

Positive interactions can produce species-rich communities and increase species turnover through time

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Abstract

Aims

The process of facilitation, where a species increases the survival, growth, and fitness of another species, is becoming increasingly recognized as a critical factor in shaping the structure of plant communities. This process is particularly important in stressful environments. Yet few studies have attempted to incorporate positive interactions into community ecological theories such as the neutral theory of biodiversity. Here, we use an equalizing trade-off model as a foundation to study the potential impact of facilitation on species richness and community temporal turnover.

Methods

Based on a spatially explicit birth–death trade-off model, we assume that the occurrence of facilitation is dependent on the presence of interspecific neighbours. We further propose that the realized birth rate for a given individual subject to facilitation is proportional to the number of interspecific neighbours within its neighbourhood. Thus, in our model, the individuals of rare species will benefit more from the existence of heterospecific individuals than common species.

Important Findings

As the facilitative coefficient increased, the species richness for simulated communities at the dynamically stochastic equilibrium was

also increasing. Simulations also demonstrated that facilitation could increase the replacement of species through time: communities with facilitation become more dissimilar (i.e. have smaller Bray–Curtis similarity values) than communities without or with a lower degree of facilitation after the same time interval. Facilitation from interspecific neighbours on rare species increased their population sizes and consequently made them less prone to extinction, thus enhancing species richness. Meanwhile, in a saturated community, with the increase of species richness, mean population size of entire communities decreased, making species more prone to extinction on average, and thus increased the community temporal turnover. Our results suggest that future experimental work on the effect of facilitation on community-level properties should focus not just on species richness but also on other descriptors of community dynamics such as the temporal species turnover.

Keywords: Bray–Curtis similarity index • positive interactions • species coexistence • species temporal turnover

Received: 6 October 2011 Revised: 4 February 2012 Accepted: 11 February 2012

INTRODUCTION

The neutral theory of biodiversity (Hubbell 2001) has contributed enormously to our understanding of the processes structuring ecological communities. In its strictest sense, neutrality

assumes that all individuals of different species are demographically identical (Hubbell 2001). This assumption of species equivalence is the most controversial aspect of the neutral theory and has attracted the most criticism (Wootton 2005; Zhang and Lin 1997; Yu *et al.* 1998; Zhou and Zhang 2008).

As a result, efforts are now being made to integrate demographic trade-offs, which reflect fitness equivalence while at the same time allowing for species differences, into neutral models (Allouche and Kadmon 2009; He *et al.* 2012; Lin *et al.* 2009; Ostling 2011; Purves and Turnbull 2010; Zhang *et al.* 2012).

The study of plant–plant interactions has been pivotal to understanding the structure of ecological communities (Callaway 2007; Gause and Witt 1935; Niu and Wan 2008). Following on from Hubbell's (2001) neutral theory, theoretical developments such as stochastic niche theory (Tilman 2004), the continuum hypothesis (Gravel *et al.* 2006) and nearly neutral theory (Zhou and Zhang 2008; He *et al.* 2012) often assume that the interactions between plant species are negative. However, these theoretical assumptions contrast markedly with many experimental studies demonstrating that positive interactions exert significant effects on the dynamics of populations (e.g. Chu *et al.* 2008, 2009b; Wang *et al.* 2008) and are key drivers of structural attributes of communities such as species richness (e.g. Cavieres and Badano 2009; Xiao *et al.* 2009; Xu *et al.* 2010; Soliveres *et al.* 2011).

Although few studies have completely integrated facilitative interactions into community assembly theory (but see Gross 2008), doing so may greatly improve our understanding of the factors shaping the structure of communities. For example, it is becoming increasingly recognized that diverse species will have different responses to neighbours in stressful conditions (Callaway 1998; Chu *et al.* 2009a; Liancourt *et al.* 2005; Wang *et al.* 2008). This kind of variation is usually dependent upon species abundance, which is itself related to species traits resulting in some species being more stress tolerant than others (Liancourt *et al.* 2005; Wang *et al.* 2008). In harshly abiotic conditions, abundant species, which are usually also stress tolerant, obtain little benefit from neighbouring plants, whereas rare species are greatly facilitated (Callaway 2007; Liancourt *et al.* 2005; Wang *et al.* 2008).

To our knowledge, no previous study has used a neutral community framework to explicitly account for the importance of positive interactions to the structure and dynamics of entire communities. In the present paper, we use a birth–death trade-off model as a foundation to study theoretically the potential impact of facilitation on community dynamics. We tested two hypotheses, both under the assumption of saturated communities: (i) positive interactions maintain higher species richness, as found by field studies in different communities (e.g. Cavieres and Badano 2009; Pugnaire *et al.* 1996; Soliveres *et al.* 2011; Xu *et al.* 2010), and (ii) if hypothesis (i) is true, facilitation will increase species turnover through time.

