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The role of local adaptation in metapopulation restorations

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Abstract

We propose an original approach to model the effect of the initial spatial distribution of a reintroduced metapopulation (one-patch release versus multi-patch release) on local adaptation. Genetic and demographic processes are considered to investigate how the different patterns of adaptation resulting from initial conditions affect metapopulation viability. In agreement with classical interpretations in the fields of population biology and evolutionary genetics, we observe an influence of the degree of environmental correlation among patches on demographic processes and an influence of inter-patch connection on genetic processes. However, our results uncover some further effects of the environment, owing to positive feedback interactions among demographic and genetic processes. When considering the one-patch release, demographic stochasticity engenders a delay in the colonization of initially empty patches. This delay enhances the genetic asymmetry among patches (in terms of local adaptation), which in turn increases demographic asymmetry. In contrast, the multi-patch release produces similar levels of adaptation among patches. Metapopulation dynamics is strongly influenced by these differences, with contrasting effects under different environments. The pattern of adaptation produced by the one-patch release strategy is optimal under a regime of recurrent slight perturbations or environmental stochasticity, while the multi-release strategy is optimal in the presence of rare and severe perturbations.

INTRODUCTION

The ability of a population to adapt to its environment depends both on its extent of genetic variation (Franklin, 1980; Lande, 1995; Frankham *et al*., 1999) and on population subdivision (Lacy, 1987). In a metapopulation context, local selection (i.e. heterogeneous selection among subpopulations) is expected to generate various levels of adaptation to the different patches (Taylor, 1976; Lacy, 1982) and to increase the variance in fitness among subpopulations. The pattern of local adaptation of a metapopulation is expected to vary with the degree of divergence of the environments in the different sites, with the sizes of subpopulations and their level of connectivity, and also with the initial population distribution.

In the context of species restoration, genetics is considered either in relation to population viability considerations, or in relation to the preservation of 'local genetic peculiarities', two problems in which local adaptation may play a role. Although the genetic and demographic characteristics of released populations depend on the origin of the founders (Griffith *et al*., 1989; May, 1991; Wolf *et al*., 1996) as well as on management and release strategy (Sarrazin & Legendre, 2000), such populations are likely to be ill adapted to their new local environments in many cases. This non-adaptation, due either to a divergence between the source population's natural environment and the release site (Montalvo & Ellstrand, 2000), or to some adaptation to captivity (Frankham, 1994), is likely to impair the success of introduction (Griffith *et al*., 1989). In translocated populations, the advantage of locally adapted individuals has been extensively discussed (Keller, Kollmann & Edwards, 2000; Montalvo & Ellstrand, 2000; Wilkinson 2001). However, the potential for rapid adaptation is rarely considered in population viability analyses (Gilligan *et al*., 1997), although it has been suggested in some species that the adaptability was sufficient to override the genetic differences between subspecies (Tordoff & Redig, 2001). Most of these results emerging from a context of conservation are consistent with long-term evolutionary studies, which have uncovered the rapid evolution of fitness owing to beneficial mutations (Lenski *et al*., 1991; Lenski & Travisano, 1994).

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When considering metapopulation viability, and more generally for conservation purposes, demographic processes must be taken into account since their impact on viability is of major importance. Demographic stochasticity is frequently invoked as an important cause of extinction for small populations (Shaffer, 1987). Its strength depends on population size, on population growth rate and on mating system (Boyce, 1992; Gabriel & Bürger, 1992; Legendre *et al*., 1999). Hence, dividing a population into several smaller ones is likely to affect its viability by increasing demographic stochasticity in each sub-population.

Besides these genetic and demographic considerations, environmental perturbations have been invoked as an important threat for the viability of natural and translocated populations in theoretical (Shaffer, 1987; Lande, 1993) and empirical studies (Griffith *et al*., 1989). Therefore, the pattern of variation of the environment and its degree of independence among subpopulations constitute a third factor that must be considered to assess metapopulation viability (Gilpin, 1987, 1988; Quinn & Hastings, 1987; Harrison & Quinn, 1989; Hanski, 1989, 1991; Earn, Levin & Rohani, 2000).

In the present work, we model a three-patch metapopulation to investigate the effect of local adaptation (a process generally considered in evolutionary topics) in a conservation perspective. The relative efficiencies of two release strategies (in terms of metapopulation viability) are compared with or without including the effect of local adaptation genes, using different life-history categories. The first strategy consists in releasing all individuals into the same site ('strategy R1') and the second one consists in allocating them equally to all three patches ('strategy R3'). In our model, the individual fitness is a function of the interaction between the genotype and the local environment, with the locally adapted individuals having a higher fitness than non-adapted individuals. From a demographic view-point, we expect that the optimal release strategy will essentially depend on the correlation of environmental fluctuations among patches (Hanski, 1989; Harrison & Quinn, 1989). However, from a genetic view-point, several mechanisms might complicate the predictions. For instance, with a one-patch release, 'niche conservatism' (Holt & Gaines, 1992; Holt, 1996) might impede local adaptation to other patches. Although these demographic and genetic processes are well studied in the respective disciplines of population biology and evolutionary genetics, their potential interactions in a metapopulation setting are generally ignored, especially in the field of conservation biology. Such considerations may be of importance, especially if these processes influence metapopulation dynamics within time frames of conservation concern. Hence two questions are raised: (1) how can the management of restoration (i.e. initial conditions) influence local adaptation processes; (2) under which environmental conditions can the resulting patterns of adaptation (in interaction with demography) influence extinction risk; and consequently, which strategy should be recommended for management of restored populations?

