Evolutionarily Stable Dispersal Rate in a Metapopulation with Extinctions and Kin Competition

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We derive an analytic expression for the evolutionarily stable dispersal rate that formalizes the balance between the effects of four factors: the cost of dispersal, the extinction rate, the coefficient of relatedness and the mode of dispersal (i.e. the probability of common origin of immigrants). This result allows us to study the effects of each factor and, more interestingly, the interactions between them. In particular, we show that the evolutionarily stable dispersal rate is not always a decreasing function of the cost of dispersal and an increasing function of relatedness. These counter-intuitive results are discussed in the light of kin selection theory. We also present the results of numerical simulations in which relatedness is not a fixed parameter but depends on different parameters including dispersal itself. We discuss these results and show how the evolutionarily stable dispersal rate is affected by the environment and the life history traits of the species. More generally, this paper presents a simple formalism allowing the study of the effects of kin selection in unstable environments (i.e. with extinctions and recolonizations). The implications of this formalism for the understanding of the evolution of other life history traits is briefly discussed.

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Introduction

The evolution of dispersal results from a balance between opposing forces. Two main factors may select against dispersal. First, the cost of dispersal: dispersing individuals might incur a cost due to either increased mortality during the dispersal phase, or disadvantages during the settling period in the novel environment. Second, the cost due to the spatial variability of the environment. In a spatially heterogeneous environment, dispersal will be selected against because it will often lead to bad environments (Balkau & Feldman, 1973; Hastings, 1983; Holt, 1985). Other factors

favour dispersal, in particular, when the environment is variable in time, some level of dispersal will be selected for (Gillespie, 1981; Levin *et al.*, 1984; McPeek & Holt, 1992). An extreme case of temporal variability is the local extinction of populations. Indeed, when extinctions occur, dispersal is favoured because each particular population will eventually become extinct and only offspring that have emigrated will be able to recolonize these sites (Comins *et al.*, 1980; Olivieri *et al.*, 1995). The degree of relatedness within each population is also involved in the evolution of dispersal since dispersal may be adaptive if it reduces competition between relatives (Hamilton & May, 1977; Comins *et al.*, 1980; Motro, 1982a, b; Frank, 1986; Taylor, 1988; Taylor & Frank, 1996).

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In this paper, we consider the evolution of dispersal under the action of four factors: the cost of dispersal, the extinction of populations, the relatedness within populations and the mode of dispersal (i.e. the probability of common origin of immigrants). Our approach allows us to unify the results of several authors and shows in a simple way how different factors (environmental or life-history traits) may interact. This approach is based on a two-step argument: first, we use the "direct fitness" formulation of inclusive fitness developed by Taylor & Frank (1996) to derive an analytic expression for the evolutionarily stable dispersal rate, where the assumption of no extinctions that was assumed in the preceding models (Frank, 1986; Taylor, 1988; Taylor & Frank, 1996) is relaxed. Throughout this first part, we consider that relatedness is a fixed parameter. In a second step, we relax this assumption and study the evolution of dispersal, where relatedness is used as a dynamical variable that depends on several factors including dispersal itself. Even though the latter situation is far more realistic, we report the results of both cases for heuristic reasons. This approach, largely inspired by the work of Frank (1986) and Taylor (1988), enables us to study both direct (when relatedness is used as a fixed parameter) and indirect effects (when

relatedness is used as a dynamical variable) of several parameters, on the evolution of dispersal. The explicit consideration of direct and indirect effects reveals some interesting interactions between the various factors affecting dispersal. Indeed, factors typically thought to select for decreased dispersal, e.g. higher cost of dispersal, may, under certain circumstances, select for increased dispersal. We report only main results in the text. The detailed mathematical derivations are confined to the appendices.

The General Model

LIFE CYCLE

The model presented below is based on the following assumptions (see also Table 1 and Fig. 1; the description of the life cycle starts right after the competition stage in Fig. 1): (1) the habitat consists of an infinite number of patches; (2) after extinctions and before reproduction, each patch is either empty or contains a population of N reproducing haploid and asexual individuals. The average within population relatedness is R. (3) Each individual produces n offspring. Generations are discrete and non-overlapping. (4) A proportion $1 - d$ of the progeny remains in the same population, while a

TABLE 1

Main parameters and variables of the model. Relatedness can either be a parameter or a variable

Parameters

c	Cost of dispersal
N	Population size
n	Fecundity
e	Extinction rate
ϕ	Dispersal mode: probability of common origin of immigrants

Variables

|	
d	Dispersal rate
d^*	ES dispersal rate
d_{ext}	Dispersal rate below which the metapopulation goes extinct
d_{lim}	Dispersal rate above which all sites are at carrying capacity
m	Immigration rate
N'	Number of individuals competing on non-extinct patches
z	Number of immigrants per generation in each patch
F_t	Frequency of population colonized t generations ago
k	Probability that a random individual is native to its patch
G_p	Marginal gain in fitness from philopatric offspring
G_d	Marginal gain in fitness from dispersing offspring
R	Average within-populations relatedness
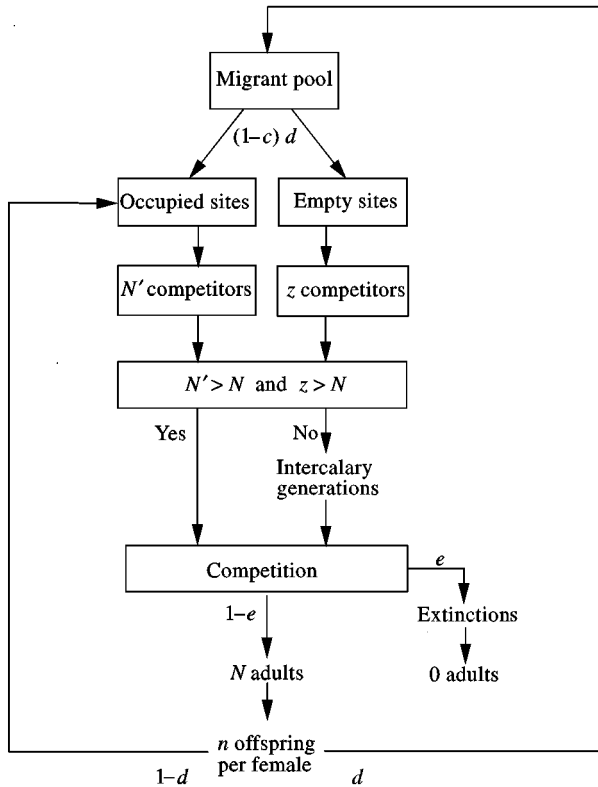
FIG. 1. General life cycle. See Table 1 for the definition of the parameters.

