

# Coexistence of nearly neutral species

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## Abstract

### Aims

The neutral theory of biodiversity provides a powerful framework for modeling macroecological patterns and interpreting species assemblages. However, there remain several unsolved problems, including the effect of relaxing the assumption of strict neutrality to allow for empirically observed variation in vital rates and the ‘problem of time’—empirically measured coexistence times are much shorter than the prediction of the strictly neutral drift model. Here, we develop a nearly neutral model that allows for differential birth and death rates of species. This model provides an approach to study species coexistence away from strict neutrality.

### Methods

Based on Moran’s neutral model, which assumes all species in a community have the same competitive ability and have identical birth and death rates, we developed a model that includes birth–death trade-off but excludes speciation. This model describes a wide range of asymmetry from strictly neutral to nearly neutral to far from neutral and is useful for analyzing the effect of drift on species coexistence. Specifically, we analyzed the effects of the birth–death trade-off on the time and probability of species coexistence and quantified the loss of biodiversity (as measured by Simpson’s diversity) due to drift by varying species birth and death rates.

### Important Findings

We found (i) a birth–death trade-off operating as an equalizing force driven by demographic stochasticity promotes the coexistence of nearly neutral species. Species near demographic trade-offs (i.e. fitness equivalence) can coexist even longer than that predicted by the strictly neutral model; (ii) the effect of birth rates on species coexistence is very similar to that of death rates, but their compensatory effects are not completely symmetric; (iii) ecological drift over time produces a march to fixation. Trade-off-based neutral communities lose diversity more slowly than the strictly neutral community, while non-neutral communities lose diversity much more rapidly; and (iv) nearly neutral systems have substantially shorter time of coexistence than that of neutral systems. This reduced time provides a promising solution to the problem of time.

**Keywords:** birth rate • ecological drift • death rate • demographic trade-off • nearly neutral theory • probability of extinction • time of coexistence

Received: 17 July 2011 Revised: 7 October 2011 Accepted: 17 October 2011

## INTRODUCTION

One of the most debated questions in the neutral theory of biodiversity is how long can neutral species coexist? Under the assumption of strict neutrality, in which species in a community are assumed to have exactly the same vital rates, Hubbell (2001) showed that species can coexist for a very long time, long enough for high species diversity to be maintained by speciation alone. This coexistence is not maintained by the ability of species to compete more effectively when rare but by the

stochasticity of ecological drift. The introduction of drift as an explanation of species assemblages, as opposed to various models of niche partitioning (Tokeshi 1999), is arguably the most significant contribution of neutral theory. This contribution has, however, been incisively debated on several fronts. Zhang and Lin (1997) first questioned the fragility of the coexistence of neutral species by analytically showing that a small departure from the assumption of equal birth rate would dramatically reduce the time of coexistence. Along this vein, Yu *et al.* (1998) demonstrated, by simulation, a similar

consequence for the violation of equal death rate. Subsequent studies have extended the work of Zhang and Lin (1997) and Yu et al. (1998) by investigating the effect of non-neutrality on community diversity patterns (species-abundance and species-area curves). Fuentes (2004) first extended Yu et al.'s work by simulating a spatially explicit nearly neutral system by considering slight differences in the viability of individuals. In Fuentes' simulation, the mortality rates of individuals are no longer equal but are determined by small differential viabilities generated by deleterious versus beneficial mutation. This nearly neutral community reduces species richness and produces species-abundance and species-area curves very different from the strictly neutral model of Hubbell. Similar results have also been reported by Zhou and Zhang (2008) that simulated the effects of differential birth rates (as proposed by Zhang and Lin 1997) on species-abundance distributions. These models depart from Hubbell's neutral model by only considering species difference in either birth rate or death rate, but not both, although in reality species differ in both rates. The effect of a birth–death trade-off on species coexistence has not yet been addressed.

As a significant step toward this problem, based on the lottery model of demographic trade-off, Lin et al. (2009) showed that although both a strictly neutral community and trade-off-based communities produce log-series species-abundance distributions, species richness is higher in trade-off communities. Similarly, Ostling (2011) and Zhang et al. (2012) relaxed Hubbell's original neutral model by considering fitness equivalence and found that high species diversity can result from an interspecific birth–death trade-off. Parsons and Quince (2007) considered a density-dependent 'quasi-neutral' model and analyzed the effect of population fluctuation on species coexistence. In these studies, fitness equivalence is defined as  $B_i/D_i = B_j/D_j = c$ , where  $B$  and  $D$  are the birth and death rates for species  $i$  and  $j$ . Therefore, species having higher birth and death rates are considered ecologically equivalent to species of lower birth and death rates. Unlike Zhang and Lin (1997) and Yu et al. (1998), the trade-off-based models of Lin et al. (2009), Ostling (2011) and Zhang et al. (2012) are still neutral by definition (Hubbell 2005), and the strictly neutral model is the special case of  $B_i = B_j$  and  $D_i = D_j$ .

Inspired by the theory of nearly neutral alleles in population genetics that extends the neutral theory of molecular evolution (Ohta 1992; Ohta and Gillespie 1996), in this study, we propose a nearly neutral model that describes a spectrum of communities ranging from strictly neutral to non-neutral. The model is derived based on two seminal works in population genetics: Moran (1962) and Karlin and McGregor (1967), and it takes account of differential birth and death rates. Although our model can describe a wide range of asymmetry (from strictly neutral to nearly neutral to non-neutral), it will become clear that the model behaviors are very similar at nearly neutral and far from neutral states. We therefore call it a nearly neutral model.

Similar to Zhang and Lin (1997) and Yu et al. (1998) but different from Lin et al. (2009), Ostling (2011) and Zhang et al.

