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Research paper

How can modelling tools inform environmental and conservation policies?

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Abstract

Among the important environmental and ecological problems are to determine the distributions of species (e.g. endangered, native and invasive species) across geographical regions and to understand the determinant of species range limits (i.e. the boundaries of the locations in which a species is found). Various studies highlight that abiotic environments (e.g. temperature, climate) and biotic interactions (e.g. competition) can influence species distributions. To investigate this problem, two mathematical models for predicting species distributions have been employed. Such models generally take the form of deterministic systems such as partial-differential equations, in which they aim to understand the interactions between species at the population scale. Thinking of interacting species as finite groups of agents, rather than continuous densities, may alter the structure of the modelling frameworks. This problem can be studied using stochastic individual-based models (IBM). These two models are used to examine the outcomes of species interactions and to understand how these species are distributed in spatially changing environments. As such, comparing and contrasting the observations between the IBM and deterministic models may offer important insights in predicting species range limits and help us to develop robust predictions of species potential distributions in nature.

Keywords: *Partial-differential equations; Stochastic individual-based models; Range limits; Environmental engineering; Conservation policies.*

1. Introduction

In general, ecological processes such as dispersal and growth can be described at the individual level or at the population level scales [1-5]. Previous studies have looked at interacting species from the population-level perspective and modelled them as continuous densities; in this case, species presence-absence can be predicted using deterministic models [3-5]. Alternatively, if the interacting species are represented as collections of discrete individuals and stochastic events (e.g. birth and death) are considered, their growth and dispersal processes can be simulated using stochastic individual-based models (IBM) [5-7].

The stochastic IBMs have been employed in scientific fields to simulate the movement and interactions between discrete agents that represent individual organisms or species [8, 9]. Generally, the interactions between these individuals are local, in which a few agents can interact at a particular time and location [6, 9]. For instance, these agents can be placed along a spatial lattice and they interact with their respective neighbours according to some rules, which are often governed by stochastic processes, such as birth-death process and random walks. The dynamics of individual-based models are often investigated using simulation study, since this modelling framework is composed of huge numbers of discrete agents and numerous variables [9].

A considerable amount of IBM studies focusses on movement of species through space. For example, Johnson et al. [10] explored the models of local movement of individual species and their interactions with complex landscape. Faugeras et al [11] developed a biased random walk model to study the movements of fish population and derived a partial-differential equation (PDE) model which approximates their IBM. Other studies on birds movement [12, 13] discussed the model of migrating birds for overwinter survival. Jongejans and Schippers [14] investigated the IBM of seeds dispersal via wind, which is a crucial mechanism for grassland vegetation. Another important ecological force that often been incorporated in IBM is biotic interactions (i.e. interactions between species) such as competition and predation. In another study, Law et al. [6] studied the IBM of plant species with local movement and competitive interactions using spatial logistic equations. They discovered that the populations can grow to asymptotic densities, which is substantially greater than or less than the carrying capacity of the non-spatial logistic model. Other studies using IBM of coral reef community demonstrated that alternative stable states may exist as a result of interspecific coral competition [15]. Some studies [9, 16] examined the Lotka-Volterra type prey-predator interactions using individual-based approach and they discovered the oscillatory behaviour is possible in this system.

Motivated by the previous deterministic models, we develop a comparable stochastic IBM whereby the interacting species are represented as collections of discrete individual agents; these agents are tracked explicitly over time while undergoing birth-death process or dispersing over adjacent locations. In the next section, we describe the development of our stochastic IBM and its deterministic counterpart. Numerical simulation results will be shown for the stochastic IBM and deterministic model and the results of the two models will be compared. Finally, we discuss several ecological implications of our results, and some of these findings have qualitative implications for conservation biology.

