



Effects of dispersal and stochasticity on the presence–absence of multiple species



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ARTICLE INFO

Article history:

Received 21 January 2016

Received in revised form

18 September 2016

Accepted 30 September 2016

Keywords:

Range limit

Priority effects

Dispersal

Stochasticity

Biotic interactions

Abiotic environments

ABSTRACT

A key problem in ecology is to predict the presence–absence of species 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 the presence–absence of species) is a challenging task because dispersal interacts with biotic and abiotic factors as well as demographic stochasticity. By using stochastic individual-based models (IBM) and deterministic models consisting of biotic interactions and environmental gradients, we investigate the joint effects of dispersal and stochasticity on the occurrence of priority effects that can shape the presence–absence of multiple species. Our analysis shows the conditions under which priority effects occur and disappear as dispersal intensity changes. Without dispersal, priority effects emerge in the presence of intense biotic interactions; only one species surviving at any given location, with no overlap in their ranges. Inclusion of dispersal first reduces the prevalence of priority effects (i.e. for weak dispersal), and then leads to their increase (i.e. for moderate dispersal); consequently, dispersal enhances the possibility for species ranges to overlap. Increasing dispersal strength above a threshold value leads to the disappearance of priority effects and causes extinction of some species. We also demonstrate contrasting observations of stochasticity on priority effects: while this phenomenon is more prevalent in the stochastic IBM than in the deterministic models for large populations, we observe fewer occurrences of priority effects in IBM for small populations; in particular, our IBM results show that priority effects are eliminated by weaker values of dispersal when population sizes are small than when they are large. This situation can induce an uncertainty in the predictions of species presence–absence. Overall, our results demonstrate how the interplay of dispersal and stochasticity can combine to result in the (dis-)appearance of priority effects that strongly determine the presence–absence of species.

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1. Introduction

When does the order in which species become established (i.e. priority effects) matter in determining presence–absence of species and when does this phenomenon depend on ecological processes such as dispersal and demographic stochasticity? These are important questions in ecology (Sexton et al., 2009; Case et al., 2005) and are crucial for making robust predictions about which species will be present (or absent) across a geographical region (Gaston, 2003; Sexton et al., 2009; Wisz et al., 2013). Some predictive models concentrate on the influence of environmental

variables (Shmida and Wilson, 1985; Pearson and Dawson, 2003; Soberón, 2007; Kearney and Porter, 2009) and biotic interactions (Wisz et al., 2013; Case et al., 2005; Gilman et al., 2010; Godsoe et al., 2015a) on presence–absence of species, yet dispersal (Sexton et al., 2009; Gaston, 2009; Bahn et al., 2006; Birand et al., 2012) and demographic stochasticity (Gaston and He, 2002; Holt et al., 2005; Simonis, 2012) can also affect the dynamics of natural communities. Generally, ecological processes such as dispersal and growth can be described at the individual level or at the population level (Nisbet and Gurney, 1982; Renshaw, 1993; DeAngelis and Matsinos, 1995; Wilson, 1998; Allen, 2003). Looking at interacting species from the population-level perspective and modelling them as continuous densities, presence–absence can be predicted using deterministic models (Nisbet and Gurney, 1982; Renshaw, 1993; Wilson, 1998). Alternatively, if the interacting species are represented as collections of discrete individuals and stochastic events

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(e.g. birth and death) are considered, their locations can be simulated using stochastic individual-based models (IBM) (Nisbet and Gurney, 1982; Renshaw, 1993; Wilson et al., 1995; Wilson, 1998; Law et al., 2003). Given these options, we propose to investigate the interaction of priority effects with dispersal and stochasticity in shaping presence–absence of species.

Priority effects have been shown to determine community assembly in various ecological systems (Sexton et al., 2009; Case et al., 2005); for instance, in a system of two interacting flour beetles (Park, 1954; Park et al., 1965), in a small food web community incorporating competition and predation (Gerla et al., 2009) and in plant (Kardol et al., 2013) and plankton (Loureiro et al., 2013) communities. These studies illustrate that biotic interactions are one of the important factors in priority effects and this process generally depends on early arrival or high initial abundances of species (Gerla et al., 2009). Other studies have also shown that priority effects can be influenced by abiotic environments: as an example, experimental works using *Daphnia* species (Loureiro et al., 2013) have found that abiotic components such as salinity levels can affect community dynamics and thus may alter priority effect outcomes. However, we know less about how the order in which species become established may alter the presence–absence of species under varying dispersal scenarios and in the presence of stochasticity. Specifically, it remains unclear whether the combined effects of dispersal and stochasticity can lead to appearance or disappearance of priority effects across heterogeneous environments with biotic interactions among multiple species.

