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Journal of Theoretical Biology 240 (2006) 662–672
Journal of Theoretical Biology
www.elsevier.com/locate/yjtbi

Seed and pollen flow in expanding a species' range

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Received 26 July 2005; received in revised form 31 October 2005; accepted 2 November 2005
Available online 20 December 2005

Abstract

The distinct processes of gene flow via seeds and pollen in hermaphrodite plants provide a biological basis for interpreting their different roles in expanding a species' range. A species' range is primarily expanded through the colonization process by seed dispersal and followed by the joint effects of both seed and pollen flow. Here we examined the effects of seed and pollen flow on shaping a species' distribution in one-dimensional space. Our results demonstrate that pollen flow can enhance range expansion when immigrating genes are adaptive to recipient populations, but can shrink a species' range when immigrating genes are maladaptive. The incompletely purging of maladaptive genes from immigrating pollen grains at the gametophyte stage can reinforce the biological barrier to range expansion. The linkage disequilibria attained by immigrating seeds and pollen grains indirectly amplify the effects of the reaction component and further limit a species' range. The cumulative effect from multiple loci each with a small effect can be substantial on altering a species' range when these genes are maladaptive. These theoretical predictions can help understand the role of pollen flow that is incapable of colonizing new habitats in range expansion.

Keywords: Species' range; Pollen flow; Seed flow; Selection; Linkage disequilibrium

1. Introduction

Gene flow in hermaphrodite plants can be mediated by either seeds or pollen grains, or both. Pollen flow refers to the process of dispersing pollen to recipient ovules, successful fertilization, and establishment of mature seeds; while seed flow refers to the process of dispersing seeds to different locations, germination, survival, and successful growth to the next adult. Biologically, an effective pollen flow should include the stage of growth to the next adult for the seeds that are formed by the combination of ovules with migrating pollen, because the death of these seeds at the sporophyte stage eventually results in unsuccessful pollen flow. These two different processes of gene flow have similar effects on homogenizing genetic divergence among populations (e.g. Hu and Ennos, 1999), on maintaining a species' integration (Mayr, 1963; Slatkin, 1976), and on spreading an advantageous allele from its residing local populations to the whole population (Fisher, 1937; Barton and Whitlock, 1997).

In spite of the same functions mentioned above between seed and pollen flow, they differ in governing population dynamics. First, their relative contributions to gene flow exhibit a wide range in magnitude and vary with species and the mode of gene inheritance (e.g. Ennos, 1994; Ennos et al., 1999; Petit et al., 2005). If the migration rate of seeds equals that of pollen, a larger effect of seed than pollen flow is predicted in reducing population genetic differentiation (Hu and Ennos, 1999). Second, when two stages of selection (gametophyte and sporophyte) are jointly considered, seed and pollen flow can create different migration loads to a recipient population (e.g. Hu and Li, 2003) and hence can result in different extents of adaptation to local environments. Third, a more critical distinction is that only seed flow can colonize empty habitats and provide a biological foundation for the subsequent pollen flow. Successful pollen flow is based on the pre-existing adult populations that are primarily established through migrating seeds (McCauley et al., 2001). The purpose of this study is to examine such distinction in order to gain insights into

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doi:10.1016/j.jtbi.2005.11.002

the effects of seed and pollen flow on expanding a species' range.

The mechanisms for forming a species' range remain an intriguing question even though several hypotheses have been presented but mostly not tested (Case et al., 2005). A species' range may be formed owning to: (1) the interaction between climate and species (Darwin, 1859); (2) the limited population genetic variation; and (3) the effect of gene flow (Haldane, 1956). Early empirical and theoretical studies demonstrate that gene flow from central populations of a species may limit adaptation at the periphery and halt range expansion (Mayr, 1963; Hoffman and Blows, 1994; Kirkpatrick and Barton, 1997; Case and Taper, 2000). Such a dispersal-dependent mechanism is basically related to the relationship between migration rate of maladaptive genes and their selection coefficients in a single recipient population (Wright, 1969, 1977, pp. 485–486). When the migration rate is greater than the selection coefficient, the frequency of maladaptive allele in the recipient population is slightly smaller than the allele frequency in migrants, leading to a large genetic load. When the migration rate is smaller than the selection coefficient, the frequency of maladaptive allele should be very small, leading to a small genetic load. As long as migration takes place and the difference between the frequencies of maladaptive alleles in migrants and in recipient populations is present, the genetic load in recipient populations always exists. In hermaphrodite plants, the migration in this relationship should include both seed and pollen flow.

In this study, we apply the dispersal-dependent mechanism to hermaphrodite plants where the two stages of genetic loads generated by pollen flow are connected through the two stages of plant life-phases (gametophyte and sporophyte). The pre-existing theories of a species' range are only based on the dispersal of diploid individuals, and the effects of haploid dispersal (pollen) have not been considered. Instead of using the approach that describes the stabilizing selection in terms of the deviation of a single polygenic quantitative trait from its optimum (e.g. Kirkpatrick and Barton, 1997), we use an evolutionary ecological approach to link per-capital growth rate with individual gene frequencies (e.g. Roughgarden, 1979, pp. 311–319), similar to MacArthur's (1962) model. The advantage of this approach is that the effects of pollen flow and the selection at the gametophyte stage can be easily incorporated although these two approaches are expected to be converged when there are infinite numbers of genes and each has an infinitesimal effect. Another advantage is that the effect of individual loci (like major quantitative trait loci) can be separately examined. Like the previous theories (e.g. Kirkpatrick and Barton, 1997; Case and Taper, 2000), a diffusion model is applied to approximate the dispersal of seeds and pollen in one-dimensional space. Two stages of selection (gametophyte and sporophyte) are included in this study, relaxing the assumption of diploid-alone selection. This is significant because about 60% of the structure genes that are expressed at the sporophyte stage of angiosperm life cycle can also be expressed and are potentially subject to selection at the gametophyte stage (Mulcahy et al., 1996).

In the following sections, we first analyse two ideal models. We then give results for one- and two-locus cases and numerically demonstrate the differences between seed and pollen flow. A multilocus model is finally analysed to evaluate the joint effects of individual quantitative trait loci on expanding the range of a species.

2. Theoretical analysis

Our model considers the case where a central population expands in two directions along one-dimensional space. The central population is assumed at steady state in demography, with a constant population density (n_0). Random combination between pollen and ovules is assumed in each established population. The gametophyte stage in the life cycle of hermaphrodite plants refers to the period from pollen and ovules formation to the time before zygote formation; while the sporophyte stage refers to the period from seed formation to adult in the same generation. For mathematical tractability, weak selection is considered at each stage so that a balance between gene flow and selection can be reached and a limit spatial distribution of a species can be formed. We begin by describing two ideal models where only seed flow and constant per-capita growth rate take place in space. The results may provide a prototype for understanding the effects of pollen flow addressed in later sections.

2.1. Ideal models

Case I: Density-independent growth. Let n be the population density at position x. For simplicity, we use notation $\dot{f}$ for $\partial f/\partial t$, f' for $\partial f/\partial x$, and f'' for $\partial^2 f/\partial x^2$. Following the same method as Nagylaki (1975) and Pease et al. (1989), we obtained the dynamic equation

$$\dot{n} = \frac{\sigma_S^2}{2} n'' + nr, \tag{1}$$

where σ_S^2 is the dispersal variance of seeds. The first term on the right-hand side of the above equation is the diffusion component and the second is the reaction component. The above equation is also applicable to animal species if σ_S^2 is replaced with the dispersal variance of animals.

