



# 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  $\sigma$  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  $\sigma$  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 $F = F_G/F_P > 1$
$\sigma$	Proportion of patches undergoing quality change at each generation
Outputs	
$d_I^*$	CS dispersal rate from I-patches (Eq. (10))
$\delta_I^*$	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)).
$\phi_{JI}^*$	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)).

Individuals are unable to predict habitat variations of a particular patch.

- (ii) Variation of habitat quality (see Section 2.1.1)
- (iii) Reproduction: offspring are produced in quantity enough to saturate all patches.
- (iv) Death of adults.
- (v) Density regulation: in each G-patch (resp. P-patch), a number of offspring proportional to  $F_G$  (resp.  $F_P$ ) are drawn at random to become individuals for the next generation, i.e. individuals equally and locally compete for resources.

## 2.2. Model analysis

We aim to determine convergence stable (CS) strategies of dispersal rates from G- and P-patches. A strategy consists of a vector  $d = (d_P, d_G)$ . The resident strategy (i.e. the mean strategy of the population) is denoted by  $d$ , a focal strategy (i.e. the strategy of a rare mutant) by  $d^o$ , and a CS strategy by  $d^*$ . To compute the fitness function, we use the direct fitness formulation of the inclusive fitness method from Taylor and Frank (1996), detailed below.

### 2.2.1. Fitness function

The fitness of a focal individual with strategy  $d^o$  is defined as the expected long-term contribution in terms of number of gene copies transmitted by this focal individual when the resident population strategy is  $d$ . As we consider a haploid model, the number of gene copies is also the number of offspring. We define two classes of individuals: individuals born in a P-patch and those born in a G-patch, denoted afterward P- and G-class individuals respectively. The fitness  $W_I(d^o, d)$  of an I-class focal individual (I=G,P) will be higher if such focal individual produces one offspring with a high probability to be the ancestor of the future population than one offspring with a low probability to be the ancestor; in other words,  $W_I(d^o, d)$  depends on the class of offspring. Then, following Taylor (1990) and Rousset (2004), the fitness  $W_I(d^o, d)$  can be defined as the expected number of gene copies that an I-class focal individual produces in a K-class (K=G,P),  $W_{KI}(d^o, d)$ , weighted by the asymptotic contribution to the future gene pool of the population of one offspring from a K-class, i.e. the mean individual reproductive values  $V_G$  and  $V_P$  (see Section 2.2.2 for their expression):

$$W_I(d^o, d) = V_P W_{PI}(d^o, d) + V_G W_{GI}(d^o, d). \quad (1)$$

Before producing offspring in a K-patch, an I-class focal individual may have dispersed and/or the quality of the patch where it is after dispersal may have changed. We can thus write

$$W_{KI}(d^o, d) = A_{KP}(d) P_{KPI}(d^o) + A_{KG}(d) P_{KGI}(d^o), \quad (2)$$

where  $P_{KJI}(d^o)$  is the probability that an I-class focal individual is in a J-patch after dispersal and in a K-patch after habitat quality variation, and  $A_{KJ}(d)$  is the expected number of offspring that survive density regulation, produced by an individual of resident strategy  $d$  which is in a J-patch after dispersal and in a K-patch after habitat quality variation.

Let us determine  $P_{KJI}(d^o)$ . We denote  $\sigma_{KJ}$  the probability that a J-patch is a K-patch after habitat quality variation, and  $P_{JI}(d^o)$  the probability that an I-class focal individual is in a J-patch after dispersal. Then,

$$P_{KJI}(d^o) = \sigma_{KJ} P_{JI}(d^o). \quad (3)$$

Recall that  $\sigma$  is the proportion of patches whose quality changes in each generation, and that the proportions of G- and P-patches,  $g$  and  $1-g$  respectively, are constant over time.  $\sigma_{KJ}$  are thus expressed by

$$\sigma_{PP} = 1 - \sigma / (2(1-g))$$

$$\sigma_{PG} = \sigma / (2g)$$

$$\sigma_{GP} = \sigma / (2(1-g))$$

$$\sigma_{GG} = 1 - \sigma / (2g). \quad (4)$$

Consider now a P-class focal individual. It has a probability  $d_P^o$  to disperse, and a probability  $1-d_P^o$  to stay in its P-patch. If it disperses, its dispersal is cost-free and it does not select the quality of the patch where it disperses. In this case, it has thus a probability  $1-g$  to reach a P-patch. Therefore, the probability that a P-class focal individual is in a P-patch after dispersal is  $1-d_P^o + (1-g)d_P^o$ . With the same reasoning we obtain all  $P_{JI}(d^o)$  terms:

$$P_{PP}(d^o) = 1 - d_P^o + (1-g)d_P^o$$

$$P_{PG}(d^o) = (1-g)d_G^o$$

$$P_{GP}(d^o) = g d_P^o$$

$$P_{GG}(d^o) = 1 - d_G^o + g d_G^o. \quad (5)$$

Let us now determine  $A_{KJ}(d)$  introduced in Eq. (2). We call a “KJ-patch” a K-patch that was a J-patch before habitat quality variation. Because we assume that offspring produced in a given patch equally compete for resources,  $A_{KJ}(d)$  is the ratio of the amount of resources in KJ-patches over the number  $N_{KJ}$  of individuals reproducing in these patches (note that we use here the resident dispersal strategy  $d$  because mutants are assumed to be rare, so that the mutant strategy does not influence the number of individuals in each patch). As the proportion of PP-patches is  $1-g-\sigma/2$ , the total amount of resources available for reproduction in PP-patches is  $F_P N (1-g-\sigma/2)$ , where  $N$  is the total number of patches. Consequently,  $A_{PP}(d)$  can be expressed as

$$A_{PP}(d) = F_P N (1-g-\sigma/2) / N_{PP}(d).$$

Similarly:

$$A_{PG}(d) = F_P N (\sigma/2) / N_{PG}(d)$$

$$A_{GP}(d) = F_G N (\sigma/2) / N_{GP}(d)$$

$$A_{GG}(d) = F_G N (g-\sigma/2) / N_{GG}(d).$$

Individuals in a J-patch that will become a K-patch after habitat quality variation may originate from G- or P-patches, so we can write:

$$N_{KJ}(d) = N_P P_{KJP}(d) + N_G P_{KJG}(d),$$

where  $P_{KJI}$  is defined by Eq. (3) and  $N_I$  is the number of I-class individuals.

The number of individuals produced in a I-patch equals the amount of resources available in this patch,  $F_I$ . Thus,

$$N_P = N(1-g)F_P$$

$$N_G = NgF_G. \quad (6)$$

Combining the equations of this section allows to express the fitness function of an I-class individual (Eq. (1)) with the four parameters of the model ( $F_G, F_P, g$  and  $\sigma$ ), the two variables ( $d^o$  and  $d$ ), and the reproductive values  $V_P$  and  $V_G$ , computed below.

### 2.2.2. Reproductive values

We recall that the mean reproductive values of a P- and G-class individual, respectively  $V_P$  and  $V_G$ , are defined as the asymptotic contribution of an individual born in a P-patch (respectively G-patch) to the future gene pool of the population (Taylor, 1990; Rousset, 2004). The vector of the individual reproductive values ( $V_P, V_G$ ) is the left eigenvector associated with the largest eigenvalue 1 of the fitness functions matrix, evaluated in the neutral model (i.e. when  $d^o = d$ ) such that:

$$(V_P, V_G) \begin{bmatrix} W_{PP}(d, d) & W_{PG}(d, d) \\ W_{GP}(d, d) & W_{GG}(d, d) \end{bmatrix} = (V_P, V_G), \quad (7)$$

where  $W_{kl}(d, d)$  is defined by Eq. (2). This system generates two collinear equations.

To solve Eq. (7), we used the normalization of reproductive values  $Q_P V_P + Q_G V_G = 1$ , where  $Q_i$  is the proportion of I-class individuals:

$$Q_P = \frac{N_P}{N_P + N_G} = \frac{F_P(1-g)}{F_G g + F_P(1-g)}$$

$$Q_G = \frac{N_G}{N_P + N_G} = \frac{F_G g}{F_G g + F_P(1-g)}$$

### 2.2.3. Convergence stability of singular strategies

The fitness of a focal individual with strategy  $d^o$  is  $W(d^o, d) = Q_P W_P(d^o, d) + Q_G W_G(d^o, d)$ . Preliminary results revealed that it is helpful to analyze the model using alternative variables: instead of writing the fitness as a function of the vectors  $d = (d_P, d_G)$  and  $d^o$  above, we now express the fitness as a function of the vectors  $v = (d_P, a)$  and  $v^o$  where  $a = F_G d_G - F_P d_P$ . Note that to make easier the biological interpretation of the results, results will however be expressed with the original variables. Selection measures (Leturque and Rousset, 2002) evaluate the probability of fixation of a rare mutant expressing the strategy  $v^o$ , weakly different from the resident strategy  $v$ . They are defined as

$$S_P(v) = \frac{\partial W(v^o, v)}{\partial d_P^o} \Big|_{v^o = v}$$

$$S_A(v) = \frac{\partial W(v^o, v)}{\partial a^o} \Big|_{v^o = v} \tag{8}$$

These probabilities vanish at singular points, i.e. CS strategies  $v^*$  necessarily satisfy:

$$S_P(v^*) = 0$$

$$S_A(v^*) = 0. \tag{9}$$

Following Leimar (2009), in the case of vector-valued traits as we use here, a sufficient criterion for a singular strategy to be convergent stable is that the Jacobian matrix of the selection gradient, evaluated at the singular strategy, is negative definite. The Jacobian matrix is defined by  $J = H + Q$  where

$$H = \begin{pmatrix} \frac{\partial^2 W(v^o, v)}{\partial d_P^o \partial d_P^o} & \frac{\partial^2 W(v^o, v)}{\partial d_P^o \partial a^o} \\ \frac{\partial^2 W(v^o, v)}{\partial a^o \partial d_P^o} & \frac{\partial^2 W(v^o, v)}{\partial a^o \partial a^o} \end{pmatrix}$$

is the selection Hessian matrix and

$$Q = \begin{pmatrix} \frac{\partial^2 W(v^o, v)}{\partial d_P^o \partial d_P} & \frac{\partial^2 W(v^o, v)}{\partial d_P^o \partial a} \\ \frac{\partial^2 W(v^o, v)}{\partial a^o \partial d_P} & \frac{\partial^2 W(v^o, v)}{\partial a^o \partial a} \end{pmatrix}.$$

This method to determine convergence stability of singular strategies allows taking into account possible mutational correlations between traits (Leimar, 2009).