METHODS

Our model is based on an equalizing birth–death trade-off model (Allouche and Kadmon 2009; He *et al.* 2012; Lin *et al.* 2009; Purves and Turnbull 2010; Ostling 2011; Zhang

et al. 2012). In this model, we assume that species could have various *per capita* birth (b_i) and death (d_i) rates, rather than all individuals being strictly neutral as in the original neutral theory (Hubbell 2001), but the b_i/d_i ratio (i.e. the birth–death trade-off) remained constant across all species.

Numerous experimental studies have demonstrated that positive interactions from neighbours could increase the birth rate by increasing fecundity and/or reproduction and decrease the mortality rate by improving survival (Callaway 2007; Chu *et al.* 2009a; Liancourt *et al.* 2005; Maestre *et al.* 2005). As well as the species-specific responses to neighbours in harsh conditions, relatively rare species will have an advantage because of neighbour facilitation on key demographic rates, i.e. the increased b_i or decreased d_i or both (Liancourt *et al.* 2005; Wang *et al.* 2008). In the present paper, we assume that the occurrence of facilitation is dependent on the presence of interspecific neighbours (Callaway 2007; Maestre *et al.* 2003; Xiao *et al.* 2009). We further propose that the realized birth rate for a given individual subject to facilitation is proportional to the number of interspecific neighbours within its neighbourhood (Callaway *et al.* 2002; Molofsky *et al.* 2001; Reisman-Berman 2007). Thus, the b_i/d_i ratio for a given species will be larger than 1 if interspecific neighbours exist in the neighbourhood of this species. Apparently, our model is non-neutral.

When a new species entered the community, its *per capita* death rate was drawn from a uniform distribution (0, 1; Lin *et al.* 2009). Thus, each empty grid due to death will be occupied by a new species with probability u and by one of the currently existing species with probability $1 - u$. Then the probability for species i occupying a given vacant grid is

$$\frac{\sum_{q=1}^{N_i(t)} b_i (1 + f \times \frac{n_{qi}}{8})}{\sum_{m=1}^{m=j} \sum_{p=1}^{p=N_m(t)} b_m (1 + f \times \frac{n_{pm}}{8})}$$

where f is a facilitative coefficient (in the present paper, we theoretically set up three levels of the magnitude of facilitation, i.e. $f=0.0, 0.5$, and 1.0 , respectively), j denotes the species richness, $N_i(t)$ and $N_m(t)$ are the total individual number of species i and m at time t , respectively, and n_{qi} and n_{pm} denote the number of interspecific neighbours of a focal individual q and p from species i and m within its Moore neighbourhood. Thus, biotic interactions among individuals are localized within the nearest eight neighbours. In the models, the dispersal of offspring and individuals of new species is global.

We constructed a saturated metacommunity consisting of $J_m = 10\,000$ individuals (on a landscape with 100×100 grids). After preliminary trials, we chose a speciation rate $u = 0.0005$, which describes the input of new species. The simulations were initiated using a single species with a death rate of 0.5 occupying all sites and continued until the community reached a stochastic equilibrium after $\sim 40\,000$ time steps. The simulations proceed in annual increments, in which three modules are executed in the following order: deaths,

reproduction and speciation, and recruitment. To calculate the changes of temporal composition of communities, we used the Bray–Curtis similarity index, which accounts for both the presence/absence and the abundance of each species (Magurran 2004; Magurran and Henderson 2010; Southwood and Henderson 2000). A set of 20 simulation runs was performed for each parameter setting, and the mean of the abundance of each of the r th ranked species was computed over the ensemble of 20 runs. A ‘wraparound’ approach (i.e. periodic boundary conditions) was used to avoid edge effects. The package *fossil* (Vavrek 2011) was used to calculate the Bray–Curtis similarity index on the R platform (R Development Core Team 2009).

RESULTS

In our model, including positive interactions by varying the birth rates of different species produced species-rich, stable communities. As the facilitative coefficient increased ($f = 0.0, 0.5, \text{ and } 1.0$), the species richness for simulated communities at the dynamically stochastic equilibrium was also increasing (Fig. 1). Additionally, positive interactions increased species turnover through time: after the same interval, the Bray–Curtis similarity index for community compositions with facilitation was lower than that of communities without or with a lower degree of facilitation (Fig. 2).

DISCUSSION

The original neutral model proposed by Hubbell (2001) is extremely sensitive to departures from the assumptions of neutrality, and even slight differences in fitness could result in a sharp decrease in species coexistence times and, consequently, a decrease in species richness (Zhang and Lin 1997; Yu *et al.* 1998). Compared with the original neutral model

(Hubbell 2001), the trade-off/neutral model used here accommodates the variability among species in the demographic parameters of birth and death rates but keeps the fitness equivalent (Allouche and Kadmon 2009; He *et al.* 2012; Lin *et al.* 2009; Ostling 2011; Purves and Turnbull 2010; Zhang *et al.* 2012). Using such fitness equivalence model as the foundation, we further account for the variation of fitness among species through facilitation that is dependent on the number of interspecific neighbours for a focal individual. The results demonstrate that positive interactions positively contribute to the maintenance of biodiversity (Fig. 1). These results imply that the trade-off neutral model may be more robust to fitness variation among species than the strictly neutral model of Hubbell’s (2001).

