

Chapter 6

**SPONTANEOUS PATTERN FORMATION
AND DIVERSITY IN SPATIALLY STRUCTURED
EVOLUTIONARY ECOLOGY**

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ABSTRACT

Spontaneous pattern formation, the appearance of inhomogeneities that are not directly imposed by external forces, can be an important but overlooked factor in the origin and maintenance of genetic diversity in populations, and in parapatric speciation. Using agent-based simulation models with multilocus genetics, we show that such patterns form in spatially distributed populations with local mating neighborhoods. Under these conditions, disruptive selection induces spontaneous pattern formation and coarsening in the spatial distribution of genotypes, and thus increases the persistence of genetic diversity. The lateral motion of hybrid zones between different genotypes of similar fitness is affected by their topological shape. Hence, the shape of these boundaries plays a crucial role in determining the rate of genetic variation and the long time behavior of the population. These patterns also interact with boundary and internal obstacles of habitat structure, so that diversity persists the longest in habitats with the most irregular geographical features. Localized obstacles contribute to the maintenance of genetic diversity even if they do not preclude interbreeding, by inhibiting the movement of hybrid zones between areas dominated by different genotypes. Our results imply that the most effective size of such obstacles for maintaining diversity is about the same as the radius of a local deme. These results are relevant to spatial ecology and conservation

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biology, in which both genetic diversity and the size and shape of population reserves have great import for the long-term survival of species in the wild. They also imply significant coupling of population level and ecological properties to evolutionary dynamics. The persistence and amount of diversity, the relationship of diversity to evolutionary change, and the survival of types is controlled by the genetically undetermined spatial distribution of types and the structure of the habitat.

INTRODUCTION

Spontaneous pattern formation describes a process in which heterogeneous structure arises within a system through internal dynamics, without external forces playing any role in either the existence or the shape of the structure. More than five decades ago British mathematician Alan Turing presented a theoretical model of spatially extended chemical reactions that could create static patterns from homogeneous initial conditions (Turing 1952). After a long period of dormancy, the dynamics of such spatial pattern formation has recently been attracting attention in developmental biology to describe various general phenomena such as spontaneous cell differentiation in embryos, and specific phenomena such as the formation of pigment patterns on animal skins. Besides Turing's static patterns, there are several other distinct classes of spontaneous pattern formation that are found theoretically to be generic to large classes of models of interacting systems and are realized in a wide range of experimental physical/chemical systems.

Dynamic domain formation and coarsening behavior was first recognized in statistical physics for systems in which components take either of two (or a few) stable states and local interactions encourage local homogeneity (Lifshitz and Slyozov 1961). Since homogeneity is local, regions of one type or another form, but there are boundaries between these regions since global homogeneity does not immediately take place. This behavior can be seen in many natural and artificial systems, especially near a phase transition in which ordering takes place. These include magnetic ordering, and vapor to liquid, or liquid to solid transitions. For example, when magnets can order in one of two opposite directions, domains of each direction form, with sharp boundaries between them. Growth of the domains occurs by the process of boundary movement, which is very slow compared to the orientation time of individual atoms.

Here we show that this same ordering in local regions and boundary movement can also arise in evolutionary ecology. The local domains are regions of similar genetic type, while diversity is maintained by having regions of different types separated by boundaries that may be mobile or static hybrid zones. The recognition of this natural mechanism of diversity maintenance has useful implications for park planning and conservation.

The spatial dynamics and characteristics of domain formation have been extensively studied using analytical and computational methods (Bray 1994). The central feature of this behavior is the characteristic time dependence of the typical domain size that increases as a function of time (coarsening) as a result of interdomain boundary motion. Spontaneous pattern formation has recently been introduced into ecology to study spatial interspecific interactions (Durrett and Levin 1994; Tilman and Kareiva 1997), where the competition between two or more species may create a spatial pattern of species that changes over time.

However, these studies do not consider the possibility or implications of such pattern dynamics for intraspecific genetic diversity.

Here we consider a theoretical model of spatially distributed mating populations with multilocus genetics and show via agent-based simulations that spontaneously forming spatial genetic patterns increase the persistence of genetic diversity when selection favors two fit genotypes over their genetic intermediates (disruptive selection) (Bar-Yam 1999; Sayama et al. 2000a, 2000b, 2003). Moreover, we show that these patterns interact with habitat structure so that the habitat structure becomes directly relevant to the maintenance of genetic diversity □ but not quite in the way that we are used to thinking about spatial heterogeneity. Most ecologists consider genetic diversity as increasing with habitat heterogeneity due to harlequin selection. In this case, however, diversity arises and persists longer in larger habitats due to the time required for pattern coarsening by the motion of boundaries between extreme genotypes (hybrid zones). The internal structure of the habitat also matters. Localized obstacles that do not preclude interbreeding nevertheless contribute to the maintenance of genetic diversity by inhibiting the movement of hybrid zones. The most effective obstacle size to maintain diversity is found to be approximately the radius of a local deme.

These results are relevant to spatial ecology and conservation biology, in which both genetic diversity and the size and shape of population reserves are of concern due to their implications for long-term survival of species (Diamond 1975; Lynch 1996; Margules and Pressey 2000). They are also relevant to understanding the coupling of ecological properties to evolutionary dynamics. The persistence of diversity due to spatial patterns is counter to the usual Fisherian relationships between population diversity as measured by genetic variance and evolutionary change in well mixed populations. Moreover, the survival of types may be dramatically affected by their spatial arrangement. The spontaneous formation of patterns also can be considered a model for parapatric speciation. All of these processes couple evolutionary and ecological dynamics.