We show that there is an infinite number of singular strategies because after changing the variables of the model, one of the two traits can be considered as selectively neutral (see Results and Appendix A.1). Consequently, our Jacobian matrix of the selection gradient evaluated at any of the singular strategies,  $J^*$ , cannot be negative definite, so that Leimar's (2009) sufficient criterion cannot be used directly. However, according to his work, the local dynamics of trait evolution around a singular strategy  $v^*$  is described by  $d(v - v^*)/dt = A J^*(v - v^*)$  where  $A$  is the mutational matrix. We will thus compute the product  $A J^*$  for all of the singular strategies and we will show that it is a semi-negative definite matrix, the non-zero eigenvalue of which corresponding to the

trait under selection. This allows us to conclude that the trait under selection of any of the singular strategies is convergent stable in the sense of Lyapunov (Leimar, 2009). The other trait can change neutrally and/or evolve following genetic correlations between the two traits, but it does not converge to a specific value.

According to Leimar (2009), a sufficient condition for convergent stable strategies to be also evolutionarily stable is that the Hessian matrix evaluated at the singular strategy,  $H^*$ , is negative definite. We show (Appendix A.1) that in our model,  $H^*$  equals the zero matrix, which does not allow us to conclude about evolutionary stability nor instability.

### 2.3. Sexual models

We modify the asexual model to take into account sexual reproduction. The life cycle is then:

- (i) Dispersal of individuals: males and females disperse from I-patches at rate  $d_{m1}$  and  $d_{f1}$  respectively.
- (ii) Mating: Males compete for the fertilization of females within each patch. We assume that males are produced in quantity enough to fertilize all females so that the number of females is limiting. Without loss of generality, we assume that the number of zygotes produced in each patch is equal to the number of females.
- (iii) Dispersal of zygotes: zygotes disperse from I-patches at rate  $d_{z1}$ . Zygote dispersal can also be interpreted as dispersal of mated females. We assume that the primary sex-ratio is balanced and that the number of zygotes produced is large enough to saturate each patch. In our model, the dispersal rate  $d_{z1}$  of zygotes may be determined by the genotype of both parents, or only by the genotype of the female parent; both assumptions lead to the same results (see Appendix B for details).
- (iv) Habitat quality variation (see section 2.1.1).
- (v) Death of adults.
- (vi) Density regulation: in each G-patch (resp. P-patch), a number of zygotes proportional to  $F_G$  (resp.  $F_P$ ) are drawn at random to become sexually mature individuals for the next generation.

When zygotes do not disperse ( $d_{z1} = 0$ ), the model is called "DDM" (for "male Dispersal, female Dispersal, Mating"; Taylor, 1994). The DDM model fits a standard animal life cycle. When females do not disperse before mating ( $d_{f1} = 0$ ), the model is called "DMD" (for "male Dispersal, Mating, zygote Dispersal"; Taylor, 1994). The DMD model fits most plant life cycles, and can also be applied to some animals (Taylor, 1994; Guillon and Bottein, 2011). A detailed presentation of the sexual models and the corresponding analyses are given in Appendix B.

### 2.4. Asexual model with three qualities of patches

The structure of an environment is usually more complex than patches of only two possible qualities. We use an asexual model with three qualities of patches (hereafter called "three-patch model") to try to generalize our results to more complex environments. A detailed presentation of the three-patch model and the corresponding analysis are given in Appendix C.

## 3. Results

### 3.1. Asexual model

We show (Appendix A.1) that CS dispersal rates from G- and P-patches are those within the interval [0,1] that satisfy the



equation:

$$F_G d_G^* - F_P d_P^* = \frac{\sigma(F_G - F_P)}{2g(1-g)}. \quad (10)$$

When habitat quality does not vary in time ( $\sigma = 0$ ), Eq. (10) becomes  $F_G d_G^* = F_P d_P^*$ . Thus, as expected, not to disperse is a CS strategy in a temporally constant environment. Nevertheless, non-zero dispersal strategies are possible. In this case, dispersal from P-patches is then  $F = F_G/F_P$  times higher than from G-patches. As a G-patch can carry  $F$  times more individuals than a P-patch, all CS dispersal strategies lead to the same distribution of individuals, with  $F$  times more individuals in a G-patch than in a P-patch. In other words, the distribution of individuals matches the distribution of resources.

In a temporally variable environment ( $\sigma > 0$ ), Eq. (10) shows that dispersal from G-patches increases relative to dispersal from P-patches when habitat quality variation increases (Fig. 1). Indeed, the more habitat quality is likely to change, the more individuals in G-patches are likely to have offspring in P-patches if they do not disperse, thus the more they should disperse. Conversely, the more habitat quality is likely to change, the more individuals in P-patches should stay in their patch which is more likely to become a G-patch. Consequently, individuals may disperse more from P-patches than from G-patches only when habitat quality variation is not too frequent.

Is the resources matching rule still valid? To answer to this question, let us define  $\delta_i(d)$  as the number of individuals (scaled relative to the total number of patches  $N$ ) after dispersal and before habitat quality variation in I-patches (we recall that  $d = (d_P, d_G)$ )

$$\begin{aligned} \delta_G(d) &= gF_G P_{GG}(d) + (1-g)F_P P_{GP}(d) \\ \delta_P(d) &= gF_G P_{PG}(d) + (1-g)F_P P_{PP}(d), \end{aligned} \quad (11)$$

with  $P_{ij}$  defined by Eq. (5). Using CS dispersal rates (Eq. (10)), the distribution of individuals can be expressed as

$$\frac{\delta_G(d^*)}{\delta_P(d^*)} = \frac{gF_G - \sigma(F_G - F_P)/2}{(1-g)F_P + \sigma(F_G - F_P)/2}. \quad (12)$$

When habitat quality varies in time, the distribution of individuals after dispersal and before habitat quality variation is thus the distribution expected in a constant environment ( $(gF_G)/((1-g)F_P)$ ), corrected by a term  $\sigma(F_G - F_P)/2$ . As this term is positive, there are fewer individuals in G-patches and more individuals in P-patches than expected in a temporally constant environment.

Let  $\phi_{ij}(d)$  be the flow of individuals that disperse from I-patches to J-patches before habitat quality variation (scaled relative to the

total number of patches  $N$ ),

$$\begin{aligned} \phi_{PG}(d) &= gF_G P_{PG}(d) \\ \phi_{GP}(d) &= (1-g)F_P P_{GP}(d), \end{aligned} \quad (13)$$

and let  $\psi_P$  (respectively  $\psi_G$ ) be the amount of resources (scaled relative to the total number of patches  $N$ ) created by habitat quality variation in P-patches (respectively G-patches) that becomes G-patches (respectively P-patches),

$$\begin{aligned} \psi_P &= (1-g)\sigma_{GP}(F_G - F_P) \\ \psi_G &= g\sigma_{PG}(F_P - F_G), \end{aligned} \quad (14)$$

with  $\sigma_{ij}$  defined by Eq. (4). Then, simple algebra shows that the condition given by Eq. (10) can be written as

$$\phi_{PG}(d^*) - \phi_{GP}(d^*) = \psi_P = -\psi_G = \frac{\sigma}{2}(F_G - F_P). \quad (15)$$

Eq. (15) can be interpreted as follows: at the CS strategies, the net flow of individuals that disperse to P-patches before habitat quality variation must equal the amount of resources created in P-patches (and the amount of resources destroyed in G-patches) due to habitat quality variation. The term  $\sigma(F_G - F_P)/2$  in Eq. (12) can thus be interpreted as an anticipation of habitat quality variation: according to Eq. (15), the number of individuals in all G- or P-patches before habitat quality variation matches the expected distribution of resources in these patches after environmental variation.

Now consider the distribution of individuals in G- and P-patches after habitat quality variation. When  $0 < \sigma < 1$ , individuals dispersing to P-patches do not know which P-patch will become a G-patch. They are uniformly distributed among all P-patches, thus with a lack of individuals in future G-patches and an excess of individuals in future P-patches. The same is true for individuals dispersing to G-patches: because they do not know which G-patch will become a P-patch, there will be a lack of individuals in future G-patches and an excess of individuals in future P-patches. Thus, except when  $\sigma = 0$  or when  $\sigma = 1$ , which make the environment completely predictable, the actual distribution of individuals after habitat quality variation necessarily undermatches resources (see Appendix A.2).

