

Sympatric speciation under incompatibility selection

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Edited by Daniel L. Hartl, Harvard University, Cambridge, MA, and approved June 20, 2006 (received for review March 22, 2006)

The existing theory of sympatric speciation assumes that a local population splits into two species under one-dimensional disruptive selection, which favors both of the opposite extreme values of a quantitative trait. Here we model sympatric speciation under selection that favors high values of either of the two independently inherited traits, each required to efficiently consume one of the two available resources, but acts, because of a tradeoff, against those possessing high values of both traits. Such two-dimensional incompatibility selection is similar to that involved in allopatric speciation. Using a hypergeometric phenotypic model, we show that incompatibility selection readily leads to sympatric speciation. In contrast to disruptive selection, two distinct modes of sympatric speciation exist under incompatibility selection: under strong tradeoffs both of the new species are specialists, each consuming its own resource, but under moderate tradeoffs speciation may be asymmetric and involve the origin of a specialist and a generalist species. Also, incompatibility selection may lead to irreversible specialization: under strong tradeoffs, the population speciates if it consists mostly of unspecialized individuals, but remains undivided if most of the individuals are specialized to consume one of the resources. Incompatibility selection appears to be more realistic than disruptive selection, implying that incompatibility between individually adaptive alleles or trait states drives both allopatric and sympatric speciation.

evolution | tradeoff | resource | hypergeometric model

Mechanisms of allopatric and sympatric speciation are thought to be very different. Allopatric speciation occurs because populations evolving in geographic isolation accumulate Dobzhansky-Muller incompatibilities, i.e., independently acquire new beneficial alleles that reduce fitness when combined in the same genotype (1, 2). In contrast, the available theory of sympatric speciation by natural selection assumes that this process is driven by disruptive selection, which favors both of the opposite extreme values of one trait (1–11).

However, this is not the only feasible assumption. Indeed, to cause sympatric speciation, natural selection must (i) protect genetic variability within the population and (ii) tear the population apart by eliminating intermediate phenotypes, such as those of hybrids between the incipient species (1–11). These conditions can be met either by frequency-dependent disruptive selection acting on one trait or frequency-dependent incompatibility selection, acting on two traits and involving a fitness tradeoff between them (12–19). Here we investigate the previously neglected possibility of sympatric speciation driven by incompatibility selection and argue that modes of selection behind allopatric and sympatric speciation can be essentially the same.

Results

Model of Disruptive Selection and Incompatibility Selection. Suppose that individuals in a local population can consume two independent resources, I and II . The expected amount of a resource consumed by an individual depends on the ratio of the individual's ability to consume this resource (c_I or c_{II}) over the corresponding average ability within the population (C_I or C_{II}). This would be the case if, for example, all of the individuals simultaneously consume a resource that is nonrenewable in the

course of a generation, with instant rates proportional to the currently available amount of the resource. The amount of resources consumed by an individual is also affected by chance. An individual needs a certain amount of consumed resources, B , for its basic metabolism, and allocates the excess to reproduction. Let us compare disruptive and incompatibility selection within this framework.

Disruptive selection depends on one quantitative trait x (size; we take all of the traits to vary between 0 and 1), with c_I being an increasing, and c_{II} being a decreasing function of x . Here B is the same for all individuals, regardless of their values of x . Thus, $R_{dis}(x)$, the expected amount of resources allocated to reproduction by individuals of phenotype x , is $c_I(x)/C_I + c_{II}(x)/C_{II} - B$.

Incompatibility selection depends on two traits, x (size) and y (agility), with c_I being an increasing function of x and c_{II} being an increasing function of y . In this case, B depends on x and y in such a way that individuals with high values of both x and y also possess higher values of B . In other words, there is a tradeoff between the abilities of an individual to consume resources I and II , mediated by the increased basic metabolism requirement. Thus, $R_{inc}(x, y)$, the expected amount of resources allocated to reproduction by individuals of phenotype (x, y) , is $c_I(x)/C_I + c_{II}(y)/C_{II} - B[1 + T(x, y)]$, where $T(x, y)$ is a tradeoff function [we assume that $T(x, y) = 0$ when $x = 0$ or $y = 0$].

