

Adaptation and propagule pressure determine invasion dynamics: insights from a spatially explicit model for sexually reproducing species

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ABSTRACT

Propagule pressure is often considered to be one of the key factors determining the probability that a species becomes invasive. However, there has been relatively little work, either empirical or theoretical, that has tested this assertion. Here, we develop a patch occupancy model for diploid organisms that reproduce sexually, and use it to investigate the dynamics of an introduced species. The model produces some interesting insights: If the introduced individuals are already well-adapted to the wild conditions, then the number of escapees is always larger when there are more introductions. However, when the introduced individuals are relatively poorly adapted to the natural conditions, this is often not the case. Under these conditions, the most rapid invasion occurs for an intermediate number of introductions. When the number of introductions is high, adaptation to local conditions is dramatically slowed and in some cases a well-adapted population never establishes. Thus, high propagule pressure does not necessarily lead to greater invasability. We believe that the model framework described in this paper can be a powerful tool for biologists interested in the genetics and evolution of invasive species, and spatially structured populations in general.

Keywords: genetics, introduced species, invasion, lattice model, patch occupancy, simulation.

INTRODUCTION

Intuitively, the number of individual introductions of a species into a non-native habitat (propagule pressure) is likely to be a key determinant of invasion dynamics. It has frequently been stated that increased availability of propagules increases the chances of an introduced species becoming invasive (see Rouget and Richardson, 2003, and references therein). While there is some support for this assertion (e.g. Green, 1997; Hutchinson and Vankat, 1997), few studies have attempted to quantify the role of propagule pressure (Williamson, 1996). Similarly, there is little

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theory on the role of propagule pressure, and Rouget and Richardson (2003) identified the need for more work in this area, arguing that ‘propagule pressure must be built into spatially explicit invasion models’.

Increasingly, ecologists are beginning to realize that evolution may frequently occur on a time-scale that is important for ecological processes and, therefore, conservation. Stockwell *et al.* (2003) review recent evidence that evolution occurs rapidly in response to ‘factors that are driving the current extinction crisis: habitat loss and degradation, overharvesting and exotic species’. They conclude by stating that, ‘In a world filled with contemporary evolution, conservation efforts that ignore its implications will be less efficient and perhaps even risk prone’. There is a real need to improve our understanding of the role of evolution in determining invasion dynamics, and propagule pressure may be an important factor in determining the ability of an introduced species to adapt and thrive in its new environment.

In this paper, we develop a spatially explicit model framework to simulate the invasion dynamics of a sexually reproducing population. In recent years, spatially explicit population models have been much used by ecologists. Spatial population models have provided some fascinating results, such as the pattern formation that permits species co-existence of hosts and parasitoids (e.g. Hassell *et al.*, 1994). They have also been used to provide insight into conservation issues. For example, many studies have investigated the likely impacts of habitat fragmentation for species persistence (e.g. Fahrig, 1997; Hill and Caswell, 1999; With and King, 1999).

While spatially explicit population models have been used quite extensively, there are far fewer examples of spatially explicit population models that incorporate genetics or evolution. In part, this discrepancy may be due to the misplaced belief that evolutionary processes occur on a different – and much longer – time-scale than ecological processes, and are thus unlikely to be important for conservation issues. In part, it may also be due to the extra computational requirements that incorporating genetics and evolution demand. With recent technological advances, computer power should not be limiting: not even for relatively complex individual-based models incorporating detailed genetic processes. The time is ripe for a concerted effort to utilize models to improve our understanding of spatial evolutionary ecology.

At least two research areas buck the trend described above. For a number of years, several authors have been publishing the results of spatial models developed to investigate the evolution of dispersal (e.g. Holt and McPeck, 1996; Travis *et al.*, 1999; Travis and Dytham, 1999, 2002; Hovestadt *et al.*, 2001; Murrell *et al.*, 2002; Poethke and Hovestadt, 2002; Cadet *et al.*, 2003). Only a subset of these models is spatially explicit, and in almost all cases the models assume organisms to be haploid. While this assumption makes the analytical models more tractable and makes the simulations faster and easier to program, it potentially compromises the models in terms of biological realism. A very similar set of approaches has been used to explore the evolution of altruism (e.g. Nakamaru *et al.*, 1997; Mitteldorf and Wilson, 2000; Irwin and Taylor, 2001; Le Galliard *et al.*, 2003). Even where simulation models have been used to look at the evolution of altruism in spatially structured populations, the model organisms have been haploid.

We believe that there is an urgent need for spatially explicit model frameworks that can be used to provide predictions for diploid organisms that reproduce sexually. Here, we propose a framework for this purpose. The method offers considerable flexibility in the spatial scale that different biological processes operate and also in the level of detail that is built into the genetic component of the model. The development of this framework has been motivated by our desire to understand how propagule pressure and the interplay of population and evolutionary dynamics determine the outcome of an introduction.