Another way to understand Eq. (10) is to decompose CS dispersal rates into two dispersal parts. First, a balanced dispersal part (i.e.  $F_G d_G^* = F_P d_P^*$ ): the number of immigrants is equal to the number of emigrants in patches of each quality. This dispersal part is the only one in a temporally constant environment. Second, an unbalanced dispersal part (term  $\sigma(F_G - F_P)/(2g(1-g))$ ), which is added to the balanced dispersal part in a temporally variable environment. This unbalanced dispersal part generates an excess of  $\sigma(F_G - F_P)/2$  individuals in P-patches (Eq. (12)), which exactly matches the amount of resources created in P-patches by habitat quality variation (Eq. (15)). As a result, unbalanced dispersal in a temporally variable environment allows anticipating habitat quality variation.

### 3.2. Sexual models

We show (Appendix B.2) that singular dispersal rates from G- and P-patches are, for the DDM model (no zygote dispersal,  $d_{z1}^0 = d_{z1} = 0$ ), those within the interval  $[0,1]$  satisfying the equations

$$\begin{aligned} F_G d_{fG}^* - F_P d_{fP}^* &= \frac{\sigma(F_G - F_P)}{2g(1-g)} \\ F_G d_{mG}^* - F_P d_{mP}^* &= \frac{\sigma(F_G - F_P)}{2g(1-g)}, \end{aligned} \quad (16)$$

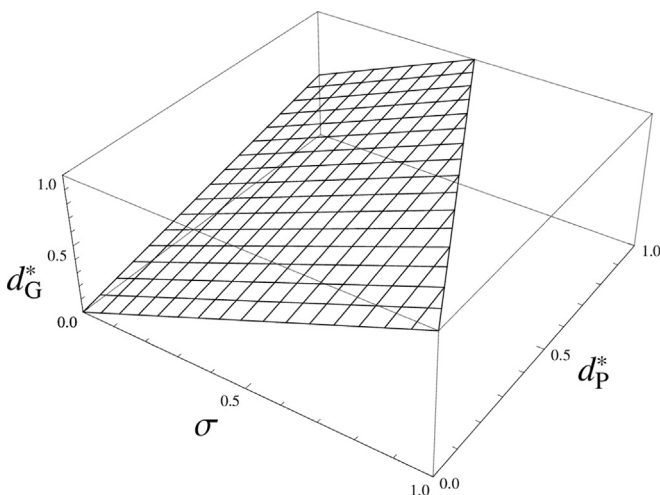


Fig. 1. Asexual model, pairs of dispersal rates from P-patches ( $d_P^*$ ) and from G-patches ( $d_G^*$ ) that are CS (Eq. (10)), as a function of the intensity of habitat quality variation ( $\sigma$ ). Parameter values:  $g = 0.5$ ,  $F_G = 2$ ,  $F_P = 1$ .

and for the DMD model (no female dispersal,  $d_{f1}^0 = d_{f1} = 0$ ), those between 0 and 1 and satisfying the equations

$$F_G d_{zG}^* - F_P d_{zP}^* = \frac{\sigma(F_G - F_P)}{2g(1-g)}$$

$$F_G d_{mG}^* - F_P d_{mP}^* = 0. \tag{17}$$

For both sexual models, we numerically verified that the above singular strategies are all convergent stable, even assuming mutational correlations between dispersal rates (see Appendix B.2 for details).

A first consequence of the above equations is that at the CS strategies the distribution of male gametes necessarily matches the distribution of female gametes after dispersal. In the case of the asexual model, we have interpreted the CS strategies using the distributions and the flows of individuals in G- and P-patches. For sexual models, it is helpful to consider the distributions and the flows of gene copies transmitted via females and males to interpret CS dispersal rates. For both DDM and DMD models, simple algebra shows that, after zygotes dispersal and before habitat quality variation, the expected number of gene copies transmitted in I-patches (scaled relative to the total number of patches  $N$ ) via females and males ( $\delta_f^m(d)$  and  $\delta_m^m(d)$ ; see Appendix B.1 for details), satisfy the following equality at the CS strategies:

$$\frac{\delta_G^f(d^*)}{\delta_P^f(d^*)} = \frac{\delta_G^m(d^*)}{\delta_P^m(d^*)} = \frac{gF_G - \sigma(F_G - F_P)/2}{(1-g)F_P + \sigma(F_G - F_P)/2}. \tag{18}$$

Moreover, for both DDM and DMD models, the net flow of gene copies (scaled relative to the total number of patches  $N$ ) transmitted to P-patches via either females or males ( $\phi_{PG}^f(d) - \phi_{GP}^f(d)$  and  $\phi_{PG}^m(d) - \phi_{GP}^m(d)$ ; see Appendix B.1 for details) matches the amount of resources created in P-patches due to habitat quality variation ( $\psi_P$ , Eq. (14)) at the CS strategies:

$$\phi_{PG}^f(d^*) - \phi_{GP}^f(d^*) = \phi_{PG}^m(d^*) - \phi_{GP}^m(d^*) = \psi_P = -\psi_G = \frac{\sigma}{2}(F_G - F_P). \tag{19}$$

These results show obvious similarities with those of the asexual model. Let us check that they can be interpreted in the same way, and notice some special features of the sexual models. According to Eqs. (18) and (19), CS dispersal rates (Eq. (16) for the DDM model and Eq. (17) for DMD model) are those leading to a number of gene copies in all G- or P-patches before habitat quality variation that matches the expected distribution of resources available in these patches after habitat quality variation. This distribution is achieved thanks to an unbalanced part of dispersal (term  $\sigma(F_G - F_P)/(2g(1-g))$ ), which generates a net positive flow of  $\sigma(F_G - F_P)/2$  gene copies to P-patches; this flow exactly matches the amount of resources created in P-patches by habitat quality variation. The results of the DDM and DMD sexual models can thus be interpreted in the same way as those of the asexual model, except that in the asexual model, the distribution of gene copies is immediately interpretable as the distribution of individuals.

In the DDM model, zygotes cannot disperse. As for the asexual model, CS dispersal rates can be decomposed into a balanced part of dispersal and an unbalanced part. Female and male unbalanced parts are necessarily identical (term  $(\sigma(F_G - F_P))/(2g(1-g))$  in Eq. (16)), allowing for a balanced sex-ratio at the time of mating (Guillon et al., 2006). The balanced part (dispersal rates such that  $F_G d_{fG}^* = F_P d_{fP}^*$  and  $F_G d_{mG}^* = F_P d_{mP}^*$ ) can be achieved with different dispersal rates for males and females.

In the DMD model, females cannot disperse before mating. CS male dispersal rates are then balanced (Eq. (17), second line): the distribution of males is identical before and after male dispersal at the CS strategies, allowing for a balanced sex-ratio at the time of mating. Then zygotes, which carry gene copies transmitted via both females and males, disperse as individuals do in the asexual model. Zygote dispersal is again in part balanced, which does not

modify their distribution, and in part unbalanced, allowing anticipating habitat quality variation (Eq. (17), first line).

In summary, the results of the asexual model and their interpretation can be extended to the DDM and DMD sexual models. CS strategies anticipate habitat quality variation, so that the number of individuals in all G- or P-patches before habitat quality variation finally matches the expected distribution of resources available in these patches after habitat quality variation.

### 3.3. Asexual model with three qualities of patches

We tried to generalize the results of the asexual model to an asexual model where there are three qualities of patches (Appendix C). Using Sage software (Sage Foundation, 2009), we found that the singular point equations (Eq. (C.4)) are satisfied for strategies with dispersal rates within the interval [0,1] that verify the following system:

$$\sum_{j=1}^3 (\phi_{1j}(d^*) - \phi_{j1}(d^*)) = \sum_{j=1}^3 p_1 \sigma_{j,1} (F_j - F_1)$$

$$\sum_{j=1}^3 (\phi_{2j}(d^*) - \phi_{j2}(d^*)) = \sum_{j=1}^3 p_2 \sigma_{j,2} (F_j - F_2)$$

$$\sum_{j=1}^3 (\phi_{3j}(d^*) - \phi_{j3}(d^*)) = \sum_{j=1}^3 p_3 \sigma_{j,3} (F_j - F_3), \tag{20}$$

where  $\sigma_{ji}$  is the proportion of  $i$ -patches ( $i \in \{1, 2, 3\}$ ) that become  $j$ -patches after habitat quality variation and  $\phi_{ji}(d_i) = F_i p_i p_j d_i$  is the flow of individuals that disperse from  $i$ -patches to  $j$ -patches before habitat quality variation (scaled relative to the total number of patches  $N$ ).  $d_i$  is the dispersal strategy from  $i$ -patches,  $p_i$  is the proportion of  $i$ -patches, and  $F_i$  is the amount of resources available in  $i$ -patches. Moreover, we verified that the solutions of Eq. (20) are the only singular strategies, by numerically solving Eqs. (C.4) for 10,000 random parameter sets and checking that the solutions verify Eq. (20). We were unable to show that the solutions of Eq. (20) are convergent stable in the general case, neither that they are unstable. However, assuming that the three dispersal rates evolve without mutational correlation, we found that dispersal rates satisfying Eq. (20) are indeed convergent stable (Appendix C).