Rescaling the spacing distance x and time t by letting $X = \sqrt{r}x/\sigma_S$ and $T = rt$, respectively, Eq. (1) becomes $\dot{N} = N''/2 + N$, where N equals $n(X, T)$, the form of population density n after transformation. This is an equation without any parameter. Similar to the case of gene frequency cline (Slatkin, 1973), $l_c = \sigma_S/\sqrt{r}$ can be termed as the *characteristic length* within which a species' density does not change. Apparently, the characteristic length (l_c) increases with the dispersal variance of seeds but decreases with the per-capita growth rate. In

one-dimensional space, the density at the central location can be expressed by $n(x,0)=n_0\delta(x)$ (initial condition) where $\delta(x)$ is a delta function. Solution to Eq. (1) is a normal distribution,

$$n(x,t)=n_0\exp(rt-(x^2/2\sigma_S^2 t))/\left(2\sigma_S\sqrt{\pi t}\right),$$

which describes a dynamic density distribution, similar to Skellam's (1951) model in one-dimensional space. The time required for establishing the population for spread, t_e, satisfies the relation of $n_0/(2\sigma_S n^*\sqrt{\pi t_e})=\exp(-rt_e)$ where n^* is the minimum detectable size of the population at the boundary (Shigesada and Kawasaki, 1997).

Under the conditions of $n(x=0)=n_0$, $n'(x=0)=n''(x=0)=0$ (*initial value* problem), and $n'(x\neq 0)<0$, we obtained

$$n'=-\frac{\sqrt{2}}{l_c}(n_0^2-n^2)^{1/2}. \tag{2}$$

Basically, a larger value of n' indicates a larger slope at each point from the central population to each direction and enhances seed dispersal and range expansion. The steady-state solution ($\dot{n}=0$) to Eq. (1) is given by

$$n=n_0\sin\left(\frac{\pi}{2}-\frac{\sqrt{2}}{l_c}x\right). \tag{3}$$

Given the minimum density n^*, the range size is $x_{\text{range}}=\sqrt{2}\left((\pi/2)-\arcsin(n^*/n_0)\right)l_c$. It can be numerically shown that the range size gradually reduces with the ratio n^*/n_0, with a maximum size being $2.22l_c$.

Case II: Density-dependent growth (the logistic model). The dynamic equation for population density is

$$\dot{n}=\frac{\sigma_S^2}{2}n''+nr\left(1-\frac{n}{K}\right), \tag{4}$$

where K is the environmental capacity in the population at position x. Eq. (4) is the same as Fisher's (1937) traveling wave model. Analytical solution to Eq. (4) is difficult to obtain due to the nonlinear reaction component, but numerical comparisons with Eq. (1) can be found in Shigesada and Kawasaki (1997, Chapter 3).

With the same setting of initial values as in the Case I and the conditions of $n'<0$ and $n''<0$, the steady-state solution to Eq. (4) is $x=(l_c/2)\int_n^{n_0}((n_0^2-n^2)/2-(n_0^3-n^3)/3K)^{-1/2}\,dn$. The condition of $n''<0$ ensures that the initial central population has a maximum density and is the source for spreading outward, which otherwise ($n''>0$) becomes concave upward in the density curve in space (Case et al., 2005). It can be numerically shown from the steady-state solution that the range size decreases with the capacity K ($<n_0$) and eventually approaches $2.22l_c$ when the capacity is sufficiently large (approaching the Case I). A species' range is proportional to $l_c/2$ when $K=n_0$. Note that the capacity at the position away from the central population (optimal fitness) is assumed to be smaller (suboptimal adaptive position) than or equal to the central population size.

In summary, the above two ideal cases describe the direct effects of seed dispersal in expanding a species' range. A species' range is proportional to the dispersal variance of seeds. Under the case of density-independent per-capital growth rate or the case of sufficient large environmental capacity, a maximum range size is about $2.22l_c$. In the next, we examine the role of pollen flow that affects a species' range via altering both adaptive and maladaptive gene frequencies in recipient populations and hence changing per-capita growth rate.

2.2. One-locus model

Consider a diallelic nuclear locus in a hermaphrodite plant species in one-dimensional space. The life cycle follows a sequence of events: pollen and ovules generation, pollen flow, haploid selection, seed formation, seed flow, and diploid selection. Let p_A and q_a ($p_A+q_a=1$) be the frequencies of alleles A and a at the locus in the population at position x, respectively. The dynamic equations for gene frequency and population density are derived in Appendix A, where pollen flow and selection at the gametophyte stage are included. At steady state the two coupled nonlinear differential equations from Eqs. (A.1) and (A.2) in Appendix A are

$$0=\frac{\sigma_S^2}{2}n''+n\bar{r}_A, \tag{5a}$$

$$0=\frac{\sigma^2}{2}p_A''+\sigma^2(\ln n)'p_A'+p_Aq_a(\delta_A/2+\Delta_A), \tag{5b}$$

where σ^2 is the total dispersal variance of seeds and pollen, $\bar{r}_A$ is the per-capital growth rate (the function of gene frequency; see Eq. (A.5) in Appendix A), δ_A is the election component at the gametophyte stage, and Δ_A is the selection component at the sporophyte stage. The analytical solutions to Eq. (5) are hard to obtain, but can be numerically evaluated. Again, note that $n''<0$ so that population density gradually reduces with the distance away from the central population.

Eq. (5) gives the approach of how pollen flow is related to the expansion of a species' range, which is distinct from seed dispersal that directly expands a species' range. The presence of pollen flow ($\sigma_P^2\neq 0$) makes the gene frequencies in the established populations approach those in the central population and reduces the genetic divergence between the central and colonized populations (i.e. the homogenizing function of gene flow). If the central population has a maximum genetic diversity, pollen flow can increase the genetic diversity in the colonized populations. As a consequence, the per-capital growth ($\bar{r}_A$) in the colonized populations approaches the one in the central population; the populations at the periphery become denser; and the range of a species' distribution is expanded. The different effects between migrants with maladaptive and adaptive genes are realized through altering per-capital growth rate ($\bar{r}_A$). The presence of maladaptive genes in migrating seeds

and pollen grains reduces the frequency of adaptive gene frequencies and hence reduces per-capital growth rate and a species' range. The relative contributions of pollen to seed flow to reducing per-capital growth rate depend on their relative dispersal variances (σ_P^2/σ_S^2). When there are maladaptive genes in migrants, the presence of selection at the gametophyte stage purges maladaptive genes to some extents and helps reduce the erosion of genetic diversity. The effects of pollen flow on altering per-capita growth rate at the sporophyte stage (mean fitness in adults) are reduced, resulting in a small influence on a species' range. The incompletely purging of maladaptive genes at the gametophyte stage reinforces the biological barrier to range expansion. These properties are numerically demonstrated as follows.

The effects of seed and pollen flow are assessed through different fitness settings for three genotypes. In the first case, all selection coefficients are assumed positive so that each genotype has a positive growth rate. In the second case, selection coefficients are set to be negative (maladaptive) for individuals with the genotype *aa* at the sporophyte stage or for pollen and ovules with the genotype *a* at the gametophyte stage. Thus, both adaptive and maladaptive genes exist in migrating seeds and pollen grains. Throughout all numerical assessments, the finite difference method is applied (see Press et al., 1992). The range size is determined according to an artificial threshold density n^* (Shigesada and Kawasaki, 1997). The basic approach for these numerical calculations is to transform a set of partial differential equations of high order to those with one order and then to use the iterative approach to calculate function values at each step. Here we concentrate on the effects of seed and pollen dispersal on the eventual distribution of a species in space, and the transient distributions which may provide us with different information are not included. Computer programs in C for numerical calculations in the steady-state case are available upon request from Hu.

