Effects of long-distance dispersal for metapopulation survival and genetic structure at ecological time and spatial scales

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Summary

1 Long-distance dispersal (LDD) of seeds by wind plays an important role in population survival and structure, especially in naturally patchy or human-fragmented metapopulations. However, no study has tested its effects using a realistic dispersal kernel in a metapopulation context with explicit spatial structure and local extinctions.

2 We incorporated such kernels into a newly proposed simulation model, which combines within-patch (population) demographic processes and a simplified maternally inherited single-locus, two-allele genetic make-up of the populations. As a test case, we modelled a typical conservation scenario of Aleppo pine (*Pinus halepensis*) populations.

3 The effects of LDD were rather diverse and depended on initial population conditions and local extinction rates. LDD increased metapopulation survival at intermediate local-extinction probabilities. LDD helped maintain higher total genetic variability in populations that were initially drifted, but facilitated random genetic loss through drift in initially 'well mixed' populations. LDD prevented population differentiation in low extinction rates but increased it at intermediate to high extinction rates.

4 Our results suggest that LDD has broader evolutionary implications and would be selected for in populations facing intermediate local-extinction pressures. Our modelling approach provides a strong tool to test the effects of LDD on metapopulation survival and genetic variability and to identify the parameters to which such effects are most sensitive, in ecological and conservational scenarios.

Key-words: conservation, demography, ecology, evolution, fragmentation, genetic diversity, local extinction, modelling, population ecology, wind dispersal

Introduction

Dispersal is among the most important processes that directly influence short- and long-term population persistence, genetic differentiation and inter- and intraspecific interactions, as well as community structure and diversity (e.g. Hastings 1993; Olivieri *et al*. 1995; Levin *et al*. 2003). Traditionally, the major interest of plant ecologists and evolutionary biologists has been in short-distance dispersal (Howe & Smallwood 1982) because only a small fraction of seeds are dispersed relatively far away from the mother plant (e.g. Howe 1989; Houle 1995; Nathan & Muller-Landau 2000). Nevertheless, long-distance dispersal (LDD) is vital for metapopulation dynamics and structure (e.g. Husband & Barrett 1996; Freckleton & Watkinson 2002; Levin *et al*. 2003) because it determines the rate of population spread (Kot *et al*. 1996; Clark 1998; Neubert & Caswell 2000), colonization of remote sites (Kawasaki *et al*. 1997; Eriksson 1996, 2000) and species survival in patchy landscapes (Malanson & Cairns 1997; Iverson *et al*. 1999; Schwartz *et al*. 2001). Increasing recognition of the importance of LDD for a variety of conservation practices (Trakhtenbrot *et al*. 2005) has driven efforts to find new ways of predicting its rate (Nathan *et al*. 2002, 2003, 2005).

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LDD is likely to underlie processes such as bet hedging under stochastic and asynchronous variation in patch conditions, so that metapopulations can persist even when the mean conditions for local populations are unfavourable (Metz *et al.* 1983; Levin *et al.* 2003; Volis *et al.* 2005). Rescue effects in source-sink metapoulations (Brown & Kodric-Brown 1977) and increasing genetic differentiation among populations (e.g. Le Corre *et al.* 1997; Sork *et al.* 1999; Austerlitz & Garnier-Géré 2003) are similarly attributable to LDD. The metapopulation concept thus provides a valuable framework for studying the consequences of LDD for plant survival and genetic diversity (Hanski 2001; Higgins & Cain 2002).

At the community level, LDD enhances metapopulation persistence in spatially and temporally heterogeneous environments (Perry & Gonzalez-Andujar 1993) and facilitates species coexistence even without a colonization-competition trade-off (Higgins & Cain 2002). At the population level, it constitutes a major determinant of spatial genetic structure and population differentiation increases as rare events result in even more distant dispersal (Le Corre *et al.* 1997; Austerlitz & Garnier-Géré 2003). These population models, however, considered populations without random or periodic catastrophic extinction (regional population assemblages *sensu* Freckleton & Watkinson 2002), whose dynamics may differ from 'true metapopulations' in which such events do occur.

Preventing accelerated reduction in a population's genetic variability is a major goal in conservation, in particular when it is fragmented or where a historically continuous population now survives as a metapopulation. Ongoing habitat fragmentation increases extinction probability, and consequently the importance of metapopulation dynamics (i.e. local extinction followed by recolonization) (Hanski 1991). Because LDD is a prerequisite for successful colonization, understanding its effects on genetic variation and survival in metapopulations has clear theoretical and applied value.

In this study, we incorporate realistic dispersal kernels into a spatially explicit scenario, which combines catastrophic extinction and colonization. Our model focuses on elucidating the importance of LDD for a metapopulation in terms of both demography and genetics, in relation to other ecological factors such as genetic drift, local extinction and spatial population arrangement.

Materials and methods

We compare the consequences of two dispersal scenarios, one incorporating LDD and the other only local dispersal, on metapopulation dynamics and genetic structure of Aleppo pine (*Pinus halepensis* Miller), a common wind-dispersed Mediterranean tree species. We use a numerical simulation model (based on Volis *et al.* 2005) with empirically derived demographic transition probabilities, dispersal rates and fecundity. We

consider various local-extinction probabilities, two initial spatial settings and two initial gene distributions. We use sensitivity analysis to highlight the variables to which the system is most sensitive, so that future research can accurately quantify the contribution of LDD to those features that are most critical for rare or endangered populations.

THE MODEL

The island model recently introduced by Volis *et al.* (2005) simulates the dynamics of subdivided populations by incorporating within-patch (population), stage-specific demographic processes, random catastrophic local-extinction events and maternally inherited single-locus population genetics. We modified this model by adjusting spatial structure, the number of patches and life stages, and by incorporating demographic stochasticity of the transition rates and realistic dispersal kernels.

Each individual is assigned one of three genotypes produced by two codominant alleles A and B (i.e. AA, AB or BB) and the number of individuals included in each transition is determined by a binomial random number, with the specified transition probability and number of draws equal to the number of individuals in the stage-genotype group. Because an individual represents one of three genotypes (i.e. AA, AB or BB), each transition changes the allele frequencies in both the source and the destination population. Migration among patches occurs only through dispersal.

