

## Symmetry breaking and coarsening in spatially distributed evolutionary processes including sexual reproduction and disruptive selection

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Sexual reproduction presents significant challenges to formal treatment of evolutionary processes. A starting point for systematic treatments of ecological and evolutionary phenomena has been provided by the gene-centered view of evolution which assigns effective fitness to each allele instead of each organism. The gene-centered view can be formalized as a dynamic mean-field approximation applied to genes in reproduction and selection dynamics. We show that the gene-centered view breaks down for symmetry breaking and pattern formation within a population and show that spatial distributions of organisms with local mating neighborhoods in the presence of disruptive selection give rise to such symmetry breaking and pattern formation in the genetic composition of local populations. Global dynamics follows conventional coarsening of systems with nonconserved order parameters. The results have significant implications for the ecology of genetic diversity and species formation.

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The dynamics of evolution can be studied by statistical models that reflect properties of general models of the statistical dynamics of interacting systems [1]. Research on this topic can affect the conceptual foundations of evolutionary biology and many applications in ecology, population biology, and conservation biology. Among the central problems is understanding the creation, persistence, and disappearance of genetic diversity. In this paper, we describe a model of sexual reproduction which illustrates mean-field approaches (the gene-centered view of evolution) and the relevance of symmetry breaking and pattern formation in spatially distributed populations as an example of the breakdown of these approximations.

Pattern formation in genomic space has been of increasing interest in theoretical studies of sympatric speciation [1–7]. These papers advance our understanding of the mechanisms of forming two species from one. However, they do not address the fundamental and practical problems of genetic diversity and spatial inhomogeneity within one species—a population whose evolution continues to be coupled by sexual reproduction. Moreover, and significantly, these papers do not address the implication of symmetry breaking and pattern formation for the gene-centered view as a fundamental framework of evolutionary theory. In the following, we demonstrate that symmetry breaking and pattern formation invalidate the gene-centered view (whether or not speciation occurs) and that they are important for the spatiotemporal behavior of the genetic composition of sexually reproducing populations. This has a wide range of implications for ecology, conservation biology, and evolutionary theory.

Before introducing the complications of sexual reproduction, we start with the simplest iterative model of exponential growth of asexually reproducing populations:

$$N_i(t+1) = \lambda_i N_i(t), \quad (1)$$

where  $N_i$  is the population of type  $i$  and  $\lambda_i$  is their fitness. If

the total population is considered to be normalized and the relevant dynamics is only of the proportion of each type. Then we obtain

$$P_i(t+1) = \frac{\lambda_i}{\sum_j \lambda_j P_j(t)} P_i(t), \quad (2)$$

where  $P_i$  is the proportion of type  $i$ . The addition of mutations to the model,  $N_i(t+1) = \sum_j \lambda_{ij} N_j(t)$ , gives rise to the quasispecies model [8] which has attracted significant attention in the physics community. Recent research has focused on such questions as determining the rate of environmental change which can be followed by evolutionary change.

Sexual reproduction causes offspring to depend on the genetic makeup of two parents. This leads to conceptual problems (not just mathematical problems) in evolutionary theory because the offspring of an organism may be as different from the parent as organisms it is competing against. A partial solution to this problem is recognizing that it is sufficient for offspring traits to be correlated to parental traits for the principles of evolution to apply. However, the gene-centered view is a simpler perspective in which the genes serve as indivisible units that are preserved from generation to generation [9]. In effect, different versions of the gene, i.e., alleles, compete rather than organisms. This view simplifies the interplay of selection and heredity in sexually reproducing organisms.

We will show, formally, that the gene-centered view corresponds to a mean-field approximation [10]. This clarifies the domain of its applicability and the conditions in which it should not be applied to understanding evolutionary processes in real biological systems. We will then describe the breakdown of the gene-centered view in the case of symmetry breaking and pattern formation and its implications for the study of ecological systems.

