

ORIGINAL ARTICLE

The maintenance of hybrid zones across a disturbance gradient

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The parapatric distribution of genetically divergent lineages in hybrid zones can be maintained by ecological differences (dispersal-independent 'ecotonal' hybrid zones), by frequency- and density-dependent interference when they intermingle and mate (dispersal-dependent 'tension' hybrid zones), or by both processes acting together. One potentially important ecological factor that has received little theoretical attention is gradients in habitat disturbance. Such gradients may be particularly important in contact zones in which the interacting lineages differ in their sexual system (e.g., self-fertile versus obligately outcrossing) because self-fertility promotes the colonization of open patches. Here we use a spatially explicit metapopulation model to examine the dynamics of a dispersal-dependent ecotonal hybrid zone across a gradient in the rate of habitat disturbance, where competing lineages differ in their sexual system. We found

that self-fertility promoted the maintenance of one lineage over its outcrossing counterpart at high extinction rates, predominantly because self-fertility confers reproductive assurance. Additionally, greater seed and pollen production promoted a lineage's persistence by reducing the seed fertility of its counterpart through hybridization. Our results draw attention to the joint effects of ecological and endogenous selection in regulating the location of hybrid zones. Our study also casts new light on the maintenance of the parapatric distribution of incompatible lineages of Spanish populations of the plant *Mercurialis annua*. In particular, we expect the rate of movement of a contact zone in eastern Spain to increase as it moves further south, contrary to earlier predictions.

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Introduction

Hybrid zones are maintained by environmental factors that cause differences in the fitness of parental genotypes across an environmental gradient (i.e., an ecotone moderated by ecological selection) and environmentally neutral dispersal-selection balance (i.e., tension zones; Barton, 1979; Barton and Hewitt, 1985). Ecotonal and tension hybrid zones are also referred to as dispersal-independent and dispersal-dependent, respectively (Barton and Hewitt, 1985). Under ecological selection, lineages are maintained in a hybrid zone because of differences in fitness between lineages across ecological gradients, with selection against the parental genotypes in non-native habitats (e.g., Fritsche and Kaltz, 2000). In contrast, in a tension zone, selection against hybrids causes the area of contact to stabilize in regions of minimal dispersal between lineages (Barton and Hewitt, 1985). The presence of ecological divergence and tension zone dynamics are not mutually exclusive, and both can affect the long-term stability of hybrid zones (e.g., Kruuk *et al.*, 1999).

Differences in ploidy between lineages are an important source of reduced hybrid fitness, especially in

plants. Selection against hybrids with mixed ploidy parentage leads to positive frequency-dependent selection in outcrossing species (Levin, 1975). This is because the proportion of mating events for each cytotype that yield unfit hybrids will more frequently involve the least common cytotype, reducing its fitness relative to the more common one, and leading to tension zone dynamics. Ultimately, this process should lead to the local extinction of the least common cytotype, a process referred to as minority cytotype exclusion (MCE; Levin, 1975; Husband, 2000). Typically, the process of MCE is considered from the perspective of the origin of novel polyploid lineages, which, upon their formation, necessarily occur at low frequencies within populations (e.g., Fowler and Levin, 1984; Husband, 2000). However, an analogous process will occur across zones of secondary contact between lineages with different ploidy levels when dispersal leads to populations of mixed ploidy levels.

Positive frequency-dependent selection and MCE result in the formation of a tension zone, along which the location of the area of contact between divergent lineages is stabilized. However, movement of the tension zone is expected to occur when there are biases in dispersal, caused, for example, by differences in fertility between lineages (Barton and Hewitt, 1985). Documentation of movement is difficult, but several cases are known (e.g., Kohlmann and Shaw, 1991; Paige *et al.*, 1991; Martin and Cruzan, 1999; Rohwer *et al.*, 2001; Blum, 2002; Dasmahapatra *et al.*, 2002). A particularly good example

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of a rapidly moving zone is the secondary contact between diploid and polyploid (hexaploid) populations of *Mercurialis annua*, a wind-pollinated annual found in ruderal habitats throughout Europe and North Africa (Durand and Durand, 1992; Pannell *et al.*, 2004). These lineages meet in two areas of secondary contact in northern Spain (Durand, 1963). Hexaploids have apparently migrated northwards from refugial areas in north-western Africa, whereas diploids have migrated westwards from refugial areas in the eastern Mediterranean (Obbard *et al.*, 2006). Importantly, these two lineages have contrasting sexual systems: diploid populations are dioecious and strictly outcrossing, whereas most populations of hexaploids are comprised of functionally hermaphroditic (monoecious) and self-fertile individuals. However, in some regions, hexaploid populations are commonly androdioecious (populations comprised of functional hermaphrodites and males) with male frequencies ranging between zero and approximately 40% (Durand, 1963; Pannell, 1997a).

Comparisons of detailed cytological studies of diploid and hexaploid *M. annua* populations in northern Spain have revealed that the contact zones are moving rapidly, with diploids displacing polyploids (Durand, 1963; Buggs and Pannell, 2006). Reciprocal transplant studies and results from experimental mixtures of diploids and hexaploids indicate that this movement results from biased gene flow between lineages (Buggs and Pannell, 2006, 2007). Specifically, the much greater pollen production by males appears to swamp hexaploid ovules, reducing their seed fertility in mixed populations. Currently, the southward movement of contact zones involves interactions between monoecious and dioecious populations. However, in areas south of the contact zones, hexaploid populations are androdioecious. Because hexaploid males also produce large quantities of pollen, it is possible that the occurrence of androdioecy will impede the southward movement of diploid populations (Buggs and Pannell, 2006).

The effects of biased dispersal on the movement of a contact zone can be expected to be offset by the existence of an ecological gradient that promotes the maintenance of lineages within local regions. Indeed, ecological or environmental gradients appear to be involved in the regulation of several animal and plant hybrid zones through their effect on the availability of suitable habitat for one or both of the hybridizing lineages (e.g., Kohlmann and Shaw, 1991; Paige *et al.*, 1991; Cruzan and Arnold, 1993; Petit *et al.*, 1997; MacCallum *et al.*, 1998; Fritsche and Kaltz, 2000; Cruzan, 2005). In *M. annua*, geographical patterns of abundance for monoecious and dioecious populations are thought to be regulated by contrasting population dynamics. Specifically, monoecious populations are smaller and occur in regions with lower rates of site occupancy than their dioecious counterparts (Eppley and Pannell, 2007). This observation is consistent with (a) the idea that reproductive assurance in self-fertile lineages promotes colonization because only one individual is required to establish a new population (Baker, 1955; Pannell and Barrett, 1998) and (b) the expectation that regional variation in the importance of metapopulation dynamics regulates the maintenance of unisexual individuals, with females, and especially males, occurring in areas where the rate of population turnover is not too high (Pannell, 1997b). We

therefore expect that an ecological gradient, namely in the rate of local extinctions, will also regulate the *M. annua* contact zone.

The previous studies of *M. annua* indicate that the stability of the contact zones will be influenced by a combination of metapopulation dynamics (Pannell, 1997b; Eppley and Pannell, 2007) and biased gene flow between lineages (Buggs and Pannell, 2006). On the one hand, population turnover in a metapopulation will act to promote the maintenance of functionally hermaphroditic hexaploids because they have a colonization advantage over dioecious diploids. On the other hand, the greater pollen fertility of diploids may allow them to overcome MCE upon migration into hexaploid populations, promoting the geographic displacement of hexaploids. In short, we expect the stability of contact zones between diploid and polyploid *M. annua* to respond to the balance between population turnover and biased gene flow between lineages.

