



## Metapopulation Genetics and the Evolution of Dispersal

Isabelle Olivieri; Yannis Michalakis; Pierre-Henri Gouyon

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METAPOPULATION GENETICS AND THE EVOLUTION  
OF DISPERSALISABELLE OLIVIERI,<sup>1,\*</sup> YANNIS MICHALAKIS,<sup>2,†</sup> AND PIERRE-HENRI GOUYON<sup>3,‡</sup>

<sup>1</sup>Institut des Sciences de l'Evolution, Université de Montpellier, Place Eugène Bataillon, 34095 Montpellier Cedex 05, France; <sup>2</sup>Institut d'Ecologie, Université Pierre et Marie Curie, Bât. A, 7e Etage, Case 237, 75252 Paris Cedex 05, France; and <sup>3</sup>Evolution et Systématique des Végétaux, Université Paris-Sud, Bât. 362, 91405 Orsay Cedex, France

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*Abstract.*—A Markovian extinction model that takes into account age structure of local populations allows consideration of the effects of demography and successional dynamics on the evolution of migration. Analytical expressions for the evolutionarily stable (ES) rates of dispersal are given for cases in which newly recolonized sites attain carrying capacity within a single season. Using a low-fecundity numerical model, we find that an increase of the level of site saturation increases the dispersal rate. Ecological successions and unequal local extinction rates between newly colonized sites and established populations strongly affect the ES dispersal rate. The frequency of genetic modifiers that enhance the rate of dispersal evolves negative correlations with deme age, with high-migration genotypes predominant among colonizers while progressively declining in frequency as a deme ages. This suggests that between-deme selection (colonization) favors migrants while within-deme selection favors low dispersers, which allows the coexistence of types with different dispersal rates. Because of the interaction between the two levels of selection, the relation between the ES dispersal rate and the deme maximal lifetime is nonmonotone. We suggest that life-history traits other than dispersal might also experience antagonistic selective forces at the between- and within-deme levels.

Migration plays a key role in the cohesion of metapopulation systems from both the demographic and genetic perspectives. Dispersal directly influences the long-term persistence of populations (Roff 1974*a*, 1974*b*, 1975; Hamilton and May 1977; Comins et al. 1980; Vance 1980; Hastings 1993; Venable and Brown 1993), coexistence of species or genotypes (Roff 1975; Levin et al. 1984; Comins and Noble 1985; Olivieri and Gouyon 1985; Yeaton and Bond 1991; Lavorel et al. 1994), and genetic differentiation among demes. In many species, there exists genetic variation in the proportion of emigrants produced per individual (e.g., seed dispersal polymorphism: Koller and Roth 1964; Venable 1979; Venable and Lawlor 1980; Clay 1982; Olivieri et al. 1983; Olivieri and Berger 1985; Schmitt et al. 1985) or in migration ability (e.g., wing dimorphism in insects: Dingle et al. 1980; Roff 1986; Kaitala 1990; Karlson 1992). Many authors have considered the

\* To whom correspondence should be sent; E-mail: olivieri@gene.univ-montp2.fr.

† E-mail: imachala@snv.jussieu.fr.

‡ E-mail: gouyon@psisun.u-psud.fr.

evolution of dispersal. In broad terms, two factors select against migration. First, migration may lead individuals to bad environments. With local adaptation, migration is selected against because of positive associations between genes coding for local adaptation and modifiers reducing the migration rate (Balkau and Feldman 1973; Frank 1986; Liberman and Feldman 1989; Wiener and Feldman 1991; Wiener and Tuljapurkar 1994). Even in the absence of genetic variability for local adaptation in a spatially heterogeneous environment, migration will be selected against because on the average an individual will disperse to an environment worse than the one it was born in, since better environments harbor more individuals (Hastings 1983; Holt 1985; see Johnson and Gaines 1990 for a review). McPeck and Holt (1992), however, found that some dispersal is the optimal solution if individuals can express patch-specific dispersal rates (i.e., habitat selection). The second factor that selects against migration is that migration entails an immediate cost in local offspring recruitment.

What then selects for dispersal? We suggest it is factors acting at the between-population level to favor migrants. Levin et al. (1984) have shown that temporal variability in population sizes may favor dispersal (see also Gadgil 1971; Roff 1975; McPeck and Holt 1992).

An extreme case of temporal variability in population size occurs with extinction. In many species, population extinction is unavoidable, either through stochastic disturbances of habitat (see Ehrlich et al. 1980; Sousa 1984; Van der Meijden et al. 1985; Dobkin et al. 1987; Harrison et al. 1988; McCauley 1989), the ecological process of succession (Horvitz and Schemske 1986; Huston and Smith 1987), or demographic stochasticity (see Harrison 1991 for a review). Global persistence in such species entails colonization subsequent to local extinction. Migration will be selected for in such systems (Van Valen 1971), because each particular deme will eventually go extinct and only offspring that have emigrated will be able to reproduce. This has been shown theoretically whether local extinctions occur because of environmental stochasticity (Van Valen 1971; Roff 1975; Motro 1982; Levin et al. 1984; Olivieri and Gouyon 1985; Venable and Brown 1988; Kaitala et al. 1989; Kaitala 1990; Cohen and Levin 1991), demographic stochasticity (Hamilton and May 1977; Crespi and Taylor 1990; Ludwig and Levin 1991; McPeck and Holt 1992), or both (Comins et al. 1980; Comins 1982).

Thus, two opposing selection pressures, selection for dispersal during recolonization and selection against dispersal once a deme is founded, act on the dispersal rate when local extinctions drive environmental variation. It follows that deme age, that is, time since deme foundation, may be a critical parameter that modulates selection on dispersal rate in a population. The probability of establishment of an immigrant is likely to depend on population age, since populations of different ages are likely to differ in size, leading to asymmetric migration rates.

Our approach is built on the results of previous articles (Van Valen 1971; Levin et al. 1984; Olivieri and Gouyon 1985). We consider local extinctions the sole cause of environmental variation and fitness variation generated solely by variable dispersal rates. We study local evolutionary dynamics in the context of a metapopulation at equilibrium (Levins 1968, 1970; Slatkin and Wade 1978; Metz and

Diekmann 1986; Lande and Barrowclough 1987; Hastings and Wolin 1989; Hanski and Gilpin 1991). A metapopulation is an assemblage of demes of common ancestry that influence each other's local dynamics via dispersal (Olivieri et al. 1990). We consider the age structure of demes within the metapopulation (see also Hastings and Wolin 1989). This allows us to study the effects of deme age and local demography on the evolution of dispersal.

Many studies (e.g., Horvitz and Schemske 1986; Alvarez-Buylla and Martinez-Ramos 1990; Alvarez-Buylla and García-Barrios 1993) have emphasized the importance for dispersal of succession (e.g., after recolonization of gaps in tropical forests). We assume that local extinction may occur because of local disturbances or successional processes. Extinction is considered a probabilistic event due to disturbance until a certain age, at which extinction is certain as a consequence of successional replacement. We allow disturbance rates to vary with time since the last disturbance. Our analysis indicates that both ecological succession and unequal extinction rates strongly affect the evolution of dispersal.

#### DESCRIPTION OF THE MODELS AND ANALYTICAL RESULTS

The models developed here are deterministic, migrant-pool island models (Slatkin and Wade 1978). All sites receive migrants. Migrants incur some mortality during transit between patches. Below we describe further assumptions about the metapopulation structure and the biology of the species under study. In the analytical models below, we assume that site carrying capacity is reached in a single generation. In the numerical model, we relax this assumption. Appendix A gives the list of main parameters and variables used in this article.

##### *A Markovian Model of Extinction*

Because dispersal evolves in the context of metapopulation dynamics and "aging" patches, it is necessary to examine the stable age distribution of demes under defined schemes. Assume a metapopulation with an infinite number of sites, each potentially with a deme (fig. 1). A "site" is the largest spatial unit for which the probability of extinction is independent of other units. A given site may exist in any of states 0, 1, 2, . . . ,  $z$ . State 0 describes unoccupied sites, state  $i$  ( $1 \leq i \leq z - 1$ ) describes occupied sites that have persisted through  $i$  consecutive time units without extinction, and state  $z$  represents climax sites, where the probability of extinction is unity (e.g., through successional replacement), in which reproduction by the organism under study is excluded by later successional species.

