On the origin of species by sympatric speciation

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Understanding speciation is a fundamental biological problem. It is believed that many species originated through allopatric divergence, where new species arise from geographically isolated populations of the same ancestral species. In contrast, the possibility of sympatric speciation (in which new species arise without geographical isolation) has often been dismissed, partly because of theoretical difficulties. Most previous models analysing sympatric speciation concentrated on particular aspects of the problem while neglecting others. Here we present a model that integrates a novel combination of different features and show that sympatric speciation is a likely outcome of competition for resources. We use multisecular genetics to describe sexual reproduction in an individual-based model, and we consider the evolution of assortative mating (where individuals mate preferentially with like individuals) depending either on an ecological character affecting resource use or on a selectively neutral marker trait. In both cases, evolution of assortative mating often leads to reproductive isolation between ecologically diverging populations. When assortative mating depends on a marker trait, and is therefore not directly linked to resource competition, our model predicts the evolution of sympatric speciation and extinction driven by environment dependent sexual selection. We start from assumptions that are likely to be satisfied in many natural populations. Individuals vary in a quantitative character x determining resource use, as for example when beak size in birds determines the size of seeds consumed. Populations consisting of individuals of a given trait value x have density-dependent logistic growth with carrying capacity K(x).


Acknowledgements. This study was supported by a grant from the NSF.

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Understanding speciation is a fundamental biological problem. It is believed that many species originated through allopatric divergence, where new species arise from geographically isolated populations of the same ancestral species. In contrast, the possibility of sympatric speciation (in which new species arise without geographical isolation) has often been dismissed, partly because of theoretical difficulties. Most previous models analysing sympatric speciation concentrated on particular aspects of the problem while neglecting others. Here we present a model that integrates a novel combination of different features and show that sympatric speciation is a likely outcome of competition for resources. We use multisecular genetics to describe sexual reproduction in an individual-based model, and we consider the evolution of assortative mating (where individuals mate preferentially with like individuals) depending either on an ecological character affecting resource use or on a selectively neutral marker trait. In both cases, evolution of assortative mating often leads to reproductive isolation between ecologically diverging populations. When assortative mating depends on a marker trait, and is therefore not directly linked to resource competition, our model predicts the evolution of sympatric speciation and extinction driven by environment dependent sexual selection. We start from assumptions that are likely to be satisfied in many natural populations. Individuals vary in a quantitative character x determining resource use, as for example when beak size in birds determines the size of seeds consumed. Populations consisting of individuals of a given trait value x have density-dependent logistic growth with carrying capacity K(x).

The theory of adaptive dynamics is a general framework for studying phenotypic evolution driven by ecological interactions. One of the phenomena unravelled by adaptive dynamics is evolutionary branching, during which directional selection drives a monomorphic population to a phenotype where ecological interactions induce disruptive selection and a subsequent split into two coexisting phenotypic clusters (Fig. 1a). Evolutionary branching explains the dynamic emergence and perpetuity of disruptive selection and serves as a unifying concept for understanding the evolution of polymorphisms. It is found in a wide range of models of sexual populations (see refs 22 and 23 for examples). Here we show that evolutionary branching also occurs in sexual populations and thus leads to a general theory for sympatric speciation. We start from assumptions that are likely to be satisfied in many natural populations. Individuals vary in a quantitative character x determining resource use, as for example when beak size in birds determines the size of seeds consumed. Populations consisting of individuals of a given trait value x have density-dependent logistic growth with carrying capacity K(x). We assume that the resource
distribution $K(x)$ is unimodal and varies according to a gaussian function $N(x_0,\sigma_K)$, with the maximum at an intermediate phenotype $x_0$ and variance $\sigma_K^2$. In polymorphic populations consisting of individuals with different trait values, dissimilar individuals interact only weakly, as, for example, when birds with different beak sizes eat different types of seed. That is, competition is not only density- but also frequency-dependent, and rare phenotypes experience less competition than common phenotypes. Specifically, we assume that the strength of competition between individuals declines with phenotypic distance according to a gaussian function $N(0,\sigma_C)$, with a maximum at zero and variance $\sigma_C^2$.