THE MODEL FRAMEWORK

Patch occupancy models

A patch occupancy model represents the landscape as a number of cells (Fig. 1). Each cell can be in one of two states, occupied or unoccupied. There are two main uses of this type of model: the first assumes that each patch can sustain one and only one individual, and in this form the model is suitable for individual-based simulations of a single population; the second assumes that each patch can support a whole subpopulation, and in this form the model can be used to describe metapopulation dynamics.

In its simplest form, a patch occupancy model is spatially implicit. This implies that colonization of a patch is equally likely to occur from any other cell. Levins's (1969) metapopulation model was the first spatially implicit patch occupancy model. This deterministic model tracks the total density of occupied and unoccupied patches. Occupied patches go extinct at rate e , and unoccupied patches are colonized at a rate determined by the species' colonization ability and the densities of occupied and unoccupied patches. Many authors have since used the model in this format (e.g. Lande, 1987; Nee and May, 1992), while others have made use of it in a stochastic form (e.g. Moilanen, 1999; Keymer *et al.*, 2000; Ovaskainen, 2002).

In the last 10 years or so, an increasing number of authors have been making use of spatially explicit patch occupancy models (e.g. Dytham, 1994, 1995; Hill and Caswell, 1999; Ellner, 2001; Travis, 2003). In a spatially explicit patch occupancy model, the landscape is represented as a lattice of habitat patches. Each patch can support one individual. In each time-step of a simulation, individuals have finite probabilities of dying and of reproducing. Stochastic death of an individual occurs with probability m . Individuals produce an offspring with probability r . Offspring move to a new patch and if the patch is not already occupied, they become established there.

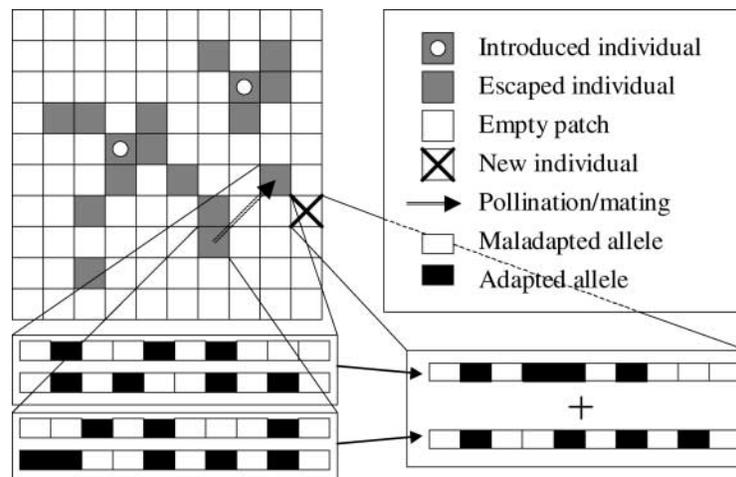


Fig. 1. A schematic representation of the model. The figure illustrates the key processes in the simulation: sexual reproduction between individuals located within a fertilization neighbourhood and dispersal.

Dispersal in a spatially explicit model

A spatially implicit model makes the assumption that offspring dispersal occurs with equal likelihood to any patch on the landscape. This is not the case when a lattice model is used: most often nearest-neighbour dispersal is assumed, offspring moving with equal probability to one of the cells immediately adjacent to their natal patch. However, a wide range of different dispersal neighbourhoods can be incorporated into this form of model (Murrell *et al.*, 2002; Travis, 2003). The simplest extension is to vary the size of the dispersal neighbourhood while maintaining the assumption that offspring move with equal likelihood to any cell within it. In a model looking at the ability of hypothetical species to shift their ranges in response to climate change, Travis (2003) used this approach with neighbourhood sizes of 8, 24 and 48.

Incorporating genotypes

We extend the framework described above so that individuals each have a genotype. An individual's genotype is represented by two copies of l loci, one inherited from each parent. Each locus can be in one of s states: the number of states that are used will depend upon the nature of the ecological problem being modelled. In some situations, different loci may have different numbers of possible states associated with them. In the simplest case, there may be two possible states for a locus: 1 indicating that the locus provides a particular fitness advantage and 0 indicating that it confers no advantage.

Incorporating sexual reproduction

For self-fertilization, the procedure remains relatively similar to a typical patch occupancy model, so we will consider it first. During an iteration of the model there is a finite probability that each adult produces an offspring, which then establishes in another patch. In a typical haploid model, the offspring's genotype would be identical to that of the parent, perhaps with a small probability of mutation at each locus. With self-fertilization in a diploid, the situation is a little more complex. Now the state of each locus is determined by simulating meiosis. If we assume there is no linkage, then the state of each of the offspring's loci is generated by selecting an allele at random from the parent's two copies of the equivalent locus.

