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Competition between fast- and slow-diffusing species in non-homogeneous environments



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HIGHLIGHTS

- We consider competition between a fast- and a slow-diffusing species.
- We study which ecological forces favor either of the two species.
- We interpret the results in terms of an "effective" selective advantage.

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ABSTRACT

We study an individual-based model in which two spatially distributed species, characterized by different diffusivities, compete for resources. We consider three different ecological settings. In the first, diffusing faster has a cost in terms of reproduction rate. In the second case, resources are not uniformly distributed in space. In the third case, the two species are transported by a fluid flow. In all these cases, at varying the parameters, we observe a transition from a regime in which diffusing faster confers an effective selective advantage to one in which it constitutes a disadvantage. We analytically estimate the magnitude of this advantage (or disadvantage) and test it by measuring fixation probabilities in simulations of the individual-based model. Our results provide a framework to quantify evolutionary pressure for increased or decreased dispersal in a given environment.

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1. Introduction

Biological species have evolved complex mechanisms to move in space. Examples range from bacterial movement by means of flagella to the capacity of swimming and flying of higher organisms. Rationalizing the evolutionary significance of movement is not an easy task, as the need to move in space can be determined by several needs (Dieckmann et al., 1999), such as the search for resources, the attempt of escaping predation or competition by conspecific, and the search for mates. On the downside, motility has a metabolic cost, which becomes particularly relevant for microorganisms swimming at low Reynolds number (Purcell, 1977). Moreover, in some circumstances, an increased motility can lead to an increased predation risk, so that a less conspicuous movement strategy can be advantageous (Visser et al., 2009; Bianco et al., 2014). Finally, in the absence of chemotaxis or environmental cues, a strongly motile species can easily abandon a patch full of

resources. For sessile species, similar tradeoffs apply to seed-dispersal strategies (Hamilton and May, 1977; Comins et al., 1980).

The combined presence of these contrasting effects implies that, in a given ecological setting, it is often difficult to determine whether evolutionary pressure tends to increase or decrease species motility. It is therefore not surprising that, on the modeling side, there exists a fairly vast literature, where different models often reach contrasting conclusions. For example, an analysis by Dockery et al. (1998), based on deterministic reaction-diffusion equations, concludes that it is always advantageous to adopt a less diffusive strategy. By means of a similar argument, Hastings (1983) concluded that, in a time-independent environment, evolutionary stable strategies do not involve dispersal. However, results from stochastic individual-based models (Kessler and Sander, 2009; Waddell et al., 2010; Lin et al., 2014; Pigolotti and Benzi, 2014; Novak, 2014; Lin et al., 2015) show that diffusing faster can indeed be advantageous. Also in the context of seed dispersal strategies, the classic analysis by Hamilton and May (1977) shows that a certain degree of dispersal is beneficial also in spatially homogeneous environments, see also Comins et al. (1980).

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In this paper, we show that an “effective” selective advantage (or disadvantage) can be associated to a higher diffusivity in different ecological settings. The effective selective advantage can be used to explicitly quantify whether evolutionary pressure promotes or disfavor an increased diffusivity. To this aim, we study a general individual-based model in which two different species, or alleles, compete stochastically in space. The model is similar in spirit to Kimura's stepping stone model (Kimura and Weiss, 1964), except that we consider a continuous space rather than a discrete array of island. Individual belonging to the two species diffuse in space with different diffusivities. Reproduction rates can depend on space and on the species. As the dynamics of the model is stochastic, the fixation of one of the two species is a random event. We study which ecological conditions lead to a bias in the fixation probability towards either the fast or the slow species and analytically quantify the selective advantage causing this bias.

In particular, we consider three different settings, which are representative of common ecological tradeoffs. In the first, the environment is spatially homogeneous, but the fastest species reproduces at a slower rate due to the cost of mobility. This simple case is useful to introduce the basic concepts and in particular to quantify the selective advantage for fast diffusing species due to demographic stochasticity. In the second setting, the two species reproduce at equal rate but the environment is spatially non-homogeneous. In the third case, reproduction rates are equal, the environment is non-homogeneous, and the two species are transported by a compressible velocity field. This latter case can be seen as an idealized example of competition in a marine environment. In all three cases, we find that, depending on parameters, diffusing faster can be either advantageous or disadvantageous, depending on trade-offs between different ecological forces that we explicitly quantify. We conclude by discussing our results in the light of existing literature.

2. Methods

2.1. Model

We consider an individual-based model in which two species (or alleles) A and B compete with each other (Pigolotti et al., 2012, 2013). Individuals of the two species diffuse in a one-dimensional space with different diffusivities $D + \delta D$ and D respectively, modeling different spatial motilities. Without loss of generality, we consider the case in which species A diffuses faster, $\delta D > 0$. Species A and B reproduce stochastically at rates $\mu(x)(1+s)$ and $\mu(x)$ respectively, where $\mu(x)$ represents the density of resources at spatial coordinate x and s is the reproductive advantage (if positive) for the fastest species. The death rates of species A and B depend on the local density of individuals. In Section 3.3, we also consider a case in which the species are transported by a velocity field $v(x)$, for example representing aquatic currents for marine organisms. Further details on the implementation of the individual-based model are discussed in Appendix A.