MODEL

We consider a spatially structured population of monoecious organisms with local but overlapping demes. Sexual reproduction of the organisms is described by a haploid, agent/individual-based model with multilocus genetics. An organism's genome has n loci, each of which has one of m possible alleles. One mature organism exclusively occupies one spatial site, reflecting the local carrying capacity. Organism reproduction generates P offspring at each site. Each of the offspring genomes is determined by random recombination of the genomes of two parent organisms randomly chosen within a distance R , the radius of a local deme. After reproduction, the fittest individual in the produced offspring at each site is selected to become a parent at the next generation.

The phenotype of each offspring is assumed to be a quantitative trait determined from its genome in such a way that each allele independently and additively contributes to the trait. Selection is applied using a fitness function that is maximal for extreme values of the quantitative trait. This has the effect of disruptive selection by selecting against organisms with intermediate trait values. It is equivalent to concave fitness sets, such as arise when a population evolves to exploit highly disparate resource types (Thoday 1972). Such disruptive

selection is considered a common and general cause of trait divergence (Kondrashov and Kondrashov 1999; Dieckmann and Doebeli 1999). The details of the model and the specific parameter settings chosen for the simulations are given in the Appendix.

Unlike many empirical studies in conservation genetics that focus on the spatial patterns of neutral markers, our study focuses on dynamic changes of adaptive genetic variation within populations under disruptive selective pressure against quantitative traits. In such settings we can characterize adaptive genetic variation by trait variation because they are strongly coupled, and in what follows we use the trait variance as a measure of genetic diversity.

In the results presented below we do not include mutation. We have also carried out simulations including mutation and found that results are not affected within the range of biologically realistic mutation rates (e.g. mutation rate per locus $\mu < 10^{-3}$). Even for unreasonably high mutation rates ($10^{-3} < \mu < 10^{-1}$) the results are only weakly affected through the slowed motion of hybrid zones. This illustrates the generic nature of coarsening behavior and its robustness to many model variations that respect the locality of interactions.

SPONTANEOUS PATTERN FORMATION

There is a dramatic contrast between theoretical predictions based on two different assumptions; (1) a panmictic population where R is infinite (i.e., mating is possible between all organisms [Figure 1; top]) and (2) a population with local demes where R is significantly smaller than the radius of the habitat (Figure 1; bottom). In the former case the population becomes restricted to one type after only a few generations. Under the latter condition the organisms locally tend to assume one or the other of two fittest types. Globally, spatial patterns with domains of two different genotypes form. Because the organisms are not physically isolated from each other, the hybrid zones between genotypes move laterally, in a direction so as to reduce their local curvature. The rate of motion increases as the local curvature increases. Inclusions of one type surrounded by the other type disappear over time, which may result in a final state that contradicts expectations based upon traditional frequency-dependent fitness (Figure 2). The spatial dynamics of the domains seen in this model is equivalent to the process of pattern formation and coarsening that occurs in nonbiological systems (Bray 1994). The robustness of these dynamics is apparent when we study the effects of variations in the model parameters n , m , R , or P . As long as there are two fittest genotypes under disruptive selection, a similar pattern formation and coarsening always results. Moreover, the observed dynamics of spatial patterns is also robust to minor fitness differences between favored genotypes (Figure 3). Even with significant fitness differences patterns still form, but they persist for shorter periods of time.

As mentioned above, such pattern forming and coarsening behavior has recently been proposed to occur in spatially distributed populations due to interspecific ecological interaction (Durrett and Levin 1994; Gandhi et al. 1998) and microevolution (Sayama et al. 2000a, 2000b, 2003). The key property common to both is the frequency-dependent dynamics in the local population growth, which is not captured by other purely random genetic drift models. The spatial patterns of genetic diversity shown in Figure 1 (bottom) are spontaneous self-organizing ones; there is no underlying spatial heterogeneity in the environment as a template. These spatial patterns of polymorphism are dynamic (due to the motion of hybrid

zones) and thus distinct from the static polymorphism found in subdivided and weakly coupled metapopulation models of ecological systems (Karlin and McGregor 1972; Levin 1974). The distinction is an important one, for the dynamics described here may be superimposed in nature on the more familiar patterns arising from habitat heterogeneity. Moreover, just as traffic jams are a spontaneous feature of heavy traffic flows, but they couple to local perturbations such as on or off ramps, the spontaneous pattern formation described here can also couple to, and thus dramatically enhance the effects of, the underlying habitat heterogeneity.