proportion d disperses and may eventually reach another patch (full or empty). (5) Dispersing progeny incur a cost of dispersal, c. (6) Different modes of dispersal are characterized by the probability ϕ of common origin of migrants (Whitlock & McCauley, 1990). For example, if $\phi = 0$, individuals emigrating from a given population will settle in different populations (or in other terms, all immigrants come from different populations). When $\phi = 1$, all immigrants come from a single population (i.e. propagule pool model of dispersal). The relatedness among immigrants is thus equal to ϕR. For example, the biological interpretation of this parameter can be easily understood within the context of host–parasite interactions. See the Discussion for more details. (7) Each population is colonized both by philopatric individuals and by immigrants. Empty patches are recolonized by immigrants. (8) For mathematical simplicity we assume that, before reproduction, both colonized and recolonized sites contain N individuals. This condition is always fulfilled if the fecundity of each

individual is very large (i.e. there are enough immigrants to fill each patch). When fecundity is limited, we assume that unsaturated populations grow to N through intercalary generations as in Comins *et al.* (1980). (9) Extinctions of populations occur after colonization and recolonization with a probability e (even newly recolonized populations may go extinct). For the sake of simplicity, we assume throughout the paper that all populations receive the same number of immigrants, $dNn(1 - c)(1 - e)$, which also corresponds to the number of founders in the case of newly colonized populations.

Under these assumptions, the metapopulation is viable if (see Appendix A)

$$d > d_{ext} = \frac{e}{Nn(1 - c)(1 - e)}. \tag{1}$$

This condition simply means that the number of successful migrants has to be greater than the extinction rate for the metapopulation to survive.

For the derivation of the evolutionarily stable (ES) dispersal rate, we will consider only the cases where the probability of recolonization of empty patches is equal to one, which leads to an even more stringent condition (see Appendix A):

$$d > d_{lim} = \frac{1}{Nn(1 - c)(1 - e)}. \tag{2}$$

If condition (2) is fulfilled, at equilibrium the metapopulation reaches a stable age structure distribution (Olivieri *et al.*, 1995):

$$F_t = e(1 - e)^t \tag{3}$$

where F_t is the frequency of patches that have been colonized t generations ago.

INCLUSIVE FITNESS

Let us focus on a particular individual i. As first pointed out by Hamilton (1964, 1970), the inclusive fitness of this individual will depend on its own success as also on the success of its related neighbours. As a consequence, the derivation of the inclusive fitness requires the incorporation of the effects of relatives through the characterization of the group j of age t that interacts with the

individual i. In this respect, let us assume that the dispersal rate of the offspring of an individual i in a population j of age t is d_{ij}^t. The average dispersal rate in a population j of age t is d_j^t and the average dispersal rate in the whole metapopulation is d. The fitness W of a randomly chosen individual in the metapopulation depends on its own phenotype, d_{ij}^t, and on the average phenotype, d_j^t, of its group of neighbours:

$$W = \sum_{t=0}^{\infty} (F_t \cdot (d_{ij}^t, d_j^t)). \qquad (4)$$

The calculation of W is given in Appendix B.

<div align="center">MARGINAL GAINS IN FITNESS</div>

Let the phenotype of individuals be determined by their genic value, x. Following the approach of Taylor & Frank (1996) and Frank (1997, 1998), we assume the population to be monomorphic (i.e. all individuals have the same genic value, x^*), select a random allele at this locus, mutate that allele and its identical by descent copies and ask if this mutant allele will increase in frequency. A standard condition for x^* to be evolutionarily stable is that the derivative of W with a deviant value x, is zero at $x = x^*$. The derivative of W (dW/dx) is the rate of change of the inclusive fitness, ΔW^{IF}, with a deviant value x and can be decomposed in the following way:

$$\Delta W^{IF} = \Delta W_1^{IF} + \Delta W_2^{IF}, \qquad (9)$$

where $G_p = -\Delta W_1^{IF}$ and $G_d = \Delta W_2^{IF}$ are the marginal gains in fitness from philopatry and from dispersal (Taylor & Frank, 1996). In Appendix C we show that

$$G_p = p[d] \left[(1-e) - Rk \right], \qquad (10)$$

$$G_d = \frac{e}{d} [1 - R\phi] + p[d](1-c)(1-e)^2$$

$$\left[\frac{1 - d + (1 - R\phi)(1-c)(1-e)d}{1 - d + (1-c)(1-e)d} \right], \quad (11)$$

where $p[d]$ is the probability that an offspring competing in a non-extinct population will win

a breeding spot multiplied by the number of offspring and k is the probability that a random individual is native to its patch (see Appendix C for their explicit formulation).

Not surprisingly, the gain from philopatry depends on the probability that an offspring will win a breeding spot in the same undisturbed population and on the average relatedness between reproducing individuals. The gain from dispersal, on the other hand, has two components. The first part on the right-hand side of eqn (11) represents the gain from offspring dispersing in previously disturbed patches, while the second part represents the gain from offspring dispersing in undisturbed patches. It is worth noting that G_p depends only on the relatedness between immigrants (i.e. the product $R\phi$), while the mode of dispersal has no effect on G_p if individuals within populations are not related (i.e. $R = 0$), just as relatedness does not affect G_p if all immigrants originate from different populations (i.e. $\phi = 0$). These observations will be very useful later to explain the effects of the various parameters on the evolutionarily stable dispersal rate.

<div align="center">EVOLUTIONARILY STABLE DISPERSAL RATE</div>

The condition on d to be evolutionarily stable (i.e. $\Delta W^{IF} = 0$) reduces to

$$G_p = G_d. \qquad (12)$$

Solving eqn (12) leads to the general solution

$$d^* = \frac{A - \sqrt{A^2 - 4e(1 - R\phi)B}}{2B}, \qquad (13)$$

where

$$A = c + e^2(1-c) + e - R(1-e)$$

$$- 2e\phi R(c + e(1-c)), \qquad (14)$$

$$B = (c + e(1-c))^2 - R(1-e) - \phi R((1-c)^2$$

$$- e(3 - 6c + 2c^2) + e^2(3 - 4c + c^2)). \quad (15)$$

In the absence of extinctions this reduces to

$$d^* = \begin{cases} \dfrac{R - c}{R - c^2 + \phi R(1 - c)^2}, & \text{if } c < R, \\[2mm] 0 & \text{if } c > R \end{cases}$$

which is a generalization of the ES dispersal rate found by Frank (1986), taking the mode of dispersal into account [Frank's result, $d^* = (R - c)/(R - c^2)$, was obtained for $\phi = 0$].

When some extinctions occur, our solution yields the result obtained by Comins *et al.* (1980), $d^* = e/(1 - (1 - c)(1 - e))$, if we assume that $N \to \infty$ (i.e. when $R \to 0$). Moreover, this solution collapses to Van Valen's (1971) result, $d^* = e$, if we further assume that $c = 1$.