In this paper, we explored the balance between the effects of intrinsic viability selection and ecological differentiation on the stability of diploid–polyploid hybrid zones in areas of secondary contact. Specifically, we used spatially explicit, stochastic simulations to examine relations between reproductive assurance, asymmetric mating, and extinction and dispersal rates on the stability of hybrid zones. We addressed the following questions: (1) How does the balance between reproductive assurance and asymmetric dispersal affect the maintenance of a contact zone across which divergent lineages possess contrasting sexual systems? (2) How does the overall rate of dispersal via seed versus pollen affect this balance and the stability of the contact zone? (3) Are androdioecious populations more resilient to displacement by dioecious populations than populations of functional hermaphrodites? Our formulation is related to other recent models of the evolution of plant mating systems (Pannell, 1997b; Heilbutth *et al.*, 2001; Wilson and Harder, 2003), which consider the outcome of competition between reproductive strategies in different environments. However, unlike these studies, which focus on the dynamics of individual populations, we were interested in the maintenance of reproductive strategies across contact zones, such as might be found in areas of secondary contact.

Model description

Overview

Our simulations used a metapopulation framework in which all sites had non-zero probabilities of extinction and recolonization. Each ‘generation’ in the model comprised: (1) mating within each extant site, which included gene flow among sites through pollen dispersal; (2) seed dispersal among sites, followed by population size regulation; and (3) the probabilistic local extinction of each site. First we describe the morph-dependent sex allocation assumed in the model, and later outline in detail the major components listed above.

Sex allocation

We assumed that all individuals made the same investment in reproduction, and that morph *i* of lineage *j* invested fractions a_{ij} and $1-a_{ij}$ towards male and female

Table 1 List of parameters used in the model

Parameter	Description
λ	The number of seeds produced by pure females
π	The amount of immigrant pollen entering a local site
γ	A constant regulating the strength of the density-dependence of selfing
δ	A constant governing the magnitude of inbreeding depression
a	The proportion of reproductive resources allocated to male function
b	A constant regulating the occurrence of pollen limitation
c	A constant governing the shape of fitness gains as a function of reproductive effort
F	A constant regulating the probability that an ovule was fertilized
H	The fraction of fertilized ovules that were fertilized by the alternate lineage resulting in a hybrid zygote
I_P	The fraction of pollen produced locally that emigrated
I_S	The fraction of seeds produced locally that emigrated
K	The carrying capacity of each site
N, N'	The number of individuals per local site before mating and following mating, dispersal, viability selection and population regulation, respectively
o	The number of seeds produced per unit of investment
p	The amount of pollen produced per unit of investment
P	The total amount of pollen in a local site during mating
s	The fraction of fertilized ovules that were self-fertilized
t	The fraction of fertilized ovules that were outcrossed

functions, respectively (see Table 1 for a complete list of all parameters used in the model). Because the translation of reproductive effort into the effective dispersal of pollen and seeds is not in general linear and may reflect diminishing or accelerating returns, we followed previous studies (reviewed in Charlesworth, 1999) by assuming that the effective amount of pollen dispersed, p_{ij} , and the effective number of seeds dispersed, o_{ij} , of morph i and lineage j was a_{ij}^c and $(1 - a_{ij})^c$, respectively, where c is a constant governing the shape of the gain curve. Models of sex allocation show that dioecy is stable to the invasion of outcrossing hermaphrodites for values of $c > 1$ (i.e., for accelerating gain curves; Charnov, 1982), although this threshold is modified under partial selfing (Charlesworth and Charlesworth, 1981). Pure males (regardless of their lineage) produced one unit of pollen, and pure females produced λ ovules. In general, then, individuals of morph i and lineage j dispersed $p_{ij} = a_{ij}^c$ units of pollen and $o_{ij} = \lambda(1 - a_{ij})^c$ seeds. The intrinsic rate of population increase was regulated through λ .

Note that sex allocation equilibrium in a randomly mating hermaphroditic population, a , is expected to equal 0.5, but that selection under local mate competition (e.g., due to inbreeding following colonization; Hamilton, 1967; Frank, 1986) is expected to bias allocation towards increased femaleness (i.e., $a < 0.5$). The value 0.5 can thus be seen as an upper threshold for a . In our simulations, we either assumed this maximum value of a , or a lower value corresponding to expectations for a metapopulation under frequent extinction/recolonization.

Mating, pollen and seed dispersal

Let N_{ijk} be the number of individuals of morph i of lineage j at site k in the metapopulation before mating, and let N'_{ijk} be the number of individuals following mating, dispersal, viability selection and density-dependent population regulation. The N'_{ijk} were determined by the numbers of ovules produced by each individual, and by the mating fate of those ovules. Ovules could have one of four different fates: unfertilized, selfed, outcrossed

or hybridized. First, an ovule might be unfertilized in pollen-limited populations, either because of insufficient pollen produced locally, or because of insufficient immigrant pollen from other populations. We assumed that the probability of fertilization for a given ovule at site k , F_k , increased linearly from zero with the total amount of pollen at the site during mating, P_{Tk} , such that $F_k = bP_{Tk}$ for $bP_{Tk} \leq 1$ and $F_k = 1$ otherwise; for self-fertile polyploid hermaphrodites, we assumed that $F = 1$. Both pollen produced locally and that dispersed from other extant populations into the site contributed to P_{Tk} , that is

$$P_{Tk} = \sum_{i,j} N_{ijk} p_{ij} + \sum_{i,j} \pi_{ijk} \quad (1)$$

where π_{ijk} is the amount of immigrant pollen of morph i of lineage j into site k and is given by

$$\pi_{ijk} = I_P \sum_{q \in J} N_{ijq} p_{ij} \quad (2)$$

Here, J is the set of sites adjacent to site k that contribute pollen to it, and I_P is the fraction of pollen produced locally that successfully emigrated. We assumed that this fraction was small and had a negligible effect on the amount of pollen remaining in the population.

Of the fertilized ovules produced by morph i of lineage j at site k , fractions s_{ijk} , t_{ijk} and H_{ijk} were self-fertilized, fertilized by pollen produced by the same lineage (i.e., outcrossed) and fertilized by pollen of the alternate lineage (i.e., hybridized). These fractions are given respectively as:

$$s_{ijk} = \frac{\gamma p_{ij}}{\gamma p_{ij} + P_{Tk} - p_{ij}}, \quad (3)$$

$$t_{ijk} = \frac{\sum_i N_{ijk} p_{ij} - p_{ij}}{\gamma p_{ij} + P_{Tk} - p_{ij}}, \quad (4)$$

$$H_{ijk} = \frac{\sum_r \sum_{q \neq j} N_{rqk} p_{rq}}{\gamma p_{ij} + P_{Tk} - p_{ij}}. \quad (5)$$

Note that the sum of terms in denominators represent the total amount of pollen expected around a given stigma of plants of morph i and lineage j ; that γ (≥ 0) is a constant governing the strength of density-dependent selfing; that, for a given i and j , $s_{ij} + x_{ij} + H_{ij} = 1$; and that therefore $(s_{ij} + x_{ij} + H_{ij})F_j + (1 - F_j) = 1$. The term p_{ij} is subtracted from the denominators and the numerator in (4) to account for pollen produced by the target plant that, accordingly, contributes self-pollen but not outcross pollen to the pollen cloud around its stigmas.