METHODS

Life-cycle and metapopulation dynamics

We use a two-sex individual-based model approach to consider both a semelparous annual life cycle (non-overlapping generations) and an iteroparous life cycle (overlapping generations). For the semelparous model, males and females pair in each time-step (year) according to their mating system and all adults die after reproduction. Fecundity is then the only parameter of fitness. The basic individual fecundity is F. For the iteroparous model, males and females pair, and reproduction is followed by differential survival according to the interaction between genotype and age for each individual. The mean fecundities F and age-specific survival rates s_x used for these models are presented in Table 1. These demographic parameters were computed to obtain different generation lengths and asymptotic growth rates, by using a deterministic matrix model (computer program ULM; Legendre & Clobert, 1995; Ferrière *et al*., 1996). In order to test the robustness of our results to different mating systems, we simulate some reintroductions using a monogamous mating system, in which males and females are paired one to one, and using a polygynous mating system, in which a single male can mate with several females, without any restriction in the number of females per male.

Demographic stochasticity for reproduction results first from the drawing of the number of offspring of each reproducing female from a Poisson distribution and second from the random determination of the sex of each individual. Each survival event is drawn from a Bernouilli function. In simulations where environmental stochasticity is considered, the average individual fecundity in patch i at generation t ($F_{(ti)}$) is obtained from a Normal distribution with a fixed mean F and a standard deviation σ (negative values of $F_{(ti)}$ are assumed to be 0). Similarly, age-specific survival rates in patch i at generation t ($s_{x(ti)}$) are obtained from a normal distribution with a fixed mean s_x and a standard deviation σ. In addition, catastrophic events occur stochastically with a probability Pc in each patch at each generation to reduce $F_{(ti)}$ or/and $s_{x(ti)}$ in a proportion C.

Table 1. Demographic parameters used for two types of species with overlapping generations. The generation time is computed as the mean age of the parents of the offspring produced by a population at the stable age distribution (Caswell, 2001).

	Short-lived species	Long-lived species
Juvenile survival (s_0)	0.415	0.7
Immature survival (s_1)	0.5025	0.7194
Immature survival (s_2)	–	0.85
Immature survival ($_s3$)	–	0.85
Adult survival (s_a)	0.6	0.9
Age at maturity	2	4
Annual individual fecundity (F)	2.64	0.35
Generation time	3.2	11.5
Life expectancy at birth (ls)	0.94	5.27
Deterministic growth rate	1.1	1.02

Initially, N_0 individuals are released. The population of each patch is truncated to the carrying capacity K in each generation, independently of the genetic qualities of individuals (K is assumed to be the same for the three patches).

The population is divided in three patches, all connected to each other, and inter-patch dispersal occurs stochastically after birth. We investigate two patterns of dispersal: an unconditional dispersal, in which the emigration rate m is constant, and a density-dependent dispersal, in which emigration takes place preferentially from the high-density patches. In the latter case, the rate of emigration from patch i at time t is $m_{ti} = m \,.\, (N_{ti}/K)$ with N_{ti} being the population size of patch i at time t. The effect of the degree of independence of the environmental variations among patches is investigated by comparing situations where fluctuations (i.e. environmental stochasticity and catastrophes) are independent with situations where fluctuations are fully correlated among patches.

Genetic characteristics

Each diploid genome is explicitly represented with 450 different diploid loci. At each locus, there are four possible alleles: '0' (wild-type allele), '1' (adaptation to the environment in patch 1, that is increase of fitness in patch 1), '2' (increase of fitness in patch 2), '3' (increase of fitness in patch 3). Consequently, an allele that is advantageous in one patch is neutral in the other patches. The initial number of alleles increasing fitness (i.e. type 1, 2 or 3) present in each founder is stochastically determined from a Poisson distribution of mean $q_0.L$ (where q_0 is the initial frequency and L is the number of loci); the remaining alleles are '0' (non-adaptive alleles). The number of independent loci considered is sufficient to assume that the initial diversity of adaptive mutations present in the founders (which determines the potential for future adaptation) increases linearly with the number of founders. During fertilisation, the probability of transmission of each allele at each locus is given by the Mendelian rules. We assume that there is no new mutation at the time scale considered and, for simplicity, we assume multiplicative interactions for fitness and free recombination of all loci.