2.2.1. *Effects of pollen flow*

The presence of pollen flow can expand a species' range in the case without maladaptive genes, although the expanded range is very smaller than that by the same amount of increment of seed dispersal (σ_S^2). For example, when all genes are adaptive, species range is slightly expanded when the dispersal variance of pollen increases from 0 to 0.1, but the range is substantially expanded when the dispersal variance of seeds increases from 0.05 to 0.1 (Fig. 1a). Per-capita growth rate increases with the dispersal variance of either seeds or pollen (Fig. 1b). Genetic loads at both the gametophyte and sporophyte stages increase from central to marginal populations, but reduce with an increase in dispersal variances of seeds and pollen (e.g. Fig. 1c).

In the second case, the growth rate of the individuals with the genotype *aa* is less than unity since the allele *a* is assumed maladaptive. Under this situation, species range reduces when the dispersal variance of pollen increases from 0 to 0.1 (Fig. 2). Another difference between these two cases is the magnitude of genetic load in marginal populations. The genetic loads at both gametophyte and sporophyte stages are negative in the first case, where mean

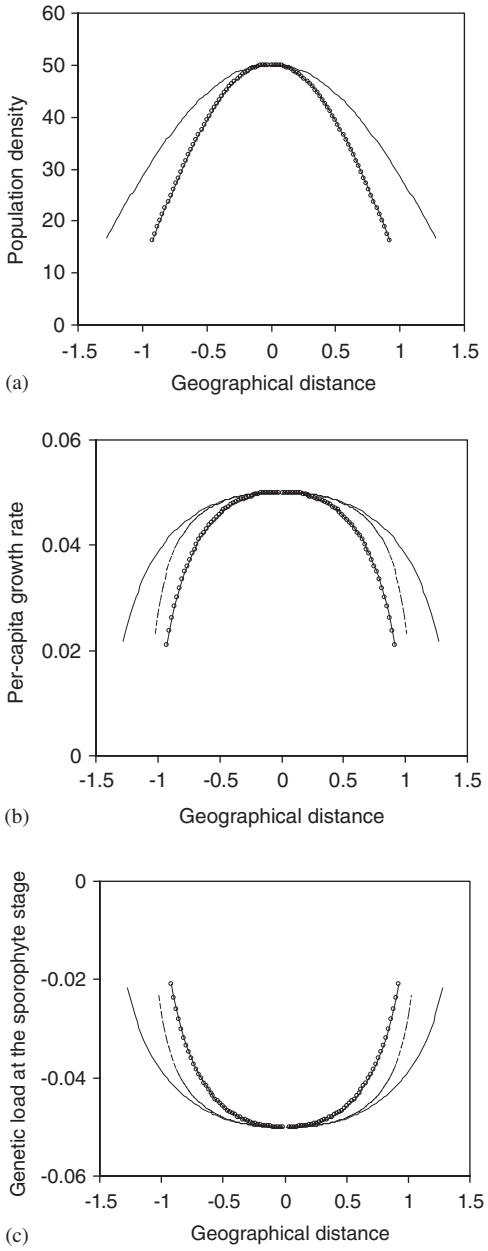

Fig. 1. Effects of pollen and seed flow on a species' distribution in space in the case without maladaptive genes: (a) population density distribution; (b) per-capita growth rate distribution; and (c) distribution of the genetic load at the sporophyte stage. The common parameters are the initial population density $n_0 = 50$, the allele frequency $p_A(x = 0) = 0.5$, the initial second-order differential of allele frequency $p''_A(x = 0) = -0.01$, the initial second-order differential of population density $n''(x = 0+$ or $0-) = -0.01$, the selection coefficients in ovules and pollen $s_{A.O} = s_{A.P} = 0.04$ for allele A and $s_{a.O} = s_{a.P} = 0.01$ for allele a, and the selection coefficients for three genotypes $s_{AA} = 0.08$, $s_{Aa} = 0.05$, and $s_{aa} = 0.02$. In each figure, the dashed line represents the case of $\sigma_S^2 = 0.05$ and $\sigma_P^2 = 0.1$, the line with open circles for the case $\sigma_S^2 = 0.05$ and $\sigma_P^2 = 0.0$, and the solid line for the case $\sigma_S^2 = 0.1$ and $\sigma_P^2 = 0.0$.

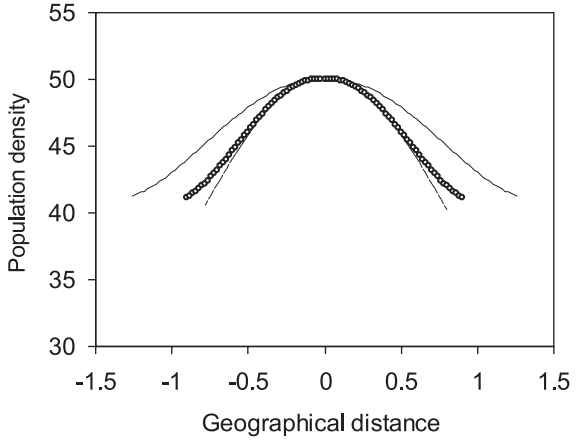

Fig. 2. Effects of pollen and seed flow on a species' distribution in space. The parameters are the initial population density $n_0 = 50$, the initial allele frequency $p_A(x = 0) = 0.5$, the initial second differential of allele frequency $p''_A(x = 0) = -0.01$, the initial second differential of population density $n''(x = 0+ \text{ or } 0-) = -0.01$, the selection coefficients in ovules and pollen $s_{A.O} = s_{A.P} = 0.04$ for allele A and $s_{a.O} = s_{a.P} = -0.02$ for allele a, and the selection coefficients for three genotypes $s_{AA} = 0.08$, $s_{Aa} = 0.02$, and $s_{aa} = -0.04$. The dashed line represents the case of $\sigma_S^2 = 0.05$ and $\sigma_P^2 = 0.1$, the line with open circles for the case $\sigma_S^2 = 0.05$ and $\sigma_P^2 = 0.0$, and the solid line for the case $\sigma_S^2 = 0.1$ and $\sigma_P^2 = 0.0$.

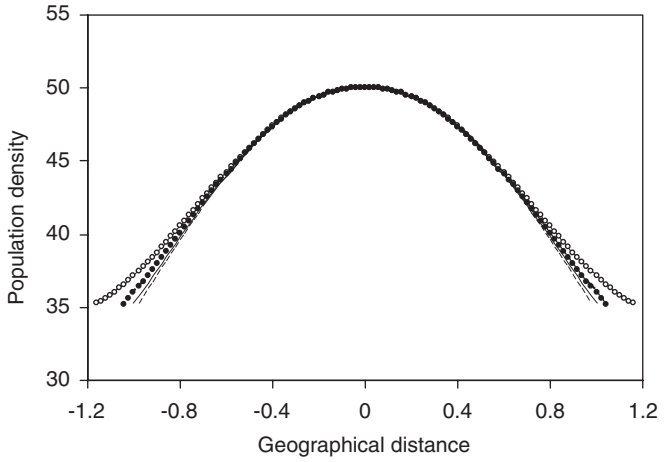

Fig. 3. Effects of selection at the gametophyte stage on a species' distribution in space. The common parameters are the initial population density $n_0 = 50$, the initial allele frequency $p_A(x = 0) = 0.5$, the initial second-order differential of allele frequency $p''_A(x = 0) = -0.01$, the initial second-order differential of population density $n''(x = 0+ \text{ or } 0-) = -0.01$, and the selection coefficients for three genotypes $s_{AA} = 0.08$, $s_{Aa} = 0.02$, and $s_{aa} = -0.04$. The line with open circles represents the case $s_{A.O} = s_{A.P} = 0.04$ and $s_{a.O} = s_{a.P} = -0.02$; the line with closed circles for the case $s_{A.P} = 0.04$, $s_{a.P} = -0.02$, and $s_{A.O} = s_{a.O} = 0.0$; and the solid line for the case with $s_{A.O} = s_{a.O} = s_{A.P} = s_{a.P} = 0.0$.

population fitness does not reduce and populations maintain positive growth rate in all expended populations. In the second case, a high genetic load in the marginal populations exists at both the gametophyte and sporophyte stages. Like in the first case, the per-capita growth rate gradually reduces with the populations away from the central population while the genetic load at both the gametophyte and sporophyte stages increase from the central to marginal populations.