We assumed that the number of seeds that immigrated into a given site was a Poisson variable with its parameter determined by the product of the size of neighbouring sites from which immigrants were drawn and a dispersal parameter I_S . In particular, the expected number of immigrants of morph i of lineage j that immigrated into site k was given by

$$\sigma_{ijk} = I_S \sum_{q \in J} N'_{ijq} \quad (6)$$

where J is the set of sites adjacent to site k , as for pollen dispersal described above. Thus, each specific morph immigrated into site k in direct proportion to its abundance in adjacent sites, with Poisson variance.

Population regulation and extinction

We assumed that a fraction δ of selfed seeds died before establishment and that all hybridized seeds were fully viable but sterile; that is, hybridized but not the fraction δ of selfed seeds contributed to the next generation of adults and thus shared in filling the population to its carrying capacity, K . We assumed that density-dependent regulation of population size operated on seedling establishment, that is populations could produce a maximum of K adult individuals. Thus, if $\sum_{i,j} N'_{ijk} > K$ at site k , then each of the N'_{ijk} were multiplied by $K / \sum_{i,j} N'_{ijk}$. Each generation, sites had a non-zero probability of experiencing a local extinction. This probability increased linearly across the rows of the lattice of the metapopulation (see below and Figure 1), with adjacent rows differing in their site extinction rate by a uniform probability (see Results for details). Extinct sites could be recolonized only through the dispersal of seeds from adjacent sites during subsequent generations.

Choice of parameter values

Simulations were run to generate qualitative inferences regarding the roles of specific parameters likely to be important in plant hybrid zones, such as differences between lineages in their dispersal rates via seed and

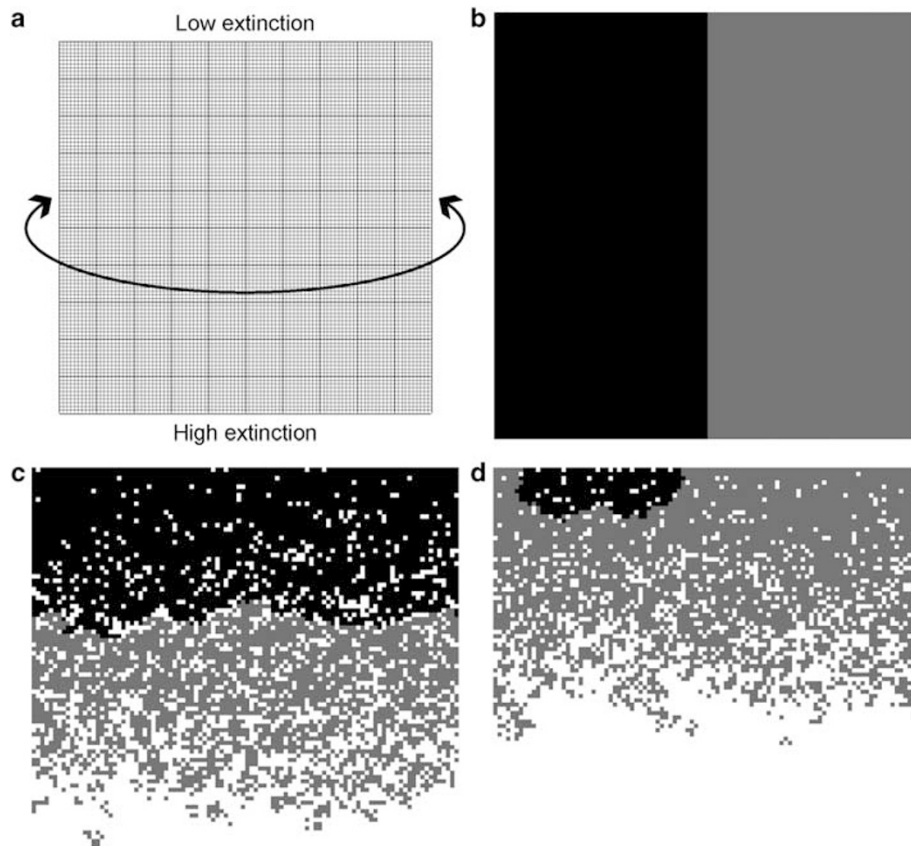


Figure 1 Two-dimensional diagrams of the 100×100 lattice used in the simulations of metapopulation dynamics. Vertical edges of the lattice had wrapping boundaries, horizontal edges had absorbing boundaries and the gradient in per site extinction rates increased from the top to the bottom of the lattice, from 0.01 to 0.26 and with a uniform increment per row of 0.0025 (a). Simulations began with the boundary between dioecious (black patches) and hermaphrodite populations (grey patches), parallel to the gradient in extinction rates (b). We considered the run to have reached equilibrium if the frequency of both lineages was constant and the boundary between them was horizontal, that is, perpendicular to the extinction gradient (c). For some values of seed and pollen immigration rates, and hermaphrodite sex allocation, the difference in fitness between lineages was negligible and the runs did not reach equilibrium (d).

pollen. To this end, we used two strategies for the choice of parameter values. First, for key parameters (e.g., relative sex allocation and seed dispersal rates), we present results for a broad range of values. Second, for other parameters (e.g., density dependence of selfing, inbreeding depression and pollen dispersal rates), we compare the effects of widely differing values. Our results do not represent an exhaustive range of parameter space, but they serve to illustrate several key features of the interactions observed during the runs performed.

Lattice shape, initialization and equilibration

The metapopulation was initialized as a 100×100 lattice of local patches of individuals with an annual life cycle (Figure 1a). The disturbance gradient was parallel to the initial boundary between lineages (Figure 1b). Edges of the lattice perpendicular to the disturbance gradient had wrapping boundaries, whereas edges at the ends of the disturbance gradient had absorbing boundaries (i.e., the lattice was tube-shaped, with populations along the 'seam' of the tube having the same per generation probability of extinction, Figure 1a). Typically, the set of sites contributing pollen and seed immigrants to any site in the metapopulation was eight. However at the top and bottom of the lattice, only five adjacent sites contributed seed or pollen immigrants.

We initialized the lattice with equal numbers of sites occupied by the two lineages, each of which was placed on opposing halves of the lattice, with the boundary between them running parallel to the disturbance gradient (Figure 1b). Through the course of the simulation, the boundary re-adjusted itself to run perpendicular to the disturbance gradient, as we would expect (see below). By initializing the lattice with the boundary and the disturbance gradient parallel to one another, we assured that the position of the final boundary would be little affected by initialization conditions. We evaluated this for a subset of the runs conducted by randomizing the location of dioecious and hermaphroditic lineages within the lattice, with each site having an equal probability of being initialized with one of the lineages. As might be expected, this alternate initialization procedure had a greater effect on the location of the boundary between lineages when equilibrium conditions were approached slowly. In these cases, the boundary between lineages differed between procedures by up to 18 rows of the lattice. However, when equilibrium conditions were reached quickly, the two initialization procedures yielded similar boundaries between lineages, differing by less than five rows in the lattice. This means that some of the individual points presented in the section Results should be treated with caution (and see below). However, our conclusions were drawn from qualitative differences between runs, and are therefore robust to variation in the location of the boundary within runs.

Within each half of the lattice at initialization, the frequencies of the morphs of the respective lineage for that simulation were set to their panmictic expectations. Thus, in the dioecious half, all populations began with equal frequencies of males and females, whereas in the monoecious half, all populations were filled with only hermaphrodites. For simulations involving

androdioecious populations, males and hermaphrodites were initialized to frequencies corresponding to their local equilibrium expectation at all sites (see section Results for further details).

