Small-scale spatial structure influences large-scale invasion rates

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Abstract

Local interactions among individual members of a population can generate intricate spatial structure, which can strongly influence population dynamics. The two-way interplay between local interactions and population dynamics is well understood in the relatively simple case where the population occupies a fixed domain with a uniform average density. However, the situation where the average population density is spatially varying is less well understood. This situation includes ecologically important scenarios such as species invasions, range shifts, and moving population fronts. Here, we investigate the dynamics of the spatial stochastic logistic model in a scenario where an initially confined population subsequently

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invades new, previously unoccupied territory. This simple model combines density-independent proliferation with dispersal, and density-dependent mortality via competition with other members of the population. We show that, depending on the spatial scales of dispersal and competition, either a clustered or a regular spatial structure develops over time within the invading population. In the short-range dispersal case, we observe a significant reduction in the invasion speed relative to standard predictions of the mean-field model. We conclude that mean-field models, even when they account for non-local processes such as dispersal and competition, can give misleading predictions for the speed of a moving invasion front.

Keywords: density-dependence; dispersal; mean-field model; plant populations; species range shifts; stochastic model.

Introduction

Spatial structure can affect population dynamics. Common examples of spatial structure are clustering, where individuals tend to occur in tightly packed groups, and regular structure, where individuals tend to be evenly spaced from one another (Pacala and Silander Jr, 1985; Mahdi and Law, 1987; Purves and Law, 2002). Spatial structure typically arises as a result of individual-level processes and interactions that occur locally in space, such as competition (Yokozawa et al., 1999; Adams et al., 2013), dispersal (Lewis and Pacala, 2000), adhesion (Johnston et al., 2013) or crowding (Binny et al., 2016a), Despite being local in origin, spatial structure can have significant large-scale effects on population size, and even determine whether the population survives or dies (Law et al., 2003). Mean-field models neglect correlations among individual locations and assume individuals interact with one another in proportion to their average densities. Hence, mean-field models cannot account for the effects of spatial structure.

Most mathematical studies that incorporate spatial structure in a lattice-free setting have focused on the relatively simple case where the initial condition is a homogeneous spatial Poisson process, and the ensemble average population density at any given time is independent of location. (e.g. Bolker and Pacala, 1999; Dieckmann et al., 2000; Murrell and

Law, 2003; Murrell, 2005; Binny et al., 2016b). This does not preclude the development of spatial structure over time. For example, individuals may become clustered and so, in any given realisation of the process, the density will be higher in some regions than others. However, the locations of the clusters are random and, when averaged over multiple realisations, the density is spatially uniform. We refer to this as the *translationally invariant* case.

The spatial stochastic logistic model (Bolker and Pacala, 1997; Law et al., 2003) is a spatially explicit, individual-based model of dispersal and competition that is translationally invariant. In this model, individuals undergo density-independent proliferation accompanied by dispersal, and density-dependent mortality, with the mortality rate being an increasing function of the number and the proximity of individuals within the local neighbourhood. The mean-field equation for the spatial stochastic logistic model is the logistic growth differential equation (Law et al., 2003). However, depending on the spatial scales of dispersal and competition, the stochastic model can produce different population dynamics to the mean-field equation, in both its transient and its long-term phase. An improvement on the mean-field model can be obtained using spatial moment dynamics (Dieckmann and Law, 2000; Plank and Law, 2015) to account for the pair density function (second spatial moment) as well as the average density (first spatial moment). Law et al. (2003) used this approach to show that, when there is a regular spatial structure, the population grows to a higher density than predicted by the mean-field equation. When there is a clustered structure, the population eventually asymptotes to a lower density than predicted by the mean-field equation, or can even die out altogether (Law et al., 2003). Translationally invariant models such as these can investigate the effect of spatial structure on population density, but cannot describe populations where the occupied region changes over time. These models are therefore not suitable for modelling ecological scenarios such as invasions, range shifts, or moving population fronts.

Some studies have investigated the more complex *translationally dependent* case, where the initial occupancy depends on position. Lewis and Pacala (2000) focused on a model of invasion with density-independent proliferation and long-range dispersal, and used a spatial moments approach to derive results for the dependence of invasion speed on

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the dispersal kernel. Lewis (2000) generalised this model to show that local density-dependent proliferation rate reduced the invasion speed in one spatial dimension, relative to mean-field predictions. However, this model only applied to a situation where density-dependence affects proliferation, and operates over a short spatial scale. Simpson and Baker (2011) investigated the dynamics of moving fronts and the invasion speed in a lattice-based model. However, this limits the types of interactions and spatial structure that the model can support (Plank and Simpson, 2012). Omelyan and Kozitsky (2019) derived a spatial moments approximation for the translationally dependent version of the spatial stochastic logistic model in one dimension. They showed that the results differed significantly from the mean-field model, which neglects correlations among individual locations. However, they did not test the predictions of their spatial moment equations against individual-based simulations, which serve as 'ground truth' for the approximation. It is therefore unknown how well the spatial moment dynamics system approximates the underlying stochastic process in practice.