(2012), our model is non-neutral by definition. It differs from the previous models in two important aspects. First, unlike the previous non-neutral models which only consider the asymmetry in either birth rates (Zhang and Lin 1997; Zhou and Zhang 2008) or death rates (Fuentes 2004; Yu et al. 1998), the simultaneous consideration of differential birth and death rates allows us to investigate the effect of a demographic trade-off on species coexistence away from the neutral state, which is otherwise impossible to do. Second, unlike the fitness-equivalence neutral models of Lin et al. (2009), Ostling (2011) and Zhang et al. (2012), what our model considers is a general case in which  $B_i/D_i$  and  $B_j/D_j$  are not necessarily equal but can vary independently. We use this model to examine the joint effect of biased birth and death rates on the probability of species extinction and the time of coexistence and show that a demographic trade-off can equalize and contribute to species coexistence without invoking stabilizing mechanisms. We then investigate the effect of ecological drift on the loss of diversity under non-neutral conditions. We conclude the study by discussing the consequences of the nearly neutral theory, including the 'problem of time'—the age of species predicted by ecological drift is simply too long to be realistic (Lande et al. 2003; Nee 2005; Ricklefs 2006; Rosindell et al. 2010).

## THE NEARLY NEUTRAL MODEL

Our departure point is Moran's neutral model, assuming all species in a community have the same competitive ability and have identical birth and death rates (Moran 1962). Moran's model is long standing, of which Hubbell's zero-sum model is a variant (Etienne and Alonso 2007; Leigh 2007). Because they differ little, we make no distinction between them. Also, because the focus of this study is to investigate species coexistence, to simplify the analysis, we only consider a system consisting of two competing species, as many competition models do. Under the assumption that the two species have the same per capita birth and death rates and within a sufficiently small time step, the transition probabilities that the abundance of the focal species increases by one, decreases by one, or remains unchanged are, respectively (Hubbell 2001; Moran 1962):

$$\begin{cases} p_{j,j+1} = \frac{N-j}{N} \frac{j}{N} \\ p_{j,j-1} = \frac{j}{N} \frac{N-j}{N} \\ p_{j,j} = 1 - p_{j,j+1} - p_{j,j-1} \end{cases}, \quad (1)$$

where  $N$  is the total number of individuals (the community size),  $j$  is the number of individuals of the focal species (species 1) at time  $t$  and  $N - j$  is the abundance of the other species (species 2). The first term,  $\frac{N-j}{N}$ , on the right-hand side of  $p_{j,j+1}$  is the probability that a death occurs in species 2. The second term,  $\frac{j}{N}$ , is the probability that a birth occurs in species 1. The transition probability ( $p_{j,j+1}$ ) can therefore be interpreted as

a joint probability of two events: first sample one individual from species 2 (to die) and then sample a second individual from species 1 (to reproduce). The random walk of model 1 describes the abundance dynamics of species with same competitive ability—the probabilities of moving one step to the right or to the left are equal:  $\frac{p_{j,j+1}}{p_{j,j-1}} = 1$ .

Model 1 can be generalized by relaxing the assumption of neutrality. This generalized model takes account of differential birth and death rates so that asymmetry in the theory is allowed. Adopting the approach proposed by Karlin and McGregor (1967) to model 1, we obtain an asymmetric model:

$$\begin{cases} p_{j,j+1} = \frac{N-j}{N-j+dj} \frac{bj}{N-j+bj} \\ p_{j,j-1} = \frac{dj}{N-j+dj} \frac{N-j}{N-j+bj} \\ p_{j,j} = 1 - p_{j,j+1} - p_{j,j-1} \end{cases} \quad (2)$$

where the differential birth and death factors are, respectively, denoted by  $b$  and  $d$ . When  $b = 1$ , the two species have the same birth rate ( $B_1 = B_2$ );  $b > 1$  means that the focal species has a higher birth rate than species 2 ( $B_1 > B_2$ ) and  $b < 1$  means that species 1 has a lower birth rate. Similar interpretations apply to death factor,  $d$ . Note that when  $d = 1$  and  $b \neq 1$ , Equation (2) reduces to Zhang and Lin's model (1997), when  $b = 1$  and  $d \neq 1$ , it is equivalent to Yu *et al.*'s (1998) model and when  $d = 1$  and  $b = 1$ , it further becomes Moran–Hubbell's zero-sum model 1.

The transition probabilities in Equation (2) are easy to derive (Karlin and McGregor 1967). They are arrived by considering birth and death as sampling events. Let us take the two terms in  $p_{j,j+1}$  as an example. Because of the species-biased death rates, we denote  $D_1$  as the probability a death occurs in species 1 (with abundance =  $j$ ) and  $D_2$  as the probability a death occurs in species 2 (with abundance =  $N - j$ ). Because the death must either occur in species 1 or 2,  $D_1 + D_2 = 1$  ( $D_1 = D_2$  for the neutral model). If we randomly sample one individual from the community (to die), the probability that the sampled individual is species 2 is  $\frac{D_2(N-j)}{D_1j + D_2(N-j)}$ . This leads to  $\frac{N-j}{N-j+dj}$ , where  $d = \frac{D_1}{D_2}$ . To derive the second term, we denote  $B_1$  as the probability of sampling an individual from species 1 and  $B_2$  the probability of sampling an individual from species 2. If we randomly sample one individual from the community (to give birth), then the probability that the sampled individual belongs to species 1 is  $\frac{B_1j}{B_1j + B_2(N-j)}$ , leading to  $\frac{bj}{N-j+bj}$ , where  $b = \frac{B_1}{B_2}$ . All the other terms in Equation (2) can be derived in the same manner. A salient feature of this nearly neutral model is that drift in abundance is no longer neutral but is biased, determined by the ratio of  $b$  and  $d$ :  $\frac{p_{j,j+1}}{p_{j,j-1}} = \frac{b}{d}$ , which is considered as a measure of fitness inequality (sensu Chesson 2000). Species 1 and 2 are said to have identical fitnesses if  $d = b$ , which is model 1.

What Equation (2) differs from Equation (1) is that the chances to walk to the right and to the left are no longer equal but determined by the difference in species competitive ability (as defined by  $b$  and  $d$ ). Competitive exclusion in the system occurs if species 1 starting from  $j$  is finally absorbed into state 0 (species

2 wins) or  $N$  (1 wins). We use two functions to investigate the effects of a birth–death trade-off on the outcome of competition.

