

## Chapter 1

# The role of spontaneous pattern formation in the creation and maintenance of biological diversity

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We show that in the presence of disruptive selection, spatial distributions of sexually reproducing organisms with local mating neighborhoods give rise to symmetry breaking and spontaneous pattern formation in the genetic composition of local populations. Global dynamics follows conventional coarsening of systems with non-conserved order parameters in statistical physics. These patterns interact with boundary and internal barrier structures so as to generate counter-intuitive increases in diversity in patches with high perimeter-to-core ratios. The results have significant implications for the creation and maintenance of biological diversity and species formation.

### 1.1 Introduction

Biological diversity in nature is known to be hierarchical and spatially heterogeneous. In conventional discussions in ecology and population biology, the observation of harlequin distribution patterns of sister forms has gener-

ally been attributed to inhomogeneities in the environment. In other words, these patterns reflect features of the underlying habitat (= selective) template. In the meantime, the study of spatially distributed ecosystems has attracted substantial modeling based both on nonlinear dynamics and statistical physics methods[3, 4, 5, 7]. Among these are studies of spontaneous pattern formation (Turing patterns) in reaction diffusion type models of ecosystems of competing organisms[6]. These models demonstrate the importance of spatial heterogeneity in the context of local biological interactions. However, this type of analysis has not yet been extended to considering restricted mating neighborhoods or the resulting multiscale relationships between allelic correlations and genetic diversity.

We will show in this article that selection against functional intermediates (i.e., disruptive selection) can, for organisms with local mating neighborhoods, give rise to spontaneous pattern formation in the genetic composition of local populations. This pattern can be independent of underlying habitat structure. Spatial separation is essentially equivalent to isolation, but instead of requiring geographical or physical barriers, virtual barriers emerge as self-consistent generated isolation. This result is a typical example of symmetry breaking in evolution to which the gene centered view, or the mean field approximation to the genetic composition, does not apply[1]. Global dynamics of these patterns follows conventional coarsening of systems with nonconserved order parameters in statistical physics. Moreover, in sharp contrast to conventional predictions, populations distributed with high perimeter-to-core area ratios generate and maintain higher spatial diversity than those with simpler, circular domains. These results have significant implications for several biological/ecological issues, such as the origins of biological diversity, the mechanisms of sympatric speciation, and the design of protected habitats that can maintain or reverse the current dramatic decrease in biological diversity.

## 1.2 Symmetry breaking and spontaneous pattern formation in spatially distributed populations

We study the relevance of spontaneous pattern formation to biological diversity within a spatially distributed versions of the model we have proposed earlier[1]. This basic model is a simplest model of sexual reproduction and disruptive selection—selection in favor of two genotypes whose hybrids are less viable. Organisms are assumed to have two nonhomologue genes with selection in favor of a particular combination of alleles on genes. Specifically, after selection, when allele  $A_1$  appears in one gene, allele  $B_1$  must appear on the second gene, and when allele  $A_{-1}$  appears on the first gene allele  $B_{-1}$  must appear on the second gene. We can write these high fitness organisms with the notation  $(1, 1)$  and  $(-1, -1)$ , and the organisms with lower fitness (for simplicity, non-viable) as  $(1, -1)$  and  $(-1, 1)$ . These assumptions give a simple update equation in terms

of the population of (1, 1):

$$p(t+1) = \frac{p(t)^2}{p(t)^2 + (1-p(t))^2} \quad (1.1)$$

For a detailed derivation see reference[1]. When correlations in reproduction are neglected, there are two stable states of the population with all organisms (1, 1) or  $p = 1$ , or all organisms (-1, -1) or  $p = 0$ . Although  $p = 0.5$  is also an unstable steady state, any small bias in the proportion of one or the other will cause there to be progressively more of one type over the other, and the population will eventually have only one set of alleles.

Assuming overlapping local reproduction neighborhoods in the model above, the relevant equations are