During the simulation, we kept track of the number of each morph and of each lineage in all sites, and of the number and morph of seed and pollen immigrants that entered each site per generation. We ran the model until one of the lineages had been excluded from the lattice, or until the metapopulation was determined to have reached equilibrium if both of the following conditions were met. First, we evaluated the change in occupied sites by each lineage over 100 generations following the method described in Hiebeler (2004). This approach involves the calculation of a running linear regression of the proportion of occupied sites over time. If the slope of the regression was less than 10^{-4} , we considered site occupancy to be stable. Second, we evaluated changes in the shape of the boundary between types by evaluating the distance to the interface between lineages from $x=0$. The obtained values of x for each y were used to calculate a slope. If the value of the slope of the regression was less than 10^{-4} for more than 100 generations, we considered the run to have reached equilibrium (i.e., equilibrium occurred when the interface was perpendicular to the disturbance gradient, having rotated 90° from initial conditions, Figure 1c). Under certain parameter combinations, equilibrium conditions were approached slowly. To limit processing time, we ended runs after 50 000 generations if equilibrium conditions had not already been reached. Runs that failed to reach equilibrium (e.g., Figure 1d) are indicated in the section Results.

Results

At equilibrium, the frequency of the two lineages was determined by the balance between (i) reproductive assurance, which promoted the spread of the hermaphroditic lineage and (ii) biased dispersal between lineages, which promoted the spread of the dioecious lineage. The contributions of reproductive assurance and biased gene flow to the maintenance of both lineages in the metapopulation varied across the disturbance gradient, stabilizing the contact zone between lineages across a narrow range of disturbance rates (Figure 1c). Thus, the average disturbance rate at the interface between the two lineages was influenced by the variables in our model that affected reproductive assurance (such as the selfing rate) and biases in gene flow (such as the rate of pollen dispersal).

Seed and pollen dispersal

Increasing the rate of dispersal between populations increased the likelihood that dioecy was maintained in the metapopulation (Figure 2a). The magnitude of gene flow between populations was governed by the gamete production of the two lineages, and the seed and pollen immigration rates. We assumed that males or females experienced an advantage in gamete production over functional hermaphrodites by setting $c > 1$, that is, by letting the gain curve accelerate. Indeed, with $c \leq 1$, dioecy was always excluded from the lattice (results not shown). Increasing the seed immigration rate, I_s , increased the likelihood that dioecious populations were maintained in the metapopulation (Figure 2a) by redu-

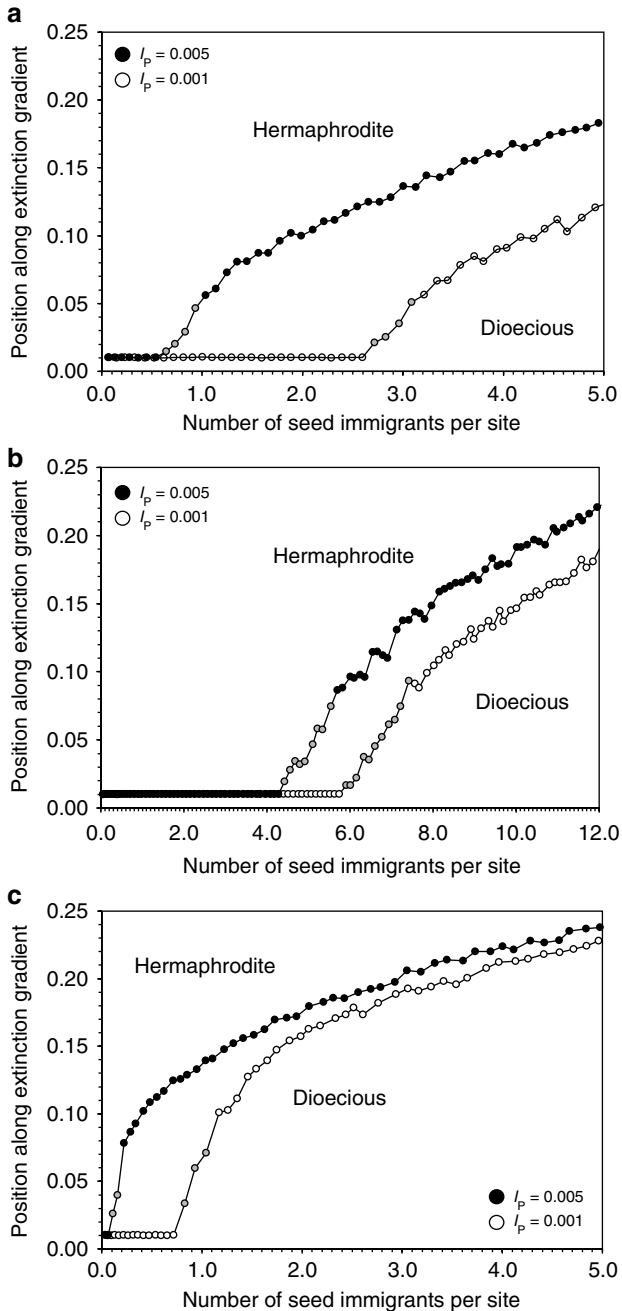


Figure 2 Relationship between the average number of seed immigrants per site and the extinction rate at the interface between dioecious and hermaphrodite lineages. The values shown on the y -axes are the average values of the extinction rate at the boundary between lineages (as depicted in Figure 1c), and thus hermaphrodite populations occurred above the curves, and dioecious populations occurred below the curves, as indicated. The average extinction rate beyond which dioecious populations were replaced by hermaphroditic populations in the metapopulation increased with increasing values of seed and pollen dispersal. In (a), we assumed no selfing ($\gamma=0$) or inbreeding depression. In (b) selfing occurred ($\gamma=10$), but inbreeding depression was assumed to be negligible. In (c), we assumed that both selfing ($\gamma=10$) and inbreeding depression ($\delta=0.5$) affected the fitness of hermaphrodites. Grey symbols indicate runs that did not reach equilibrium (as depicted in Figure 1d). Note the different scale for x -axis in Figure 2b. For the results in each panel, we set $a=0.5$ and $c=1.2$, corresponding to relative seed fertility of females: hermaphrodites of 2.3:1.0, respectively.

cing the colonization advantage of the self-fertile lineage. The greater pollen production by males in comparison with hermaphrodites led to biased pollen dispersal between populations, favouring the maintenance of the dioecious lineage in the metapopulation under increased levels of pollen dispersal (compare the two lines in Figure 2a–c).

Selfing and inbreeding depression

Competitive selfing by hermaphrodites inhibited the spread of dioecious populations by protecting hermaphrodite ovules from mating with diploid males (Figure 2b). Selfing was density-dependent, and under a selfing parameter of $\gamma=10$, selfing rates were $s=0.75$ in sites with two plants, for example, and $s=0.09$ for sites at the carrying capacity. Inbreeding depression ($\delta=0.5$) more than offset the advantage of selfing (Figure 2c), and promoted the maintenance of dioecious populations.

Subpopulation dynamics

The persistence of either hermaphroditic or dioecious populations under a given colony extinction rate depended on the process of colonization and the subsequent loss of one lineage through MCE. These dynamics can be understood by considering events in newly colonized populations at the boundary between the two lineages (Figure 3). For low immigration rates, that is, those resulting in two or fewer seed immigrants per generation, reproductive assurance of hermaphrodites resulted in the exclusion of the dioecious lineage. The colonization advantage to hermaphrodites was reduced by increasing the number of immigrants (Figure 3b) and rates of pollen dispersal (Figure 3c). As explained above, selfing promoted the maintenance of hermaphroditism (Figure 3d), but this was offset by inbreeding depression (Figure 3e) or pollen dispersal (Figure 3f).