The first function is the probability of absorption, defined as the probability that the focal species starting from  $j$  will go extinct (Taylor and Karlin 1998):

$$e_j = \frac{\sum_{i=j}^{N-1} \rho_i}{1 + \sum_{i=1}^{N-1} \rho_i}, \quad 0 < j < N, \quad (3)$$

where  $\rho_i = \frac{q_1 q_2 \dots q_i}{p_1 p_2 \dots p_i}$ ,  $0 < i < N$ .  $p_i$  and  $q_i$  are the transition probabilities, defined by  $p_i = p_{i,i+1}$  and  $q_i = p_{i,i-1}$ . The extinction probability can be analytically derived by substituting Equation (2) into (3):

$$e_j = \begin{cases} \frac{(d/b)^j [1 - (d/b)^{N-j}]}{1 - (d/b)^N} & b \neq d \\ \frac{N-j}{N} & b = d \end{cases} \quad (4)$$

Note that in Lin *et al.* (2009), only the probabilities for  $b = d$  are considered (e.g. see Fig. 1 of Lin *et al.* 2009). This study generalizes the previous results by considering any ratio of  $b/d$ .

The second function is the time to absorption. This time can be measured either by relative time or absolute time. The relative time is defined as the average number of steps for the focal species traveling from  $j$  to either 0 or  $N$ . It can be derived following the procedure of Taylor and Karlin (1998):

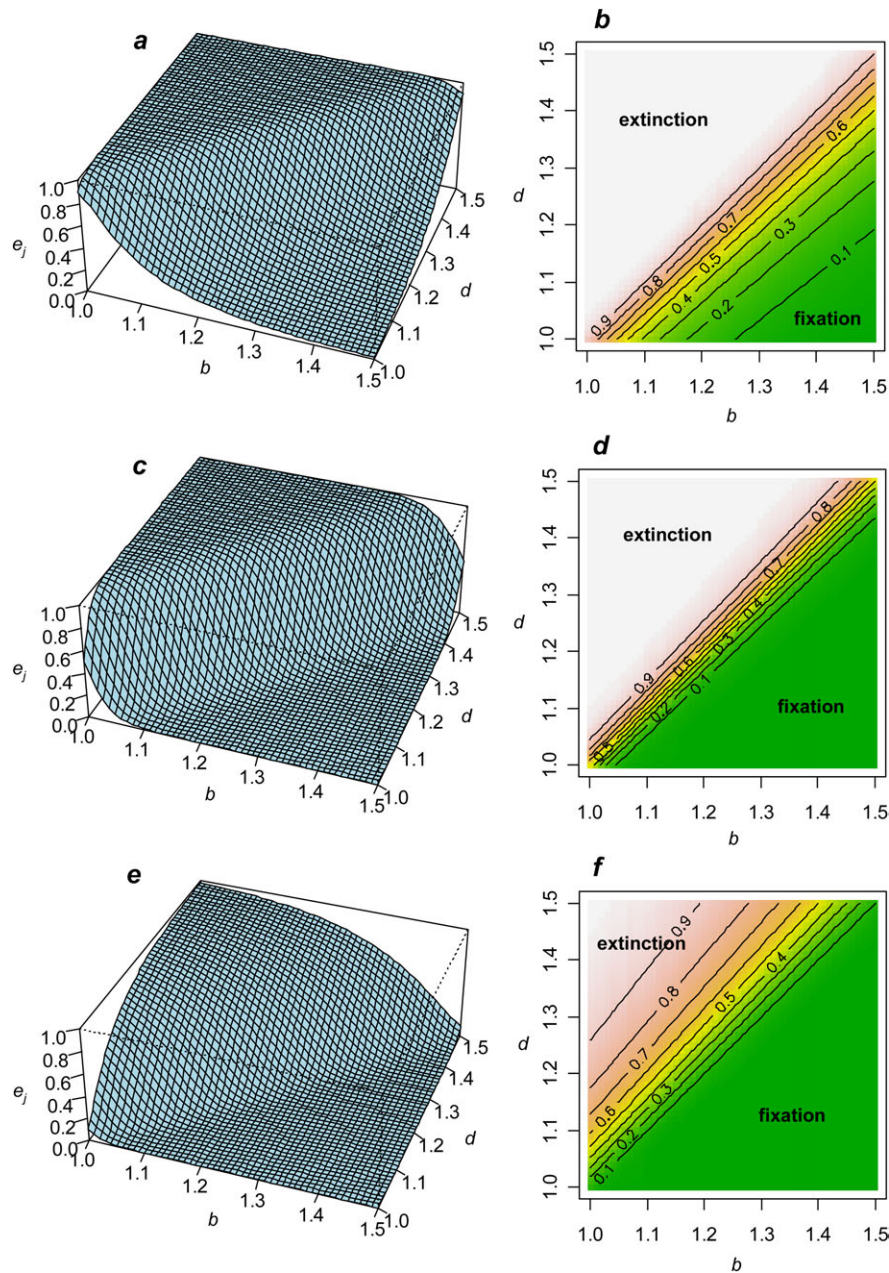
$$t_j = \left(1 + \sum_{i=1}^{j-1} \rho_i\right) \frac{\sum_{i=1}^{N-1} R_i}{1 + \sum_{i=1}^{N-1} \rho_i} - \sum_{i=1}^{j-1} R_i, \quad 1 < j < N, \quad (5)$$

where  $R_i = \frac{1}{p_i} \left(1 + \frac{q_i}{p_{i-1}} + \frac{q_i q_{i-1}}{p_{i-1} p_{i-2}} + \dots + \frac{q_i q_{i-1} \dots q_2}{p_{i-1} p_{i-2} \dots p_1}\right)$ . Substituting Equation (2) into (5), we obtain

$$t_j = \begin{cases} = \frac{1}{1 - d/b} \\ \left[ \frac{1 - (d/b)^j}{1 - (d/b)^N} \sum_{i=1}^{N-1} \frac{1}{p_i} \left(1 - \left(\frac{d}{b}\right)^{N-i}\right) \right. \\ \left. - \sum_{i=1}^{j-1} \frac{1}{p_i} \left(1 - \left(\frac{d}{b}\right)^{j-i}\right) \right] & b \neq d \\ = \frac{j}{N} \sum_{i=1}^{N-1} \frac{N-i}{p_i} - \sum_{i=1}^{j-1} \frac{j-i}{p_i} & b = d \end{cases} \quad (6)$$

The absolute time to extinction is the actual time for the focal species traveling from  $j$  to either 0 or  $N$  state. The derivation of this absolute time requires reformulation of Equation (2) and can only be done for the case of fitness equivalence, as given in Appendix 1. Because relative time is most commonly used in the literature (Ewens 2004; Hubbell 2001; Zhang and Lin 1997) and is also more useful to present the concept of nearly neutral theory, in the rest of this study, relative time is used.