The method described above is easily extended to two hermaphrodite parents reproducing sexually. Now in each time-step there is a finite probability r that each individual will bear an offspring (be a mother). The offspring's genotype will consist of one set of loci from its mother and a second set from another individual (the father). The identity of the father is drawn at random from all the individuals that are found within a critical distance of the mother. The two simplest *fertilization neighbourhoods* are global (where all individuals within the arena are equally likely to be the father) and nearest neighbour (where fertilization is limited to those individuals located in adjacent cells to the mother). More complex fertilization neighbourhoods can be employed where the probability of being the father is a function of distance from the mother. Once the identity of the two parents has been determined, the states of the offspring's first set of loci is determined by selecting alleles at random from the mother's two copies. Similarly, the states of the offspring's second copy are randomly assigned from the father.

Incorporating separate sexes within the framework described so far is straightforward. Individuals simply carry a label indicating whether they are male or female, and only the females bear young. The probability that a newly born individual is male (or female) will depend upon the sex ratio of the species that is being modelled. Mutation is incorporated immediately after meiosis. There is a fixed probability γ that a mutation occurs at each locus.

USING THE FRAMEWORK TO STUDY THE EVOLUTIONARY ECOLOGY OF AN INTRODUCED SPECIES

Invasion dynamics may be driven by evolutionary processes (Hänfling and Kollmann, 2002; Lee, 2002). Also, invasion frequently has a strong spatial pattern (e.g. Collingham *et al.*, 2000; Wadsworth *et al.*, 2000; Higgins *et al.*, 2001). Given these characteristics of invasion biology, we believe that the framework we have developed can be a useful tool for investigating the evolutionary ecology of invasion. In this paper, we are particularly interested in how propagule pressure drives the evolutionary and population dynamics of the invasion process. We ask one quite specific question: If we have a number of constant points of introduction (POI), how does the size of the population in the wild (PIW) depend upon the number of POI? We illustrate what we mean by a constant POI with two examples. First, consider a plant species that is maintained within gardens. Assume that when one individual dies it is replaced immediately by another plant of the same species. Under these conditions, gardens will provide a constant source of this species' seeds. Second, consider the case of mink escaping from fur farms. If we assume that the rate of mink escaping remains steady through time, and the size and location of fur farms is constant, then we have a constant source of individuals being released into the wild. Intuitively, one would probably expect that as the number of POI increases, the PIW should increase. However, under some circumstances it may be possible that a continuous flow into the wild of large numbers of maladapted individuals can suppress the ability of a PIW to adapt to the wild conditions, and can thus limit the size of the PIW. Here, we use the model framework described above to provide some insights into the relationship between POI and PIW.

The model

Each simulation starts by designating a number of patches, n , on the lattice as sources of invasion or POI. The location of these patches is chosen at random. An individual is placed onto each of these patches: its genotype is generated by assigning 1 to each locus with probability a (otherwise it is assigned 0). These individuals are assumed to suffer no mortality (imagine, for example, a garden plant that is replaced with an identical specimen if it dies).

Now the simulation is implemented for γ years. Every year reproduction is followed by mortality. In the reproduction phase of the model, every individual on the lattice is the maternal parent of an offspring with probability r . We generate results for four different fertilization neighbourhoods. First, global fertilization is assumed: the paternal parent of an offspring is determined by selecting an individual at random from all the other individuals on the lattice. Second, we assume nearest-neighbour (i.e. an individual located in one of the eight cells neighbouring the potential mother). Global and nearest-neighbour fertilization represent extreme abstractions, and intermediate neighbourhoods better represent reality for most species. Therefore, we have also run the model assuming 80 cell

and 440 cell neighbourhoods, where pollen can disperse up to 4 and 10 cells, respectively, along both the x and y axes. Self-fertilization occurs only when an individual has no fertilization partner within its neighbourhood. The genotype of the offspring is determined as described in the previous section. When a mutation occurs at a locus, it changes state (i.e. if it is initially in state 1, it changes to state 0 and vice versa). The offspring disperses to one of the eight cells neighbouring its natal patch. If the destination patch is not already occupied, it successfully establishes there with a probability dependent on its genotype. Here we assume that the probability of establishment is simply $f/20$, where f is the number of well-adapted alleles possessed by an individual. Thus an individual that has no well-adapted alleles has no chance of establishment, while one that has well-adapted alleles at every locus always establishes. After every individual has had a chance to reproduce, mortality is implemented. Every individual (other than the introduced individuals) dies with probability m .