In this study, we investigate the dynamics of the spatial stochastic logistic model in the translationally dependent case. Similarly to Omelyan and Kozitsky (2019), we focus on the case where the population is initially confined to a subregion of the domain and subsequently invades via dispersal of individuals into previously unoccupied regions. However, unlike Omelyan and Kozitsky (2019), we carry out individual-based simulations of the translationally dependent spatial stochastic logistic model and we work in a two-dimensional domain. We systematically investigate scenarios with different spatial scales for competition and dispersal, and compare them to predictions of the mean-field model. This allows us to quantify the departure of the stochastic process from mean-field dynamics in terms of the spatial structure. To provide insight into how spatial structure affects population spreading, we test how the speed of the invasion and the population density behind the invasion front depends on the spatial scales of competition and dispersal by quantifying the spatial structure of the population. We interpret these results in light of what is already known about the translationally invariant form of the spatial stochastic logistic model.

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Translationally dependent spatial stochastic logistic model

Individual-based model

We consider a population of $N(t)$ individuals with locations $z_i(t) = (x_i(t), y_i(t)) \in \Omega \subseteq \mathbb{R}^2$ ($i = 1, \ldots, N(t)$). The spatial stochastic logistic model consists of two individual-level mechanisms: density-independent proliferation accompanied by dispersal; and density-dependent mortality modelling local competition. Specifically, in a short time interval δt, each of the $N(t)$ agents has a probability $\lambda \delta t + O(\delta t^2)$ of proliferating, independent of all other agents. Offspring are dispersed to a location at a displacement ξ from the parent, where ξ is a random variable from a bivariate probability distribution with density function $w_d(\xi)$, referred to as the dispersal kernel. In addition, agent i has a probability $\mu_i(t)\delta t + O(\delta t^2)$ of dying in time interval δt. The mortality rate for individual i at time t consists of a constant density-independent term μ_0 and a contribution from neighbouring individuals μ_c, weighted by a competition kernel $w_c(\xi)$:

$$\mu_i(t) = \mu_0 + \mu_c \sum_{j \neq i} w_c\left(z_j(t) - z_i(t)\right). \tag{1}$$

The dispersal and competition kernels are assumed to be isotropic and symmetric about the origin and to integrate to 1 over Ω. We consider a rectangular domain $\Omega = [-L_x, L_x] \times [0, L_y]$ with periodic boundaries, such that dispersal and competition are wrapped across opposing boundaries. This is equivalent to the spatial stochastic logistic model studied by Bolker and Pacala (1997) and Law et al. (2003) for a translationally invariant population. To investigate the dynamics of a translationally dependent population, we consider an initial condition where N_0 agents are distributed independently and uniformly at random in the region $-x_0 \leq x \leq x_0$, where $x_0 < L_x$.

Since the population is translationally invariant in the vertical direction, we calculate the

average agent density $\hat{u}(x,t)$ in thin vertical strips of width δx:

$$\hat{u}(x,t) = \frac{1}{\delta x L_y} \sum_{i=1}^{N(t)} \mathbb{I}\left(x - \delta x/2 \leq x_i(t) < x + \delta x/2\right), \tag{2}$$

where $\mathbb{I}$ is an indicator function.

To quantify the spatial structure of the population, we compute the pair correlation function at time t defined by:

$$g(r,t) = \frac{\sum_{i=1}^{N(t)} \sum_{j \neq i} I\left(r - \delta r/2 \leq |z_i(t) - z_j(t)| < r + \delta r/2\right)}{2r\delta r \sum_{i=1}^{N(t)} \int_0^\pi \hat{u}\left(x_i(t) + r\cos(\theta), t\right) d\theta}. \tag{3}$$

This corresponds to the ratio of the number of pairs a distance r apart to the expected number of pairs a distance r apart, in a population with density $\hat{u}(x,t)$ that is in a state of complete spatial randomness. The integral in Eq. (3) is approximated numerically by discretising the integration variable θ and using linear interpolation for the required values of $\hat{u}(x,t)$. In principle, the nature and strength of spatial structure could vary across the spatial domain Ω. This can be allowed for calculating different pair correlation functions in different regions $R \subset \Omega$ by restricting the index i to individuals that are in the region R. However, in practice we find that the pair correlation function is very similar throughout Ω, so for simplicity we calculate a single pair correlation function across the whole of the spatial domain.

We measure the extent of the invasion at time t by calculating the mean squared displacement, defined as the average value of $x_i(t)^2$ across all $N(t)$ agents. We also measure the location of the invasion front at time t as the location of the agent with the 10th largest value of $|x_i(t)|$. We use the 10th largest value as opposed to the largest value to reduce noise caused by outlying agents, but the qualitative results are not sensitive to this choice.