**Figure 1:** effects of different birth ( $b$ ) and death ( $d$ ) rates on the extinction probability of the focal species for three initial states  $j = 10$  (a, b), 50 (c, d) and 90 (e, f) for model 2. The right-hand panels are the contour plots of their left-hand 3D plots.

Ecological drift is the only force regulating species coexistence in models 1 and 2. It causes the loss of species and over time produces a march to fixation. A classical model of population genetics is that genetic drift drives the loss of alleles at the rate of  $H_t = H_0 \left(1 - \frac{1}{N}\right)^t$ , where  $H_t$  is the heterozygosity in population genetics at time  $t$  and  $N$  is population size. This model can be generalized to quantify the effect of ecological drift on species diversity. Considering a lottery model of strictly neutral species (i.e. all species have the same annual death rate  $D$  and the same annual birth rate  $B$ ), we derived the effect of ecological drift on the loss of species diversity as (Appendix 2)

$$H_t = H_0 \left(1 - \frac{2D - D^2}{N}\right)^t, \quad (7)$$

where  $H_t$  is the Simpson diversity index (i.e. heterozygosity) at time  $t$ . It is clear that under ecological drift, communities are bound to fixation over time, resulting in  $H_\infty = 0$ . Note that Equation (7) is a general model that applies to communities of multiple species, not just two species.

We conducted simulations based on the lottery model to evaluate the effect of drift on non-neutral communities by varying species birth and death rates. The lottery model describes the

same drift process of model 2 but is easier to program when dealing with multiple species (Lin *et al.* 2009). The detail of the simulation algorithm is described in Appendix 3. To sketch the algorithm, we started off with communities of 100 equally abundant species with community size = 10 000 individuals. Thus,  $H_0 = 100/101$  (calculated from sampling without replacement). To generate the non-neutral communities, for each species, we first chose a death rate  $D$  from a uniform distribution,  $U(0, 1)$ . The birth rate  $B$  for that species is then defined as  $B \sim N(D, \sigma^2)$  and  $B > 0$ . Note that here, without loss of generality, the birth rates of species are scaled to lie also between 0 and 1. In this study, we present results for four scenarios with  $\sigma = 0.01, 0.001, 0$  (trade-off communities) and a strictly neutral configuration with the death rate  $D = B = 0.5$  for each species, since each simulated community has an average death rate of 0.5 at start. In total, the simulation took 100 runs. For each run, the observation time is 60 000 birth–death cycles.

## RESULTS

We analyzed the combined effects of biased birth ( $b$ ) and death ( $d$ ) rates on  $e_j$  and  $t_j$ . In the following evaluations,  $N = 100$  was used. Larger  $N$  can be used, but the summation term involving  $(d/b)^x$  in the first equation of Equation (6) causes numerical overflow.  $N = 8$  or 16 are commonly used in numerical evaluations of Hubbell (2001) due to the computation problem. Experimentation with other  $N$  did not change the qualitative results.

To evaluate the effect of initial state  $j$  on  $e_j$  and  $t_j$ , we considered three initial abundances from which the focal species started:  $j = 10, 50$  and  $90$  (corresponding to 10, 50 and 90% of  $N$ ). In the evaluations, the ranges of  $b$  and  $d$  were varied from 1 to 1.5. Higher  $b$  ( $d$ ) means the focal species has higher birth (death) rates than species 2.

The effects of  $b$  and  $d$  on the extinction probability ( $e_j$ ) of the focal species are shown in Fig. 1. For small initial  $j$ ,  $e_j$  is high (Fig. 1a). This trend is reversed with the increase of  $j$  (Fig. 1c and e). In all of the three cases, extinction increases with  $d$  but decreases with  $b$ . There is a clear trade-off between  $b$  and  $d$ : the adverse effect of  $d$  is compensated for by  $b$ .

Unlike the probability of extinction, which describes the extinction of the focal species, the time of coexistence as defined by Equation (6) is the time for which the system wanders before a species (1 or 2) hits an absorption state (0 or  $N$ ). The effects of  $b$  and  $d$  on the time of coexistence are shown in Fig. 2. Across  $j$ , the coexistence time is highest when  $j = 50$  (half of the community size). With each  $j$ , for a fixed  $b$ , the time increases with  $d$  to a peak and then decreases (Fig. 2). This trajectory also applies to the effect of  $b$  by fixing  $d$ . The peak ridges shown in Fig. 2 are maintained by the trade-off of  $b$  and  $d$ —a high birth rate  $b$  is offset by a high death rate  $d$ .

However, the trade-offs are not symmetric— $b$  needs to be slightly higher than  $d$  to maintain the ridge when  $j < N/2$  (Fig. 2b) or  $d$  slightly higher than  $b$  (Fig. 2f). An interesting result is that the highest coexistence time is not maintained at  $b = d = 1$  (strictly neutral state) but at the state away from

the strictly neutral around  $b \approx d > 1$  (along the red lines of Fig. 2b, d and f) that represents a neutral model of approximate fitness equivalence. Note coexistence time is the same, as long as  $b = d$  since  $t_j$  in Equation (6) only depends on  $d/b$ .

The effect of ecological drift on the loss of biodiversity varies between neutral and non-neutral communities (Fig. 3). Simpson's diversity for the simulated strictly neutral community ( $B/D = 1$ ; Fig. 3a) is well predicted by the theoretical model (Eq. 7). However, demographic differentiation plays a sharply contrasting role in maintaining diversity, depending on whether there is trade-off in demographic difference or not. For trade-off communities, the loss of diversity is slower than the strictly neutral community (Fig. 3b), while for non-trade-off communities, the loss of Simpson's diversity is accelerated over time (Fig. 3c and d). These results are in agreement with the finding that demographic trade-off prolongs coexistence time (Fig. 2).