Results

Figure 2 shows a typical set of population trajectories for a few selected parameterizations of the model. Most of the trajectories shown in Fig. 2 are characterized by a long lag phase when the PIW is rather small, followed by rapid population increase up to an asymptote. For a particular parameterization, the population trajectories can differ considerably from one simulation to another. This is illustrated well by Fig. 2c: in one of the five replicate simulations shown here the lag phase lasts 400 time-steps, while in another rapid population growth still hasn't occurred after 1000 time-steps. This highlights the stochastic nature of the model and illustrates the importance of running a sufficient number of replicate simulations for each parameter set. In general, a greater variability between replicate simulations is obtained when POI and γ are small. All of the results in Fig. 2 are for a global fertilization neighbourhood. Qualitatively similar results are obtained for all the other fertilization neighbourhoods that we implemented. However, when reproduction is asexual the trajectories are quite different: steady population increase occurs through time, rather than the very rapid increase following a lag.

Time lags between introduction and the establishment and spread of invasive species can be caused by several different mechanisms (see Sakai *et al.*, 2001). Genotypic adaptation provides the mechanism for the lags observed in Fig. 2. In all these cases, the rapid increases in population density follow an increase in the extent to which the PIW are adapted to the environment. Figure 3 illustrates this for one realization of the model: very similar results are obtained for a wide range of parameter space and for different fertilization neighbourhoods. Within the model, well-adapted individuals arise through a combination of recombination and mutation. The stochastic nature of both these processes partly accounts for the variability that is observed between the length of time lags in replicate simulations where the same parameter values are used.

When the introduced individuals are well adapted to the wild conditions, then increasing the number of POI always reduces the time taken for a large wild population to establish. However, when the introduced individuals are relatively poorly adapted to the environment, the relationship between the number of POI and PIW becomes more complex (see Fig. 4). For a period after introductions commence, the relationship is simple: the more POI, the greater the PIW (Fig. 4a). However, after POI have been present for longer the relationship changes, and the highest PIW are found for intermediate POI (Fig. 4b). This effect becomes

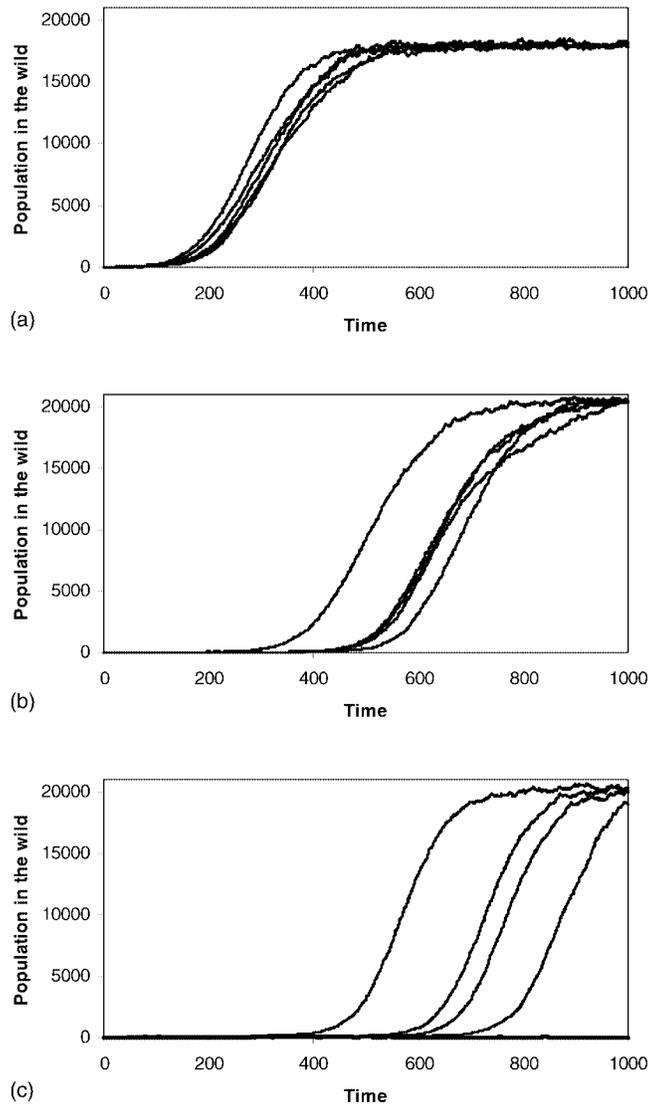


Fig. 2. Typical results from the simulation. There is often a considerable lag time between introductions commencing and the invasion taking hold. The five lines shown in each box are the results from five runs of the model using identical parameter values. Here, a global fertilization neighbourhood is used and dispersal is nearest neighbour. In (a) $a = 0.01$, $\text{POI} = 50$ and $\gamma = 0.1$. In (b) $a = 0.04$, $\text{POI} = 20$ and $\gamma = 0.05$. In (c) $a = 0.04$, $\text{POI} = 50$ and $\gamma = 0.05$. In all three, $m = 0.12$.