Then, disruptive fitness function $w_{dis}(x)$ is:

$$w_{dis}(x) = \int_0^{\infty} zn_{\sigma}(z - R_{dis}(x))dz, \quad [1]$$

where $n_{\sigma}(z)$ is a normally distributed random variable with mean 0 and variance σ^2 , which describes random fluctuations in consumption. Informally, Eq. 1 is based on the probability $p_x(z)$ that an individual of phenotype x allocates for reproduction the amount z of consumed resources, after satisfying its basic metabolism requirement and with fluctuations in consumption taken into account. The fitness of phenotype x is obtained by integrating $zp_x(z)$ from 0 to infinity, because only those individuals who have some resources left can reproduce. Analogously, incompatibility fitness function $w_{inc}(x, y)$ is:

$$w_{inc}(x, y) = \int_0^{\infty} zn_{\sigma}(z - R_{inc}(x, y))dz. \quad [2]$$

For disruptive selection we assume the consumption functions to be $c_I(x) = \exp(Ax)$ and $c_{II}(x) = \exp[A(1 - x)]$, where A is the unevenness of consumption. Analogously, for incompatibility selection, we assume that $c_I(x) = \exp(Ax)$, $c_{II}(y) = \exp(Ay)$, and $T(x, y) = \exp(Dxy) - 1$, where D is the tradeoff strength. With both modes of selection, the two resources are assumed to be equally abundant, because c_I and c_{II} depend on the same

Conflict of interest statement: No conflicts declared.

This paper was submitted directly (Track II) to the PNAS office.

Freely available online through the PNAS open access option.

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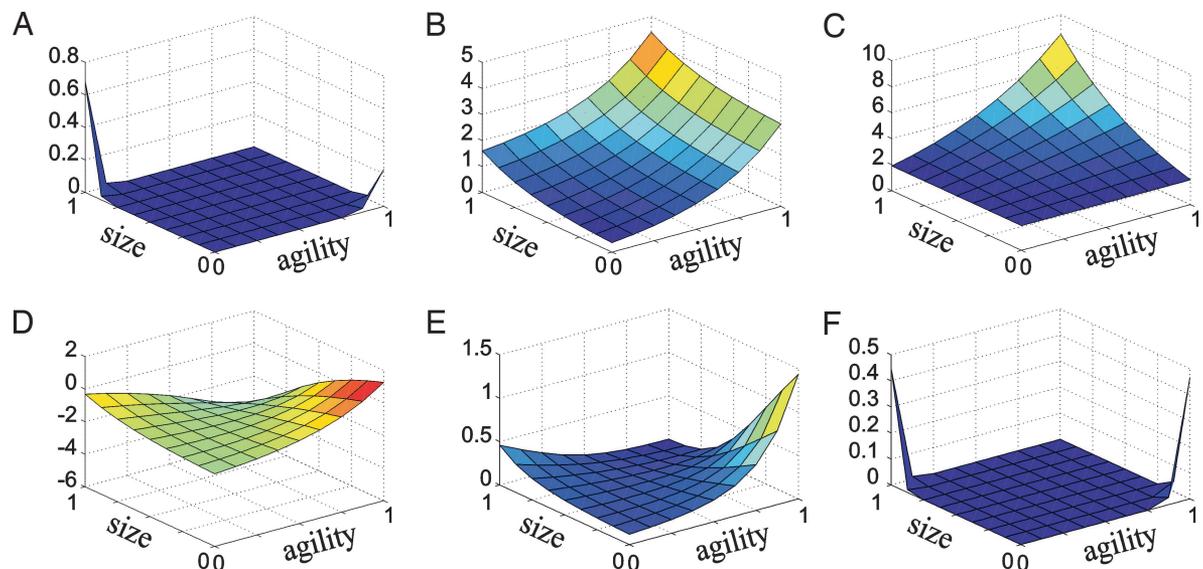