We assume constant fecundity, but the offspring genotype is randomly selected. Our model only simulates a single maternally inherited gene, so that the effects of seed LDD could be determined independently, for example from pollen LDD. When offspring numbers are small (less than 1000) a random draw determines which gametes would pair. When offspring numbers are high, this individually based random process can be approximated by a statistical approach, such that the distribution of offspring genotypes is determined by the Hardy–Weinberg (H-W) principle, assuming random mating, and multivariant-normal random deviation

$$\mathbf{C} = \begin{bmatrix} P\{A\}^2(1 - P\{A\}^2) & -P\{A\}^2 * P\{B\}^2 \\ -P\{A\}^2 * P\{B\}^2 & P\{B\}^2(1 - P\{B\}^2) \end{bmatrix} \quad \text{eqn 1}$$

$$\begin{pmatrix} F_{AA} \\ F_{BB} \end{pmatrix} = NF \begin{pmatrix} P\{A\}^2 \\ P\{B\}^2 \end{pmatrix} + \sqrt{NF} *$$

$$\left(\begin{bmatrix} \sqrt{\lambda_{C1}} & 0 \\ 0 & \sqrt{\lambda_{C2}} \end{bmatrix} * \begin{bmatrix} \mathbf{v}_{C11} & \mathbf{v}_{C21} \\ \mathbf{v}_{C12} & \mathbf{v}_{C22} \end{bmatrix} \right) * \begin{pmatrix} X_1 \\ X_2 \end{pmatrix} \quad \text{eqn 2}$$

$$F_{AB} = NF - F_{AA} - F_{BB} \quad \text{eqn 3}$$

where $\mathbf{C}$ is the covariance matrix of the genotype probabilities, $P\{A\}$ and $P\{B\}$ are the allele frequencies of A and B in the reproductive adult population, F_{AA}, F_{BB} and F_{AB} are the number of offspring that carry each, NF

is the total number of offspring produced by the population, X_1 and X_2 are standard normal random numbers, and λ_{C1}, λ_{C2}, V_{C1} and V_{C2} are the eigenvalues and corresponding eigenvectors of **C** (Volis *et al*. 2005).

MODEL APPLICATION: ALEPPO PINE METAPOPULATION DYNAMICS

Aleppo pine is the most common pine species of the Mediterranean Basin (Barbéro *et al*. 1998). Contrary to previous beliefs that dispersal and germination in this species are solely stimulated by fires, the majority of seeds during a tree's lifetime are actually dispersed during fire-free periods (Nathan *et al*. 1999), and germination is abundant in non-fire-generated disturbed habitats (e.g. Nathan *et al*. 2000). Indeed, the species is considered one of the most invasive pines, rapidly colonizing disturbed habitats, even in the absence of fire (Nathan *et al*. 1999; Richardson 2000). Fire-induced dispersal kernels, and LDD in particular, are virtually unknown (Ne'eman *et al*. 2004) and, although adjustment of our model parameters to fire-stimulated metapopulation dynamics is feasible, we prefer to introduce here a general model for fire-free plant metapopulation dynamics, rather than restricting the scope to a specific type of disturbance.

Aleppo pine has rather small (*c*. 22 mg) winged seeds, whose relatively low mean terminal velocity (*c*. 0.81 ms^{-1}) indicates better dispersal capacity than other wind-dispersed pines (Nathan & Ne'eman 2000). Seed release depends on the opening of closed partially serotinous cones, either by fire or during dry and hot spells (Sirocco-type events called Sharav in the eastern Mediterranean) that occur in spring and fall (Nathan *et al*. 1999). Sharav events, which are characterized by strong easterly winds with significantly higher vertical and horizontal wind velocities, promote LDD (the proportion of seeds trapped relatively far (> 20 m) from adult trees is twice as high as during non-Sharav periods, Nathan *et al*. 1999). While Sharav events may occasionally be associated with fire, the vast majority induce massive seed release in its absence (Nathan *et al*. 1999; Nathan & Ne'eman 2000, 2004).

To estimate the parameters required for the dispersal model, and to quantify seed survival and stage-transition rates, we use data collected during a 5-year study in two presumably native Aleppo pine populations in fire-free conditions (Nathan *et al*. 1999, 2000, 2001). The long-term history of population dynamics in one of these sites, located on Mt Pithulim in the Judean Hills, can be reconstructed in exceptionally fine detail (Nathan 2004). The earliest records (air photos confirmed by annual growth rings) indicate a severe bottleneck, with only five trees inhabiting the site at the beginning of the 20th century. The population has expanded since the 1940s, and *c*. 1500 adult individuals are now located in an area of 60 ha near the core of the old stand (Nathan 2004). This rapid and intensive regeneration has occurred in the absence of fire.

Intensive seed predation by ants, rodents and birds leads to very low seed survival and practically no effective soil seed-bank between years (Nathan & Ne'eman 2000, 2004). Some ant (e.g. *Messor* spp.) and rodent (e.g. *Apodemus* spp.) species may transport seeds over short distances to their mounds or caches, but these dispersal events rarely, if ever, result in seedling emergence (Nathan & Ne'eman 2000), and all bird species observed consume Aleppo pine seeds immediately after detection. As LDD by animals is therefore very unlikely, we focus on wind as the most important vector for dispersal of Aleppo pine seeds over both short and long distances.

Mechanistic and phenomenological modelling approaches (Nathan & Muller-Landau 2000; Levin *et al*. 2003) constitute two alternative ways to incorporate seed dispersal in a reasonably realistic manner. The mechanistic approach can predict dispersal under specific conditions (e.g. strong winds) that promote LDD and Nathan and Ne'eman (2004) have parameterized the model of Nathan *et al*. (2002) for Aleppo pine seeds under two wind conditions. The seasonal average horizontal wind velocity (5.46 m s^{-1}, hereafter 'typical winds') was used to estimate the short-distance dispersal of most seeds and the maximum 10-minute average horizontal wind velocity recorded during the dispersal season (21.20 m s^{-1}, 'extreme winds') to estimate LDD. We emphasize that both conditions were derived from measurements taken only during the (short) dispersal season (i.e. when Sharav events occur). Even under such extreme winds, the probability of dispersal to distances greater than 1 km is in the order of 10^{-5}, and the behaviour of the tail suggests that at 10 km (the spatial scale relevant to the present study) the probability could well be < 10^{-10} (Nathan & Ne'eman 2004). Mechanistic simulation of > 10^{10} dispersal events is not practical, and, although dispersal kernels can be estimated from analytical functions, the parameters in phenomenological models cannot be associated directly with realistic conditions that give rise to short- or long-distance dispersal. Therefore, we used a combined approach, in which the parameters of a phenomenological model are fitted to dispersal kernels predicted by a mechanistic model.

NUMERICAL EXPERIMENT SETTINGS

We use a simplistic scenario of a spatially structured population (metapopulation) comprised of 12 linearly arranged circular (200 m radius) patches. The first and last (12th) populations are at the edges of the domain and the centres of neighbouring populations are separated by 1 km.