2.2.2. Selection at the gametophyte stage

The selection at the gametophyte stage can influence a species' distribution through altering the frequencies of adaptive genes and hence changing per-capital growth rate. Removing the maladaptive genes at the gametophyte stage can enhance range expansion. Fig. 3 shows that a species' range is greater in the case with selection at the gametophyte stage, compared with the case without selection at the gametophyte stage. The joint effect of ovule and pollen selection is greater than that of each individual selection on range expansion. When pollen flow is absent, there is no difference between ovule and pollen selection in shaping range expansion since both of them equally transmit nuclear genes to progeny. However, there are differences when pollen flow with maladaptive migrating genes is present. Pollen selection is more effective than ovule selection in expanding a species' range (Fig. 3).

2.2.3. Density-dependent selection

The objective here is to look at the effects of pollen flow on range expansion under the density-dependent reaction. Suppose that there is no density-dependent regulation in the number of pollen grains and ovules (Wright–Fisher's model), but there is density-dependent regulation in the number of adults. According to Roughgarden (1979, p. 313), let $s'_{AA} = s_{AA}(1 - n/K_{AA})$, $s'_{Aa} = s_{Aa}(1 - n/K_{Aa})$, and $s'_{aa} = s_{aa}(1 - n/K_{aa})$, where K_{AA}, K_{Aa}, and K_{aa} are the environmental capacities in the population at position x for genotypes AA, Aa, and aa, respectively. Replacing s_{AA}, s_{Aa}, and s_{aa} in Eq. (A.2) in Appendix A with s'_{AA}, s'_{Aa}, and s'_{aa}, respectively, gives the density-dependent expressions. The per-capita growth rate then equals

$$\bar{r}'_A = s_{AA}\left(1 - \frac{n}{K_{AA}}\right)p^2 + s_{Aa}\left(1 - \frac{n}{K_{Aa}}\right)\cdot 2pq + s_{aa}\left(1 - \frac{n}{K_{aa}}\right)q^2, \quad (6)$$

which is the same as Roughgarden's (1979, p. 313) expression.

There is a very complicated relationship between the per-capital growth rate and the capacity for each genotype, but the assumption of a tradeoff between them is often used (Roughgarden, 1979, pp. 313–319). Our numerical results show that the effects of pollen flow in the case of density-dependent selection remain the same as those in the preceding cases, that is the reduction in a species' range in the presence of migrating pollen with maladaptive genes (e.g. Fig. 4).

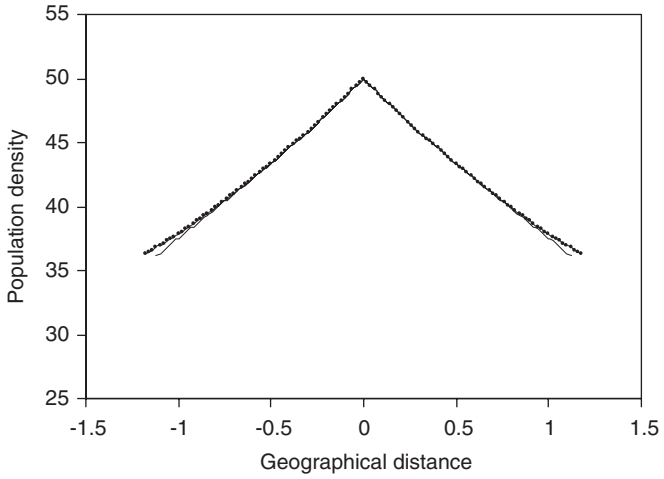

Fig. 4. Effects of pollen flow in the case of density-dependent capacity for each genotype. Parameters are the initial population density $n_0 = 50$, the initial allele frequency $p_A(x = 0) = 0.5$, the initial second-order differential of allele frequency $p''_A(x = 0) = -0.01$, the initial second differential of population density $n''(x = 0+ \text{ or } 0-) = -0.01$, the dispersal variance of seeds $\sigma_S^2 = 0.05$, the selection coefficients in ovules and pollen $s_{A.O} = s_{A.P} = 0.04$ for allele A and $s_{a.O} = s_{a.P} = -0.02$ for allele a, and the selection coefficients for three genotypes $s_{AA} = 0.08$, $s_{Aa} = 0.02$, and $s_{aa} = -0.04$. The capacities are $K_{AA}(x) = 40$, $K_{Aa}(x) = 45$, and $K_{aa}(x) = 50$. The line with closed circles represents the case of $\sigma_P^2 = 0.0$, and the solid line for the case of $\sigma_P^2 = 1.0$.

