Evolutionary Branching and Sympatric Speciation Caused by Different Types of Ecological Interactions

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abstract: Evolutionary branching occurs when frequency-dependent selection splits a phenotypically monomorphic population into two distinct phenotypic clusters. A prerequisite for evolutionary branching is that directional selection drives the population toward a fitness minimum in phenotype space. This article demonstrates that selection regimes leading to evolutionary branching readily arise from a wide variety of different ecological interactions within and between species. We use classical ecological models for symmetric and asymmetric competition, for mutualism, and for predator-prey interactions to describe evolving populations with continuously varying characters. For these models, we investigate the ecological and evolutionary conditions that allow for evolutionary branching and establish that branching is a generic and robust phenomenon. Evolutionary branching becomes a model for sympatric speciation when population genetics and mating mechanisms are incorporated into ecological models. In sexual populations with random mating, the continual production of intermediate phenotypes from two incipient branches prevents evolutionary branching. In contrast, when mating is assortative for the ecological characters under study, evolutionary branching is possible in sexual populations and can lead to speciation. Therefore, we also study the evolution of assortative mating as a quantitative character. We show that evolution under branching conditions selects for assortativeness and thus allows sexual populations to escape from fitness minima. We conclude that evolutionary branching offers a general basis for understanding adaptive speciation and radiation under a wide range of different ecological conditions.

Keywords: adaptive dynamics, evolutionary branching, sympatric speciation, competition, mutualism, predation, quantitative genetics.

Understanding the origin of new species remains one of the core problems in evolutionary biology. Whether one

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believes that there are many (Hutchinson 1959) or actually only a few species (Felsenstein 1981) compared to what one would expect from general niche space considerations, the actual mechanisms by which a phenotypic cluster of individuals splits into two distinct descendant clusters with restricted gene flow between them are only poorly understood. Traditionally, there are two basic approaches to understanding this evolutionary process. In the first, subpopulations of a given species are thought to become geographically isolated, after which they follow separate evolutionary paths, eventually leading to different species that are reproductively isolated even after secondary contact (Mayr 1963). Since the particular cause for geographic isolation is not part of the description, this is a kind of "black box" mechanism. Given such isolation, it is rather easy to imagine that separate evolution in different habitats during many generations would lead to phenotypic differences and to reproductive incompatibility. Indeed, such allopatric speciation is quite well understood experimentally (Rice and Hostert 1993). Theoretically, the basic ingredients for allopatric speciation are isolated habitats in which selection pressures are different and in which different realizations of the stochastic process underlying genetic drift can occur. Habitat differences have also been the starting point for the second traditional approach, which studies the conditions under which speciation occurs in sympatry, that is, when gene flow is possible between two incipient species. In this approach, it is also often assumed that there are different habitats favoring different genotypes, but the different genotypes occur sympatrically and are pooled for mating. One then studies the conditions necessary for reproductive isolation to evolve between the genotypes that are favored in the different habitats (e.g., Maynard Smith 1966; Felsenstein 1981; Kawecki 1996). Depending on whether one thinks that such conditions are easy or hard to meet, one leans toward sympatric or allopatric speciation as the dominant mode for the origin of new species.

The difficulties in the theory of sympatric speciation are twofold (Kondrashov and Mina 1986). On the one hand, ecological conditions must induce disruptive selection in

such a way that the population does not become monomorphic for one of the favored phenotypes. On the other hand, given such ecological conditions, the mating system must evolve such that reproductive isolation ensues between the phenotypes that are favored by disruptive selection. In the history of the theory of sympatric speciation, the focus has shifted between these two difficulties (e.g., Maynard Smith 1966; Felsenstein 1981). In this article, we present an integrative framework for studying sympatric speciation that simultaneously addresses both issues.

In genetic models for sympatric speciation, the maintenance of a polymorphism in the presence of disruptive selection is often a delicate affair (Maynard Smith 1966; Udovic 1980; Felsenstein 1981; Kawecki 1996), thus narrowing the basis for the evolution of reproductive isolation. In our theory, such problems of ecological fine tuning do not arise because disruptive selection is not an externally imposed assumption. Instead, the system automatically converges to a state in which it experiences disruptive selection and in which the conditions for the evolution of polymorphisms are satisfied. We will show that such a course of events is a general phenomenon and can occur under a wide range of ecological interactions.