The effects of the four parameters of the model (e, ϕ, R, c) on d^* are summarized in Fig. 2 and Table 2. The major results are:

(1) *The effect of e*: as previously shown by several authors (Comins *et al.*, 1980; Comins, 1982; Levin *et al.*, 1984; Olivieri *et al.*, 1995) d^* always increases with e. Contrary to the "stable" case treated by Frank, when extinctions occur, some level of dispersal is always selected for. A special case occurs when $\phi = 1$ and $R = 1$. In this case, d^* is equal to 0.5, whatever be the cost of dispersal and the extinction rate [Fig. 2(f)].

(2) *The effect of ϕ*: not surprisingly, when all individuals are unrelated (i.e. $R = 0$), the mode of dispersal (ϕ) does not affect the evolution of dispersal [cf. Figs. 2(a) and (d)]. When $R > 0$, d^* is lowered by an increase of the probability of common origin, ϕ, because then the immigrants increasingly compete against relatives. This effect can be seen in the expression of the marginal gains in fitness from dispersal: G_d is a decreasing function of ϕR.

(3) *The effect of R*: when $\phi = 0$, d^* always increases with R. Dispersal evolves in order to avoid kin competition (Hamilton & May, 1977; Comins *et al.*, 1980; Frank, 1986). Note that the marginal gain in fitness from philopatry, G_p, is always a decreasing function of relatedness (see also Fig. 3). However, when $\phi > 0$ and the cost of dispersal is low, d^* can decrease when relatedness increases [see Fig. 2(d)–(f)]. This counter intuitive result can be explained by the kin competition that occurs between immigrants as soon as they are related (i.e. $\phi R > 0$). This effect is especially important in newly colonized populations where competition takes place only between immigrants. In this case, higher levels of relatedness induce an extra cost of dispersal, i.e. the cost of competing against relatives in newly founded populations.

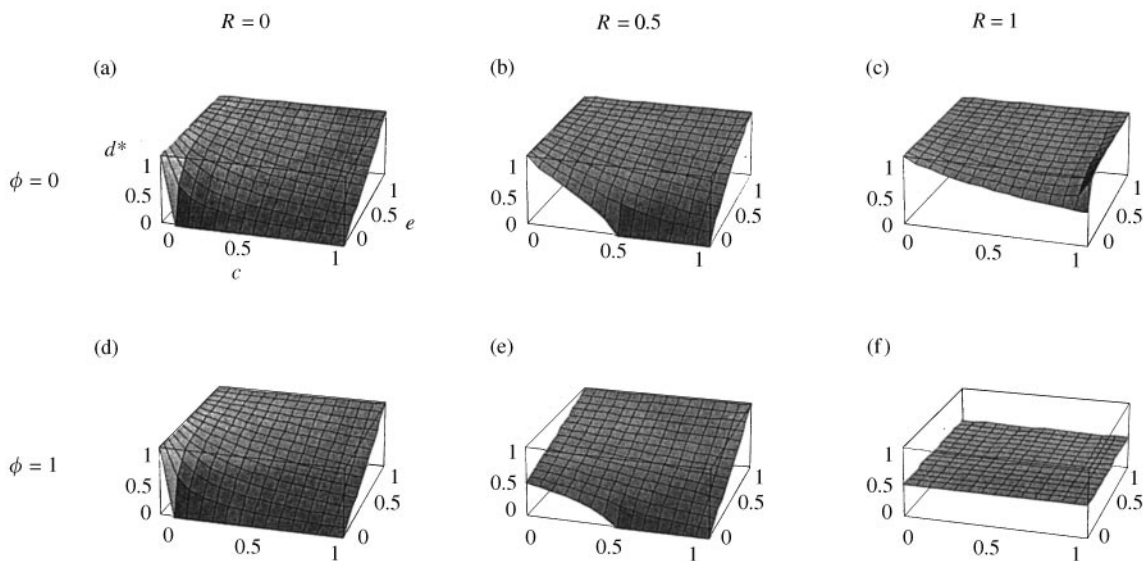(4) *The effect of c*: Frank (1986) showed that in the absence of extinctions d^* always decreases

FIG. 2. Evolutionary stable dispersal rate (d^*) vs. the cost of dispersal, c, and the extinction rate (e). On the upper row $\phi = 0$ and (a) $R = 0$, (b) $R = 0.5$ and (c) $R = 1$. On the lower row $\phi = 1$ and (d) $R = 0$, (e) $R = 0.5$ and (f) $R = 1$.

Main effects of increases of various parameters and variables on d^*. The last two parameters, N and n, only affect d^* through their effects on relatedness

Parameter	Condition	Effect on d^*	Mechanism
e		↗	Colonization of new sites
ϕ		↘	Kin competition among immigrants
R	$\phi = 0$	↗	Kin competition in the natal site
	$\phi > 0, e > 0$	↘	Kin competition among immigrants
c	$e = 0$	↘	Avoid cost of dispersal
	$\phi = 0, e > 0, R \to 1, c \to 1$	↗	Kin competition in newly founded populations
N	$\phi = 0$	↘	Kin competition in the natal site
	$\phi > 0, e > 0$	↗	Kin competition among immigrants
n	$c \to 0, e = 0$	↗	Because R ↗
	$c \to 1, e > 0$	↘	Because R ↘

when the cost of dispersal, c, increases. This is not always the case when extinctions occur. In particular, when relatedness is very high d^* can increase with c [see Fig. 2(c)]. Comins *et al.* (1980) found a similar result (an increase of d^* for high c) which they interpreted as a way to avoid the extinction of the entire metapopulation. Indeed, when c and e are large, the recolonization process may not be sufficient to compensate for the extinction of populations [see eqn (1)]. However, this explanation cannot account for our results because the increase of d^*, with increases in the cost of dispersal, can be observed even when the entire metapopulation is viable. For instance, the metapopulation is always viable if we assume infinite fecundity (i.e. $n \to \infty$) though this assumption does not alter the result [see eqn (13)].

We propose an alternative explanation based on the comparison of the marginal gains in fitness from philopatry, G_p, and from dispersal, G_d. Indeed, it can be shown that the return from dispersal is always a decreasing function of the cost of dispersal. The return from philopatry, however, has a complex interaction with c mediated by the level of relatedness. To understand this interaction, it is useful to notice that increases in the cost of dispersal result in lower numbers of successful immigrants, and hence as c increases each population contains a larger proportion of philopatric individuals. When relatedness is low, such increases of the cost of dispersal increase the return from philopatry, since at the same time the return from dispersal

decreases, overall, selection favours decreases of the dispersal rate. When relatedness is large, however, increases in c cause more and more competition between highly related philopatric individuals and hence decrease the return from philopatry (see Fig. 3). Actually, when both c and R are large, marginal gains in fitness from both dispersal and philopatry decrease with higher costs of dispersal. Extinctions, through the benefit accrued to dispersing individuals during the colonization of empty sites, provide an extra benefit from dispersal and thus lead to the increase of d^* with higher cost of dispersal when c and R are very large [see Fig. 3(b)]. This last benefit is in turn cancelled if dispersing individuals are highly related (i.e. large ϕ) and indeed, in that case, we do not observe any increase of d^* for very large c. [see Fig. 2(f)].