2. The Models

2.1. A Deterministic PDE Model

We consider a multispecies deterministic model by extending the Lotka-Volterra competition equations along environmental gradients, *x*. Specifically, we employ a PDE model for the densities $\mathrm{N_i(x,t)}$ of multiple species (with $i = 1,2,\dots,m$) in a one-dimensional domain [17-20]:

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

where r_i is the intrinsic growth rate of species *i*, K_i is the carrying capacity, D_i is the diffusion coefficient and $\propto_{ij}$ is the competitive effect of species *j* on species *i* (with $\propto_{ii} = 1$). Equation (1) is subjected to the following no-flux boundary conditions:

$$D_i \frac{\partial N_i}{\partial x} = 0 \tag{2}$$

The boundary conditions (2) are used because we assume that the region is closed, and no migration occurs across boundaries. The change in environment is modelled by incorporating a spatial dependence *x* into the carrying capacities K_i i.e. $K_i(x)$ [17-20]. The abiotic environments can be associated with numerous factors such as temperature, moisture and elevation. For instance, the term *x* can be considered as a geographical region, which may vary in climatic conditions and thus may affect the distributions of species. The effects of biotic interactions on range limits may depend on how each species responds to the environmental gradient. To illustrate these effects in a multispecies community, we use a linear environmental gradient in a three-species model ($m = 3$):

$$K_i(x) = m_i x + c_i \tag{3}$$

where $\mathrm{K_i(x)}$ is the carrying capacity of species *i* at spatial location *x*, $\mathrm{m_i}$ is the change in environmental suitability with respect to abiotic component *x* and $\mathrm{c_i}$ is the carrying capacity of species i when *x = 0*.

2.2. A Stochastic IBM

To investigate how the underlying population-level information relates to a smaller individual scale, we develop a stochastic IBM, which was motivated by the deterministic model (1). We assumed that we have a one-dimensional uniform lattice (i.e. a line splits into finitely many sites) and each individual can reproduce, die (due to local competitive interactions) or move to the left or to the right between these sites following an unbiased random walk. The random walk theory gives us the relationship between the probability of an individual moves, v_i, a short distance Δx at each time step Δt in the stochastic IBM, with diffusion coefficient D_i in the deterministic model (1):

$$\mathrm{D_i} = \frac{\mathrm{v_i}\,(\Delta \mathrm{x})^2}{\Delta \mathrm{t}} \tag{4}$$

Now, let us define $n_i(x,t)$ as the number of individuals of species *i* at location *x* and time *t*, where $n_i = N_i \Delta x$ and $n_i \in \{0,1,2,\dots\}$. To model the birth-death process, we define the birth rate B_i and death rate μ_i of this stochastic process, which is motivated by the reaction term of the deterministic model (1). We assume that competition is only local (meaning that μ_i depends on the number of individuals at a particular site, not at neighbouring sites). We also assume that Δt is small such that at most one transition can occur per site and depend on the current state of the population at that site. The possible types of transition are: birth (with probability $B_i \Delta t$); death (with probability $\mu_i \Delta t$); move left or right (with probability $v_i n_i$, in which v_i corresponds to equation (4)). So, if there are *n* sites and *m* species, then there can be *n x m* set of transition rates. At the right boundary i.e. $x_{max} = 1$ (respectively left boundary i.e. $x_{min} = 0$), the individual is unable to move right (respectively left). Thus, we have a 'reflecting barrier', which is analogous to no-flux boundary conditions (2) [4]. Notice that the changes in state will not be actioned until the following time step, in which all sites are simultaneously updated. We constructed the stochastic IBM in this way to keep a close connection to the deterministic model; the deterministic model (1) is the mean-field equation to the stochastic IBM, in the limits when $\Delta x, \Delta t \to 0$ and the population size is sufficiently large.

3. Methodology

Numerical simulations are conducted using MATLAB for the stochastic IBM and deterministic models and the results of the two models are compared in the next sections. For the deterministic model, equation (1) with zero-flux boundary conditions (2) is solved numerically using MATLAB *pdepe* solver. This solver computes the numerical solutions of PDE in one spatial variable *x* and time *t* using the method of lines. In the method of lines, the spatial domain is divided into a mesh with *A + 1* equally spaced nodes x_j = *jh* for *j* = 0,1,...,*A*, where $h = \frac{1}{A}$ is the uniform mesh size. The spatial derivative in equation (1) is replaced by a second central difference approximation. This leads to a system of *3(A + 1)* ordinary-differential equations (ODE), one for the density of each species at a series of equally spaced *x* points. The *pdepe* package then solves the resulting system of ODE by a standard ODE solver, *ode15s* for t = 1000s. We used $h = 2 \times 10^{-3}$ and initial conditions as indicated in each figure section. The results are insensitive to a reduction in grid spacing *h*. We also determined the stability of these steady states. To do this, the time derivative in equation (1) is set to zero and the spatial derivative in equation (1) is replaced by a second central difference approximation, with constant grid spacing *h*. The zero-flux boundary conditions (3) are coded in the equations for the end points using a finite difference approximation. This results in a system of *3(A+1)* non-linear equations, one for the density of each species at a series of uniformly spaced *x* points, x_j = *jh* for *j=0,1,…,A*, where $h = \frac{1}{A}$. This system is solved for steady state using MATLAB *fsolve*. To determine the stability of steady state, the Jacobian matrix is calculated numerically in *fsolve* and then the eigenvalues are computed using *eig* function. The steady state is stable if all eigenvalues have negative real parts. Unless otherwise stated, the parameter values employed in this work are given by Table 1.