An example of simulation of the model is shown in Fig. 1, where the two species compete for a localized patch of resources. Simulations are run until fixation, i.e. the time at which either species A or B goes extinct. We anticipate that all parameters of the model, including the size of the total population size N as in the case of the figure, can be responsible for biasing fixation towards the fast or the slow diffusing species. The macroscopic dynamics can be analyzed by deriving stochastic evolution equations for the concentrations $c_A(x, t)$ and $c_B(x, t)$ of the two species (Pigolotti et

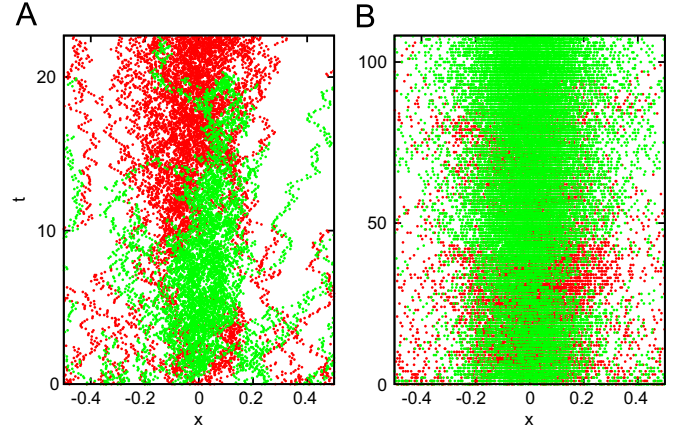


Fig. 1. Examples of the dynamics of the individual-based model. In both panels, $\mu(x)$ is a Gaussian distribution with average zero and variance $\sigma = 0.1$. The red species is the fastest: in both panels, $\delta D/D = 0.2$ and $D = 10^{-3}$. The two species are reproductively neutral, $s = 0$ and are initially present at the same density. The total number density is (A) $N = 50$ and (B) $N = 300$. By performing several realizations of the two simulations, we find that the fixation probability of the fastest species in (A) is $P_{fix} \approx 0.62$ and in (B) is $P_{fix} \approx 0.57$. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this paper.)

al., 2012, 2013), that read

$$\begin{aligned} \partial_t c_A &= \overbrace{-\nabla[v(x)c_A]}^{\text{Advection}} + \overbrace{(1+s)\mu(x)c_A}^{\text{Growth}} - \overbrace{c_A(c_A+c_B)}^{\text{Competition}} + \overbrace{(D+\delta D)\nabla^2 c_A}^{\text{Diffusion}} + \overbrace{\sigma_A \xi_B(x, t)}^{\text{Fluctuations}} \\ \partial_t c_B &= -\nabla[v(x)c_B] + \mu(x)c_B - c_B(c_A+c_B) + D\nabla^2 c_B + \sigma_B \xi_B(x, t) \end{aligned} \quad (1)$$

where $\xi_A(x, t)$, $\xi_B(x, t)$ are Gaussian, independent, delta-correlated noise sources representing demographic stochasticity. The noise amplitudes are $\sigma_A^2 = c_A[\mu(x) + c_A + c_B]/N$ and similarly for c_B . The intraspecific and interspecific competition coefficients in Eq. (1) are set to one by an appropriate choice of the density-dependent death rates and the interaction length in the individual-based model, see Pigolotti et al. (2012, 2013) and Appendix A for details.

The dynamics embodied in Eq. (1) is characterized by a very rich phenomenology (Pigolotti et al., 2013). In this broad framework, we focus on the specific problem of understanding when having a larger diffusivity $\delta D > 0$ confers a selective advantage or disadvantage to species A . We shall study this problem in different settings, where different terms in Eq. (1) dominate. A possible way to analytically study the problem is the following. Consider Eq. (1) and change variables to the total concentration $c_T(x, t) = c_A + c_B$ and the relative fraction of species A , $f(x, t) = c_A/c_T$. We begin by writing the equation for c_T . We always consider cases in which the difference in growth rate and diffusivities are both small, $s \ll 1$ and $\delta D/D \ll 1$. Under these approximations, c_T evolves according to a closed equation:

$$\partial_t c_T = -\nabla[v(x)c_T] + \mu(x)c_T - c_T^2 + D\nabla^2 c_T + \delta D\nabla^2 c_A + \sqrt{\sigma_A^2 + \sigma_B^2} \xi. \quad (2)$$

When the diffusion length scale is much smaller than the typical length scale of the gradient of $\mu(x)$ (in other words, $D \ll 1$) and the velocity field vanishes, $v(x) = 0$, the stationary solution can be approximated as $c_T \approx \mu(x)$, i.e. the total population is close to an ideal free distribution (IFD) (Fretwell and Lucas, 1969). In the last part of the Results section, we also consider an example in which $v(x) \neq 0$ and the distribution of the total population is not necessarily close to an IFD.

Once the equilibrium value of c_T is known, it can be substituted in the equation for the fraction f , which is the relevant quantity to determine which of the two species fixates. By analyzing this equation, we shall see that one can identify the effects leading to selective advantages to the fastest or the slower species.

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