The formalization that we used explicitly identifies the effects of kin selection through the coefficient of relatedness, R. Including this parameter explicitly, allows us to derive an analytic expression that clarifies the effect of several parameters [see eqn (13)]. Moreover, the marginal gains in fitness analysis untangles the effects of these parameters and provides explanations for counter-intuitive results (e.g. increase of d^* with higher c or with lower R). Although very useful, the assumption that relatedness is a fixed parameter is unrealistic. Indeed, relatedness depends on the dispersal rate, the mode of dispersal, as well as on several other demographic and environmental factors (see Fig. 4 and Appendix D). In
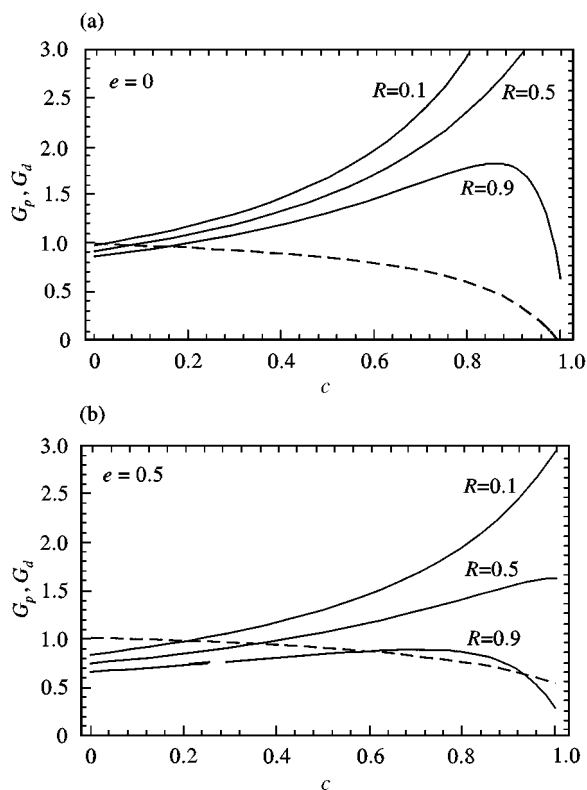
FIG. 3. Marginal gains in fitness from philopatry, G_p (full line) and from dispersal, G_d (dashed line) vs. the cost of dispersal, c, for three levels of relatedness ($R = 0.1$, 0.5 and 0.9), for $d = 0.85$, $\phi = 0$ and for (a) $e = 0$ and (b) $e = 0.5$. For these parameter values the benefit to produce a disperser, G_d, always decreases with c and does not depend on relatedness. When relatedness increases the return from philopatry, G_p, may decrease with c (for high values of c). When some extinctions occur, this can lead to an increase of the ES dispersal rate when c increases (see explanations in the text).
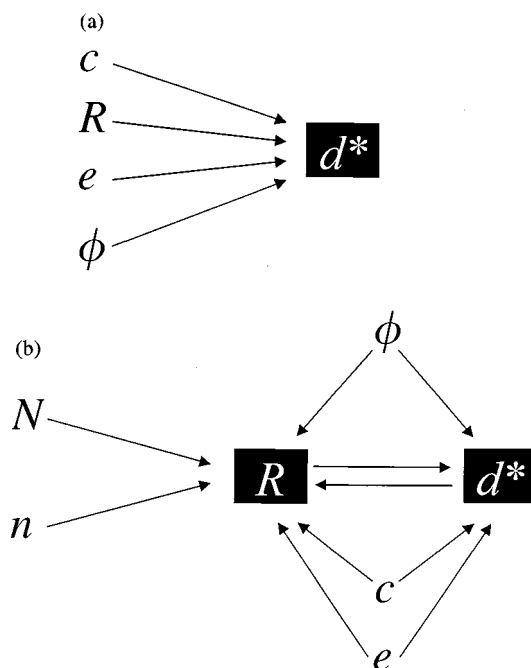

FIG. 4. Direct and indirect effects of various parameters on the evolution of dispersal. When relatedness is used as a fixed parameter (a), we study the direct effects of parameters on the evolution of dispersal. When relatedness is used as a dynamical variable (b), we study both the direct and the indirect effects of parameters on the evolution of dispersal

the following section, we extend the previous model by taking into account the indirect effects of these parameters on the evolution of dispersal.

Relatedness as a Dynamical Variable

In the first subsection, we outline the main results of the effects of life-history traits and environmental parameters on relatedness (the derivation of relatedness is given in the Appendix D and a summary of these effects is presented in Table 3). We assume that each individual has an infinite number of offspring ($n \to \infty$). This assumption simplifies the algebra, ensures that the metapopulation is viable and all the sites are occupied as soon as some dispersal occurs [see

eqns (1) and (2)] and helps to better understand the effects of the other parameters. We then relax the hypothesis of infinite fecundity.

In the second subsection, we discuss how these parameters affect dispersal directly and indirectly through their effects on relatedness.

RELATEDNESS

The derivation of relatedness presented in Appendix D allows us to study the effects of the environment (cost of dispersal, extinction rate, population size) and of the life-history traits of the species (mode of dispersal, fecundity) on relatedness. A summary of these effects is presented in Table 3. Below we comment on the main results.

First, consider the case $\phi = 0$ and $n \to \infty$. As already noted by many authors, relatedness decreases when either the size of the populations, N, or the immigration rate, m, increases (m is the probability that a randomly chosen individual is

TABLE 3

Main effects of increases of various parameters and variables on relatedness

Parameter	Condition	Effect on R
N		↘
n	$e = 0$	↗
	$e > 0$	↘
	$\phi = 0$	↘
d	d small, $\phi = 1$	↘
	d large, $\phi = 1$	↗
ϕ		↗
c		↗
e	$\phi = 0$	↘
	$\phi = 1$	↗

an immigrant). The immigration rate depends on several factors (d, c, e; see Appendix D.1). When d increases or when c decreases, immigration increases and relatedness decreases. Since extinct populations are always recolonized in our model, higher extinction rates, like immigration, increase the "turn over" of the metapopulation and tend to decrease relatedness.

Second, when immigrants originate from the same population (i.e. $\phi > 0$), R increases because immigrants are related. An increase of ϕ, may also affect qualitatively the effects of dispersal. In particular, when $\phi = 1$, relatedness is minimized for intermediate values of dispersal. Indeed, if dispersal is very low, relatedness is very high because of the classical effect of migration. If dispersal is very high, relatedness is very high as well, but this is so, because there are almost no philopatric individuals and immigrants are all related (i.e. $\phi = 1$). For intermediate values of dispersal, relatedness is minimized since immigrants and philopatric individuals are not related.

