Integrating Ecology and Evolution in a Spatial Context

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EDITED BY

JONATHAN SILVERTOWN

Department of Biological Sciences
The Open University

AND

JANIS ANTONOVICS

Department of Biology
University of Virginia

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Chapter 5

Spatially explicit studies on the ecology and genetics of population margins

J. Antonovics, T. J. Newman† and B. J. Best‡*

Introduction

There has been a growing realization that the numerical and genetic dynamics of populations can be profoundly different when individuals do not have equal probabilities of interacting with every other individual, but instead interact in a distance-dependent way with a local subset of the population (Kareiva 1994; Rhodes *et al.* 1996; Tilman & Kareiva 1997). Much of this realization has come from comparing the outcome of spatially explicit simulations with standard unstructured population models (so called 'mean-field' models; Levin & Pacala 1997). For example, the inclusion of spatial structure in host–parasitoid models not only increases the likelihood of long-term host–parasitoid coexistence, but it also leads to complex spatio-temporal patterns, even in homogeneous external environments (Comins *et al.* 1992). Such complexity occurs quite generally when these models are applied to other host–pathogen systems (J. Antonovics and M. P. Hassell, unpublished).

Most of such studies have focused on the emergence of patterns within large patches, and edges have been seen as 'nuisances' to be taken care of by algorithms that wrap, reflect or absorb at boundary regions. However, in nature, populations are characterized by real borders and edges. The processes and dynamics occurring at such margins have been shown to be critical for understanding limits to range extension (Antonovics 1976; Carter & Prince 1981; Watkinson 1985; Best 1990), responses to environmental change (Camill & Clark 1998), genetic divergence (Slatkin 1973; Endler 1977; Mallet & Barton 1989) and speciation (Caisse & Antonovics 1978).

Nevertheless, processes at margins and zones of contact have generally been described in terms of the behaviour of 'one-dimensional', transect-like, mean-field models. These studies have used either 'connected lattice' models in one dimension (e.g. 'stepping-stone' models in population genetics), or partial differential equations describing spatial change in abundance or gene frequency over one or two dimensions (Fisher 1937; Turchin 1998). While there have been a number of spatially explicit studies of dispersal from point sources (Turchin 1998) and the spread of in-

* *Department of Biology, University of Virginia, Charlottesville, VA 22904-4328, USA.*
† *Departments of Biology and Physics, University of Virginia, Charlottesville, VA 22904-4328, USA.*
‡ *Department of Botany, Duke University, Durham, NC 27708, USA. Current address: Department of Economics, University of Washington, Seattle, WA 98195-3330, USA.*

vading populations into 'empty' habitat (Hengeveld 1989; Lewis 1997), there have been almost no studies of spatially explicit processes in marginal populations. In this chapter we will use spatially explicit, individual-based models to study the patterns and dynamics that develop in population margins as they expand into regions that become more and more unsuitable (or perhaps as they retreat in response to environmental change). We begin by considering purely ecological models where there is no genetic variation in the population and only environmentally imposed variation in demographic parameters. Then, we examine colonization of a novel habitat, where genetic change accompanies the range expansion of a population.

Demographic limits to population spread

The basic model

To investigate the dynamics of populations at the edges of their range, we use a spatially explicit model of a distributional limit caused by an environmental gradient which imposes an increasing death rate in one dimension. We use a two-dimensional square lattice, where each cell represents a site that can be potentially occupied by an individual plant. Each individual (with some probability) can then die or reproduce, and the ensuing offspring are dispersed according to a normal distribution around the centre point of the parent (which itself is immobile). Dispersal involves placing an individual into an unoccupied cell using a smooth bivariate Gaussian weighting function so as to minimize the anisotropic influence of the underlying lattice. We impose exclusion dynamics, meaning that each cell of the lattice can at most be occupied by a single individual. This represents density dependence at the smallest scale. We model an environmental gradient as a sigmoid increase in individual mortality rate in one direction, perpendicular to a boundary. We use the hyperbolic tangent function to describe this mortality rate $\mu(x)$, where x measures the distance along the gradient from the mid-point of the gradient. If reproduction exceeds mortality, and the gradient is sufficiently steep, a margin to the population is established at some position on the gradient. We use serial updating (representing perennials), and use a $n \times n$ lattice with wrap-around edges perpendicular to the margin. All runs are started by allowing invasion of a few individuals in the region of the gradient where population growth is positive (i.e. in the figures, the gradient of increasing mortality runs from bottom to top). Simulations are run until there is visually an overall steady state with only random fluctuations (i.e. the population has reached an ergodic state).

The influence of space on species margins determined by an environmental gradient

The distribution pattern of the individuals at the population edges is extremely different from that obtained by simple diffusion theory with only dispersal (Figure 5.1). In the former, biologically more realistic case, the edges are much 'rougher' because clusters of individuals arising by chance at the margins produce invading