## DISCUSSION

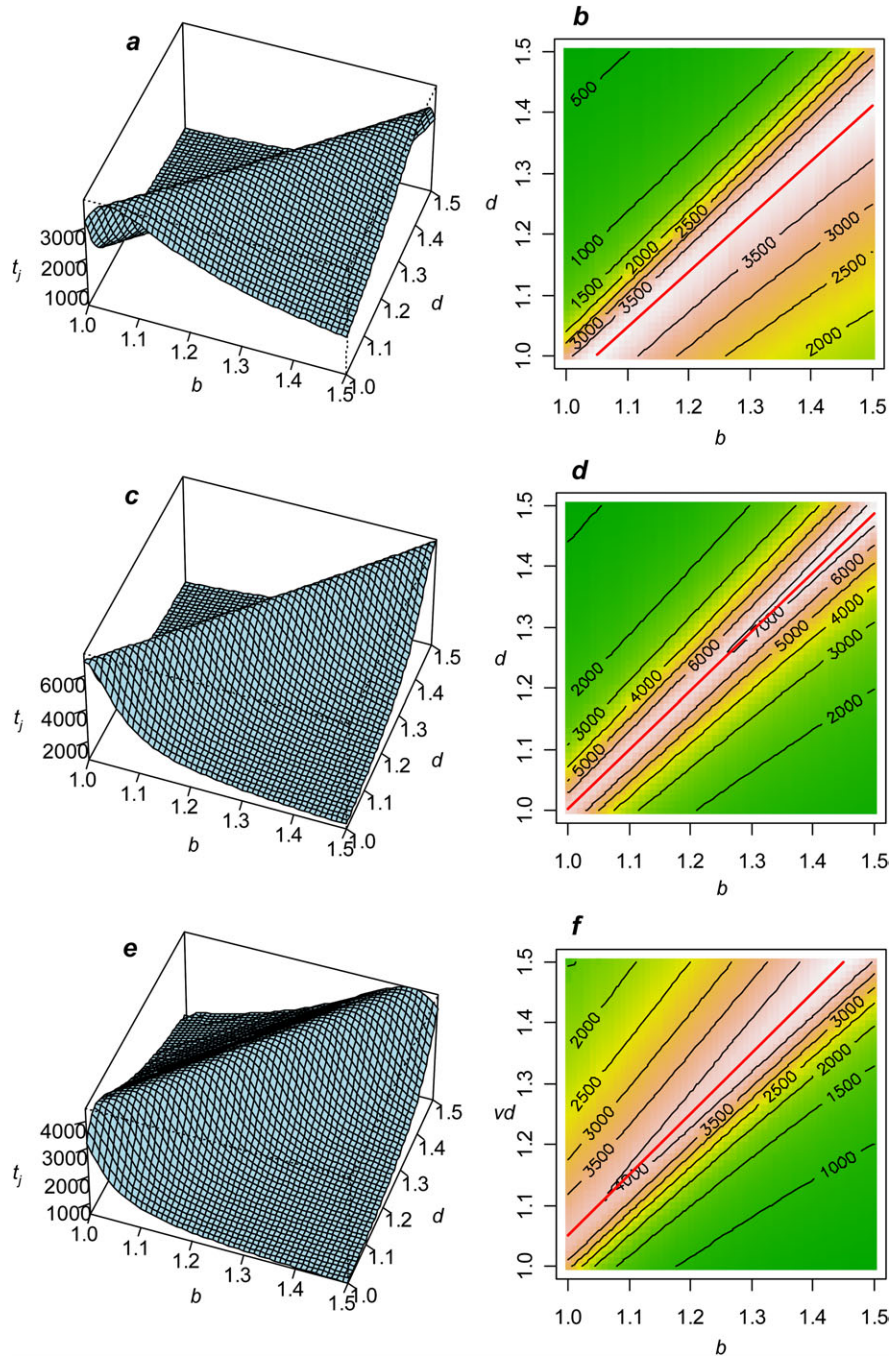
The debate over the neutral theory of biodiversity is ongoing (Clark 2009; Rosindell *et al.* 2011). Among the several unsolved problems, the strongest criticism of the theory is its unrealistic assumption of perfect neutrality, which ignores observed difference in species fitness. Attempts have been made to reconcile the neutral and niche theories and to generalize neutral theory by incorporating asymmetry (Adler *et al.* 2007; Allouche and Kadmon (2009); Alonso *et al.* 2006, 2008; Cadotte 2007; Gravel *et al.* 2006; Hubbell 2005; Leibold and McPeck 2006; Ostling 2011; Peng *et al.* 2012; Rosindell *et al.* 2010, 2012; Tilman 2004; Volkov *et al.* 2005; Zhang *et al.* 2012; Zillio and Condit 2007). Our study is a useful step along this direction. We term this theory as nearly neutral theory sensu the nearly neutral theory of molecular evolution (Ohta 1992; Ohta and Gillespie 1996). It is nearly neutral because our results (Figs 1 and 2) show that a small perturbation to the symmetry assumption of birth and death rates dramatically reduces species coexistence; the effect decelerates as the differences in birth and death rates increase.

Equation (2) is a generalization of previous models that take account of demographic differentiation. It becomes a strictly neutral model when  $b = d = 1$ . The increase or decrease of  $b$  and  $d$  describes departure from the neutral model and reflects differences in species fitness. Neutral-dominated communities will have  $b$  and  $d$  near 1, while non-neutral communities have  $b$  and  $d$  larger than 1. The fitness equivalent models of Lin *et al.* (2009), Ostling (2011) and Zhang *et al.* (2011) correspond to the special case of  $b = d \neq 1$ . It is obvious from Equations (4) to (6) that the extinction probability and coexistence time not only depend on the  $d/b$  ratio but also on the initial size of the focal species. This makes the behavior of the fitness equivalent models be the same as the strict neutral community of Equation (1). When  $b \neq d$ , Equation (2) corresponds to the non-neutral models of Zhang and Lin (1997) and Yu *et al.* (1998), and the analysis of Yu *et al.* (1998) is

equivalent to that of Zhang and Lin (1997). This finding is previously unrecognized and reveals that the effect of differential death on species coexistence is very similar to the effect of differential birth.