The frequency of sites in state  $i$  at time  $t$  is represented by  $V_i(t)$ . If population density is the same in all occupied sites,  $V_i(t)$  represents the proportion of the metapopulation in sites where the most recent extinction episode occurred  $i$  time units ago. Extinction occurs at a rate depending exclusively on the time since the most recent extinction. The probability that a site in state  $i$  escapes extinction is  $A_i$  ( $0 \leq i \leq z$ ). Sites in state  $i$  that escape extinction enter state  $i + 1$  in the next season. We assume that all empty sites are colonized and proceed to state

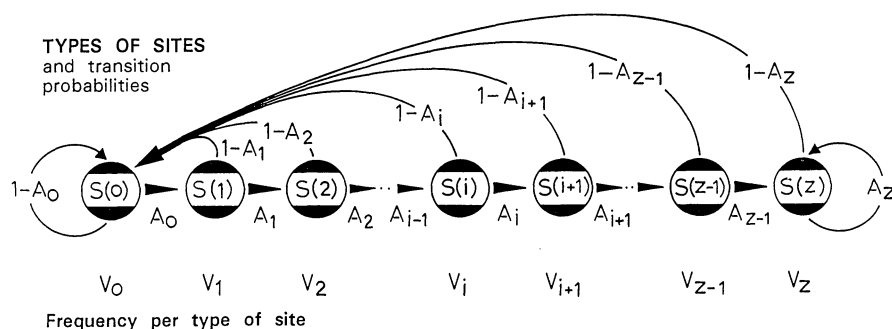


FIG. 1.—The metapopulation. In a viable metapopulation, the different types of sites are as follows. Empty sites are those in which the species considered is missing because of a recent disturbance. Such sites can either remain vacant because of disturbance or be recolonized, leading to the foundation of a new population. Colonized sites are those in state  $i = 1, \dots, z - 1$ ,  $i$  being the age of the population. Uncolonizable, climax sites (end of successions) are those in which the species is not present (or where it cannot reproduce) and cannot establish in the absence of disturbance, for example, one in which competitively superior species are present.

1 with probability  $A_0$ . These assumptions lead to the following transition equations:

$$V_0(t) = \sum_{j=0}^z (1 - A_j) V_j(t - 1), \tag{1}$$

$$V_i(t) = A_{i-1} V_{i-1}(t - 1) \quad \text{for } 1 \leq i \leq z - 1, \tag{2}$$

and

$$V_z(t) = A_{z-1} V_{z-1}(t - 1) + A_z V_z(t - 1). \tag{3}$$

For all  $t$ ,  $\sum_{j=0}^z V_j(t) = 1$  and, at equilibrium,  $V_i(t) = V_i(t - 1) \equiv V_i$ . Solving the transition equations using the stationary persistence parameters ( $A_i$ ) and maximal population life span ( $z$ ) leads to the distribution of the  $V_i$  (equivalent to the patch age distribution described by Hastings and Wolin [1989]).

If we assume all occupied sites have identical persistence probabilities ( $A_i = A_1$  for  $1 \leq i \leq z - 1$ ),

$$V_0 = \frac{1}{1 + A_0 \left[ \frac{1 - A_1^{z-1}}{1 - A_1} + \frac{A_1^{z-1}}{1 - A_z} \right]}, \tag{4}$$

$$V_i = V_0 A_0 A_1^{i-1}, \quad \text{for } 1 \leq i \leq z - 1, \tag{5}$$

and

$$V_z = \frac{V_0 A_0 A_1^{z-1}}{1 - A_z}. \tag{6}$$

Among occupied sites, the frequency of sites of type  $i$  ( $1 \leq i \leq z - 1$ ) is

$$\tilde{V}_i = \frac{V_i}{1 - V_0 - V_z} = \frac{A_1^{i-1}(1 - A_1)}{1 - A_1^{z-1}} = A_1^{i-1}\tilde{V}_1, \quad (7)$$

where, since  $\sum_{i=1}^{z-1} \tilde{V}_i = 1$ ,

$$\tilde{V}_1 = \frac{1 - A_1}{1 - A_1^{z-1}}. \quad (8)$$

Both the frequency of occupied sites ( $1 - V_0 - V_z$ ) and the age distribution among occupied sites affect the evolution of dispersal.

#### *Evolutionarily Stable Dispersal Rates*

The evolution of dispersal depends on the relative expected success via dispersing and nondispersing offspring. We used two approaches to study the evolution of dispersal: a nondynamic strategy analysis, in which we compare a measure of expected fitness through dispersing and nondispersing offspring, and a dynamic genetic analysis, in which we derive conditions for initial increase of genetic modifiers of dispersal. Numerical analysis (see Numerical Studies) permits us to compare these two approaches. We also examine the evolutionarily stable (ES) dispersal rate in an extended model that contains more realistic within-patch dynamics.

*An asexual model of dispersal evolution.*—Assume the metapopulation has the stationary age distribution among sites, determined by the extinction regime. Because the probabilities of persistence ( $A_i$ ) depend exclusively on the time since the last extinction, extinction proceeds independently of the evolution of dispersal. Different predictions may arise if dispersal influences extinction rates.

At the beginning of each generation, residents of a given deme undergo asexual reproduction. Juveniles disperse at genetically determined rates, and a fraction  $q$  of dispersers survive to form the migrant pool. Adults die at a rate  $1 - s$ , and these dead adults are replaced either by nondispersing local juveniles or by migrants. Each deme receives an equal fraction of the migrant pool. All unoccupied sites receive migrants, but effective recolonization occurs (with probability  $A_0$ ) if this immigration event is not followed by disturbance. Juveniles that fail to become established are eliminated.

*Evolutionarily stable dispersal rate obtained from strategy analysis.*—Evolutionarily stable strategies (ESS; Maynard Smith 1982) have been determined in studies of dispersal (e.g., Hamilton and May 1977) by considering the fitness of a rare mutant that determines a strategy different from the predominant strategy. We assume that the population is nearly monomorphic for a genotype that has dispersal rate  $d^*$  and study the fate of a rare genotype with rate  $d$ . The strategy  $d^*$  is said to be ES if either (1)  $W(d^*) > W(d)$  for all rare  $d \neq d^*$  or (2)  $W(d^*) = W(d)$  for rare  $d$  and  $W(d^*) > W(d)$  for common  $d$  (see Maynard Smith 1982). We consider a simple case in which reproduction and survival rates are independent of genotype and equal extinction rates of all occupied sites ( $A_i = A_1$  for  $1 \leq i < z$ ). We assume newly colonized sites attain carrying capacity within a single season.

The full analysis is given in appendix B. We give the main results in what follows. For fixed  $d^*$ ,  $W(d)$  is linear in  $d$ , so  $W(d^*) = W(d)$  for all  $d$  at the putative ESS. We thus consider the second definition of an ESS:  $W(d) = W(d^*)$  for rare  $d$ , and  $W(d^*) > W(d)$  for common  $d$ . The candidate for the ESS obtained by setting  $W(d) = W(d^*)$  for rare  $d$  is

$$d^* = \frac{A_0 V_0}{[1 - q(1 - V_0 - V_z)][A_0 V_0 + A_1(1 - s)(1 - V_0 - V_z - V_{z-1})]}. \quad (9)$$

It can be shown that maximal dispersal ( $d^* = 1$ ) is favored unless migration is sufficiently hazardous ( $q$  low enough; see app. B). Intermediate ES dispersal rates, however, may evolve even when  $q = 1$ .

The quantity  $d^*$  increases with adult survival rate, survival to migration, and recolonization rate of empty sites ( $A_0$ ). It decreases with increasing extinction rate of occupied sites. Thus, matching earlier studies (e.g., Van Valen 1971; Comins et al. 1980), the ES dispersal rate increases with extinction rates. Successional dynamics result in higher  $d^*$  compared with a model with strictly random patch turnover.

With complete adult replacement ( $s = 0$ ), arbitrarily large  $z$ , and identical extinction rates of all sites, equation (9) further reduces to the evolutionarily stable dispersal rate obtained by Comins et al. (1980) and Levin et al. (1984) (see app. B). When survival during migration ( $q$ ) tends to zero,  $d^*$  further reduces to  $1 - A_1$ , the value found numerically by Van Valen (1971). By relaxing the hypothesis of  $A_0 = A_1$ , it is possible to express overall survival to migration as a function of  $q$ ,  $A_0$ , and  $A_1$  and get an expression similar to that of previous authors, with  $q$  replaced by  $Q$ :

$$Q = \frac{A_0 q}{A_1(1 - A_1 + A_0)}. \quad (10)$$

The effective survival rate  $Q$  exceeds  $q$  only if  $A_0$  exceeds  $A_1$ , indicating that the possibility of becoming established in an unoccupied site in which the probability of persistence is increased ( $A_0 > A_1$ ) has the same effect on the ES dispersal rate as a reduction in migration hazard (higher  $q$ ).

*A dynamic evolutionary stability analysis.*—The above strategy analysis assumes that the gene frequency distribution is identical among demes and, in particular, independent of deme age. Enhancers of dispersal, however, would be expected to be overrepresented among migrants and underrepresented in long-established demes. As our analysis shows, this might not be important in the absence of successions, because deme age and deme extinction probability are then uncorrelated. In the more general case in which successions occur ( $z$  finite), there is a positive correlation between deme age and deme expected future lifetime. An explicit dynamic analysis of gene frequency change (which forces one to take into account deme age and, thus, expected future lifetime of each deme) shows that this effect can influence the ES dispersal rate.

We now assume that the gene frequency distribution is the same for demes of

the same age but varies among demes of different ages. Local stability analysis provides a method for obtaining expressions for ES rates through the direct study of the dynamic process of exclusion or invasion of rare genotypes with different dispersal rates. We assume, once again, that demes constituting the metapopulation have attained the stationary patch age distribution and that newly colonized sites attain carrying capacity within a single season.