The individual-based structure of the model allows the alleles on these independent loci to evolve in interaction with the demographic characteristics of the population. Adaptive alleles act at the individual level by influencing the fitness of each individual according to its location. In the semelparous model, adaptive alleles are assumed to increase fecundity only, whereas in the iteroparous model, adaptive alleles increase fecundity, survival, or both. In cases where mutations increase fecundity, the genetic factor wfj that characterises the relative fecundity of individual j is $\mathrm{wf_j} = (1 + hs)^{n1} \,.\, (1 + s)^{n2}$; where s is the fractional increase in fecundity caused by a homozygous mutation, $n1$ and $n2$ are the numbers of loci in the individual that are respectively heterozygous and homozygous for a locally adaptive mutation (depending on which patch the individual stays in), and h is the dominance coefficient. Similarly, in cases where mutations increase survival rates, the genetic factor wsj that characterises the relative survival (at any age) of individual j is $\mathrm{ws}_j = (1 + hs/ls)^{n1} \,.\, (1 + s/ls)^{n2}$; where ls is the lifespan of the species.

The size of each patch determines the magnitude of the deviation of the allelic frequencies from the frequencies expected without drift, according to the individual realizations of genetic and demographic stochastic processes (mating, fertilization, death, birth, dispersal, fluctuation in sex-ratio, etc.). In cases where mutations increase fecundity, the deterministic number of offspring of the particular pair (j, k) in patch i at generation t is given by $F_{(t,i,j,k)} = 2.\mathrm{w}f_j.\mathrm{w}f_k.F_{(ti)}$. The integer number of offspring is then obtained from a Poisson distribution of mean $F_{(t,i,j,k)}$. In cases where mutations increase survival (only in the iteroparous models), the age-specific survival rate of the individual j in patch i at generation t is given by $S_{x(t,i,j)} = \mathrm{ws}_j.S_{x(ti)}$.

Extinction occurs when metapopulation size is equal to zero. The evolution of the genetic characteristics and extinction probabilities are investigated in different scenarios, by using Monte Carlo simulations in which 1000 population trajectories are drawn over 100 years.

RESULTS

Influence of the initial spatial population distribution on allelic frequencies

Strategies R1 and R3 lead to two distinct patterns of local adaptation. In the case of strategy R3, we note a progressive increase of the mean frequencies of the three types of selected alleles in each patch, with the frequency of each allele increasing more in the patch where it is locally adaptive (despite inter-site connection). This genetic differentiation among the three patches results in a homogeneous increase of the mean fitness in each patch.

In the case of strategy R1, the frequency of type 1 alleles (which are locally adaptive in the release patch) largely increases in the three patches, while the frequencies of the two other types of alleles do not change within 100 generations. This absence of genetic differentiation results in a divergence of the mean fitness in the three patches. Fitness increases largely in the release patch (patch 1), while it remains close to its initial level in patches 2 and 3.

Quantitatively, the divergence between strategies R1 and R3 depends substantially on the rate of dispersal. However, the above result remains qualitatively unchanged for a broad array of inter-patch dispersal rates (Fig. 1): the efficiency of local adaptation (expressed as the frequency of locally adaptive alleles) is always high in the release patch and low in the other patches for strategy R1 (left), while it is intermediate in all sites for strategy R3 (right). This divergence is maximal for relatively low dispersal rates ($m < 0.05$). The type of dispersal (density dependent versus constant-not shown) does not qualitatively affect these results.

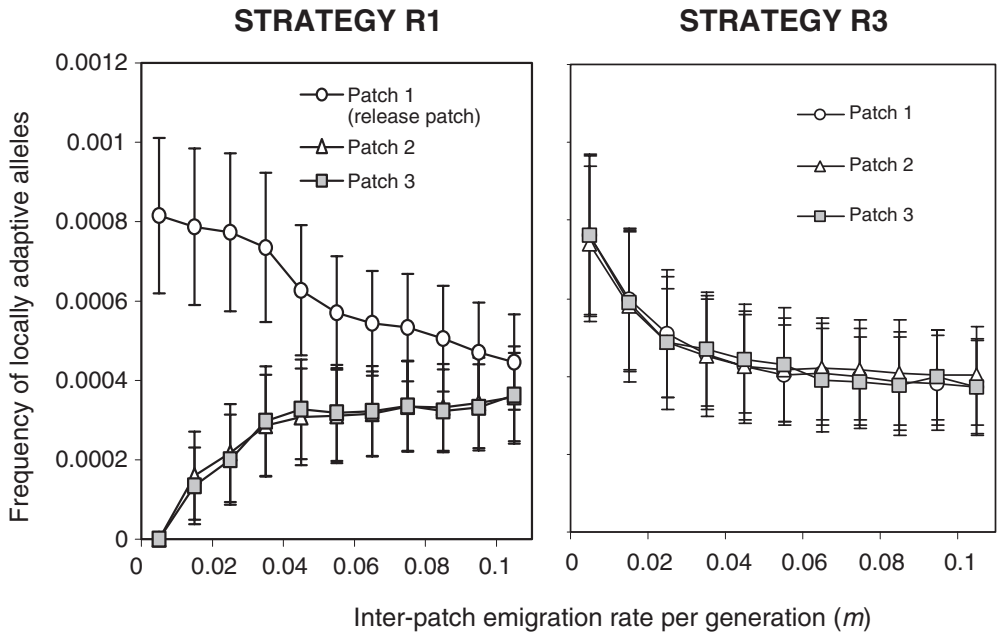

Fig. 1. Frequencies of locally adaptive alleles in each patch according to the dispersal rate (after 100 generations). Semelparous monogamous population with density-dependent dispersal; perturbations are not synchronized; $N_0 = 75$ individuals; $F = 1.6$; $K = 75$; $P_c = 0.16$; $C = 0.2$; $\sigma = 0.1$; $q_0 = 0.0005$; $s = 0.1$; $h = 0.5$.