The left parts of Eq. (20) are the net flows of individuals into a given patch type due to dispersal at the CS strategies, whereas the right parts represent the amount of resources created in the same patch type by habitat quality variation. Eq. (20) is thus the parallel of Eq. (15) in the case of an environment with three habitat qualities: again, a dispersal strategy such that the net flow of individuals equals the flow of resources in each habitat is a CS strategy.

It can be shown that Eq. (20) are equivalent to the following system:

$$\frac{\delta_1(d^*)}{\delta_2(d^*)} = \frac{p_1 F_1 + p_1 \sigma_{2,1} (F_2 - F_1) + p_1 \sigma_{3,1} (F_3 - F_1)}{p_2 F_2 + p_2 \sigma_{1,2} (F_1 - F_2) + p_2 \sigma_{3,2} (F_3 - F_2)}$$

$$\frac{\delta_1(d^*) p_1 F_1 + p_1 \sigma_{2,1} (F_2 - F_1) + p_1 \sigma_{3,1} (F_3 - F_1)}{\delta_3(d^*) p_3 F_3 + p_3 \sigma_{1,3} (F_1 - F_3) + p_3 \sigma_{2,3} (F_2 - F_3)}$$

$$\frac{\delta_2(d^*)}{\delta_3(d^*)} = \frac{p_2 F_2 + p_2 \sigma_{1,2} (F_1 - F_2) + p_2 \sigma_{3,2} (F_3 - F_2)}{p_3 F_3 + p_3 \sigma_{1,3} (F_1 - F_3) + p_3 \sigma_{2,3} (F_2 - F_3)}, \tag{21}$$

where  $\delta_i(d)$  is the number of individuals (scaled relative to the total number of patches  $N$ ) after dispersal and before habitat quality variation in  $i$ -patches:

$$\delta_i(d) = p_i F_i (1 - d_i) + \sum_{j=1}^3 p_j F_j p_i d_j.$$

Eq. (21) is thus the parallel of Eq. (12) in the case of an environment with three habitat qualities. This analysis leads us to conclude that our main results for the asexual model (Eqs. (12) and (15)) may be

generalized to environments with more than two qualities of patches, at least when there is no mutational correlation between dispersal rates.

#### 4. Discussion

We developed an analytical model to investigate the distribution of individuals resulting from convergence stable (CS) dispersal rates in a temporally variable environment. For an organism reproducing asexually and assuming an environment with two qualities of patches, we found that CS dispersal rates satisfy two conditions: (i) the net flow of individuals that disperse into patches of a given quality before variation of habitat quality equals the expected amount of resources created in these patches after environmental variation (Eq. (15)), and (ii) the distribution of individuals in patches of a given quality before habitat quality variation matches the expected distribution of resources in these patches after environmental variation (Eq. (12)). It can also be demonstrated that reproductive values in different patches are equal at the CS strategies, fitnesses in different patches as well, which is also equivalent to equal fitnesses for dispersing and non-dispersing individuals from each patch (results not shown). It must be noticed that our CS strategies are not proved to be evolutionarily stable. However, in a similar model where dispersal did not depend on habitat quality ( $d_p = d_C$ ) Cohen and Levin (1991) found that the predicted dispersal rates are evolutionarily stable when comprised in the interval [0,1]. When dispersal is habitat-dependent as in our study (i.e.  $d_p$  and  $d_C$  not necessarily equal), CS strategies form a continuum of strategies and a polymorphism may evolve.

We showed that our results can be generalized to sexually reproducing organisms following a DDM or DMD life cycle. For the 3-patch model, we were unable to conclude about convergence stability or instability in the general case. Nevertheless, when there is no mutational correlation between traits, we demonstrated that our results can be generalized to an environment with three qualities of patches.

The classical result that the fitness of dispersers and non-dispersers are equalized (Slatkin, 1978) is a simple translation of Eq. (9). That dispersal evolution in a structured population should tend to equalize reproductive values among patches has also been consistently reported (McPeck and Holt, 1992; Lemel et al., 1997; Lebreton et al., 2000; Greenwood-Lee and Taylor, 2001; Holt and Barfield, 2001; Padrón and Trevisan, 2006). The equalization of reproductive values can be viewed as the achievement of an ideal free distribution (Holt and Barfield, 2001; Greenwood-Lee and Taylor, 2001; Rousset, 2004). A continuum of CS dispersal rates is obtained here, as usually observed when dispersal is assumed to be habitat-dependent (McPeck and Holt, 1992; Doebeli, 1995; Lemel et al., 1997; Lebreton et al., 2000).

The present model describes the evolution of dispersal in an environment which is temporally variable, following a stationary Markovian process. At any given time, the environment is spatially variable because patches differ in their present state, i. e. in their quality. Patch quality is here defined as the amount of resources available, determining carrying capacities. However, the environment may be qualified as spatially homogeneous in the sense that all patches will experience the different states a constant proportion of time. In a temporally variable environment described as a stationary Markov chain, like in our model, habitat quality is partly predictable because the proportion of patches that will change quality is constant over time. However, the exact quality of a given patch at the next time step cannot be predicted: quality variation is a stochastic process that can only be anticipated in expectancy. These two properties of the model explain the two results at the

CS strategies: (i) resource matching is realized in expectancy *before* habitat quality variation, and (ii) the distribution of individuals undermatches resources *after* habitat quality changes, i.e. there is a lack of individuals in the more rewarding patches, and an excess in the less rewarding patches after habitat quality changes.

Result (i) means that individuals distribute in different patches *before* habitat quality variation according to the expected distribution of resources available in these patches after habitat quality variation (Eq. (12)). This result is reminiscent of the resource matching rule (Parker, 1978; Recer et al., 1987). Temporally variable environments have been the object of few experiments in the test of the ideal free distribution theory, but Recer et al. (1987) examined the effect of varying resource input rates on the distribution of mallards between two patches. In their experimental setting, when resource supply rate was varied rapidly enough, individuals could no longer track the variation of the environment, settled in one patch, and their distribution was matching the mean input rates in different patches. In our model, we also find that individuals distribute themselves before habitat quality variation by averaging future available resources.

Result (ii) is due to the fact that individuals have partial information about habitat quality: they cannot know whether a given patch will change quality, so they distribute at random between patches of the same present quality though differing in their future quality. This is analogous to perception limits: with perception limits, foraging individuals get imprecise information about the suitability of different patches and undermatching is observed because some individuals distribute randomly between patches (Abrahams, 1986; Gray and Kennedy, 1994; Hakoyama and Iguchi, 1997). The theoretical distribution of individuals in stochastic environments has already been studied (Hakoyama, 2003; Schreiber, 2012) and undermatching was also found even if hypotheses differ between these models and ours, as detailed hereafter.

Contrary to e.g. McPeck and Holt (1992) (as well as Hakoyama, 2003; Schreiber, 2012), the present model is based on temporal disturbance of patch quality when there is no spatial variation of the environment: here, all patches are equivalent in the long term. Other models have already studied the evolution of dispersal in such a context (Comins et al., 1980; Cohen and Levin, 1991; Olivieri et al., 1995; Olivieri and Gouyon, 1997; Gandon and Michalakis, 1999) but they considered that dispersal is not habitat-dependent. Fixing equal dispersal rates among patches  $d_p^* = d_C^*$  is a special case of our model. In the case of random patch extinction ( $F_p = 0$  and  $\sigma_{pp} = \sigma_{pC}$ ), our model gives the same solution as in previous studies:  $d_C^* = 1$ . Cohen and Levin (1991) used a Markovian process to model temporal variation of habitat quality in a metapopulation. In the case when dispersal is costless and when there are two qualities of habitat, we find the same solution as Cohen and Levin (1991):  $d_p^* = d_C^* = \sigma / (2g(1-g))$ . The CS dispersal rate thus only depends on the statistical structure of the environment ( $\sigma$  and  $g$ ), and not on resources  $F_p$  and  $F_C$ . As in previous models, we make the strong assumption that habitat quality change ( $\sigma$  or  $\sigma_{i,j}$ ) is constant over time, as well as the proportion of different patch types ( $g$  or  $p_i$ ). The effects of relaxing this assumption should depend on individual cases, and no general prediction can be made.

Dispersal may be decomposed in three successive steps: emigration, movement and immigration (Bowler and Benton, 2005; Clobert et al., 2009). Considering emigration, our model assumes that dispersal is habitat-dependent. Habitat quality here determines how many individuals may establish in one patch. In this case, habitat quality may be perceived as the local intensity of competition between individuals for establishment. Our model may also describe the case when the number of individuals per patch is the same in all patches and individuals must share resources. In this case,  $F_C$  and  $F_p$  represent the amount of resources available to one individual that



linearly determines its fecundity. Habitat quality may here be perceived as the amount of resources available to an individual or its condition before dispersal and mating.

Concerning movement between patches, our model assumes that dispersal is cost-free. Cost-free dispersal allows a straightforward interpretation of our analytical results in terms of distribution or flow of individuals in different patches. However this assumption may prove inadequate in many real situations where mortality occurs during movement or dispersers are less competitive (Roncè, 2007). When the assumption of cost-free dispersal is relaxed in our two patch asexual model, the CS dispersal rate from poor patches should always be nil ( $d_p = 0$ ), since this limits the overall costs. Whether there is dispersal from good patches should depend on the relative values of the cost of dispersal and the ratio in resources  $F$ , i.e. whether the benefit in resources available to dispersers is high enough to compensate for the cost of dispersal.