It is helpful to explain the gene-centered view using the ‘‘rowers analogy’’ introduced by Dawkins [11]. In this analogy boats of mixed English- and German-speaking rowers are filled from a common rower pool. Boats compete in heats and it is assumed that a speed advantage exists for boats with more same-language rowers. The successful rowers are then returned to the rower pool for the next round. Over time, a predominantly and then totally same language rower pool will result. Thus, the selection of boats serves, in effect, to select rowers who therefore may be considered to be competing against each other [12]. In order to make the competition between rowers precise, an effective fitness can be assigned to a rower. We will make explicit the rowers model (in the context of genes and sexual reproduction) and demonstrate the assignment of fitness to rowers (genes).

The rowers analogy can be directly realized by considering genes with selection in favor of a particular combination of alleles on genes. Specifically, for two genes, 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 as  $(1,-1)$  and  $(-1,1)$ . For simplicity, we assume below that the lower-fitness organisms are nonreproducing. Models which allow them to reproduce, but with lower probabilities than the high-fitness organisms, give similar results.

The assumption of placing rowers into the rower pool and taking them out at random is equivalent to assuming that there are no correlations in reproduction (i.e., no correlations in mate pairing) and that there is a sufficiently dense sampling of genomic combinations by the population (in this case only a few possibilities). Then the offspring genetic makeup can be written as a product of the probability of each allele in the parent population. This assumption describes a ‘‘panmictic population’’ which forms the core of the gene-centered view often used in population biology. The assumption that the offspring genotype frequencies can be written as a product of the parent allele frequencies is a dynamic form of the usual mean-field approximation neglect of correlations in interacting statistical systems [13]. While the explicit dynamics of this system is not like the usual treatment of mean-field theory, e.g., in the Ising model, many of the implications are analogous.

In our case, the reproducing parents [either  $(1,1)$  or  $(-1,-1)$ ] must contain the same proportion of the correlated alleles ( $A_1$  and  $B_1$ ) so that  $p(t)$  can represent the proportion of either  $A_1$  or  $B_1$  and  $1-p(t)$  can represent the proportion of either  $A_{-1}$  or  $B_{-1}$ . The reproduction equations specifying the offspring (before selection) for the gene pool model are

$$P_{1,1}(t+1) = p(t)^2, \quad (3)$$

$$P_{1,-1}(t+1) = P_{-1,1}(t+1) = p(t)[1-p(t)], \quad (4)$$

$$P_{-1,-1}(t+1) = [1-p(t)]^2, \quad (5)$$

where  $P_{1,1}$  is the proportion of  $(1,1)$  among the offspring, and similarly for the other cases.

The proportion of the alleles in generation  $t+1$  is given by the selected organisms. Since the less fit organisms  $(1,-1)$  and  $(-1,1)$  do not survive, this is given by  $p(t+1) = P'_{1,1}(t+1) + P'_{-1,-1}(t+1) = P'_{1,1}(t+1)$ , where primes indicate the proportion of the selected organisms. Thus

$$p(t+1) = \frac{P_{1,1}(t+1)}{P_{1,1}(t+1) + P_{-1,-1}(t+1)}. \quad (6)$$

This gives the update equation

$$p(t+1) = \frac{p(t)^2}{p(t)^2 + [1-p(t)]^2}. \quad (7)$$

There are two stable states of the population with all organisms  $(1,1)$  or all organisms  $(-1,-1)$ . If we start with exactly 50% of each allele, then there is an unstable steady state. In every generation 50% of the organisms reproduce and 50% do not. 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. This problem is reminiscent of an Ising ferromagnet at low temperature: A statistically biased initial condition leads to alignment.