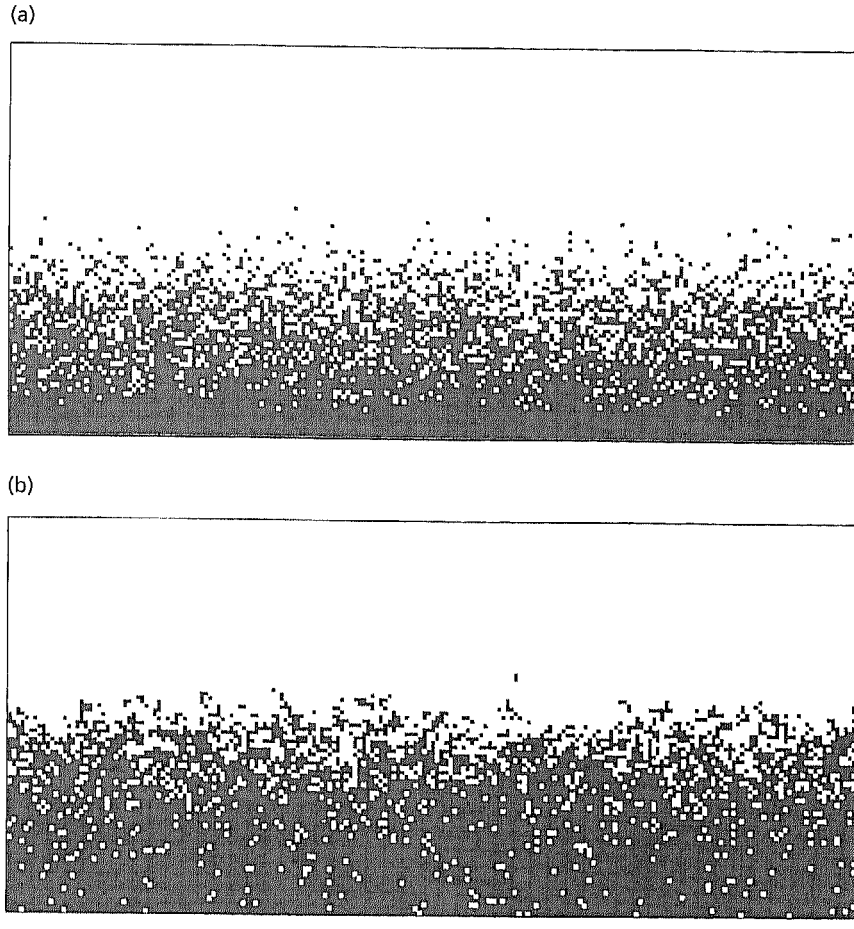

Figure 5.1 Typical spatial structure of a population margin where there is either, (a) movement of adults (= diffusion) but no births, or (b) no movement of adults, but dispersal of newly born individuals. In both cases mortality rate increases smoothly towards the top of the figure, but is uniform in the horizontal direction. Note the rough edge and flame-like extensions of the population margin boundary in (b)

flame-like phalanxes maintained by high local recruitment rates. We have also found from our simulation that the mean-field estimate of the steady-state density profile may substantially overestimate the ability of the population margin to advance along the gradient, depending on the steepness of the gradient relative to the dispersal distance (Figure 5.2). Note that the agreement is worse for one dimension than for two dimensions. To estimate the expected population profile we invoke a spatially implicit mean-field model which includes density-dependent reproduction and mortality. Denoting the density of the population as $\rho(x,t)$, the birth term is $r\rho(1-\rho)$ and the death term is $-\mu(x)\rho$ (where we have scaled the density to its carrying capacity). Equating these two in the steady-state yields $\rho(x) = 1 - \mu(x)/r$.

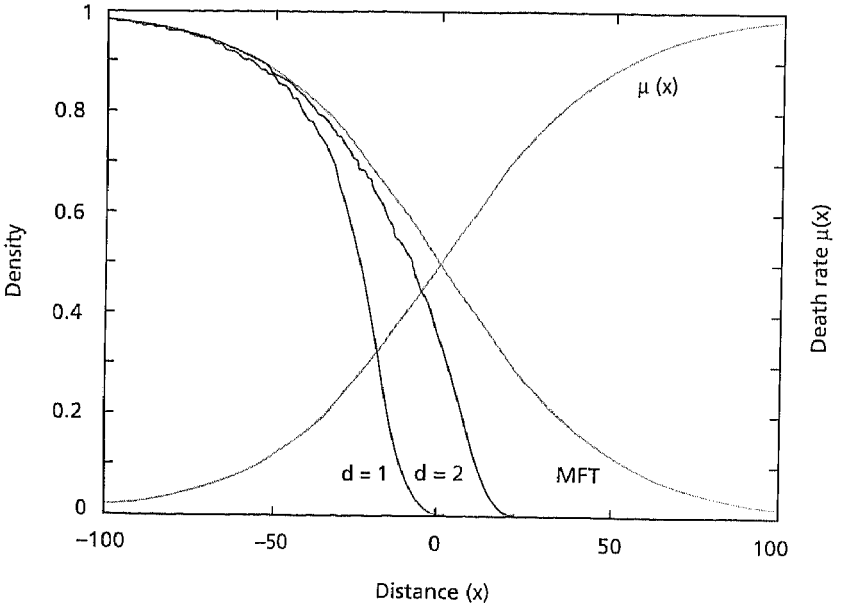

Figure 5.2 Density profiles as a function of distance along the environmental gradient (represented by increasing mortality rate, μ) for a marginal population with dispersal of newborns, but no adult movement (case b, Figure 5.1). Density profiles are plotted for the cases of one dimension ($d = 1$, a linear habitat) and two dimensions ($d = 2$), compared to expectations from mean-field theory (MFT)

This discrepancy may be understood heuristically as follows. As a cluster of individuals climbs the environmental gradient, its size fluctuates through birth and death processes. In a mean-field description, the individuals are described by a density which, however small, never vanishes. However, in our simulations, as in the real world of discrete organisms, the population is composed of clusters of a finite number of individuals. As a cluster extends into the margin it often becomes reduced to a single organism. This is where discrete effects are crucial. If this single organism dies, the entire cluster dies as there can be no subsequent recovery. It is the finite time extinction of clusters due to large fluctuations that is lost in mean-field theories.

We have also contrasted instantaneous and cumulative population distributions. The former is a snapshot of the population at a given time, while the latter is a time-integrated distribution such as would be obtained by sampling specimens over a period of time (as occurs when collections are accrued by museums and herbaria). We find that the cumulative distributions are (as expected) broader than the instantaneous distributions. But the edges of such cumulative distributions are not smoother. Instead, they are much rougher and have a great deal of spatial and temporal structure that seems to bear no consistent relationship to the instantaneous distributions (Figure 5.3). This is because the cumulative distribution incorporates