Immigration is random in our model because dispersing individuals have the same probability to settle in any patch. If dispersers select habitat, i.e. prefer to establish in one kind of patches, the distribution and flow of individuals at CS strategies should be unchanged, compared to the situation without habitat selection. Hence, dispersal rates from good and poor patches should be modified to satisfy Eqs. (12) and (15). Habitat selection has thus the potential to modify CS dispersal rates.

Compared to the dispersal strategies examined in the present study, a superior strategy is to delay dispersal after habitat quality variation. Indeed, delaying dispersal allows to assess future patch quality before deciding to leave or not (informed dispersal; Clobert et al., 2009). If investigators also sample habitat quality after environmental variation, this may explain why a majority of studies report dispersal from low-quality/high-density habitats toward good-quality/low-density habitats (Bowler and Benton, 2005). Delayed dispersal, coupled with habitat selection, even has the potential to result in resource matching if information can be gathered about the suitability and occupancy of different patches before settling (Clobert et al., 2009). In our model, dispersal occurs before variation of habitat quality, a strategy that results in undermatching but that may still be selected for in short-lived species when time constraints dictate to disperse at an early stage (e.g., insects; McCauley, 1989).

Provided that the CS strategies we found are also evolutionarily stable, the model makes additional predictions. At first, dispersal rates should increase when habitat disturbance increases (Fig. 1). This is in agreement with observations showing that species occupying disturbed habitats and early successional stages often have very good dispersal mechanisms (Pickett and Thompson, 1978; Washburn and Cornell, 1981; Levin et al., 1984; Wissinger, 1997). Concerning the values of CS dispersal rates, the model's predictions are not clear-cut because a family of co-existing CS strategies is found: only the distribution and flow of individuals at the CS strategies are unique. Complicating further the picture, dispersal may be higher from good or from poor habitats, depending on the values of parameters  $F$ ,  $g$  and  $\sigma$ . Testing the predictions of the model may therefore prove tricky in the absence of a controlled experimental setting. Measuring the distribution of short generation time organisms in an experiment that varies the environment temporally is more likely to bring the appropriate information.

Disturbance and succession are ubiquitous landscape features. Natural exogenous disturbance, subsequent succession, or habitat-use by man all affect the compositions of vegetable and animal assemblages (Heinselman, 1973; Schowalter, 1985). Forests or shrublands are modeled by fire, wind and water motion (Christensen 1985). Forests are also exploited for wood through logging activity. Cultivated fields are ephemeral and disturbed habitats, varying in habitat quality with crop type and crop growth (Thorbeck and Topping 2005; Benvenuti, 2007). Patterns of succession can also be found in marine ecosystems (Huston and Smith,

1987). Such processes, either stochastic or deterministic, sometimes have the properties of a Markov chain (Wagooner and Stephens 1970; Horn, 1975; Olivieri et al., 1995; Valverde and Silvertown, 1997). In this context, dispersal may evolve in a way similar to that described in our model. Among insects, for example, frequent changes in land use modify habitat quality in milkweed beetle populations, independently from the age of these populations (McCauley, 1989). Forked fungus beetles live in connected populations around logs appropriate for fungal growth that slowly decompose and lose their suitability (Whitlock, 1992). Concerning dispersal strategy, the rodents *Microtus pennsylvanicus* live in ephemeral early successional patches of vegetation and massive emigration can be observed from populations while the habitat is still capable of supporting a large number of mice (Christian, 1970), a behavior that may be expected from our model.

One may also wonder whether the present model can predict the behavior of foraging animals in a temporally variable environment. Because reproductive values in different patches are equal at the CS strategies, the distribution of individuals in our model seems only driven by the availability of resources at any generation. However, because in a stationary Markov chain all patches spend the same proportion of time in different states, averaging resources over time should lead individuals to distribute equally among the different patches. The specificity in our model is that individuals are free to disperse between two time steps, enabling them to anticipate the variation of resources. We do not know of an experiment studying the distribution of individuals in such a context. Implementing a Markovian process for resources input while allowing for dispersal may thus give valuable information concerning the ability of animals to learn the pattern of variation and anticipate the distribution of resources.

### Authors' contribution

RA performed the analyses and wrote the manuscript. PdV performed analyses and contributed to the writing of the manuscript. JMG designed the study, contributed to the analyses and wrote the manuscript.

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### Appendix A. Proofs of the results for the asexual model

#### A.1. Model analysis

We computed a simplified analytical expression of the fitness function  $W(v^0, v)$  with variables  $v = (d_p, a)$  and  $v^0$  where  $a = F_C d_C - F_P d_P$  using Mathematica (Wolfram, 2008). Then, we computed the selection measures (Eq. (8)); we found that  $S_P(v) = 0$  whatever



parameters values and whatever variables values. This means that, after changing variables  $(d_p, d_G)$  to  $(d_p, a)$ , the dimension along  $d_p$  can be considered as selectively neutral. Consequently, Eq. (9) becomes  $S_A(v^*) = 0$ , and solving it leads to  $a^* = (\sigma(F_G - F_P)) / (2g(1 - g))$ . There is thus an infinite number of singular strategies which can be written as  $v^* = (d_p^*, a^* = \sigma(F_G - F_P) / (2g(1 - g)))$  where  $d_p^*$  is not subject to selection and hence can take any value within  $[0, 1]$ .

As explained in Section 2.2.3, the trait under selection of any of the singular strategies,  $a^*$ , is convergent stable if the eigenvalue of the matrix  $AJ^*$  (where  $J^*$  is the Jacobian matrix of the selection gradient evaluated at the singular strategy and  $A$  is the mutational matrix) corresponding to this trait is negative. The Jacobian of our system evaluated at any of the singular strategies  $v^*$  reads  $J^* = \begin{pmatrix} 0 & 0 \\ 0 & \lambda \end{pmatrix}$  where  $\lambda$  is a negative term. For any mutational matrix  $A = \begin{pmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{pmatrix}$ , the product  $AJ^*$  equals  $\begin{pmatrix} 0 & \alpha_{12}\lambda \\ 0 & \alpha_{22}\lambda \end{pmatrix}$ . Its eigenvalues are 0 and  $\alpha_{22}\lambda$ . The non-zero eigenvalue corresponds to the evolution of the trait  $a$ , i.e. the trait under selection and is negative (because  $\alpha_{22}$  is a mutation rate, a positive term). Therefore any strategy  $a^*$  is convergent stable in the sense of Lyapunov (Section 2.2.3; Leimar, 2009). The other trait,  $d_p$ , is not subject to selection so that we do not expect its convergence to a specific value. Finally, any singular strategy  $v^* = (d_p^*, a^* = \sigma(F_G - F_P) / (2g(1 - g)))$ , where  $d_p^*$  can take any value within  $[0, 1]$ , is thus locally convergent stable.

Note that because  $d_p$  can change neutrally and  $a$  in fact depends on  $d_p$  ( $a = F_G d_G - F_P d_p$ ), we expect  $a$  to converge to any value such that  $a = a^*$ ; we do not expect  $d_p$  to converge to a specific value along the “line”  $a = a^*$ . The term  $d_p$  can also change while  $a$  converges to  $a^*$  because of mutational correlations between the two traits (term  $\alpha_{12}\lambda$  in matrix  $AJ^*$  above).

For the biological interpretation of the results, it is helpful to come back to the original variable  $d = (d_p, d_G)$ : locally convergent stable singular strategies are the vectors  $d^* = (d_p^*, d_G^*)$  such that  $F_G d_G^* - F_P d_p^* = (\sigma(F_G - F_P)) / (2g(1 - g))$ , with dispersal rates within the interval  $[0, 1]$ .

The selection Hessian matrix of our system evaluated at any singular strategy,  $H^*$ , equals the zero matrix whatever parameter values. This does not allow us to conclude about evolutionarily stability or instability (Section 2.2.3). Given that the CS strategies we find form a continuum of strategies, a polymorphism of dispersal strategies may evolve once a CS strategy has been reached.