Finally, higher fecundity tends to increase relatedness in the absence of extinctions (see Appendix D.2). This effect is due to an increase of the probability that two randomly chosen offspring are sibs. However, when some extinctions occur, relatedness increases when fecundity decreases. This arises because reduced fecundity results in lower numbers of immigrants and, more importantly, in lower numbers of founders in empty patches. When newly founded popula-

tions are founded by fewer colonizers, relatedness tends to increase. This increase of relatedness because of founding events occurs when either fecundity, the size of the populations or dispersal decreases but also when the cost of dispersal or the extinction rate increases.

COEVOLUTION OF THE DISPERSAL RATE AND RELATEDNESS

Let us first assume that each individual produces an infinite number of offspring (i.e. $n \rightarrow \infty$). The results obtained through numerical simulations are qualitatively very similar to those obtained when relatedness is used as a fixed parameter. Below we report the main results:

(1) *The effect of e*: d^* always increases with e (Fig. 5). A special case is when $N = 1$. Indeed, if $N = 1$ relatedness is equal to one. If $\phi = 1$, we are exactly in the case shown in Fig. 2(f) and $d^* = 0.5$ whatever be the cost of dispersal and the extinction rate.

(2) *The effect of N*: the carrying capacity acts only indirectly (via its effect on relatedness) on the evolution of dispersal (see Fig. 4). Indeed, increase in population size decreases relatedness and, as a consequence, greatly affect d^* (Fig. 5). When $\phi = 0$, lower relatedness always decreases dispersal (Fig. 2) and, not surprisingly, larger carrying capacity decreases d^* [see Figs 5(a) and (b); see also Taylor, 1988]. However, when $\phi > 0$ and when extinctions occur, lower relatedness may select for higher dispersal rates (see Fig. 2). Consequently, in this situation, larger carrying capacity may increase the evolutionarily stable dispersal rate [see Fig. 5(c) and (d)].

(3) *The effect of c*: d^* decreases with the cost of dispersal (Fig. 5). The only exception occurs when N is small (i.e. $N < 5$) where d^* can increase with c [see Fig. 5(a) and (b)]. However, we show in the following subsection that, when the assumption of infinite fecundity is relaxed, d^* may increase when c is high under a much wider range of population sizes.

(4) *The effect of ϕ*: an increase in the probability of common origin has two effects. It increases the relatedness among immigrants and, at the same time it increases the average within-population relatedness, R. The first effect is an
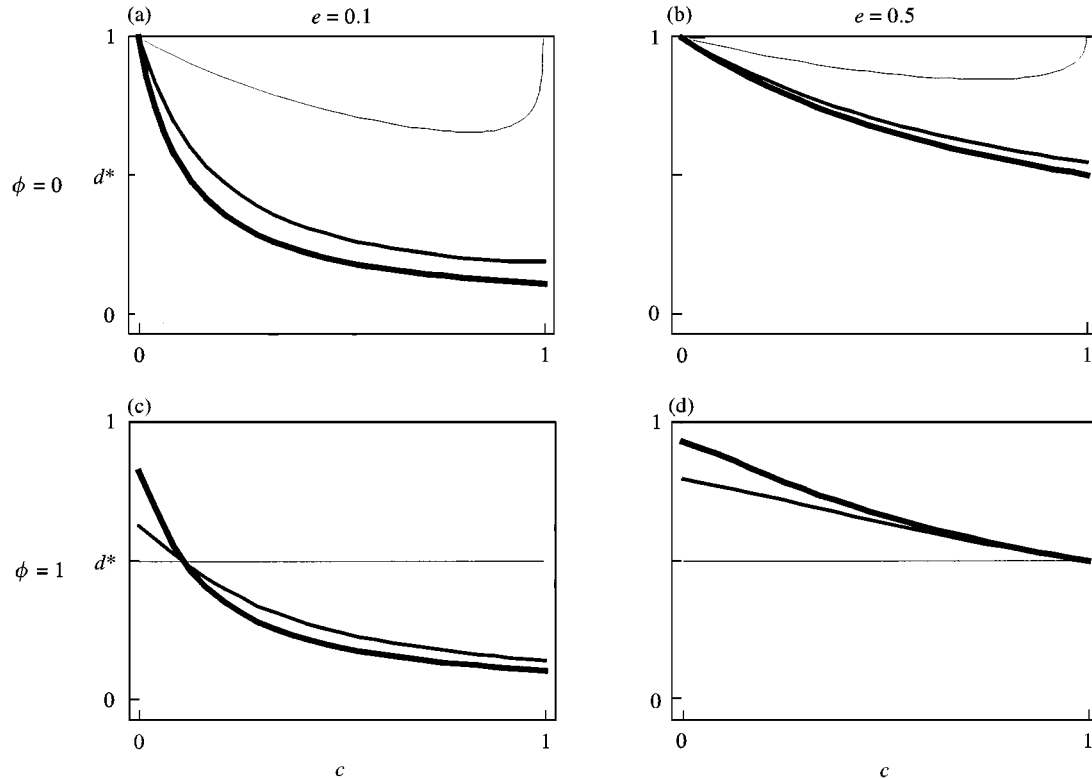
FIG. 5. Numerical solutions of the ES dispersal rate (d^*) vs. the cost of dispersal for asexual organisms for different sizes of the population: $N = 1$ (light), $N = 10$ (medium) and $N = 100$ (bold). On the upper row $\phi = 0$ and on the lower row $\phi = 1$. On the left, $e = 0.1$; on the right, $e = 0.5$.

additional cost of dispersal, while the second one is an additional cost of philopatry. Overall, numerical simulations show that the extra cost due to kin competition is higher for immigrants than for philopatric individuals and, as a consequence, higher ϕ generally decreases the ES dispersal rate (see Fig. 5).

We now assume that each individual produces a finite number, n, of offspring. This more realistic assumption has mainly two effects. First, the dynamics of the metapopulation can be greatly affected by a finite fecundity. In particular, when some extinctions occur, the whole metapopulation can get extinct (see Appendix A). Second, it modifies the calculation of relatedness (see Appendix D.2). We first show the effects of relaxing the assumption of infinite fecundity on the evolution of dispersal. Since we know from Appendix A that if $d < d_{lim}$, a certain proportion of the metapopulation will be empty even after the dispersal phase, we will consider only the cases where $d^* > d_{lim}$. Indeed, if some populations stay

empty after the recolonization phase, both the derivation of the ES dispersal rate and the calculation of relatedness would not be correct.

Figure 6 shows the effect of fecundity on the ES dispersal rate. The effects of fecundity are only indirect (see Fig. 4). When c is very low, d^* tends to increase with higher fecundity. This is due to the increase of relatedness with higher fecundity when the average number of immigrants is very large (i.e. when e and c are very low; see explanations in the previous subsection on relatedness). When c is very high, higher fecundity decreases d^* because it also decreases relatedness.