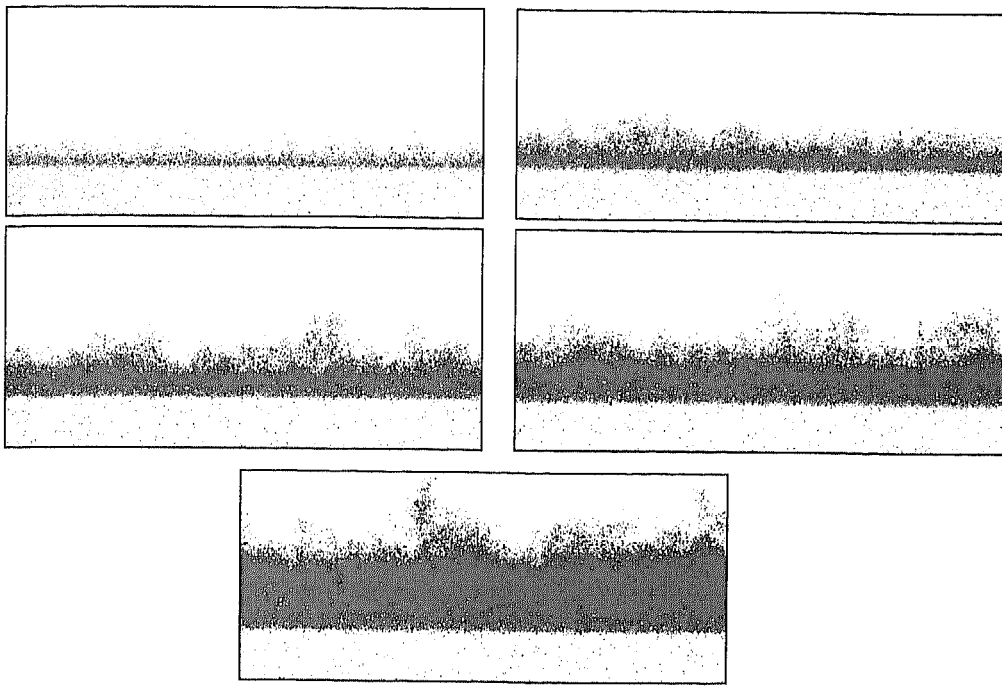

Figure 5.3 Time sequence (left to right, top to bottom) of typical distribution patterns at a population boundary as seen from a single generation census (grey) and as seen from a cumulative census (dark) obtained when all occupied sites are noted over successive periods of several hundred time steps.

rare events which include individuals at extreme points along the gradient. As time proceeds, the cumulative distribution changes increasingly slowly because increasingly extreme events are required to effect any change. However, no matter how long one observes the system, the cumulative distribution remains spatially inhomogeneous.

On viewing the cumulative distribution one would be tempted to infer much about the underlying environmental gradient, especially regarding its position and shape. However, one's inferences would be false, as the real demographic gradient lies hidden far behind the edge of the cumulative distribution and is much smoother. In our own studies, we have recorded similar differences between distributions obtained by a one-time intensive sampling vs. that obtained from cumulative sampling as occurs, for example, with collections of herbarium specimens (Figure 5.4).

Populations which are colonizing a new area across a demographic barrier

The study of a demographic barrier is a natural extension to our study of an environmental gradient. It is also of prime ecological significance in questions of species colonization. We represent this barrier by a bell-shaped (normally distributed)

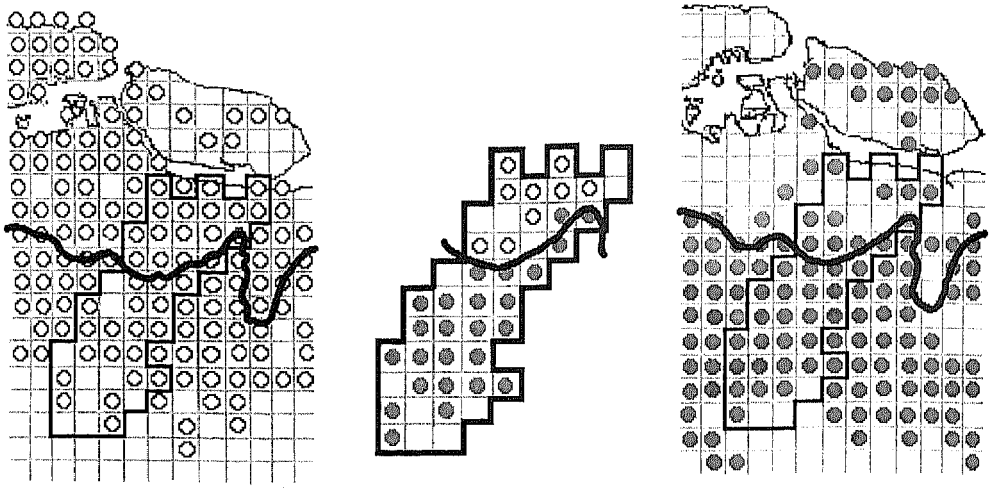

Figure 5.4 Distribution of *Silene alba* (left, open circles) and *Silene dioica* (right, solid circles) in north-central Kent, England, as given by the cumulative county distribution maps (Philp 1982), and distributions recorded in a 1992 census of part of the same region (centre figure). Data are from J. Antonovics and W. E. Kunin, unpublished results. Each square is 2 × 2 km. The dark line shows the approximate position of the fall line between the North Downs and the lowland, arable region of the Thames Valley. Note the relatively sharp boundary seen in the 'instantaneous' census, and the broad overlap seen in the cumulative census.

region of increased mortality centred across the lattice in one direction. So long as the demographic barrier is not too small (in which case it is easily surmounted by an advancing population), we can expect that colonization will occur via individuals in the advancing front of the population distribution. However, as we saw in the previous section, the position of this leading edge is strongly suppressed in the spatially explicit model as compared to the predictions of mean-field theory. Thus, we expect colonization to be more difficult when spatial stochastic effects are correctly accounted for! As pointed out already, the overall effect of fluctuations at a margin appear to be antidiffusional due to the finite time extinction of small outlying clusters. It is very interesting to see that even when outlying clusters diffuse over the peak of the barrier, colonization does not necessarily occur. Although over the barrier, the cluster is still in a very unfavourable region and its most likely fate is to shrink to zero before making it far enough into the favourable habitat to begin prospering.

The colonization time scale depends on the model parameters. For example, increasing the reproduction rate enables clusters to live longer and thus have a higher probability of descending far enough down the far side of the barrier to firmly seed the colonization event. One can view this process as that of condensation, in which a bubble of sufficient size is required to initiate the condensation process. Such a critical nucleation size is a well-known concept in the field of phase transitions in

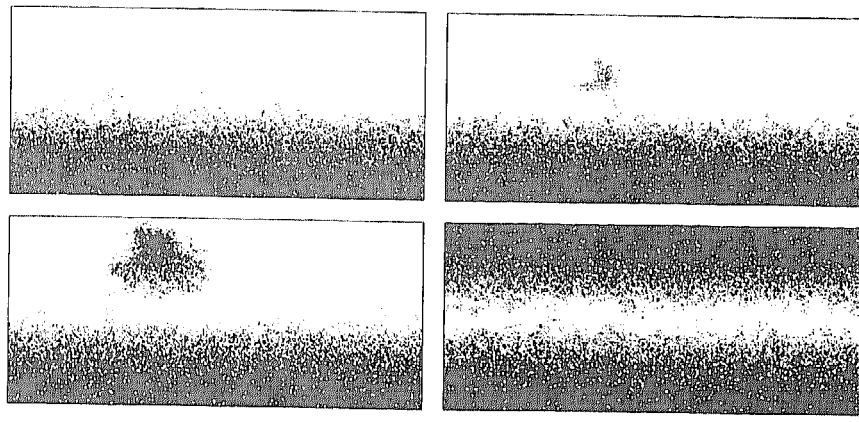

Figure 5.5 Time sequence (left to right, top to bottom) of colonization over a demographic barrier. The demographic barrier is a Gaussian-shaped region of increased mortality (not shown) across the centre of the region being colonized. Top left, outlying clusters at barrier; top right, successful cluster seeding new habitat; bottom left, growth of new population; and bottom right, complete population on both sides of barrier.

liquid–gas systems (Gunton *et al.* 1983). When colonization does occur it is often due to a single cluster, with the spread of the new population starting at a single longitudinal point in the virgin habitat (Figure 5.5).