We perform M independently initialised realisations of the individual-based model (IBM) and average $\hat{u}(x,t)$ and $g(r,t)$ over the M realisations. The dispersal and competition

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Parameter	Value
Proliferation rate	$\lambda = 1$
Intrinsic mortality rate	$\mu_0 = 0.01$
Neighbour-dependent mortality rate	$\mu_c = 0.1$
Dispersal kernel standard deviation	σ_d (variable)
Competition kernel standard deviation	σ_c (variable)
Domain size	$L_x = 20,\ L_y = 10$
Width of the initially occupied region	$x_0 = 1$
Initial population size	$N_0 = 20$
Threshold density for invasion front	$u_{\text{thresh}} = 1$

Table 1: Model parameter values.

kernels are set to be bivariate Heaviside functions:

$$w_{[c,d]}(\xi) = \frac{1}{4\sigma_{[c,d]}^2} \begin{cases} 1, & |\xi_x|, |\xi_y| \leq \sigma_{[c,d]} \\ 0, & \text{otherwise} \end{cases}$$

Parameter values are shown in Table 1.

Mean-field dynamics

The mean-field equation for the translationally dependent spatial stochastic logistic model is:

$$\frac{\partial u(x,t)}{\partial t} = \lambda \int \tilde{w}_d(x - y)u(y,t)dy - \left(\mu_0 + \mu_c \int \tilde{w}_c(x - y)u(y,t)dy \right) u(x,t), \quad (4)$$

where $x \in [-L_x, L_x]$. This formulation makes use of the translational invariance in the vertical direction to write the average population density $u(x,t)$ in terms of the horizontal coordinate x only, where $\tilde{w}_d(x)$ and $\tilde{w}_c(x)$ are the marginal distributions over x of the dispersal and competition kernels $w_d(x,y)$ and $w_c(x,y)$ respectively. Eq. (4) neglects correlations in the locations of pairs of agents and assumes that the system is locally well mixed. Formally, this corresponds to approximating the joint density of pairs of agents at x and y in the second integral in Eq. (4) by the product of the average agent densities $u(x,t)$ and $u(y,t)$.

The population carrying capacity K (i.e. equilibrium average density in a uniformly

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occupied domain) can be found from Eq. (4). This corresponds to a solution u to Eq. (4) that is independent of both x and t, which is uniquely given by $K = (\lambda - \mu_0)/(\mu_c)$. We can also calculate the total population size $N(t)$ and mean squared displacement $MSD(t)$ at time t under the mean-field equation via:

$$N(t) = \int u(x,t)dx, \qquad MSD(t) = \frac{\int x^2 u(x,t)dx}{N(t)}.$$

The location of the invasion front at time t is defined to be the smallest value of $|x|$ for which $u(x,t) > u_{\text{thresh}}$.

The integro-differential equation (4) is solved by discretising x using a mesh spacing $\delta x = 0.01$ and solving the resulting system of ordinary differential equations using Matlab's *ode45* routine. To implement periodic boundaries, we set $\tilde{w}_d$ and $\tilde{w}_c$ to be periodic extensions of the dispersal kernel and competition kernel respectively on $x \in [-L_x, L_x]$. This means that population members located near the boundary at $x = -L_x$ are interacting with population members located near the boundary at $x = L_x$ and vice versa.

Results

First, we test the behaviour of the translationally dependent spatial stochastic logistic model when both dispersal and competition operate over a long range ($\sigma_d = \sigma_c = 5$, Fig. 1). In this case, agents compete weakly with neighbours over a relatively large neighbourhood (encompassing the full height L_y of the domain), and the correlation between locations of parent and offspring is weak. As a consequence, spatial structure is close to random (pair correlation function close to 1, Fig. 1c) and the IBM results are close to the predictions of the mean-field equation (Fig. 1d-e).