increasingly obvious as the simulation proceeds (Fig. 4c). One consequence of this result is that under some circumstances reducing the number of POI actually results in an increase in the PIW. Figure 5 illustrates this effect. It is important to note that reducing POI to a particular value N after a period when it has been higher does not necessarily result in the same PIW as if the POI was always N . In Fig. 5, when POI is reduced from 5000 to 0, there

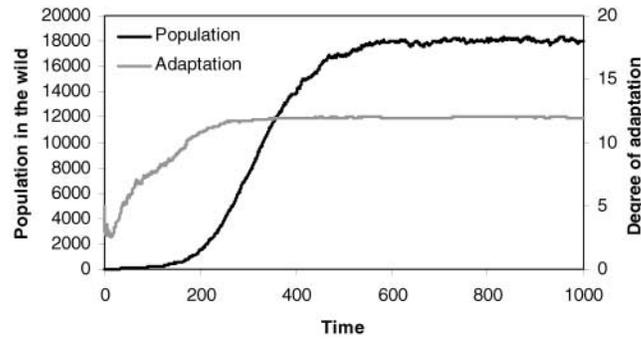


Fig. 3. The time lag between introduction and rapid population increase is due to the time required for genetic adaptation to occur. Here, $a = 0.01$, $m = 0.12$, $\text{POI} = 50$ and $\gamma = 0.1$. Dispersal is nearest neighbour and fertilization is global.

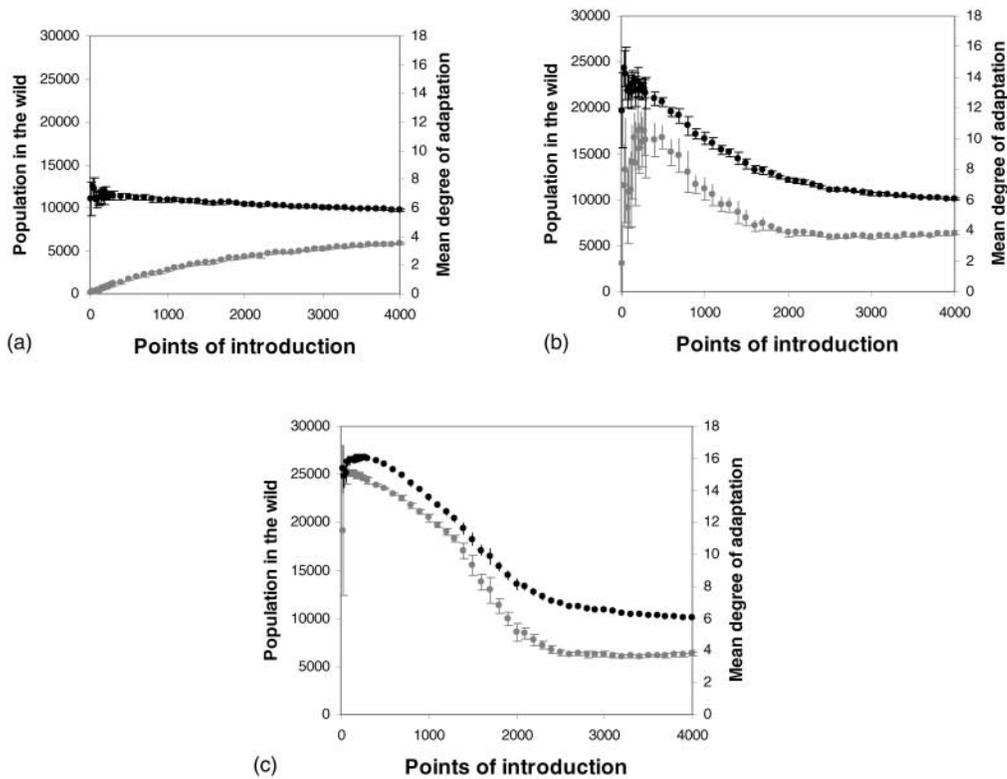


Fig. 4. More points of introduction do not always mean a larger population in the wild. Here, $m = 0.12$, $a = 0.2$ and $\gamma = 0.0001$; dispersal is local, fertilization is global. (a) After 100 time-steps, (b) after 300 time-steps, (c) after 500 time-steps. Means and standard errors for 10 simulations at each POI are shown. Black symbols show the degree of adaptation, and grey symbols show the size of the population in the wild.