This model can be reinterpreted by assigning a mean fitness (analogous to a mean field) to each allele as in Eq. (2). The fitness coefficient for allele  $A_1$  or  $B_1$  is  $\lambda_1 = p(t)$  with the corresponding  $\lambda_{-1} = 1 - \lambda_1$ . The assignment of a fitness to an allele reflects the gene-centered view. The explicit dependence on the population composition (an English-speaking rower in a predominantly English-speaking rower pool has higher fitness than one in a predominantly German-speaking rower pool) has been objected to on grounds of biological appropriateness [14]. For our purposes, we recognize this dependence as the natural outcome of a mean-field approximation.

We can describe more specifically the relationship between this picture and the mean-field approximation by recognizing that the assumption of no correlations in reproduction, a random mating pattern of parents, is the same as a long-range interaction in an Ising model. If there is a spatial distribution of organisms with mating correlated by spatial location and fluctuations so that the starting population has more of the alleles represented by 1 in one region and more of the alleles represented by  $-1$  in another region, then patches of organisms that have predominantly  $(1,1)$  or  $(-1,-1)$  form after several generations. This symmetry breaking, like in a ferromagnet, is the usual breakdown of the mean-field approximation. Here, it creates correlations and patterns in the genetic makeup of the population. When correlations become significant, then the species has two types, though they are still able to crossmate and are doing so at the boundaries of the patches. Thus the gene-centered view breaks down when multiple organism types form.

Understanding the spatial distribution of organism genotype is a central problem in ecology and conservation biology [15,16]. The spatial patterns that can arise from spontaneous symmetry breaking through sexual reproduction, as implied by the analogy with other models, may be relevant. A systematic study of the relevance of symmetry breaking to ecological systems begins from a study of spatially distrib-

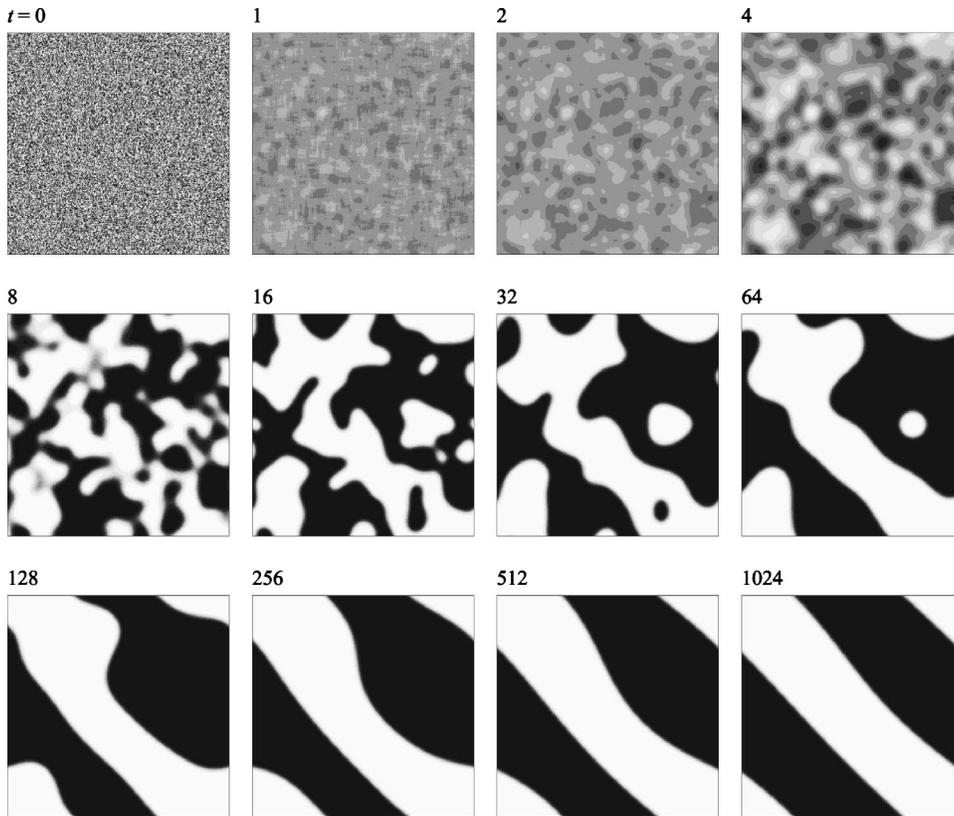


FIG. 1. Spatially distributed evolution with disruptive selection giving rise to two types appearing in patches and coarsening. The space is periodic and has  $256 \times 256$  sites, and the mating neighborhood radius is  $R = 5$ .

