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Evolution of natal dispersal in spatially heterogenous environments

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ABSTRACT

Understanding the evolution of dispersal is an important issue in evolutionary ecology. For continuous time models in which individuals disperse throughout their lifetime, it has been shown that a balanced dispersal strategy, which results in an ideal free distribution, is evolutionary stable in spatially varying but temporally constant environments. Many species, however, primarily disperse prior to reproduction (natal dispersal) and less commonly between reproductive events (breeding dispersal). These species include territorial species such as birds and reef fish, and sessile species such as plants, and mollusks. As demographic and dispersal terms combine in a multiplicative way for models of natal dispersal, rather than the additive way for the previously studied models, we develop new mathematical methods to study the evolution of natal dispersal for continuous-time and discrete-time models. A fundamental ecological dichotomy is identified for the non-trivial equilibrium of these models: (i) the per-capita growth rates for individuals in all patches are equal to zero, or (ii) individuals in some patches experience negative per-capita growth rates, while individuals in other patches experience positive per-capita growth rates. The first possibility corresponds to an ideal-free distribution, while the second possibility corresponds to a "source-sink" spatial structure. We prove that populations with a dispersal strategy leading to an ideal-free distribution displace populations with dispersal strategy leading to a source-sink spatial structure. When there are patches which cannot sustain a population, ideal-free strategies can be achieved by sedentary populations, and we show that these populations can displace populations with any irreducible dispersal strategy. Collectively, these results support that evolution selects for natal or breeding dispersal strategies which lead to ideal-free distributions in spatially heterogenous, but temporally homogenous, environments.

1. Introduction

Dispersal is an important aspect of the life histories of many if not most organisms. However, it was shown by Hastings [19] that selection generally favors slower rates of dispersal in spatially varying but temporally constant environments. This is an example of a widespread feature of spatial models in population dynamics and genetics known as the reduction phenomenon, which is that movement or mixing generally reduces growth [2]. Hastings considered types of dispersal such as simple diffusion and symmetric discrete diffusion that did not allow organisms to perfectly match the distribution of resources in their environment. There are dispersal strategies that do allow organisms to match the distribution of resources in their environment, and it was shown by McPeek and Holt [28] in numerical experiments with discrete time models on two habitat patches that such strategies were favored by selection. At equilibrium the populations using those strategies had equal fitness in the two patches, which is one of the characteristics of an ideal free distribution. The ideal free distribution was introduced by Fretwell and Lucas [15] as a heuristic theory of how organisms would distribute themselves if individuals could assess their fitness in all locations and were free to move so as to optimize their fitness. In a population that is at equilibrium and has an ideal free distribution all individuals would have equal fitness and there would be no net movement of individuals, as a change in local densities would lead to a reduction of fitness for some individuals. In the context of population models it is natural to use the per capita growth rate as a proxy for fitness, in which case the per-capita growth rates of all ideal-free individuals equal zero at equilibrium. This observation can be used to characterize the ideal free distribution in population models. It turns out that in many

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modeling contexts ideal free dispersal strategies are evolutionarily stable in the sense that a population using one cannot be invaded by an ecologically similar population using a dispersal strategy that does not result in an ideal free distribution.

In his dissertation, Altenberg [1] conjectured that strategies leading to an ideal free distribution would be evolutionarily stable. It turns out that is indeed the case in various types of models. One approach to modeling the evolution of dispersal, which we shall not pursue here, is based directly on game theory. The implications of the ideal free distribution in that context are described in [4,11,25,26,34]. The approach that we will take is inspired by the theory of adaptive dynamics. We will consider models of populations dispersing in patchy landscapes and perform what amounts to a pairwise invasibility analysis to compare different dispersal strategies. A dispersal strategy is evolutionarily stable if a population using it can resist invasion by other populations using other strategies. In fact, we will show that in many cases populations using dispersal strategies leading to an ideal free distribution can actually exclude ecologically similar competitors that are using other strategies. Results on the evolutionary stability of ideal free dispersal have been obtained in various modeling contexts, including reaction-diffusion-advection equations [3,7,24], discrete diffusion models [6,8,31], nonlocal dispersal models [9,10], and discrete time models [6,23]. All of these models, however, assume that individuals are either semelparous, as in the case of the discrete-time models, or assume that individuals disperse throughout their lifetime.

In many species, dispersing prior to reproducing (natal dispersal) is much more common than dispersing between successive reproductive events (breeding dispersal) [18]. Natal dispersal is the only mode of dispersal for sessile species such as plants with dispersing seeds or sessile marine invertebrates with dispersing larvae. Many territorial species, such as birds or reef fish, often exhibit long natal dispersal distances and little or no dispersal after establishing a territory [16]. For example, Paradis et al. [32] found that the mean natal dispersal distance for 61 of 69 terrestrial bird species was greater than their mean breeding dispersal distance. For species exhibiting significant natal dispersal, the assumption of individuals dispersing throughout their lifetime is inappropriate. A more appropriate simplifying assumption is that these species only disperse a significant amount prior to reproduction and negligible amounts after reproduction. Many continuous time metapopulation models [17,29] and discrete time models for iteroparous, as well as semelparous, populations [20,23] have a structure consistent with this assumption: individuals disperse between patches right after birth and settle on one patch for the remainder of their lifetime.