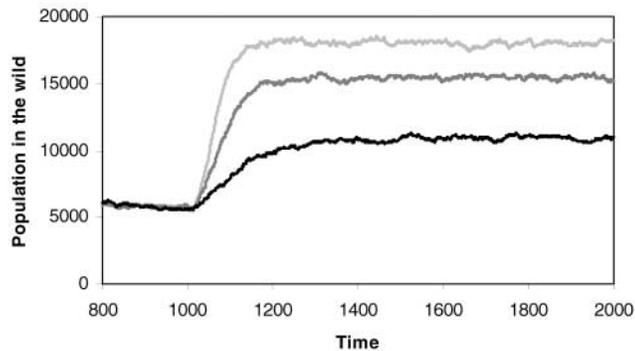


Fig. 5. Reducing the number of POI can increase the PIW. Here, $m = 0.12$, $a = 0.01$ and $\gamma = 0.1$; dispersal is local and fertilization is global. In each simulation there are 5000 POI for the first 1000 time-steps. Then the number of POI is reduced. The results for three levels of reduction are shown. The black line depicts the result with a reduction to 2500 POI, the dark grey line with a reduction to 1000 POI, and the light grey line with removal of all the POI.

is a rapid increase in the PIW as the population is able to adapt to the wild conditions no longer hindered by the constant flow of maladapted genes from the POI.

Our results emphasize the importance of sexual reproduction for the adaptation of a population to novel conditions. If an asexually reproducing organism is introduced to a novel environment, adaptation is likely to take far longer than for a sexual organism and hence its potential as an invasive is lessened (compare Fig. 6 with Fig. 4). We were interested to determine whether the adaptive potential of an organism with a restricted fertilization neighbourhood would be similarly limited. Our results indicate that when POI is low (< 300), adaptation is somewhat slower with smaller fertilization neighbourhoods. This results in a slower increase in population size. However, with larger POI, the reverse is true: adaptation is greater with more restricted fertilization neighbourhoods and hence the size of the PIW is greater. These effects are clearly illustrated in Fig. 7.

We have also run the model with nearest-neighbour fertilization excluding selfing. This imposes a severe Allee effect. Most of the POI will not have another POI in a neighbouring cell and will be unable to reproduce. When we implemented the model using the parameters used to produce Fig. 4, but with local fertilization and no selfing, there was no significant establishment of a PIW even when POI was as high as 4000 – the results were very similar to those for an asexual population

DISCUSSION

In this paper, we have developed a spatially explicit patch occupancy model for sexually reproducing species. We have used the model framework to investigate the evolutionary ecology of the invasion process, and ask one specific question: How does the number of introductions (propagule pressure) influence the dynamics of invasion? Our results clearly show that under certain conditions, having a greater number of introductions can reduce the number of individuals in the wild. This is most likely to occur when the introduced individuals are poorly adapted to the natural environment. Under these conditions, considerable genetic adaptation is necessary before the population in the wild is able to grow

