity factors in metacommunities with and without CA or NDD. Parameter values: $J_m=10^5$, $\theta=100$ and $\sigma=0.003$ except for the neutral case where $\sigma=0$. The curves are the mean of 100 repeated simulations.

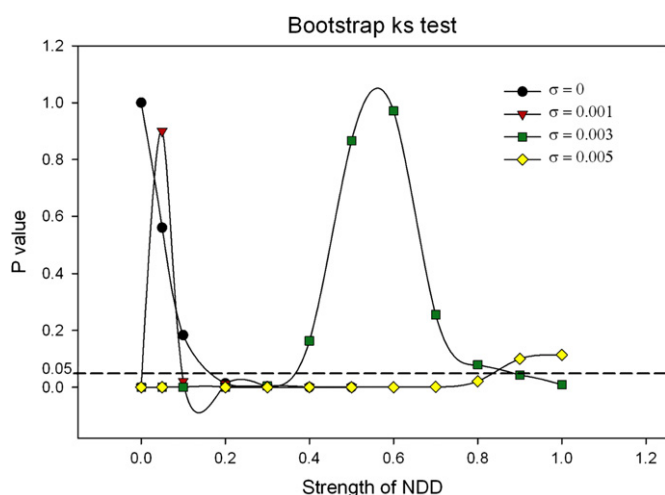


Fig. 3. The significance analysis of SADs, which are produced by the neutral and non-neutral model, using the bootstrap Kolmogorov–Smirnov (Boot ks) test for relative SADs. We chose 0.05 as the critical significance level.

localized dispersal can strengthen intra-specific competition relative to inter-specific competition, thereby facilitating species coexistence, it may also cause decreased mean fitness due to inbreeding depression and increased competition between relatives (Keller and Waller, 2002; Latter and Robertson, 1962; West et al., 2001). If this happens, species may evolve long-distance dispersal strategies to avoid inbreeding depression and competition between relatives (Hamilton and May, 1977; Szulkin and Sheldon, 2008). Hence, localized dispersal is not always selected for. Furthermore, when dispersal is locally limited, the effect of dispersal limitation in offsetting the negative effect of CA on coexistence is relatively small (see also Zhou and Zhang, 2008). Therefore, we hypothesize that NDD, rather than dispersal limitation, slows down competitive exclusion caused by CA and then gives rise to neutral-like SADs.

Third, although neutral theory has proved to be successful in producing realistic SADs, it rarely provided insight in the relationship between biodiversity and ecosystem functioning. In our model, community structure and species fate are highly deterministic. The positive relationship between species competitive ability and its relative abundance for common species

predicted by our model may provide some insights into the relationship between biodiversity and ecosystem functioning. However, neutrality is still likely to hold for the rare species (see Figs. 2(b) and 4(b)). The reason why the neutral model fits SADs so well might be that the visual fit applies mostly to less abundant species (Etienne et al., 2007). In fact, the neutral model's fit of abundant species is known to be very poor (Etienne et al., 2007). Hence, we question the method of curve-fitting in detecting mechanisms of species coexistence and maintenance of biodiversity (McGill et al., 2007). For real communities, more careful investigations are needed to understand community assembly. Zillio and Condit (2007) offered an alternative reason why neutral-like SADs are often obtained: they argue that the species-introduction process plays a crucial role in shaping SADs and this process is exactly one of the few ingredients of neutral theory.

With respect to species differences in competitive ability, Chesson and Warner (1981) provided another mechanism for species with unequal demographic rates to coexist. They constructed a general model for lottery competitive systems and demonstrated that variance in species' demographic rates caused by environmental variability, given it is large enough, can promote species coexistence when there are asymmetric competitive abilities among species. However, species coexistence is not stable in that framework – there is no mechanism to rescue species from extinction when it is rare. The mechanism we proposed in this paper can ensure stable coexistence for species with asymmetric demographic rates. Although asymmetric competitive ability i.e. different fecundities may speed up competitive exclusion, NDD constrains the advantage in growth arising from high fecundity. In other words, the increase in the strength of intra-specific interactions due to NDD reduces the effect of inter-specific interactions (competitive asymmetry), and vice versa. Although it is difficult to distinguish different coexistence mechanisms in real communities, we state that stable coexistence based on NDD may be more common, given that NDD has been so widely detected (Comita et al., 2010; Harms et al., 2000; Hubbell et al., 1990; Peters, 2003; Wills et al., 1997).