$$p(x, t+1) = D(\bar{p}(x, t)) \quad (1.2)$$

$$D(p) = \frac{p^2}{p^2 + (1-p)^2} \quad (1.3)$$

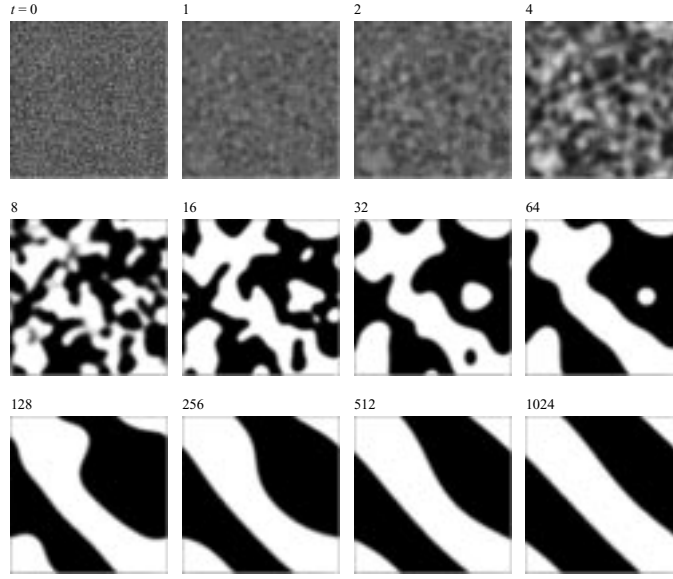
$$\bar{p}(x, t) = \frac{1}{N_R} \sum_{|x_j| \leq R} p(x + x_j, t) \quad (1.4)$$

$$N_R = |\{x_j \mid |x_j| \leq R\}| \quad (1.5)$$

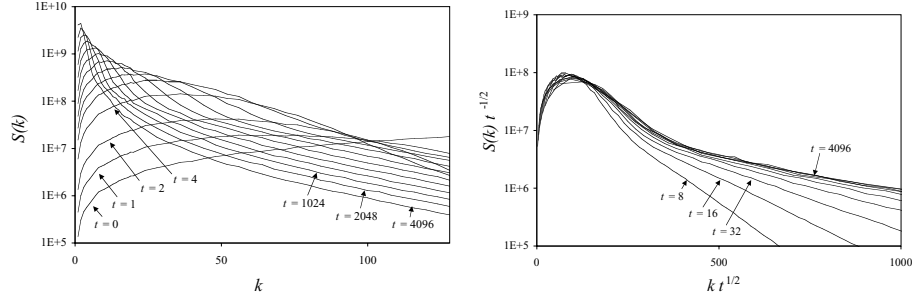
where the organisms are distributed over a two-dimensional grid and the local genotype averaging is performed over a preselected range of grid cells around the central cell ((1.4) and (1.5)). Under these conditions the organisms locally tend to assume one or the other type. In contrast to conventional insights in ecology and population biology, there is no need for either complete separation of organisms or environmental variations to lead to spatially varying genotypes. However, because the organisms are not physically isolated from each other, the boundaries between neighboring domains will move, and the domains will follow conventional coarsening behavior for systems with non-conserved order parameters in statistical physics, such as an Ising ferromagnet model with low temperature, as demonstrated below.

A simulation of this model starting from random initial conditions is shown in Fig. 1.1. These initial conditions can arise when selection becomes disruptive after being non-disruptive due to environmental change. The formation of domains of the two different types that progressively coarsen over time can be seen.

While the evolutionary dynamics describing the local process of organism selection is different, the spatial dynamics of domains is equivalent to the process of coarsening that occurs in many other systems[2]. Fourier transformed power spectra (Fig. 1.2 and Fig. 1.3) confirm the correspondence to conventional coarsening by showing that the correlation length grows as  $t^{1/2}$  after initial transients. Since flat boundaries do not move except by random perturbations, a non-uniform final state is possible in a finite sized system. The addition of noise will cause slow relaxation of flat boundaries but they can also be trapped by quenched (frozen) inhomogeneity.

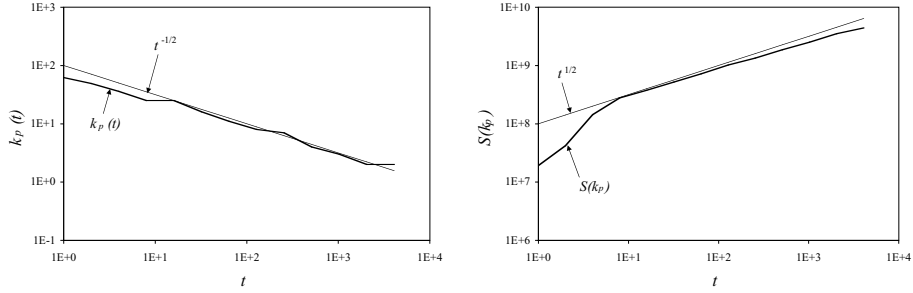


**Figure 1.1:** Spatially distributed evolution with disruptive selection giving rise to two types appearing in patches and coarsening. The space is periodic and has  $256 \times 256$  sites, and the mating neighborhood radius is  $R = 5$ .