Consistent with our two hypotheses, the results demonstrate that facilitation could indeed have a substantial impact on community structure (Figs 1 and 2). In the simulations, the rare species advantage resulting from facilitation increased the population sizes of rare species and made them less prone to extinction, increasing species richness (Fig. 1). This result is consistent with empirical observations from recent experimental studies conducted in harsh conditions (e.g. Cavieres and Badano 2009; Mulder *et al.* 2001; Soliveres *et al.* 2011; Xu *et al.* 2010). However, in a saturated community following the zero-sum game, the increase of species richness definitely causes the decrease of population size of all species on average. At the level of entire communities, facilitation could make species more prone to extinction on average and thus increase the species temporal turnover (Fig. 2), although this supposition will need further experimental validation. We propose that future experiments on the effect of facilitation on community-level properties should not only focus on species richness but also other descriptors of community dynamics such as species temporal turnover, as shown in the present work.

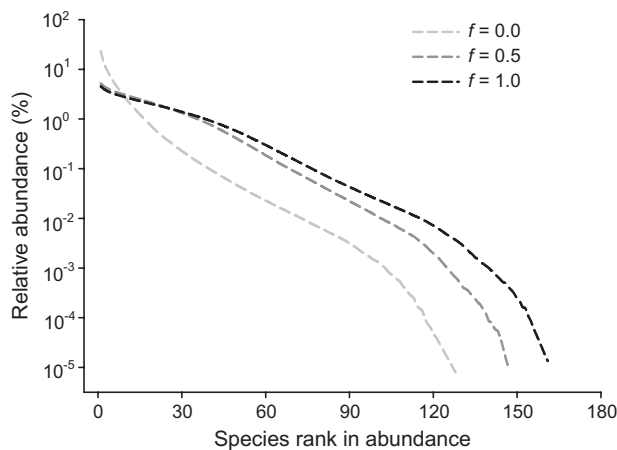


Figure 1: species abundance distributions for saturated multispecies communities at the dynamically stochastic equilibrium when using the facilitative coefficient of $f = 0.0, 0.5, \text{ and } 1.0$, respectively. Note the y-axis log scale.

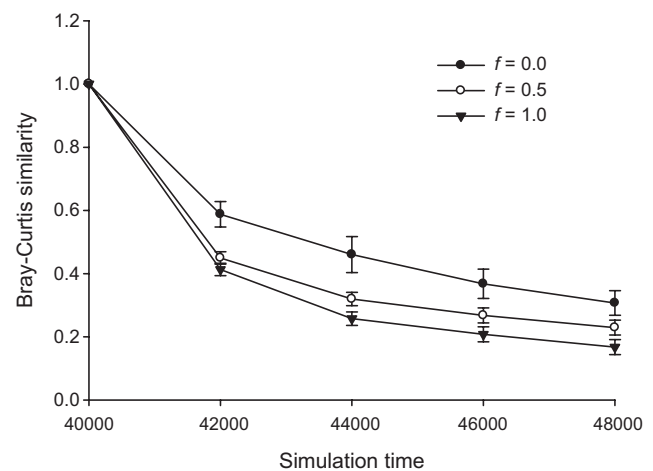


Figure 2: temporal turnover of species composition, as measured with the Bray–Curtis similarity index with the facilitative coefficient of $f = 0.0, 0.5, \text{ and } 1.0$, respectively. Data represent means \pm SE ($n = 20$). The sampling interval is 2000 time steps in our simulations.

Our model presents a novel demonstration of how we might explore the effects of positive plant–plant interactions on community dynamics using a neutral model as the foundation. Though equalizing trade-off neutral models can maintain high biodiversity (Lin *et al.* 2009; Ostling 2011; Zhang *et al.* 2012), the inclusion of positive interactions among species could make these models more realistic, especially for communities in stressful environments, which are largely structured by facilitation.

FUNDING

National Natural Science Foundation of China (31000199, 30970543, 30770360, 41021091); the Fundamental Research Funds for the Central Universities (lzujbky-2012-133, lzujbky-2009-88, lzujbky-2010-49); the Youth Innovation Research Fund for Interdiscipline of Lanzhou University (LZUJC200915); the Department of Zoology, University of Cambridge (to M.D.F.E.); the European Research Council (the European Community's Seventh Framework Programme FP7/2007-2013 to F.T.M./ERC grant agreement no. 242658 [BIOCOM]).

ACKNOWLEDGEMENTS

We are grateful to James Rosindell, Da-Yong Zhang, Adrian Friday, Fangliang He, and one anonymous reviewer for valuable and constructive comments on the earlier versions of the manuscript. *Conflict of interest statement.* None declared.

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