Finite fecundity also interacts with the effects of other parameters. In particular, when each individual produces only a finite number of offspring, d^* tends to increase with very high values of the cost of dispersal, whatever be the size of the populations. This result is similar to the results obtained by Comins *et al.* (1980) where they always found an increase of d^* with very high c.
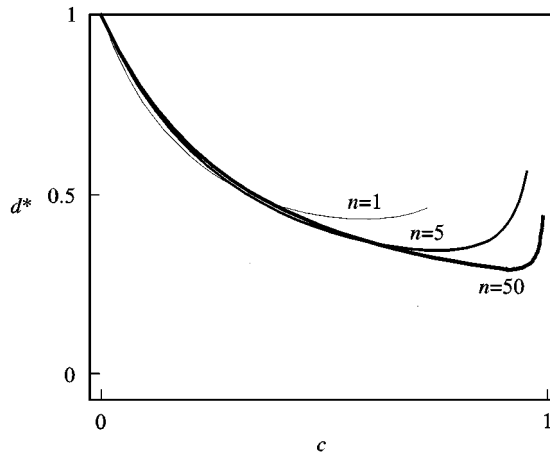
FIG. 6. Effect of fecundity on ES dispersal rate. Numerical solutions of the ES dispersal rate (d^*) vs the cost of dispersal for $n = 1$ (light), $n = 5$ (medium) and $n = 50$ (bold). Other parameter values: $N = 10$, $e = 0.2$, $\phi = 0$. When c is very large the evolutionarily stable dispersal rate can lead to situations where the metapopulation occupancy is not maximized (i.e. $d^* < d_{\lim}$). We did not derive d^* in these cases.

There is a large amount of theoretical work on differences between evolutionarily stable and optimal dispersal rates (Hamilton & May, 1977; Comins et al., 1980; Motro, 1982a; Olivieri et al., 1995; Olivieri & Gouyon, 1997). An optimal dispersal rate is the one that maximizes the occupancy of the metapopulation (see Hamilton & May, 1977; Comins et al., 1980). In our case, it would correspond to a dispersal rate $> d_{lim}$. In agreement with several previous studies (Comins et al., 1980; Olivieri et al., 1995; Olivieri & Gouyon, 1997), we found that, when we assume a finite fecundity, selection could lead to suboptimal situations where $d^* < d_{lim}$ (Fig. 6).

Discussion

We studied the evolution of dispersal in a metapopulation subject to extinction and re-colonization. The kin selection model that we used allowed us to derive an analytic formulation of the ES dispersal rate. This expression formalizes the intuitive prediction that the ES dispersal rate results from a balance between the effects of the cost of dispersal, the probability of extinction, the coefficient of relatedness and the mode of dispersal (i.e. the probability of common origin of immigrants, ϕ). Our analysis revealed some non-

intuitive results, in that factors usually known to select for increased (or decreased) dispersal rates, may under certain circumstances have the opposite effect. For instance, increases in the cost of dispersal do not necessarily select for decreases in the dispersal rate. In particular, we developed a kin selection argument to explain the fact (already noted by Comins et al., 1980) that when some extinctions occur, the ES dispersal rate may increase with the cost of dispersal, when c and the average within-population relatedness are large. Interestingly, we also found that higher relatedness does not always select for higher dispersal rates. When immigrants originate from the same population (i.e. ϕ is very high), the ES dispersal could decrease with relatedness because of the kin competition that occurs between immigrants.

In a second step, following Frank (1986) and Taylor (1988), we studied the evolution of dispersal, where relatedness is a dynamical variable depending on various parameters including the dispersal rate itself. This approach allowed us to study the effects of parameters that indirectly affect the evolution of dispersal through their effects on relatedness. For example, when the size of the population and fecundity increase, the ES dispersal rate generally decreases. Moreover, it appears very clearly from our approach that the mode of dispersal (i.e. the probability of common origin) affects the evolution of dispersal both directly and indirectly through its effect on relatedness (see Fig. 4). Very interestingly these two effects may, in certain cases, act in opposing directions. First, higher values of ϕ increase the intensity of kin competition among dispersers. This selects against dispersal. Second, higher ϕ values increase the average within population relatedness which in turn tends to increase d^*. The evolutionary outcome results from a balance between these opposing effects. However, numerical simulations show that higher ϕ, very generally, selects for lower dispersal rates, d^*.

Our results can be compared to those obtained by Comins (1982), who found that the dispersal pattern (i.e. island model vs. stepping-stone model) did not affect the ES dispersal rate. In the stepping-stone model, it does not pay to disperse more than in the island model because the strength of kin competition increases in both the natal site and in the neighbouring site. In other

words, there is a higher cost to be philopatric but a lower benefit to disperse. There is one major difference between our model and that used by Comins (1982) which stems from our assumption that individuals from different populations are unrelated. By relaxing this assumption, Comins (1982) considered yet another cost of dispersal which arises from the relatedness between philopatric and immigrant individuals. This difference may explain the fact that we do find an effect of the mode of dispersal on the ES dispersal rate. Our formulation of the mode of dispersal is more related to, though different than, the concept of kin-structured migration (Fix, 1975, 1978; Rogers, 1987) than to the restriction of dispersal to neighbouring sites. As noted by Hedrick & Levin (1984), there is a number of species in which this kin-structured migration may occur. For example, there is some evidence for this type of migration in humans (Fix, 1978, 1981; Smouse et al., 1981), monkeys (Chepko-Sade & Olivier, 1979; Cheverud et al., 1978), voles (Beacham, 1979) and acorn wood-peckers (Koenig & Pitelka, 1979). Another special case of this type of migration may occur in numerous plants where migration involves multiseeded fruits, all individuals emerging from the same fruit being sibs. We therefore expect a higher effect than that of ϕ, since some immigrants (e.g. seeds of the same fruit) will not only share the same population of origin but the same mother as well. An example closer to our definition of ϕ is provided by parasite life cycles, where the mode of dispersal ϕ fully describes the different type of transmission from host to host. For example, in an air-borne disease, $\phi \to 0$ and for a vector-borne disease or a sexually transmitted disease, $\phi \to 1$. This formalism may help to understand the consequences of the type of transmission on parasite evolution (Frank, 1994; Gandon, 1999).

The assumptions concerning the genetic system could be easily modified to study the evolution of dispersal of diploid and haplodiploid organisms. Other assumptions concerning the demography could also be relaxed (e.g. non-equal densities, overlapping generations). This would allow us to test the robustness of our predictions under more realistic assumptions. Moreover, assuming a sexual mode of reproduction would allow us to study whether a maternal or an off-spring control of dipersal affects the evolution of dispersal. It has been shown that a parent–offspring conflict can emerge over the evolution of dispersal (Hamilton & May, 1977; Motro, 1983; Frank, 1986; Taylor, 1988). In this respect, it would be particularily interesting to see how the mode of dispersal and the extinctions of populations may affect this conflict.