Our approach is based on the phenomenon of evolutionary branching and on the theory of adaptive dynamics (Metz et al. 1992, 1996; Dieckmann 1994; Dieckmann and Law 1996; Dieckmann 1997; Geritz et al. 1997, 1998; Meszéna et al. 2000). In this approach, ecological interactions are the evolutionary driving force, and the feedback between evolutionary change and the ecological conditions experienced by individuals is considered. Evolutionary dynamics are studied using the concept of invasion fitness (Metz et al. 1992). This quantity measures the long-term per capita growth rate of a rare mutant in an environment that is determined by externally fixed parameters on the one hand and by the population density and the phenotype of the resident population(s) on the other. In particular, the invasion fitness of a mutant explicitly depends on the resident phenotype, reflecting the consequences of frequency-dependent ecological interactions. For deriving analytical results, one makes a number of simplifying assumptions, for example, that mutations are sufficiently rare so that mutants encounter monomorphic resident populations that are at their ecological equilibrium. This corresponds to assuming a separation of ecological and evolutionary timescales, with the ecological dynamics occurring faster than the evolutionary dynamics. Under the further assumption that mutants whose invasion fitness is >0 not only can invade (with some probability) but also can replace the former resident and thus become the new resident, it is possible to study the evolutionary dynamics by analyzing a function $f(y, x)$ describing the invasion fitness of a mutant

y in a resident population x. Here x may be a multidimensional vector, either because the trait under study has more than one component or because there are more than one species involved. Evolutionary dynamics then follow selection gradients determined by derivatives of the invasion fitness function $f(y, x)$, as will be explained in the next sections.

Phenotypes of special interest are those where the selection gradient is 0, and the first question is whether these points actually are evolutionary attractors. In classical optimization models of evolution, reaching such attractors implies that evolution comes to a halt because evolutionary attractors only occur at fitness maxima. However, in the wider framework of adaptive dynamics, this need not be the case (Geritz et al. 1998; Meszéna et al. 2000). When frequency-dependent ecological interactions drive the evolutionary process, it is possible that an evolutionary attractor represents a fitness minimum at which the population experiences disruptive selection. In fact, evolution toward fitness minima due to frequency-dependent selection has been found in a number of previous studies (e.g., Christiansen 1991; Ludwig and Levin 1991; Abrams et al. 1993). Adaptive dynamics takes these analyses one step further by asking what happens after the fitness minimum has been reached. The ensuing evolutionary dynamics can indeed be very interesting because after attaining the fitness minimum the population may split into two distinct and diverging phenotypic clusters. Thus, in adaptive dynamics, evolutionary convergence toward a fitness minimum can lead to evolutionary branching. It is important to note that such a sequence of events is entirely explained by frequency-dependent ecological interactions and does not require any extrinsically imposed disruptive selection pressures.

Evolutionary branching has been found in a number of models, including models for the evolution of dispersal rates (Doebeli and Ruxton 1997; Parvinen 1999) and for the evolution of seed size (Geritz et al. 1999), in host-parasite models (Boots and Haraguchi 1999; Koella and Doebeli 1999), in models for habitat specialization (Geritz et al. 1998), and in models for the evolution of quantitative characters determining competitive interactions (Metz et al. 1996; Dieckmann and Doebeli 1999; Kisdi 1999). These results already hint at the possibility that evolutionary branching might be a ubiquitous phenomenon. To support and to substantiate this claim in a more systematic way, our goal in this article is to demonstrate the phenomenon of evolutionary branching in a number of classical models covering a wide range of ecological interactions. In the next section, we review evolutionary branching in single-species models for symmetric and asymmetric resource competition. It serves to recall basic concepts of the theory of adaptive dynamics and paves the way for the more

complicated two-species models analyzed in the following two sections, where we extend our considerations to co-evolutionary scenarios and show that evolutionary branching is a generic and robust phenomenon in ecological models for two mutualistic species and for predator-prey interactions. Our analytical theory is always supplemented by computer simulations of stochastic individual-based models, which overall confirm the analytical results and thereby show that the assumptions used to derive the analytical theory are sensible.