Denote the frequency in the metapopulation of the rare genotype associated with dispersal rate  $d$  by

$$X = \sum_{i=1}^{z-1} \tilde{V}_i X_i, \quad (11)$$

in which  $\tilde{V}_i$  represents the frequency of demes of type  $i$  among occupied sites (see eq. [7]) and  $X_i$  is the frequency of the rare genotype in demes of type  $i$ .

In the next generation, the frequency of the rare genotype in newly recolonized sites,  $X'_1$ , is the frequency in the migrant pool, while the frequency in occupied sites of type  $i + 1$  (for  $1 \leq i \leq z - 2$ ) reflects adult mortality and immigration into sites of type  $i$ :

$$X'_1 = \frac{dX}{dX + d^*(1 - X)} \quad (12)$$

and

$$X'_{i+1} = sX_i + \frac{(1 - s)[(1 - d)X_i + dq(1 - V_0 - V_z)X]}{1 - \bar{d}_i + \bar{d}q(1 - V_0 - V_z)}, \quad (13)$$

in which  $d^*$  represents the dispersal rate of the common resident genotype,  $\bar{d}_i$  is the average dispersal rate among juveniles of sites of type  $i$ , and  $\bar{d}$ , the average dispersal rate in the metapopulation, corresponds to the denominator of  $X'_1$  in equation (12). Because the probabilities of extinction of demes are independent of dispersal rates, the persistence parameters ( $A_i$ ) influence the genotypic dynamics only through the age distribution of demes ( $V_i$ ).

For the case of equal extinction probabilities of occupied sites, it is shown in appendix C that the candidate ES dispersal rate is then given by

$$d^* = \frac{1 - A_1}{(1 - sA_1)[1 - q(1 - V_0 - V_z)] - A_1 \tilde{V}_{z-1}(1 - s) \frac{1 - a(d^*)^{z-1}}{1 - a(d^*)}}. \quad (14)$$

The ES dispersal rate is obtained by solving equation (14), where  $a(d^*)$  is defined in appendix C and is biologically related to adult survival and probability of establishment of nondispersing offspring of the rare type. A proof by Ovide Arino in appendix D shows there is at most a single solution to equation (14). All introduced genotypes, irrespective of their dispersal rates, fail to undergo geometric increase in monomorphic populations with ES dispersal rate. Moreover, it is shown in appendix C that the ES dispersal rate is evolutionarily attracting.

A metapopulation initiated within a sufficiently small neighborhood around the

initial equilibrium state converges to the eigenvector associated with the leading eigenvalue of the matrix in appendix C (eq. [C2]). Given this distribution, enhancers of dispersal are negatively correlated with deme age. The rate of decline in gene frequency with deme age depends on  $a(d)$ :

$$X_i - X_{i-1} = a(d)(X_{i-1} - X_{i-2}) . \quad (15)$$

The difference between frequency in demes of age 1 and the average frequency is proportional to the difference between the predominant and minority dispersal rates:

$$X_1 - X \propto (d - d^*) . \quad (16)$$

Enhancers of dispersal ( $d > d^*$ ) decline in frequency as demes age. This finding was verified numerically (see next section).

The ES dispersal rate determined from dynamics (eq. [14]) and the nondynamic strategy analysis (eq. [9]) agree only in the absence of succession (arbitrarily large  $z$ ): for infinite  $z$ ,  $V_0/(1 - V_0)$  reduces to  $(1 - A_1)/A_0$  and equation (14) reduces to equation (9). Our analysis suggests that the nondynamic analysis implicitly assumes the virtual absence of structure in the metapopulation; in particular, the expected future lifetime of a deme is assumed to be independent of its current age. This assumption holds only in the absence of successions. Thus, the gene frequency distribution per se does not affect the result. But its study in the dynamics analysis allowed us to take into account deme age and, thus, deme expected future lifetime.

#### NUMERICAL STUDIES

Here, we first show numerically that stable polymorphisms can be maintained between genotypes far from the ES dispersal rate and give an example of local evolutionary dynamics for such a polymorphism. Second, we study the effect of the population life span,  $z$ , on the ES dispersal rate and compare the results obtained from the dynamic, nondynamic, and numerical analyses. In the numerical studies, we relax the assumption that newly recolonized sites immediately reach carrying capacity, so as to assess the robustness of our dynamic analysis. Third, we study in detail the effect of fecundity and adult survival and show that fecundity may strongly affect the ES dispersal rate.

Our numerical model is the same as the analytical model, except that local dynamics (population size as a function of deme age) depends on fecundity and adult survival rates. When fecundity is low, few dispersers arrive per site (in particular unoccupied sites) and population growth is low. When fecundity is large, local growth is fast and carrying capacity is reached in a single time unit, as in the "site-saturation" model of Levin et al. (1984) and the analytical model above.

In particular, we assume local growth is exponential until carrying capacity ( $K$ ) is reached, with no overshooting. Each adult produces offspring, dispersed at a genetically determined rate. Dispersed offspring reach sites of age  $i$  with a frequency equal to  $V_i$ ; a proportion  $1 - V_0 - V_z$  are lost, as in the analytical

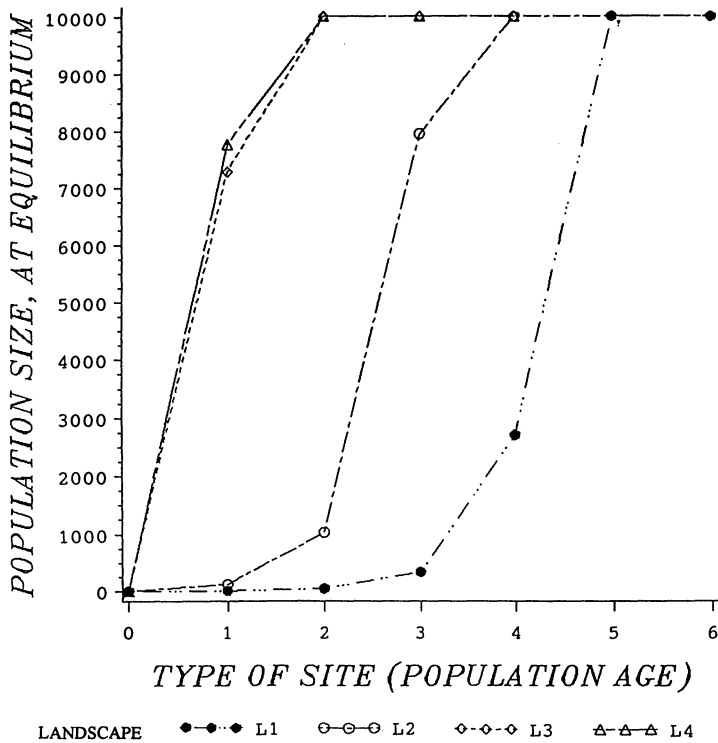


FIG. 2.—Local population dynamics within any given undisturbed site at equilibrium of the metapopulation, in each of four landscapes. Landscapes are described in tables 1 and 2. An annual species with a fecundity of 10 was considered.

TABLE 1  
PARAMETERS CHARACTERIZING THE FOUR LANDSCAPES USED IN  
NUMERICAL ANALYSES

	$A_0$	$A_i$	$A_z$	$z$
L1	.3	.99	.9999	7
L2	.1	.9	.999	7
L3	.1	.9	.9	5
L4	.4	.9	.95	5

NOTE.— $i = 1$  to  $z - 1$ .

model. The probability of surviving migration ( $q$ ) is one in all our examples. There is local competition between immigrants and resident offspring for space left by adults. When the number of competing offspring is less than the space left, all offspring survive; otherwise, survival occurs as in the analytical model.

Numerical calculations were performed from arbitrary initial population sizes. For given genotypes, several initial conditions were tried; we observed no cases of dependence of equilibrium values on initial values. These equilibrium local dynamics are described in figure 2 for four landscapes described in tables 1 and

TABLE 2  
EQUILIBRIUM RELATIVE FREQUENCIES OF EACH SITE AGE CLASS IN EACH OF THE FOUR LANDSCAPES  
DESCRIBED IN TABLE 1

	$V_0$	$V_1$	$V_2$	$V_3$	$V_4$	$V_5$	$V_6$	$V_7$	$V_0 + V_z$
L1	.00035	.00011	.00011	.00010	.00010	.00010	.00010	.99924	.99959
L2	.01831	.00183	.00175	.00148	.00133	.00120	.00108	.97311	.99142
L3	.50000	.05000	.04500	.04050	.03645	.32805	.82805	...	...
L4	.13116	.05246	.04722	.04250	.03825	.68842	.81958	...	...

NOTE.— $V_z = V_5$  or  $V_7$ .

2. These stable patterns were obtained after only a few generations and showed a strict association between local population size and deme age. In all following analyses,  $K$  is a constant, in effect a scaling parameter. The following examples show that local dynamics influenced the model outcome.

