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Effects of biotic interactions and dispersal on the presence-absence of multiple species

Mohd Hafiz Mohd[a,b,*], Rua Murray[b], Michael J. Plank[b], William Godsoe[c]

[a] School of Mathematical Sciences, Universiti Sains Malaysia, Penang, 11800 USM, Malaysia
[b] School of Mathematics and Statistics, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand
[c] Bio-Protection Research Centre, Lincoln University, P.O. Box 85084, Lincoln 7647, New Zealand

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ABSTRACT

One of the important issues in ecology is to predict which species will be present (or absent) across a geographical region. Dispersal is thought to have an important influence on the range limits of species, and understanding this problem in a multi-species community with priority effects (i.e. initial abundances determine species presence-absence) is a challenging task because dispersal also interacts with biotic and abiotic factors. Here, we propose a simple multi-species model to investigate the joint effects of biotic interactions and dispersal on species presence-absence. Our results show that dispersal can substantially expand species ranges when biotic and abiotic forces are present; consequently, coexistence of multiple species is possible. The model also exhibits ecologically interesting priority effects, mediated by intense biotic interactions. In the absence of dispersal, competitive exclusion of all but one species occurs. We find that dispersal reduces competitive exclusion effects that occur in no-dispersal case and promotes coexistence of multiple species. These results also show that priority effects are still prevalent in multi-species communities in the presence of dispersal process. We also illustrate the existence of threshold values of competitive strength (i.e. transcritical bifurcations), which results in different species presence-absence in multi-species communities with and without dispersal.

1. Introduction

How do dispersal process and biotic interactions combine to determine species presence-absence and its dependency on initial abundances (i.e. priority effects)? This is an interesting question because empirical evidence suggests that the joint effects of biotic interactions and dispersal affect species range limits across heterogeneous environments [1–4]. In general, there is a suite of ecological forces that can determine the presence-absence of species: abiotic environments [5–8], biotic interactions [9–12] and dispersal process [1,13–15]. While various ecological forces have been examined, much remains unknown about the combined influences of dispersal and biotic interactions on the occurrence of priority effects and species coexistence in multi-species communities. In this paper, we fill part of this knowledge gap by investigating the interaction of priority effects with biotic factor and dispersal in shaping the presence-absence of species along environmental gradients.

Environmental factors such as climate can affect the presence-absence of species across a geographical region [5,7,8,16,17]. It has been demonstrated through empirical evidence that environmental factors can determine species range limits in marine and terrestrial communities [18,19]. For instance, Barry et al.[20] discover that changes in shore temperature can affect species presence-absence in intertidal communities; Perry et al.[18] demonstrate that the distributions of fish species have shifted in mean latitude (or depth) because of increases in sea temperature; Comte and Grenouillet [21] suggest that climate can affect the distributions of stream fish species along environmental gradients; Moritz et al.[22] illustrate that the distributions of some small mammals have changed due to the influence of climate.

Apart from environmental components, biotic interactions has also been proposed as another crucial factor that can shape species range limits [9–11]. The notion that biotic interactions such as competition can influence the presence-absence of species has long been recognised [23–26] and is evident in numerous studies [9,27–30]. For instance, experimental works by Davis et al.[2,3] illustrate that biotic interactions, dispersal and climate all affect the abundances of three competing fruit fly species as temperature changes. Other studies [12,31,32] show how competition among species and dispersal along environmental gradients can shape species presence-absence. It has also been observed in different studies

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[*] Corresponding author.
E-mail address: mohdhafizmohd@gmail.com (M.H. Mohd).

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that both biotic and abiotic components can influence community compositions [33–35]. For example, by studying the competition between exotic and native Daphnia species, Wittmann et al. [36] illustrate that the competitive outcomes depend on temperature and strength of biotic interactions.

When biotic interactions are relatively intense, priority effects can occur in which initial species abundances affect species presence-absence [1,10,37,38]. In this case, the order in which species become established or their history of arrival can determine the community structure [39,40]. Experimental studies have manipulated initial abundances or the establishment order of species to explore the occurrence of priority effects [41,42]. Other experimental studies using a microbial community [43] demonstrate that variation in the timing of species introduction can lead to different community assembly. Additionally, some studies observe that priority effects can also be influenced by abiotic environments: experimental work using *Daphnia* species [44] find that abiotic components such as salinity levels can affect community dynamics and thus may alter priority effect outcomes. Experimental studies of Park [41,42] also show how important such an interaction between biotic factor and abiotic environments (e.g. temperature and humidity) in determining the occurrence of priority effects.

Dispersal process also plays an important role in structuring community assembly [1–3]. It has been demonstrated that dispersal can allow species to be present in otherwise unsuitable environments, as shown by the experimental studies of Davis et al.[2,3]. In an ecological community, dispersal can increase species diversity by immigration of species from other locations [45]; it has been shown that sink populations (i.e. low quality habitat with few individuals) can only persist if they receive sustained dispersal from source populations (i.e. high quality habitat with more abundant individuals) [46–48]. Dispersal can also facilitate local coexistence of species across heterogeneous environments as a consequence of source-sink dynamics [47].