We now focus on the deviation from mean-field dynamics as the range for dispersal σ_d and/or competition σ_c are reduced. In all cases, the long-term statistical equilibrium of the model is a spatially structured population with uniform average agent density, consistent with the translationally invariant version of the spatial stochastic logistic model (Law et al., 2003). Here, we focus on the population dynamics in the transient phase
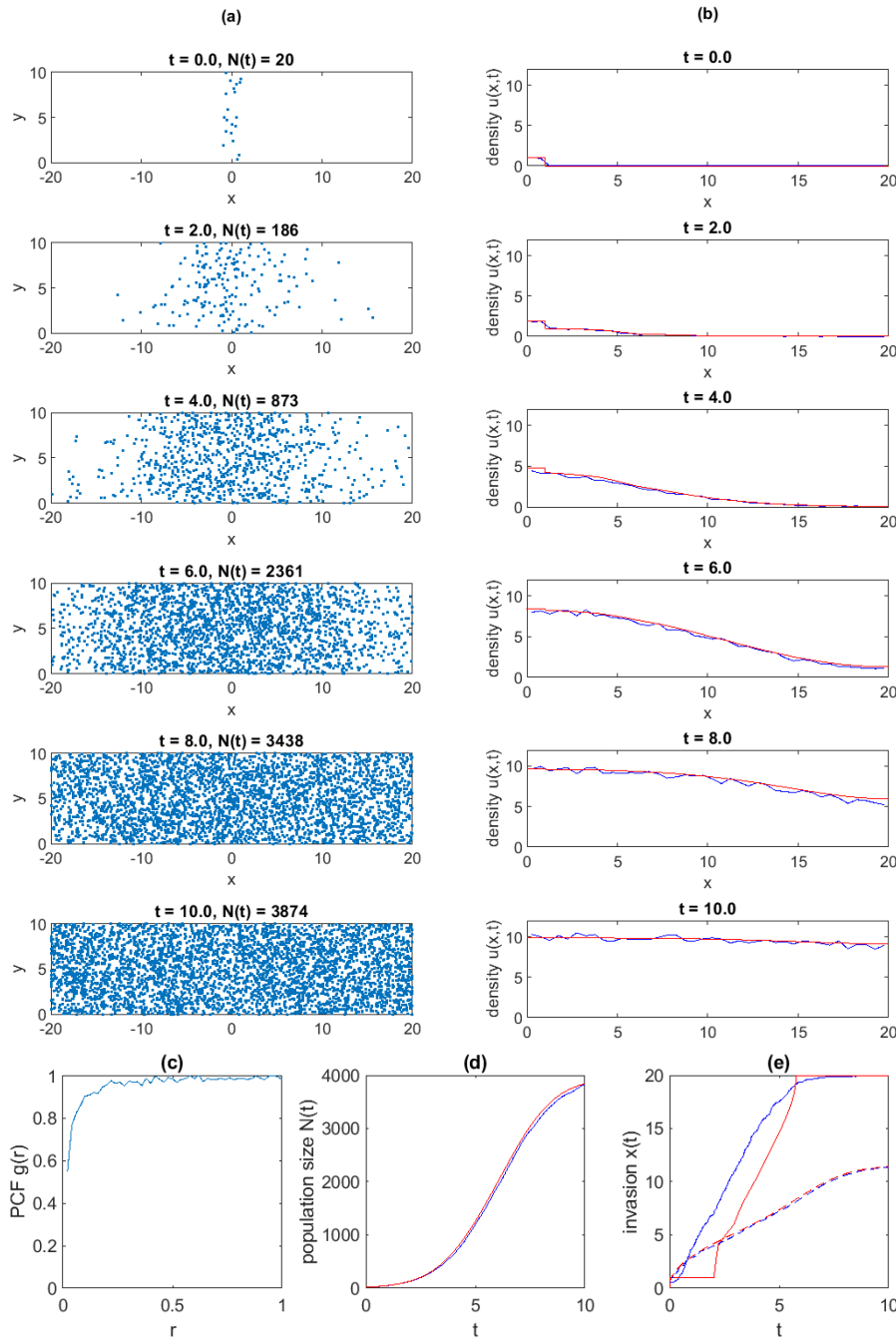
Figure 1: IBM and mean-field results for long-range competition and long-range dispersal ($\sigma_c = 5, \sigma_d = 5$): (a) snapshots of a single realisation of the IBM; (b) average agent density in the IBM (blue) and mean-field equation (red) at $t = 0, 2, 4, 6, 8, 10$. (c) pair-correlation function (PCF) at $t = 10$; (d) time series of the average population size in the IBM (blue) and mean-field equation (red); (e) time series of the invasion size measured by the location of the invasion front (solid) and the root mean squared displacement (dashed) in the IBM (blue) and mean-field equation (red). IBM results in (b-e) are averaged across $M = 10$ independent realisations, each initialised with N_0 agents randomly placed in the region $|x| < x_0$.
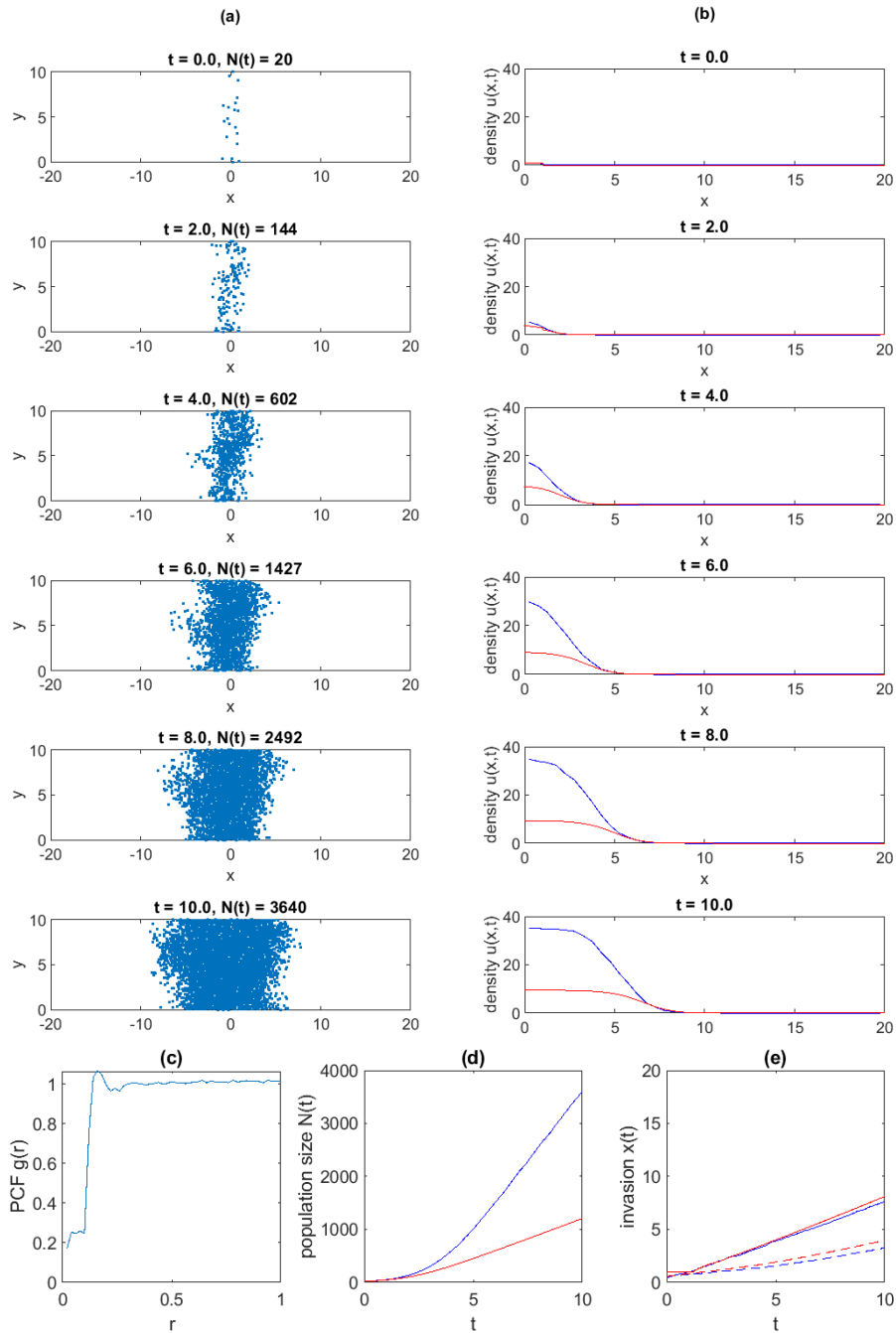
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Figure 2: IBM and mean-field results for short-range competition and long-range dispersal ($\sigma_c = 0.1$, $\sigma_d = 1$): (a) snapshots of a single realisation of the IBM; (b) average agent density in the IBM (blue) and mean-field equation (red) at $t = 0, 2, 4, 6, 8, 10$. (c) pair-correlation function (PCF) at $t = 10$; (d) time series of the average population size in the IBM (blue) and mean-field equation (red); (e) time series of the invasion size measured by the location of the invasion front (solid) and the root mean squared displacement (dashed) in the IBM (blue) and mean-field equation (red). IBM results in (b-e) are averaged across $M = 10$ independent realisations, each initialised with N_0 agents randomly placed in the region $|x| < x_0$.