To determine the ES dispersal rate for each parameter set, we performed pairwise comparisons between dispersal rates, starting with  $d = 0$  or  $d = 1$ , compared with the next  $d$  at a 0.01 interval. The winning dispersal rate was then competing against the dispersal rate at the next 0.01 interval. The dispersal rate that won all such contests is the ES dispersal rate. To test for uniqueness and attractiveness, we started contests from both extremes, zero and one. With the ESS determined, we introduced randomly chosen genotypes in a metapopulation fixed for the ESS and checked that all other genotypes disappeared, whatever their initial frequency. This happened in all cases examined.

#### *Stable Polymorphism versus ES Dispersal Rate*

Van Valen (1971) suggested that polymorphisms could be maintained as a result of selection operating differently within and between groups. Our analytical results (see Description of the Models and Analytical Results, *Evolutionarily stable dispersal rate obtained from strategy analysis*, and app. C) suggest that polymorphisms between modifiers of the dispersal rates surrounding the ESS can be protected. Our numerical model allows us further to make pairwise contests between genotypes that are far from the ESS and to study the stability of polymorphisms. Using this numerical model, with no assumption on site saturation, we found that two genotypes straddling the ESS could indeed be maintained together stably as suggested by Van Valen (1971). For example, figure 3 shows the equilibrium frequencies of two annual genotypes (i.e., adult survival rate equal to zero).

At equilibrium, for those cases with a stable polymorphism, all sites of a given age  $i$  had the same genotypic frequencies. These frequencies differed among sites by age, as observed in the analytical model. The trait thus evolves within local populations, while the metapopulation as a whole is ES. Figure 3 shows that the frequency of the genotype with the lowest migration rate increases with local population age. Each population evolves toward fixation of the nonmigrating genotype. This pattern reflects the opposition between selection at colonization and selection thereafter. In any contest, the genotype with the largest dispersal rate is overrepresented in the migrant pool, whereas the genotype with the small-

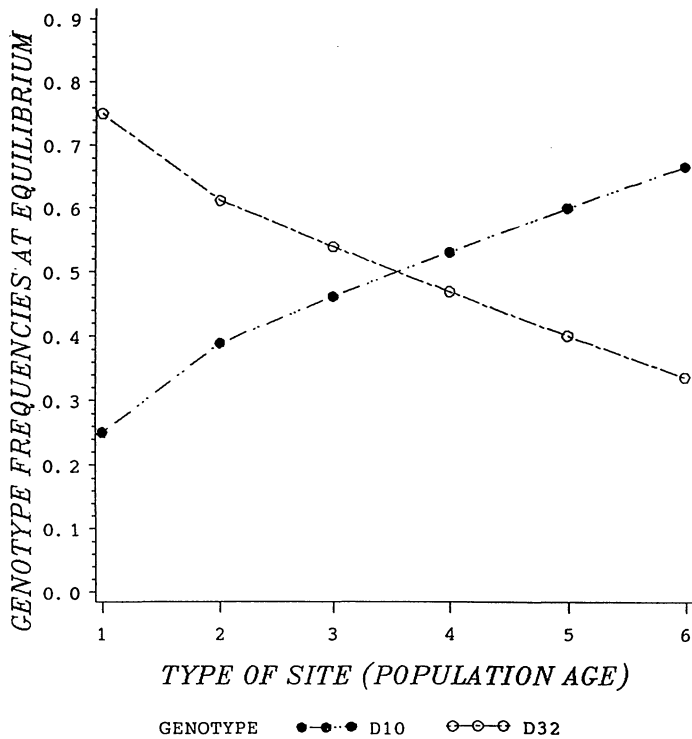


FIG. 3.—Stable polymorphism for dispersal: equilibrium frequencies of two genotypes with different dispersal rates (.10 and .32), as a function of population age; the ESS is  $d^* = .19$ . An annual species with a fecundity of 10 was considered in landscape L1 (see table 1).

est dispersal rate is overrepresented in the “resident” pool (adults plus nondispersers). If there were no cost to dispersal ( $q = 1$ ,  $A_0 = A_1$ , and  $z$  is arbitrarily large, so that  $V_z = 0$ ), emigration and immigration would exactly compensate one another. Dispersal would then not be selected against locally (e.g., as in Campbell 1982). With some mortality during dispersal, however, or if the recolonization rate is smaller than the persistence probability of occupied sites ( $A_0 < A_1$ ), the number of juveniles leaving a deme is necessarily larger than the number of juveniles entering a deme: emigration and immigration no longer compensate one another. As the overall cost incurred by the genotype with the largest dispersal rate is larger as well, this genotype is less represented in occupied sites after the emigration-immigration phase than it was before. There is thus selection against dispersal within each deme.

We studied numerically the conditions for a protected polymorphism. We found that stable polymorphisms could be maintained only when the two competing genotypes were straddling the ESS, but with both far from it. When they were close to the ESS, one of the two genotypes would dominate. Figure 4 shows an example. This contradicts the prediction derived from the dynamic strategy analysis (eq. [C5] in app. C; see also app. E) that a polymorphism between two types

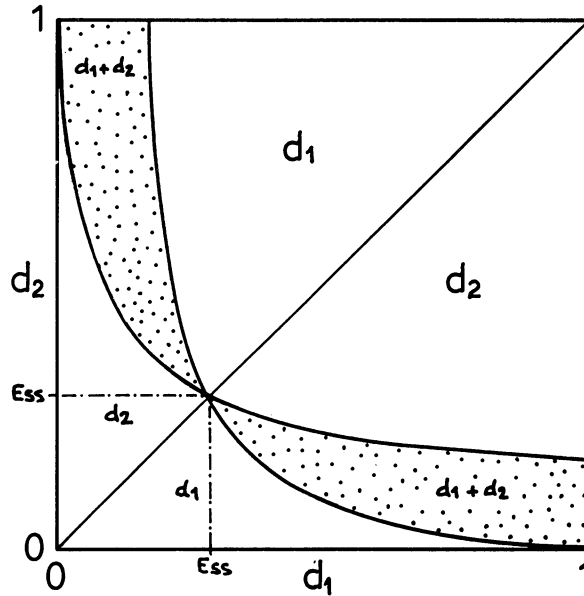


FIG. 4.—Values of dispersal rates in the parameter space ( $d_1$ ,  $d_2$ ) of two competing genotypes that allow the maintenance of a stable polymorphism (dotted area). Polymorphism can occur only if  $d_1$  and  $d_2$  straddle the ES dispersal rate. When coexistence is not allowed, the winning genotype is indicated.

straddling the ESS should always be protected. Numerically, we found that the nonprotection of polymorphism occurred when sites of type  $z - 1$  were sufficiently common among occupied sites (i.e.,  $\bar{V}_{z-1}$  was large enough). It appears that their presence induces negative frequency dependence in the rare genotype frequency, as suggested by the analysis in appendix E. Genotypes present in sites of type  $z - 1$  do not contribute offspring to the following generation. The more the genotype is represented in those sites (and, thus, the less it is represented elsewhere, for a given overall frequency), the more it should be affected by the presence of sites of type  $z - 1$ . We should thus expect the protection of polymorphism to be nonsymmetric: when the rare genotype disperses at a rate less than the ES dispersal rate (while the common genotype disperses more), it should be more affected by sites of type  $z - 1$  and less easily protected than when the rare genotype disperses at a rate higher than the ESS (while the common genotype disperses less). This disymmetry can actually be observed in figure 4. Take a given value of  $d_1$ . If  $d_1$  is less than the ES dispersal rate, the range of protected values of  $d_2$  is large. Conversely, if  $d_1$  is above the ESS, the range of protected values of  $d_2$  is small. Thus, the protection of a rare low disperser is much less likely to occur than the protection of a rare high disperser.

Although such polymorphisms were stable (i.e., gene frequencies return to an equilibrium value when displaced from it), we found that they were not ESSs (sensu Maynard Smith 1982): in particular, in all cases examined, the introduction

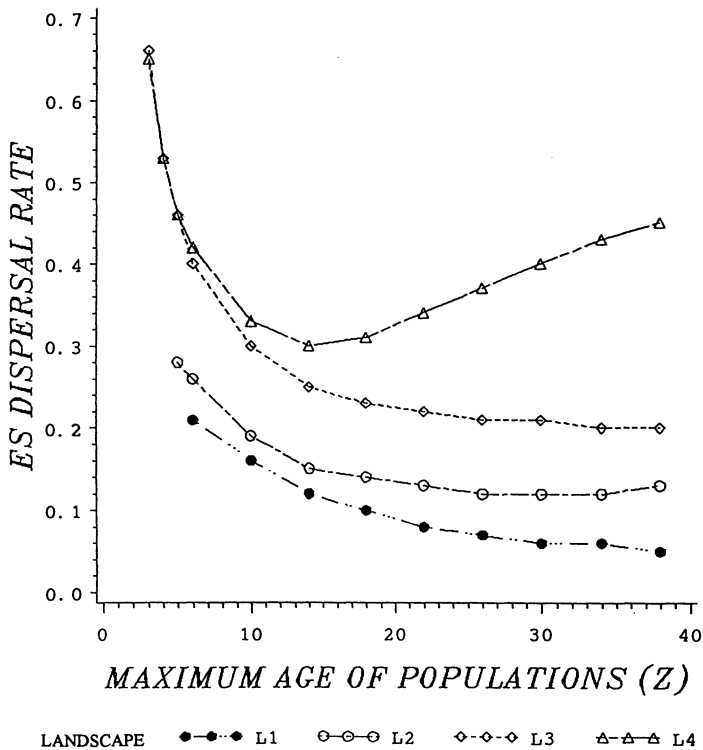


FIG. 5.—Influence of  $z$ , maximal age of a population, on the ES dispersal rate, for each landscape (see text). An annual species with a net fecundity of 10 was considered.

of a genotype with a dispersal rate closer to the ES rate led to the loss of one of these types. Polymorphic states were never ES to the introduction of the ES dispersal rate. We are aware of only two studies that have experimentally demonstrated that recently founded populations show greater dispersal abilities than more established populations (Olivieri and Gouyon 1985; Peroni 1994).