One can then ask about the ensuing patterning of population spread along and further down the far side of the demographic barrier. Our initial results show that spread into the favourable habitat is not necessarily as an ever-widening wedge/triangle as might be expected intuitively, but that it is more often relatively amorphous. After colonization has occurred, the instantaneous distribution reflects two thriving populations separated by a very sparsely populated region (the barrier). As might be expected, the cumulative distribution comes to show no features whatsoever, because traversal events back and forth across the barrier eradicate any signal of the barrier.

Populations whose margins are determined by the changes in abundance of another species: host–pathogen interactions at a species boundary

We have seen that populations at margins have complicated spatial patterning and are dominated by spatiotemporal fluctuations. It is therefore extremely interesting to examine the process of infection of such a population by an invading species, for example a pathogen. It is intuitively appealing to imagine that marginal populations, although fragile, may actually be refugia from pathogen spread. An example of this is the persistence of healthy stands of American chestnut in marginal areas of the species distribution, following the spread of chestnut blight.

In our model, we establish the host species on an environmental gradient, and after a steady state has been reached we introduce a pathogen into the bulk of the host

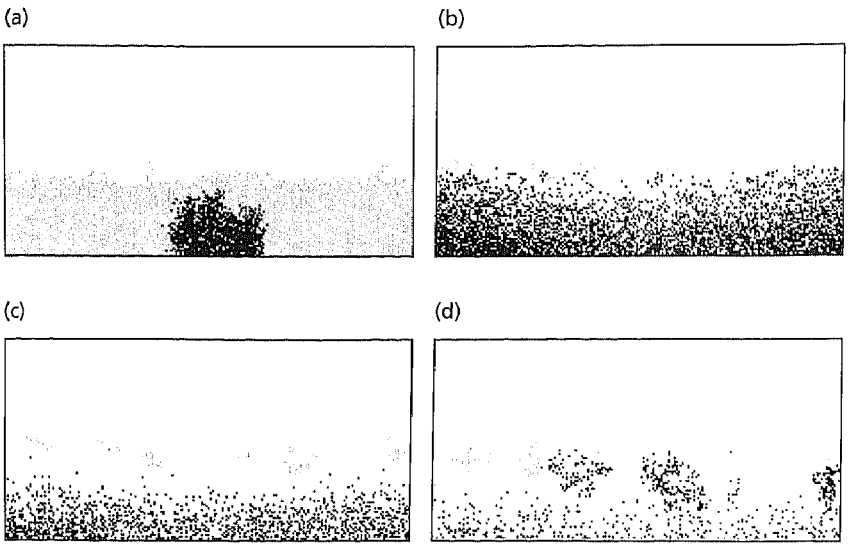

Figure 5.6 Time sequence (left to right, top to bottom) of pathogen spread into a marginal population. The healthy host individuals are represented by grey squares and the diseased hosts by black squares. Panels are: (a) early stages of pathogen spread; (b) a few individuals in the margin escape infection; (c) retreat of infected individuals and regrowth of healthy population; and (d) subsequent reinfection of advancing healthy population. Disease transmission is a Gaussian function around infected individuals, there is no recovery, and the disease increases host mortality rate.

population. The pathogen spreads, sterilizes the host, and slightly increases its mortality (cf. *Silene alba* and *Microbotryum violaceum*; Alexander & Antonovics (1988), Alexander *et al.* (1996)).

In many cases the population furthest up the gradient does act as a refuge, at least in the early stages of the pathogen spread (Figure 5.6). We then have a strip of healthy individuals high up on the gradient and a sea of infected individuals lower down which gradually die off. Because of the increased mortality further up the gradient, the infected individuals higher up die off faster leaving an empty band between the healthy marginal population and the infected central population. The healthy individuals then exploit this empty habitat and begin reclaiming the gradient lower down. However, they inevitably make contact with long-lived infected individuals in the bulk which reinfect them sending a wave of infection back up the gradient, and so the process repeats itself (Figure 5.6).

It is important to stress that this process of infection, recovery and reinfection (which is accompanied by advancement and recession of the healthy population) is dominated by rare events at the population margin. Thus, the cycles are not periodic, but seemingly random, in both size and duration. Such cycles are not seen in the 'body' of the population. In this sense, the mass infection events resemble earthquakes and avalanches, which are events on a wide range of spatiotemporal scales.

Such systems have attracted a lot of interest over the past 10 years under the heading 'self-organized criticality' (Bak 1994).

Genetic limits to population spread

Most natural plant populations have distinct boundaries, but it is often unclear why the boundaries occur precisely where they do. In the previous section we tacitly assumed that population limits were due to some physiological tolerance, perhaps modulated by the effects of competition, disease and predation (Harper 1977). These explanations are mechanistic, making the assumption that the observed tolerances or competitive abilities are fixed. However, physiological limits are under selection, and should continue to evolve. Viewed in this light, our explanations for the species distributions we observe must include factors which limit the rate and extent of evolutionary change (Chapter 17; Antonovics 1968, 1976).

On a large geographic scale, ecotypic variation allows individuals of a species to occupy a wide range of environmental conditions (Turesson 1922; Clausen *et al.* 1948). Similarly, the adaptation of individuals within a population to local conditions should lead to the exploitation of novel resources (Wilson & Turelli 1986) or the colonization of adjacent habitats and microsites (Ludwig 1950; Levene 1953; Antonovics *et al.* 1971; Antonovics 1990).

Genetic differentiation and expansion of a population into a different marginal habitat can be reduced to a three part process.

1 Production of 'preadapted' genotypes. This may occur by mutation and/or recombination. This may be limited by finite population size since rare mutations and gene combinations may be effectively unachievable.

2 Dispersal. High seed dispersal will increase the frequency with which a neighbouring habitat is sampled by offspring from the original habitat.

3 Gene flow through seed and pollen dispersal. This will determine the degree which the offspring of any new colonists resemble their parents.