Consequences of the pattern of adaptation on extinction

In order to evaluate precisely the effect of local adaptation on extinction, Figures 2, 3 and 4 compare the results obtained with and without the effect of adaptive genes. The genetic factor w of all individuals is fixed to 1 in the latter case so there is no selection.

Not surprisingly, for strategies R1 and R3, adaptive genes have a beneficial impact on viability in all cases. However, the magnitude of this impact is not equivalent for the two strategies and depends largely on the type of environment considered. Under environmental stochasticity, local adaptation genes slightly increase the relative efficiency of strategy R1, whatever the strength of perturbations (compare the left and right sides of Fig. 2(a). Under a regime of punctual perturbations, the relative impacts of the two strategies depend on the types of perturbations. The pattern of adaptation generated by strategy R1 is more beneficial if perturbations are relatively frequent and of weak effect, while the pattern of adaptation generated by strategy R3 is optimal if perturbations are less frequent and of strong effect (catastrophes) (compare the left and right sides of Fig. 2(b).

From a demographic view-point, the degree of correlation of environmental fluctuations among patches has two effects (Fig. 3). First, the efficiency of strategy R3 relative to strategy R1 increases when perturbations occur independently among patches, owing to a lowered probability of global extinction via environmental perturbations when the three sites are initially occupied. Secondly, for both strategies, high dispersal rates are more beneficial than low dispersal rates if perturbations act independently, owing to a more efficient demographic rescue (no synchronization of subpopulations' dynamics). From a genetic view-point, the impact of adaptive genes remains qualitatively unchanged (i.e. a relative increase of the efficiency of strategy R3 in this case) whether perturbations are correlated or not. Above results are presented using a semelparous annual life cycle, in which a duration of 100 years exactly corresponds to 100 generations. By using an iteroparous model with overlapping generations, we found similar results concerning the qualitative impact of adaptation in relation to the release strategy (i.e. an important increase of the relative efficiency of R3 in the presence of catastrophes (Fig. 4a) and a slight increase of the relative efficiency of strategy R1 in the presence of frequent/slight perturbations or environmental stochasticity (Fig. 4(b)). In Fig. 4, deterministic growth rates are different in order to obtain similar extinction rates). However, although no qualitative difference exists between overlapping and non-overlapping generations models, comparisons between different life-history categories uncover substantial variations in the impact of local adaptation on metapopulation dynamics. In particular, for iteroparous life cycles, adaptive mutations have a very much more beneficial impact on metapopulation persistence in the case of the short-lived compared with the long-lived species.

In order to test the robustness of these results to a change in some demographic and genetic parameters, some additional simulations were performed with different growth rates (ranking from 1 to 2.5 for semelparous and from 1 to 1.2 for iteroparous species), carrying capacity K (from 75 to 500), coefficient of selection s (from 0.01 to 0.5) and coefficient of dominance h (from 0 to 1). In each case, a comparison of the