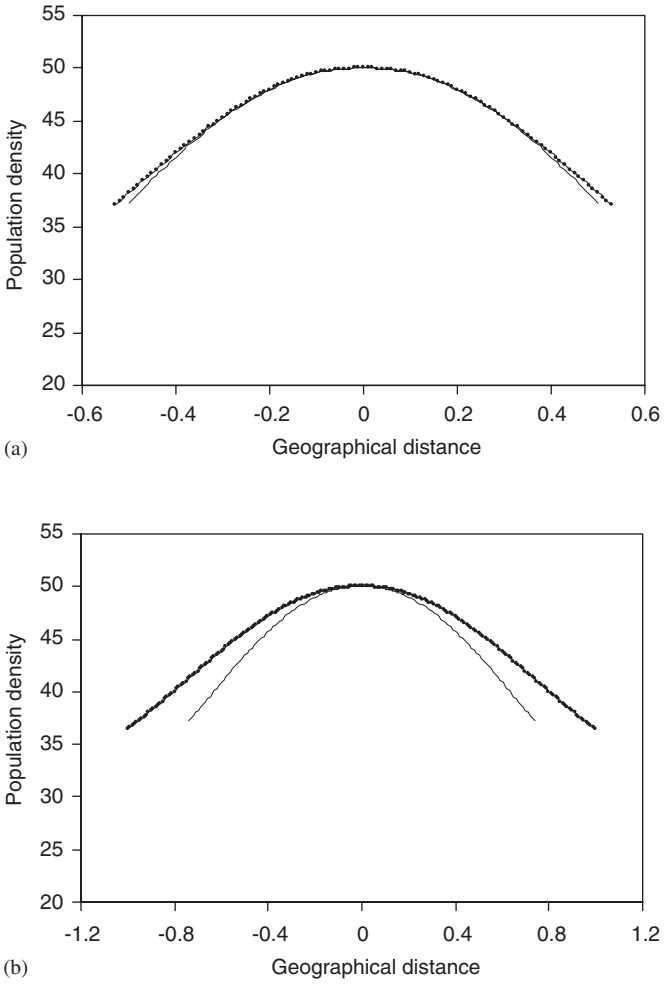

Fig. 5. Effects of recombination rate (r) on a species' distribution in space: (a) dispersal variance seeds $\sigma_S^2 = 0.05$ and pollen $\sigma_P^2 = 0.1$ and (b) $\sigma_S^2 = 0.1$ and $\sigma_P^2 = 0.0$. Common parameter settings are the initial population density $n_0 = 50$, the initial allele frequency $p_A(x = 0) = 0.5$, the initial second-order of allele frequency $p''_A(x = 0) = p''_B(x = 0) = -0.01$, the initial second-order of population density $n''(x = 0+ \text{ or } 0-) = -0.01$, the selection coefficients in ovules and pollen $s_{A.O} = s_{A.P} = s_{B.O} = s_{B.P} = 0.04$ for alleles A and B and $s_{a.O} = s_{a.P} = s_{b.O} = s_{b.P} = -0.01$ for alleles a and b, the selection coefficients at the A and B loci $s_{AA} = s_{BB} = 0.08$, $s_{Aa} = s_{Bb} = 0.03$, and $s_{aa} = s_{bb} = -0.02$. In each figure, the dashed represents the case of $r = 0.05$, and the line with closed circles for the case of $r = 0.5$.

2.3. Two-locus model

The objective here is to examine the effects of linkage disequilibrium (LD) on range expansion. When LD equals zero, the two loci evolve independently. Here LD is mainly generated by the migrating seeds and pollen but reduced by the recombination. Consider that two diallelic nuclear loci are involved in population fitness, with alleles A and a at the first locus and B and b at the second one. Let r be the recombination rate between the A and B loci. Let p_B and $q_b (p_B + q_b = 1)$ be the frequencies of the alleles B and b, respectively. Let D be the linkage disequilibrium between these two loci in the current adult stage. The dynamic equations for the changes in gene frequency, LD, and population density are derived in Appendix B. From Eqs. (B.1) and (B.2) in Appendix B, the function of LD is equivalent to creating an additional reaction component that increases the steepness of gene frequency distribution and hence reduces a species' range.

The steady-state equations can be obtained simply by setting $\dot{p}_A = \dot{p}_B = \dot{D} = \dot{n} = 0$. It can be seen from Eq. (B.4) in Appendix B that D is the function of the joint dispersal variances of seeds and pollen, indicating that the relative effects of seed versus pollen dispersal directly rely on their relative magnitudes in quantity. Fig. 5a demonstrates that the range reduction due to the tightly linked genes is small when $\sigma_S^2 = 0.05$ and $\sigma_P^2 = 0.1$, compared with that due to the loosely linked genes (Fig. 5a). However, a substantial range reduction due to the tightly linked loci is resulted when $\sigma_S^2 = 0.1$ and $\sigma_P^2 = 0.0$ (Fig. 5b), indicating that seed flow has a greater effect than pollen flow in generating LD.

2.4. Multiple-locus model

We now examine the cumulative effects from multiple loci. Multiple genes that are linked on the same chromosomes in migrating pollen or seeds can simultaneously spread in space since pollen and seeds carry a half and a whole set of genomes, respectively. The governing equations for population dynamics are given in Appendix C.

In our numerical analyses, suppose that multiple linked loci are distributed on the same chromosome, with a recombination rate between adjacent loci being 0.05. Each diallelic locus has the same selection coefficient at both the gametophyte and sporophyte stages. Thus, allele frequencies among all loci are coincident in space. Numerical results show that a species' range reduces with the number of loci, indicating that the cumulative effect becomes substantial when the number of loci increases (Fig. 6a). The cumulative effects from pollen flow are also substantial in the presence of maladaptive migrating genes (e.g. Fig. 6b).

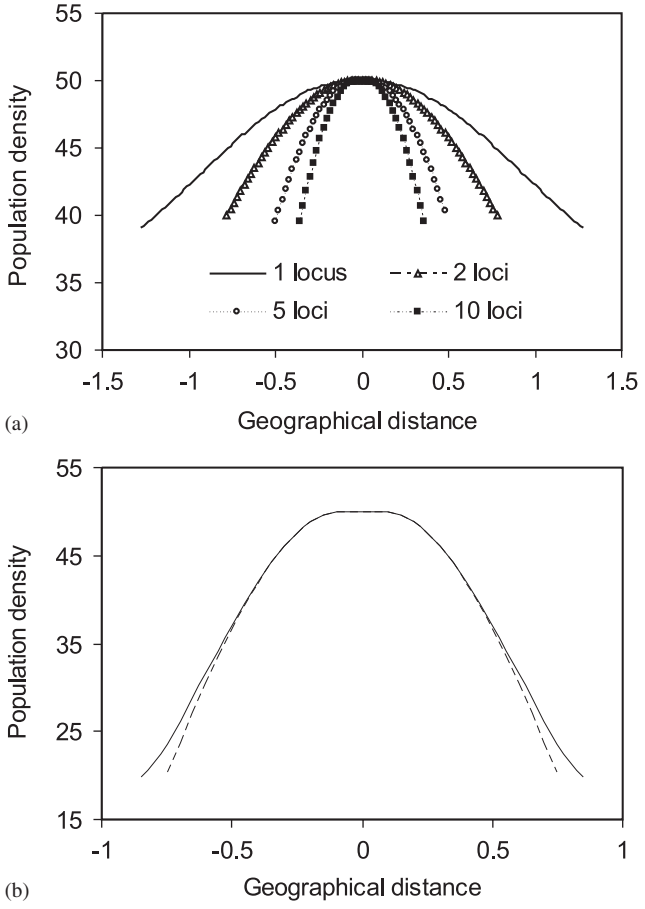

Fig. 6. Effects of multiple loci on a species' distribution in space: (a) comparison of different number of loci under the dispersal variances of seeds $\sigma_S^2 = 0.05$ and pollen $\sigma_P^2 = 0.05$; (b) effects of pollen flow in the case of four loci, with $\sigma_S^2 = 0.05$. In (a), the selection coefficients in ovules and pollen $s_{i_1.O} = s_{i_1.P} = 0.02$ for allele i_1 and $s_{i_2.O} = s_{i_2.P} = -0.01$ for allele i_2, the selection coefficients for genotypes $s_{i_1i_1} = 0.04$, $s_{i_1i_2} = 0.01$, and $s_{i_2i_2} = -0.02$. In (b), selection coefficients are $s_{i_1.O} = s_{i_1.P} = 0.04$ and $s_{i_2.O} = s_{i_2.P} = -0.02$, $s_{i_1i_1} = 0.08$, $s_{i_1i_2} = 0.02$, and $s_{i_2i_2} = -0.04$. The solid line represents the case of $\sigma_P^2 = 0.0$, and the dashed line for the case of $\sigma_P^2 = 0.1$. The common parameters for (a) and (b) are the initial population density $n_0 = 50$, the initial allele frequency for allele $i_1 p_{i_1}(x = 0) = 0.5$, the initial second-order differential of allele frequency $p''_{i_1}(x = 0) = -0.01$, the initial second-order differential of population density $n''(x = 0+ \text{ or } 0-) = -0.01$, and the recombination rate between adjacent loci equals 0.05.