Sex allocation

Varying the proportion of reproductive resources invested by hermaphrodites in their male function, a_h , substantially altered the ability of the dioecious lineage to be maintained in the metapopulation (Figure 4). This effect was complex, with a bimodal distribution of the persistence of dioecious populations across the range of a_h values explored. Under low values of a (corresponding to low pollen and high seed allocation of hermaphrodites), dioecious populations were maintained in regions of low population turnover. For intermediate levels of a_h , dioecious populations were excluded from the metapopulation. Finally, for levels of a_h corresponding to roughly equal allocation to pollen and seed, dioecious populations were maintained across a range of population turnover rates. Again, increasing the amount of pollen dispersal among the patches of the metapopulation had a positive effect on the maintenance of dioecious populations.

Androdioecy versus monoecy

Androdioecy promoted the spread of dioecious populations. As in Figure 2, low rates of seed and pollen dispersal led to the exclusion of the dioecious lineage from the metapopulation (Figure 5a and b). However, under rates of seed and pollen immigration that caused

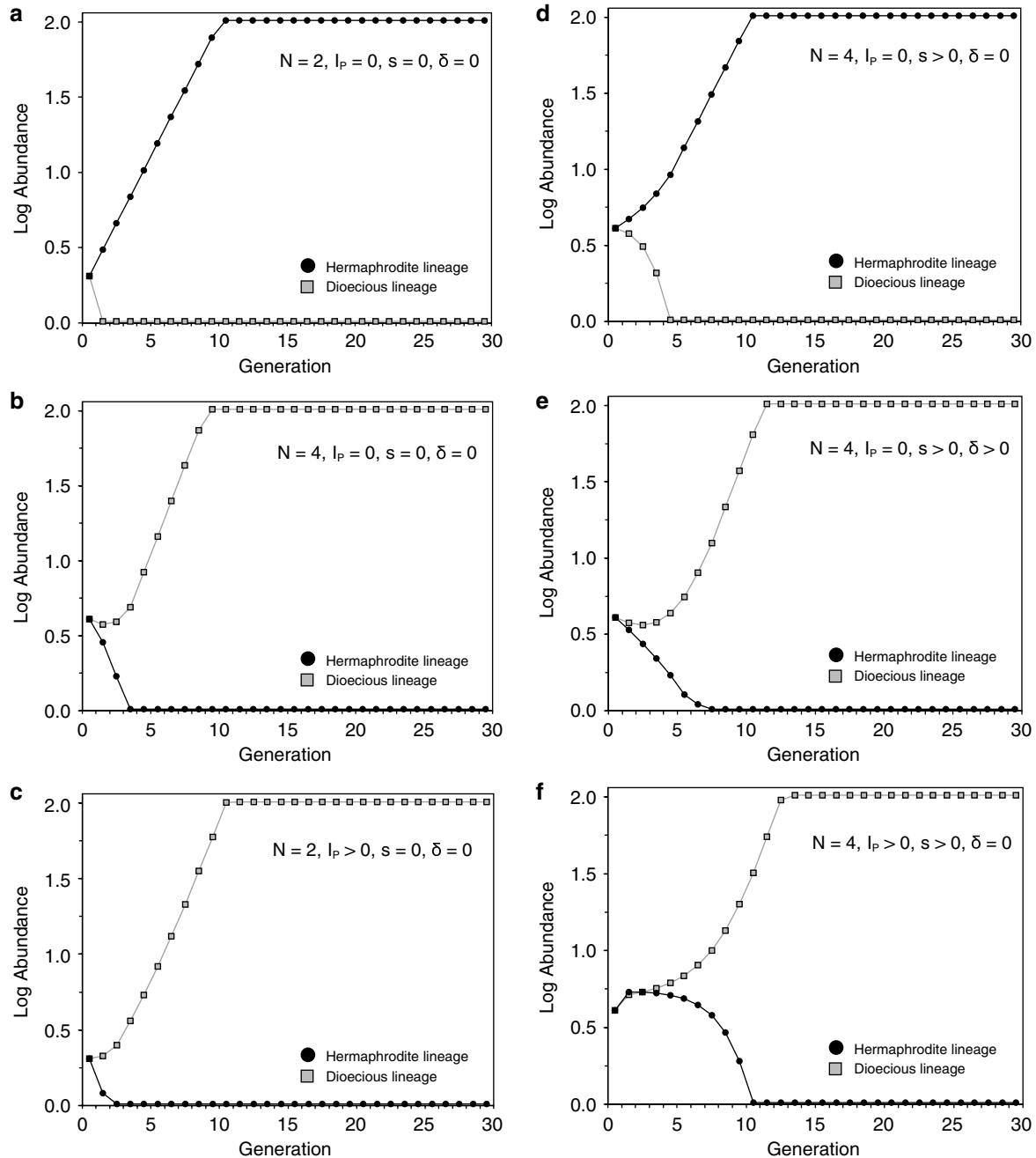


Figure 3 Examples of the dynamics of individual sites within the metapopulation following colonization by the dioecious lineage (grey squares) and the hermaphrodite lineage (black circles). The comparison between panels (a), (b) and (c) demonstrate the roles of immigration (via either seed or pollen) and reproductive assurance in the contact zone between lineages. In (a), there were two colonists of each lineage, and in the example depicted, diploids were rapidly lost from the population because they had no compatible mates. However, in (b), there were four colonists of each lineage and thus, in the majority of cases, diploids had at least one compatible mate. In this example, hybridization initially reduced the frequency of each lineage in the next generation; however, the greater pollen fertility of diploid males had a larger effect on hermaphrodites than the reverse, and as the frequency of hermaphrodites decreased, unisexuals increased in frequency. In (c), pollen flow from neighbouring sites promoted the persistence of unisexuals. Comparison between panels (d, e and f) demonstrates the role of selfing in promoting the spread of polyploids and how selfing can be counterbalanced by inbreeding depression or pollen flow. In (d), selfing by hermaphrodites protected their ovules from fertilization by males. However, inbreeding depression (e) or pollen flow (f) cancelled the effect of selfing, promoting the spread of the dioecious lineage.

the exclusion of dioecy under competition with the hermaphroditic lineage, the presence of an androdioecious lineage promoted the maintenance of dioecious populations (Figure 5c versus d). Moreover, even under conditions that allowed dioecious populations to be

maintained in the metapopulation, the occurrence of androdioecious populations yielded increased frequencies of dioecious populations over a greater range of the per site extinction rate compared to runs with exclusively hermaphroditic populations (Figure 5e versus f).

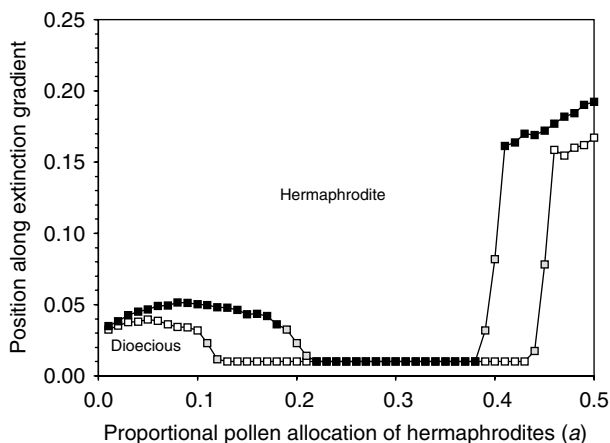


Figure 4 The effect of varying a , the sex allocation parameter defining the allocation to male sex function, on the persistence of the dioecious lineage in the metapopulation. The y -axis is the same as in Figure 2, with dioecious populations occurring below the curves, and hermaphrodite populations above the line, as indicated. Again, as in Figure 2, the two curves represent different values of the pollen immigration parameter, I_P (open squares, $I_P=0.001$, closed squares, $I_P=0.005$).