Demography within each patch is described by stage-transition and dispersal probabilities between four life stages (seeds, juveniles, i.e. seedlings and saplings from years 1–4 after germination, old saplings, i.e. young adults from years 5–8, which are not reproductive yet, and reproductive adults; Izhaki *et al*. 2000; Nathan &
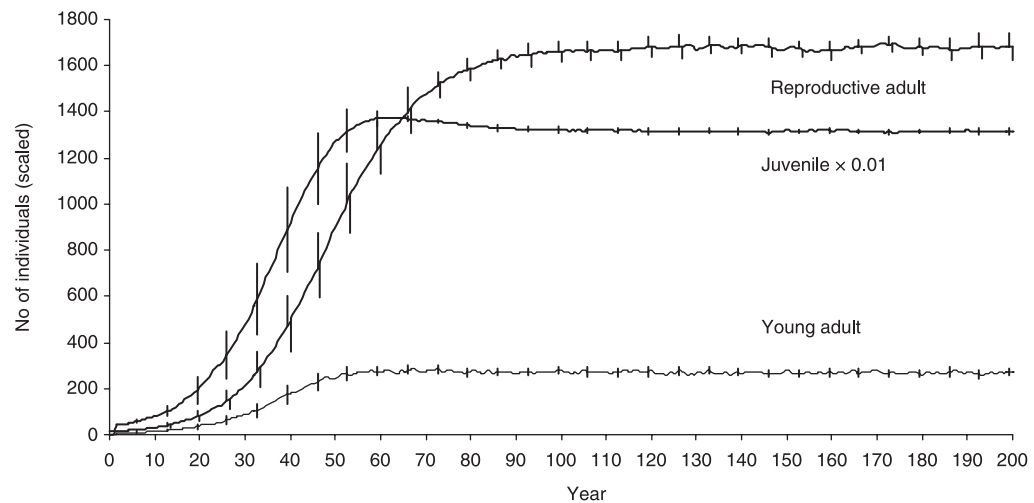
Fig. 1 Population dynamics. The number of juveniles, young adults and reproductive adults each year, throughout 200 simulated years. The numbers shown are the means of 100 simulations of a single patch population without catastrophic extinction and without migration. Error bars (marked only every 10th year) represent the standard deviation between simulated populations. Juvenile numbers are scaled by a factor of 0.01 in order to be presented on the same axis as other life stages. All life stages reached stable size before 100 years. The mean stable adult population size of a single population was 1657.

Ne'eman 2000, 2004). Seeds can only make the transition to juveniles, and do not survive to the next year (i.e. no seed bank). Juveniles and saplings can either survive at their current stage (survival rate = 0.001, 0.51, respectively) or make the transition to the next life stage (transition rate = 0.001, 0.25, respectively). Adults can survive and reproduce (survival rate = 0.96, fecundity = 10 000 seeds adult^{-1}). There is no transition between genotypes, except by fecundity. Our reanalysis of the data of Nathan & Ne'eman (2004) found significant negative density-dependent seed survival and we therefore included density-dependent response at the seed stage, in which the probability a_{12} of transition from seed to seedling is

$$a_{12} = 0.03 * e^{(-0.01 * \mathbf{Ns}/\mathbf{A})} \qquad \text{eqn 4}$$

where **Ns** is the number of seeds in the population patch and **A** is the population patch area (m^2).

We use the two-parameter Weibull function as the phenomenological model, because it has been applied successfully to simulate seed dispersal in general (Muller-Landau 2001) and wind dispersal in particular (Tufto *et al.* 1997), and shows flexibility in producing both thin- and fat-tailed dispersal kernels. The cumulative density function $F(x; k, l)$ of the probability of dispersed seeds travelling distance x(m) from the source is

$$F(x; k, l) = 1 - \exp\left[-\left(\frac{x}{k}\right)^{l}\right] \qquad \text{eqn 5}$$

where k and l are, respectively, scale (m) and shape (dimensionless) parameters.

We fit this function to the tails of two mechanistically derived dispersal kernels presented by Nathan & Ne'eman (2004), i.e. to all observations behind the kernel's mode.

The Weibull distribution fitted the 'typical winds' scenario very well ($r^2 = 0.96$), but not the 'extreme winds' scenario, consistent with the complex shape of its kernel (see Fig. 1 in Nathan & Ne'eman 2004). To provide a mechanistic interpretation of the Weibull parameters, we fix the shape parameter in both scenarios to a value ($l = 0.50$) that is close to the one fitted to 'typical winds' kernel ($l = 0.57$). This value corresponds to a fat-tailed distribution, i.e. one whose tail drops off more slowly than the negative exponential ($l = 1$) (e.g. Turchin 1998). We then estimate the scale parameter (k) for each of the two scenarios using a relationship derived from the Weibull's moment-generating function (see Evans *et al.* 2000)

$$k = \frac{\bar{x}}{\Gamma(1 + \frac{1}{l})} \qquad \text{eqn 6}$$

where $\bar{x}$ is the mean dispersal distance ($\bar{x} = 6.07$ m and 125.13 m and, hence, $k = 3.03$ m and 62.57 m, for the 'typical winds' and 'extreme winds' scenarios, respectively), and Γ is the gamma function.

To match the discrete spatial setting of the simulated landscape, we use the two Weibull functions to calculate the probability of wind-dispersed seeds arriving at neighbouring circular patches (populations). We assume, for simplicity, that all seeds are released from one point at the centre of each patch. Under the 'typical winds' scenario, the vast majority (99.97%) of dispersed seeds deposit within the 200-m radius of source population, and the probability of dispersal to other populations is very low (Table 1). Under stronger and more variable wind conditions, most (83.27%) dispersed seeds still deposit within the limits of the source population, but some are expected to reach neighbouring populations, including the most distant one. However, as many seeds land in the matrix between patches, where the probability of survival is assumed to be zero, the 'extreme

Table 1 Dispersal kernels. Dispersal rates between populations, calculated by discretized Weibull probability distribution functions of the distance between patches with two wind intensities – typical and extreme winds. The metapopulation (12 populations) statistics of the fraction of seeds lost, average dispersal distance, standard deviation (SD) of dispersal distance and effective mean wind velocity are also presented

Destination population number	Dispersal distance (km)	Dispersal rate from population #1	
		Typical winds	Extreme winds
			8.33E-01
1	0	9.99E-01	1.55E-02
2	1	8.61E-08	2.02E-03
3	2	2.43E-11	4.60E-04
4	3	5.60E-14	1.36E-04
5	4	0	4.72E-05
6	5	0	1.83E-05
7	6	0	7.74E-06
8	7	0	3.49E-06
9	8	0	1.65E-06
10	9	0	8.20E-07
11	10	0	4.22E-07
12	11	0	
Average fraction lost		0.03%	13.46%
Average dispersal distance (m)		6.07	125.13
SD of distance		71.55	1987.74
Mean wind velocity (m s^{-1})		5.46	21.20

winds' scenario entails much lower survival at the seed dispersal stage (13.46% vs. 0.03% seeds lost, Table 1). Although most seeds are dispersed relatively short distances in both scenarios, 'typical winds' accounts exclusively for short-distance dispersal, and comparison with 'extreme winds' therefore enables examination of the independent effects of LDD.