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corresponding to the invasion of the initially unoccupied region.

When competition is short-range and dispersal is long-range ($\sigma_c = 0.1$, $\sigma_d = 1$, Figure 2), a regular spatial structure develops, indicated by values of the pair correlation function less than 1 for pairs less than distance 0.1 apart (Fig. 2c). These results are consistent with the translationally invariant spatial stochastic logistic model: strong competition in small neighbourhoods makes the probability of more than one agent persisting in such a neighbourhood very small. Conversely, offspring have a high probability of escaping the competitive influence of their parent and finding an empty neighbourhood. The population in the region behind the invasion front reaches a substantially higher density then predicted by the mean-field equation (Fig. 2b,d) because a typical agent experiences a lower-density neighbourhood, and therefore a lower mortality rate, than in the mean-field model. However, the speed of the invasion, as measured by the root mean squared displacement or by the location of the invasion front, is well predicted by the mean-field equation (Fig. 2e).

When competition is long-range and dispersal is short-range ($\sigma_c = 1$, $\sigma_d = 0.1$, Fig. 3), a strongly clustered spatial structure develops. This can be seen in individual realisations of the IBM (Fig. 3a) and values of pair correlation function greater than 1 for pairs less than distance $r = 0.5$ apart (Figure 3a). The pair correlation function drops below 1 for $r > 0.5$, indicating that the clusters are not randomly distributed, but are spaced regularly apart from one another. This is a consequence of competition making it difficult for any individual to survive in the neighbourhood surrounding an established cluster. These results are consistent with the translationally invariant version of the spatial stochastic logistic model. The cause of the clustering is the short dispersal distances leading to an accumulation of offspring around a common ancestor. This cluster eventually reaches a critical size where proliferation by individuals in the cluster is balanced by the elevated mortality rates due to competition. Because competition operates over a relatively long range, all individuals in a cluster tend to compete with all other individuals in the same cluster and hence experience similar mortality rates. Short-range dispersal makes it very difficult for new offspring to escape the cluster.

In the very early stages on the invasion up to around $t = 20$, the population size and
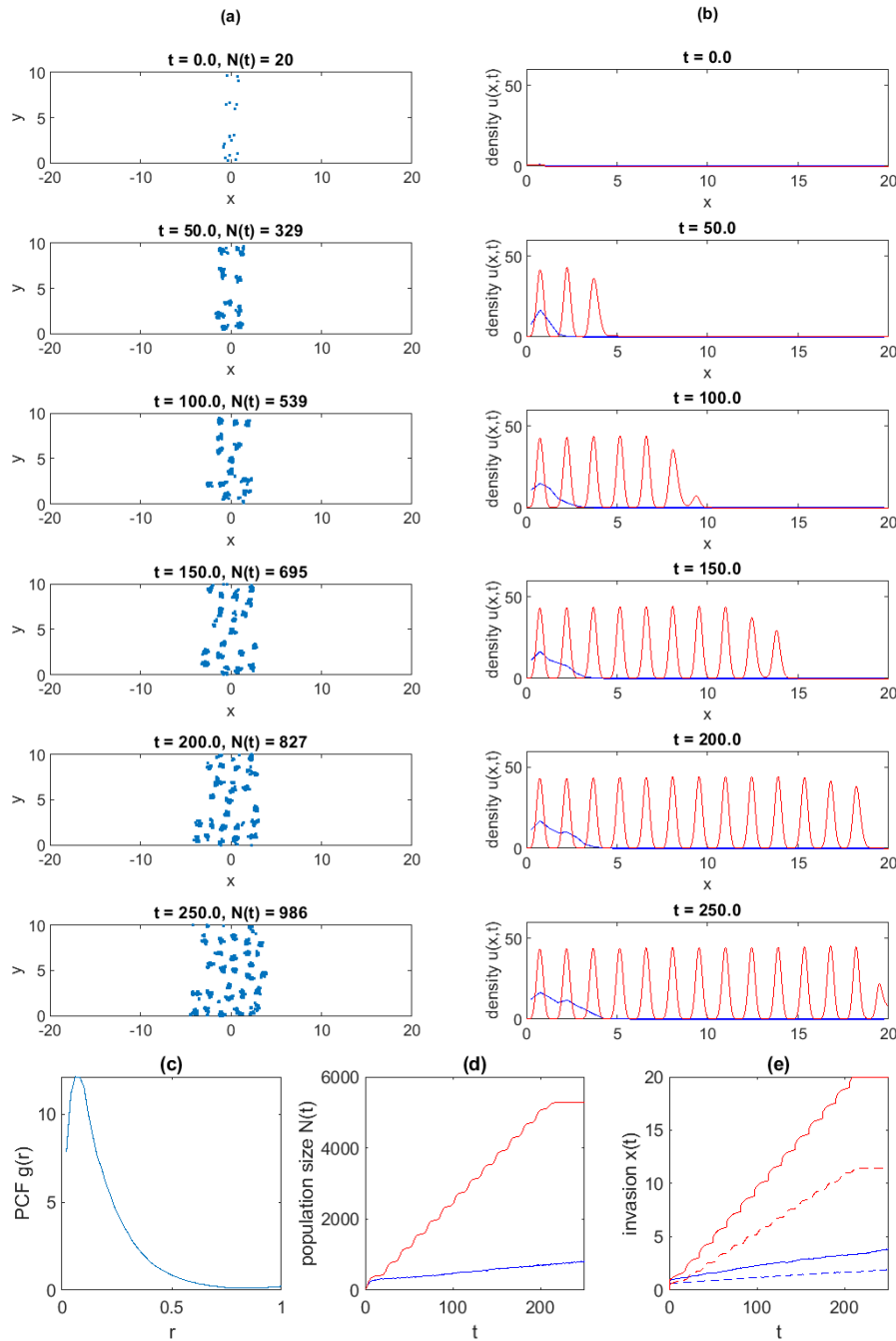
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Figure 3: IBM and mean-field results for long-range competition and short-range dispersal ($\sigma_c = 1$, $\sigma_d = 0.1$): (a) snapshots of a single realisation of the IBM; (b) average agent density in the IBM (blue) and mean-field equation (red) at $t = 0, 50, 100, 150, 200, 250$. (c) pair-correlation function (PCF) at $t = 250$; (d) time series of the average population size in the IBM (blue) and mean-field equation (red); (e) time series of the invasion size measured by the location of the invasion front (solid) and the root mean squared displacement (dashed) in the IBM (blue) and mean-field equation (red). IBM results in (b-e) are averaged across $M = 10$ independent realisations, each initialised with N_0 agents randomly placed in the region $|x| < x_0$.