Some of the predictions of our model could be tested either experimentally or using the comparative approach. For instance, the comparative approach could be used to test the effect of the mode of dispersal on the evolution of dispersal. Our model would predict that species adopting a kin structured type of migration (i.e. high ϕ) should tend to have lower dispersal rates. However, we are rather pessimistic because the difficulty in measuring the dispersal rate itself in a large number of cases is likely to be a major constraint for such tests.

An experimental approach, using host–parasite systems in particular, could perhaps prove more fruitful. A population of infected hosts can be regarded as a metapopulation of parasites, the death of hosts being analogous to parasite population extinctions. Within that context, relevant experiments may have already been performed. Indeed, Ebert & Mangin (1999) recently conducted a study on the relationships between within-host growth rate, parasite virulence, host extrinsic death rate and parasite dispersal rate in a system composed of the crustacean *Daphnia magna* and its microsporidian gut parasite *Glucoides intestinalis*. The authors showed that parasite transmission was positively correlated to host extrinsic death rate. One possible interpretation proposed by the authors, is that, increased host mortality selects for increased parasite dispersal rates. This interpretation is in agreement with a classical result of models on the evolution of dispersal, showing that higher extinction rates select for increased dispersal. We believe that more complex predictions of our model could be tested using a similar experimental approach.

In a broader perspective, this work presents a general model to study the evolution of altruism in a metapopulation with extinctions and recolonization. Both processes have been shown to play a determinant role in the evolution of social behaviours (Cohen & Eshel, 1976; Eshel,

1977). This model could be easily modified to study the evolution of other life-history traits such as parasite virulence (Frank, 1994, 1996a; Gandon, 1998) or policing behaviours (Frank, 1995, 1996b).

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APPENDIX A

Metapopulation Viability and Dispersal

Let us assume that, after dispersal, the metapopulation consists of two different types of patches: full and empty patches with respective frequencies F_f and $1-F_f$. The following recurrence equation describes the dynamics of such a system:

$$F_f' = (1 - e)F_f + r(eF_f + (1 - F_f)),$$

where the prime indicates subsequent generations and r is the probability that a patch is recolonized. At equilibrium $F_f' = F_f = \hat{F}_f$. There are two equilibria for this system, $\hat{F}_f = 0$ and

$$\hat{F}_f = \frac{r}{r + e(1 - r)}.$$

We modify the general model proposed by Levins (1969, 1970) by considering that r depends on the dispersal strategy. Let us assume that M is the average number of immigrants in each population:

$$M = (1 - e)\hat{F}_f Nn(1 - c)d.$$

If we further assume that each population receives exactly M immigrants we get

—If $M \geq 1$, $r = 1$.
—If $M < 1$, $r = M$.

The condition for the viability is $(1 - e)F_f > 1/T$, if T is the total number of populations in the metapopulation (i.e. at least one population must be present after extinctions for the metapopulation to be viable). This leads to the following condition on the dispersal rate:

$$d > d_{ext} = \frac{eT}{Nn(1 - c)(1 - e)(T - 1)}. \quad \text{(A.1)}$$

When $T \to \infty$,

$$d_{ext} \to \frac{e}{Nn(1 - c)(1 - e)}. \quad \text{(A.2)}$$

The limit dispersal rate, d_{lim}, is the rate above which all the sites will be occupied after the dispersal phase (i.e. $r = 1$ or $F_f = 1$):

$$d \geq d_{lim} = \frac{1}{Nn(1 - c)(1 - e)}. \quad \text{(A.3)}$$

It follows from this derivation that three cases are possible:

(1) If $d > d_{lim}$ the metapopulation is viable and all sites are occupied.
(2) If $d_{lim} > d \geq d_{ext}$ the metapopulation is viable but only a fraction ($\hat{F}_f$) of the metapopulation is occupied.
(3) If $d < d_{ext}$ the metapopulation is not viable.

In the present paper, we restrict our analysis to the case (1).

APPENDIX B

The Inclusive Fitness

The fitness of an individual i in a population j of age t is

$$W(d_{ij}', d_j^t) = W_1 + W_2,$$

where W_1 and W_2 are the expected numbers of progeny via philopatry or dispersal, respectively.

$$W_1 = n(1 - e)(1 - d_{ij}^t)p_{philo}[d_j^t], \quad \text{(B.1)}$$

where

$$p_{philo}[d_j^t] = \frac{1}{n(1 - d_j^t + (1 - e)(1 - c)d)}$$

is the probability that a philopatric offspring from a population of age t (that did not go extinct) will win a breeding spot.

$$W_2 = W_{2a} + W_{2b},$$

where W_{2a} and W_{2b} refer to the contribution to fitness through dispersed offspring that reach a population that did not go extinct [with probability $(1 - e)$] or an empty patch (with probability e), respectively. In populations that did not go extinct the dispersers compete with other immigrants as well as the residents. This leads to

$$W_{2a} = nd_{ij}^t(1 - e)(1 - c) \sum_{t'=1}^{\infty} (F_{t'} \cdot p_{disp}[d^{t'}]), \quad \text{(B.2)}$$

where $p_{disp}[d^{t'}]$ is the probability that a dispersed offspring competing on a random population of age t' will win a breeding spot:

$$p_{disp}[d^{t'}] = \frac{1}{n(1 - d^{t'} + (1 - e)(1 - c)((1 - \phi)d + \phi d_j^t))}.$$

The summation in eqn (B.2) gives the probability that a dispersed offspring competing on a random population that did not go extinct will win a breeding spot.

In newly colonized populations, dispersers compete only with other immigrants and therefore

$$W_{2b} = e \frac{(1 - c)d_{ij}^t}{((1 - \phi)d + \phi d_j^t)}. \quad \text{(B.2)}$$

This leads to

$$W(d_{ij}^t, d_j^t) = n(1 - e)((1 - d_{ij}^t)p_{philo}[d_j^t]$$

$$+ d_{ij}^t(1 - c) \sum_{t'=1}^{\infty} (F_{t'} \cdot p_{disp}[d^{t'}]))$$

$$+ e \frac{(1 - c)d_{ij}^t}{((1 - \phi)d + \phi d_j^t)}. \quad \text{(B.4)}$$

APPENDIX C

Marginal Gains in Fitness

The marginal gains in fitness from philopatry, G_p, and from dispersal, G_d, can be derived from:

$$G_p = -\Delta W_1^{IF} = -\sum_{t=0}^{\infty} F_t \left[\frac{dW_1}{d\,d_{ij}^t} \right]$$

$$= -\sum_{t=0}^{\infty} F_t \left[\frac{\partial W_1}{\partial d_{ij}^t} + \frac{\partial W_1}{\partial d_j^t} R_t \right],$$

$$G_d = \Delta W_2^{IF} = \sum_{t=0}^{\infty} F_t \left[\frac{dW_2}{d\,d_{ij}^t} \right]$$

$$= \sum_{t=0}^{\infty} F_t \left[\frac{\partial W_2}{\partial d_{ij}^t} + \frac{\partial W_2}{\partial d_j^t} R_t \right],$$

where

$$R_t = \frac{d d_j^t}{d d_{ij}^t} \quad \text{(C.1)}$$

is the relatedness between two random individuals in a population of age t (see Appendix D). If we further assume that the dispersal rate individuals adopt does not vary with the age of the populations (i.e. $d_{ij}^t = d_{ij}$ and $d_j^t = d_j$) we get

$$G_p = -\frac{\partial W_1}{\partial d_{ij}} - \frac{\partial W_1}{\partial d_j} \sum_{t=0}^{\infty} (F_t\, R_t), \quad \text{(C.2)}$$

$$G_d = \frac{\partial W_2}{\partial d_{ij}} + \frac{\partial W_2}{\partial d_j} \sum_{t=0}^{\infty} (F_t\, R_t) \quad \text{(C.3)}$$