Random catastrophic local extinctions, simulating deforestation events (for example due to logging, agriculture or development), are prescribed locally to each population patch at each time step with uniform distribution. The local-extinction probability is constant over time throughout each simulation, but ranges from 0% (no deforestation) to 7.5% in different simulations (higher probabilities drive the entire population to inevitable extinction within 100 years).

The optimal length for simulations was determined from a preliminary experiment to identify the time to reach equilibrium size. Dynamics of a single patch was followed, starting from a small (24 adults), genetically mixed population (at H-W equilibrium), without extinction or interpatch dispersal for 300 simulated years. Once the populations reached an equilibrium size of about 1650 adults (its carrying capacity), density-dependent transition from seeds to juveniles limited growth and the mean growth rate reached equilibrium, $\lambda = 1$. Juveniles and young reached equilibrium after about 50 years, while the adult numbers stabilized after about 90 years (Fig. 1) and a period of 100 years was therefore selected in simulations testing the effects of wind dispersal.

We use two different initial spatial structures: 'all-occupied', where all 12 patches were initially occupied at low densities, and 'spreading', where only the central six patches were initially occupied. The simulation starts with a total of 192 adults in the metapopulation, divided equally between populated patches (16 and 36 adults per patch in the all-occupied and spreading populations, respectively). We also test two different initial gene distributions. In 'mixed' populations we assume a H-W genotype distribution of 0.25 : 0.5 : 0.25 (AA : AB : BB), and initial values of the genetic indexes at $F_{ST} = 0$, $H_t = 0.5$ and $H_s = 0.5$, where F_{ST} denotes the population differentiation, H_t the total metapopulation heterozygosity, and H_s the expected population heterozygosity. In 'drifted' populations, the genotype distribution of local populations was initially skewed to 0.0 : 0.25 : 0.75 (AA : AB : BB) in half of the populations and 0.75 : 0.25 : 0.0 in the other half, with $F_{ST} = 0.562$, $H_t = 0.5$ and $H_s = 0.219$. In all cases, the total metapopulation initial gene distribution was 0.5 : 0.5 (A : B). We test each initial case with a full range of local extinction probabilities (0–7.5%, increment of 0.5%) and with the two dispersal scenarios. We repeat each simulation setting 100 times.

Results

EFFECTS OF LDD ON METAPOPULATION SIZE AND SURVIVAL

In the absence of both LDD (i.e. the typical-wind dispersal scenario) and local extinction, the initially homogeneous populations (12 occupied patches) reach carrying capacity (*c*. 1650 adults each, determined from Fig. 1) (results not shown). Although adding LDD (i.e. the extreme-wind dispersal scenario) decreases seed survival (Table 1), thus reducing the population growth rate, populations still re-colonize newly extinct patches and metapopulations survive even when all patches suffered local extinction at some time (but not simultaneously) and no population reached carrying capacity. As a result, LDD improves survival at intermediate local-extinction probabilities (Fig. 2), even though it decreases the mean total metapopulation size. In both all-occupied and spreading populations, the probability of survival drops with increasing probability of local extinction until the whole metapopulation becomes extinct at values > 7.5% and drops faster in the absence of LDD (Fig. 2). Confidence limits are calculated by assuming that the survival of a metapopulation is drawn from a binomial distribution, with probability specified by the survival rate and number of draws equal to the number of simulations (i.e. 100), and marking the 95th percentile of the resulting distribution. This intermediate range is much larger in spreading populations (1–6%) than in initially all-occupied populations (2.5–4%) (Fig. 2) and the benefits of LDD (faster and more efficient re-colonization of extinct patches) are therefore more advantageous under these conditions.
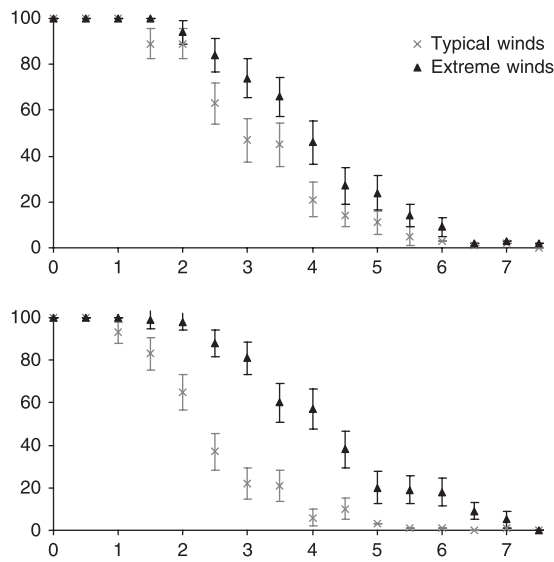
Fig. 2 Probability of survival of the metapopulation in 100 years at two wind levels in initially all-occupied (top) and spreading (bottom) populations. All metapopulations went extinct when local extinction probability was higher than 7.5%. The points mark the averages of 100 simulations; error bars mark the two-tailed 95% confidence limits based on binomial distribution.

Table 2 Four-way fully factorial ANCOVA on the genetic indexes H_t (the total metapopulation heterozygosity), H_s (the expected population heterozygosity, and F_{ST} (population differentiation). The affecting variables are 'Gene' (i.e. initial gene distribution: initially mixed vs. initially drifted), 'Space' (i.e. initial spatial arrangement: initially all occupied vs. initially spreading), and 'Wind' (i.e. wind dispersal scenario: typical winds with local dispersal only vs. extreme winds with local dispersal + LDD). Extinction probability is a covariate. × marks an interaction term. Significant effects are highlighted in bold

Effect	H_t	H_s	F_{ST}
Gene	**< 0.001**	**< 0.001**	**< 0.001**
Space	**< 0.001**	**< 0.001**	**< 0.001**
Wind	**< 0.001**	0.8518	**< 0.001**
Extinction	**< 0.001**	**< 0.001**	**< 0.001**
Extinction × Gene	**< 0.001**	**< 0.001**	**< 0.001**
Extinction × Space	0.779	0.5762	0.743
Extinction × Wind	**0.008**	**< 0.001**	**< 0.001**
Wind × Genes	**< 0.001**	**< 0.001**	**< 0.001**
Wind × Space	0.082	0.540	0.215
Gene × Space	**< 0.001**	**< 0.001**	**< 0.001**
Gene × Space × Extinction	0.086	0.146	0.215
Gene × Extinction × Wind	**< 0.001**	**0.004**	**< 0.001**
Space × Extinction × Wind	0.269	0.547	0.214
Gene × Space × Wind	**0.007**	**< 0.001**	0.693
Gene × Space × Wind × Extinction	0.204	0.360	0.077

EFFECTS OF LDD ON METAPOPULATION GENETIC DIVERSITY

Under all combinations of settings, local-extinction probabilities have pronounced effects on expected population heterozygosity (H_s) and total metapopulation heterozygosity (H_t) (Extinction effects, Table 2). In the absence of local extinction, both heterozygosity measures remain high and close to the initial value (0.5 in initially mixed populations, Figs 3 and 4). The high variation in the estimated genetic indexes among simulations can be attributed to the stochasticity of the modelled processes of gene transmission and extinction, and to the single locus effect.