4 Population growth within the newly exploited habitat. This will affect the availability of colonists and the level of effective gene flow. Gene flow will depend on the number of individuals in the new habitat relative to the number of individuals in the source population. Because this ratio will change as colonization proceeds, population size should be included explicitly in any model of the invasion of new habitats.

Population growth itself will depend on several conflicting factors.

1 Continued immigration from the source population by seed may augment population size. Immigration by pollen dispersal may also result in additional fertilizations if, for example, the colonizing population is sparse.

2 Gene flow either by seed or pollen may serve to limit adaptation to the new habitat. Alternatively, it may reduce the effects of inbreeding that might be occurring in the individuals at the margins.

3 Stochastic spatial processes may allow immigration where in deterministic models such immigration may be impossible. The effects may be genetical (e.g. chance increase and fixation of chromosome variants that are disadvantageous in the het-

erozygous condition) or they may be ecological (e.g. spatial clumping of individuals in one region may minimize gene flow into that clump).

Numerous empirical and theoretical studies have now demonstrated localized differentiation for adaptive characters and determined the conditions that are likely to promote or retard such adaptation. Several studies (see Chapter 17) have recently modelled gene flow and selection where the number of surviving individuals is a direct function of localized genetic differentiation along an environmental gradient. However, these studies have not considered finite populations from an individually based context, where chance processes may be particularly important at boundaries. We therefore simulated conditions at the margin of a finite, two-dimensional plant population to test the general hypothesis that population boundaries may be determined by ecological factors which limit local adaptation to novel conditions, rather than by an absolute lack of genetic variation for the character(s) determining distribution.

The model

A source population was placed in one habitat, next to an unexploited habitat. The source population held rare alleles at three loci, and these alleles had low fitness in the source habitat but very high fitness in the novel environment. The actual ability of the source population to colonize the adjacent, novel habitat was monitored for varying seed and pollen dispersal distances under different spatial patterns of natural selection. Several specific questions were addressed in the context of whether the source population colonizes the unexploited habitat. In particular we asked: How long does the colonization process take? What are the specific effects of the patterns of natural selection and seed and pollen dispersal distances on population expansion? How are genetic differentiation and population growth in the new habitat related?

A two-dimensional area was defined with a grid of cells arranged on 50 rows and 100 columns. A maximum of seven different habitat types, numbered 0 to 6, were also defined to represent different selection regimes. Each point on the grid could be assigned a different habitat type, and any seed landing at that point would be subject to the corresponding selection regime. Thus, any spatial pattern of natural selection could be imposed by assigning groups of points the same number in the desired pattern.

Selection acted on phenotypes determined by three unlinked loci in the simplest possible model for a quantitative trait. Each locus had two alleles (0 or 1) with completely additive effects, so phenotypic values ranged from 0 (homozygous for 0) to 6 (homozygous for 1). Each phenotype had its maximum fitness in the habitat defined by the same number, and its fitness decreased in habitats defined by smaller or larger numbers according to a normal density function with a standard deviation of one habitat (Figure 5.7). Thus, the 0 allele was favoured in habitats with low numbers, the 1 allele was advantageous in habitats defined by high numbers. Relative fitnesses were translated into absolute fitnesses by multiplying by the maximum possible seed production for an individual. If the absolute fitness (seed number per individual)

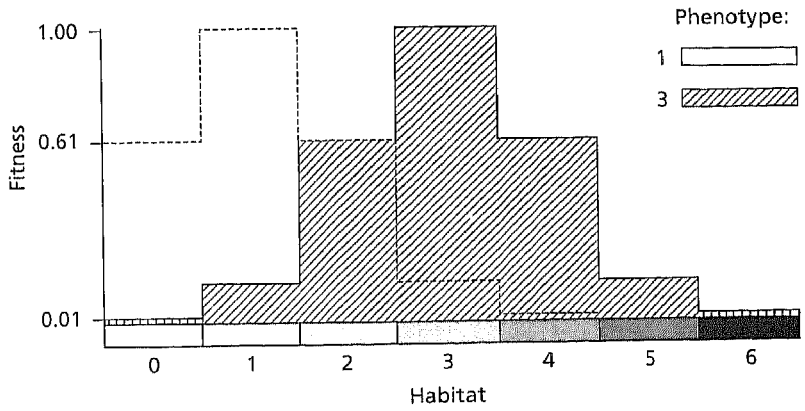

Figure 5.7 Relative fitnesses of two representative phenotypes, 1 and 3, in six habitats of differing quality. Note that each phenotype has the highest fitness in its correspondingly numbered habitat.

was less than 1, a fitness of 0 was assigned to the individual. We assumed no pollen limitation to seed set.

Population dynamics were determined by the occupancy of individual cells or sites on the grid, but only 10% of the points on the grid were designated at random as safe sites (i.e. occupiable). The maximum possible population size was 500, but actual sizes were less if safe sites were not colonized.

Each generation, the following series of events occurred. Maternal parents were mated to pollen parents, randomly one seed at a time. Gametes were sampled randomly from the maternal and paternal genotypes in each mating event, and no selfing was allowed. Seeds were dispersed individually onto the grid. At sites in which more than one seed landed, the surviving occupant was chosen at random. Seeds became the new adults, and their fitnesses (seed production) were calculated as above.

Dispersal of pollen and seed followed a normal distribution. For seeds, the site to which a seed was dispersed was selected randomly from among all sites the chosen distance away from the maternal parent. For pollen dispersal, a pollen parent was selected randomly for each mating event from among all plants the chosen distance away from the maternal parent. The average dispersal distances used (measured in rows and columns) were low (s.d. = 2), and high (s.d. = 10). Seeds that were dispersed to unsafe sites on the grid, or to sites off the grid, were lost (absorbing boundaries).