3. Discussion

Although species' geographic ranges under a variety of biological mechanisms have been intensively studied (Case et al., 2005; Holt and Keitt, 2005), the effects of pollen flow have surprisingly never been investigated. Much of our interest often focuses on the dispersal of seeds or other types of diploid propagules that are capable of colonizing new habitats, and the effects of pollen flow on a species range have been neglected. Haldane (1956) pointed out that population adaptation at the periphery would be countered by the maladaptive genes immigrated from interior populations, and thus limit a species' range even in the absence of physical barriers to dispersal. This prediction has been theoretically confirmed in recent studies where dispersal refers to diploid individuals (Kirkpatrick and Barton, 1997; Barton, 2001). The present study demonstrates the distinct roles of seed and pollen flow in expanding a species' range. In particular, it shows that the maladaptive genes from migrating pollen can further shrink a species' range, especially when many maladaptive genes are simultaneously involved. However, pollen flow can also help range expansion when all migrating genes are adaptive to local environments even if they are unequal in adaptation among different genotypes. This function is analogous to that of pollen flow in spreading an advantageous allele in a clinal situation where pollen flow can extend the width of gene frequency cline (Hu and Li, 2002).

Our results imply the importance of selection at the gametophyte stage in shaping a species' range. The genetic load at the gametophyte sage has not been stressed so far (Hu and Li, 2003). The maladaptive genes from migrating pollen grains can be partially purged at the gametophyte stage at the expense of increasing immigration load. The incompletely removing of maladaptive genes at the gametophyte stage adds an additional genetic load to recipient populations at the sporophyte stage and hence reinforces the biological barrier to range expansion.

Because the immigrating genes via pollen vector are involved in two stages of selection, pollen flow contributes to the genetic load at both the sporophyte and gametophyte stages. In a different model, Hu and Li (2003) showed that immigration load at the sporophyte stage is more related to seeds than to pollen. The ratio of $m_P/2m_S$ (the migration rate of pollen to two times the migration rate of seeds) can be used to assess the relative contributions of pollen and seed flow to the immigration load at the sporophyte stage when the total migration rate is smaller than the total selection coefficients at the two stages (Hu and Li, 2003). Thus, those species with a large ratio of pollen to seed flow, such as *Quercus petraea*/*Q. robur* and *Pinus sylvestris* (Ennos, 1994), may have a large immigration load attributable to pollen flow other than seed flow at the sporophyte stage. Using a different approach, Burt (1995) estimated the contributions to population fitness reduction from pollen and seeds. For example, seed and

pollen flow in *Ipomopsis aggregate* can reduce the fitness at the sporophyte stage by ~0.002 and ~0.0008 per generation, respectively. In relation to the present results, estimation of the relative rate of pollen to seed flow can be applied for gaining insights into the role of pollen flow in shaping a species' range.

In addition to the direct effects of pollen flow on the immigration load at both the sporophyte and gametophyte stages, the indirect effects of pollen flow by generating linkage disequilibrium among linked genes are also important. Linkage disequilibrium has a similar function to natural selection as a reaction component and hence amplifies the biological barrier to range expansion in the presence of maladaptive migrating genes. These indirect effects have not been examined in previous theories where haploid migration is not considered. Our results show that the relative contribution of pollen and seed flow to linkage disequilibria is proportional to the ratio of their dispersal variances (σ_P^2/σ_S^2). As implied from previous studies (Petit et al., 2005), migration rate of pollen grains among established populations is often much greater than that of seeds, especially for plants with wind pollinations. Thus, the indirect effect of pollen flow through generating linkage disequilibrium can be substantial when the dispersal variance of pollen is much greater than the recombination rates or when a large number of tightly linked adaptive genes are involved.

Another effect is the cumulative effect from multiple loci that can be substantial in shaping a species' range although individual gene effects may be small. This is of practical significance since many quantitative trait loci each with small effects can be detected with the development of genome-wide screening techniques in future. These multiple loci can be simultaneously transferred by either seed or pollen flow to the colonized populations. As implied from our present results, the cumulative genetic load is likely large if multiple loci are maladaptive. Thus, the biological barrier owing to the incompletely purging at the gametophyte stage is reinforced.

Finally, it is necessary to point out that the effects of pollen flow are related to the founder effect during the colonization process, the demographic properties of the established populations, and the type of mating system. These factors can affect genetic diversity within and between colonized populations (e.g., Austerlitz et al., 2000; Ingvarsson, 1997) and hence influence range expansion. When the number of initial individuals in a new habitat is small but the per-capita growth rate is high in an outcrossing species, the subsequent pollen flow may have a significant effect on changing the genetic diversity in the newly established populations, as evidenced in the case of *Silene alba* (McCauley et al., 2001). If the initial population size is small and the per-capita growth rate is also small, the contribution from pollen flow may be negligible, such as in those species with insect pollination and ruminant dispersal of seeds where migration rate of pollen is small or comparable to that of seeds. Under this situation, seed dispersal plays a dominant role in expanding a species' range.

Acknowledgments

We greatly appreciate a referee for helpful comments. This work is financially supported by the Alberta Ingenuity Fund and the Natural Sciences and Engineering Research Council of Canada.

Appendix A. Equations for one locus

Consider a diallelic nuclear locus with alleles A and a in a hermaphrodite plant species in one-dimensional space. The analytical derivation follows a sequence of events in life cycle: pollen and ovules generation, pollen flow, haploid selection, seed formation (random combination between pollen and ovules), seed flow, and diploid selection. For mathematical rigor in deriving partial differentials of allele frequencies, the sequence of events are assumed to occur within a time interval, Δt (e.g. Nagylaki, 1975; Hu and Li, 2001). Let n be the population density (number of individuals) at position x. According to previous studies (Nagylaki, 1975; Pease et al., 1989; Kirkpatrick and Barton, 1997), the population dynamics can be described by a diffusion-reaction equation

$$\dot{n} = \frac{\sigma_S^2}{2} n'' + n\bar{r}_A, \tag{A.1}$$

where $\bar{r}_A$ is the per-capita growth rate in the one-locus case.

For mathematical tractability, weak selection is assumed at both the gametophyte and sporophyte stages so that all terms containing the second or higher orders of selection coefficients are negligible. Let $s_{A.P}$ and $s_{A.O}$ be the selection coefficients of allele A in pollen and ovules, respectively; $s_{a.P}$ and $s_{a.O}$ be the selection coefficients of allele a in pollen and ovules, respectively. Let the fitness at the sporophyte stage be $1 + s_{AA}$ for genotype AA, $1 + s_{Aa}$ for Aa, and $1 + s_{aa}$ for aa. Density-independent selection is assumed to take place independently in each local population.

Let p_A and $q_a (p_A + q_a = 1)$ be the frequencies of alleles A and a in the population at position x, respectively. Let $\delta_A = s_{A.P} + s_{A.O} - s_{a.P} - s_{a.O}$, the selection component related to the gametophyte stage, and $\Delta_A = p_A s_{AA} + (q_a - p_A)s_{Aa} - q_a s_{aa}$, the selection component related to the sporophyte stage. According to the life cycle and the direction of dispersal from high to low density populations in space, the dynamic equation for allele frequency is derived as

$$\dot{p}_A = \frac{\sigma^2}{2} p_A'' + \sigma^2 (\ln n)' p_A' + p_A q_A (\delta_A/2 + \Delta_A), \tag{A.2}$$

where $\sigma^2 = \sigma_S^2 + \sigma_P^2/2$ in which σ_P^2 is the dispersal variance of pollen grains. Note that the first term on the right-hand side of Eq. (A.2) represents the diffusion component. The second term on the right-hand side of Eq. (A.2) represents the joint effect of gene flow and the change in density over

space (a nonlinear component); and the last term (the reaction component) represents the changes due to the selection at both the gametophyte and sporophyte stages. An expression similar to Eq. (A.2) can also be found in Barton (2001) except that the reaction component in the present model includes the selection at the gametophyte stage and that the diffusion component includes the haploid dispersal.