uted versions of the model just described. This model is a simplest model of disruptive selection, which corresponds to selection in favor of two genotypes whose hybrids are less viable. Assuming overlapping local reproduction neighborhoods, called demes, the relevant equations are

$$p(x, t+1) = D(\bar{p}(x, t)), \quad (8)$$

$$D(p) = \frac{p^2}{p^2 + (1-p)^2}, \quad (9)$$

$$\bar{p}(x, t) = \frac{1}{N_R} \sum_{|x_j| \leq R} p(x + x_j, t), \quad (10)$$

$$N_R = |\{x_j | |x_j| \leq R\}|, \quad (11)$$

where the organisms are distributed over a two-dimensional grid and local genotype averaging is performed over a pre-selected range of grid cells around the central cell. 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 nonconserved order parameters.

A simulation of this model starting from random initial conditions is shown in Fig. 1. This initial condition can arise when selection becomes disruptive after being nondisruptive 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 and pattern formation that occurs in many other systems such as an Ising model or similar cellular automata models [17,18]. Fourier-transformed power spectra (Figs. 2–4) confirm the correspondence to conventional coarsening by showing that the correlation length grows as  $t^{1/2}$  after initial transients. In a finite-sized system, it is possible for one type to completely eliminate the other type. However, the time scale over which this takes place is much longer than the results assuming complete reproductive mixing, i.e., the mean-field approximation. Since flat boundaries do not move except by random perturbations, a nonuniform final state is possible. The addition of noise will cause a slow

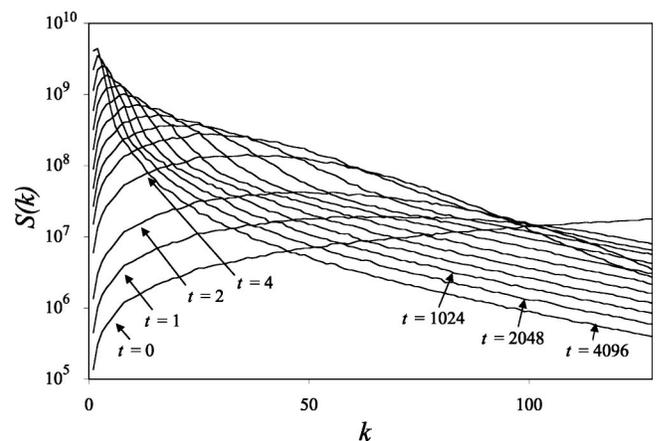


FIG. 2. Fourier power spectra averaged over ten simulations of evolutionary processes like that shown in Fig. 1 ( $512 \times 512$  sites and  $R = 1$ ).