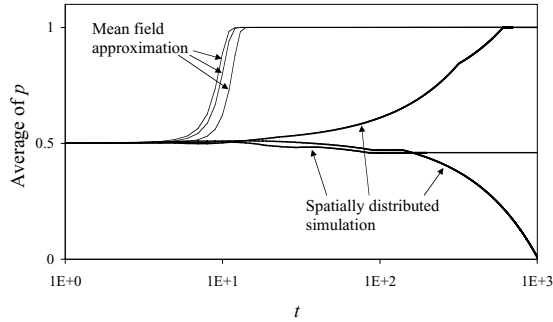
**Figure 1.2:** Fourier power spectra averaged over ten simulations of evolutionary processes like that shown in Fig. 1.1 ( $512 \times 512$  sites and  $R = 1$ ). Left: Raw spectra. Right: Collapsed version demonstrating the scaling form  $S(k) = t^{1/2} f(kt^{1/2})$ .

A dramatic contrast between theoretical predictions which can be studied through experimental observations is the comparison between expectations under the mean field approximation (which corresponds to the gene centered view of evolution[1]) and predictions of simulations that allow for symmetry breaking and spontaneous pattern formation. An example of such a comparison is shown in Fig. 1.4 where the population averaged time dependence of  $p$  is shown. The persistence of diversity in simulations with symmetry breaking, as compared to its disappearance in the mean field approximation, is clear. The mean field ap-



**Figure 1.3:** Temporal behavior of the peak of a Fourier power spectrum in the shown case. Left: The peak frequency  $k_p(t)$  which follows approximately  $t^{-1/2}$ . Right: The peak power  $S(k_p)$  which follows approximately  $t^{1/2}$ .

proximation would predict a rapid homogenization over the entire population. The spatially distributed simulation with symmetry breaking predicts that when population diversity is measured locally, rapid homogenization similar to the mean field prediction will apply, while when they are measured over areas significantly larger than the expected range of reproduction, extended persistence of diversity should be observed.



**Figure 1.4:** Comparison of the time dependence of type probability in the mean field approximation and the spatially distributed simulation with symmetry breaking, calculated using different random number sequences. Diversity persists much longer in the latter. In some cases, forever.

### 1.3 Implications to ecology and conservation biology

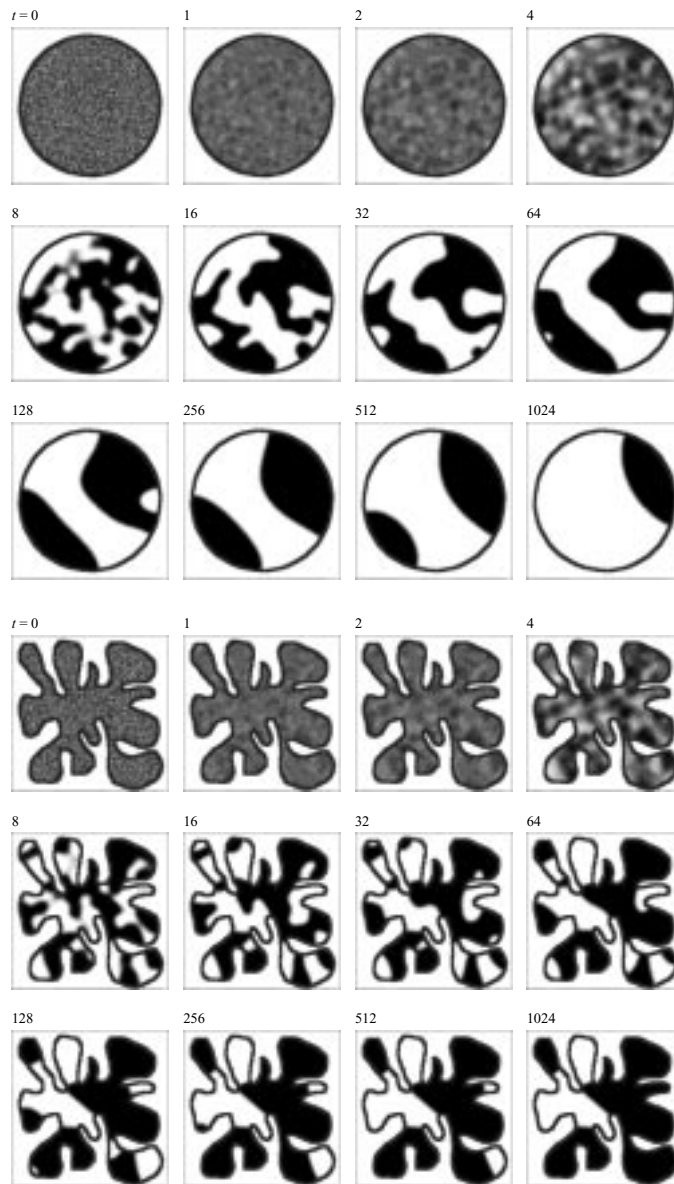
It is important to emphasize that the patterns of genetic diversity in the pictures shown above do not arise from any underlying spatial inhomogeneities in the environment. They are completely spontaneous / self-organizing patterns.

