



Dispersal evolution and resource matching in a spatially and temporally variable environment



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HIGHLIGHTS

- We model the evolution of dispersal rates in a temporally variable environment.
- We develop asexual and sexual life-cycle models that we solve analytically.
- Resource matching is predicted in expectation before habitat quality variation.
- The individuals' distribution undermatches resources after habitat quality variation.
- The overall flow of individuals matches the overall flow of resources between patches.

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ABSTRACT

Metapopulations may consist of patches of different quality, and are often disturbed by extrinsic processes causing variation of patch quality. The persistence of such metapopulations then depends on the species' dispersal strategy. In a temporally constant environment, the evolution of dispersal rates follows the resource matching rule, i.e. at the evolutionarily stable dispersal strategy the number of competitors in each patch matches the resource availability in each patch. Here, we investigate how the distribution of individuals resulting from convergence stable dispersal strategies would match the distribution of resources in an environment which is temporally variable due to extrinsic disturbance. We develop an analytically tractable asexual model with two qualities of patches. We show that convergence stable dispersal rates are such that resource matching is predicted in expectation before habitat quality variation, and that the distribution of individuals undermatches resources after habitat quality variation. The overall flow of individuals between patches matches the overall flow of resources between patches resulting from environmental variation. We show that these conclusions can be generalized to organisms with sexual reproduction, and to a metapopulation with three qualities of patches when there is no mutational correlation between dispersal rates.

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1. Introduction

Many natural populations occupy a spatially fragmented landscape and may be satisfactorily described as metapopulations, i.e. as arrays of subpopulations connected by dispersal. The persistence of metapopulations depends both on the rate of disturbance and succession – an extrinsic variable – and on the species' dispersal properties (Levin and Paine, 1974). Dispersal may thus be

viewed as an adaptation to ephemeral habitats: dispersal may allow tracking favorable environments (Recer et al., 1987), or, if tracking is not possible, may be a bet-hedging strategy (Philippi and Seger, 1989; McPeck and Holt, 1992). Analyzing the distribution of individuals across space and time is another way to look at dispersal strategies which has been fruitful for decades.

Fretwell and Lucas (1969) introduced the concept of ideal free distribution to predict the distribution of organisms competing for resources in patchy, heterogeneous landscapes. Their seminal work assumed that competitors are equal in food acquisition ability, move between patches at no cost, and have perfect information of the resource supply and competitors' distribution. In these conditions, the number of competitors in each patch is predicted to match the resource availability in each patch. More generally, the ideal free distribution is the one such that an

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individual could not attain higher fitness by relocating to another patch. This distribution has been shown to be evolutionarily stable when fitness is a negative function of density (Cressman and Krivan, 2006; Krivan et al., 2008). However, experiments often report undermatching, i.e. a lack of individuals in the more rewarding patches, and an excess in the less rewarding patches (Kennedy and Gray, 1993). This may be the result of deviations from the initial hypotheses, such as imperfect knowledge of patch quality or unequal competitive abilities (Abrahams, 1986; Houston and McNamara, 1988). Undermatching is also the outcome of most experiments when the resource supply rate varies within patches (Recer et al., 1987; Earn and Johnstone 1997; but see Hakoyama, 2003).

Spatial and temporal variability of the environment may be satisfactorily described as Markovian process, where the probability to reach a given state at the next time step only depends on the state at its present time. For example, a Markovian process has been used to describe the states of vegetation in a forest with tree replacement (Wagooner and Stephens, 1970; Horn, 1975), and to describe disturbed environments submitted to fires (Callaway and Davis, 1993; Hibbard et al., 2003). Theoretical studies also have consistently applied a Markovian process to variable environments, e.g. to model environments subject to climate disturbance (Casagrandi and Gatto, 2002; Tuljapurkar et al., 2003). In a metapopulation, Olivieri et al., (1995) described a general stochastic process of patch extinction and succession with a Markov chain at stationarity (see also Valverde and Silvertown, 1997). At stationarity, a Markov chain has a convenient property: the proportions of time spent in the different states are constant over time. In addition, a Markov chain allows to characterize the environmental noise with its color (Vasseur and Yodzis, 2004), since a colored noise can be interpreted as a continuous limit of a discrete Markovian process (Ezard and Coulson, 2010). Although a Markov chain may only approximate reality, it still provides an operational and fruitful framework to understand the evolution of dispersal (Cohen and Levin, 1991; Olivieri et al., 1995).