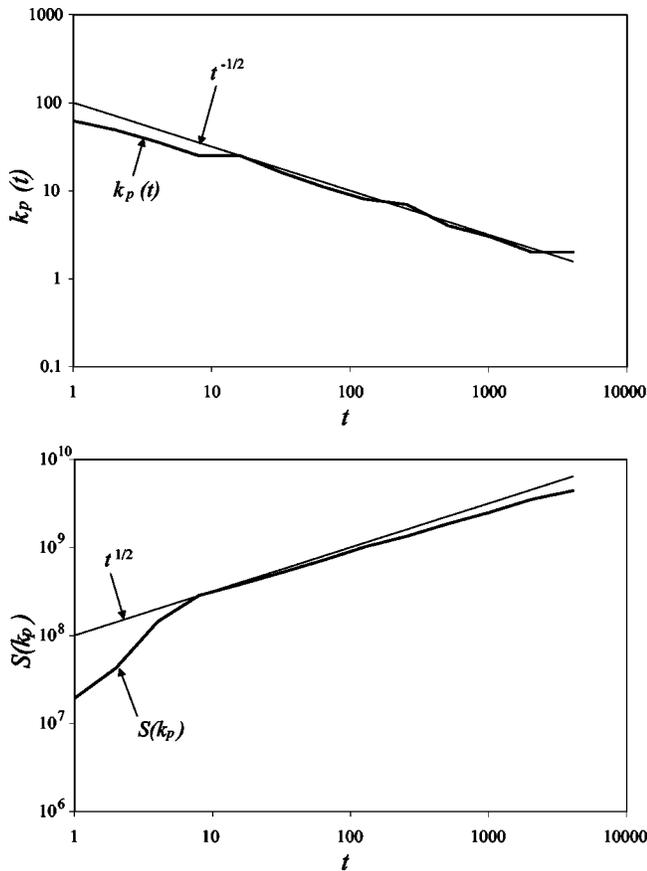


FIG. 3. Temporal behavior of the peak of a Fourier power spectrum in the shown case. Top: the peak frequency  $k_p(t)$  which follows approximately  $t^{-1/2}$ . Bottom: the peak power  $S(k_p)$  which follows approximately  $t^{1/2}$ .

relaxation of flat boundaries but they can also be trapped by quenched (frozen) inhomogeneity.

The results have significant implications for ecology of genetic diversity and species formation. The observation of harlequin distribution patterns of sister forms is generally attributed to nonhomogeneities in the environment, i.e., that these patterns reflect features of the underlying habitat (=selective) template. Our results show that disruptive selection can give rise to spontaneously self-organized patterns of

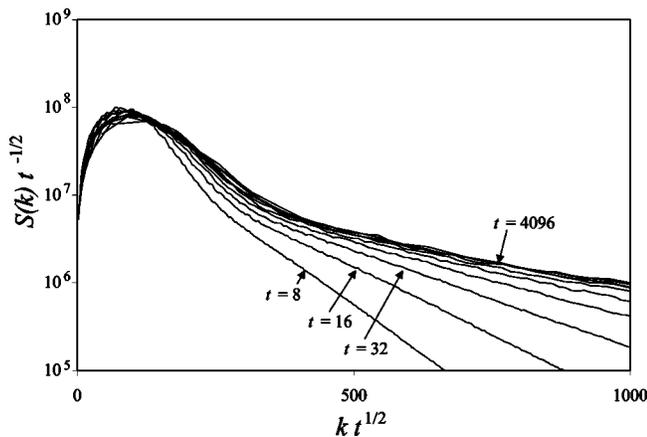


FIG. 4. Collapsed version of the Fourier power spectra demonstrating the scaling form  $S(k) = t^{1/2} f(k t^{1/2})$ .

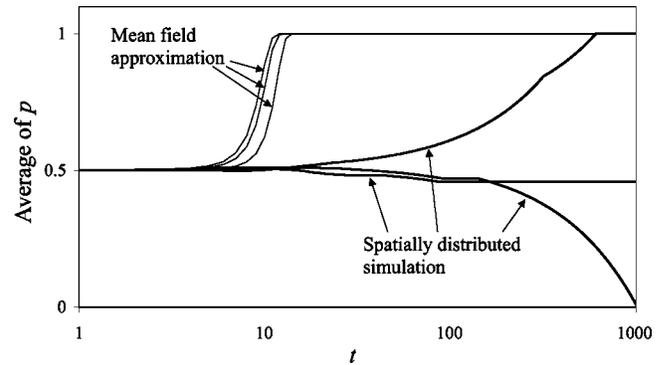


FIG. 5. Comparison of the time dependence of type probability in the mean-field approximation and symmetry breaking, calculated using different random number sequences. Diversity persists much longer in the latter, in some cases forever.

spatial distribution that are independent of underlying habitat structure. At a particular time, the history of the introduction of disruptive selection events would be apparent as a set of overlapping patterns of genetic diversity that exist on various spatial scales.