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invasion speed are reasonably well approximated by the mean-field equation (Fig. 3d,e). During this phase of the invasion, the population is increasing in density, but is mostly restricted to the initially occupied region, $|x| \leq x_0$. At around $t = 20$, the mean-field model establishes a newly occupied region and undergoes a second wave of rapid population growth. This pattern repeats periodically with the mean-field population alternating between phases of growth (increasing density in situ) and expansion (occupying new areas). In contrast, the clustered structure in the IBM makes it very difficult for a daughter agent to escape the influence of its ancestral cluster and establish a new cluster. Only occasionally can a new cluster establish and this means that the invasion proceeds very slowly relative to mean-field.

When both competition and dispersal and short-range ($\sigma_c = \sigma_d = 0.1$, Fig. 4), the spatial structure is also clustered, although not as strongly as when competition acts over a longer range (Fig. 3). Short-range dispersal means that individuals with a common ancestor have strongly correlated locations, but tend to be thinned out by short-range competition. Although the clustering is weaker than in Fig. 3, it still severely limits the ability of the population to invade, with population growth and the invasion speed much lower than predicted by the mean-field equation (Fig. 4d-e).

Discussion

The effect of spatial structure on average population density has been investigated previously (Law et al., 2003; Binny et al., 2016b). However, in some situations, understanding and predicting how spatial structure affects a biological invasion is more relevant than predictions of population density. Examples include the invasion of a pest species (Sprague et al., 2019), species range shifts due to climate change (Godsoe et al., 2014; Hurford et al., 2019), wound healing where cells migrate to fill injured tissue (Maini et al., 2004), or invasion of cancer cells into healthy tissue.

We have investigated the dynamics of translationally dependent populations under the spatial stochastic logistic model. This is a simple individual-based model (IBM) that consists of two mechanisms: density-independent proliferation accompanied by dispersal;
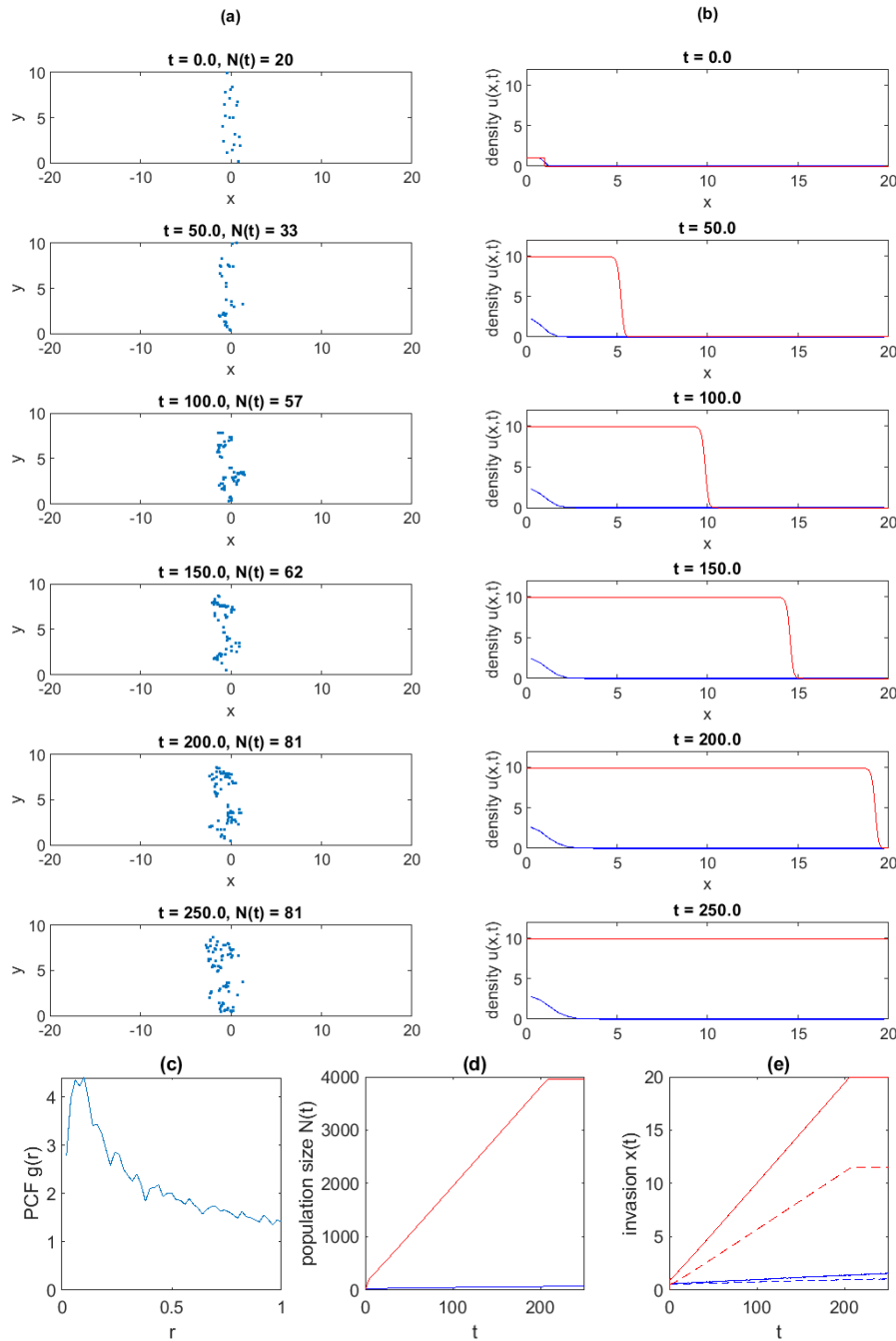
Figure 4: IBM and mean-field results for short-range competition and short-range dispersal ($\sigma_c = 0.1$, $\sigma_d = 0.1$): (a) snapshots of a single realisation of the IBM; (b) average agent density in the IBM (blue) and mean-field equation (red) at $t = 0, 50, 100, 150, 200, 250$. (c) pair-correlation function (PCF) at $t = 250$; (d) time series of the average population size in the IBM (blue) and mean-field equation (red); (e) time series of the invasion size measured by the location of the invasion front (solid) and the root mean squared displacement (dashed) in the IBM (blue) and mean-field equation (red). IBM results in (b-e) are averaged across $M = 50$ independent realisations, each initialised with N_0 agents randomly placed in the region $|x| < x_0$.