The genetic load at the gametophyte stage equals the reduction in average fitness in the population. Let l_P and l_O be the genetic loads in pollen and ovules at the gametophyte stage, respectively. We obtained

$$l_P = s_{A.P}p_A^* + s_{a.P}q_a^*, \tag{A.3}$$

$$l_O = s_{A.O}p_A + s_{a.O}q_a, \tag{A.4}$$

where p_A^* and q_a^* are the gene frequencies after pollen flow. The allele frequencies in ovules are assumed equal to those in the preceding adults. At the steady state, $p_A^* = p_A$ and $q_a^* = q_a$. The average per-capita growth rate at the sporophyte stage can be expressed as

$$\bar{r}_A = p_A^2 s_{AA} + 2p_A q_a s_{Aa} + q_a^2 s_{aa}, \tag{A.5}$$

which links Eq. (A.1) with Eq. (A.2). The genetic load at the sporophyte stage equals $-\bar{r}_A$.

Appendix B. Equations for two loci

Suppose that two diallelic nuclear loci are involved in the population fitness, with alleles A and a at the first locus and B and b at the second one. Let r be the recombination rate between the two loci. Let p_B and $q_b (q_b = 1 - p_B)$ be the frequencies of alleles B and b, respectively. Let $s_{B.P}$ and $s_{B.O}$ be the selection coefficients for allele B in pollen and ovules, respectively; and $s_{b.P}$ and $s_{b.O}$ for allele b in pollen and ovules, respectively. The fitness at the sporophyte stage is set as $1 + s_{BB}$ for genotype BB, $1 + s_{Bb}$ for Bb, and $1 + s_{bb}$ for bb. The model of additive viabilities is applied to calculating the fitness of any two-locus genotype.

Let p_{AB}, p_{Ab}, p_{aB}, and p_{ab} be the frequencies of gametes AB, Ab, aB, and ab, respectively. Let D $(= p_{AB}p_{ab} - p_{Ab}p_{aB})$ be the linkage disequilibrium between these two loci at the current adult stage. Similarly, let $\delta_B = s_{B.P} + s_{B.O} - s_{b.P} - s_{b.O}$ and $\Delta_B = p_B s_{BB} + (q_b - p_B)s_{Bb} - q_b s_{bb}$ be the selection components at the gametophyte and sporophyte stages at the B locus, respectively. According to the same approach as in the one-locus case, the dynamic equations for allele frequencies are given by

$$\dot{p}_A = \frac{\sigma^2}{2}p_A'' + \sigma^2(\ln n)'p_A' + p_A q_a(\delta_A/2 + \Delta_A) + (1-r)D(\delta_B/2 + \Delta_B), \tag{B.1}$$

$$\dot{p}_B = \frac{\sigma^2}{2}p_B'' + \sigma^2(\ln n)'p_B' + p_B q_b(\delta_B/2 + \Delta_B) + (1-r)D(\delta_A/2 + \Delta_A). \tag{B.2}$$

The fourth term on the right-hand side of Eq. (B.1) or Eq. (B.2) is the changes due to the presence of linkage disequilibrium between the two loci. When linkage disequilibrium equals zero ($D = 0$), these two loci evolve independently.

The changes in the four gamete frequencies with time are derived as

$$\dot{p}_{AB} = \frac{\sigma^2}{2}p_{AB}'' + \sigma^2(\ln n)'p_{AB}' + p_{AB}((q_a\delta_A + q_b\delta_B)/2 + q_a\Delta_A + q_b\Delta_B), \tag{B.3a}$$

$$\dot{p}_{Ab} = \frac{\sigma^2}{2}p_{Ab}'' + \sigma^2(\ln n)'p_{Ab}' + p_{Ab}((q_a\delta_A - p_B\delta_B)/2 + q_a\Delta_A - p_B\Delta_B), \tag{B.3b}$$

$$\dot{p}_{aB} = \frac{\sigma^2}{2}p_{aB}'' + \sigma^2(\ln n)'p_{aB}' + p_{aB}((-p_A\delta_A + q_b\delta_B)/2 - p_A\Delta_A + q_b\Delta_B), \tag{B.3c}$$

$$\dot{p}_{ab} = \frac{\sigma^2}{2}p_{ab}'' + \sigma^2(\ln n)'p_{ab}' + p_{ab}(-(p_A\delta_A + p_B\delta_B)/2 - p_A\Delta_A - p_B\Delta_B). \tag{B.3d}$$

From these expressions of gamete frequencies, the change in the linkage disequilibrium with time can be derived according to the relation $\dot{D} = \partial(p_{AB}p_{ab} - p_{Ab}p_{aB})/\partial t$, that is

$$\dot{D} = -rD + (1-r)\sigma^2 D''/2 + \sigma^2 p_A' p_B' + (1-r)\sigma^2(\ln n)'D' + (1-r)D[(q_a - p_A) \times (\delta_A/2 + \Delta_A) + (q_b - p_B)(\delta_B/2 + \Delta_B)]. \tag{B.4}$$

It can be seen from Eq. (B.4) that if D has the order in magnitude similar to the selection coefficients, the selection component in the above equation is negligible. The linkage disequilibrium is mainly generated by migration but reduced by recombination.

Using the same approach as in the one-locus case, the population dynamics can be obtained by replacing $\bar{r}_A$ in Eq. (A.1) with the per-capita growth rate under the two-locus case ($\bar{r}_{AB}$),

$$\bar{r}_{AB} = p_A^2 s_{AA} + 2p_A q_a s_{Aa} + q_a^2 s_{aa} + p_B^2 s_{BB} + 2p_B q_b s_{Bb} + q_b^2 s_{bb}. \tag{B.5}$$

The genetic loads at the gametophyte stage, denoted by L_P and L_O in pollen and ovules, respectively, are given by

$$L_P = s_{A.P}p_A^* + s_{a.P}q_a^* + s_{B.P}p_B^* + s_{b.P}q_b^*, \tag{B.6}$$

$$L_O = s_{A.O}p_A + s_{a.O}q_a + s_{B.O}p_B + s_{b.O}q_b, \tag{B.7}$$

where $p_\bullet^*$ and $q_\bullet^*$ are the gene frequencies after pollen flow. The allele frequencies in ovules are assumed equal to those in the preceding adults. Again, at steady state, $p_\bullet^* = p_\bullet$ and $q_\bullet^* = q_\bullet$. The genetic load at the sporophyte stage equals $-\bar{r}_{AB}$.