### A.2. Undermatching after habitat quality change

Let us define  $\Delta_{JI}(d)$  as the number of individuals (scaled relative to the total number of patches  $N$ ) after dispersal and habitat quality variation in  $J$ -patches, formerly  $I$ -patches:

$$\Delta_{JI}(d) = \sigma_{JI} \delta_I(d)$$

with  $\sigma_{JI}$  and  $\delta_I(d)$  defined by Eqs. (4) and (11) respectively. Let us define  $F_{JI}$  as the amount of resources (scaled relative to the total number of patches  $N$ ) in  $J$ -patches, formerly  $I$ -patches:

$$F_{GG} = F_G \left( g - \frac{\sigma}{2} \right)$$

$$F_{PG} = F_P \frac{\sigma}{2}$$

$$F_{GP} = F_G \frac{\sigma}{2}$$

$$F_{PP} = F_P \left( 1 - g - \frac{\sigma}{2} \right).$$

After simplification,

$$\frac{\Delta_{GG}(d)}{F_{GG}} = \frac{\delta_G(d)}{gF_G}$$

$$\frac{\Delta_{PG}(d)}{F_{PG}} = \frac{\delta_G(d)}{gF_P}$$

$$\frac{\Delta_{GP}(d)}{F_{GP}} = \frac{\delta_P(d)}{(1-g)F_G}$$

$$\frac{\Delta_{PP}(d)}{F_{PP}} = \frac{\delta_P(d)}{(1-g)F_P}.$$

At the CS strategies,

$$\delta_G(d^*) = gF_G - \frac{\sigma}{2}(F_G - F_P)$$

$$\delta_P(d^*) = (1-g)F_P + \frac{\sigma}{2}(F_G - F_P).$$

When  $0 < \sigma < 1$ , because  $\sigma/2 < g$  and  $\sigma/2 < (1-g)$ , it comes that:

$$\frac{\Delta_{GG}(d^*)}{F_{GG}} < 1$$

$$\frac{\Delta_{PG}(d^*)}{F_{PG}} > 1$$

$$\frac{\Delta_{GP}(d^*)}{F_{GP}} < 1$$

$$\frac{\Delta_{PP}(d^*)}{F_{PP}} > 1.$$

Thus, the distribution of individuals after habitat quality change undermatches the distribution of resources. However, for  $\sigma = 0$  (no variation of habitat quality),

$$\frac{\Delta_{GG}(d^*)}{F_{GG}} = 1 \text{ and } \frac{\Delta_{PP}(d^*)}{F_{PP}} = 1$$

and for  $\sigma = 2g = 2(1-g)$ , which implies that  $g = 1/2$  and  $\sigma = 1$  (the quality of all patches changes),

$$\frac{\Delta_{PG}(d^*)}{F_{PG}} = 1 \text{ and } \frac{\Delta_{GP}(d^*)}{F_{GP}} = 1.$$

In these two special cases, when environmental change is perfectly predictable, the distribution of individuals after habitat quality change matches the distribution of resources.

## Appendix B. Sexual models

### B.1. Models writing and analysis

For the DDM model, only males and females disperse. A dispersal strategy thus consists of a vector  $d = (d_{fP}, d_{fG}, d_{mP}, d_{mG})$ . For the DMD model, only males and zygotes disperse. A dispersal strategy thus consists of a vector  $d = (d_{mP}, d_{mG}, d_{zP}, d_{zG})$ .

For both sexual models, let  $W_I(d^0, d)$  be the fitness of an  $I$ -class focal individual with strategy  $d^0$  in a resident population with strategy  $d$ . Recall that the fitness is defined as the expected number of gene copies transmitted to the next generation by the focal individual. As for the asexual model, we can write the fitness of an  $I$ -class individual as

$$W_I(d^0, d) = V_P W_{PI}(d^0, d) + V_G W_{GI}(d^0, d)$$

where  $V_I$  is defined by Eq. (7). We then split the expected number of gene copies that an  $I$ -class focal individual produces in a  $L$ -patch,  $W_{LI}(d^0, d)$ , into a female and a male term:

$$W_{LI}(d^0, d) = W_{LI}^f(d^0, d) + W_{LI}^m(d^0, d).$$

Let  $P_{JI}^f(d^0)$  be the probability that an  $I$ -class female will be fertilized in a  $J$ -patch, and  $Z_{IJ}(d^0, d)$  the probability that a zygote produced in a  $J$ -patch will be a  $L$ -class reproducing individual in the next generation. As a female can be fertilized either in a  $G$ -

in a P-patch, and because each gene copy is transmitted to a female gamete with probability 1/2, we can write

$$W_{II}^f(d^o, d) = \frac{1}{2} (Z_{LP}(d^o, d)P_{PI}^f(d^o) + Z_{LG}(d^o, d)P_{GI}^f(d^o)).$$

With the same reasoning as that used to obtain Eq. (5), we express  $P_{JI}^f(d^o)$  terms:

$$\begin{aligned} P_{PP}^f(d^o) &= 1 - d_{fP}^o + (1 - g)d_{fP}^o \\ P_{PG}^f(d^o) &= (1 - g)d_{fG}^o \\ P_{GP}^f(d^o) &= gd_{fP}^o \\ P_{GG}^f(d^o) &= 1 - d_{fG}^o + gd_{fG}^o \end{aligned} \tag{B.1}$$

The competition between zygotes depends on the quality of their habitat, therefore

$$Z_{LJ}(d^o, d) = Z_{LPJ}(d^o, d) + Z_{LGJ}(d^o, d).$$

A zygote produced in a J-patch becomes a reproducing individual in a L-patch which was a K-patch before habitat quality variation if (i) this zygote disperses from its J-patch to a K-patch (and/or stay if  $J = K$ ) (probability  $P_{KJ}^z(d^o)$ ), and (ii) the K-patch becomes a L-patch because of habitat quality variation (probability  $\sigma_{LK}$ , Eq. (4)), and (iii) the zygote, now in a L-patch, formerly K-patch, survives density regulation to become a reproducing individual for the next generation (probability  $P_{LK}^c(d)$ ):

$$Z_{LKJ}(d^o, d) = P_{KJ}^z(d^o)\sigma_{LK}P_{LK}^c(d).$$

The zygote dispersal term  $P_{KJ}^z(d^o)$  is expressed similarly to the female dispersal term:

$$\begin{aligned} P_{PP}^z(d^o) &= 1 - d_{zP}^o + (1 - g)d_{zP}^o \\ P_{PG}^z(d^o) &= (1 - g)d_{zG}^o \\ P_{GP}^z(d^o) &= gd_{zP}^o \\ P_{GG}^z(d^o) &= 1 - d_{zG}^o + gd_{zG}^o \end{aligned} \tag{B.2}$$

The competition term  $P_{LK}^c(d)$  is the ratio of the number of sexually mature individuals that all L-patches, formerly K-patches, can carry, over the number of zygotes that are produced in these patches. Recall that we assume the number of males is large enough to fertilize all females while the number of females is limiting. The number of zygotes produced is thus equal to the number of females. Let  $\zeta_K(d)$  be the amount of females in all K-patches after female dispersal. Then, the competition terms are

$$\begin{aligned} P_{PP}^c(d) &= \frac{N(1 - g)\sigma_{PP}F_P}{\zeta_G(d)P_{PG}^z(d)\sigma_{PP} + \zeta_P(d)P_{PP}^z(d)\sigma_{PP}} \\ P_{PG}^c(d) &= \frac{Ng\sigma_{PG}F_P}{\zeta_G(d)P_{GG}^z(d)\sigma_{PG} + \zeta_P(d)P_{GP}^z(d)\sigma_{PG}} \\ P_{GP}^c(d) &= \frac{N(1 - g)\sigma_{GP}F_G}{\zeta_G(d)P_{PG}^z(d)\sigma_{GP} + \zeta_P(d)P_{PP}^z(d)\sigma_{GP}} \\ P_{GG}^c(d) &= \frac{Ng\sigma_{GC}F_G}{\zeta_G(d)P_{GG}^z(d)\sigma_{GC} + \zeta_P(d)P_{GP}^z(d)\sigma_{GC}} \end{aligned}$$

where  $\zeta_K(d)$  is expressed by

$$\zeta_K(d) = N_G P_{KG}^f(d) + N_P P_{KP}^f(d)$$

with  $N_I$  defined by Eq. (6).

Let us now determine the male fitness term  $W_{II}^m(d^o, d)$ . We define  $P_{JI}^m(d^o)$  as the probability that an I-class male is in a J-patch after dispersal and  $\mu_J(d)$  as the amount of males in J-patches after dispersal. Consequently,  $P_{JI}^m(d^o)\zeta_J(d)/\mu_J(d)$  is the probability that an I-class male will fertilize a female in a J-patch. The same decomposition as for the female fitness leads to the following expression of the male fitness:

$$W_{II}^m(d^o, d) = \frac{1}{2} \left( Z_{LP}(d^o, d)P_{PI}^m(d^o)\frac{\zeta_P(d)}{\mu_P(d)} + Z_{LG}(d^o, d)P_{GI}^m(d^o)\frac{\zeta_G(d)}{\mu_G(d)} \right)$$

This expression assumes that the dispersal rate  $d_{zI}$  of zygotes is determined by the genotype of both parents. Assuming that it is

determined by the genotype of the female parent only (which may be more relevant for the DMD life cycle as it should mimic a plant life cycle), the terms  $Z_{LJ}(d^o, d)$  are to be replaced by  $Z_{LJ}(d, d)$ . Using this different assumption does not change any of our results and conclusions (not shown).

The term  $P_{JI}^m(d^o)$  is expressed similarly to female and zygote dispersal

$$\begin{aligned} P_{PP}^m(d^o) &= 1 - d_{mP}^o + (1 - g)d_{mP}^o \\ P_{PG}^m(d^o) &= (1 - g)d_{mG}^o \\ P_{GP}^m(d^o) &= gd_{mP}^o \\ P_{GG}^m(d^o) &= 1 - d_{mG}^o + gd_{mG}^o \end{aligned} \tag{B.3}$$

and the term  $\mu_J(d)$  similarly to  $\zeta_J(d)$ :

$$\mu_J(d) = N_G P_{JG}^m(d) + N_P P_{JP}^m(d).$$

Combining the equations of this section and computing the reproductive values with Eq. (7) allows to express the fitness of an I-class individual with the four parameters of the model ( $F_P, F_G, g$  and  $\sigma$ ) and the two variables ( $d^o$  and  $d$ ).