There is a long tradition of studies in distribution and abundance that attribute pattern formation to various types of interactions between organism and environment, between organisms and each other, and between organisms and agents of disturbance. It is also widely recognized that many aspects of distribution and abundance are the result of historical contingency or stochastic dispersal processes. What is needed for a better understanding of spatial diversity seen in nature is a grasp of the types of patterns that can arise through self-organization, or of the interaction between pattern generators, like the results shown in this article. The notion of self-organization does not contradict the possibility of the influence of environmental inhomogeneity; on the contrary, the two processes can work together. The impact of environmental variations is reinforced by the processes that would spontaneously cause inhomogeneity. Environmental variations directly couple to the effects of genetic diversity due to disruptive selection, through symmetry breaking. Specifically, spatial variation in environments will reinforce particular spatial patterns and tend to “freeze” them.

In addition, the effects of the boundary structure of ecological systems can be directly studied in this model.

Conservation biologists are very concerned about the size and shape of population reserves, due to their implications for long-term survival of threatened and endangered species. Conventional wisdom holds that a high perimeter-to-core area ratio leads to increased rates of extinction due to exaggerated edge effects—the notion that individuals close to the edge of a reserve boundary (or habitat interface) are at increased risk due to a constellation of physiological and ecological considerations. One would thus predict that reserves with convoluted boundaries will exhibit high rates of decay in species and genetic diversity.

However, this tenet is relevant only to the process of diversity decay. It ignores other processes responsible for the generation and maintenance of diversity. Our results show that generative processes such as those demonstrated here can give rise to complex spatial patterns of genetic diversity, with important implications for conservation biology and evolutionary theory. In Fig. 1.5 we show simulations of the pattern formation process starting from the identical initial condition but clipped out using two different boundary templates; one is a simple circle and the other is in an elaborated shape. It is clear that features of the boundary that are of a particular size tend to trap patterns at that scale maintaining the diversity in the face of the processes of reproductive mixing that tend to homogenize the population. The implications for the design of habitats for endangered species can be understood from this result as follows: During the process of restoration of population size, organism survival is generally promoted and the development of diversity of the population arises from multiple cross breeding. However, once the population achieves a size which is significant compared to the carrying capacity of the land, the effects of selection will tend to reduce the diversity which is created. When this selection takes place in the context of complete reproductive mixing of the population, the population diversity will rapidly decline. To avoid this effect, partial isola-



**Figure 1.5:** Simulations in a simple (circular) domain, and in a domain with elaborated boundary shape. The space is periodic and has  $256 \times 256$  sites, and the mating neighborhood radius is  $R = 5$ .

tion of reproducing populations will retain higher diversity. Complete isolation is not desirable as it will result in small unstable communities. However, partial isolation through spatial distribution can be effective in maintaining ecological

diversity in a unified population.

## 1.4 Conclusion

We showed using a simple model that spatial distribution of sexually reproducing and locally mating organisms spontaneously generates spatial patterns of segregated genotypes in the presence of disruptive selection. The global dynamics of these patterns is the same as that of conventional domain coarsening models in statistical physics. These results can be viewed as a spatially distributed trait divergence in a single ecosystem and has significant implications in the creation and maintenance of biological diversity. In particular, the spatial patches will more likely to last when the boundary of a domain is more complex and more capable of holding different types of subpopulations, which is counter-intuitive to conventional predictions in conservation biology.

To understand the more general implications for diversity it is necessary to consider the population of organisms that arise from multiple disruptive selection events, not just a single one as shown in this article. Each of these events can affect a different aspect of the organism / different sets of genes. Thus, in a more complete model, the introduction of disruptive selection would occur not once, but many times. Single organism evolution in the above discussion can also be replaced throughout by co-evolution of organisms.

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