Three spatial patterns of natural selection were imposed. Each used habitat 0 as the native habitat and habitat 5 as the new habitat to be colonized, but the patterns differed at the transition zone between the two habitats (Figure 5.8). The 'sharp' pattern of selection had no intermediate habitat between habitats 0 and 5, the 'stepped' pattern of selection had a region of habitat 2 between habitats 0 and 5, and the

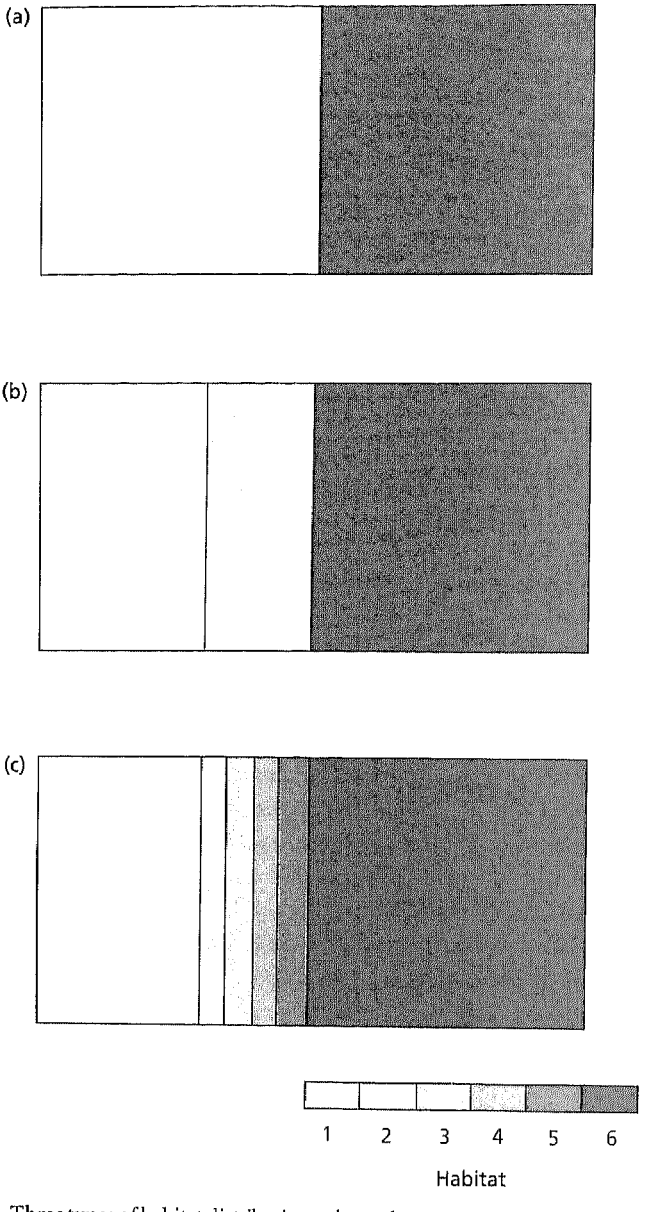

Figure 5.8 Three types of habitat distribution at boundary regions: (a) sharp; (b) stepped; (c) gradual.

'graded' pattern of selection had sequentially arranged sections of habitats 1 to 4 between habitats 0 and 5.

Each run started with a source population of 125 individuals in habitat 0. Most of these individuals were phenotype 0, but randomly chosen individuals were assigned

Table 5.1 Colonization success and average time to start of colonization for a population adapting to an adjacent marginal habitat characterized by three spatial patterns of selection at the boundary, and with different levels of seed and pollen dispersal (see text). Based on 50 simulation runs.

	Spatial pattern of selection	Seed dispersal low		Seed dispersal high	
		Pollen low	Pollen high	Pollen low	Pollen high
Percentage colonization success and time to colonization (generations)	Sharp	0 (–)	0 (–)	32 (45)	8 (52)
	Stepped	16 (29)	0 (–)	100 (4)	100 (4)
	Graded	82 (45)	0 (–)	100 (14)	100 (15)

a single 1 allele (and therefore were phenotype 1) such that the initial frequency of the 1 allele was 0.05 at each locus. The frequency of the 1 allele at any locus was not allowed to fall below 0.05 because preliminary simulations had shown that without resetting gene frequency, rare alleles were frequently lost at one locus.

The following information was obtained for each run:

1 colonization success—the new habitat was considered colonized when it held more than 50 individuals;

2 time to start of colonization defined as the generation at which the novel environment was continuously occupied by at least one individual;

3 distributions of gene frequency and plant density across the habitat boundary. At five-generation intervals, average gene frequency and population size were calculated for regions of each habitat defined by adjacent five-column sections of the grid.

Results

Colonization success

Invasion of a new habitat was much more likely when seed dispersal was high, and when intermediate habitats were included between the source population and the novel environment (Table 5.1). The stepped and graded spatial patterns of selection had similar effects on colonization success, except when seed and pollen dispersal distances were both low. In this case, individuals were more likely to colonize the new area when the change in selection was graded than when it was stepped. The average distance travelled by pollen had little effect on colonization success when seed dispersal was high, but when seed dispersal was low, long-distance pollen dispersal prevented population expansion under all three patterns of natural selection (Table 5.1). A supplemental run of 1000 generations with graded selection, and with low seed and high pollen dispersal distances showed successful colonization at generation 975, indicating that colonization under such conditions is not impossible, but rather highly improbable.

Time to start of colonization

In runs with no selection, it always took 10 generations for seeds to colonize the new habitat when seed dispersal was low, and one generation when seed dispersal was

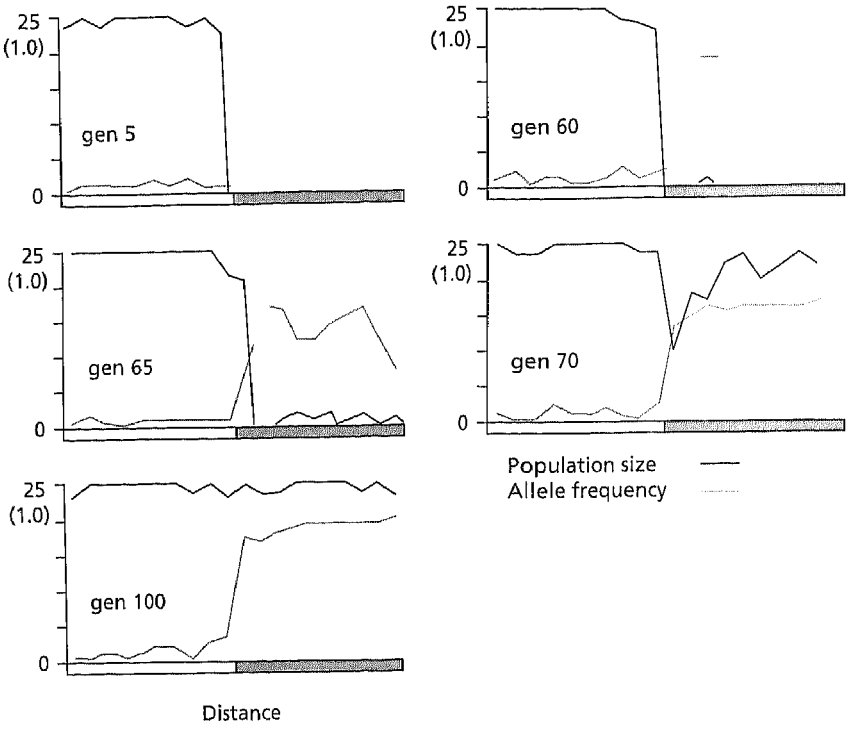

Figure 5.9 Plant density (solid line) and gene frequency (grey line) of a population colonizing and simultaneously adapting to a new habitat across an abrupt gradient, and where there is low pollen dispersal but high seed dispersal.

high. When selection was applied and colonization was successful, the generation in which colonization occurred was highly variable among replicates. Despite this variability, a trend towards earlier colonization can be seen under stepped selection as compared to graded selection (Table 5.1).