We now describe the influence of population life span on the ES dispersal rate and compare the various models of this article.

#### *Influence of Maximal Population Lifetime on the ES Migration Rate*

We have already studied in the analytical section the influence on  $d^*$  of  $A_0$ ,  $A_1$ , and  $s$  when  $z$ , the maximal population lifetime, is large. Numerical studies (not shown) give the same patterns for smaller  $z$ .

Provided  $z$  was small enough, we found either in saturation models (dynamic and nondynamic) or in a numerical model (with low or high fecundities) that increasing  $z$  tended to reduce the ES migration rate (see fig. 5 for the numerical model). However, for sufficiently large  $z$ , the ES dispersal rate had a lower bound and, in fact, in some landscapes (L4 in fig. 5) the ESS increased with  $z$  for very large  $z$  until a plateau was attained (numerical results from the various models are shown in table 3).

TABLE 3

OBSERVED AND EXPECTED EVOLUTIONARILY STABLE DISPERSAL RATES AS A FUNCTION OF POPULATION MAXIMAL LIFE SPAN  $z$  IN EACH OF THE FOUR LANDSCAPES PREVIOUSLY DESCRIBED

LANDSCAPE AND $z$	EXPECTED ESS		OBSERVED ESS	
	$d_1^*$	$d_2^*$	$m = 1,000$	$m = 10$
L1:*				
7	.17	.29	.29	.19
20	.06	.10	.10	.09
50	.03	.04	.04	.04
100	.02	.02	.02	.02
1,000	.28	.28	.28	.28
$\infty$	.31	.31	NA	NA
L2:†				
7	.22	.31	.31	.24
20	.12	.15	.15	.13
50	.16	.16	.16	.15
100	.20	.20	.20	.20
$\infty$	.20	.20	NA	NA
L3:‡				
5	.35	.48	.48	.46
7	.28	.38	.38	.37
20	.20	.23	.23	.22
50	.20	.20	.20	.20
$\infty$	.20	.20	NA	NA
L4:§				
5	.36	.48	.48	.46
7	.29	.39	.39	.39
20	.31	.32	.32	.32
50	.48	.48	.48	.48
$\infty$	.50	.50	NA	NA

NOTE.—An annual species with a fecundity  $m$  of either 10 or 1,000 was considered (in the last case, site saturation occurs at recolonization). The expected ES dispersal rates were obtained by assuming that sites are saturated readily after recolonization (eqq. [9] and [14] for  $d_1^*$  and  $d_2^*$ , respectively). The first expected value ( $d_1^*$ ) further assumes that  $z$  is large enough for succession to be neglected. When fecundity is equal to 10 only, the assumption of site saturation at recolonization is verified only for high values of  $z$  and favorable landscapes such as L3 or L4. The symbol NA means that no simulation was performed for those cases (see text for discussion).

\*  $A_0 = .3$ ;  $A_1 = .99$ ;  $A_z = .9999$ .

†  $A_0 = .1$ ;  $A_1 = .9$ ;  $A_z = .9999$ .

‡  $A_0 = .1$ ;  $A_1 = .9$ ;  $A_z = .9$ .

§  $A_0 = .4$ ;  $A_1 = .9$ ;  $A_z = .95$ .

The reason for this particular behavior is that the adaptiveness of exporting offspring depends both on the expected future lifetime of the home deme and the expected success of offspring elsewhere. The presence of climax communities affects both factors. The home deme can be terminated either by disturbance or by attaining the climax state. An increase in  $z$  increases the expected future lifetime of the home deme. But if  $z$  is very large, the expected lifetime depends

more on the probability of disturbance than on the maximum life span. Considering only the persistence of the home deme, then, increasing  $z$  tends to reduce migration, but this effect diminishes at large  $z$ .

Climax states are excluded as possible sites of establishment until a disturbance restores them to state 0. If climax sites are common, migration is discouraged because the probability of offspring establishment is low. As  $z$  increases, climax states become rarer because the probability of a site persisting through  $z$  seasons becomes less likely. Considering only the establishment of offspring, then, increasing  $z$  tends to increase migration.

These two effects of increasing  $z$  operate in opposite directions. For small  $z$ , the first effect predominates: higher  $z$  means the home demes will persist with higher probability and migration is thus less imperative. For large  $z$ , the first effect becomes weaker (the future of the home deme depends less on  $z$ ) and allows the second effect to arise: increasing  $z$  reduces the fraction of climax sites and improves the prospects for migrant establishment. As  $z$  grows large, however, this effect is also expected to diminish, because the probability of a site attaining climax will be very low. In summary, the ES dispersal rate will tend to decline as  $z$  increases for small  $z$  but may increase with  $z$  for large  $z$ ; for very large  $z$ , the ES dispersal rate will be insensitive to  $z$ , as the age distribution of demes will be governed mainly by disturbance probabilities.

When sites reach carrying capacity just after colonization, it is possible to obtain an analytical expression of the ES migration rate (see Description of the Models and Analytical Results, *A Markovian Model of Extinction*). Comins et al. (1980) and others assumed infinite  $z$  (no succession), immediate site saturation, and constant local extinction rates. We now compare numerical and analytical results (e.g., eq. [9] from the strategy analysis and eq. [14] from the stability analysis, with  $s = 0$  and  $q = 1$ ; see table 3). If sites reach carrying capacity immediately after colonization (e.g., high fecundity in table 3), the stability analysis solution (eq. [14]) equals simulation results. The analytical solution obtained using a strategy analysis (eq. [9]) gives the correct value only for large  $z$ : when  $z$  is too small, the ES dispersal rate is underestimated. This is because this nondynamic analysis implicitly assumes the absence of an association between gene frequency and deme age, thus preventing one from taking into account the association between deme expected future lifetime and deme age. For finite  $z$ , older demes have shorter expected future lifetimes, and the advantage of exporting offspring increases with deme age. The ES dispersal rate increases when this effect is taken into account, as in the local stability analysis.

#### *Influence of Genotypic Parameters*

When  $z$  and fecundity are low enough that carrying capacity is not reached in a single season, the value given by equation (14) exceeds the value obtained numerically with no assumption on site saturation (see table 3). Increasing fecundity or adult survival reduces the opportunity for establishment of nonmigrating offspring within their demes of origin. Thus, the ES migration rate increases with both, as shown in figure 6, where landscape L4 was considered using the numerical model, under no assumption on site saturation. The effect of adult survival