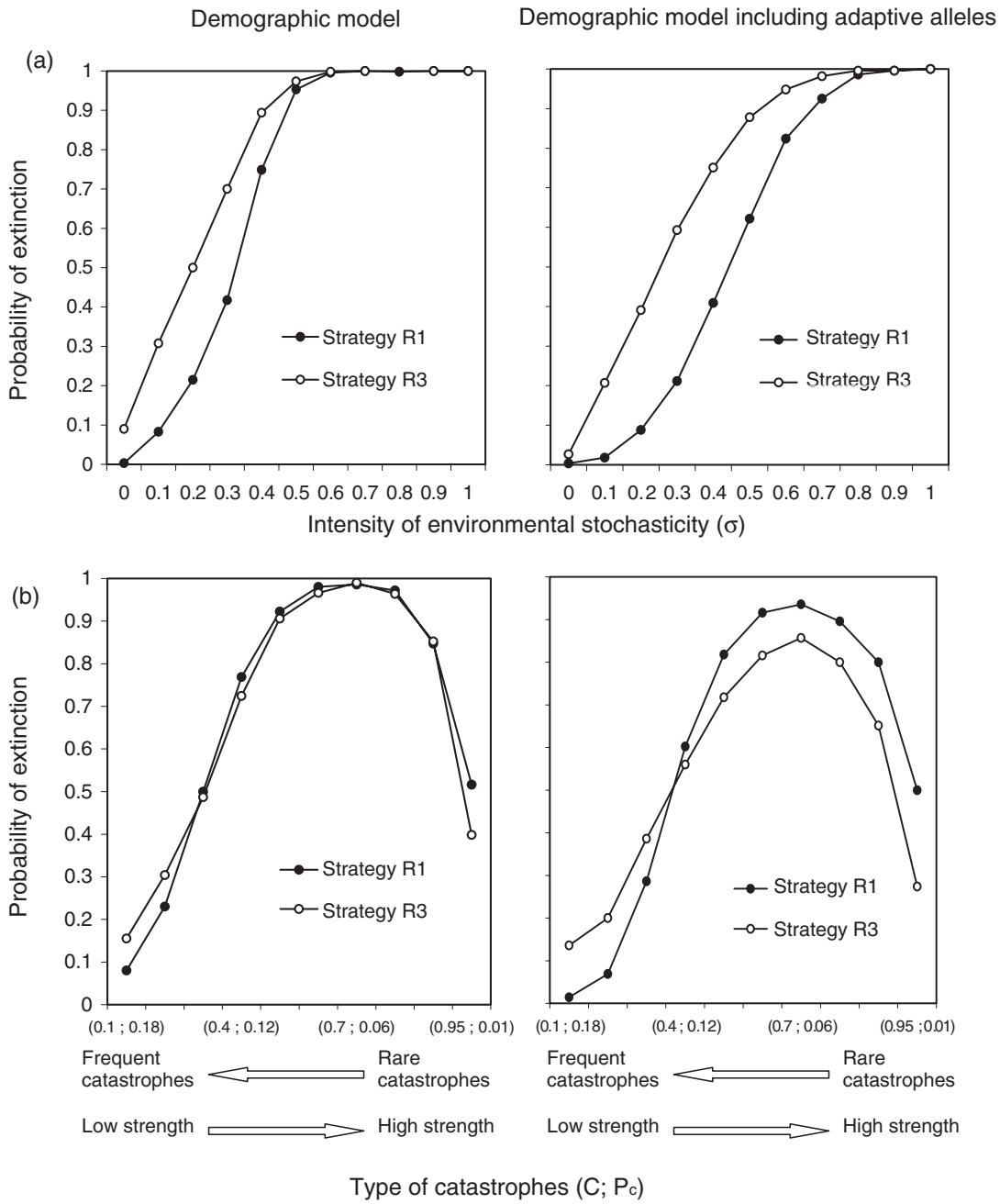

Fig. 2. Influence of environmental stochasticity (a), and catastrophes (b) on metapopulation viability, in the absence/presence of a possibility of local adaptation. Probability of extinction after 100 generations. Semelparous monogamous population with a density dependent dispersal; perturbations are not synchronised; $N_0 = 75$ individuals; $F = 1.6$; $K = 75$; $m = 0.02$; $q_0 = 0.0005$; $s = 0.1$; $h = 0.5$.

viabilities with and without the effect of local adaptation genes was made. Our results indicate that the efficiency of strategy R1 increases with the carrying capacity of patches (for an equivalent number of released individuals) and decreases with the basic individual fecundity. However, when comparing models in which adaptation genes are considered with models without possibility of adaptation, the impact of local adaptation remains in conformity with the above results in every cases. Similarly, variations in the genetic parameters *s* and *h* do not qualitatively affect these results.

Comparisons between a monogamous and a polygamous population indicate that the changes in allelic frequencies are not affected by the mating system. The impact of demographic stochasticity is substantially reduced with a polygamous mating system (Legendre *et al.*, 1999), which decreases the efficiency of strategy R3 relative to strategy R1, particularly under frequent catastrophes or strong environmental stochasticity, but it does not affect our general conclusions, from a genetic view-point.

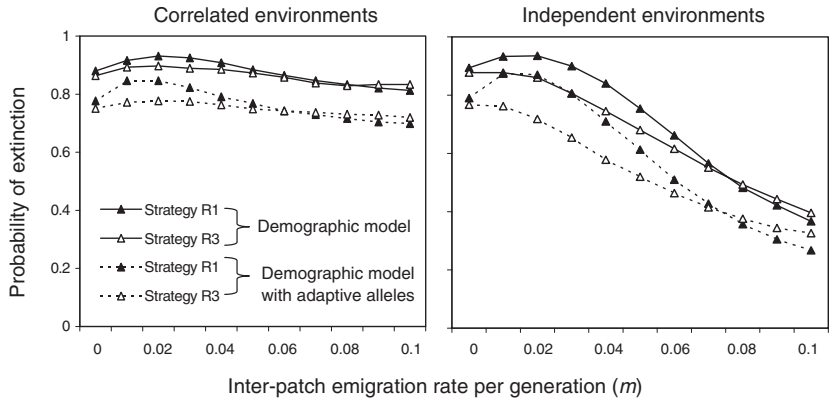

Fig. 3. Influence of the rate of inter-patch dispersal rate on metapopulation viability, in the presence of correlated/independent environmental fluctuations. Probability of extinction after 100 generations. Semelparous monogamous population with a density dependent dispersal; $N_0 = 75$ individuals; $F = 1.6$; K = 75; $P_c = 0.04$; $C = 0.8$; $\sigma = 0.1$; $q_0 = 0.0005$; $s = 0.1$; $h = 0.5$.