In this paper, we address the following question: in a spatially and temporally variable environment described as a stationary Markov chain, how would the distribution of individuals resulting from dispersal evolution match the distribution of resources? We develop an analytically tractable asexual model of dispersal evolution with two qualities of patches in order to describe the convergence stable (CS) strategies of dispersal rates. We show that CS dispersal rates allow individuals to anticipate habitat quality variation. The distribution of individuals is such that the number of individuals in each kind of patch before habitat quality variation matches the expected distribution of resources in these patches after environmental variation. The overall flow of individuals between patches then matches the overall flow of resources

between patches resulting from environmental variation. We show that these conclusions can be generalized to organisms with sexual reproduction, and to a metapopulation with three qualities of patches when there is no mutational correlation between dispersal rates.

2. The models

2.1. Asexual model

2.1.1. Environment properties

We consider a metapopulation with N patches large enough to ignore kin effects and demographic stochasticity. Patches switch between two quality states, “good” and “poor”, and are then called “G-patches” and “P-patches” respectively. G-patches (respectively P-patches) contain F_G (respectively F_P) resources. G-patches contain $F = F_G/F_P > 1$ more resources than P-patches. The amount of resources available in a patch is proportional to its carrying capacity, so that G-patches can carry F times more individuals than P-patches. At time t , G- and P-patches are in proportions g_t and $1 - g_t$, respectively.

We model temporal variation of the environment by changing the quality of a proportion σ of the total number of patches in each generation. A proportion $\sigma/2$ is G-patches that become P-patches, and a proportion $\sigma/2$ is P-patches that become G-patches. We assume that temporal variation of the environment is due to external factors and does not depend on individuals' properties and how they exploit resources, i.e. we assume that σ is a constant parameter. The environment may be described as a two-state Markov chain. This Markov chain has a stationary state, and g_t can be considered to be constant over time provided that N is large enough. Our models assume such stationary state of the environment, and hereafter we denote g the constant proportion of G-patches. Note that g is also the proportion of time that a patch spends in state G (see Table 1 for a summary of the notation).

2.1.2. Individuals' properties

The asexual model describes an asexual life cycle with non overlapping generations. A generation consists of

- (i) Dispersal of individuals: dispersal follows an island model. Dispersal rates depend on the quality of patches: a fraction d_G and d_P of individuals disperse from G- and P-patches respectively. Each dispersal rate is determined by a single haploid locus. Dispersers do not select their destination according to its quality. They are thus distributed in G- and P-patches according to the proportions of these patches, respectively g and $1-g$. We assume cost-free dispersal.

Table 1

Notation used in the asexual model.

Variables	
d_I	Dispersal rate of individuals of the resident population from I-patches
d_I^0	Dispersal rate of a focal (mutant) individual from I-patches
Parameters	
g	Proportion of G-patches
F_I	Carrying capacity of a I-patch $F = F_G/F_P > 1$
σ	Proportion of patches undergoing quality change at each generation
Outputs	
d_I^*	CS dispersal rate from I-patches (Eq. (10))
δ_I^*	Number of individuals (scaled relative to the total number of patches N) in I-patches after dispersal and before habitat quality variation, at the CS strategies (Eqs. (11) and (12)).
ϕ_{JI}^*	Flow of individuals that disperse from I-patches to J-patches before habitat quality variation (scaled relative to the total number of patches N), at the CS strategies (Eqs. (13) and (15)).

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