Discussion

The location and stability of hybrid zones is often considered to be the result of either endogenous selection against hybrid genotypes, exogenous selection of genotypes along an ecological gradient, or a combination of both processes acting in concert (Barton and Hewitt, 1985; Arnold, 1997). Our study has drawn attention to the joint effects of endogenous and ecological selection in regulating the location of a contact zone between lineages with contrasting reproductive systems. However, in contrast to previous investigations that have considered ecological selection in terms of ecophysiological adaptations across an environmental gradient, we have modelled selection across a gradient in the disturbance regime, that is, in the probability of local population extinction. We found that this gradient could promote the stable coexistence of two lineages with different sexual systems at opposite ends of a disturbance gradient. Although our results are complex in their detail, they can be understood broadly in terms of the relative advantages and disadvantages of contrasting sex-allocation strategies. These can be grouped loosely under three broad concepts: (1) effects of contrasting reproductive assurance; (2) effects of contrasting seed dispersal; and (3) effects of contrasting pollen dispersal. Below, we discuss these three aspects of our results in turn. We then discuss the assumptions of our model concerning the relative advantages of combined versus separate sexes in terms of female and male fitness gain curves and inbreeding depression. Finally, we consider the extent to which our results may contribute to an understanding of the moving *M. annua* contact zone, upon which several important details of our model were based.

Reproductive assurance

Reproductive assurance provided a colonization advantage to hermaphrodites that led to the exclusion of

unisexuals under low dispersal rates and low population densities. This occurred because low dispersal and population densities reduced the probability that females would acquire compatible mates in newly colonized populations. These findings are consistent with those of previous studies of the dynamics of reproductive assurance in a metapopulation (Pannell, 1997b; Pannell and Barrett, 1998). In particular, Pannell (1997b) showed that the probability that obligate outcrossers (e.g., unisexuals) are maintained in a metapopulation is a positive function of their fertility and the immigration rate. Moreover, Pannell and Barrett (1998) showed that the advantage of reproductive assurance increased with the extinction rate and decreased with the density of occupied sites. However, neither Pannell (1997b) nor Pannell and Barrett (1998) evaluated conditions that promoted the stable maintenance of self-fertile and obligately outcrossing lineages. The present study has shown that this can occur via an ecological gradient that favours contrasting lineages at its extremes.

Our study has focussed on the dynamics of lineages with different sexual systems, such as one might find between different ploidy levels. The evolution of uniparental reproduction often accompanies polyploidization, e.g., through the evolution of apomixis (e.g., Bayer and Stebbins, 1987) or the loss of self-incompatibility (e.g., Miller and Venable, 2000). Accordingly, differences in reproductive assurance (or uniparental reproduction more generally) between lineages with contrasting ploidy may be expected to occur across areas of secondary contact for a number of plant groups. In general, differences in the reproductive traits of contrasting cytotypes occurring in hybrid zones have been viewed from the perspective of the advantages of isolating mechanisms to prevent the negative effects of MCE, with a focus on individual populations (e.g., McCarthy and Quinn, 1990; Petit *et al.*, 1997; Segraves and Thompson, 1999; Husband and Sabara, 2003). To date, there has been little empirical work examining the dynamics of contact zones between lineages with both contrasting ploidy and reproductive systems, even though there is some evidence that variation in the ability to reproduce uniparentally is a factor regulating the distribution of diploid and polyploid contact zones. For example, in *Antennaria parvifolia*, the polyploid, apomictic lineage occurs in the glaciated regions of North America, whereas its diploid, sexual (and dioecious) ancestor is restricted to the southern parts of the species' range (Bayer and Stebbins, 1987). Similarly, there is a suggestion by Naiki and Nagamasu (2004) that polyploid populations in *Damnacanthus indicus* are more highly selfing than their diploid counterparts, and which also occur at higher latitudes, because polyploidy in this species is associated with the breakdown of distyly (a sexual polymorphism that promotes outcrossing; Barrett, 2002).

Seed dispersal

Colony establishment governed the dynamics of the contact zone in our simulations by allowing each lineage to colonize unoccupied areas of the metapopulation. Thus, local extinctions and seed dispersal were the key processes governing the maintenance of the contact zone through their effects on establishment dynamics. Indeed,