In many runs, the novel habitat was continuously inhabited from an early generation (often as early as generation 15 or 20), but was not colonized by the criteria used here, because the population of colonists never grew beyond about 10 individuals. This situation was seen frequently in the stepped pattern of selection, when seed- and pollen-dispersal distances were both low.

Spatial distribution

When seed dispersal was high, the temporal changes in the distribution of individuals during a successful colonization event were similar for all spatial patterns of selection and all pollen dispersal distances (Figures 5.9 and 5.10). Within approximately 10 generations, the density rose so that more than 90% of all safe sites were occupied. A cline in gene frequency was quickly established.

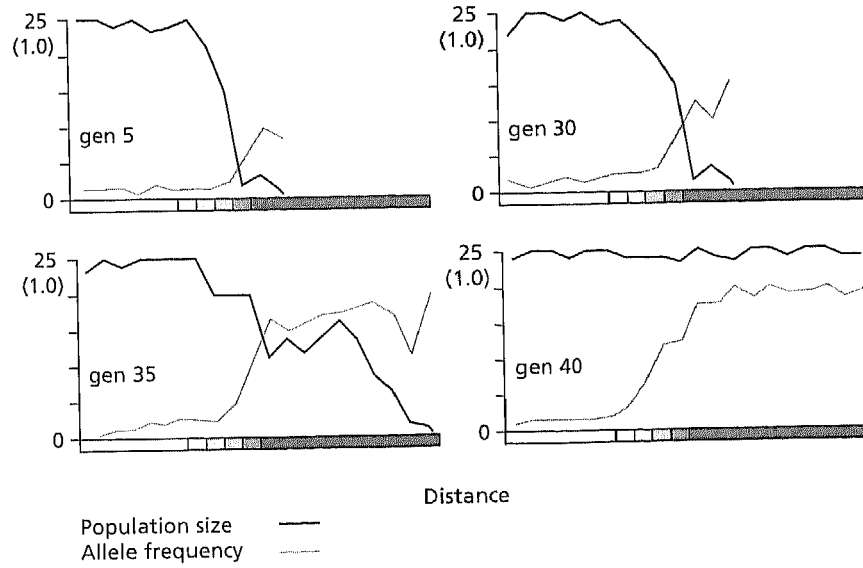

Figure 5.10 Plant density (solid line) and gene frequency (grey line) of a population colonizing and simultaneously adapting to a new habitat across a gradual habitat gradient, and where there is low pollen dispersal but high seed dispersal.

With a low seed-dispersal distance, the changes in population distribution depended on the spatial pattern of selection and on the pollen-dispersal distance. Under the sharp pattern of selection, no local adaptation occurred regardless of the pollen-dispersal distance, and the population ended abruptly at the edge of the novel habitat. An occasional colonist, weakly genetically adapted, extended the population boundary beyond the source habitat, but complete colonization never followed. When the selection pattern included intermediate habitats, the low and high pollen-dispersal distances gave different results. The low pollen-dispersal distance led to considerable local differentiation in the intermediate habitat, even when colonization was unsuccessful. When colonization occurred, the population advanced slowly at its margin into the new habitat (Figure 5.10), so that much of the time the margin of the population was characterized by a gradual decrease in population density. When the pollen-dispersal distance was high, colonization never occurred (within 100 generations) but genetic differentiation nevertheless developed in the intermediate habitats. (Figure 5.11).

Discussion

These simulations indicate it may be erroneous to make the simple inference that the absence of a species from a particular habitat means that neighbouring populations hold no genetic variation for the relevant characters. Instead, there are ecological and genetic factors which could inhibit the evolution of locally adapted subpopulations, thereby decreasing the likelihood that a new habitat can be exploited.

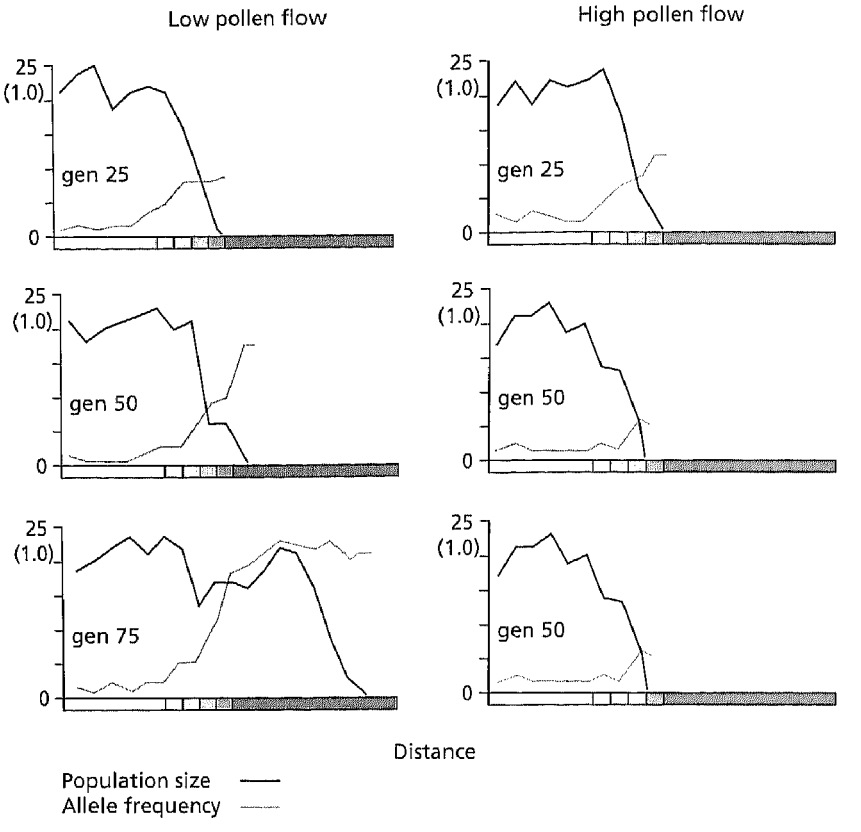

Figure 5.11 Plant density (solid line) and gene frequency (grey line) of a population colonizing and simultaneously adapting to a new habitat across a gradual habitat gradient, under conditions of low seed dispersal and either low or high pollen dispersal.