Table 1: Parameter Values

Parameter	Parametrisation of the Models	
	Description	Value
r_i	The intrinsic growth rate of species *i*	1
m_1	The change in environmental suitability of species 1 with respect to *x*	100
m_2	The change in environmental suitability of species 2 with respect to *x*	0
m_3	The change in environmental suitability of species 3 with respect to *x*	90
c_1	Carrying capacity of species 1 when *x* = 0	0
c_2	Carrying capacity of species 2 when *x* = 0	400
c_3	Carrying capacity of species 3 when *x* = 0	0
D	Diffusion coefficient	0.001
Δx	Space step	0.1
Δt	Time step	0.0005
v	Probability of moving left or right (calculated using equation (4))	0.00005
$\propto$	Competition coefficient (as indicated in each figure section)	

4. Results and Findings

To illustrate the possible competitive outcomes of the IBM which correspond to the dynamical behaviour of the PDE model, we conducted the simulation studies for PDE and IBM models and, the results of both models are compared. As an example, Figure 1 illustrates the possible outcome of species interactions predicted by the two models when the interspecific competition is relatively weak ($\alpha < 1$).

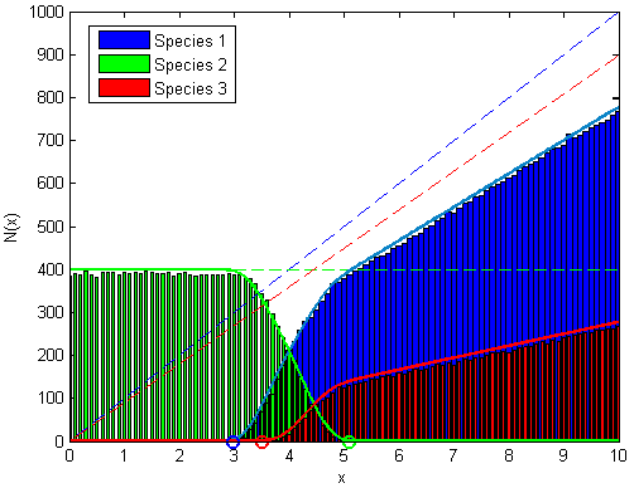
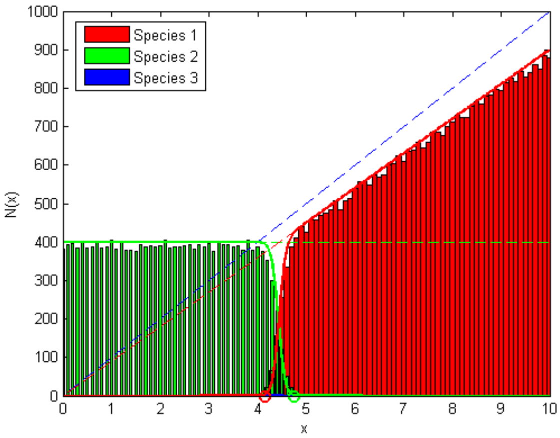
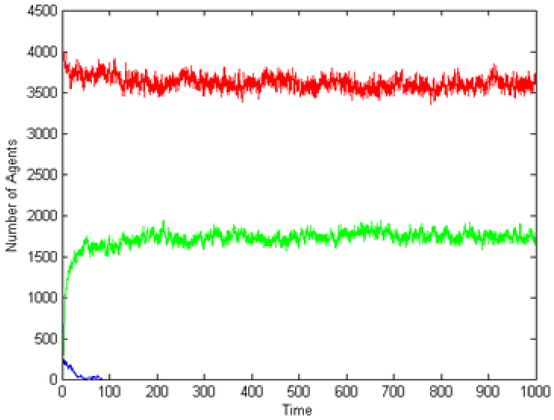