For both DDM and DMD models, let us define  $\delta_I^f(d)$  and  $\delta_I^m(d)$  as the expected number of gene copies transmitted in I-patches via females and males respectively, after zygote dispersal and before habitat quality variation (scaled relative to the total number of patches  $N$ ). Because zygotes are produced in number equal to the number of females, and each zygote carries one gene copy from each of its female and male parent:

$$\delta_I^f(d) = \delta_I^m(d) = \zeta_G P_{IG}^z(d) + \zeta_P P_{IP}^z(d).$$

We define  $\phi_{JI}^f(d)$  and  $\phi_{JI}^m(d)$  as the flow of gene copies transmitted from I-patches to J-patches before habitat quality variation via females and males respectively (scaled relative to the total number of patches):

$$\begin{aligned} \phi_{PG}^f(d) &= gF_G (P_{PG}^z(d)P_{GG}^f(d) + P_{PP}^z(d)P_{PG}^f(d)) \\ \phi_{GP}^f(d) &= (1 - g)F_P (P_{GG}^z(d)P_{GP}^f(d) + P_{GP}^z(d)P_{PP}^f(d)) \\ \phi_{PG}^m(d) &= gF_G \left( P_{PG}^z(d)P_{GG}^m(d)\frac{\zeta_G(d)}{\mu_G(d)} + P_{PP}^z(d)P_{PG}^m(d)\frac{\zeta_P(d)}{\mu_P(d)} \right) \\ \phi_{GP}^m(d) &= (1 - g)F_P \left( P_{GG}^z(d)P_{GP}^m(d)\frac{\zeta_G(d)}{\mu_G(d)} + P_{GP}^z(d)P_{PP}^m(d)\frac{\zeta_P(d)}{\mu_P(d)} \right). \end{aligned}$$

For the DDM model, zygotes do not disperse ( $d_{zI}^o = d_{zI} = 0$ ). Similarly to the asexual 2-patch model (see Section 2.2.3), it is helpful to analyze the model using alternative variables: we now write the fitness as a function of the vectors  $v = (d_{fP}, d_{mP}, a_f, a_m)$  and  $v^o$  where  $a_f = F_G d_{fG} - F_P d_{fP}$  and  $a_m = F_G d_{mG} - F_P d_{mP}$ . Selection measures are then defined as

$$\begin{aligned} S_{fP}(v) &= \frac{\partial W(v^o, v)}{\partial d_{fP}^o} \Big|_{v^o = v} \\ S_{mP}(v) &= \frac{\partial W(v^o, v)}{\partial d_{mP}^o} \Big|_{v^o = v} \\ S_{fA}(v) &= \frac{\partial W(v^o, v)}{\partial a_f^o} \Big|_{v^o = v} \\ S_{mA}(v) &= \frac{\partial W(v^o, v)}{\partial a_m^o} \Big|_{v^o = v}. \end{aligned}$$

These probabilities vanish at singular points, i.e. CS strategies  $v^*$  necessarily satisfy:

$$S_{fP}(v^*) = 0, S_{mP}(v^*) = 0, S_{fA}(v^*) = 0, S_{mA}(v^*) = 0. \tag{B.4}$$

For the DMD model, females do not disperse ( $d_{fI}^o = d_{fI} = 0$ ), and it is again helpful to analyze the model using alternative variables: we now write the fitness as a function of the vectors  $v = (d_{zP}, d_{mP}, a_z, a_m)$  and  $v^o$  where  $a_z = F_G d_{zG} - F_P d_{zP}$ . Selection measures are then

defined as

$$S_{zP}(v) = \frac{\partial W(v^o, v)}{\partial d_{zP}^o} \Big|_{v^o = v}$$

$$S_{mP}(v) = \frac{\partial W(v^o, v)}{\partial d_{mP}^o} \Big|_{v^o = v}$$

$$S_{zA}(v) = \frac{\partial W(v^o, v)}{\partial a_z^o} \Big|_{v^o = v}$$

$$S_{mA}(v) = \frac{\partial W(v^o, v)}{\partial a_m^o} \Big|_{v^o = v}.$$

These probabilities vanish at singular points, i.e. CS strategies  $v^*$  necessarily satisfy:

$$S_{zP}(v^*) = 0, S_{mP}(v^*) = 0, S_{zA}(v^*) = 0, S_{mA}(v^*) = 0. \tag{B.5}$$

We determined convergence stability of singular strategies as done with the asexual 2-patch model (see Section 2.2.3 and Appendix A.1). Specifically, the local dynamics of trait evolution around a singular strategy  $v^*$  is described by  $d(v - v^*)/dt = AJ^*(v - v^*)$  where  $A$  is the mutational matrix. We show (Appendix B.2) that (i) after changing the variables of the models, some of the traits can be considered as selectively neutral, and (ii) the product  $AJ^*$  is a semi-negative definite matrix, the non-zero eigenvalues of which corresponding to the traits under selection. This allows us to conclude that the traits under selection of the singular strategies are convergent stable in the sense of Lyapunov (Leimar, 2009). The other traits can change neutrally and/or evolve following genetic correlations between the different traits, but they do not converge to a specific value. For both sexual models, the matrix  $J^*$  is not simple and we were not able to determine the sign of each element. We thus computed the product  $AJ^*$  numerically. To do so, we generated 10,000 random singular strategies (with dispersal rates within  $[0,1]$ ), with parameters drawn in uniform distributions:  $g$  drawn in  $]0, 1[$ ,  $F_C$  drawn in  $]1, 10[$ ,  $F_P$  drawn in  $[1, F_C[$ , and  $\sigma$  drawn in  $]0, \min(2g, 2(1-g))]$ . For the mutational matrix, we generated random positive definite matrices using the Wishart distribution with 2 degrees of freedom.

According to Leimar (2009), a sufficient condition for convergent stable strategies to be evolutionarily stable is that the Hessian matrix evaluated at the singular strategy,  $H^*$ , is negative definite. We show (Appendix B.2) that in our sexual models,  $H^*$  equals the zero matrix, which does not allow us to conclude about evolutionarily stability nor instability.

## B.2. Proofs of the results for the sexual models

### B.2.1. DDM model

We computed a simplified analytical expression of the fitness function  $W(v^o, v)$  with variables  $v = (d_{fP}, d_{mP}, a_f, a_m)$  and  $v^o$  where  $a_f = F_C d_{fG} - F_P d_{fP}$  and  $a_m = F_C d_{mG} - F_P d_{mP}$  using Mathematica (Wolfram, 2008). Then, we computed the selection measures; we found that  $S_{fP}(v) = 0$  and  $S_{mP}(v) = 0$  whatever parameters values and whatever variables values. This means that, after changing variables  $(d_{fP}, d_{mP}, d_{fG}, d_{mG})$  to  $(d_{fP}, d_{mP}, a_f, a_m)$ , the dimensions along  $d_{fP}$  and  $d_{mP}$  can be considered as selectively neutral. Consequently, Eq. (B.4)

$$\text{becomes } \begin{cases} S_{fA}(v^*) = 0 \\ S_{mA}(v^*) = 0 \end{cases}, \text{ and solving it leads to } \begin{cases} a_f^* = \frac{\sigma(F_C - F_P)}{2g(1-g)} \\ a_m^* = \frac{\sigma(F_C - F_P)}{2g(1-g)}. \end{cases}$$

There is thus an infinite number of singular strategies which can be written as  $v^* = (d_{fP}^*, d_{mP}^*, a_f^* = \sigma(F_C - F_P)/(2g(1-g)), a_m^* = \sigma(F_C - F_P)/(2g(1-g)))$  where  $d_{fP}^*$  and  $d_{mP}^*$  are not subject to selection and hence can take any value within  $[0,1]$ .

We numerically computed the matrix  $AJ^*$  for 10,000 random singular strategies (see Appendix B.1). For all random singular strategies, we found that the eigenvalues of  $AJ^*$  corresponding to

the traits under selection ( $a_f$  and  $a_m$ ) are negative. Therefore, the singular strategies  $v^* = (d_{fP}^*, d_{mP}^*, a_f^* = \sigma(F_C - F_P)/(2g(1-g)), a_m^* = \sigma(F_C - F_P)/(2g(1-g)))$ , where  $d_{fP}^*$  and  $d_{mP}^*$  can take any value within  $[0,1]$ , are locally convergent stable.

For the biological interpretation of the results, it is helpful to come back to the original variable  $d = (d_{fP}, d_{mP}, d_{fG}, d_{mG})$ : locally convergent stable singular strategies are the vectors  $d^* = (d_{fP}^*, d_{mP}^*, d_{fG}^*, d_{mG}^*)$  such that  $F_C d_{fG}^* - F_P d_{fP}^* = F_C d_{mG}^* - F_P d_{mP}^* = \sigma(F_C - F_P)/(2g(1-g))$ , with dispersal rates within the interval  $[0,1]$ .

The selection Hessian matrix of our system evaluated at any singular strategy,  $H^*$ , equals the zero matrix whatever parameter values. This does not allow us to conclude about evolutionarily stability nor instability. Given that the CS strategies we find form a continuum of strategies, a polymorphism of dispersal strategies may evolve once a CS strategy has been reached.