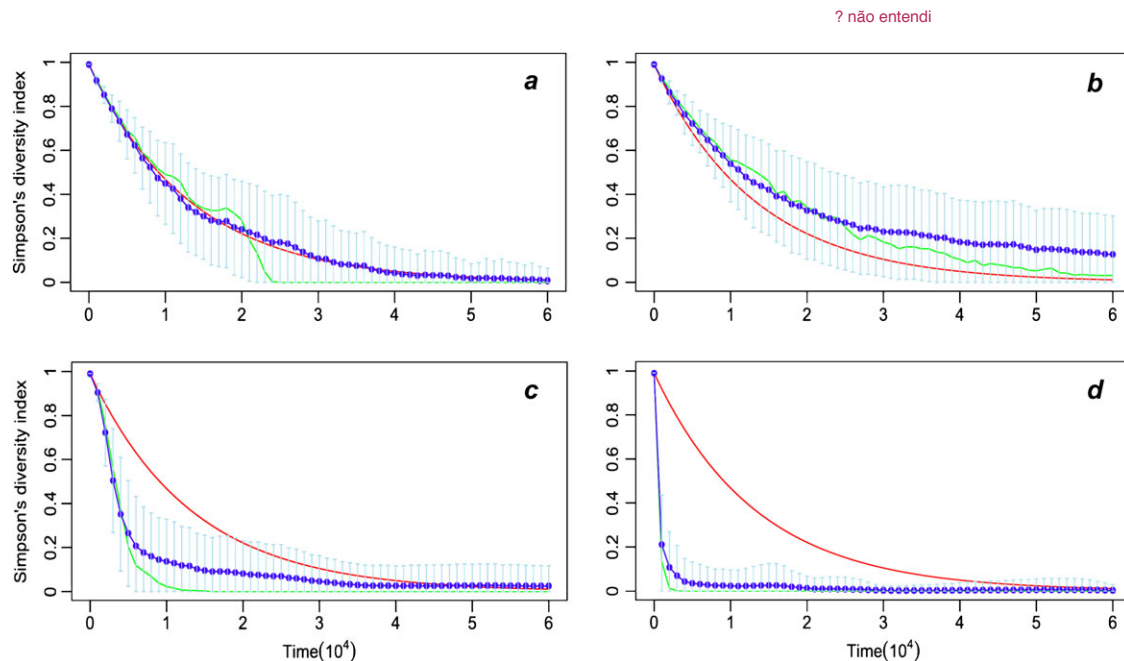
However, it is important to note two points. The first is that the compensatory effects of birth and death on coexistence are not completely symmetric as shown by Fig. 2 (if the effect were

completely symmetric, the slope of the red line in Fig. 2d would be 1 with intercept = 0). The second point is that the simultaneous consideration of birth and death in the nearly neutral model has greatly generalized our understanding of the effect of demographic trade-off on coexistence. Previous results (Fuentes 2004; Yu *et al.* 1998; Zhang and Lin 1997; Zhou and Zhang 2008), by only considering birth differentiation or death



**Figure 2:** effects of different birth ( $b$ ) and death ( $d$ ) rates on the time of coexistence for three initial states  $j = 10$  (a, b), 50 (c, d) and 90 (e, f) for model 2. The right-hand panels are the contour plots of their left-hand 3D plots. The peak ridge of the coexistence time is shown by the red line in each contour plot:  $d = 0.0468 + 0.909b$ ,  $d = 0.0315 + 0.971b$  and  $d = 0.05 + b$ , respectively, for panels b, d and f.





**Figure 3:** effect of ecological drift on the loss of diversity as measured by Simpson's index (heterozygosity). Red curves: the theoretical prediction with a death rate of 0.5 for each species (Eq. 7); blue curves: mean  $\pm$  standard error; green curves: median. The simulated communities are strictly neutral (a), trade-off (b), and non-neutral (c for  $\sigma = 0.001$  and d for  $\sigma = 0.01$ ).

differentiation, just correspond to slice profiles of Figs 1 and 2 by fixed  $b$  or  $d$  and thus could not unveil the effect of demographic trade-off. Furthermore, the consideration of both birth and death is necessary if other processes (e.g. density dependence) in addition to the neutral process are considered (Parsons and Quince 2007).

Species of the strictly neutral model have identical fitness, and their dynamics are solely driven by random drift. This system does not involve non-linearity to ensure rare species advantage (Chesson and Warner 1981). By this criterion, the nearly neutral model is also an unstable model that does not involve stabilizing (rare species advantage) but equalizing mechanisms (demographic stochasticity) that maintain coexistence. Figure 2 shows that coexistence time is higher at states away from the strictly neutral along the fitness-equivalence manifold. This occurs due to a strong birth-death trade-off between  $b$  and  $d$  by which symmetry ( $b \approx d \neq 1$  but not  $b = d = 1$ ) is nearly met (Fig. 2b, d and f). In this region, species coexist for a very long time, even longer than strictly neutral species. This result is consistent with the finding of Lin *et al.* (2009), Ostling (2011) and Zhang *et al.* (2011) that higher diversity can be maintained by neutral model of equivalent fitness than by the strictly neutral model. The demographic trade-off here operates as an equalizing force that tends to minimize fitness difference between species. This result provides a support to Hubbell's claim that interspecific differentiation can promote coexistence without invoking niche mechanisms (stabilizing force). It is worth noting that trade-offs in life history traits are typically regarded as a niche stabilizing mechanism (Grubb 1977). As we have shown here

this is not necessarily true as far as demographic trade-off is concerned.

Ecological drift, dispersal limitation and speciation are the three major community assembly rules in Hubbell's neutral theory. However, little is currently understood on how drift would reduce the diversity of communities. For example, how should effective community size (analogous to effective population size in population genetics) be defined to measure the loss of diversity due to drift (Hu *et al.* 2006; Lande *et al.* 2003; Orrock and Fletcher 2005)? Results in Fig. 3 show that fitness equivalent neutral communities (Fig. 3b) lose diversity more slowly than the strictly neutral community, while nearly neutral communities (Fig. 3c and d) lose diversity much more rapidly than the strictly neutral community. Clearly, the effective community size for nearly neutral communities should be smaller than the neutral community. The challenge is how we may analytically define an effective community size that incorporates  $b$  and  $d$  (and also immigration and speciation processes) (Hu *et al.* 2009).