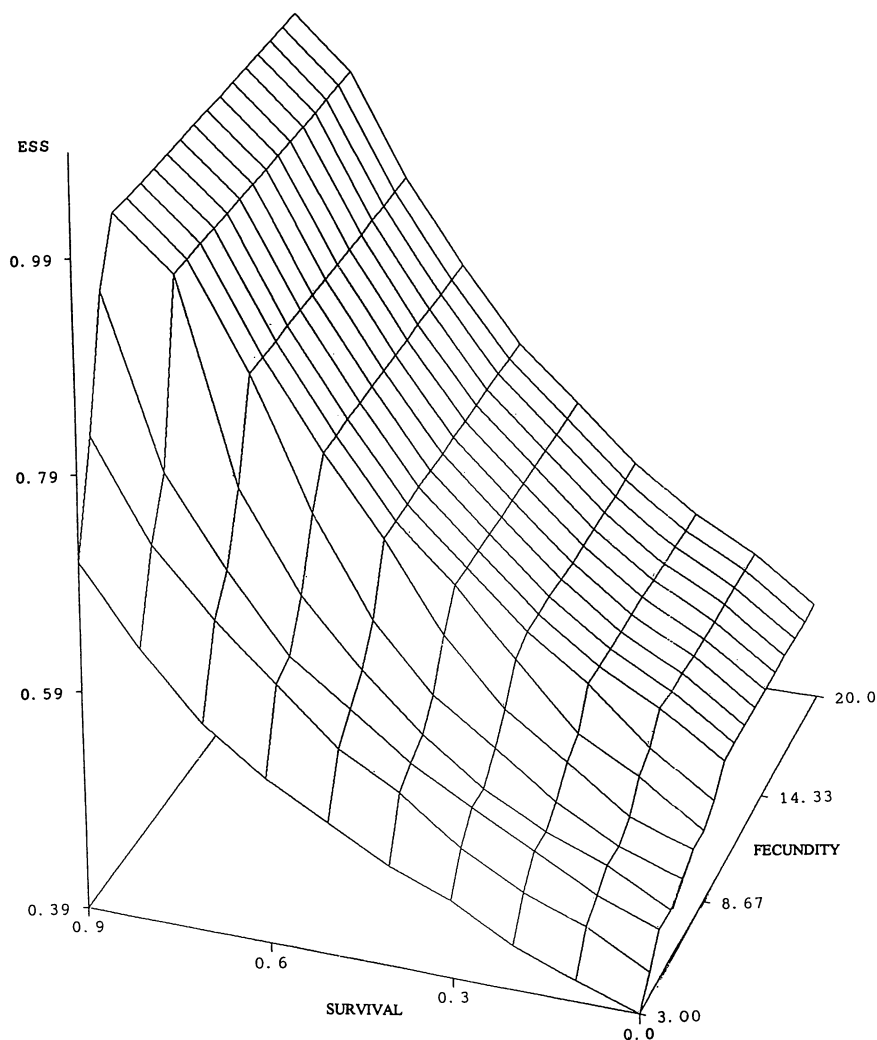


FIG. 6.—Evolutionarily stable dispersal rate, as a function of adult survival rate and fecundity, in landscape L4. Landscape L4 is described in tables 1 and 2.

was thus the same as the one found in the analytical model, while fecundity had no effect under the saturation model. When sites reach carrying capacity in a single generation, the probability of establishment in extant populations is very low, and an increase in fecundity no longer affects the local population dynamics (see the upper bound reached by  $d^*$  in fig. 6). This corresponds to the site saturation models studied analytically in the section *A Markovian Model of Extinction*, in which the ES dispersal rate was not affected by fecundity.

That an increase of fecundity increases the ES migration rate was found by Roff (1975), Levin et al. (1984), and Motro (1982) in a particular case. When local

extinctions, however, are due to demographic stochasticity (i.e., stochasticity in offspring number), as in models considered by Comins et al. (1980) and Motro (1982), the ES dispersal rate decreases with increasing fecundity, because of the resulting decrease in local extinction probability.

#### DISCUSSION

The comparisons of the dynamic and the nondynamic analyses demonstrate the importance of local evolutionary dynamics, which depend on the relation between deme age and deme expected future lifetime. Neglecting such a relation when maximal population lifetime is low (below 20 yr in the examples studied) leads to an underestimation of the ES dispersal rate. For many early colonizers, it is likely that low values of  $z$ , the maximal population lifetime, are common (Horvitz and Schemske 1986).

We found an interesting nonmonotone relation between  $z$  and the ES dispersal rate. This nonmonotony is due to an interaction between the effect of  $z$  on the persistence probability of the home deme on one side, and its effect on establishment of migrating offspring on the other side. It thus directly reflects the antagonistic selective forces at within- and between-deme levels. Individuals carrying dispersal genes tend to leave the local deme, resulting in a progressive decline in such genes within demes. This reduction with increasing deme age (see eq. [16] and fig. 3) reflects selection opposing migration at the within-deme level. The high-migration genotype will, however, be overrepresented in newly recolonized sites, favoring migration at the between-deme level. Conflict between within-deme and between-deme selection is a metapopulation effect.

Our numerical analysis allowed us to relax the assumption of immediate site saturation and study the effect of fecundity. We then found that, other things being equal, high-fecundity species should disperse more than low-fecundity species. We thus found that the site-saturation models overestimate ES dispersal rates, compared with models with more realistic within-patch dynamics. Under both the saturation and the low-fecundity models, the ES dispersal rate increases with adult survival rate. This results from the negative influence of adult survival on offspring establishment in the home deme. While high fecundities seem to be associated with high dispersal rates in nature (the "colonizer" syndrome; Baker and Stebbins 1965), this is not observed for high adult survival rates. Other factors (e.g., trade-offs between fecundity and survival) may be involved.

While the ES dispersal rate is the strategy that should evolve under natural selection, we may define an optimum dispersal rate as the rate that maximizes the probability of metapopulation persistence. We define an optimum "strategy" at the metapopulation level as the value that maximizes the equilibrium metapopulation size (the equivalent "site occupancy" was used by Hamilton and May [1977] and Comins et al. [1980]). Analytical and numerical results (not shown) indicate that some positive dispersal rate is always favored but that the ES dispersal rate tends to fall below the rate that would maximize total metapopulation size, in agreement with the numerical results of Roff (1975) and the analytical results of Comins et al. (1980).

## CONCLUSION

In this article, we showed that successional dynamics results in higher ES dispersal rates compared with a model with strictly random patch turnover. Conversely, realistic local population growth patterns result in lower ES dispersal rates, compared with models with immediate site saturation. Successions create a positive correlation between deme age and deme expected future lifetime. Only the dynamic analysis, in which local evolution of gene frequencies is explicitly studied, allows one to take this effect into account. This results in a correct determination of the ES dispersal rate, compared with the nondynamic analysis. Note that the disparity between the two approaches occurs only in the presence of successions.

The metapopulation effect examined in this article (selection in different directions at population foundation and during following generations) may be very general. For instance, after a local extinction event that prevents reproduction in a given season, recolonization is often derived from the seed bank (see Venable and Brown 1988 for a model of the evolution of seed dormancy). The seed bank comprises seeds produced during previous seasons. Selection during recolonization thus favors genotypes that produced offspring with a high dormancy rate. Within each deme, however, genotypes producing nondormant seeds will be selected, just as nonmigrants were selected in the models presented in this article. Many other traits, such as age-specific fecundities and survival rates (I. Olivieri and P.-H. Gouyon, unpublished manuscript), mating systems (D. Couvet and C. Gliddon, unpublished manuscript), and possibly disease resistance, are likely to experience different selection patterns through time, from the founding to the extinction of a population. Such traits thus should not be analyzed as if they were fixed entities, either when one studies the genetics of subdivided populations or when one designs optimum biological reserves. The determinants of the ability of a species to persist globally (its fecundity, survival rate, and dispersal rate among other factors) are themselves evolving in response to a host of factors, including the disturbance regime.

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## APPENDIX A

## LIST OF MAIN VARIABLES AND PARAMETERS

$V_i (i = 0, \dots, z)$	Frequency of sites in state $i$
$\bar{V}_i (i = 1, \dots, z)$	Frequency of sites in state $i$ , relative to the total frequency of occupied sites
$z$	Maximal deme lifetime
$A_0$	Recolonization probability
$A_i (i = 1, \dots, z)$	Persistence probability of a site in state $i$
$d^*$	Evolutionarily stable dispersal rate (ES dispersal)
$d, d_1, d_2$	Dispersal rate of various genotypes
$d_1^*, d_2^*$	Expected dispersal rates under the nondynamic and the dynamic models, respectively
$s$	Adult survival rate
$q$	Survival rate of dispersing offspring during dispersal
$W(d)$	Fitness of a genotype with dispersal rate $d$
$X$	Frequency of a rare genotype with dispersal rate $d$
$X_i$	Frequency of a rare genotype with dispersal rate $d$ in demes of age $i$

## APPENDIX B

## EVOLUTIONARILY STABLE DISPERSAL RATE OBTAINED FROM STRATEGY ANALYSIS

Consider the fitness of dispersing and nondispersing offspring of a mutant adult with a dispersal rate of  $d$  in a metapopulation in which the predominant strategy is  $d^*$ . A fraction  $(1 - d)$  of offspring remain in the home deme. Because the genotype that determines  $d$  is rare, the number of nondispersing juveniles and migrants competing within an occupied deme is proportional to  $1 - d^* + d^*q(1 - V_0 - V_z)$ . The probability that a given nondispersing juvenile becomes established is

$$\frac{(1 - s)A_1(1 - \bar{V}_{z-1})}{1 - d^* + d^*q(1 - V_0 - V_z)}, \quad (\text{B1})$$

where  $s$  is probability of survival for adults,  $A_1$  the probability the deme escapes extinction, and  $1 - \bar{V}_{z-1}$  the probability that the site is not in the state  $z - 1$ .

A fraction  $d$  of the offspring disperse. These offspring survive migration and enter an occupied deme of age  $< z - 1$  with probability  $q(1 - V_0 - V_z - V_{z-1})$ . They establish with a probability  $A_1(1 - s)$  divided by the number of competing juveniles. Dispersing offspring survive migration and enter an unoccupied deme with probability  $qV_0$  and establish with probability  $A_0$  (the probability that demes of this kind escape extinction) divided by the total number of competitors of unoccupied demes,  $d^*q(1 - V_0 - V_z)$ .