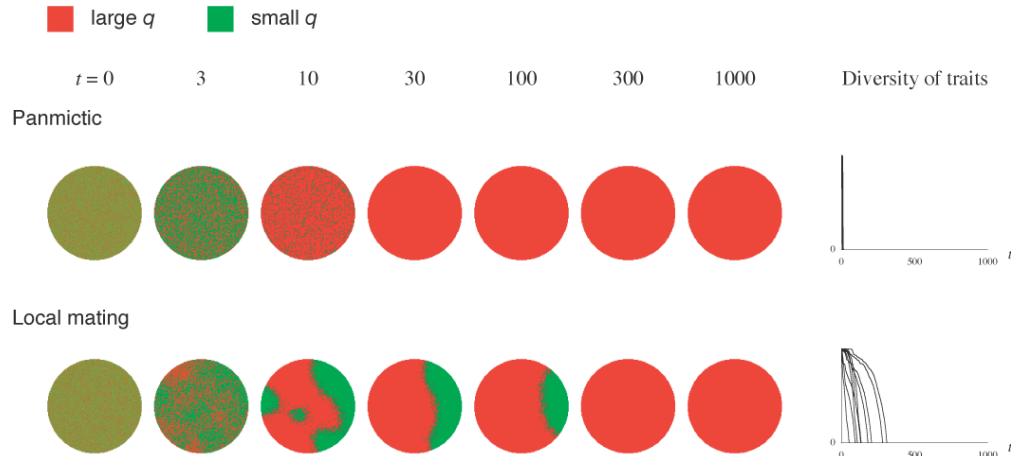


Figure 1. Simulations of pattern formation in a spatially distributed mating population undergoing disruptive selection initiated at $t=0$. Organisms are characterized by a quantitative trait q (see Appendix). Large and small q are favored over intermediate values of q by disruptive selection. On the right, the time dependence of the diversity is plotted for 10 sample simulation runs. Diversity is characterized by the variance of the trait distribution. These also apply to Figs. 2 to 5. **Top:** Simulations of a panmictic population, where organisms can mate regardless of spatial distance (i.e. the radius of the local deme R is infinite). In this case diversity vanishes only a few generations after the introduction of disruptive selection. **Bottom:** Simulations with local mating, where the size of local demes of organisms is smaller than the size of the habitat. Local mating causes pattern formation and thus persistence of genetic diversity.

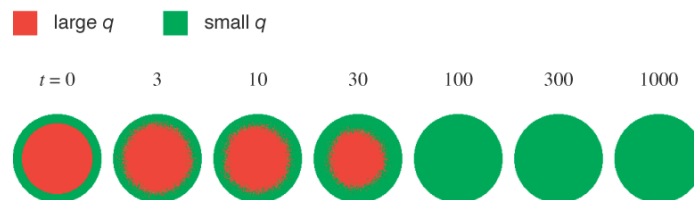


Figure 2. An extreme example of genetic changes determined by topological shape of hybrid zones. Initially, one of the two fittest genotypes (with large q) forms a big flock in the middle of the habitat, surrounded by a thin band of the other type (with small q). The flock occupies more than 60% of the total population so that frequency-dependent fitness difference predicts their dominance over the other type. Due to the circular shape of the hybrid zones, however, the initially dominant genotype is eventually dominated by the other. This result is robust to small changes in the model. Remarkably, even if the small q type has a slightly lower fitness than the high q type, it will still dominate over the long term (see also Figure 3).

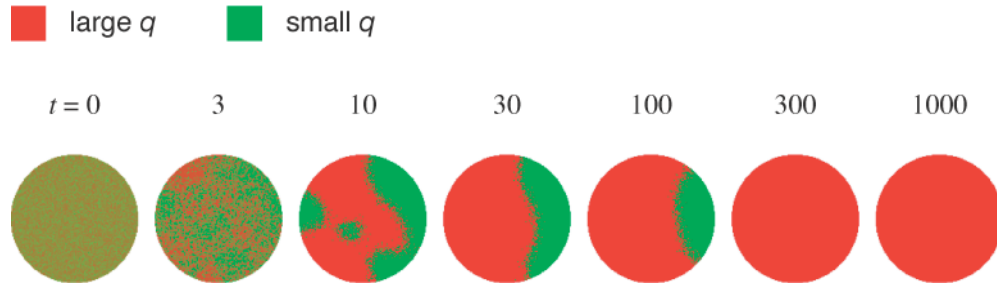


Figure 3. A simulation of pattern formation with small selection bias added to favor species of large q . The fitness of species of large q is increased by 1% compared to species of small q . The seed value of random numbers for this run is the same as that used in Figure 1 (bottom). While the fitness difference slightly promotes the propagation of hybrid zones from large q domains to small q domains, its effect is hard to detect visually. This implies the robustness of spontaneous pattern formation and coarsening dynamics against minor fitness differences between types.

The genetics of hybrid zones has been studied with increasing attention (Endler 1977; Barton 1979; Barton and Hewitt 1981, 1989; Harrison 1986, 1993; Nurnberger et al. 1995; Hewitt 2001), and the motion of hybrid zones has been seen in experimental observations (Pearson 2000; Britch et al. 2001; Rohwer et al. 2001). These studies typically analyze the dynamics of hybrid zones based on the difference between inherent fitness of two competing species where their domains meet. In contrast, our study deals with the spontaneous emergence of spatial separation between two equally favored types and the motion of hybrid zones by a particular kind of context-dependent fitness difference that arises from spatial distribution and dynamics, not simply from inherent biological superiority of one genotype. In our model, the local curvature of hybrid zones gives a local context-dependence to effective fitness. This may have a real-world significance, but has not yet been considered in studies on hybrid zones in the wild.