More specific relevance of these results to the theoretical understanding of genetic diversity can be seen in Fig. 5 where the population-averaged time dependence of  $p$  is shown. The gene-centered-view and mean field approximation predicts a rapid homogenization over the entire population. The persistence of diversity in simulations with symmetry breaking, as compared to its disappearance in the mean-field approximation, is significant. Implications for experimental tests and methods are also important. 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.

The divergence of population traits in space studied in our work can also couple to processes of speciation, i.e., processes that prevent interbreeding or doom the progeny of such breedings. These may include assortative mating, whereby organism traits inhibit interbreeding. Such divergences can potentially lead to the formation of multiple species from a single connected species (sympatric speciation). By contrast, allopatric speciation, where disconnected populations diverge, has traditionally been the more accepted process even though experimental observations suggest sympatric speciation is important.

Recent studies [1–7] have begun to connect the process of symmetry breaking to sympatric speciation. Without considering pattern formation in physical space, we and other researchers have been investigating the role of pattern formation in genomic space as a mechanism or description of sympatric speciation. These studies include a model of stochastic branching and fixation of subpopulations due to genetic drifts and local reproduction in genome space [2], general reaction-diffusion Turing pattern formation models in genomic space [1,3,4], and specific individual-based models of reproductive isolation involving assortative mating and disruptive selection (intrinsic disruptive selection or disrupt-

tive selection arising from competition or sexual selection) [5–7]. Our work, presented here, is unique in discussing spatial inhomogeneity and genetic diversity within one species.

In conclusion, in formalizing sexual reproduction in evolutionary theory, we have found fundamental justification for rejecting the widespread application of the gene-centered view. The formal mathematical analysis we presented to demonstrate the lack of applicability of the gene-centered view is an essential step toward developing a sound conceptual foundation for evolution. We also showed that the gene-centered view breaks down for species where local mating and disruptive selection give rise to symmetry breaking and pattern formation, which correspond to genetic inhomogeneity and trait divergence of subpopulations. The patterns formed undergo coarsening, following the usual universal spatiotemporal scaling behavior. The slow movement of

boundaries between types cause long-term persistence of genetic diversity through the local survival of (partially) incompatible types. This provides a new understanding of the development and persistence of spatiotemporal patterns of genetic diversity within a single species.

One should note that the context in which the gene-centered view breaks down is of profound significance in applied aspects of modern ecology and conservation biology. The preservation of endangered species and ecosystems is currently at risk due to a dramatic decrease in their genetic diversity. We have described the implications of our results for the experimental observation of genetic diversity in endangered species. Our study of spatial patterns of genetic diversity in populations may also help guide the design of conservation areas and human-directed breeding programs for endangered organisms.

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- $$\{N(s;t)\} = R[\{N'(s;t-1)\}],$$
- $$\{N'(s;t)\} = D[\{N(s;t)\}],$$
- where  $s$  is a particular genome and  $N, N'$  are numbers of reproduced, selected organisms, respectively. Using a mean-field approximation for offspring, the probability of a particular genome  $s$  is the product of probabilities of the alleles  $a_i$ :  $P(a_1, \dots, a_N) = \prod P(a_i)$ . This enables the two-step update equations to be written as a one-step update equation for each allele:
- $$n'(a_i;t) = \tilde{D}[\{n'(a_i;t-1)\}] = \lambda(\{n'\})n'(a_i;t-1),$$
- where  $n'(a_i)$  is the number of allele  $a_i$ . For details see [10].
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