The overall fitness of an individual with dispersal rate  $d$  is, then,

$$W(d) = A_1(1 - s) \frac{(1 - d)(1 - \bar{V}_{z-1}) + dq(1 - V_0 - V_z - V_{z-1})}{1 - d^* + d^*q(1 - V_0 - V_z)} + \frac{A_0dqV_0}{d^*q(1 - V_0 - V_z)}. \quad (\text{B2})$$

For fixed  $d^*$ ,  $W(d)$  is linear in  $d$ , so  $W(d^*) = W(d)$  for all  $d$  at the putative ESS. We thus consider the second definition of an ESS:  $W(d) = W(d^*)$  for rare  $d$ , and  $W(d^*) \geq W(d)$  for common  $d$ . The candidate for the ESS obtained by setting  $W(d) = W(d^*)$  for rare  $d$  is

$$d^* = \frac{A_0V_0}{[1 - q(1 - V_0 - V_z)][A_0V_0 + A_1(1 - s)(1 - V_0 - V_z - V_{z-1})]}, \quad (\text{B3})$$

which is equation (9) in the text.

When the genotype that exports offspring at rate  $d$  is common,  $W(d) - W(d^*)$  is proportional to

$$(d^* - d)^2 [1 - q(1 - V_0 - V_z)] [A_0 V_0 + A_1(1 - s)(1 - V_0 - V_z - V_{z-1})], \quad (B4)$$

which is positive for all values of  $d \neq d^*$ .

Equation (9) is sensible (i.e.,  $0 \leq d^* \leq 1$ ) if

$$q \leq \frac{A_1(1 - s)(1 - V_0 - V_z - V_{z-1})}{(1 - V_0 - V_z)[A_0 V_0 + A_1(1 - s)(1 - V_0 - V_z - V_{z-1})]}. \quad (B5)$$

Maximal dispersal ( $d^* = 1$ ) is favored unless migration is sufficiently hazardous ( $q$  satisfying eq. [B5]). Because the upper limit of  $q$  given by equation (B5) may exceed unity, intermediate ES dispersal rates may evolve even under very high probabilities of surviving migration (even when  $q = 1$ ).

In the absence of succession (arbitrarily large  $z$ ),  $V_{z-1}$  and  $V_z$  are negligible (see eqq. [5] and [6]), and equation (9) reduces in this case to

$$d^* = \frac{(1 - A_1)(1 - A_1 + A_0)}{[1 - A_1 + A_0(1 - q)](1 - A_1 s)}. \quad (B6)$$

The quantity  $d^*$  increases with  $s$ ,  $q$ , and  $A_0$ , up to  $d^* = 1$ . It can be shown that either  $d^*$  is equal to 1 or  $d^*$  decreases when  $A_1$  increases. This is true whether  $A_0$  is equal to  $A_1$  or independent of  $A_1$ .

For identical persistence probabilities for all sites ( $A_i = A_1$  for all  $i$ ), equation (9) reduces to

$$d^* = \frac{1 - A_1}{[1 - q(1 - V_0 - V_z)][1 - A_1 s - (1 - s)A_1^{z-1}]}. \quad (B7)$$

With complete adult replacement ( $s = 0$ ) and arbitrarily large  $z$ , equation (B7) reduces to the ES dispersal rate obtained by Comins et al. (1980) and Levin et al. (1984):

$$d^* = \frac{1 - A_1}{1 - qA_1}. \quad (B8)$$

APPENDIX C

DYNAMIC ANALYSIS OF THE ES DISPERSAL RATE

Making the system of equations given by equations (11), (12), and (13) linear (ignoring second-order and higher terms in frequency of the rare genotype) produces the recursion

$$\mathbf{X}' = \mathbf{M}\mathbf{X}. \quad (C1)$$

Here,  $\mathbf{X}$  denotes the vector of frequencies of the rare genotype among demes ( $\mathbf{X} = [X_i, i = 1, 2, \dots, z - 1]$ ),  $\mathbf{X}'$  the vector in the next generation, and  $\mathbf{M}$  a  $(z - 1)$ -dimensional square matrix:

$$\mathbf{M} = \begin{bmatrix} \frac{d}{d^*} \bar{V}_1 & \frac{d}{d^*} \bar{V}_2 & \cdots & \frac{d}{d^*} \bar{V}_{z-2} & \frac{d}{d^*} \bar{V}_{z-1} \\ a + b\bar{V}_1 & b\bar{V}_2 & \cdots & b\bar{V}_{z-2} & b\bar{V}_{z-1} \\ b\bar{V}_1 & a + b\bar{V}_2 & \cdots & b\bar{V}_{z-2} & b\bar{V}_{z-1} \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ b\bar{V}_1 & b\bar{V}_2 & \cdots & a + b\bar{V}_{z-2} & b\bar{V}_{z-1} \end{bmatrix}, \quad (C2)$$

in which

$$a = a(d) = s + (1 - s) \frac{1 - d}{1 - d^*[1 - q(1 - V_0 - V_z)]} \quad (C3)$$

and

$$b = b(d) = (1 - s) \frac{dq(1 - V_0 - V_z)}{1 - d^*[1 - q(1 - V_0 - V_z)]} \quad (C4)$$

Each frequency  $X'_{i+1}$  ( $i > 0$ ) has thus the form  $aX_i + \sum b\bar{V}_i X_i$ . The quantity  $a$  corresponds to residents (adults plus offspring produced locally), and the quantity  $b$  corresponds to immigrants. The first row of  $\mathbf{M}$  corresponds to recolonization of empty sites by immigrants from all other sites.

The rare genotype successfully invades if the absolute value of the dominant eigenvalue of  $\mathbf{M}$  exceeds unity. If the rare genotype disperses at the same rate as the common genotype ( $d = d^*$ ),  $a(d^*) + b(d^*) = 1$ . All rows of  $\mathbf{M}$  sum to unity, so  $\text{Det}[\mathbf{I} - \mathbf{M}]_{d=d^*} = 0$ . Such neutral genotypes neither increase nor decline in frequency. For sufficiently small effects (small  $[d - d^*]$ ), rare genotypes affecting dispersal rate increase geometrically only if

$$\text{Det}[\mathbf{I} - \mathbf{M}] < 0 \quad (C5)$$

Ignoring terms of order  $(d - d^*)^2$  or smaller, we obtain

$$\text{Det}[\mathbf{I} - \mathbf{M}] = \frac{d - d^*}{d^*} \left[ -1 + \sum_{i=2}^{z-1} \bar{V}_i \frac{1 - a(d^*)^{i-1}}{q(1 - V_0 - V_z)} \right] \quad (C6)$$

Introduced dispersal modifiers increase when rare if equation (C6) is negative. Neither enhancers ( $d > d^*$ ) nor suppressors ( $d < d^*$ ) of dispersal invade at geometric rates if the resident dispersal rate satisfies

$$q(1 - V_0 - V_z) = \sum_{i=2}^{z-1} \bar{V}_i [1 - a(d^*)^{i-1}] \quad (C7)$$

This equation implicitly defines the candidate ES dispersal rate.

For the case of equal extinction probabilities of occupied sites ( $A_i = A_1$  for  $1 \leq i \leq z - 1$ ),  $\bar{V}_i$  and  $\bar{V}_1$  are given by equations (7) and (8), and the candidate ES dispersal rate is given by

$$d^* = \frac{1 - A_1}{(1 - sA_1)[1 - q(1 - V_0 - V_z)] - A_1 \bar{V}_{z-1}(1 - s) \frac{1 - a(d^*)^{z-1}}{1 - a(d^*)}} \quad (C8)$$

which is equation (14) in main text.

Because of the dependence of  $a(d^*)$  on  $d^*$ , equation (C8) in fact corresponds to a polynomial of potentially high order in  $d^*$ . The ES dispersal rate is obtained by solving equation (C8).

Both the dynamic and nondynamic analyses have addressed evolutionary stability with respect to convergence in frequency space by determining the dispersal rate that would prevent the initial increase of genotypes that exhibit any other dispersal rate. A distinct kind of evolutionary stability entails convergence in parameter space. We consider the fate of modifiers of the dispersal rate introduced into a population for which the dispersal rate differs from the ES rate. We say that a dispersal rate is evolutionarily attracting if suppressors of dispersal invade only if the prevailing dispersal rate exceeds the ES rate (see Christiansen 1991), even if the ultimate fixation of the invading genotypes would entail

even greater deviations from the ES dispersal rate. In terms of the present analysis, equation (C6) indicates that, in the absence of succession (arbitrarily large  $z$ ), rare modifiers increase if

$$(d - d^*) \left[ -1 + \frac{d^*(1-s)A_1(1-A_1)}{1 - d^* \left(1 - \frac{qA_0}{1 + A_0 - A_1}\right)} \right] < 0 . \tag{C9}$$

The ES dispersal rate is defined as the value of  $d^*$  for which the second bracket in equation (C9) is zero. If the prevailing dispersal rate  $d^*$  exceeds the ES rate, this second bracket is positive, and modifiers that reduce dispersal ( $d < d^*$ ) invade. Enhancers of dispersal ( $d > d^*$ ) invade only if the prevailing dispersal rate  $d^*$  falls below the ES rate. We conclude that the ES dispersal rate is in fact evolutionarily attracting.