Appendix C. Equations for multiple loci

Suppose there are m diallelic loci that are involved in controlling the genetic variation of fitness. The fitness for any multilocus genotype is calculated according to the assumption of additive viabilities. For simplicity, let i_1 and i_2 be the capital and small alleles at the ith locus ($i = 1,\ldots, m$), respectively. Let p_i and q_i be the frequencies of alleles i_1 and i_2 at the ith locus ($p_i + q_i = 1$), respectively. Let r_{ij} and $D_{ij}(i \neq j)$ be the recombination rate and linkage disequilibrium between the ith and jth loci, respectively. Using the same approach as in Appendices A and B, we obtained the general expressions

$$\dot{p}_i = \frac{\sigma^2}{2} p_i'' + \sigma^2(\ln n)' p_i' + p_i q_i(\delta_i/2 + \Delta_i) + \sum_{j \neq i}^{m} (1 - r_{ij}) D_{ij}(\delta_j/2 + \Delta_j), \quad \text{(C.1)}$$

$$\dot{D}_{ij} = -r_{ij} D_{ij} + \frac{1 - r_{ij}}{2} \sigma^2 D_{ij}'' + \sigma^2 p_i' p_j' + (1 - r_{ij})\sigma^2(\ln n)' D_{ij}' + (1 - r_{ij}) D_{ij}((q_i - p_i) \times (\delta_i/2 + \Delta_i) + (q_j - p_j)(\delta_j/2 + \Delta_j)), \quad \text{(C.2)}$$

where $\delta_i = s_{i_1 \cdot P} + s_{i_1 \cdot O} - s_{i_2 \cdot P} - s_{i_2 \cdot O}$, the component related to the selection at the gametophyte stage at the ith locus, and $\Delta_i = p_i s_{i_1 i_1} + (q_i - p_i) s_{i_1 i_2} - q_i s_{i_2 i_2}$, the component related to the selection at the sporophyte stage at the ith locus. The number of linkage disequilibria equals $m(m-1)/2$ for a given m loci.

The equation for the dynamics of population density has the same form as in Eq. (A.1) except that $\bar{r}_A$ in Eq. (A.1) is replaced with the following per-capita growth rate in the multilocus case

$$\bar{r}_M = \sum_{i=1}^{m} (p_i^2 s_{i_1 i_i} + 2 p_i q_i s_{i_1 i_2} + q_i^2 s_{i_2 i_2}). \quad \text{(C.3)}$$

The genetic load at the gametophyte stage can be expressed as

$$L_P = \sum_{i=1}^{m} (s_{i_1 \cdot P} p_i^* + s_{i_2 \cdot P} q_i^*), \quad \text{(C.4)}$$

$$L_O = \sum_{i=1}^{m} (s_{i_1 \cdot O} p_i + s_{i_2 \cdot O} q_i), \quad \text{(C.5)}$$

where p_i^* and q_i^* are the gene frequencies after pollen flow, and the allele frequencies in ovules are assumed equal to those in the preceding adults. Again, at steady state, $p_i^* = p_i$ and $q_i^* = q_i$. The genetic load at the sporophyte stage equals $-\bar{r}_M$.

References

Austerlitz, F., Mariette, S., Machon, N., Gouyon, P.H., Godelle, B., 2000. Effects of colonization processes on genetic diversity: differences between annual plants and tree species. Genetics 154, 1309–1321.

Barton, N.H., 2001. Adaptation at the edge of a species' range. In: Silvertown, J., Antonovics, J. (Eds.), Integrating Ecology and Evolution in a Spatial Context. Blackwell Science, Oxford, pp. 365–392.

Barton, N.H., Whitlock, M.C., 1997. The evolution of metapopulations. In: Hanski, I.A., Gilpin, M.E. (Eds.), Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego, pp. 183–210.

Burt, A., 1995. The effect of fitness. Evolution 83, 47–52.

Case, T.J., Taper, M.L., 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. Am. Nat. 155, 583–605.

Case, T.J., Holt, R.D., McPeek, M.A., Keitt, T.H., 2005. The community context of species' borders: ecological and evolutionary perspectives. Oikos 108, 28–46.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection or Preservation of Favored Races in the Struggle for Life, first ed. J. Murrary, London.

Ennos, R.A., 1994. Estimating the relative rates of pollen and see migration among plant populations. Heredity 72, 250–259.

Ennos, R.A., Sinclair, W.T., Hu, X.S., Langdon, A., 1999. Using organelle markers to elucidate the history, ecology and evolution of plant populations. In: Hollingsworth, P.M., Bateman, R.M., Gornall, R.J. (Eds.), Molecular Systematics and Plant Evolution. Taylor & Francis, London, pp. 1–19.

Fisher, R.A., 1937. The wave of advance of advantageous genes. Ann. Eugenics 7, 355–369.

Haldane, J.B.S., 1956. The relation between density regulation and natural selection. Proc. Roy. Soc. London B, Biol. Sci. 145, 306–308.

Hoffman, A.A., Blows, M.W., 1994. Species borders: ecological and evolutionary perspectives. Trends Ecol. Evol. 9, 223–227.

Holt, R.D., Keitt, T.H., 2005. Species' borders: a unifying theme in ecology. Oikos 108, 3–6.

Hu, X.S., Ennos, R.A., 1999. Impacts of seed and pollen flow on population differentiation for plant genomes with three contrasting modes of inheritance. Genetics 152, 541–552.

Hu, X.S., Li, B., 2001. Assessment of the ratio of pollen to seed flow in a cline for genetic variation in a quantitative trait. Heredity 87, 400–409.

Hu, X.S., Li, B., 2002. Seed and pollen flow and cline discordance among genes with different modes of inheritance. Heredity 88, 212–217.

Hu, X.S., Li, B., 2003. On migration load of seeds and pollen grains in a local population. Heredity 90, 162–168.

Ingvarsson, P.K., 1997. The effect of delayed population growth on the genetic differentiation of local populations subject to frequent extinctions and recolonizations. Evolution 51, 29–35.

Kirkpatrick, M., Barton, N.H., 1997. Evolution of a species' range. Am. Nat. 150, 1–23.

MacArthur, R.H., 1962. Some generalized theorems of natural selection. Proc. Natl Acad. Sci. USA 48, 1893–1897.

Mayr, E., 1963. Animal Species and Evolution. Harvard University Press, Cambridge, MA.

McCauley, D.E., Richards, C.M., Emery, S.N., Smith, R.A., McGlothlin, J.W., 2001. The interaction of genetic and demographic process in plant metapopulations: a case study of Silene alba. In: Silvertown, J., Antonovics, J. (Eds.), Integrating Ecology and Evolution in a Spatial Context. Blackwell Science, Oxford, pp. 177–196.

Mulcahy, D.L., SariGorla, M., Mulcahy, G.B., 1996. Pollen selection-past, present and future. Sex. Plant Rep. 9, 353–356.

Nagylaki, T., 1975. Conditions for the existence of clines. Genetics 80, 595–615.

Pease, C.M., Lande, R., Bull, J.J., 1989. A model of population growth, dispersal and evolution in a changing environment. Ecology 70, 1657–1664.

Petit, R.J., Duminl, J., Fineschi, S., Hampe, A., Salvini, D., Vendramin, G.G., 2005. Comparative organization of chloroplast, mitochondrial and nuclear diversity in plant populations. Mol. Ecol. 14, 689–701.

Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P., 1992. Numerical Recipes in C. The Art of Scientific Computing, second ed. Cambridge University Press, Cambridge.

Roughgarden, J., 1979. Theory of Population Genetics and Evolutionary Ecology: An Introduction. Macmillan Publishing Co., Inc., New York.

Shigesada, N., Kawasaki, K., 1997. Biological Invasions: Theory and Practice. Oxford University Press, Oxford.

Skellam, J.G., 1951. Random dispersal in theoretical populations. Biometrika 38, 196–218.

Slatkin, M., 1973. Gene flow and selection in a cline. Genetics 75, 733–756.

Slatkin, M., 1976. The rate of spread of an advantageous allele in a subdivided population. In: Karlin, S., Nevo, E. (Eds.), Population Genetics and Ecology. Academic Press, New York, pp. 767–780.

Wright, S., 1969. Evolution and the Genetics of Populations. The Theory of Gene Frequencies, vol. 2. University Chicago Press, Chicago.

Wright, S., 1977. Evolution and the Genetics of Populations. Experimental Results and Evolutionary Deductions, vol. 3. University Chicago Press, Chicago.