MAINTENANCE OF GENETIC DIVERSITY

We consider the relevance of the dynamics of such heterogeneous spatial patterns in the genotypes (and their associated hybrid zones) to the persistence of genetic diversity and, particularly, the significant role of habitat size and shape. These issues are typically not considered in theoretical or laboratory experimental studies that assume spatially homogeneous populations and that may specifically exclude consideration of edge and boundary effects.

Our results show that spontaneous pattern formation implies that the genetic diversity persists significantly longer in a population with local demes, as compared to a panmictic population when they are subject to disruptive selection (diversity plots in Figure 1). The time until homogenization increases with the size of the habitat (Figure 4), because the characteristic length scale of spatial patterns showing coarsening behavior grows as a square root of the elapsed time (Sayama et al. 2000a, 2000b) and therefore a longer time is needed to reach homogenization in larger areas. This suggests that protected habitats substantially smaller than natural ones will tend to lose genetic diversity more rapidly when disruptive selection occurs. This is of concern because high genetic diversity is widely considered to be

a key to the robustness and resilience of biological systems (Tilman and Downing 1994; Holling et al. 1995). The loss of diversity when only one of two original types is left is not just the loss of the other type, but also of the many possible crosses between them that might be of higher fitness if environmental changes occur.

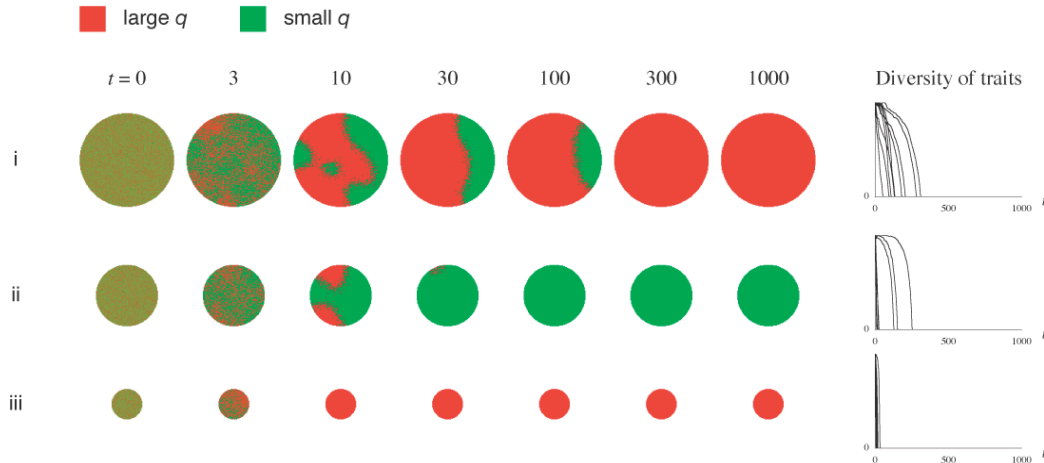


Figure 4. Simulations of pattern formation with local mating for three cases with different habitat sizes. The ratio of the diameter of one local deme to the total habitat diameter is about 16% for i, 25% for ii, and 50% for iii. The results for i is the same as shown in Figure 1. The time of diversity persistence is shorter for smaller habitats.

EFFECTS OF GEOGRAPHICAL IRREGULARITIES

The results in Figs. 1 to 4, and those obtained in other studies (Durrett and Levin 1994; Gandhi et al. 1998; Sayama et al. 2000a, 2000b), all apply only to simple habitat structures. To further study the implications of pattern formation, we consider the irregular geographical features that natural and protected habitats have. The effects of spatial barriers on static clines have been studied using reaction/diffusion equation models of gene frequency (Slatkin 1973; Nagylaki 1976; Fife 1979). Also, the effects of population subdivision on neutral genetic variation and effective population size have been studied using metapopulation models (Gilpin 1991; Gliddon and Goudet 1994; Hedrick and Gilpin 1997). In contrast with these earlier studies that calculated only stationary solutions (final structures) of genetic variation that reflect reduced migration rates between subpopulations in zero- or one-dimensional spaces, we consider the dynamic movement and transformation of curved hybrid zones and their interactions with localized obstacles in two dimensions.

Figure 5 shows examples of simulations representing habitats with internal obstacles of different sizes. Such irregular features inhibit and sometimes eventually stop the motion of hybrid zones and thus freeze coarsening patterns, preventing the reduction of genetic diversity through homogenization by reproductive mixing. We systematically evaluate the effectiveness of the internal obstacles in freezing the coarsening patterns by measuring the probability of persistence of polymorphism over time. Two parameters are varied: the size of an obstacle and the obstacle area fraction inside the habitat (the ratio of the area of the obstacles to the total area of the habitat). We have carried out over 10,000 simulation runs to

explore the parameter space. We define an *effectiveness index*, which measures the efficiency per unit area of internal obstacles, as the slope of a hyperbolic tangent fitted to $p(x)$, where p is the probability of maintenance of polymorphism and x is the obstacle fraction. Generally, the probability of polymorphism increases as the density of obstacles increases (Figure 6; embedded graphs). This is due to a decrease in the rate of local patch extinction through the pinning of hybrid zone motion. More significantly, the effectiveness index is found to be maximal when the size of obstacles is equal to the radius of a local deme (Figure 6; main plot). This can be understood in that obstacles smaller than the radius of a deme are not large enough to hamper local reproductive mixing and thus do not effectively freeze coarsening patterns. Obstacles at the size of the radius of a deme can freeze the patterns. Obstacles larger than this are not much more effective, but use a larger area and thus have a lower effectiveness. This result weakly depends on the circular shape of the obstacles we use. It is expected that if one used star-shaped obstacles, polymorphism would be retained with smaller covered areas having larger perimeters. However, the specific scale (diameter) of the most effective obstacles should be independent of their shape because it corresponds to the range of the mating processes.