Fig. 1: Solution of the PDE model (solid lines) and 500 averaged realisations of the IBM (bar graphs) at final time T = 1000. Solid lines indicate the steady-state solution of the PDE model (1) with no-flux boundary conditions (2) following linear environmental gradient (3); dotted lines indicate carrying capacity $K_i(x) = m_i x + c_i$; circles show the range limits of species 1, 2 and 3. Bar graphs correspond to the average density of the IBM. Competition coefficient: $\alpha = 0.8$. Initial abundances: $N_1(x) = 0.9K_1(x)$, $N_2(x) = 0.05K_2(x)$, $N_3(x) = 0.05K_3(x)$. Other parameter values as in Table 1. The steady-state solution of the PDE is calculated using MATLAB *pdepe* solver.

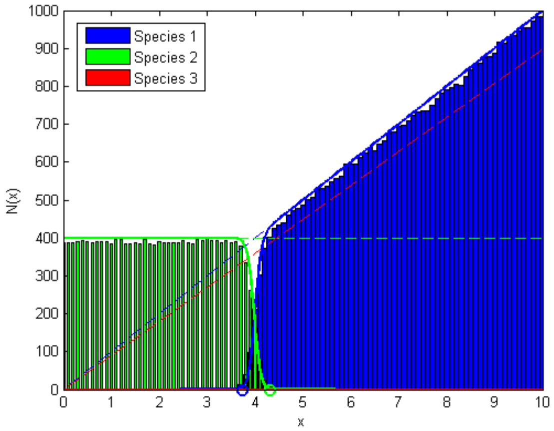
Figure 1 illustrates the average density of the IBM (bar graphs) when $\alpha < 1$, in contrast to the PDE model (solid lines). Note that the vertical axis corresponds to the density of species i.e. the number of individuals across the sites divided by Δx. The average density of the IBM appears to follow closely the steady-state solution of the PDE. The range limits of species (circles) predicted by the stochastic IBM resemble those observed in the PDE model. These range limits divide the spatial domain into several regions. Each one of these regions corresponds to different possible outcomes of the two models as x changes. For instance, species 2 (green) dominates over the left region; and species 1 (blue) and 3 (red) coexist over the right-hand part of spatial domain. The central region corresponds to the zone of coexistence between these three-competing species.



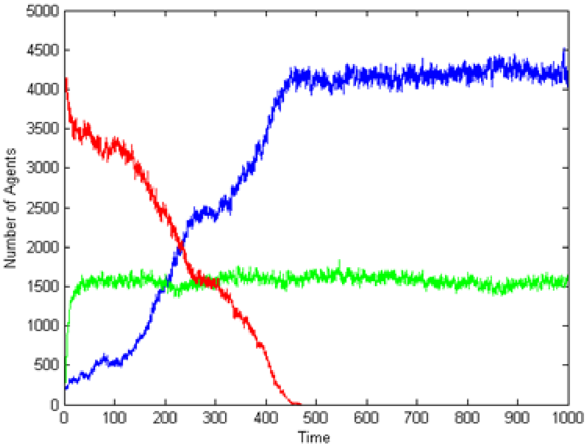
(a) 85 realisations (out of 300 simulations)



(b) Time series plot of 1 selected realisation showing species 3 can persist.



(c) 215 realisations (out of 300 simulations)



(d) Time series plot of 1 selected realisation showing species 1 can persist

Fig. 2: (a)-(c) Solution of the PDE model (solid lines) and of the IBM (bar graphs) at final time T = 1000 when initial abundances favour species 3. Solid lines indicate the steady-state solution of the PDE model (1) with no-flux boundary conditions (2) following linear environmental gradient (3); dotted lines indicate carrying capacity $K_i(x) = m_i x + c_i$; circles show the range limits of species 1, 2 and 3. Bar graphs correspond to the average density of the IBM. (b)-(d) Time series plots of two selected realisations of the IBM. Competition coefficient: $\alpha = 1.2$. Initial abundances: $N_1(x) = 0.05K_1(x)$, $N_2(x) = 0.05K_2(x)$, $N_3(x) = 0.9K_3(x)$. Other parameter values as in Table 1. The steady-state solution of the PDE model is calculated using MATLAB *pdepe* solver.