We also observed that NDD and immigration have similar roles in producing SADs patterns: from logseries to lognormal distribution. In local communities we found a more significant influence of the immigration rate on SADs without or with a slight NDD than with a large NDD (see Supplementary Fig. A4). This suggests that

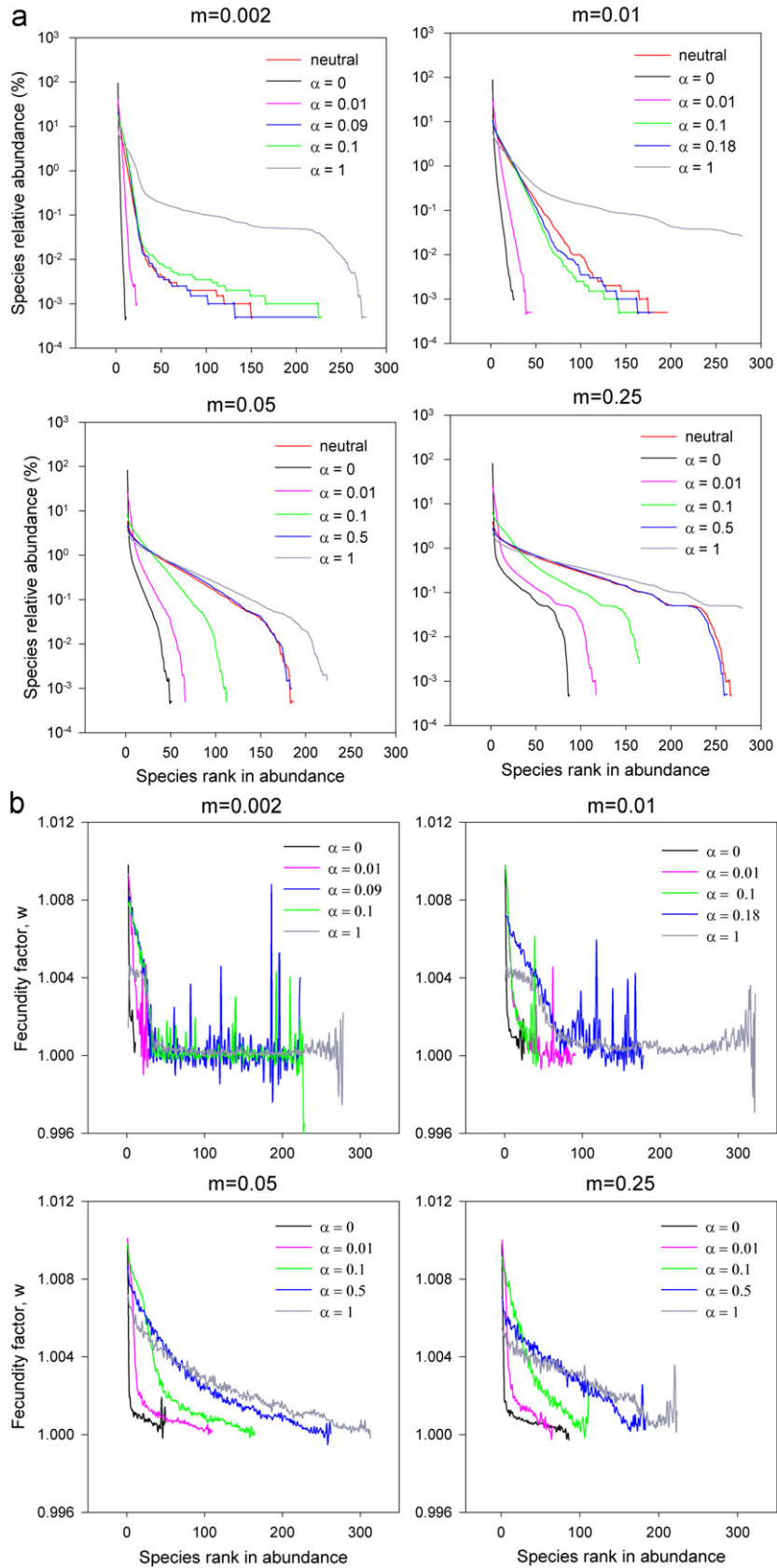


Fig. 4. (a) Local community equilibrium rank-abundance curves of models with and without differences in species' per capita fecundities or NDD, for different immigration rates from the metacommunity. The blue lines are the best fit to the neutral-like patterns. (b) Relationship between species abundances and their fecundity factors in local communities with and without differences in species' per capita fecundities or NDD, for different immigration rates from the metacommunity. Other parameters: $J=2000$, $\theta=100$, $\sigma=0.003$ (except neutral case), $m=0.002, 0.01, 0.05$ and 0.25 .