These assumptions are integrated into an asexual individual-based model in which each individual is characterized by its trait value $x$. Individuals give birth at a constant rate and die at a rate that is determined by frequency- and density-dependent competition (see Methods). Evolutionary dynamics occur because offspring phenotypes may deviate slightly from parent phenotypes. The quantitative character first evolves to the value $x_0$ with maximal carrying capacity. After that, two things can happen: either $x_0$ is evolutionarily stable and evolution comes to a halt at $x_0$, or $x_0$ is actually a fitness minimum and can be invaded by all nearby phenotypes$^{19,21,22}$. In the latter case, evolutionary branching occurs

Figure 1 Convergence to disruptive selection. a, Evolutionary branching in the individual-based asexual model: at the branching point $x_0 = 0$, the population splits into two morphs. Three insets show fitness functions (continuous curves) generated by the ecological interactions at different points in time (indicated by horizontal dotted lines). Selection changes from directional to disruptive when evolution reaches $x_0$. The resource distribution $K(x)$ has its maximum at $x_0$ and is shown for comparison (dashed curve). b, As in a, but with multilocus genetics for the ecological character and random mating. Shading represents phenotype distributions (5 diploid and diallelic loci result in 11 possible phenotypes). Despite disruptive selection at the branching point (see insets), branching does not occur.

Figure 2 Mating probabilities as determined by mating character and difference in ecological or marker character between mates. The mating character $m$ is scaled to vary between $-1$ (all $-$ alleles) and $+1$ (all $+$ alleles). Mating probabilities vary with differences in either ecological or marker character, depending on the scenario. If the mating character in the focal individual is close to $+1$, it has a high probability of mating with similar individuals. If its mating character is close to $-1$, it is more likely to mate with dissimilar individuals. Intermediate mating characters (close to 0) correspond to random mating.

Figure 3 Evolutionary branching in sexual populations. a, First scenario: mating probabilities (vertical axes) depend on the ecological character (horizontal axes), which first evolves to intermediate values (50 generations). Then the mean mating character increases to positive values (180 generations) and induces a bimodal split in the ecological character (200 generations). b, Second scenario: mating probabilities (vertical axes in upper panels) depend on a marker trait (vertical axes in lower panels). The ecological trait (horizontal axes in all panels) first evolves to intermediate values (100 generations). Owing to temporary correlations between marker and ecological trait, assortative mating increases, which in turn magnifies these correlations (generations 400-1,090). This positive feedback eventually leads to speciation (1150 generations). In b branching typically takes longer than in a. The summary panels depict the evolution of mean character values schematically. Grey arrows in the bottom summary panel show an alternative, equally likely, evolution of linkage disequilibrium between ecological and marker character.
(Fig. 1a). This happens for \( \sigma_C < \sigma_C^* \), that is, if the curvature of the carrying capacity at its maximum is less than that of the competition function. Then the advantage of deviating from the crowded optimal phenotype \( x_0 \) more than compensates for the disadvantage of a lower carrying capacity.

Sexual reproduction is incorporated by assuming that character values are determined by many additive, diploid loci with two alleles, + and −, and are proportional to the number of ‘plus’ alleles. Offspring inherit maternal and paternal alleles at each locus independently (free recombination). As in the asexual case, the sexual population evolves to a mean phenotype \( x_0 \). If mating is random, however, evolutionary branching does not occur for any values of \( \sigma_C \) and \( \sigma_C^* \); the split into two distinct phenotypic morphs is prevented by the continual generation of intermediate phenotypes through recombination (Fig. 1b). Thus, in sexual populations, non-random mating is a prerequisite for evolutionary branching.

To model the evolution of assortative mating we assume that individuals express an additional quantitative character that determines mating probabilities according to two scenarios. In the first, mating probabilities are based on similarity in the ecological character, and in the second they are based on similarity in a third, ecologically neutral ‘marker’ trait (see Methods). Mating character and marker trait are also determined by many additive diallelic loci. Individuals with an intermediate mating character mate randomly. Individuals carrying mostly ‘minus’ alleles at the mating loci mate disassortatively, and hence are more likely to mate with individuals with very different ecological or marker phenotypes. Individuals carrying mostly plus alleles at the mating loci mate assortatively: the probability of mating increases with phenotypic similarity to the partner (Fig. 2).

Figure 3a shows the evolutionary dynamics of an initially randomly mating population when mating probabilities depend on the ecological character. While this character evolves to \( x_0 \), the mating character initially changes only slowly, but it picks up speed and evolves towards positive assortativeness when the ecological character reaches \( x_0 \). Once assortativeness is strong enough, the population splits into two ecologically different morphs which eventually are almost completely reproductively isolated. These results confirm and extend those of ref. 24 and occur because, near the dynamically emerging fitness minimum at \( x_0 \), selection favours mechanisms that allow for a split in the phenotype distribution and hence for a departure from the fitness minimum. Assortative mating is such a mechanism, because it prevents the generation of intermediate offspring phenotypes from extreme parent phenotypes. Parameter requirements for evolutionary branching in sexual populations appear to be only slightly more restrictive than in the asexual case (Fig. 4).