We also explore the behaviour of the IBM and the corresponding PDE model under linear environmental gradient when $\alpha > 1$. Our observations suggest that the IBM exhibits the alternative stable states behaviour leading to competitive exclusion that depends on initial abundances of species. This can be illustrated by Figure 2 as an example, which depicts the difference between the possible outcomes of the IBM in the alternative stable states case: either species 1 or species 3 persist over the right-hand part of spatial domain. When initial abundances favour species 3, this situation sometime lead to the survival of species 3 and the extinction of species 1 (Figure 2 (a)). Given the initial head start (Figure 2 (b)), species 3 can possibly suppress other competitors over the right-hand side of spatial domain and species 2 can dominate the left region. This is one of the possible outcomes of the IBM when initial abundances favour species 3. However, some stochastic event may tip the system into an alternative basin of attraction [21]; in this stochastic model, the same set of parameter and initial abundances sometime may also result in the extinction of species 3 and thus species 1 can persist (Figure 2 (c)). Even though species 3 initially have an early advantage (Figure 2 (d)), the physiologically similar species i.e. species 1 have the potential to increase their abundances by reproducing more; as opposed to species 3, these species may experience strong intraspecific competition because they are more abundant. Consequently, due to the possibility of strong competition within the same species, the number of individual of species 3 can decrease and in the long run; species 1 can exclude species 3 and dominate over the right side of spatial domain.

5. Conclusion

In this work, we investigate the dynamics of species interactions along environmental gradients using different modelling frameworks. We observe that the deterministic model and stochastic IBM give qualitatively similar predictions on species distributions as the strength of competition changes. The good agreement between the PDE and IBM results seems plausible because in developing the stochastic IBM, we incorporate an unbiased random-walk process (which can be approximated as diffusion term in the PDE model) and, the birth-death process (which correspond to the reaction term in the PDE model). Thus, the competitive outcome predicted by the stochastic IBM resembles those in the PDE model.

Our findings also demonstrate how different ecological forces driving species coexistence and alternative stable states can strongly shape the presence-absence of multiple species. In the absence of biotic interactions, abiotic environments determine the fundamental niches of species. Biotic interactions such as competition eliminate interacting species from some locations and affect their range limits. Dispersal affects species ranges in the presence of biotic and abiotic components. We also observe that multi-species coexistence is possible near the central region, with species diversity peaks at this location. Ecologically, this observation illustrates an example of a mid-domain effect, meaning that more species ranges overlap near the centre of a geographical region [22, 23].This pattern of species diversity has been observed empirically; for instance, different studies of small mammals along elevational gradients observe patterns of mid-domain effect in which species diversity peaks at an intermediate elevation [24, 25].

Alternative stable states are known as priority effects, where species establishment order can determine the presence-absence of species [26, 27]. The initially more abundant species have the potential to predominate and exclude the others [28, 29]. In our studies, we find that initial species abundance is a critical feature in determining the range limits of interacting species. This critical feature could be employed as a bio-control strategy: our result suggests that we could release specified abundances of bio-control agents, and these agents can reduce the competitive advantage of certain species. The bio-control agents may tip the balance between the competitors and may induce the switch between the long-term distributions of species. In practice, it has been observed through different studies [30-32] that initial abundances can affect species presence-absence in biological control strategies, and our finding is consistent with these observations.

From a modelling point of view, our simulation results on the occurrence of stable coexistence and alternative stable states in a multispecies community can be considered as realistic phenomena since these common predictions are given by different modelling frameworks e.g. deterministic PDE and stochastic IBM. By examining a family of related models and trying to obtain similar predictions between these modelling frameworks, we establish that these phenomena are robust, and they are not restricted to specific details and assumptions of the models. Thus, comparing and contrasting the dynamics of different models can help in understanding the generality of ecological results [9], and may offer important insights into the robustness of model-based predictions of species' distributions. With this in mind, we suggest the use of multi-scale modelling approaches to scientists in order to predict the spatial distributions of species across a geographical region.

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