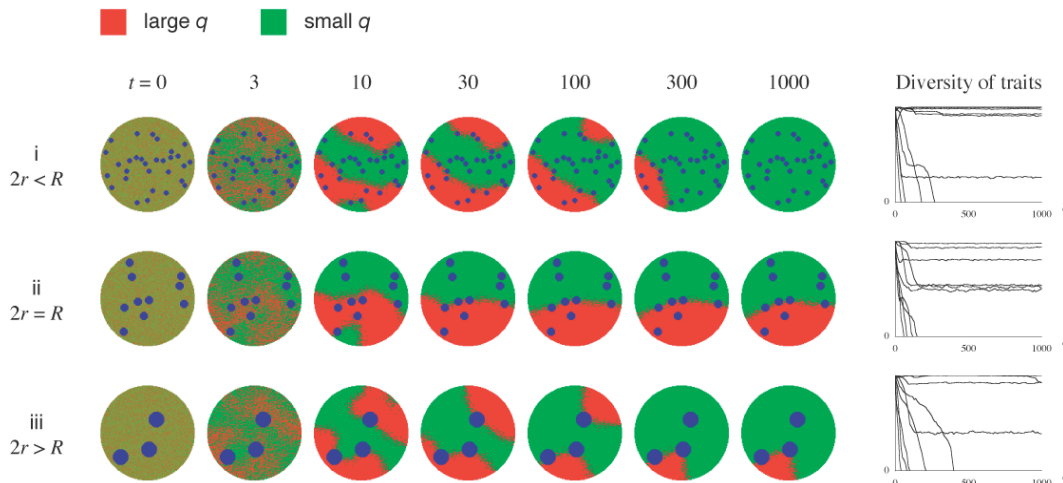


Figure 5. Simulations of pattern formation with local mating in a habitat that contains internal obstacles (blue spots). Three cases with different obstacle sizes (i, ii, iii) are shown, keeping the total obstacle area almost the same (r is the radius of the obstacles). Habitats with obstacles have a longer persistence of diversity due to the pinning of the motion of hybrid zones at the obstacles. The obstacles with a size $2r=R$ are found to be most effective (see Figure 6).

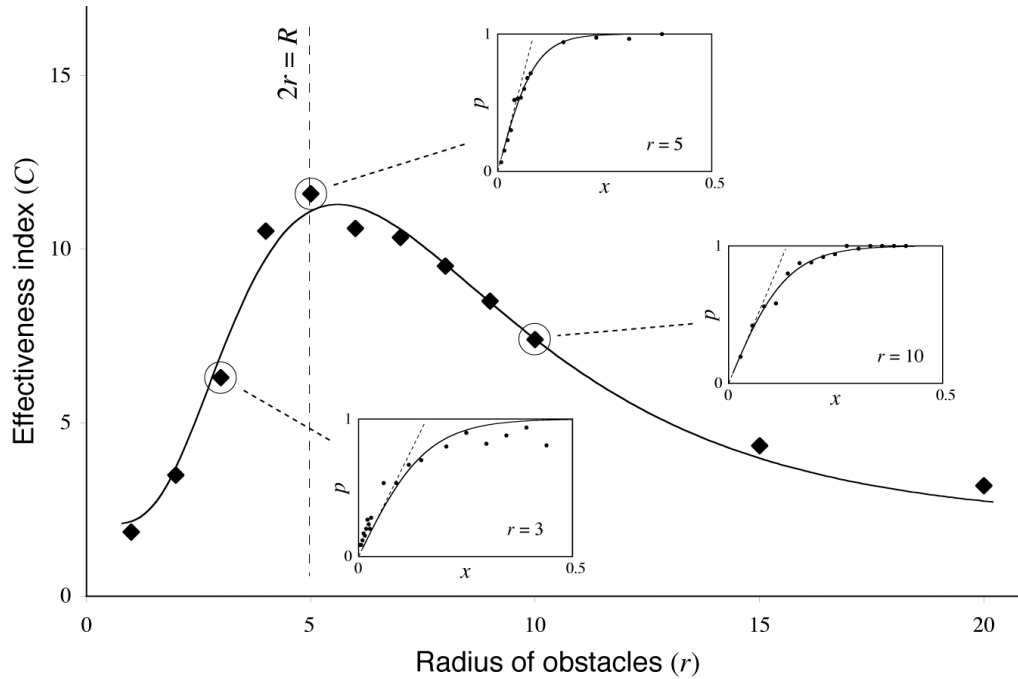


Figure 6. The relationship between obstacle size and effectiveness of obstacles in preserving diversity as measured by the effectiveness index C as a function of the radius of obstacles r . The effectiveness index is the initial slope of a hyperbolic tangent $p = \tanh(Cx)$ fitted to the simulation results $p(x)$, where p is the probability of maintenance of polymorphism and x is the obstacle fraction (the ratio of obstacle area to total area of the habitat). This measures the efficiency per unit area of the obstacles. A lognormal curve is fitted to the results for reference. This plot has a peak near $2r = R$. Thus, obstacles that are about as large as the radius of local demes are the most effective in maintaining polymorphism (Figure 5). The probability of maintenance of polymorphism was measured for each r and x using the final outcomes of multiple simulations for 500 generations, thus without obstacles the result would be zero. Each data point plotted in the embedded $p(x)$ graphs reflects the results of at least 20 runs, with an average of over 50 runs per point. The total number of runs used to obtain these results is over 10,000.