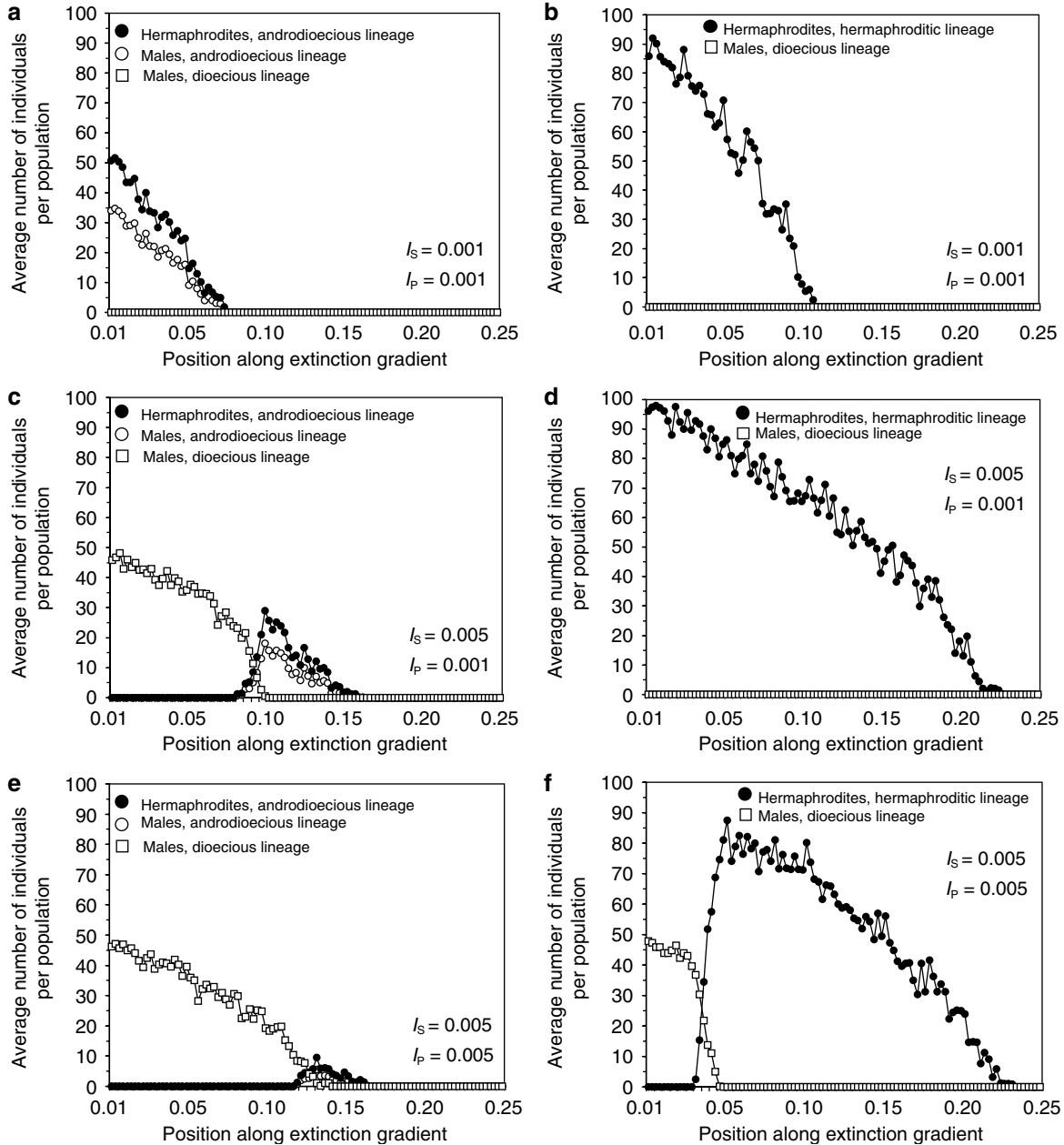


Figure 5 Comparison of the frequency of males from the dioecious lineage when these co-occurred with an androdioecious or hermaphroditic lineage across rows of the lattice (i.e., values of the per site extinction rate) for individual runs of the simulation at equilibrium (note that this is not the position of the interface between lineages as in previous figures). The left-hand series of panels (i.e., a, c and e) depict scenarios involving a dioecious–androdioecious contact zone. The right-hand series (b, d and f) depict a dioecious–hermaphrodite contact zone. Left and right pairs of panels (e.g., a and b) provide comparisons of the two types of contact zones for the same combinations of parameter values. Under low values of seed and pollen dispersal, dioecious populations were excluded from the metapopulation in the presence of androdioecious populations (a), or purely hermaphroditic populations (b). Under higher values of seed dispersal, dioecious populations were maintained in the metapopulation when competing with androdioecious populations (c), but not hermaphroditic populations (d). Further increases in pollen dispersal from adjacent sites also promoted the maintenance of dioecious populations, allowing them to persist in competition with either androdioecious (e) or monoecious populations (f). For the runs depicted in each panel, we set $a = 0.2$ and $c = 1.2$, corresponding to equilibrium male frequencies of 41%; these values are similar to those found in large, stable populations of *M. amua* (Dorken and Pannell, unpublished data).

without colony extinctions, the contact zone between lineages did not move from its initial conditions, even under substantial differences in fitness between them (data not shown). By increasing the amount of seed dispersal across the metapopulation, we altered the relative abilities of each lineage to compete for the

colonization of sites opened up by extinction events. Under low seed dispersal, the dioecious lineage was restricted to areas of low extinction rates, or excluded from the metapopulation altogether. However, under higher dispersal rates, males and females were more likely to disperse into populations together and, and

once a dioecious population was established, it could prevent the hermaphroditic lineage from establishing in the same site.

The maintenance of hybrid zones is determined not only by the net direction of dispersal, but also the strength of selection against individuals dispersing into a site (Slatkin, 1973; reviewed in Barton and Hewitt, 1985). Although we assumed very strong selection against hybrids, whether selection occurred at all was frequency- and density-dependent, increasing with higher frequencies of the opposing lineage within a site. In this way, the disturbance gradient used in our simulations affected the strength of selection against dispersers into a site by moderating the probability that a disperser would hybridize. At higher extinction rates, selection was reduced because of the greater likelihood that neighbouring sites were unoccupied. However, closer to the boundary between lineages, and thus at lower extinction rates, selection against dispersers increased because of the greater likelihood that they would potentially hybridize with the occupants of the site.

Differences in patterns of seed dispersal between dioecious and hermaphrodite lineages have been modelled in detail by Heilbut *et al.* (2001) and Wilson and Harder (2003). As in the present study, these authors showed that dioecious individuals required at least double the seed or pollen fitness of hermaphrodites to persist (i.e., equivalent to $c > 1$ in our formulation). However, there were two key differences between our study and these previous models. First, we ignored spatial dynamics occurring within populations, focussing instead on dispersal between the subpopulations of a metapopulation. Although spatial effects occurring within populations are no doubt important for the maintenance of dioecy, the persistence of dioecious lineages will ultimately depend on patterns of colonization and population establishment (i.e., events occurring at the metapopulation level). Selection on sex allocation does not necessarily act in the same direction at the population and metapopulation levels (e.g., Pannell, 1997b). Within established populations, selection will often favour traits promoting outcrossing, and thus unisexuality, especially if unisexuals have a fertility advantage over hermaphrodites. In contrast, at the metapopulation level, traits promoting colonization (e.g., self-fertility and reproductive assurance) are favoured. Dioecious lineages, therefore, are not only expected to compete against their hermaphrodite progenitors within populations, where they may have a selective advantage, but also at the landscape level for access to unoccupied sites, where they are expected to have a colonization disadvantage compared with hermaphrodites. To our knowledge, these dynamics have not previously been taken into account when modelling the ability of dioecious lineages to compete with hermaphrodites.

Second, we assumed that dioecious and hermaphrodite lineages interacted with each other during mating, forming sterile hybrids. Indeed, under the strong positive frequency-dependent selection resulting from selection against hybrids, the least common species was rapidly excluded from mixed populations. It seems unlikely that relatively weaker selection pressures, such as those resulting from variance in patterns of seed dispersal between hermaphrodite and unisexual species (Heilbut *et al.*, 2001; Wilson and Harder, 2003), would

have altered the outcome of this process. Instead, persistence was determined by colonization dynamics and its effect on the success of diploid versus polyploid lineages at the level of the metapopulation. In spite of the different spatial scales and modes of selection considered, it is notable that our results are consistent with the conclusion of Wilson and Harder (2003) that limitations on colonization success (e.g., Baker's Law as modelled here, or variance in seed dispersal as modelled by Wilson and Harder (2003)) should favour traits that promote extensive dispersal.

Pollen dispersal

Dispersal via pollen promoted the maintenance of the dioecious lineage within our simulations via two key effects on population dynamics. First, pollen flow from neighbouring populations promoted colonization by dioecious populations by allowing lone females to produce seeds, thereby reducing the advantage of reproductive assurance possessed by self-fertile hermaphrodites. Second, $c > 1$ meant that, on average, dioecious populations produced more pollen than hermaphrodite populations. High levels of pollen dispersal between sites thus led to a reduction in the seed fertility of hermaphrodites, and thus their ultimate displacement from sites adjacent to those occupied by dioecious populations. The joint action of these two processes was particularly clear in comparisons between simulations that assumed different hermaphroditic allocation. Under low allocation to seeds, the colonization ability of hermaphrodites was reduced, limiting their distribution in the metapopulation (Figure 4). However, under low allocation to pollen, hermaphrodite ovules were easily swamped by the dioecious lineage, again limiting their spread.

Several empirical studies have highlighted the role played by pollen dispersal in regulating the maintenance of hybrid zones. For example, greater pollen production of the invasive *Spartina alterniflora* has led to the displacement of native *Spartina foliosa* (Antilla *et al.*, 1998; Ayres *et al.*, 2004). Polyploidization is well known to affect reproductive traits such as the size of flowers and pollen (Stebbins, 1950), but its effects on patterns of sex allocation are poorly understood. Fukuhara (2000) found an overall trend for reduced allocation to male function with polyploidization in two species of *Corydalis*, but whether these differences affect patterns of colonization and the directionality of gene flow between the lineages studied is not known. Our results indicate that patterns of sex allocation are of substantial importance for regulating the maintenance of lineages in a hybrid zone. We found that even subtle differences in sex allocation had a dramatic effect on the maintenance of a hybrid zone regulated by colonization and extinction events. Specifically, our results draw attention to the possibility of a threshold level of allocation to seed production for the maintenance of parapatric lineages along disturbance-regulated gradients (Figure 4).