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and density-dependent mortality as a result of local competition (Bolker and Pacala, 1997; Law et al., 2003). Our results have revealed that spatial structure can affect invasion speed and population density in different ways. In the long-range competition, short-range dispersal regime, the clustered spatial structure reduces both population density and invasion speed. The spatial structure in the occupied region rapidly reaches a strongly clustered state. This strong localised clustering makes it difficult for offspring to escape the competitive influence of their cluster and this is the limiting factor both for the effective carrying capacity and the speed at which the invasion front can advance. In the short-range competition, long-range dispersal regime, a regular spatial structure develops. This allows the population to grow to higher densities than predicted by the mean-field, as previous studies of the translationally invariant form of the model have shown. However, the speed of the invasion remains close to the mean-field prediction.

In all situations investigated, the IBM population invades at a similar or slower rate than the standard mean-field, suggesting that the mean-field equation provides an upper bound for the true invasion speed. The main factor that limits the invasion is the dispersal distance. Populations with short-range dispersal tend to invade more slowly, relative to mean-field predictions, because it is difficult for daughter agents to escape from the competitive influence of their ancestral cluster.

The scenarios we have tested are similar to those investigated by Omelyan and Kozitsky (2019), who developed spatial moment dynamics approximation for the translationally dependent spatial stochastic logistic model in one spatial dimension. However, the solutions of Omelyan and Kozitsky (2019), particularly the speed of the invasion front, are yet to be tested against IBM simulations. Our individual-based simulations exhibit similar spatial structure to that predicted by Omelyan and Kozitsky (2019), i.e. clustered in the short-range dispersal regime and regular in the short-range competition regime. However, the spatial moment dynamics system of Omelyan and Kozitsky (2019) predicted that, in the short-range dispersal regime, the invasion speed would be similar to that of the mean-field equation and the population size would be larger. In contrast, our results for this case show that both the invasion speed and the population size in the IBM are much lower than mean-field. It is possible that differences between our results and

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those of Omelyan and Kozitsky (2019) are due to differences between one-dimensional and two-dimensional versions of the model, or the impact of approximations inherent in the analysis based upon a moment closure approximation (Murrell et al., 2004).

We have focused on the spatial stochastic logistic model (Bolker and Pacala, 1997; Law et al., 2003), which is the simplest IBM that is capable of generating non-trivial spatial structure. There are other individual-level mechanisms that generate and/or are influenced by spatial structure. Examples include density-dependent proliferation (Lewis, 2000), movement (Dieckmann and Law, 2000; Murrell and Law, 2000), directional bias (Binny et al., 2015), and interspecific interactions (Bolker and Pacala, 1999; Murrell and Law, 2003). The interplay between these mechanisms and spatial structure has been investigated for translationally invariant populations, i.e. when the average density is spatially uniform (Binny et al., 2016b; Surendran et al., 2018; Binny et al., 2019). Extending the analysis of these mechanisms to a translationally dependent population will be an objective of future work.

Acknowledgements

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