As extinction probability increases, the effects of LDD on both heterozygosity measures become more pronounced (Figs 3 and 4, Extinction × Wind, Table 2). These effects can be understood by considering the nature of the surviving metapopulations: in the absence of LDD, these consisted of the few populations that had never experienced local extinction and had reached carrying capacity, whereas in its presence they were made up of smaller populations, most of which had experienced local extinction and recovery during the simulated period.

The effect of LDD on H_s depends on the initial genetic settings of the metapopulation (Wind by itself has no significant effect on H_s, but Wind × Gene and Wind × Gene × Extinction are significant, Table 2). In large 'well mixed' populations, genetic drift is extremely rare due to the high fecundity of adult trees: without LDD, surviving populations are large and therefore genetic drift is highly unlikely. Furthermore, founder

effects are negligible because of lower colonization probabilities and, consequently, H_s does not decrease with increasing local extinction probability (Table 3). In 'well mixed' populations with LDD, however, recolonization is frequent and rapid, enabling more populations to persist and accelerating the probability of genetic drift (Fig. 3a,b, Table 3).

Persisting 'initially drifted' populations exhibit, by definition, low genetic diversity; hence founder effects are less likely to further reduce genetic diversity. Accordingly, increased local extinction probability causes little or no effect on H_s in drifted populations, regardless of LDD (Fig. 3c,d, Table 3).

LDD strongly affects the relationship between H_t and local-extinction probabilities (Extinction × Wind, Table 2), with the effect depending on the initial genetic setting (Gene × Extinction × Wind, Table 2). H_t declines much less rapidly with increasing local-extinction probability in mixed than in drifted populations, in both dispersal scenarios (Fig. 4, Table 3), as gene distribution is similar among local populations and local extinction does not therefore cause substantial loss of interpopulation diversity. LDD has opposite effects on genetic variability in mixed and drifted populations, respectively accelerating and slowing the reduction of genetic variability (Fig. 4, Table 3). This could be attributed to the decrease in population size with LDD, making genetic drift in the 'mixed' case more probable.

In initially drifted populations, H_t rapidly declines with increasing local-extinction probability in both dispersal scenarios, especially in the absence of LDD
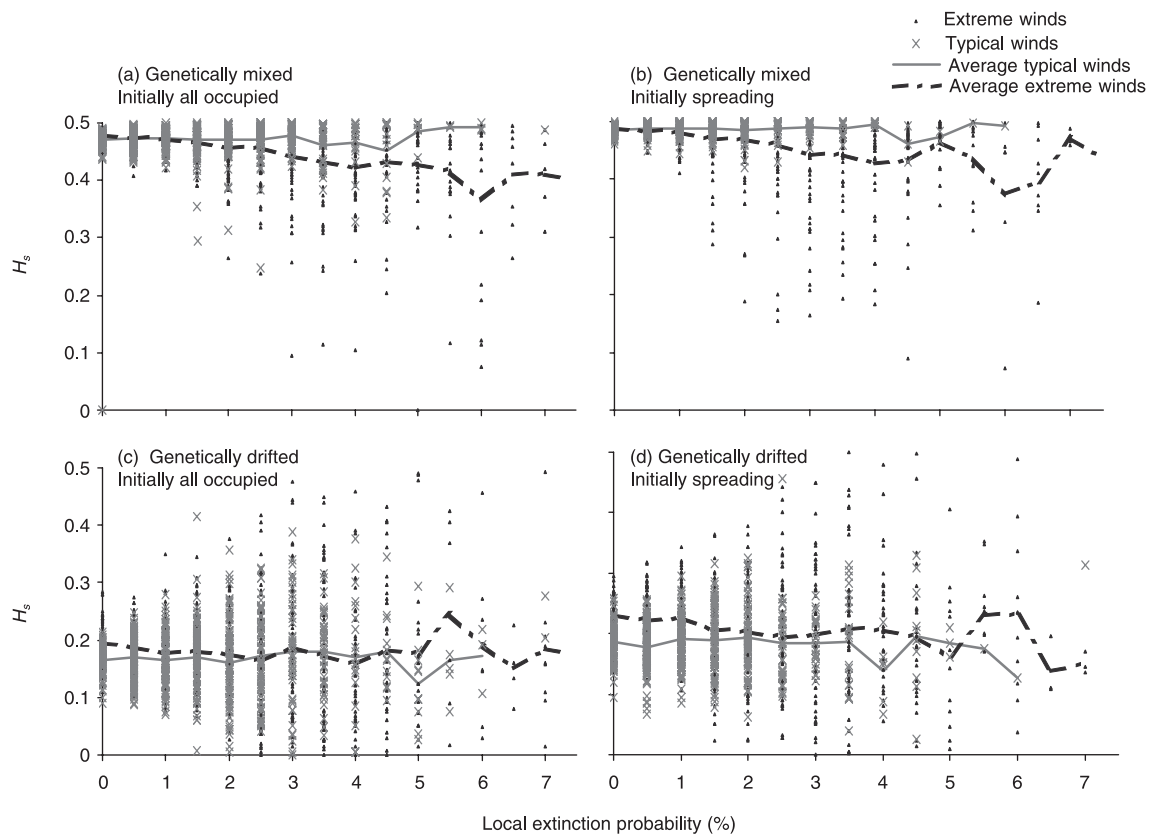
Fig. 3 Expected population heterozygosity, H_s, under different local extinction probabilities in the presence and absence of LDD (typical and extreme winds, respectively). Points mark H_s in surviving metapopulations after 100 simulated years. Lines mark the means: solid lines for typical winds, dashed for extreme winds. (a) Initially all-occupied genetically mixed populations. (b) Initially spreading genetically mixed populations. (c) Initially all-occupied genetically drifted populations. (d) Initially spreading genetically drifted populations.