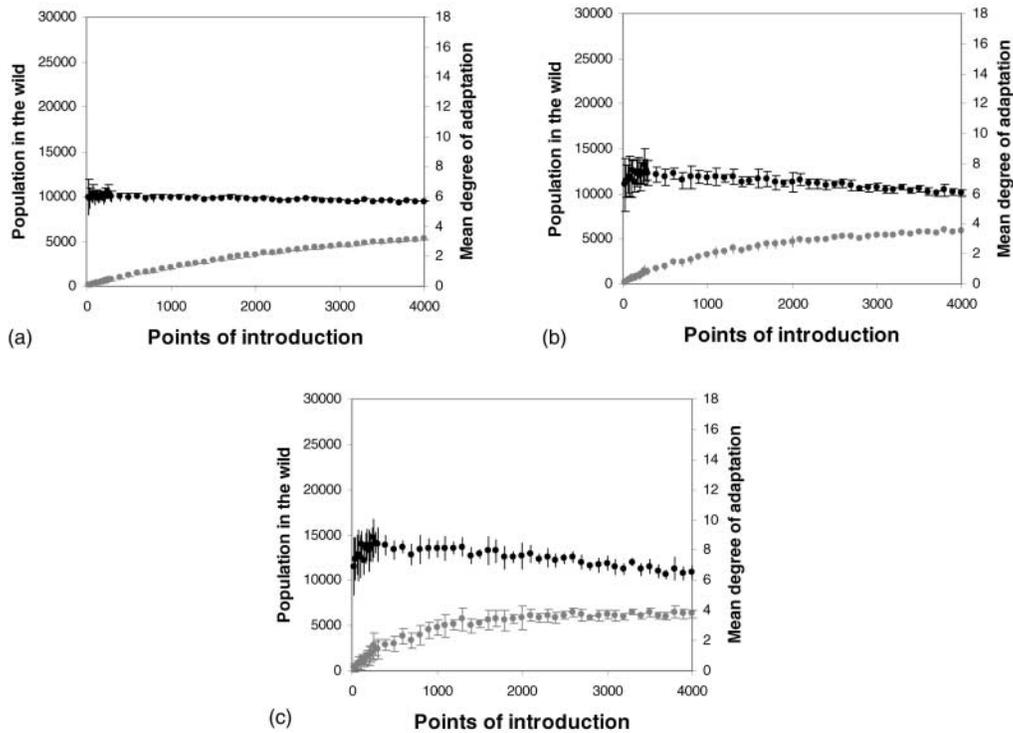


Fig. 6. Asexual populations are less able to adapt to novel environmental conditions. The parameters used to produce these results are identical to those in Fig. 4, except that here reproduction is asexual. Part (a) shows population size and mean adaptation after 100 time-steps, (b) after 300 time-steps and (c) after 500 time-steps. Black symbols show the degree of adaptation, and grey symbols show the size of the population in the wild.

appreciably. Genetic adaptation occurs through a combination of mutation and recombination of genes that are present within the introduced individuals. Up to a point, increasing the number of introductions increases invasion potential. This is partly due to simple demographics, but also because the introduced population contains a greater proportion of the total number of well-adapted alleles, providing more material for recombination to work on (and reducing the need for mutations). However, as the number of introduced individuals with mainly poorly adapted genes increases beyond this point, it becomes ever more difficult for a PIW to become well adapted. The constant flux of poor genes from the introduced population has the effect of genetically trapping the PIW.

One implication of this result is that reducing the number of individuals of an exotic organism escaping into the wild may not always have the desired result. In Denmark, there are more than 2000 operating mink fur farms, from which mink escape. A recent study showed that nearly 80% of 213 mink caught in the wild had been born in farms (M. Hammershøj *et al.*, unpublished). This could imply that the free-ranging mink population has not been able to become well-adapted to natural conditions in Denmark, and that the constant supply of escaping farm mink is actually keeping numbers of free-ranging mink down. Limiting the number of farms (or escapees) could thus have the effect that a well-

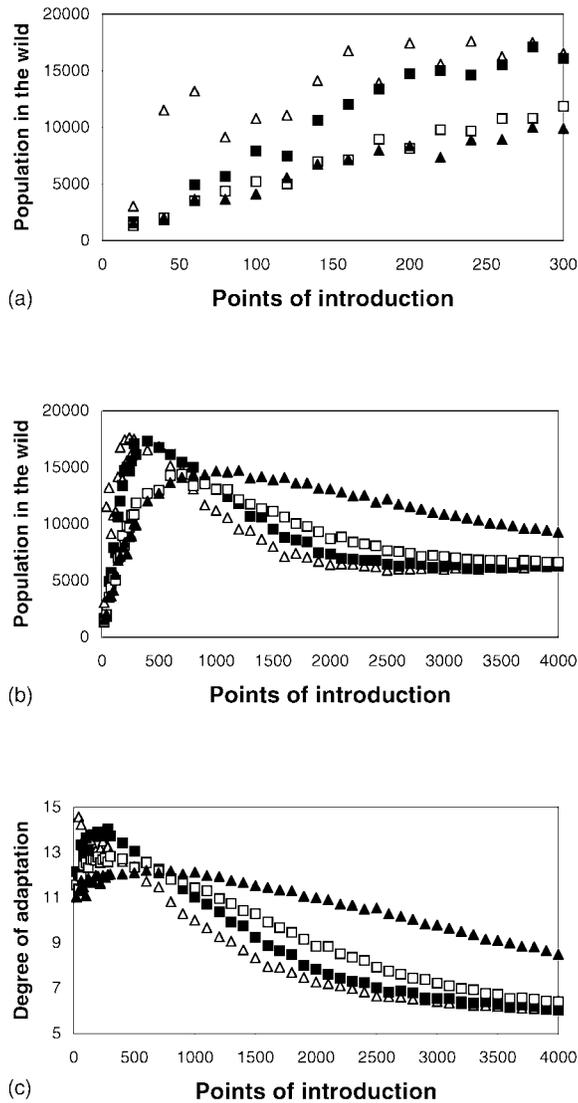


Fig. 7. The influence of fertilization neighbourhood. When POI is small, invasion tends to be greater with larger fertilization neighbourhoods. However, when POI is large, a population with smaller fertilization neighbourhoods may be more invasive. ▲, 8 patch neighbourhood; △, global neighbourhood; □, 80 patch neighbourhood; ■, 440 patch neighbourhood. (a) Results for POI between 0 and 300; (b) between 0 and 4000. Part (c) shows how well adapted the populations are. $m = 0.12$, $a = 0.2$ and $\gamma = 0.0001$.

adapted, truly feral mink population will establish itself. Similarly, it is possible that some popular garden plant species may not have become invasive because they are found in so many gardens! A change in fashion that reduces their popularity could result in a belated invasion.