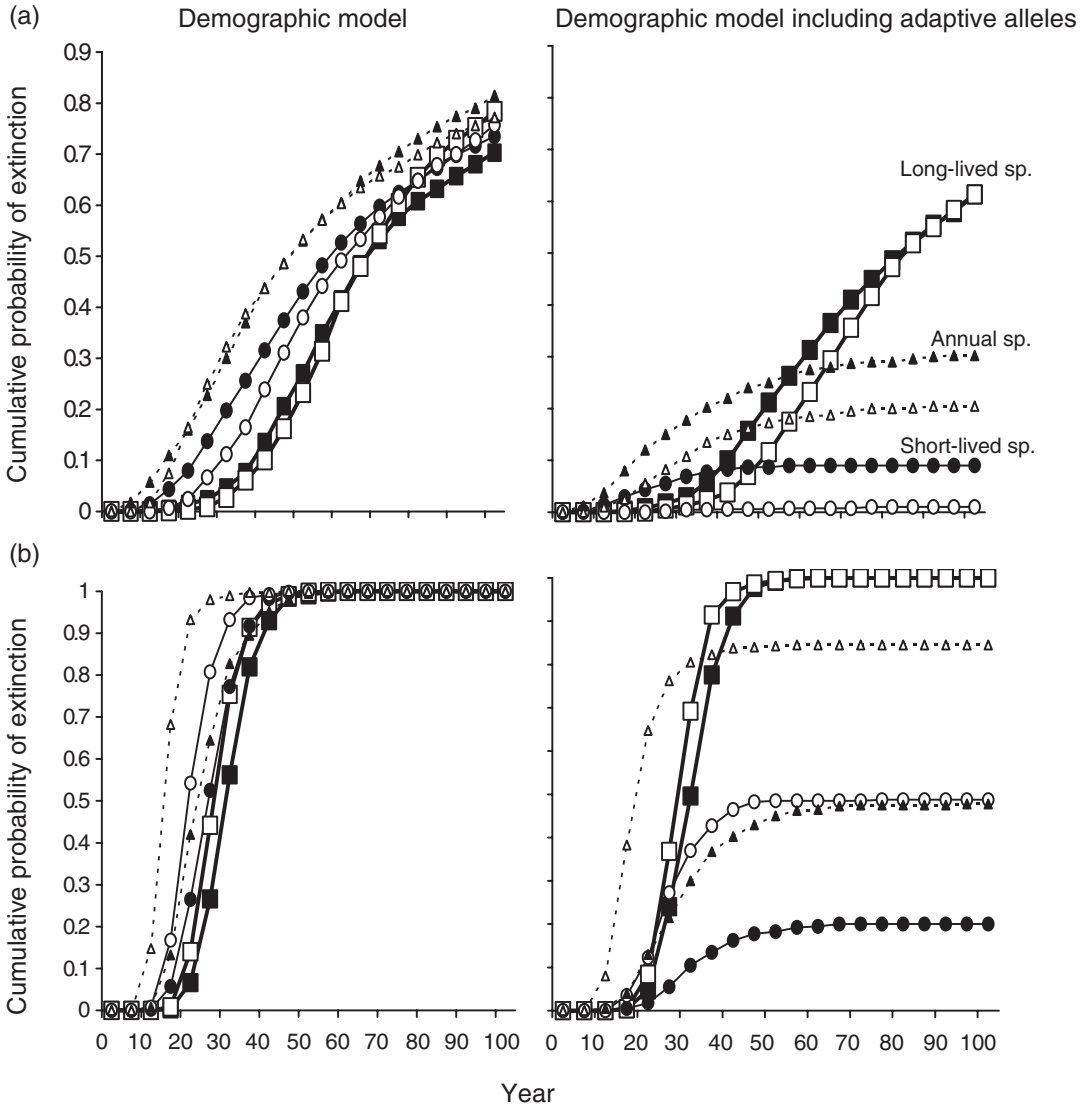

Fig. 4. Influence of the life-history category on metapopulation extinction. Solid symbols: strategy R1; open symbols: strategy R3. Monogamous population with a density-dependent dispersal; perturbations are not synchronized; in all cases, $N_0 = 75$ individuals; $K = 500$; annual dispersion rate $m = 0.01$; $q_0 = 0.0005$; $s = 0.1$; $h = 0.5$. For the semelparous species, $F = 1.6$; for iteroparous species, perturbations act on survival, demographic parameters are presented in Table 1. (a), catastrophes, $P_c = 0.02$; $C = 0.9$. (b), environmental stochasticity, $\sigma = 0.35$.