In the present paper we will derive results on the evolutionary stability of ideal free dispersal strategies for a general class of models accounting for natal dispersal. We begin by examining the structure of their equilibria and their global stability. The nontrivial equilibrium, when it exists, will be shown to exhibit a dichotomy: per-capita growth rates are equal to zero in all patches (i.e. an ideal free distribution), or some individuals experience negative per-capita growth rates while others experience positive per-capita growth rates. We identify which density-independent dispersal strategies give rise to the ideal-free distributions under equilibrium conditions and show that populations employing these dispersal strategies exclude populations employing non-ideal free dispersal strategies. In the process, we verify a conjecture of Kirkland et al. [23] and extend some of the results of that paper. Furthermore, we show that in models where some dispersing individuals are forced to disperse into patches only supporting negative per-capita growth rates (sink patches), there is selection for slower dispersal. (In such situations the only strategy that can produce an ideal free distribution is the strategy of no dispersal at all.)

2. Sources, sinks, and single species dynamics

2.1. The general model and assumptions

We consider two types of models of populations in patchy environments: (i) models which track population densities in a network of patches, and (ii) patch occupancy models which track the frequencies of occupied sites in a collection of patches, i.e. metapopulation models. For both models, we assume that individuals only disperse shortly after reproduction, e.g. plants via seeds, sessile marine invertebrates via larvae, territorial species such as reef fish, etc. For these types of organisms, individuals can experience density- or frequency-dependence in three demographic phases: fecundity (pre-dispersal), settlement (post-dispersal), or survival (adults). Let $u_i(t)$ denote the population density or frequency in patch i at time t, where $t \in [0, \infty)$ in continuous time and $t = 0, 1, \ldots$ in discrete time. Adults living in patch i produce offspring at a rate $f_i(u_i)$ and experience mortality at a rate $m_i(u_i)$. A fraction d_{ji} of offspring disperse from patch i to patch j and only fraction $s_j(u_j)$ of these offspring survive upon arriving in patch j. If there are n patches, then the governing equation for u_i is given by

$$\Delta u_i = s_i(u_i) \sum_{j=1}^{n} d_{ij} f_j(u_j) u_j - m_i(u_i) u_i, \quad 1 \le i \le n, \tag{2.1}$$

where $\Delta u_i = \frac{du_i}{dt}$ in continuous time and $\Delta u_i = u_i' - u_i$ in discrete time; u_i' denotes the population density in patch i in the next time step, i.e. $u_i'(t) = u_i(t+1)$. Denote $\mathbb{R}_+ = [0, \infty)$. Let $\mathcal{S} = \mathbb{R}_+$ for the population density models and $\mathcal{S} = [0, 1]$ for the population frequency models. Then $\mathcal{S}^n$ is the state space for the models. We make the following assumptions.

(A1) Matrix (d_{ij}) is non-negative, column stochastic, and irreducible in the continuous time case and primitive in the discrete time case. A square matrix is irreducible if it is not similar via a permutation to a block upper triangular matrix. A primitive matrix is a square nonnegative matrix some power of which is positive. Biologically, no individuals are lost while dispersing and after enough generations, the descendants of an adult from patch i can be found in all patches.

(A2) $f_i, s_i : \mathcal{S} \to \mathbb{R}_+$ are continuous, positive, non-increasing functions, and $m_i : \mathcal{S} \to \mathbb{R}_+$ is continuous, positive, non-decreasing. Biologically, reproduction and survival rates decrease with population density, while mortality increases with density.

(A3) $u_i f_i(u_i) : \mathcal{S}_+ \to \mathbb{R}_+$ is strictly increasing. Biologically, as the population gets larger in patch i, the more offspring are produced by the population in patch i. In the discrete-time case, we require the stronger hypothesis that

$$\frac{\partial}{\partial u_i}(s_i(u_i) d_{ii} f_i(u_i) + (1 - m_i(u_i)) u_i) > 0 \text{ for } u_i \in \mathcal{S}, i = 1, 2, \ldots, n.$$

This stronger hypothesis is needed to ensure monotonicity of the discrete time population dynamics.

For each i and population density u_i, define

$$g_i(u_i) := \frac{s_i(u_i) f_i(u_i)}{m_i(u_i)}. \tag{2.2}$$

If the population density were held constant at u_i, then $g_i(u_i)$ equals the mean number of surviving offspring produced by an individual remaining in patch i during its life time. Namely, $g_i(u_i)$ is the reproductive number of individuals living in patch i with the fixed local density u_i. Hence, we view $g_i(u_i)$ as the fitness of an individual remaining in patch i. By **(A2)**, g_i are continuous, positive, decreasing functions. We make the following stronger assumption on g_i:

(A4) g_i is strictly decreasing on $\mathcal{S}$ and $\lim_{u_i \to \infty} g_i(u_i) < 1$ for the population density models and $g_i(1) < 1$ for the population frequency models. Biologically, fitness within a patch decreases with