DISCUSSION

Our results on the implications of spatial pattern formation for genetic diversity in natural and artificial habitats can be summarized as follows: In the reference case, when selection occurs in the context of complete reproductive mixing of the population, the population diversity declines rapidly. Local mating results in the preservation of trait variation and genetic diversity over substantially longer times according to our spatially extended population model. Even in the context of local mating, however, the diversity eventually declines, and does so more rapidly for smaller habitats. Local geographical irregularities can further extend the retention of a higher diversity. The effect of localized irregularities should be contrasted with the effect of habitat partitioning. Absolute partitioning is not desirable because it will result in small populations with a high probability of extinction. Spatial obstacles, even though they do not partition the space, inhibit complete reproductive mixing and are effective in maintaining genetic diversity in a geographically contiguous population.

The effect of local obstacles is not restricted to their immediate vicinity. By impeding the motion of hybrid zones, these obstacles can impact on the diversity of the entire habitat, a substantial long-range or non-local effect. Our results imply that where it is possible to design such obstacles, using obstacles whose size approximates the radius of the local demes may lead to maintenance of polymorphism with a minimal sacrificed habitat area. Other factors should also be considered in practical planning (e.g., total availability of suitable habitats, potential influences of obstacle construction, etc.).

In additional studies we found that convoluted habitat boundaries also freeze coarsening patterns (Sayama et al. 2000b). The implications of this result are counter-intuitive, for it implies that genetic diversity could be enhanced by increasing the ratio of habitat edge to area. For actual habitat design, however, taking advantage of this effect would also increase undesirable edge effects, such as microclimate deterioration or invasion by predator and weed species. Thus, from a practical viewpoint, external boundaries of protected habitats should probably be kept as short as possible because they are generally sources of environmental degradation and encroachment.

Our results suggest that internal obstacles in habitats might be introduced to enhance the maintenance of genetic diversity. What would the internal obstacles implied here actually be in any practical application? In an aquatic system they could be islands of a different physical environment, such as rocky reef on a mud or sand bottom. In a terrestrial park they could be fenced-off areas whose inside and outside are both protected and in which, for example, conservation and ecology management experiments could be conducted. In an era where the trend in zoological parks is to become as natural as possible, it might seem abhorrent to unleash interior designers upon the small nature reserves that we fondly but erroneously regard as accessible miniwildernesses (Nairobi National Park comes to mind). With few vast areas of true wilderness remaining in the world, current strategies for endangered species survival call for the maintenance of as many independent, self-sustaining populations as possible to maximize both total population size and genetic diversity. Our work suggests that, at least for some species, careful planning can maximize the conservation value of any one of these highly constrained remnant habitats.

To understand the more general implications for diversity, it is necessary to consider the population of organisms that arise from multiple disruptive selection events occurring at different times, as opposed to a single one. Each of these events may affect different aspects of the organismal traits corresponding to different but possibly overlapping sets of genes. As environmental changes occur, disruptive selection affecting various traits and/or loci introduces new patterns of covariance in the allele population that correspond to patterns of population differences. If the correlation between these distinct disruptive selection events is sufficiently weak, these patterns coarsen over time almost independently. Otherwise they may interfere with each other. Figure 7 shows preliminary studies on spontaneous pattern formation due to sequential introduction of disruptive selection. Two distinct disruptive selection events, which are orthogonal to each other in genome space, create two overlapping and independently coarsening patterns, which divide the population into four different types. In such cases, at a particular time, the history of introduction of disruptive selection events is apparent as a set of overlapping patterns that exist on various spatial scales. Larger scale features correspond to differences that were introduced earlier in time (or had a stronger type dominance).