Given these observations, much remains unknown about how dispersal process, in interaction with other ecological forces, shapes a multi-species community assembly. Specifically, it is unclear what effects dispersal and biotic interactions can have on the outcomes of species interactions if priority effects are important in determining presence-absence of species along environmental gradients. To address this problem, we extend previous theoretical studies [49,50] involving two-species to model biotic interactions and dispersal among multiple species across heterogeneous environments. To model dispersal between adjacent locations, we incorporate a local dispersal process into our systems. This inclusion leads to a system of partial-differential equations (PDE) consisting of interspecific competition, environmental suitability (carrying capacity) and local dispersal terms. We investigate the joint effects of dispersal and biotic interactions on community dynamics by comparing results of the models with and without dispersal. We also aim to provide theoretical explanations for the effects of biotic interactions and dispersal on multi-species community dynamics.

The article is organised as follows. After describing the model, we illustrate the effects of dispersal in the presence of weak and intense biotic interactions. We highlight these observations using our simulation results, with respect to the occurrence of priority effects and the possibility of species coexistence. By using numerical continuation, we discuss some mathematical insights on the effects of dispersal on the presence-absence of species. Finally, we discuss several ecological implications of our results.

2. The models

We consider a partial differential equation (PDE) model for the densities $N_i(x,t)$ of m species in a one-dimensional domain $0 \leq x \leq 1$ [4,51]:

$$\frac{\partial N_i}{\partial t} = \frac{r_i N_i}{K_i(x)}\left(K_i(x) - \sum_{j=1}^{m}\alpha_{ij}N_j\right) + D_i\frac{\partial^2 N_i}{\partial x^2} \qquad (i = 1, 2, \ldots, m) \tag{1}$$

where r_i is the intrinsic growth rate, K_i is the carrying capacity and D_i is the diffusion coefficient of species i, and α_{ij} is the coefficient for competition of species j on species i. By rescaling the density of species i relative to its intraspecific competition coefficient α_{ii}, we may effectively set the intraspecific competition coefficients α_{ii} to equal 1, and the remaining competition coefficients α_{ij} represent the ratio of intraspecific to interspecific competition. Eq. (1) is a spatially extended Lotka–Volterra competition model[10,12,50], which becomes a PDE with the addition of the diffusion term.

In the absence of dispersal ($D_i = 0$), the dynamical behaviour of Eq. (1) at a specific location x is independent of the behaviour at all other locations. Competition is assumed to be local (meaning that species only compete with other species at the same location) and we also assume that interspecific competition is symmetric e.g. $\alpha_{ij} = \alpha_{ji} = \alpha$. Following these assumptions, the simplest equation of type (1) is in the case of two-species (e.g. $m = 2$): competitive interactions within each location x lead to several outcomes, depending on the competition coefficient α and the ratio of the carrying capacities $\frac{K_1}{K_2}$: local coexistence (when $\alpha < \frac{K_1}{K_2} < \frac{1}{\alpha}$) and priority effects (when $\frac{1}{\alpha} < \frac{K_1}{K_2} < \alpha$). The analysis can be extended for the cases of asymmetric competition ($\alpha_{ij} \neq \alpha_{ji}$) and more than two interacting species . For instance, in the case of asymmetric competition for the three-species models with equal carrying capacity (e.g. all $K_i = 1$), different dynamical behaviours are possible: periodic limit cycle solutions [52–55] and nonperiodic population oscillations [52]. The reader is also referred to [54,56–59] for further details and extensions of these dynamical systems results. Because of the uncertainty in choosing the competition coefficient α, we have examined the dynamics of Eq. (1) for a realistic range of values of α.

The suitability of a particular environment or location is modelled by incorporating a spatial dependence x into the carrying capacity term; each species' carrying capacity $K_i(x)$ can vary with location x. x could be a location within a geographical region, or used as a proxy for representing abiotic environmental factors such as temperature, moisture or elevation that affect the carrying capacity of species. The effects of biotic interactions on range limits can depend on how each species responds to the environmental gradient. To illustrate these effects in a multi-species community, we use a linear environmental gradient (i.e. carrying capacity varies linearly with x) in a three-species model ($m = 3$) [10,32,50,51]:

$$K_i(x) = m_i x + c_i \tag{2}$$

where $K_i(x)$ is carrying capacity of species i at location x, m_i is the change in environmental suitability with respect to abiotic component x and c_i is the carrying capacity of species i when $x = 0$. To ensure Eq. (1) is well defined, we set $K_i(x)$ to a small but non-zero value (0.001) outside the fundamental niche.

The diffusion term models dispersal among locations, with the parameter D_i representing the strength of dispersal for species i. We assume that interacting species have the same dispersal rate ($D_i = D$) and no migration occurs across boundaries (by imposing zero-flux boundary conditions for each species):

$$D_i \frac{\partial N_i}{\partial x}\bigg|_{x=0,1} = 0. \tag{3}$$

To solve the model (1), we employed numerical simulation using MATLAB for sufficient time until steady state is reached. In particular, we used MATLAB `ode15s` solver and we also verified