This work is inspired by some experimental studies which show that biotic interactions, dispersal, abiotic environments (Davis et al., 1998a,b) and priority effects (Loureiro et al., 2013) can alter the presence–absence of species. Our goal is to explore the possible mechanisms for priority effects in community assembly using modelling approaches. The deterministic models that we employ describe an example of biotic interactions, namely competition between species along environmental gradients, which are essential forces in shaping the presence–absence of species (MacLean and Holt, 1979; Roughgarden, 1979). We extend previous deterministic theoretical studies involving two interacting species (MacLean and Holt, 1979; Roughgarden, 1979) to model biotic interactions among multiple species across heterogeneous environments. We also assume that dispersal between adjacent locations can affect the dynamics of natural communities. This assumption is motivated by several studies of two-species systems (Case et al., 2005; Godsoe et al., 2015a,b); for instance, Case et al. (Case et al., 2005) show that dispersal and biotic interactions may determine range limits of species. They demonstrate that in the face of severe competitive pressure, priority effects occur with the range limits of species depending on initial abundances and the strength of dispersal (Case et al., 2005). Relatively weak dispersal can mitigate the effect of intense biotic interactions and cause species ranges to overlap (Case et al., 2005; Cantrell and Cosner, 1998). Conversely, when dispersal is strong, dramatic changes in range limits are possible with some species being excluded from otherwise suitable environments (Case et al., 2005; Cantrell and Cosner, 1998; Levin et al., 2009). By extending two-species deterministic models, we investigate the conditions under which priority effects occur and disappear as dispersal intensity changes in a multi-species community.

We also examine the impact of stochasticity on the community dynamics, in the presence of dispersal, biotic and abiotic forces that can limit the presence–absence of species. For such situations, some stochastic models have been formulated (Wilson, 1998; Law et al., 2003), but the interaction of priority effects with dispersal and stochasticity in shaping species range limits has not been investigated explicitly. Motivated by our deterministic models, we develop a comparable stochastic IBM that captures the dynamics

at an individual scale. In the IBM, each individual from each species is an agent that is tracked explicitly over time while undergoing a birth–death–movement process (DeAngelis and Mooij, 2005; Dieckmann et al., 2000; Faugeras and Maury, 2007). We aim to explore the occurrence of priority effects in our stochastic IBM by considering various dispersal scenarios and different population sizes, and to check whether the range-limit predictions are similar using the stochastic and deterministic models. It is demonstrated that even simple stochastic models can show dynamical behaviour that contrasts with the predictions of deterministic models (Wilson, 1998; Law et al., 2003). For instance, Law et al. (Law et al., 2003) study a single-species IBM and discover that the IBM predictions can be different compared to the logistic equation. Wilson (Wilson, 1998) investigates the dynamics of an IBM with biotic interactions and dispersal; he demonstrates qualitative agreement between the IBM and deterministic results. He also illustrates the disagreement between the IBM and deterministic predictions when the total population size is reduced (Wilson, 1998).

The article is organised as follows. After describing the two models, we discuss the effects of dispersal on patterns of species presence–absence. The focus of our analysis is the identification of three important patterns associated with the presence–absence of species: (i) the prevalence of priority effects (i.e. the range of competitive strength for which priority effects determine species presence at some spatial locations); (ii) the possibility of species range overlap (i.e. the range of spatial locations at which more than one species are found); (iii) the possibility of species exclusion (i.e. the situation in which we observe a species is absent at all spatial locations). We then demonstrate the agreement between deterministic models and IBM for large populations, but disagreement for small populations. Additionally, we also illustrate priority effects are more (respectively, less) prevalent in IBM for large (respectively, small) populations as dispersal strength changes. Finally, we discuss several ecological implications of our results.

2. The models

2.1. Population-level (deterministic) model

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

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

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 (Case et al., 2005; Godsoe et al., 2015a; Roughgarden, 1979), 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

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