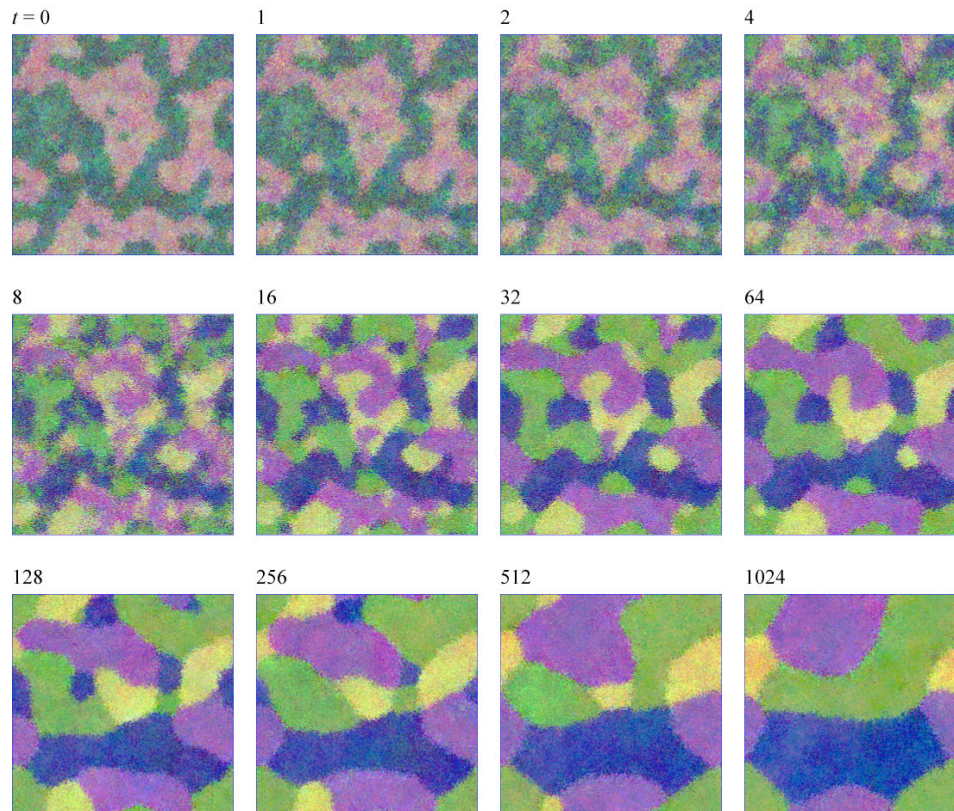


Figure 7 A simulation of pattern formation with local mating under sequential introduction of disruptive selection. The parameters used are $n=10$, $m=10$, $P=2$, $R=3$, and the space is a square area of 256×256 sites with periodic boundary conditions applied to its edges. These choices are to make the overlapping coarsening behavior more visible. $t = 0$ is 32 generations after the first disruptive selection was introduced to the population. At this time, the second selection that is orthogonal to the first one in genome space is introduced, leading to overlapping coarsening patterns of four different genotypes. During the coarsening process, the characteristic scale of patterns caused by the first selection (blue-green vs. yellow-purple) is larger than that by the second (blue-purple vs. green-yellow), reflecting its earlier introduction to the population.

This study also provides new insight into the origins of genetic diversity as a possible precursor of speciation. Recent studies have acknowledged the relevance of symmetry breaking to speciation (Kondrashov and Kondrashov 1999; Dieckmann and Doebeli 1999). Our results indicate that a spatially distributed species may spontaneously split into multiple different types that keep physical contact with each other in the absence of inhomogeneous habitat structure. At the hybrid zones between these types, mechanisms for reproductive isolation would be favored since they would increase reproductive success, facilitating trait divergence and formation of multiple species. The first step would be the appearance of a mutation leading to reproductive isolation at a location along the boundary. The benefits of reproductive isolation would cause this trait to propagate along the boundary, but also away from boundaries. The propagation away from boundaries would occur because reproductive isolation at boundaries would enable the types to coexist spatially, leading the boundaries to thicken, increasing the boundary area and consequently the benefit of reproductive isolation would extend to neighboring areas. Thus, the evolutionary benefit of reproductive isolation

would spread throughout the population propagating outward from the point of origin both along and away from the original boundaries. This process would give rise to parapatric speciation – speciation that takes place in a spatially distributed population with no geographical barriers. Previous studies on parapatric speciation (Manzo and Peliti 1994; Gavrillets et al. 1998, 2000) used stepping-stone models with several subpopulations and weak migration between them. Our model is unique compared to these earlier models in that it considers a spatially contiguous population in two dimensions with overlapping demes and the behavior of coarsening domains of different genotypes.

Finally, our results demonstrate the existence of powerful linkages between biological processes at three different scales. Spontaneous pattern formation and its interplay with geographical features are emergent traits of ecological populations, caused by attributes of the organismal reproductive process that reflect genetic recombination inside each organism. This is an important example that contradicts the erroneous but commonly held assumption that it is possible to neatly partition evolutionary effects at different spatial scales (i.e., the study of molecule, individual, population, metapopulation, species, or ecosystem). Indeed, when hierarchical structure is considered as a signal attribute of complex systems, it is the dynamic linkages among the levels, rather than the number of levels themselves, that should probably be the focus of attention. We emphasize that the self-organization of dynamic patterns through multiscale interactions is a characteristic of properties of diverse complex systems, including spatially distributed living systems (Bar-Yam 1997), and that recognition of this can lead to deeper insights into community organization and evolution.

APPENDIX : DETAILS OF THE SIMULATION MODEL

The model used for this research is an agent-based model with a two-dimensional spatial grid of sites in which each site can contain one mature monoecious organism with an n -locus genome (also see Figure 8). Haploid and diploid models both yield similar results, and we present the results obtained with haploid models in this chapter. There are m possible alleles for each locus. The genome of an organism determines a quantitative trait q . Each allele is assumed to independently and linearly contribute to the trait (i.e., $q = \sum a_i$, where a_i is an integer ranging from 0 to $m-1$ that represents the effect of the allele at the i th locus). The possible traits range from 0 to $n(m-1)$. Modifying the assumption of linearity of allelic effects to traits can change the relative allelic diversity between different loci, but does not significantly change the general results on the dynamics of spatial patterns reported in this chapter. Fitness is a function of the quantitative trait, $f(q)$, which is lowest for intermediate values of the trait and highest for the two extreme values. We have tested several different fitness assignments, including V-shaped, quadratic, and discrete (stepwise) dependences of the fitness as a function of the trait. All these assignments yield the same results. Reproduction in the model assumes random genetic crosses between two parent organisms (i.e., the allele at each locus is inherited from either of two parents independently). The parent organisms are chosen randomly out of a local neighborhood of radius R around each site. Such mating processes are repeated P times per site per generation, then the fittest individual

of the P offspring at each site becomes the selected parent at the next generation. We do not consider the effects of mutation for simplicity.