It is important to note here that, even if dispersal does not vary with the age of the population, relatedness does vary with the age of the population (Withlock, 1992). As we can see in eqs (C.2) and (C.3), we will have to consider the average relatedness, R, within populations given by

$$R = \sum_{t=0}^{\infty} (F_t\, R_t). \quad \text{(C.4)}$$

At the first sight, it might appear surprising to neglect the variations among populations of

different ages at the phenotypic level (i.e. $d_{ij}^t = d_{ij}$) but not at the genotypic level (R varies with t). This apparent discrepancy can be justified if phenotypic variations are assumed to be very small. However, variation of the genetic structure cannot be neglected since the concept of relatedness does not depend on phenotypic *similarity* but on genetic *identity*.

The explicit derivation of eqs (C.2) and (C.3) yields

$$G_p = p[d]\,[(1-e) - Rk],\qquad \text{(C.5)}$$

$$G_d = \frac{e}{d}[1 - R\phi] + p[d](1-c)(1-e)^2$$

$$\left[\frac{1 - d + (1 - R\phi)(1-c)(1-e)d}{1 - d + (1-c)(1-e)d}\right],\quad \text{(C.6)}$$

where

$$p[d] = \frac{1}{1 - d + (1-e)(1-c)d}$$

is the probability that an offspring competing in a non-extinct population will win a breeding spot multiplied by the number of offspring and

$$k = \frac{(1-e)(1-d)}{1 - d + (1-c)(1-e)d}$$

is the probability that a random individual is native to its patch.

APPENDIX D

The Calculation of Relatedness

Since we assume haploidy and asexuality, R is equivalent to the coefficient of consanguinity, f (Michod and Hamilton, 1980; Taylor, 1988). It is important to note that relatedness is measured among juveniles after reproduction and before dispersal because only juveniles disperse and compete against each other.

D.1. INFINITE FECUNDITY

Whitlock and McCauley (1990) developed an analytic formulation of the coefficient of consan-

guinity in the population recolonized t generations ago, f_t. Using a similar recurrence equation we get

$$f_t = M_1 + M_2((1-m)^2 f_{t-1} + m^2\gamma),$$

where M_1 and M_2 are the probabilities that two individuals in the population are or are not sibs, respectively. When fecundity is very large

$$M_1 = \frac{1}{N},$$

$$M_2 = \frac{N-1}{N},$$

m is the immigration rate,

$$m = \frac{(1-c)(1-e)d}{1 - d + (1-c)(1-e)d}.$$

We assume that individuals of different populations are not related and therefore immigrants may be related only if they have emigrated from the same population. γ is the probability of identity of two immigrants and is equal to ϕR.

For newly founded populations we have

$$f_0 = R_0 = M_1 + M_2\gamma.$$

At the scale of the metapopulation this leads to

$$R' = \sum_{t=0}^{\infty} F_t R_t = \sum_{t=0}^{\infty} F_t f_t,$$

$$R' = eR_0 + (1 - e)$$

$$\times \sum_{t=1}^{\infty} [F_{t-1}[M_1 + M_2((1-m)^2 R_{t-1}$$

$$+ m^2\gamma)]]$$

$$R' = eR_0 + (1-e)[M_1 + M_2((1-m)^2 R + m^2\gamma)].$$

At equilibrium this yields

$$R = \frac{M_1}{1 - M_2((1-m)^2(1-e) + \phi((1-e)m^2 + e))}.$$

$$\text{(D.1)}$$

D.2. FINITE FECUNDITY

Using a similar recurrence equation we get

$$f_t = M_1 + M_2(P_p f_{t-1} + P_m \gamma),$$

where M_1 and M_2 are the probabilities of being sibs or non-sibs, respectively.

Different cases will have to be considered depending of the number of individuals, N', competing on non-extinct sites.

$$N' = immigrants + philopatric = z + Nn(1 - d),$$

where z is the number of immigrants per generation in each population, given by

$$z = M = Nn(1 - e)(1 - c)d,$$

where M is given in A:

if $N' > N$: $M_1 = \dfrac{n-1}{Nn-1}$, $M_2 = \dfrac{n(N-1)}{Nn-1}$;

if $N' < N$: $M_1 = \dfrac{\dfrac{Nn}{N'}-1}{Nn-1}$, $M_2 = \dfrac{n\left(N-\dfrac{N}{N'}\right)}{Nn-1}$.

P_p and P_m are the probabilities of choosing two different philopatric individuals or two different immigrants,

$$P_m = m\frac{Nn(1-c)(1-e)d-1}{Nn(1-d+(1-c)(1-e)d)-1},$$

$$P_p = (1-m)\frac{Nn(1-d)-1}{Nn(1-d+(1-c)(1-e)d)-1},$$

We assume that individuals from different populations are not related and therefore immigrants may be related only if they had emigrated from the same population which yields $\gamma = \phi R$.

For newly founded populations we again have

$$f_0 = R_0 = M_1^0 + M_2^0 \gamma,$$

where M_1^0 and M_2^0 are the probabilities of being sibs or non-sibs in newly founded populations, respectively. Different cases need to be considered depending on the number of individuals, z, competing on empty patches

if $z > N$: $M_1^0 = \dfrac{n-1}{Nn-1}$, $M_2^0 = \dfrac{n(N-1)}{Nn-1}$;

If $z < N$: $M_1^0 = \dfrac{Nn/z-1}{Nn-1}$, $M_2^0 = \dfrac{n(N-N/z)}{Nn-1}$.

At the scale of the metapopulation, this leads to

$$R' = \sum_{t=0}^{\infty} R_t = \sum_{t=0}^{\infty} [F_t f_t],$$

$$R' = eR_0 + (1-e)\sum_{t=1}^{\infty}$$

$$\times [F_{t-1}[M_1 + M_2(P_p R_{t-1} + P_m \gamma)]],$$

$$R' = eR_0 + (1-e)[M_1 + M_2(P_p R + P_m \gamma)].$$

At equilibrium, this yields

$$R = \frac{e(M_1^0 - M_1) + M_1}{1 - \phi e M_2^0 (1-e) M_2 (P_p + \phi P_m)}. \qquad (D.2)$$