APPENDIX D

DEMONSTRATION OF THE UNIQUENESS OF THE ES DISPERSAL RATE

OVIDE ARINO

I.P.R.A. Mathématiques, 64000 Pau, France

Let  $r(d)$  be the largest eigenvalue of  $\mathbf{M}$  in equation (C2). Let  $\mathbf{Y}(d)$  be a row eigenvector of  $\mathbf{M}$  for the eigenvalue  $r(d)$ . We can normalize  $\mathbf{Y}(d)$  so that it is unique, in order for the application of  $d$  into  $\mathbf{Y}(d)$  to be regular. Thus,  $\mathbf{Y}(d)$  is the solution of

$$\mathbf{Y}(d)\mathbf{M}(d) = r(d)\mathbf{Y}(d) . \tag{D1}$$

All components of  $\mathbf{Y}(d)$  are positive. Let  $\mathbf{e}$  represent the column vector in which all elements are unity. By applying  $\mathbf{e}$  to equation (D1), we obtain

$$\mathbf{Y}(d)\mathbf{M}(d)\mathbf{e} = r(d)\mathbf{Y}(d)\mathbf{e} . \tag{D2}$$

We then calculate the derivative of this equality with respect to  $d$ , at the value  $d = d^*$ . Noting that  $r(d^*) = 1$  and  $\mathbf{M}(d^*)\mathbf{e} = \mathbf{e}$ , we obtain

$$\mathbf{Y}(d^*)\mathbf{M}'(d^*)\mathbf{e} = r'(d^*)\mathbf{Y}(d^*)\mathbf{e} , \tag{D3}$$

in which the primes stand for the derivatives with respect to  $d$ .

The ES dispersal rate is determined by  $r(d^*) = 1$  and  $r'(d^*) = 0$ . Value  $r'(d^*)$  has the sign of

$$\phi(d^*) = \mathbf{Y}(d^*)\mathbf{M}'(d^*)\mathbf{e} . \tag{D4}$$

Letting  $l = a'(d^*) + b'(d^*)$ , we have

$$\mathbf{M}'(d^*)\mathbf{e} = \begin{pmatrix} 1 \\ d^* \\ l \\ \vdots \\ l \end{pmatrix} . \tag{D5}$$

We thus have

$$\phi(d^*) = \frac{t_1}{d^*} + (t_2 + \dots + t_{z-1})l , \tag{D6}$$

where  $t_1, t_2, \dots, t_{z-1}$  are the components of  $\mathbf{Y}(d^*)$ :

$$\begin{aligned} t_1 &= at_2 + c\bar{V}_1 \\ t_2 &= at_3 + c\bar{V}_2 \\ &\vdots \\ t_{z-2} &= at_{z-1} + c\bar{V}_{z-2} \\ t_{z-1} &= c\bar{V}_{z-1}, \end{aligned} \tag{D7}$$

where  $c = t_1 + b(t_2 + \dots + t_{z-1})$ , with  $a = a(d^*)$  and  $b = b(d^*)$ .

We normalize the vector  $\mathbf{Y}(d^*)$  by letting  $c = 1$ . We then have

$$\phi(d^*) = \frac{t_1}{d^*} + \frac{(1 - t_1)l}{b}. \tag{D8}$$

Using equation (D8), we obtain

$$t_1 = \bar{V}_1 + a\bar{V}_2 + \dots + a^{z-2}\bar{V}_{z-1}, \tag{D9}$$

and thus

$$\begin{aligned} \phi(d^*) &= \frac{\bar{V}_1 + a\bar{V}_2 + \dots + a^{z-2}\bar{V}_{z-1} + [1 - (\bar{V}_1 + a\bar{V}_2 + \dots + a^{z-2}\bar{V}_{z-1})]l}{d^*} \\ &= \frac{\bar{V}_1 + a\bar{V}_2 + \dots + a^{z-2}\bar{V}_{z-1} + q(1 - V_0 - V_z) - 1}{d^*q(1 - V_0 - V_z)}. \end{aligned} \tag{D10}$$

It is easily shown that  $a(d^*)$ , and thus  $\phi(d^*)$ , are decreasing functions of  $d^*$  (the derivative of  $a(d^*)$  with respect to  $d^*$  is proportional to  $-[1 - s]q[1 - V_0 - V_z]$ ). The quantity  $\phi(d^*)$  therefore takes the zero value at most once, and thus the solution to  $r'(d^*) = 0$  is unique.

Moreover, if  $d_0^*$  is the solution of  $\phi(d^*) = 0$ , then  $r'(d^*) > 0$  for  $d^* < d_0^*$ , and  $r'(d^*) < 0$  for  $d^* > d_0^*$ . Thus,  $r(d^*) < r(d_0^*)$  for  $d^* \neq d_0^*$  and in the neighborhood of  $d_0^*$ . This implies that the ES dispersal rate always invades a population in which the dispersal rate is close to but different from the ES dispersal rate.

### APPENDIX E

#### INFLUENCE OF SITES OF TYPE $z - 1$ ON THE MAINTENANCE OF A POLYMORPHISM BETWEEN TWO GENOTYPES STRADDLING THE ES DISPERSAL RATE

We consider a metapopulation with two annual genotypes 1 and 2, determining dispersal rates of  $d_1$  and  $d_2$ , respectively. Let  $X_i$  be the frequency of genotype 2 in sites of type  $i$ . We assume that genotype 2 is rare, so that  $X_i \approx 0$  for all  $i$ .

The number of immigrants per site is equal to

$$C_i = \sum_{i=1}^{z-1} V_i K m [X_i d_2 + (1 - X_i) d_1] \tag{E1}$$

$$\approx K m d_1 (1 - V_0 - V_z). \tag{E2}$$

The frequency of the rare genotype among the immigrants of the following generation is (see eq. [12])

$$X'_1 = \frac{\sum_{i=1}^{z-1} V_i X_i K m d_2}{C_i} = \frac{d_2}{d_1} X, \tag{E3}$$

with  $X = \sum \bar{V}_i X_i$ .

The frequency of the rare genotype in established populations is

$$X'_i = \frac{Km(1 - d_2)X_{i-1} + q_{1,t}C_t}{(1 - d_1)Km(1 - X_{i-1}) + (1 - d_2)KmX_{i-1} + C_t} \tag{E4}$$

$$\approx \frac{X_{i-1}(1 - d_2) + d_2X(1 - V_0 - V_z)}{1 - d_1(V_0 + V_z)} \tag{E5}$$

The overall frequency of the rare genotype in the next generation is

$$X' = \sum_{i=1}^{z-1} \bar{V}_i X'_i = \bar{V}_1 X'_1 + \sum_{i=2}^{z-1} \bar{V}_i X'_i \tag{E6}$$

By replacing  $\bar{V}_i$  with  $A_1 \bar{V}_{i-1}$  for  $i \in [2, \dots, z - 1]$ , and  $X'_i$  with the expression above, we obtain

$$X' \approx X \left\{ \frac{d_1}{d_1} \bar{V}_1 + \frac{A_1[1 - d_2(V_0 + V_z + V_{z-1})]}{1 - d_1(V_0 + V_z)} \right\} - \frac{A_1(1 - d_2)\bar{V}_{z-1}X_{z-1}}{1 - d_1(V_0 + V_z)} \tag{E7}$$

When sites of type  $z - 1$  are negligible ( $\bar{V}_{z-1} \approx 0$ ),  $X'$  is a linear function of  $X$ ,  $\bar{V}_1 = 1 - A_1$ , and the relative variation of gene frequency from one generation to the next is

$$\frac{\Delta X}{X} \approx \frac{d_2(1 - A_1)}{d_1} + A_1 \frac{1 - d_2(V_0 + V_z)}{1 - d_1(V_0 + V_z)} - 1 \tag{E8}$$

The value  $\Delta X$  has the sign of  $S = (d_2 - d_1)[1 - A_1 - d_1(V_0 + V_z)]$ . In this expression, one can recognize  $(1 - A_1)/(V_0 + V_z)$ , the ESS when  $V_{z-1}$  is negligible (see eq. [B7] or [14] in main text with  $q = 1$  and  $s = 0$ ).

Thus  $S \propto (d_2 - d_1)(d^* - d_1)$ . This equation clearly shows that the genotype determining a dispersal rate  $d_2$  increases when rare either if  $d_1 < d^*$  and  $d_2 > d_1$  or if  $d_1 > d^*$  and  $d_2 < d_1$ . In particular, any polymorphism between two genotypes straddling the ESS (but not necessarily close to it) should be protected when  $\bar{V}_{z-1}$  is negligible. This was checked numerically in the case of landscape L4, with  $z = 100$  and a high fecundity.

When  $\bar{V}_{z-1}$  is not negligible, there is an extra (negative) term to  $X$  that seems (numerically) to prevent protection of genotypes with dispersal rates that are too far from the ESS, compared with the resident genotype. As this term is proportional to  $\bar{V}_{z-1}X_{z-1}$  it is likely to induce some negative frequency dependence (the larger the frequency of genotype 2 in sites  $z - 1$ , the more it is selected against).

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*Associate Editors: Robert D. Holt  
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