Table 3 Parameters of linear regression lines between extinction probability and the genetic indexes (H_t, the total metapopulation heterozygosity, H_s, the expected population heterozygosity, and F_{ST}, population differentiation), in the presence or in the absence of LDD. Values of the intercept and slope of the regression lines are shown ± 95% confidence limits (*t*-test). Slopes that lie within the confidence limits of each other are not significantly different. Significance of the regression line is indicated in superscript next to r^2: *** < 0.001, ** < 0.01, * < 0.05, NS = not significant

	Initial gene distribution	Initial structure	Typical winds (LDD absent)			Extreme winds (LDD present)		
			Intercept	Slope	r^2	Intercept	Slope	r^2
H_t	Mixed	All-occupied	0.498 ± 0.003	−0.625 ± 0.137	0.328***	0.505 ± 0.006	−1.479 ± 0.195	0.440***
		Spreading	0.497 ± 0.001	−0.244 ± 0.075	0.268***	0.499 ± 0.006	−1.176 ± 0.209	0.353***
	Drifted	All-occupied	0.499 ± 0.013	−7.279 ± 0.605	0.672***	0.492 ± 0.012	−5.884 ± 0.464	0.648***
		Spreading	0.468 ± 0.014	−7.911 ± 0.807	0.638***	0.466 ± 0.013	−5.726 ± 0.513	0.612***
H_s	Mixed	All-occupied	0.472 ± 0.003	−0.030 ± 0.153	0.015[NS]	0.482 ± 0.006	−1.295 ± 0.208	0.375***
		Spreading	0.487 ± 0.002	0.038 ± 0.088	0.037[NS].	0.487 ± 0.006	−1.154 ± 0.228	0.323***
	Drifted	All-occupied	0.166 ± 0.007	0.142 ± 0.335	0.032[NS]	0.184 ± 0.009	−0.243 ± 0.342	0.048[NS]
		Spreading	0.186 ± 0.006	0.084 ± 0.354	0.020[NS]	0.223 ± 0.009	−0.654 ± 0.349	0.129**
F_{ST}	Mixed	All-occupied	0.053 ± 0.004	−1.194 ± 0.180	0.202***	0.046 ± 0.005	−0.285 ± 0.180	0.010**
		Spreading	0.000 ± 0.001	−0.566 ± 0.100	0.189***	0.025 ± 0.005	0.027 ± 0.170	0.000[NS]
	Drifted	All-occupied	0.690 ± 0.025	−15.155 ± 1.172	0.488***	0.650 ± 0.024	−10.497 ± 0.899	0.379***
		Spreading	0.580 ± 0.029	−16.320 ± 1.604	0.426***	0.520 ± 0.022	−9.863 ± 0.890	0.371***

(Fig. 4c,d, Table 3). In this case, the initial allele frequencies in the populations are different and loss of interpopulation diversity occurs with the extinction of each populated patch. LDD enables re-colonization and, thus, alleles that would have otherwise disappeared as populations went extinct are more likely to be rescued.

LDD leads to lower population differentiation (F_{ST}) when local-extinction rates are low, and to higher F_{ST} when local-extinction rates are intermediate-high (Fig. 5, Table 3, effect of Wind × Extinction, Table 2). In mixed populations, where F_{ST} is initially zero and remains low after 100 years (the overall mean is below 0.1), this
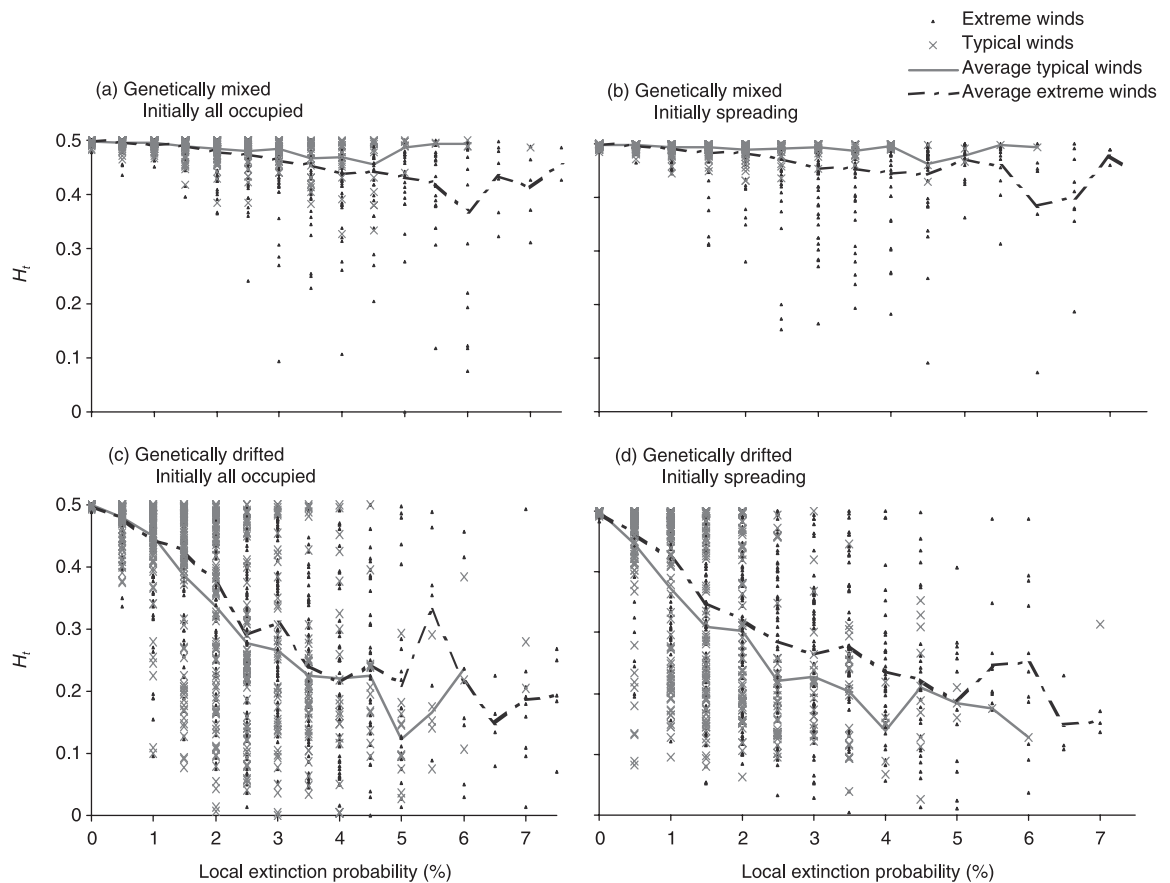
Fig. 4 Total metapopulation heterozygosity, H_2, under different local extinction probabilities in the presence and absence of LDD (typical and extreme winds, respectively). Points mark H_t at surviving metapopulations after 100 simulated years. Lines mark the means: solid lines for typical winds, dashed for extreme winds. (a) Initially all-occupied genetically mixed populations. (b) Initially spreading genetically mixed populations. (c) Initially all-occupied genetically drifted populations. (d) Initially spreading genetically drifted populations.

effect of LDD is weaker than in initially drifted populations, where F_{ST} at the start of the simulation is high (0.562) (Fig. 5, Table 3, effect of Wind × Extinction × Gene, Table 2). The effect of LDD on F_{ST} is similar regardless of the initial spatial structure of the populations (non-significant effect of Wind × Extinction × Space, Table 2).