NDD can reduce the effect of immigration on SADs in local communities. In addition, the effects of speciation and NDD on community structure are oppositely correlated with spatial scale: as the effect of NDD decreases with larger spatial scales, NDD plays a weaker role in metacommunities than in local communities, whereas speciation is more important at large scales.

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Appendix A. Supplementary Information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2011.03.003.

References

- Adler, P.B., HilleRisLambers, J., Levine, J.M., 2007. A niche for neutrality. *Ecology Letters* 10, 95–104.
- Alonso, D., Etienne, R.S., McKane, A.J., 2006. The merits of neutral theory. *Trends in Ecology and Evolution* 21, 451–457.
- Amarasekare, P., 2004. Spatial variation and density-dependent dispersal in competitive coexistence. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271, 1497–1506.
- Bell, F., Freckleton, R., Lewis, O., 2006. Plant pathogens drive density-dependent seedling mortality in a tropical tree. *Ecology Letters* 9, 569–574.
- Bell, G., 2001. Ecology—neutral macroecology. *Science* 293, 2413–2418.
- Chase, J.M., 2005. Towards a really unified theory for metacommunities. *Functional Ecology* 19, 182–186.
- Chase, J.M., 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 104, 17430–17434.
- 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.
- Chave, J., Alonso, D., Etienne, R.S., 2006. Theoretical biology: comparing models of species abundance. *Nature* 441 E1.
- Chesson, P., 1998. Recruitment limitation: a theoretical perspective. *Austral Ecology* 23, 234–240.
- Chesson, P., 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31, 343–366.
- Chesson, P.L., Warner, R.R., 1981. Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist* 117, 923–943.
- Comita, L.S., Muller-Landau, H.C., Aguilar, S.n., Hubbell, S.P., 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329, 330–332.
- Etienne, R.S., 2005. A new sampling formula for neutral biodiversity. *Ecology Letters* 8, 253–260.
- Etienne, R.S., Alonso, D., 2005. A dispersal-limited sampling theory for species and alleles. *Ecology Letters* 8, 1147–1156.
- Etienne, R.S., Apol, M.E.F., Olff, H., Weissing, F.J., 2007. Modes of speciation and the neutral theory of biodiversity. *Oikos* 116, 241–258.
- Freckleton, R.P., Lewis, O.T., 2006. Pathogens, density dependence and the coexistence of tropical trees. *Proceedings of the Royal Society B—Biological Sciences* 273, 2909–2916.
- Goldenheim, W., Irving, A., Bertness, M., 2008. Switching from negative to positive density-dependence among populations of a cobble beach plant. *Oecologia* 158, 473–483.
- Hamilton, W.D., May, R.M., 1977. Dispersal in stable habitats. *Nature* 269, 578–581.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A., Herre, E.A., 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404, 493–495.
- Harpole, W.S., Tilman, D., 2006. Non-neutral patterns of species abundance in grassland communities. *Ecology Letters* 9, 15–23.
- Hubbell, S.P., 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* 16, S9–S21.
- Hubbell, S.P., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Hubbell, S.P., 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19, 166–172.
- Hubbell, S.P., 2006. Neutral theory and the evolution of ecological equivalence. *Ecology* 87, 1387–1398.
- Hubbell, S.P., Condit, R., Foster, R.B., 1990. Presence and absence of density dependence in a neotropical tree community. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 330, 269–281.
- Jabot, F., Chave, J., Etienne, R.S., 2008. Reconciling neutral community models and environmental filtering: theory and an empirical test. *Oikos* 117, 1308–1320.
- Keller, L.F., Waller, D.M., 2002. Inbreeding effects in wild populations. *Trends in Ecology and Evolution* 17, 230–241.
- Kraft, N.J.B., Valencia, R., Ackerly, D.D., 2008. Functional traits and niche-based tree community assembly in an amazonian forest. *Science* 322, 580–582.
- Latter, B.D.H., Robertson, A., 1962. The effects of inbreeding and artificial selection on reproductive fitness. *Genetics Research* 3, 110–138.
- Leibold, M.A., McPeck, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87, 1399–1410.
- Levine, J.M., HilleRisLambers, J., 2009. The importance of niches for the maintenance of species diversity. *Nature* 461, 254–257.
- Lin, K., Zhang, D.-Y., He, F., 2009. Demographic trade-offs in a neutral model explain death-rate-abundance-rank relationship. *Ecology* 90, 31–38.
- McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benccha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F.L., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I., White, E.P., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10, 995–1015.
- Mitchell, C.E., Power, A.G., 2003. Release of invasive plants from fungal and viral pathogens. *Nature* 421, 625–627.
- Packer, A., Clay, K., 2000. Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* 404, 278–281.
- Peters, H.A., 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters* 6, 757–765.
- Præstgaard, J.T., 1995. Permutation and bootstrap Kolmogorov–Smirnov tests for the equality of two distributions. *Scandinavian Journal of Statistics* 22, 305–322.
- Purves, D.W., Pacala, S.W., 2005. *Ecological Drift In Niche-Structured Communities: Neutral Pattern Does Not Imply Neutral Process*. Cambridge University Press, Cambridge.
- Purves, D.W., Turnbull, L.A., 2010. Different but equal: the implausible assumption at the heart of neutral theory. *Journal of Animal Ecology* 79, 1215–1225.
- Rominger, A., Miller, T., Collins, S., 2009. Relative contributions of neutral and niche-based processes to the structure of a desert grassland grasshopper community. *Oecologia* 161, 791–800.
- Rosindell, J., Cornell, S.J., 2007. Species-area relationships from a spatially explicit neutral model in an infinite landscape. *Ecology Letters* 10, 586–595.
- Rosindell, J., Cornell, S.J., 2009. Species-area curves, neutral models, and long-distance dispersal. *Ecology* 90, 1743–1750.
- Rosindell, J., Wong, Y., Etienne, R.S., 2008. A coalescence approach to spatial neutral ecology. *Ecological Informatics* 3, 259–271.
- Rosindell, J., Cornell, S.J., Hubbell, S.P., Etienne, R.S., 2010. Protracted speciation revitalizes the neutral theory of biodiversity. *Ecology Letters* 13, 716–727.
- Swaine, M.D., Lieberman, D., Putz, F.E., 1987. The dynamics of tree population in tropical forest—a review. *Journal of Tropical Ecology* 3, 359–366.
- Szulkin, M., Sheldon, B.C., 2008. Dispersal as a means of inbreeding avoidance in a wild bird population. *Proceedings of the Royal Society B: Biological Sciences* 275, 703–711.
- Tilman, D., Kilham, S.S., Kilham, P., 1982. Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics* 13, 349–372.
- Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J., Kuris, A.M., 2003. Introduced species and their missing parasites. *Nature* 421, 628–630.
- Vandermeer, J.H., 1972. Niche theory. *Annual Review of Ecology and Systematics* 3, 107–132.
- 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., Hubbell, S.P., Maritan, A., 2007. Patterns of relative species abundance in rainforests and coral reefs. *Nature* 450, 45–49.
- Volkov, I., Banavar, J.R., He, F.L., Hubbell, S.P., Maritan, A., 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438, 658–661.
- Volkov, I., Banavar, J.R., He, F.L., Hubbell, S.P., Maritan, A., 2006. Theoretical biology—comparing models of species abundance—reply. *Nature* 441, E1–E2.
- Walker, S.C., 2007. When and why do non-neutral metacommunities appear neutral? *Theoretical Population Biology* 71, 318–331.
- West, S.A., Murray, M.G., Machado, C.A., Griffin, A.S., Herre, E.A., 2001. Testing Hamilton's rule with competition between relatives. *Nature* 409, 510–513.
- Whitfield, J., 2002. Ecology: neutrality versus the niche. *Nature* 417, 480–481.
- Wills, C., Condit, R., Foster, R.B., Hubbell, S.P., 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences of the United States of America* 94, 1252–1257.
- Wootton, J.T., 2005. Field parameterization and experimental test of the neutral theory of biodiversity. *Nature* 433, 309–312.
- Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130, 1–14.
- Yu, D.W., Terborgh, J.W., Potts, M.D., 1998. Can high tree species richness be explained by Hubbell's null model? *Ecology Letters* 1, 193–199.

- Yu, D.W., Wilson, H.B., Frederickson, M.E., Palomino, W., De La Colina, R., Edwards, D.P., Balareso, A.A., 2004. Experimental demonstration of species coexistence enabled by dispersal limitation. *Journal of Animal Ecology* 73, 1102–1114.
- Zhang, D.Y., Lin, K., 1997. The effects of competitive asymmetry on the rate of competitive displacement: how robust is Hubbell's community drift model? *Journal of Theoretical Biology* 188, 361–367.
- Zhou, S.R., Zhang, D.Y., 2006. Allee effects and the neutral theory of biodiversity. *Functional Ecology* 20, 509–513.
- Zhou, S.R., Zhang, D.Y., 2008. A nearly neutral model of biodiversity. *Ecology* 89, 248–258.
- Zillio, T., Condit, R., 2007. The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. *Oikos* 116, 931–940.