### B.2.2. DMD model

We computed a simplified analytical expression of the fitness function  $W(v^o, v)$  with variables  $v = (d_{zP}, d_{mP}, a_z, a_m)$  and  $v^o$  where  $a_z = F_C d_{zG} - F_P d_{zP}$  and  $a_m = F_C d_{mG} - F_P d_{mP}$  using Mathematica (Wolfram, 2008). Then, we computed the selection measures; we found that  $S_{zP}(v) = 0$  and  $S_{mP}(v) = 0$  whatever parameters values and whatever variables values. This means that, after changing variables  $(d_{zP}, d_{mP}, d_{zG}, d_{mG})$  to  $(d_{zP}, d_{mP}, a_z, a_m)$ , the dimensions along  $d_{zP}$  and  $d_{mP}$  can be considered as selectively neutral.

Consequently, Eq. (B.5) becomes  $\begin{cases} S_{zA}(v^*) = 0 \\ S_{mA}(v^*) = 0 \end{cases}$ , and solving it leads

to  $a_z^* = \sigma(F_C - F_P)/(2g(1-g))$  and  $a_m^* = 0$ . There is thus an infinite number of singular strategies which can be written as  $v^* = (d_{zP}^*, d_{mP}^*, a_z^* = \sigma(F_C - F_P)/(2g(1-g)), a_m^* = 0)$  where  $d_{zP}^*$  and  $d_{mP}^*$  are not subject to selection and hence can take any value within  $[0,1]$ .

We numerically computed the matrix  $AJ^*$  for 10,000 random singular strategies (see Appendix B.1). For all random singular strategies, we found that the eigenvalues of  $AJ^*$  corresponding to the traits under selection ( $a_z$  and  $a_m$ ) are negative. Therefore, the singular strategies  $v^* = (d_{zP}^*, d_{mP}^*, a_z^* = \sigma(F_C - F_P)/(2g(1-g)), a_m^* = 0)$ , where  $d_{zP}^*$  and  $d_{mP}^*$  can take any value within  $[0,1]$ , are locally convergent stable.

For the biological interpretation of the results, it is helpful to come back to the original variable  $d = (d_{zP}, d_{mP}, d_{zG}, d_{mG})$ : locally convergent stable singular strategies are the vectors  $d^* = (d_{zP}^*, d_{mP}^*, d_{zG}^*, d_{mG}^*)$  such that  $F_C d_{zG}^* - F_P d_{zP}^* = \sigma(F_C - F_P)/(2g(1-g))$  and  $F_C d_{mG}^* - F_P d_{mP}^* = 0$ , with dispersal rates within the interval  $[0,1]$ .

As for the previous models, the Hessian selection matrix evaluated at the singular strategy equals the zero matrix, which does not allow us to conclude about evolutionarily stability nor instability. Given that the CS strategies we find form a continuum of strategies, a polymorphism of dispersal strategies may evolve once a CS strategy has been reached.

## Appendix C. Asexual model with three qualities of patches (“three-patch model”)

We define the environment as a stationary Markov chain consisting of three kinds of patches in proportion  $p_i$  ( $i \in \{1, 2, 3\}$ ). The amount of resources available in  $i$ -patches is  $F_i$ . The parameter  $\sigma$  is no more convenient and we have to solve the system:

$$p_1 \sigma_{1,1} + p_1 \sigma_{2,1} + p_1 \sigma_{3,1} = p_1 \sigma_{1,1} + p_2 \sigma_{1,2} + p_3 \sigma_{1,3}$$

$$p_2 \sigma_{1,2} + p_2 \sigma_{2,2} + p_2 \sigma_{3,2} = p_1 \sigma_{2,1} + p_2 \sigma_{2,2} + p_3 \sigma_{2,3}$$

$$p_3 \sigma_{1,3} + p_3 \sigma_{2,3} + p_3 \sigma_{3,3} = p_1 \sigma_{3,1} + p_2 \sigma_{3,2} + p_3 \sigma_{3,3},$$

where  $\sigma_{ji}$  is the proportion of  $i$ -patches that become  $j$ -patches after habitat quality variation:

$$\forall i \in \{1, 2, 3\}, \sum_{j=1}^3 \sigma_{ji} = 1.$$

Then we have the solutions:

$$\begin{aligned} \forall (r_1, r_2, r_3, r_4) \in [0, 1]^4, \\ \sigma_{2,1} &= \frac{(r_1 + r_3 + r_4)p_2 + p_1 r_1 - r_1}{p_1} \\ \sigma_{3,1} &= \frac{r_1 + r_2 - (r_1 + r_2)p_1 - (r_1 + r_2 + r_3)p_2}{p_1} \\ \sigma_{1,2} &= r_4 \\ \sigma_{3,2} &= r_3 \\ \sigma_{1,3} &= r_2 \\ \sigma_{2,3} &= r_1. \end{aligned}$$

A dispersal strategy consists of three dispersal rates:  $d = (d_1, d_2, d_3)$ .

The fitness  $W_i(d^o, d)$  of an  $i$ -class individual ( $i \in \{1, 2, 3\}$ ) is now expressed as

$$W_i(d^o, d) = \sum_{k=1}^3 V_k W_{k,i}(d^o, d). \tag{C.1}$$

where  $W_{k,i}(d^o, d)$  is the expected number of offspring that an  $i$ -class focal individual produces in a  $k$ -patch, and  $V_i$  is the asymptotic contribution of an individual born in a  $i$ -patch to the future gene pool of the population. The vector of the individual reproductive values  $(V_1, V_2, V_3)$  is now defined as

$$(V_1, V_2, V_3) \begin{bmatrix} W_{1,1}(d, d) & W_{1,2}(d, d) & W_{1,3}(d, d) \\ W_{2,1}(d, d) & W_{2,2}(d, d) & W_{2,3}(d, d) \\ W_{3,1}(d, d) & W_{3,2}(d, d) & W_{3,3}(d, d) \end{bmatrix} = (V_1, V_2, V_3)$$

with

$$\sum_{i=1}^3 Q_i V_i = 1$$

where  $Q_i$  is the proportion of  $i$ -class individuals:

$$Q_i = \frac{p_i F_i}{\sum_{j=1}^3 p_j F_j}.$$

The fitness function can be expressed as

$$W(d^o, d) = \sum_{i=1}^3 Q_i W_i(d^o, d). \tag{C.2}$$

To produce offspring in a  $k$ -patch, an  $i$ -class focal individual may disperse to a  $j$ -patch ( $j \in \{1, 2, 3\}$ ) which becomes a  $k$ -patch after habitat quality variation or not disperse from a  $i$ -patch which becomes a  $k$ -patch after habitat quality variation. Thus we can write:

$$W_{k,i}(d^o, d) = (1 - d_i^o) \sigma_{k,i} A_{k,i}(d) + d_i^o \sum_{j=1}^3 p_j \sigma_{k,j} A_{k,j}(d) \tag{C.3}$$

$A_{k,i}(d)$  is the ratio of the amount of resources in  $k$ -patches, formerly  $i$ -patches, over the number of individuals reproducing in these patches:

$$A_{k,i}(d) = \frac{F_k N p_i \sigma_{k,i}}{N_i (1 - d_i) \sigma_{k,i} + p_i \sigma_{k,i} \sum_{j=1}^3 N_j d_j}$$

Combining the equations of this section allows to express the fitness function of an  $i$ -class individual with the parameters of the model ( $F_i, p_i$  and  $\sigma_{j,i}$ ) and the two variables ( $d^o$  and  $d$ ).

Selection measures are defined by

$$\begin{aligned} S_1(d) &= \frac{\partial W(d^o, d)}{\partial d_1^o} \Big|_{d^o = d} \\ S_2(d) &= \frac{\partial W(d^o, d)}{\partial d_2^o} \Big|_{d^o = d} \\ S_3(d) &= \frac{\partial W(d^o, d)}{\partial d_3^o} \Big|_{d^o = d}. \end{aligned}$$

These probabilities vanish at singular points, i.e. CS strategies  $d^*$  necessarily satisfy:

$$\begin{aligned} S_1(d^*) &= 0 \\ S_2(d^*) &= 0 \\ S_3(d^*) &= 0. \end{aligned} \tag{C.4}$$

After changing the variables of the model similarly to what we did for the other models, we found that the Jacobian matrix  $J^*$  of the selection gradient evaluated at any of the singular strategies (Eq. (20)) equals the zero matrix. Therefore, we cannot conclude about convergence stability or instability of these strategies. However, assuming that there is no mutational correlation between dispersal rates, singular strategies are convergent stable if the following relation is satisfied:

$$\begin{aligned} \frac{\partial S_1(d)}{\partial d_1} \Big|_{d = d^*} &< 0 \\ \frac{\partial S_2(d)}{\partial d_2} \Big|_{d = d^*} &< 0 \\ \frac{\partial S_3(d)}{\partial d_3} \Big|_{d = d^*} &< 0. \end{aligned} \tag{C.5}$$

We numerically verified that these inequalities are verified for candidate CS strategies (dispersal rates satisfying Eq. (20)) with the same method as in Appendix B.2.1 for the DDM model. For all strategies tested, we found that Eq. (C.5) is verified. We concluded that dispersal rates satisfying Eq. (20) are convergent stable dispersal strategies, at least when there is no mutational correlation between dispersal rates.

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