Model assumptions

For our simulations, we set $c = 1.2$ for determining the relative pollen and ovule fertilities of each lineage; under equal allocation to pollen and ovules by hermaphrodites ($a = 0.5$) this corresponds to a relative fertility of females

to hermaphrodites of 2.3. This value for the relative fertility of females to hermaphrodites falls within the range of estimates measured in natural populations of co-occurring females and hermaphrodites (i.e., gynodioecious populations; e.g., *Phacelia linearis*, Eckhart, 1992; *Geranium sylvaticum*, Ramula and Mutikainen, 2003; and *Bidens sandwicensis*, Schultz and Ganders, 1996), and well below the estimates of the difference in pollen production between males and hermaphrodites of *M. annua* (Pannell, 1997a).

We further assumed that selfing rates were density-dependent, varying in our simulations between $s=1.0$ and $s=0.09$ in populations of 1 and 100 individuals, respectively (i.e., the minimum and maximum number of individuals per population). Density-dependent selfing will usually be expected in self-compatible, wind-pollinated species, and has indeed been found in herbaceous *M. annua* (Eppley and Pannell, unpublished data) and woody *Pinus sylvestris* (Robledo-Arnuncio *et al.*, 2004). At inbreeding equilibrium, the selfing rate is expected to affect the magnitude of inbreeding depression, with sustained inbreeding expected to result in the purging of genetic load (reviewed in Crnokrak and Barrett, 2002), and a reduction in the negative effects of inbreeding (Lande and Schemske, 1985; Charlesworth *et al.*, 1990). Because selfing rates fluctuated over the course of population growth, we might have assumed that the magnitude of inbreeding depression should also vary during the life span of a deme. However, it is not known how inbreeding depression should evolve under metapopulation dynamics, although severe population bottlenecks are expected to have only a minor effect on the magnitude of inbreeding depression (Kirkpatrick and Jarne, 2000). Moreover, dispersal from surrounding demes should slow or prohibit evolutionary changes in the magnitude of inbreeding depression that is caused by variation in the selfing rate. Our assumption of a constant value for the magnitude of inbreeding depression is a simplification, but it is clear from our results that the advantages of selfing for reproductive assurance and the sheltering of hermaphrodite ovules from hybridization could be counteracted by other selective factors, such as viability differences due to inbreeding.

The moving *M. annua* contact zone

Diploid, dioecious populations of *M. annua* are rapidly displacing hexaploid, monoecious populations in the two regions in which they form contact zones (Buggs and Pannell, 2006). What do our results contribute to understanding the processes responsible for this displacement? As noted above, movement of a tension zone occurs when the balance between dispersal and selection against hybrids favours one lineage over another (reviewed in Barton and Hewitt, 1985). We assumed no asymmetry in selection against hybrids, so that movement was the result of biased patterns of dispersal between lineages. In this section we discuss some of the specific details of *M. annua* biology that (a) motivate a key assumption of our model, the occurrence of metapopulation dynamics, and (b) that appear to be responsible for biased dispersal from diploid to polyploid populations.

In *M. annua*, contact zones between dioecious and functionally hermaphroditic populations in Spain coin-

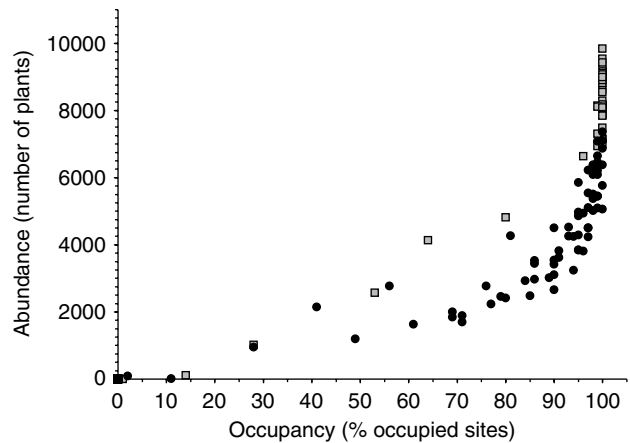


Figure 6 Plot of the percentage of sites occupied by the dioecious lineage (grey squares) and the hermaphroditic lineage (black circles) against the abundance of individuals per row of the lattice (the maximum value of which is 10000 when all sites in a row are at carrying capacity).

cide with gradients in patterns of population occupancy and abundance (Eppley and Pannell, 2007). In these regions, monoecious populations are smaller and occur at lower densities than dioecious populations (Eppley and Pannell, 2007). The patterns of occupancy and abundance found by Eppley and Pannell (2007) are consistent with the regulation by metapopulation dynamics of dimorphic (e.g., dioecious), and especially monomorphic (i.e., monoecious), populations, as assumed in this study. Indeed, the patterns of occupancy versus abundance found in natural dimorphic and monomorphic populations match those found in our simulations (compare Figure 3 of Eppley and Pannell, 2007 with Figure 6 of this study). Thus, it appears that in natural populations, as in our simulations, the dioecious lineage is favoured under higher rates of site occupancy and abundance; all else being equal, this corresponds with lower rates of population turnover.

As argued above, the direction and rate of dispersal between populations of each lineage governs the movement of the contact zone. Because hybrids are sterile, the establishment of one lineage in areas occupied by the other ultimately requires dispersal through seed. However, our simulations indicate that pollen dispersal can facilitate this process, both by simultaneously increasing the likelihood that females will acquire compatible mates, and by reducing the seed fertility of hexaploids by swamping their ovules with diploid pollen. There is good experimental evidence that these processes are likely to affect contact zone dynamics in *M. annua*. Buggs and Pannell (2006) showed that the presence of diploid males, even if they occur at low frequencies, leads to substantial reductions in the seed fitness of polyploids. However, hybridization rates for female ovules remained low, even when hexaploid hermaphrodites occurred at high frequencies. These findings led Buggs and Pannell (2006) to conclude that biased pollen dispersal between diploids and hexaploids is the primary factor responsible for the displacement of hexaploids.

If dioecious diploids of *M. annua* move further south they will come into contact with androdioecious populations of the hexaploid lineage. We found in our

simulations that androdioecy in one lineage allowed the persistence of the dioecious lineage under a greater range of conditions than pure monoecy. This finding runs counter to the speculations of Buggs and Pannell (2006) that dioecious diploid populations of *M. annua* might be less able to displace androdioecious populations than populations of functionally hermaphrodite plants because: (a) similar levels of pollen fertility between diploid and polyploid males might prevent the swamping of polyploid ovules by diploid males; and (b) functional hermaphrodites in androdioecious populations would retain the ability to colonize unoccupied sites by themselves. However, in our simulations we found that the high equilibrium frequency of males in androdioecious populations reduces the colonization advantage possessed by polyploids because fewer individuals from polyploid populations can establish populations by themselves. Without the advantage of reproductive assurance, polyploid populations should be easily displaced by diploids, which possess a marginal fertility advantage through female function over functionally hermaphroditic polyploids. Thus, our results indicate that we should expect the displacement of polyploids to accelerate as diploids move into areas occupied by androdioecious populations.

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