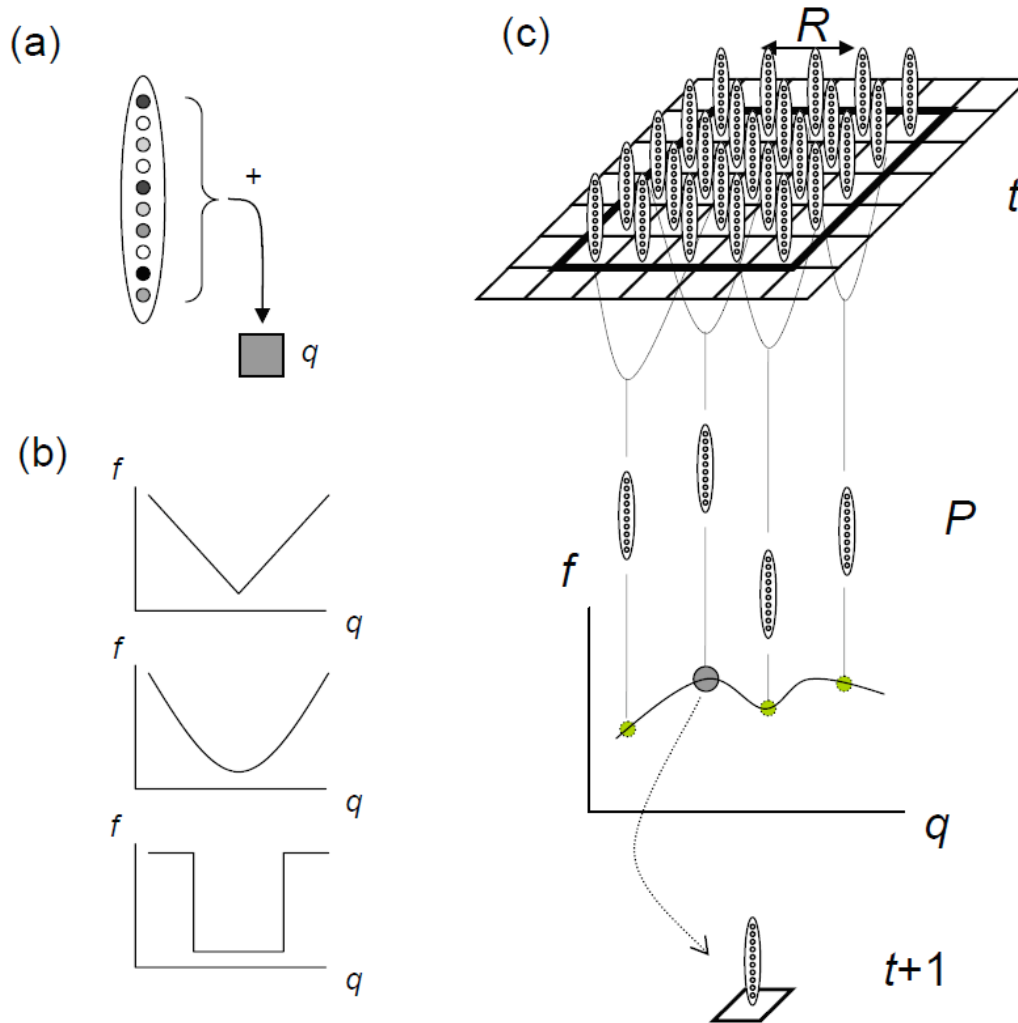


Figure 8. Schematic illustration of the simulation model. (a) An organism has a haploid n -locus genome. Each locus takes one of the m different alleles (shown in grey-scale shades). The quantitative trait of the organism q is determined by the sum of the effects of alleles on all loci. (b) Fitness f is given by a nonlinear function of the quantitative trait q that is lowest for intermediate values of the trait and highest for the two extreme values. (c) Each spatial site in a two-dimensional domain is occupied by one organism. In reproduction, two organisms are randomly picked up within a local neighborhood of radius R (either square or circular) and their genomes are randomly recombined to produce an offspring. Such mating is repeated for P times per each spatial site. The offspring with largest f wins to occupy the site in the next generation.

The parameters used in the figures are $n=10$, $m=10$, $P=10$, $R=10$ unless otherwise noted, and the fitness of a trait is a V-shaped curve (i.e., the fitness is linearly related to the trait value distance from the median possible value [$f(q) = |q - n(m-1)/2|$]). The habitat is a circular space with a diameter of 127 site widths long (except for Figs. 4ii, 4iii and 7). For

simulations described in Figs. 5 and 6, circular obstacle patterns on which organisms cannot exist are randomly placed inside the habitat in such a way that they neither overlap each other nor stick out from the habitat. The initial conditions consist of organisms with randomly assigned genotypes. This can arise when selection becomes disruptive after being nondisruptive.

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