Fig. 1. Structure of incompatibility selection (Eq. 2). Size and agility are each controlled by eight loci, $A = 2.5$, $B = 1.9$, $\sigma = 1.5$, and $D = 1.5$. (A) Distribution of phenotypes before selection. (B) The expected amount of resources consumed, $\exp(Ax)/C_I + \exp(Ay)/C_{II}$. (C) Basic metabolism requirement, $B_{\text{exp}}(Dxy)$. (D) The expected amount of consumed resources left for reproduction, $R_{\text{inc}}(x)$. (E) Fitness, $w_{\text{inc}}(x, y)$. (F) Distribution of phenotypes after selection.

parameter A . Naturally, Eqs. 1 or 2 lead to a wider range of fitness values, i.e., to a more stringent selection, when A and/or B increase and σ declines (Fig. 1).

Conditions and Modes of Sympatric Speciation. With both disruptive and incompatibility selection, we assume that nonrandom mating is caused by variability in either one trait z (color; matings occur preferably between similar individuals) or in two traits, male color z and female preference u . As before (11), we use a hypergeometric phenotypic model (20–23) and assume independent inheritance of all of the traits, the worst case for sympatric speciation (3, 10), which is facilitated when the same variable loci pleiotropically control both fitness and mate choice (1–3).

An ecologically explicit model of disruptive selection (Eq. 1) leads to sympatric speciation under conditions similar to those required with an ad hoc rectangular fitness function used in ref. 11, which represents the most conducive to sympatric speciation form of selection (24). As expected, two outcomes are possible as long as $A > 0$ (data not reported): (i) nonspeciation, when an equilibrium distribution of x is symmetric ≈ 0.5 and the mating trait(s) are monomorphic, and (ii) speciation, the formation of two equally abundant species with $x = 0$ and $x = 1$, which are reproductively isolated from each other because of recruitment of the mating trait(s) through expansion of linkage disequilibria (11).

Incompatibility selection (Eq. 2) also readily leads to sympatric speciation, but displays a wider variety of qualitatively different outcomes (Fig. 2). If the population fails to speciate, three outcomes are possible: (i) fixation, under low D , of a single “jack-of-all-trades” phenotype $x = 1, y = 1$ (generalist nonspeciation); (ii) fixation, under high D , of one of the two possible specialized phenotypes, either of $x = 1, y = 0$ or of $x = 0, y = 1$, depending on the initial distribution of phenotypes (specialist nonspeciation); and (iii) fixation of the highest value, 1, of either x or y , depending on the initial distribution of phenotypes, and stable polymorphism of the other trait (polymorphic nonspeciation). In contrast to the case of disruptive selection, the population never remains unspecialized, with the $x = 0, y = 0$ phenotype the most common, because to increase x (with $y = 0$) or to increase y (with $x = 0$) is always advantageous under incompatibility selection.

Speciation can occur in two ways: (i) with high D the two new

species have phenotypes $x = 1, y = 0$ and $x = 0, y = 1$, so that each one is a specialist adapted to its own resource (specialist–specialist speciation) or (ii) with moderate D one of the new species is generalist with phenotype $x = 1, y = 1$, and the other is a specialist with either phenotype $x = 1, y = 0$ or $x = 0, y = 1$, depending on the initial distribution of phenotypes (generalist–specialist speciation). This latter mode of sympatric speciation provides the first example of generalist–specialist coexistence that can be reached through gradual evolution (25). The two new species are reproductively isolated because of acquisition, by ecologically distinct phenotypes, of different values of one or two traits that control mate choice. If speciation does not occur, these traits remain monomorphic.