Discussion

We investigate the effects of LDD on persistence and genetic diversity at both the population and metapopulation levels. Realistic dispersal kernels have been incorporated in models of population spread (e.g. Le Corre *et al.* 1997; Neubert & Caswell 2000; Austerlitz & Garnier-Géré 2003) and multispecies community context (Higgins & Cain 2002; Verheyen *et al.* 2004). However, to our knowledge, our model is the first to incorporate such kernels, as well as realistic (empirically derived) stage-specific demography and catastrophic local extinctions, in a metapopulation context. We also examine, for the first time, the effects of LDD on metapopulation survival and genetic diversity over the relatively short temporal and spatial scales relevant to ecological processes.

Our combined phenomenological-mechanistic approach to estimating dispersal kernels is aimed at addressing the problems of highly subjective parameterization of phenomenological models and the heavy computation demands of mechanistic models. A phenomenological model, parameterized by fitting it to dispersal kernels predicted by a mechanistic model, and applied to wind dispersal of Aleppo pine, performed very well under typical winds but not under extreme winds (Nathan *et al.* 2001). Nevertheless, we propose that the combined approach should be preferred over the purely phenomenological approach, because it makes the parameterization scheme transparent, less subjective and comparable with mechanistically derived predictions.

We apply the model to explore the consequences of LDD for population dynamics of Aleppo pine, where LDD depends critically on wind. We focus on primary seed dispersal by wind and on fire-free dynamics, despite the importance of post-fire regeneration in this species (the species recruits abundantly and colonizes new sites following disturbances other than fire, and fire-stimulated dispersal kernels, and LDD in particular, are virtually unknown). Our modelling approach can, nevertheless, easily be adjusted to incorporate other seed dispersal
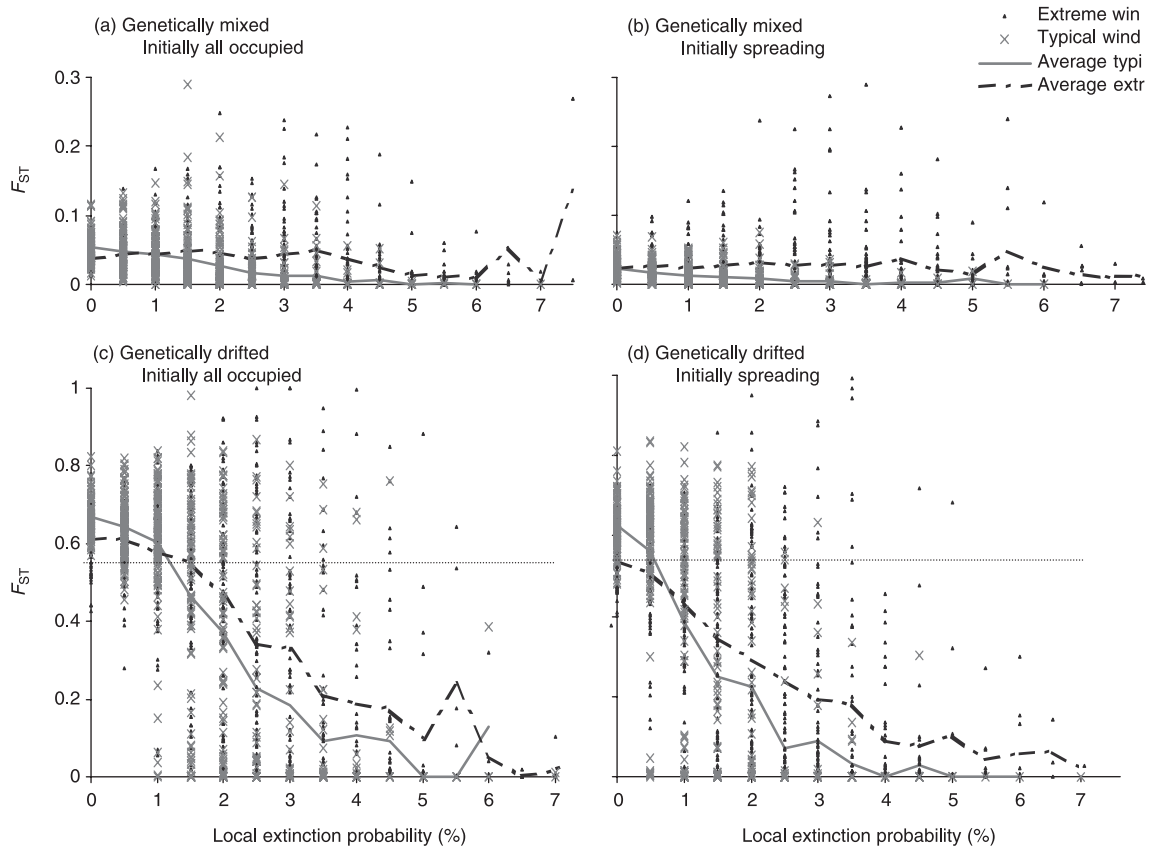
Fig. 5 Population differentiation index, F_{ST}, under different local extinction probabilities in the presence and absence of LDD (typical and extreme winds, respectively). Points mark F_{ST} at surviving metapopulations after 100 simulated years. Lines mark the means: solid lines for typical winds, dashed for extreme winds. (a) Initally all-occupied genetically mixed populations. (b) Initially spreading genetically mixed populations. (c) Initially all-occupied genetically drifted populations. (d) Initially spreading genetically drifted populations. Dotted line in 5.c and 5.d marks the initial $F_{ST} = 0.562$ of metapopulations from the genetically drifted scenario at the time of the simulation start.

processes (mediated by animals or other abiotic vectors), and can account for fire-stimulated dynamics. It is also straightforward to relax other simplifying assumptions, such as the absence of a persistent soil seed bank and vegetative propagation. Overall, this modelling framework is general and flexible enough to be generalized to other species of various life-forms (with either overlapping or non-overlapping generations), to other types of dispersal kernel, demographic transitions and spatial representation of landscape heterogeneity and even to animal populations.

DEMOGRAPHIC CONSEQUENCES OF LDD

Our simulations are in general agreement with the current understanding of LDD effects on metapopulation demography, including a trade-off between seed survival and colonization ability in fragmented landscapes (Levin *et al*. 2003). Although increasing dispersal distance is likely to reduce the probability that seeds will reach a suitable habitat, as some are 'lost' in the unsuitable matrix between habitat patches, LDD is needed to transport seeds from local, high-competition patches to remote, low-competition patches and, thus, enhance seed germination rates and seedling survival. LDD thus generates a 'rescue effect' (Brown & Kodric-Brown 1977) at the metapopulation level.