When assortative mating depends on the ecological character, speciation is not hindered by recombination between mating loci and ecological loci. However, when mating depends on an ecologically neutral marker trait, a linkage disequilibrium between marker loci and ecological loci, leading to a correlation between mating character and ecological character, is required for the evolution of assortative mating and for speciation. Classical, deterministic models (such as Felsenstein’s ‘two-allele’ models) predict that such linkage disequilibria are unlikely because of recombination between ecological and marker loci. In our individual-based model, however, genetic drift due to stochastic demographic effects readily leads to speciation despite the opposing force of recombination. Figure 3b shows the adaptive dynamics when mating probabilities depend on a neutral marker trait. Genetic drift temporarily results in small and localized linkage disequilibria between some marker loci and some ecological loci. Positive and negative correlations both select for assortative mating, which in turn magnifies the local disequilibrium into a global linkage disequilibrium between marker and ecological trait. This feedback eventually induces the sympatric split into reproductively isolated phenotypic clusters. Thus, stochastic fluctuations in finite populations can spontaneously break the symmetry of linkage equilibria seen in determi-

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**Figure 4** Combinations of standard deviations \( \sigma_C \) and \( \sigma_C^* \) of the resource distribution \( K(x) \) and competition function \( C(x) \), respectively, that allow for evolutionary branching. Analytical results are available for the asexual model (see Methods) and predict branching for \( \sigma_C < \sigma_C^* \), that is, below the diagonal. Conditions for branching in sexual populations (within 20,000 generations) are shown in grey when mating probabilities depend on the ecological character and in black when they depend on a marker trait.

**Figure 5** Average waiting times for evolutionary branching with different numbers of loci when assortative mating depends on a marker trait. **a**, Variable numbers of loci for marker and ecological trait with a fixed number of loci (5) for assortative mating. **b**, Variable numbers of loci for assortative mating and ecological trait with a fixed number of loci (5) for the marker trait. Other parameters are as in Fig. 3; each column represents the average waiting time from 60 simulation runs.
The deterministic dynamics of a resident population of phenotype $x$ arise more rarely. Branching triggered by drift becomes less likely in tative characters (Fig. 5). Evolutionary branching is more likely nistic models. Recombination between marker loci and ecological phenotype is chosen from a normal distribution $N(x, \sigma)$, where $\sigma$ is the individual's ecological trait and variance $\sigma = \sigma_0$. If $m = 0$, the focal indi

Our results extend and contrast previous insights into showing that competition for unimodal resources can initiate sympatric speciation even if assortative mating depends on an ecologically neutral marker trait. The results are robust against changes in the models such as varying numbers of loci (Fig. 5), assuming different mutation rates per locus, different functions for the carrying capacities, $K(x)$, and for the strength of competition, $C(x)$, while maintaining their qualitative characteristics. Evidence is accumulating that ecology is important for speciation, and our theory may provide an integrative framework for understanding otherwise puzzling evidence for monophyletic origins of many sympatric species, including cichlids, sticklebacks, and snails, giant seedcobs, and anolis lizards. In all these cases, it is likely that frequency-dependent mechanisms are important determinants of the species' ecologies. Based on this and previous work on sympatric speciation, the model could be used to predict the formation of new species in accordance with the theory presented here. We expect our theory to work best in relatively recently colonized habitats, in which sympatric divergence is not strongly opposed by competition from other species already present. In fact, a striking example of incipient sympatric speciation due to ecological interactions in a new habitat has recently been documented in a pair of cichlid morphs (U. K. Schleien et al., submitted), in which restricted gene flow has evolved through size-assortative mating. The mechanisms of speciation are rarely as clear as in this example, but our theoretical evidence generally suggests a prominent role for ecologically driven speciation in sympatry.

Methods

The deterministic dynamics of a resident population of phenotype $x$ are

$$\frac{dN(x, t)}{dt} = rN(x, t) \left[1 - \frac{N(x, t)}{K_x}\right]$$

where $N(x, t)$ is the population size at time $t$. The carrying capacity, $K(x) = K_x \exp\left(-\frac{x - x_0}{\sigma_x}\right)$, is the stable equilibrium. When a rare mutant $y$ appears in a resident $x$ at carrying capacity $K(x)$, it competes with the discounted density $C(x - y)K(x)$, where $C(x - y) = \exp\left(-\frac{|x - y|}{\sigma_c}\right)$ describes the strength of competition between phenotypes. Therefore, the per capita growth rate $s(x, y)$ of the rare mutant $y$ is $r \left[1 - \frac{N(y, t)}{K_x}\right]$. The derivative $\frac{dN(x, t)}{dx}$ at $y = x_0$ is an attractor for the adaptive dynamics $\frac{dN(x, t)}{dx}$. In addition, if $s(x, y) = 0$ at $x = y = x_0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0$, then $x_0$ is a branching point. If $s(x, y) < 0