The strictly neutral theory has been criticized for failing to correctly predict the time of species existence (Lande *et al.* 2003; Nee 2005; Ricklefs 2006). Theories in population genetics establish that the average age of a population in a community is approximately  $2N$  ( $N$  is community size) (Kimura 1983; Leigh 1981). This leads to the prediction that the average age of a tree species, even if rare, in a region of size of Central America would be billions of years, long before plants originated (Nee 2005). Therefore, the process of drift is just too slow to account for rapid species turnover over time. There have been attempts to explain this problem. For

example, it has been hypothesized that the division of a large ecosystem into smaller homogeneous neutral communities, climate change, coevolutionary interactions and gradual (rather than instantaneous) speciation within ecological systems may each contribute to reducing the time of coexistence (Lande *et al.* 2003; Nee 2005; Ricklefs 2006; Rosindell *et al.* 2010). Our results show that a small relaxation from the neutral assumption can substantially reduce the time of coexistence (Fig. 2). Although this reduction may still not be large enough to fully account for the problem, nearly neutral theory coupling with other processes (e.g. division of a large system, reduced effective community size, gradual speciation) can offer a promising solution.

It is worth mentioning that although Equation (2) is in essence a demographic model, it can also be used to model the effect of environmental stochasticity on species coexistence. Birth and death factors  $b$  and  $d$  in Equation (2) are the ratios of the probabilities of sampling species 1 over species 2 (to die or to reproduce). **Environmental factors that affect birth and death could thus be incorporated into the nearly neutral models through  $b$  and  $d$ , and, in turn, their effects on the transition probabilities can be modeled. This may be an opportunity to introduce stabilizing mechanisms into the unstable nearly neutral model.**

The nearly neutral theory developed here generalizes the neutral theory while not compromising the analytical tractability of the theory. The theory provides a promise to reconcile mismatching predictions of the current neutral theory. Here we would like to raise an overlooked issue in the current study. In fitness equivalent models, species of high birth and high death are considered ecologically equivalent to species of low birth and low death. This is true for species coexistence as measured by Equations (4) and (6) but may not be so with regard to other community properties, especially, in response to environmental stochasticity. The high birth–high death versus low birth–low death trade-off will induce a difference in variance along the trade-off manifold that could have important implications to population survival and thus community organization. This is not a straightforward question but deserves a closer attention.

## FUNDING

National Natural Science Foundation of China (D.Y.Z. and K.L.); Ministry of Science and Technology of China (D.Y.Z. and K.L.); Geomatics for Informed Decisions Network of Canada (F.H.); Natural Sciences and Engineering Research Council of Canada (F.L.); University of Alberta International (the China-UofA Joint Research Lab program).

## ACKNOWLEDGEMENTS

We thank Douglas Yu for their constructive comments, which have much improved this study.

*Conflict of interest statement.* None declared.

## APPENDIX 1

### Derivation of the absolute coexistence time for the trade-off-based drift model

The derivation of the absolute coexistence time requires a reformulation of the asymmetric Moran–Hubbell model 2 in terms of a non-linear one-step stochastic process. Let's start by assuming that the probability for a given individual of the focal species to die in the time interval  $(t, t + \Delta t)$  is  $D_1 \Delta t$ , where  $D_1$  is a species-specific 'death rate'. From this assumption, it follows that the probability of one death occurring in  $(t, t + \Delta t)$  in the focal species is  $jD_1 \Delta t + o(\Delta t)$ , where  $o(\Delta t)$  is a higher order term of  $\Delta t$  and can be disregarded when  $\Delta t$  is small. The above probabilities then is  $jD_1 \Delta t$ .

The one-step transition probabilities that the abundance of the focal species increases or reduces by one individual, or unchanged are, respectively:

$$\begin{cases} p_{j,j+1} = [(N-j)D_2 \Delta t] \left( \frac{B_1 j}{B_1 j + B_2(N-j)} \right) \\ p_{j,j-1} = [jD_1 \Delta t] \left( \frac{B_2(N-j)}{B_1 j + B_2(N-j)} \right), \\ p_{j,j} = 1 - p_{j,j+1} - p_{j,j-1} \end{cases} \quad (A1)$$

where  $B_i$  is the birth rate of species  $i$  ( $i=1, 2$ ). The first term,  $[(N-j)D_2 \Delta t]$ , on the right-hand side of  $p_{j,j+1}$  is the probability of a death occurring in species 2 during the interval  $(t, t + \Delta t)$ . The second term,  $\frac{jB_1}{B_1 j + B_2(N-j)}$ , is the probability of a birth (immediately following the death event) occurring in species 1. The transition probability,  $p_{j,j+1}$ , is a joint probability of a death in species 2 followed by a birth in species 1. The probabilities above are the continuous time version of Equation (2) in the main text.

The time to fixation or absorption,  $t_j$ , is defined as the average number of time steps for the focal species traveling from  $j$  to either  $N$  or 0 (Ewens 2004; Zhang and Lin 1997):

$$\begin{aligned} t_j &= \frac{j}{N} \sum_{i=1}^{N-1} \sum_{k=1}^i \frac{1}{p_{k,k+1}} - \sum_{i=1}^{j-1} \sum_{k=1}^i \frac{1}{p_{k,k+1}} \\ &= \frac{j}{N} \sum_{i=1}^{N-1} \sum_{k=1}^i \frac{B_1 k + B_2(N-k)}{(N-k)k B_1 D_2 \Delta t} - \sum_{i=1}^{j-1} \sum_{k=1}^i \frac{B_1 k + B_2(N-k)}{(N-k)k B_1 D_2 \Delta t}, \quad 1 \leq j < N. \end{aligned} \quad (A2)$$