In contrast to disruptive selection, the possibility of sympatric speciation under incompatibility selection may depend on the state of the initial population, leading to irreversibility of ecological specialization. This phenomenon was observed under high D (Fig. 2), where, under intermediate values of A , the population speciates if initially the unspecialized phenotype $x = 0, y = 0$ is common, but remains essentially unchanged if initially either of the specialist phenotypes $x = 1, y = 0$ or $x = 0, y = 1$ is common. Indeed, incompatibility selection never favors just a decline of either size or agility, and a population consisting mostly of, say, phenotype $x = 1, y = 0$ can speciate only if the decline of size is accompanied by the increase in agility. However, too strong a tradeoff makes this impossible. In contrast, under one-dimensional disruptive selection a change that impairs the individual’s ability to consume one resource automatically improves its ability to consume the other resource, which prevents dead-end specialization. Both the possibility of specialist–generalist speciation and irreversibility of specialization are observed only when variability in fitness-controlling traits depends on a relatively high number of loci (Fig. 2, compare C and D with E and F). Apparently, there is not enough room for complex dynamics on the (size \times agility) plane when these traits are affected by too small a number of loci.

Under both disruptive selection (figures 1 and 3 in ref. 11) and incompatibility selection (Fig. 3), the process of sympatric speciation involves an intermediate phase of isolation by natural selection (11), during which the distribution of fitness-controlling traits is bimodal, because of strong selection against the intermodal hybrids,