One feature of our results is the time lag between introduction and the rapid increase of the PIW. Lag times between initial colonization and the onset of rapid population growth and range expansion are a common feature of invasions (e.g. Mack, 1985; Kowarik, 1995) and in some cases can be in the order of several hundred years (Kowarik, 1995). There are at least three possible causes of these lags (Sakai *et al.*, 2001): exponential population growth, a shift in environmental conditions that favours the invading species, or an evolutionary change in the population. The lengthy lag times observed in our simulations are due to the time it takes for the PIW to become well enough adapted to exhibit rapid population growth. We have not fully explored the dependence of lag time on the different parameters in the model, and one obvious avenue for future work will be to use this type of model framework to establish how lag times depend upon factors such as propagule pressure, the genetic system and the spatial structure of the population. Figure 2 shows that there can be considerable variability in the lag time, even for replicate simulations using the same parameter values. What determines the degree of variability is an interesting question, and one that might also be answered by further use of this type of model.

Fertilization neighbourhood influences the ability of an introduced population to adapt and become invasive. If introductions are few and far between, then a wider fertilization neighbourhood permits greater recombination and facilitates more rapid adaptation than is possible when the fertilization neighbourhood is limited. In this case, adaptation is mainly limited by the need for well-adapted mutations. Once the PIW reaches a reasonable size, the dilution effect from the POI is small. However, when introductions are many, a wider fertilization neighbourhood can be a disadvantage. Now, there is plenty of scope for acquiring beneficial mutations through recombination for all fertilization neighbourhoods. However, for a population with a large fertilization neighbourhood, there is no way of escaping the genetic dilution effect from the POI. However, some areas of the landscape will by chance have lower densities of POI, and a population with a small fertilization neighbourhood can benefit from these areas, as pockets of individuals will be able to escape the dilution effect and become well-adapted. Further work investigating the consequences of different spatio-temporal patterns of introductions might prove valuable.

It is worth comparing our results with those obtained in theoretical work investigating the evolution of range margins (Kirkpatrick and Barton, 1997; see also Holt, 2003). Kirkpatrick and Barton (1997) demonstrate that gene flow from the core to the margins of a species' range can stymie adaptation at the periphery and thus prevent the range from expanding outwards. Under some conditions, the periphery of the range can act as a demographic sink. The mechanism behind the result in our model is essentially the same as that in Kirkpatrick and Barton's: a large number of maladapted individuals continuously arriving in a novel environment prevents local adaptation that might otherwise occur.

Here, we have chosen to use the model framework to ask one particular question relating to the evolutionary ecology of invasion. There is much more that can be done with this type of model in that particular area. However, we believe that this framework opens many exciting possibilities for future work in a range of ecological fields and here we make a few suggestions. In the Introduction, we suggested that the evolution of dispersal was one of the few areas where evolutionary processes have regularly been incorporated into spatial population models. Most models looking at the evolution of dispersal assume asexual organisms and thus do not incorporate inbreeding depression. This is a considerable drawback, as it is widely acknowledged that inbreeding depression is one of the main potential

drivers of dispersal strategy (see Gandon, 1999). Using the framework described here, it should be possible to gain a better insight into the role that inbreeding depression has in selecting for dispersal behaviour on fragmented landscapes, and during range expansions. Patch occupancy models are ideal for looking at questions relating to patterns of habitat loss. Using the framework we have developed, it will be possible to investigate how different patterns of habitat loss impact on the genetic structure of a population. There is currently considerable interest in the dynamics of high mutability clones (mutators) in bacteria (Sniegowski *et al.*, 2000; Tenaillon *et al.*, 2000; Travis and Travis, 2002, 2004). Much of this interest stems from a probable link between mutators and the evolution of drug resistance (Oliver *et al.*, 2000). Several model studies have investigated how mutators increase within a population following an environmental change (Taddei *et al.*, 1997; Tenaillon *et al.*, 1999, 2000). All these models are spatially implicit. However, many bacteria inhabit environments with considerable spatial structure. For example, mutator clones have been found in populations of *Pseudomonas aeruginosa* inhabiting the lung (Oliver *et al.*, 2000). A very real need exists for models that can be used to assess how sensitive mutator dynamics are to different spatial population structures. The framework described in this paper is ideally suited to this purpose.

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