Dispersal polymorphism in stable habitats

Eva Kisdi [1]

Department of Mathematics and Statistics, University of Helsinki, PO Box 68, FIN-00014, Finland

HIGHLIGHTS

- I consider an analytically highly tractable model for the evolution of dispersal under contrasting levels of kin competition.
- I use both adaptive dynamics and an inclusive fitness approach.
- Dispersal may evolve to an ESS or undergo evolutionary branching, but it always has an evolutionarily stable dimorphic attractor.
- The model exhibits unprotected dimorphisms and loss of diversity via a catastrophic bifurcation.

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ABSTRACT

In fragmented but temporally stable landscapes, kin competition selects for dispersal when habitat patches are small, whereas the loss of dispersal is favoured when dispersal is costly and local populations are large enough for kin interactions to be negligible. In heterogeneous landscapes with both small and large patches, contrasting levels of kin competition facilitate the coexistence of low-dispersal and high-dispersal strategies. In this paper, I use both adaptive dynamics and inclusive fitness to analyse the evolution of dispersal in a simple model assuming that each patch supports either a single individual or a large population. With this assumption, many results can be obtained analytically. If the fraction of individuals living in small patches is below a threshold, then evolutionary branching yields two coexisting dispersal strategies. An attracting and evolutionarily stable dimorphism always exists (also when the monomorphic population does not have a branching point), and contains a strategy with zero dispersal and a strategy with dispersal probability between one half and the ESS of the classic Hamilton–May model. The present model features surprisingly rich population dynamics with multiple equilibria and unprotected dimorphisms, but the evolutionarily stable dimorphism is always protected.

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1. Introduction

In a landmark paper, Hamilton and May (1977) showed that kin competition can maintain dispersal in stable habitats. The simplest version of their model assumes that the habitat consists of many small sites, each supporting just one adult individual. All offspring born in a site are therefore siblings, and the offspring who remain in their natal site kill their own siblings when they compete for establishment. Dispersal can be seen as an altruistic act; the dispersed offspring accept the cost of dispersal, such as the associated mortality risk, in order to save their siblings (Taylor, 1988; Ronce, 2007). If the habitat consists of larger patches that can support more than one adult, then the offspring are not all relatives and

therefore kin competition weakens, resulting in less dispersal (Comins et al., 1980; Taylor, 1988; Ajar, 2003).

In natural habitats, the size of habitat patches is likely variable. Since differently sized patches select for different levels of dispersal, variable patch size offers an attractively economical explanation for the evolution of dispersal polymorphisms. The expectation that variable patch size can select for the diversification of dispersal strategies was shown to be correct by Massol et al. (2011), who found evolutionary branching of dispersal when patch size is distributed with positive skew. The model of Massol et al. (2011) excels at combining analytical results with biological realism (and indeed they demonstrate that their condition for evolutionary branching is satisfied in several natural systems), but is relatively technical.

In this paper, I propose a simpler model to demonstrate evolutionary branching and to explore the joint evolution of coexisting dispersal strategies under contrasting levels of kin competition. The

advantage of the present model is threefold. First, it is a direct extension of the Hamilton–May model, and hence easier comparable to the classic results than the continuous-time model of Massol et al. (2011; see Section 6 for details). Second, the analysis is carried beyond evolutionary branching, i.e., I investigate how two dispersal strategies coevolve. For some dimorphisms, I find multiple population dynamic equilibria such that the dimorphism is not protected and can be lost without warning, through a catastrophic bifurcation, when an environmental change induces changes in the model parameters. Third, the simplicity of the present model makes it analytically highly tractable.

In the first part of the paper, I obtain simple formulas for the invasion boundaries of pairwise invasibility plots (Geritz et al., 1998), for the evolutionarily singular strategies and their bifurcations, and also for the evolutionarily stable dimorphisms. The adaptive dynamics of this model can be analysed with simple mathematics to an almost unprecedented degree. In the second part, I use the inclusive fitness approach to obtain the monomorphic and dimorphic singularities and their convergence stability in a highly intuitive way (Section 7 can be read directly after the model description). I also extend the inclusive fitness approach to derive the condition for evolutionary stability (Section 8). Although the latter is technically more cumbersome, it shows explicitly how contrasting habitat sizes facilitate evolutionary branching via spatial sorting of dispersal strategies.

2. The model

I consider a population of an annual organism where juveniles compete for breeding sites. A fraction p of the breeding sites are solitary sites, whereas the remaining fraction $1-p$ of the sites form one large, well mixed patch, where all juveniles compete equally for all sites. The life cycle consists of reproduction, dispersal, and competition. At reproduction, each breeding site is occupied by one adult, who produces C offspring and dies. I assume $C \to \infty$ so that the dynamics is deterministic within each site. A fraction d of the offspring is dispersed and the remaining fraction $1-d$ remains in the natal site. Dispersed offspring survive dispersal with probability s and land either in a solitary site with probability p or in the large patch with probability $1-p$. Hence I assume that immigration is simply proportional to the area covered by the breeding sites, so that the model has no inherent source–sink structure (this is different from the model of Massol et al. (2011), who assumed that each location receives the same number of immigrants irrespectively of its carrying capacity). After dispersal, juveniles compete for a breeding site according to a fair lottery. Kin competition within solitary sites selects for dispersal (Hamilton and May, 1977), whereas kin competition vanishes in the large patch and dispersal is selected against due to the mortality cost associated with it.