DISCUSSION

Our results suggest that, in a metapopulation, the initial distribution of individuals may affect the efficiency of local adaptation, which can in turn influence metapopulation viability. From a demographic view-point, our results underline the influence of the degree of correlation of environmental perturbations on the relative efficiencies of the two release strategies, in agreement with previous theoretical work on demographic synchrony and rescue effect (Hanski, 1989, 1991; Earn *et al*., 2000). More surprisingly, from a genetic view-point, the optimal strategy depends on the type of perturbations and not on their correlation. One-patch release is advantageous in the presence of frequent slight perturbations, while multi-release strategy is optimal in the presence of rare severe perturbations. Although the influence of these processes of adaptation may vary quantitatively and qualitatively with a number of genetic and demographic parameters, our results suggest that they play a substantial role in metapopulation extinction (see the impact of genetics in Fig. 2(b) according to the type of perturbations) and should therefore be considered in PVA models. This result may be of importance in the context of restorative conservation of populations or metapopulations, in which only unconditionally deleterious genes are generally considered (Lynch *et al*., 1999).

Influence of initial conditions on adaptation

In the case of strategy R1, the frequency of allele that is locally adaptive in the release site is largely increased in the three subpopulations after 100 generations, contrary to the frequencies of the two other types of selected alleles. This difference is caused by a delay in the colonization of the two initially empty sites. Indeed, a small number of immigrants towards an empty site are vulnerable to strong demographic stochasticity. During this delay, adaptation can only occur in the release site and dispersal only takes place from the release site to the two others. Such a one-way gene flow tends to be enhanced by selection, which engenders a positive feedback by making the mean fitness in the release site and in the other sites diverge. The two initially empty patches remain then demographically and genetically dependent on the release site for several generations. Despite a progressive increase of population size in the release patch, allelic diversity decreases during that period, which limits the possibility of future adaptation to the two empty patches through a loss of adaptive alleles. Adaptation reaches consequently a high level in the release site and remains low in the other sites even after 100 generations. This process of extinction and recolonization, which acts as a form of gene flow and limits the differentiation of populations (Slatkin, 1977; Wade & McCauley, 1988), is, in our case, mainly dependent on the initial population distribution (strategy R1 or R3). Admittedly, this process also depends on the duration needed to colonize the two initially empty patches. This duration is a function of the rate and the pattern of dispersal, and on the time needed for the release patch to become saturated (which varies with the ratio N_0/K and the rate of increase R). In particular, for very high dispersal rates, the difference between the two strategies becomes weak, owing to rapid colonization (Fig. 1). However, since colonization requires several generations on average (owing to demographic stochasticity), the process described above appears qualitatively to generate demographic and genetic asymmetries among patches independently of m, N_0/K and R.

In the case of strategy R3, contrary to strategy R1, selection occurs equally in the three sites and inter-patch dispersal allows an increase of the mean frequency of each type of adaptive allele in the whole population. However, in each patch the mean frequency of locally adaptive alleles increases less than it does in the case of the release site in strategy R1 (Fig. 1). Two main reasons explain this result. As a first reason, the initial population size in each patch is three times smaller than the initial population size in the release patch with strategy R1. This smaller population size results both in a lower genetic variation on which local selection will act in each patch, and in smaller local effective population sizes, which reduce the effective selection coefficients owing to increased effects of genetic drift (Lacy, 1987; Frankham *et al*., 1999). The second reason is immigration. In the case of strategy R1, no dispersal (or very little) occurs to the release site from the others, while in the case of strategy R3, the demographic balance of the three sites allows a homogenous continuous gene flow among them, which reduces local adaptation. Hedrick (1995) observed such a reduction owing to migration by using a continent-island model. Here, the rapidity of adaptation is diminished by immigration but the feedback of the gene flow among patches allows a better local adaptation than does the continent-island model. From a genetic view-point, these results remain true for a broad array of dispersal rates (Fig. 1) and for density dependent as well as density independent dispersal. However, owing to demographic stochasticity, metapopulation size and persistence are greatly decreased in all cases if dispersal is density-independent (Nachman, 2000).

The genetics-demography-environment interaction

One characteristic of catastrophes, compared to demographic and environmental stochasticities, is that their impact on viability remains important for relatively large populations (Ewens *et al*., 1987). However, the global impact of catastrophes depends on their severity and their frequency (Shaffer, 1987; Lande, 1993). Particularly, the dynamics of extinction is expected to vary according to whether frequent perturbations of moderate effect or rare and severe catastrophes are considered. In the former case, the repetition of slight negative events progressively reduces population size, while in the latter case one single rare severe catastrophe can lead a population to rapid extinction. Hence, a single large population (or a population with a high growth rate) will endure frequent perturbations of low severity because each perturbation has a low probability of reducing

population size to a point where demographic stochasticity becomes an important factor of extinction. By contrast, in the case where catastrophes are rare and severe, a single catastrophic event can lead the large population to extinction and the best strategy to maximize the viability of the whole population is to divide it into several subpopulations more or less independent of each other.