Long-distance seed dispersal had quite different effects from long-distance pollen dispersal. In fact, colonization was more likely when seed dispersal was greater, and the latter could completely mask the inhibitory effects of high pollen dispersal on colonization. There are several reasons why long-distance seed dispersal would have different consequences from long-distance pollen dispersal. First, selection acted on diploids, so ill-adapted seeds were screened from the migrants. Genes carried by migrant pollen, however, were not selected before mating, and so colonists often produced offspring ill-adapted to the new habitat. Secondly, if seeds are dispersed far into the new habitat, they may receive smaller amounts of ill-adapted pollen from the source population, making local differentiation easier to maintain. Thirdly, by increasing the number of offspring landing in the novel environment, a high seed-dispersal distance provided a greater number of opportunities for selection to pick out a locally adapted type. And finally, rapid population growth in the new habitat resulting from wide seed dispersal could have quickly increased the population size

above some critical level, so that enough pollen was available from colonists to proportionally reduce the amount of ill-adapted pollen received from elsewhere. If long-distance seed dispersal had any negative effect on the maintenance of local differences in gene frequency, the effect was confounded with, and counteracted by, other effects which promoted colonization.

The presence of intermediate habitats greatly facilitated the colonization of the extreme habitat because incremental selection promoted a local increase in the frequency of genes favoured in the new habitat, ultimately resulting in a genetic change that could not be achieved in a single step. This is not unlike methods employed in artificial selection programmes, where breeders can achieve drastic results, but only through gradual, incremental changes. It has never been demonstrated in the field to what extent the power of natural selection to achieve certain results is determined by spatial patterns of selection.

Replicate runs often gave qualitatively different outcomes, such that predictions could only be made in probabilistic terms about whether or not a colonization would occur in a particular ecological situation. The most striking illustration of the stochastic nature of colonization was the supplemental run of 1000 generations, using a high pollen-dispersal distance, a low seed-dispersal distance, and graded selection. For the first 974 generations, the population boundary remained static (as in the 100-generation replicate runs), with little or no evidence of local differentiation. Colonization suddenly occurred at generation 975. If this was a real population under observation for a substantial period of time (5, 10, or even 100 years), one might conclude erroneously that the population had reached the extent of its distribution, and would not invade adjacent habitats without the input of new genetic variation. This indicates that there is (as above in the purely ecological model) some critical event necessary for colonization that may or may not occur by chance. The critical event could be the chance production of a well preadapted genotype, genetic drift towards the favourable state in the new habitat, or the attainment of a local threshold population size which decreases effective pollen flow from the original habitat. To determine this, future studies will need to include 'pedigree tracing' (to show whether new establishments were migrants from the source population or offspring of the colonists), and explicit study of the two-dimensional spatial distribution of genotypes in successful vs. unsuccessful colonization events.

Conclusions

While there has been general recognition that processes at population margins are critical in determining the distribution and abundance of species, there has been remarkably little study of such margins at a population level. The goal of the studies presented here has been to develop a rigorous theory of such margins. Such a theory is timely because of the recent advances in computational techniques associated with mapping and remote sensing technology. Until now, the time and effort needed to do fine-scale mapping has been prohibitive, with the consequence that ecological margins have largely been studied at a coarse scale in terms of the correlation

of individual abundance with topographic, climatic or other readily measured variables.

Processes occurring at marginal populations may not only determine range extension and distribution, but these marginal populations may in turn have an influence on the dynamics of the more 'central' or source population. This is particularly likely where populations are small (or localized to small habitat patches), because in these cases boundary conditions will contribute relatively more to global dynamics than where populations are large. For example, we have shown (using mean-field models) that the presence of a 'passive refuge' can greatly influence the conditions for chaotic behaviour to emerge in the parent population (Newman *et al.* 2001). It is also well known that seed banks and resting stages (which can be considered as passive refuges) can have large consequences for above ground dynamics (Cohen & Levin 1991; Ellner & Hairston 1994), as can source–sink structuring of populations (Pulliam 1996).

Our studies have shown that processes occurring at margins can have counter-intuitive outcomes, and reaffirm that a simple correlational approach to causes of species distributions may be very misleading. In addition, we can expect that detailed analysis of marginal patterns (which we have not attempted) may give substantial insight into factors limiting populations at their ranges, as well as whether such ranges are expanding or retreating. Clearly this is important in understanding the effect of climatic or other environmental changes on distribution patterns, as well as in understanding the processes impinging on rare species and small populations where edge effects may predominate.

Summary

The distribution of species is often limited by environmental gradients, such that the abundance of a species declines in concert with some spatial change in biotic or abiotic factors. We use spatially explicit individually based models to investigate the patterns that occur at these boundaries, and to investigate range extension beyond the boundary as a result of genetic change. Our results show that patterns at population margins that result form birth, death and dispersal are quite different from those observed as a result of simple diffusion against a gradient. Distance moved along such a gradient is less than would be predicted by a mean field model. At the margins, local, short-lived 'flame-like' patterns develop, and such heterogeneity is accentuated rather than minimized in cumulative plots of individual distributions. Classical distribution maps based on cumulative records are therefore likely to exaggerate the heterogeneity of species boundaries and show poorer correlation with environmental gradients, relative to distributions obtained by intensive one time sampling. Interaction of abiotic gradients with biotic gradients was investigated by introducing a pathogen and allowing it to spread into the margin of the host population. While the low density of individuals at population margins initially prevents the invasion of disease into those margins, in the long term marginal populations and disease are sustained by a complex colonization–extinction dynamic where

there is no clear gradient in pathogen abundance at the margin. When genetic variants are introduced that can colonize an extreme habitat at the edge of a population, the success of these variants depends not only on the patterns of seed and pollen movement, but also on the steepness of the environmental gradient connecting the habitats. Colonization accompanied by genetic change is facilitated by a gradual environmental change. Even when colonization is unsuccessful, local clinal patterns can develop at the population margins. In simulation runs, the time to colonization was often highly variable, suggesting that spatially driven stochastic events (e.g. local aggregation) may be extremely important for successful invasion of a new habitat in the face of gene flow.

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