From (A2), it is obvious that a natural measure of coexistence time is given by

$$\begin{aligned} T_j &= t_j \Delta t = \frac{j}{N} \sum_{i=1}^{N-1} \sum_{k=1}^i \frac{B_1 k + B_2(N-k)}{(N-k)k B_1 D_2} - \sum_{i=1}^{j-1} \sum_{k=1}^i \frac{B_1 k + B_2(N-k)}{(N-k)k B_1 D_2} \\ &= \frac{j(N-1)}{N D_2} + \frac{j}{N} \sum_{i=1}^{N-1} \frac{B_2}{B_1 D_2} \frac{N-i}{i} - \sum_{i=1}^{j-1} \left[ \frac{j-i}{D_2(N-i)} + \frac{B_2}{B_1 D_2} \frac{j-i}{i} \right] \\ &\quad 1 \leq j < N. \end{aligned} \quad (A3)$$

The above absolute coexistence time  $T_j$  can be further simplified for fitness equivalent neutral communities by assuming equivalent fitness, i.e.  $B_1/D_1 = B_2/D_2$ . This fitness equivalence



(corresponding to the scenario of  $b = d$  of Eq. 6) removes  $B_1$  and  $B_2$  from (A3).

The above model becomes the Moran–Hubbell model if the time step is defined as  $\Delta t = \frac{1}{jD_1 + (N-j)D_2}$ . This is the implicit assumption behind the Moran model and all subsequent Markov-chain models in discrete times. Here,  $\Delta t$  is no longer invariant but varies with relative species abundances of the community if species differ in their death rates. This property, which makes the transition probabilities no longer suitable for use in the master equation, has passed practically unnoticed in the literature. Of course, this is not a problem if only demographically symmetric species are considered. This perhaps explains why it was not noticed before.

In the Moran–Hubbell model, the relative coexistence time is measured in terms of the average number of deaths required for the focal species to drift to 0 or  $N$ . Substituting  $\Delta t = \frac{1}{jD_1 + (N-j)D_2}$  into the relative time of Equation (A2), one obtains Equation (6) of the main text. The relative time and absolute time are qualitatively similar in most cases except that when death rate is very low in which the absolute time can be longer than the relative time. In all cases, both times show that strictly neutral species (i.e. having exactly the same birth and death rates) in general do not constitute maximum coexistence, particularly when viewed from the relative time. This is an important result of this study, new to the literature.

## APPENDIX 2

### Derivation of diversity decay for strictly neutral species with identical vital rates in a lottery model

Define  $F_t$  as the probability that two randomly sampled individuals at generation  $t$  are of the same species.  $1 - F_t$  is thus Simpson's diversity index, commonly denoted by  $H_t$  in population genetics. In the lottery model (Lin *et al.* 2009), a portion  $D$  of individuals die and are replaced by offspring of all individuals with equal probability. When two individuals are sampled at random, there is a probability of  $(1 - D)^2$  that neither of these two is the new individual and the probability that at least one is the new individual is  $1 - (1 - D)^2$ . If neither of the sampled individuals is new, then the probability they are of same species is simply  $F_{t-1}$ . If two sampled individuals are both new, the probability that they are the progeny of the same individual in the previous generation is  $1/N$ ; if they are the progeny of different individuals, which occurs with probability  $(1 - 1/N)$ , then the probability they are of the same species is  $F_{t-1}$ . Putting together, the probability two sampled individuals are of the same species is  $[\frac{1}{N} + (1 - \frac{1}{N})F_{t-1}]$  when they are both new. By the same argument we can derive the same result when only one sampled individual is new. We thus have the recursion

$$F_t = [1 - (1 - D)^2] \left[ \frac{1}{N} + \left(1 - \frac{1}{N}\right) F_{t-1} \right] + (1 - D)^2 F_{t-1}. \quad (\text{A3})$$

After some rearrangement, we obtain

$$1 - F_t = \left(1 - F_{t-1}\right) \left(1 - \frac{2D - D^2}{N}\right). \quad (\text{A3})$$

Therefore, Simpson's diversity index changes with time as

$$H_t = 1 - F_t = H_0 \left(1 - \frac{2D - D^2}{N}\right)^t. \quad (\text{A3})$$

Obviously, if  $D = 1$ , it reduces to the Wright–Fisher model with non-overlapping generations, which is  $H_t = H_0 \left(1 - \frac{1}{N}\right)^t$ . The larger  $D$ , the quicker the diversity decays. This must be the case because higher annual mortality rates imply more turnovers, which in turn leads to more effective drift.

## APPENDIX 3

### Simulation based on the lottery model for evaluating the effect of ecological drift on non-neutral communities

We performed the simulation by running 100 independent communities. For each of the 100 communities, its size is set to be 10 000. At the beginning of each simulation, the community is occupied by 100 species with equal abundance, and each species is characterized with a death rate ( $D_i$ ) randomly drawn from a uniform distribution  $U(0, 1)$  and a birth rate ( $B_i$ ) randomly drawn from a normal distribution  $N(D_i, \sigma^2)$ , where  $\sigma^2$  is the variance and  $B_i > 0$ .

With the above general setting, each simulation goes forward as follow.

#### STEP 1 (death process):

- For each species, its abundance is denoted as  $N_i$ .
- For each individual of the species, a number is randomly generated from a uniform distribution  $U(0, 1)$ .
- If the random number generated is less than or equal to its death rate ( $D_i$ ), the individual is designated as dead, and the abundance of the species ( $N_i$ ) decreases by one.
- Thus, the total number of dead individuals across all existent species in the community could be counted and is denoted as  $tNum$ .

#### STEP 2 (birth process):

- For each of these  $tNum$  vacant sites released from the deaths of STEP 1, a new individual is recruited, which is sampled from one of the existent species in the community (before the death process) in accordance to its birth rate ( $B_i$ ) and its abundance ( $N_i$ ).
- One cycle (from death to birth process) of the simulation is counted as one time unit. Each simulation continues till the total time unit reaches 60 000. During the course of

simulation, the community was sampled once per 1000 time units (hence there are 60 Simpson's indices for each simulation).

The above STEP 1 and STEP 2 were repeated for 100 communities (i.e. 100 independent runs). The resultant curves (Fig. 3) and their error bars were calculated based on mean and standard error of these 100 communities.

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