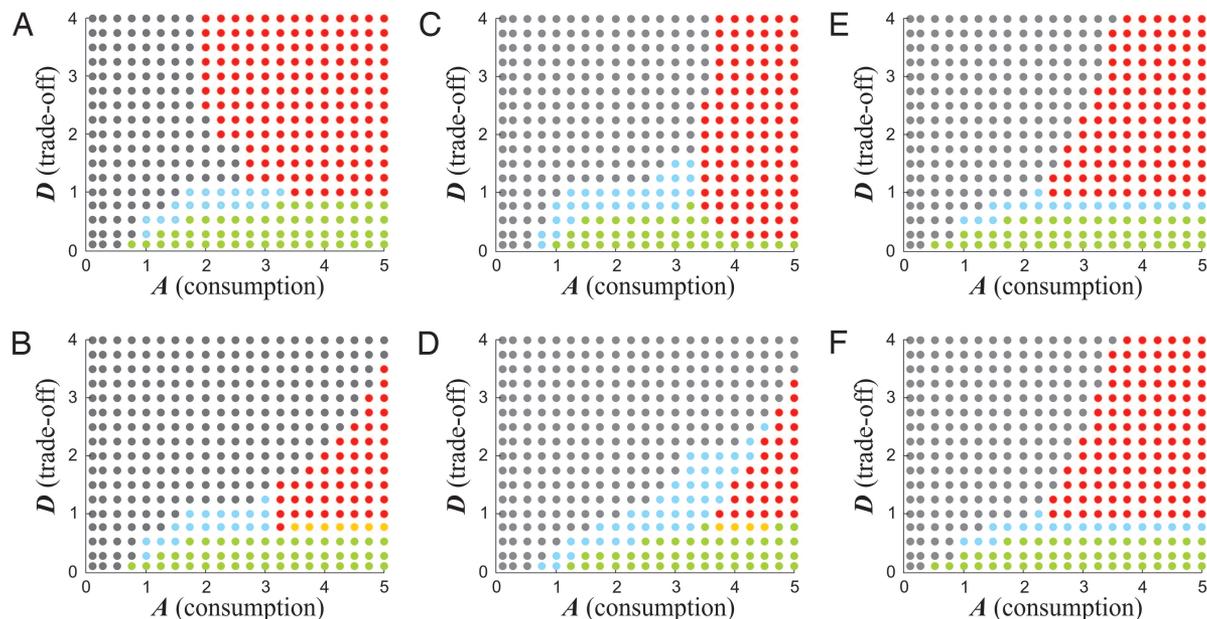


Fig. 2. Possible outcomes under incompatibility selection with $B = 1.9$ and $\sigma = 1.5$. Speciation: red, the two new species have phenotypes $x = 1, y = 0$ and $x = 0, y = 1$, i.e., they are specialists each adapted to consume one of the two resources; yellow, one of the two new species is generalist with phenotype $x = 1, y = 1$, and the other is specialist with phenotype $x = 1, y = 0$ or $x = 0, y = 1$. Nonspeciation: gray, all of the individuals eventually become specialists, either with $x = 1, y = 0$ or with $x = 0, y = 1$ phenotype; blue, all individuals acquire the highest value, 1, of either x or y , and remain polymorphic in the other trait; green, all individuals become generalists with $x = 1$ and $y = 1$. (A and B) Size and agility are controlled by eight loci each, mating depends on one trait (color) controlled by four loci. (C and D) Size and agility are controlled by eight loci each, mating depends on two traits (color and preference) each controlled by four loci. (E and F) Size and agility are controlled by four loci each, mating depends on two traits (color and preference) each controlled by four loci. The initial population was close to $x = 0, y = 0$ (A, C, and E) or $x = 1, y = 0$ (B, D, and F).

but the mating is still essentially random. This phase is apparently unavoidable as long as fitness and mate choice depend on non-overlapping sets of polymorphic loci. In both cases, isolation by natural selection may progress, after a delay caused by slow accumulation of variability in the mate choice trait(s), to reproductive isolation between the modes, if the mate choice trait(s) can be recruited into the process of speciation, because of establishment of linkage disequilibria between the mate choice and the fitness-controlling trait(s). This final stage of speciation is essentially identical under the two types of selection: by the time isolation by natural selection is achieved, there is little difference between disruptive and incompatibility selection, both of which eliminate F_1 hybrids between the incipient species and rare backcrosses. However, the processes that lead to establishment of isolation by natural selection are much more complex under two-dimensional incompatibility selection (Fig. 3) than under one-dimensional disruptive selection.

As under disruptive selection (11), speciation under incompatibility selection may be facilitated by high numbers of loci affecting fitness-controlling traits and by low numbers of loci affecting mating-related traits and requires stronger selection under two-trait “color preference” than under one-trait “similar-mates-similar” mode of mate choice (Fig. 2, compare C and D with A and B). High values of A and B , as well as low values of σ , cause the fitness of less adapted phenotypes to be close to zero and also facilitate speciation. Still, speciation may occur under moderate selection, with the genetic load never exceeding ≈ 0.7 (Fig. 3). This value of the genetic load is close to the theoretical minimum (6, 22, 24) necessary to double the phenotypic variance in each generation and eventually establish isolation by natural selection. Of course, if variability of fitness and mate choice is controlled by overlapping sets of loci (3, 9), a much weaker selection could be sufficient. Unequal amounts of the two resources, modeled by letting c_I and c_{II} depend on different parameters, does little to affect speciation (data not reported).

Discussion

Our results demonstrate that incompatibility selection that favors individuals possessing high values of either one or the other of two quantitative traits, but not those possessing high values of both traits, can cause sympatric speciation as easily as disruptive selection acting on one trait. Not surprisingly, the variety of possible outcomes is greater under two-dimensional incompatibility selection. Biologically, incompatibility selection may be more plausible than disruptive selection.

Indeed, two ecological mechanisms of one-dimensional disruptive selection have been proposed. First, such selection may occur when two distinct resources or habitats, such as two host species, are available (4, 15, 26). However, incompatibility selection appears to be more realistic in this case: exploitation of substantially different resources or habitats probably depends on different traits, and the impaired ability to exploit one of them does not *per se* help to exploit the other. Ecological tradeoffs, which force resource specialization and are necessary for speciation, are well documented in a variety of situations (12–19, 27–29). Here, we assumed that the environment is homogeneous, as of free-swimming fish in a lake. Presence of habitats, which must be taken into account if the life cycle involves long sedentary stages, as it is the case for many phytophagous insects (4), has to be considered separately.

Second, disruptive selection was proposed to result from competition for a continuously distributed resource (9, 30, 31) (Roughgarden/Dickmann-Doebeli model; ref. 32). However, this mechanism is controversial (32–34), and strong disruptive selection reported in ref. 9 appears to be an artifact (32). Indeed, if the resource is distributed continuously, substantial flattening of the population distribution can reduce competition for intermediate phenotypes and lead to stabilizing, instead of disruptive, selection (5). One-dimensional selection may also favor speciation under mutational pressure (35), but the importance of this effect remains unknown.

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