Suppose that L dispersal strategies coexist in the population (later I shall focus on $L=1$ and $L=2$). Let d_k denote the fraction of offspring dispersed by strategy k ($k=1, \ldots, L$), let $n_{1k}(t)$ be the fraction of all breeding sites that is solitary and is occupied by an adult of strategy k in generation t ($\sum_{k=1}^{L} n_{1k}(t) = p$), and let $n_{2k}(t)$ be the fraction of all sites that is in the large patch and is occupied by strategy k ($\sum_{k=1}^{L} n_{2k}(t) = 1-p$).

In order to describe the population dynamics concisely, I start with defining three quantities that will play the role of the environmental feedback variables (Metz et al., 1992; Diekmann et al., 2001; see below). The first environmental feedback variable is

$$E_1 = s \sum_k (n_{1k} + n_{2k}) \, d_k \tag{1a}$$

so that $E_1 C$ is the number of immigrants per site. If a solitary site was occupied by an adult of strategy i, then the site is won by one of the adult's non-dispersed offspring with probability

$$\frac{1 - d_i}{1 - d_i + E_1}.$$

The second environmental feedback variable is

$$E_2 = \frac{1 - p}{\sum_k n_{2k}(1 - d_k) + (1 - p)E_1} \tag{1b}$$

so that E_2/C is the probability that a specific juvenile secures a breeding site if it is competing in the large patch. To interpret this quantity, note that all juveniles in the large patch compete for $(1-p)N$ sites (where N is the total number of breeding sites), $\sum_k n_{2k} NC(1-d_k)$ is the number of non-dispersed offspring produced in the large patch and $(1-p)NE_1C$ is the number of immigrants into the large patch (this is $(1-p)N$ times what a solitary site receives because the large patch covers $(1-p)N$ times the area of a single site). The probability of success is the number of sites divided with the number of competitors. Finally, the third environmental feedback variable is defined as

$$E_3 = \sum_k \frac{n_{1k}}{p} \cdot \frac{1}{1 - d_k + E_1} \tag{1c}$$

so that E_3/C is the probability that a specific immigrant offspring who landed in a solitary site wins the site. Here n_{1k}/p is the probability of landing in a site occupied by an adult of strategy k conditioned on landing in a solitary site, and $(1 - d_k + E_1)C$ is the number of competitors within the site.

Let D denote an arbitrary dispersal strategy (either one of the coexisting L strategies or a new mutant) and let the vector $\mathbf{m}(t) = (m_1(t), m_2(t))^T$ be the population vector of this strategy, containing the fraction of all sites that are occupied with an adult of this strategy and are solitary (m_1) or in the large patch (m_2). Hence if D stands for the kth strategy present in the resident population, then $D = d_k$ and $\mathbf{m} = (n_{1k}, n_{2k})^T$. The projection matrix $\mathbf{A}$, which determines the population vector in the next generation according to $\mathbf{m}(t+1) = \mathbf{A}\mathbf{m}(t)$, is given by

$$\mathbf{A} = \begin{bmatrix} \dfrac{1 - D}{1 - D + E_1} + DspE_3 & DspE_3 \\ Ds(1-p)E_2 & (1 - D + Ds(1-p))E_2 \end{bmatrix} \tag{2}$$

Here the element A_{11} is the number of solitary sites won by the offspring of a parent currently in a solitary site, given by the sum of the probability that a solitary site is won by a non-dispersed offspring (first term of A_{11}) and the number of offspring dispersed from a solitary site who survive dispersal, land in a solitary site, and win that site (second term of A_{11}). A_{12} is the number of offspring dispersed from a site in the large patch who survive dispersal, land in a solitary site, and win that site. Similarly, A_{21} is the number of offspring dispersed from a solitary site who survive dispersal, land in the large patch, and secure a site in the large patch. Finally, A_{22} is the number of offspring born in a site of the large patch who either did not disperse or survived dispersal and landed back in the large patch, times the probability of securing a site in the large patch.

Notice that the elements of $\mathbf{A}$ are not constants because the environmental feedback variables E_1, E_2, E_3 depend on the variables $n_{ik}(t)$. However, all non-linearities in the population dynamics act through the environmental feedback variables, i.e., the three environmental feedback variables fully describe all biotic interactions between an individual and the resident population (Metz et al., 1992; Diekmann et al., 2001). When the resident population has equilibrated so that the densities n_{ik} are constants, then the dynamics of a mutant is linear as long as its own density is negligible.