Such processes, which integrate both demographic and environmental mechanisms, can be generalized with some genetic considerations. The pattern of local adaptation engendered by strategy R1 (i.e. one high-fitness patch and two low-fitness patches) is optimal in an environment with frequent slight perturbations. Indeed, each single perturbation is insufficient to provoke a local extinction in the high-fitness patch, and the high growth rate in this patch decreases the chance of extinction due to consecutive perturbations. Conversely, the pattern of local adaptation engendered by strategy R3 (i.e. three patches with an intermediary fitness) is optimal in an environment with rare severe catastrophes, owing to the low probability that catastrophes lead simultaneously the three patches to extinction, particularly if perturbations are not synchronized.

Comparisons among life-history categories

Although no qualitative difference exists in adaptation between overlapping and non-overlapping generations species, the number of generations elapsed for a given period of time varies with the life cycle considered, depending on the generation length. Since genetic processes operate on a per-generation basis, the relative importance of local adaptation and environmental variations is expected to vary as well with the generation length. The impact of adaptation on extinction and on the relative efficiencies of release strategies is therefore reduced in the case of the long-lived species (Fig. 4), for which the number of generations elapsed within 100 years is only 8.7 (the numbers of generations elapsed are respectively 31.3 and 100 for the iteroparous short-lived and the annual species). Since the adaptive processes considered here can have a substantial effect on the short run (the processes do not involve new mutations), their impact on viability is real at time scales of conservation concern (100–200 years). This impact remains however relatively minor for species with large generation lengths. Short-lived species typically exhibit higher annual growth rates than long-lived ones. However, for equivalent growth rates, demographic stochasticity has a stronger impact on short-lived species, owing to a rapid turnover, which amplifies the stochastic fluctuations in the number of descendants (Legendre *et al.*, 1999). The interaction among the genetic and demographic mechanisms leads to contrasting influences of the generation length on short- and long-term persistence. Short-lived species extinct more at short term owing to demographic stochasticity (left side of Fig. 4). However, when adaptation processes are considered, the rate of extinction of short-lived species decreases more than for long-lived ones after few generations (right side of Fig. 4).

In the case of the iteroparous life cycle, in above results we assumed that environmental perturbations affect survival rates rather than fecundity. In the case where perturbations act on fecundity, the fluctuations in population size engendered by rare/severe catastrophes are buffered by the pool of individuals that remain from one year to the next (for both long- and short-lived species). As a consequence, there is no qualitative difference between rare/severe perturbations and frequent/slight ones. Additional simulations show that local adaptation is always more beneficial with strategy R1 if perturbations decrease fecundity in iteroparous species. However, empirical data suggest that, in many cases, environmental catastrophes (such as severe winters, fires, floods, drought and disease epidemics) act primarily on survival (for mammals, see a review in Young, 1994).

Although our results are qualitatively robust to some variations in the coefficient of selection and the coefficient of dominance, quantitative assessments of the impact of local adaptation on viability are limited by the lack of empirical data concerning the characteristics of beneficial mutations. Although the occurrence of advantageous mutations has been documented in bacteria, fungi and *Drosophila* (Ayala, 1969; Lenski *et al.*, 1991; Wilkes & Adams, 1992), little is known about the magnitude of the effect of a single mutation on fitness. In their study on the long-term evolution in *E. coli*, Lenski *et al.* uncover the rapid evolution of fitness owing to beneficial mutations, particularly during the first generations (Lenski *et al.*, 1991; Lenski & Travisano, 1994). However, Lenski *et al.* (1991) do not present any particular value of coefficient of selection per locus. Rather they emphasize that some combinations of u and s may fit their experimental results. We have focused our work on genes that increase fitness on a particular patch, and genes that have an unconditionally positive effect on fitness have not been considered, nor deleterious genes. Additional results suggest that in the case where an allele is advantageous in one patch and gives a disadvantage in all the others, the metapopulation evolves to give more generalists (i.e. individuals with few advantageous/disadvantageous alleles and a high proportion of '0' alleles) if the dispersal rate is high, while it gives more specialists if the dispersal rate is low. However, the interaction between the type of environmental fluctuations and the initial spatial distribution is not affected: rare strong perturbations are always more harmful in the case of strategy R1.

In our model, density dependence results from truncating population size to the carrying capacity. An alternative would have been to consider a competition among genotypes in this mechanism. Since the two alternatives are plausible, depending on the mechanisms on which act respectively local adaptation and density dependence, we have considered the simplest option, although it probably results in reduced selective coefficients. The influence of a variety of demographic characteristics, such as age-classes structure, more detailed mating system, etc., could be assessed by addressing these issues more specifically. However, the aim of this work is primarily to uncover that initial

conditions (naturally or artificially created) may influence metapopulation persistence, not only for demographic reasons, but also through a substantial influence on adaptation. In a conservation context where genetic considerations are not always relevant and may even sometimes obscure the more vital demographic issues (Caughley, 1994; Gilligan *et al*., 1997), a multidisciplinary approach which integrates both demography and genetics may be a fruitful method to evaluate the extents of their respective effects as well as the unexpected consequences of their interaction. (Gilpin & Soulé, 1986; Lande, 1988; Mills & Smouse, 1994; Sarrazin & Barbault, 1996; Clarke & Young, 2000).

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