The trade-off between the effects of LDD at the population and metapopulation levels is directly related to the probability of local catastrophic population extinction. When local extinction probability is low, intense competition in local patches favours LDD, but high patch occupancy negates the advantage of LDD. When extinction probability is high, seed removal through LDD accelerates local extinction, but seeds arriving to distant suitable patches are not likely to survive. At intermediate levels of local extinction, LDD clearly raises metapopulation survival as compared with short-distance dispersal (Verheyen *et al*. 2004), especially in spreading populations, where half of the suitable patches were initially unoccupied. These unoccupied patches are rarely colonized in the absence of LDD, and thus the entire metapopulation is more sensitive to extinction. LDD more efficiently and rapidly reduces the number of unoccupied patches, making the entire metapopulation less susceptible to extinction at intermediate local-extinction levels.

GENETIC CONSEQUENCES OF LDD

The effects of LDD on metapopulation genetics (measured by H_s and H_t) depend on the initial population state. Generally, LDD leads to loss of genetic variability in initially homogenous H-W populations, but slows the rate of genetic-variability loss in initially drifted populations. This implies that LDD is of increased importance in populations that went through extreme fragmentation, founder effects and bottlenecks for maintenance of genetic variability, in contrast to the positive effects always observed on the metapopulation demography, independent of the initial state. We suggest that the reason for this difference is associated with the relative importance of the two levels at which genetic loss occurs.

At the local-population level, genetic drift causes loss of some alleles in small populations. At the metapopulation level, extinction-recolonization processes reduce the within-population and total-metapopulation genetic-diversity under both the propagule-pool (i.e. single source of immigrants) and the migrant-pool (i.e. multiple sources of immigrants) colonization modes (Slatkin & Wade 1978; Pannell & Charlesworth 1999, 2000). This loss can be partly offset if the recolonized local populations are initiated by a diverse group of founders or if they receive intensive gene flow immediately after colonization (McCauley *et al.* 2001). In our model, dispersal is distance dependent and spatially explicit; therefore, it is an intermediate dispersal mode between the propagule pool and the migrant pool. In addition, our model includes post-colonization gene flow, which has been shown to be important for population persistence (Lubow 1996; Thrall *et al.* 1998).

Even though LDD increases the viability of metapopulations, it leads to lower genetic diversity (on average) in the surviving local populations when the metapopulation consists of replicated ideal ('at-equilibrium') populations (i.e. in mixed populations). This agrees with the results of Austerlitz & Garnier-Gere (2003), who describe a case of an 'at-equilibrium' spreading population with no local extinction. Nevertheless, we show that in a metapopulation where local populations have already been through an extreme genetic drift, this trend changes. At low local-extinction probabilities, the effects of LDD on genetic diversity are positive and stronger than the effects of short-distance dispersal, whereas, at high local-extinction probabilities, LDD has a similar effect to that of short-distance dispersal. The positive effect of LDD especially is evident in the case of initially spreading metapopulations.

Independent of the level of initial mixing and of the spatial structure of the population, LDD has two general effects on F_{ST}. Long-distance dispersed seeds arriving in occupied patches have a homogenizing effect on the metapopulation genetic structure, while seeds that reach an unoccupied patch act as founders of a new population and thus have a subdividing effect. The former reduces F_{ST}, the latter increases it. Our simulations show, for the first time, that this homogenizing effect of LDD prevails under low local extinction probability (especially in spreading populations), whereas the subdividing effect prevails at intermediate to high local extinction probabilities.

EVOLUTIONARY IMPLICATIONS

In an evolutionary context, our findings suggest that selection forces favouring LDD would be effective in populations that face intermediate local-extinction pressures. In comparison, at the two ends of the local-extinction scale, populations with extremely high extinction pressure would have to adapt by improving their local patch survivability, and populations living with very low local-extinction pressures would not benefit from LDD because most available patches would eventually be occupied and patch turnover would be very slow. Only at the intermediate local-extinction levels, would LDD facilitate a rescue effect that would be beneficial to survival and therefore selected for.

These results agree with the theoretical predictions for evolutionarily stable dispersal rates (Olivieri & Gouyon 1997; Ronce *et al.* 2000a,b). In studies that used the classic metapopulation framework of Levins (1968) (i.e. identical patches, no within-patch local dynamics and saturation just after colonization), evolutionarily stable dispersal rates were predicted to be proportional to the local extinction rates (Levin *et al.* 1984; Olivieri *et al.* 1995) and to increase monotonically as extinction rates increase. However, incorporating local population-dynamics into these models revealed that beyond some level of extinction pressure, increase in the extinction rates might decrease the evolutionarily stable dispersal rates (Karlson & Taylor 1992, 1995; Ronce *et al.* 2000a,b). Ronce *et al.* (2000a) suggested two possible reasons why increased dispersal rates are not advantageous under high extinction rates: first, the decreasing intensity of competition within local populations with high local-extinction rates (Ronce *et al.* 2000a, 2000b), and secondly, the decreasing importance of bet-hedging (Karlson & Taylor 1992, 1995).

We find that LDD has a homogenizing effect under low local extinction probability (especially in spreading populations), but a subdividing effect at intermediate to high local extinction probabilities. Putting together theoretical predictions and our simulation results, we may conclude that LDD should be selected for under moderate intensity/frequency of disturbance and be characteristic of species with high fecundity. At the same time, in a stable near-equilibrium metapopulation LDD will keep population differentiation low and total genetic diversity low to moderate. This agrees with published data on temperate forest tree species (Hamrick & Godt 1990). LDD might foster speciation in cases of global catastrophes and climate changes when many habitat patches become available, and increasing probability of founder events are coupled with continuing patch turnover and moderate local-extinction rates.

However, if local extinction is absent or too intensive, the genetic homogenizing effect of LDD will prevent speciation.

IMPLICATIONS FOR CONSERVATION

We simulate the dynamics of Aleppo pine populations, which typically exhibit a patchy distribution throughout the native geographical range (Barbéro *et al.* 1998). Many populations of Aleppo pine in Israel and elsewhere went through an extreme bottleneck and expanded in the last 50 years. Therefore, the combination of a 'drifted' genetic structure and a 'spreading' scenario (Figs 3d, 4d and 5d) in our simulations is of special relevance for this species. Accordingly, low levels of H_s have been observed in all populations of *P. halepensis* across its geographical range (Korol *et al.* 2002). Our simulations suggest that LDD enhances metapopulation survival and decelerates the rate of genetic variability loss in this particular species. Given the evidence for relatively high dispersal capacity (Nathan & Ne'eman 2000), this may imply that recovery of native populations, without further interference, is highly probable. However, we emphasize that, in other cases, LDD may accelerate genetic variability loss, especially if extinction probability is high. Efforts to maintain the species genetic diversity should therefore consider the interactions between LDD, population history and expected local-extinction risks. Such considerations could be made using simulation tools similar to our model.

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