The framework of adaptive dynamics has so far mainly been developed as an asexual theory that lacks population genetic considerations. In particular, most previous models of evolutionary branching have assumed clonal organisms (for recent exceptions, see Dieckmann and Doebeli 1999; Kisdi and Geritz 1999; Van Dooren 1999). Therefore, the theory of adaptive dynamics may appear not to be relevant for evolution in sexual populations. Quite to the contrary, we suggest that adaptive dynamics and, in particular, processes of evolutionary branching, can have interesting implications for understanding general evolutionary principles. We think that evolutionary branching is a unifying concept that helps us to understand speciation under a wide range of ecological conditions. However, for evolutionary branching to become a model for sympatric speciation, population genetics and mating mechanisms must be incorporated into the underlying ecological models. In this article, we do this by assuming that the quantitative characters influencing ecological interactions are determined by many additive diploid loci (for an alternative approach, see Kisdi and Geritz 1999). In fact, there is a valid caveat against considering evolutionary branching in asexual models as a basis for understanding aspects of speciation: in sexual populations, branching could be prevented by the continual production of intermediate offspring phenotypes through recombination between incipient branches. If mating is random, this indeed is the case. However, if mating is assortative with respect to the ecological characters under study, evolutionary branching is possible in sexual populations and can lead to speciation. This will be demonstrated in "Evolutionary Branching in Sexual Populations," where we will also show that assortative mating is a mechanism allowing the escape from fitness minima. In initially randomly mating populations under branching conditions, assortativeness can therefore be favored by natural selection. Our conclusion is that evolutionary branching can serve as a general paradigm for sympatric speciation once multilocus genetics and the evolution of assortative mating are included in the underlying ecological models.

Evolutionary Branching in Models for Symmetric and Asymmetric Competition

In order to introduce some basic concepts and notation, we begin with single-species competition models that are based on the classical Lotka-Volterra population dynamics. More extensive discussions of related material can be found in Metz et al. (1996), Dieckmann and Doebeli (1999), and Kisdi (1999). We assume that individuals are characterized by a quantitative trait x, for example, body size, which affects intraspecific competition between individuals. Let $N(x, t)$ be the population density of individuals with character value x at time t. Then their ecological dynamics are given by

$$\frac{dN(x, t)}{dt} = rN(x, t)\left[1 - \frac{N_{\text{eff}}(x, t)}{K(x)}\right]. \quad (1)$$

Here, $K(x)$ is the carrying capacity of populations that are monomorphic for trait x. For simplicity, it is assumed that $K(x)$ varies with the trait x and that the intrinsic growth rate r is independent of x. The quantity $N_{\text{eff}}(x, t)$ is the effective population density that an individual with character value x experiences at time t. The effective density is determined by the distribution of phenotypes in the population and by the function $\alpha(x - y)$, which measures the strength of competition exerted by an individual with phenotype y on an individual with phenotype x. Here, we take the function $\alpha(x - y)$ to be

$$\alpha(x - y) = \exp\left(\frac{\sigma_\alpha^2 \beta^2}{2}\right)\exp\left[\frac{-(x - y + \sigma_\alpha^2\beta)^2}{2\sigma_\alpha^2}\right], \quad (2)$$

which has been previously used in the study of character displacement (Rummel and Roughgarden 1985; Taper and Case 1992). For $\beta = 0$, this function describes symmetric competition; that is, $\alpha(x - y)$ is a symmetric function of the difference $x - y$ with a maximum at 0 (see fig. 1A). This implies that individuals with similar phenotypes compete more strongly with each other than individuals with dissimilar phenotypes, as, for example, when beak size in birds determines the type of seeds eaten. If $\beta > 0$, $\alpha(x - y)$ describes asymmetric competition, with $\alpha(x - y)$ being maximal for some negative difference in character values (see fig. 1A). This implies that larger individuals tend to have a competitive advantage over smaller individuals. In contrast to the asymmetric competition models in Law et al. (1997) and in Kisdi (1999), in which the competitive advantage or disadvantage increased monotonically with phenotypic distance, the function $\alpha(x - y)$ used here implies that competition between very different phenotypes is always weak. Such
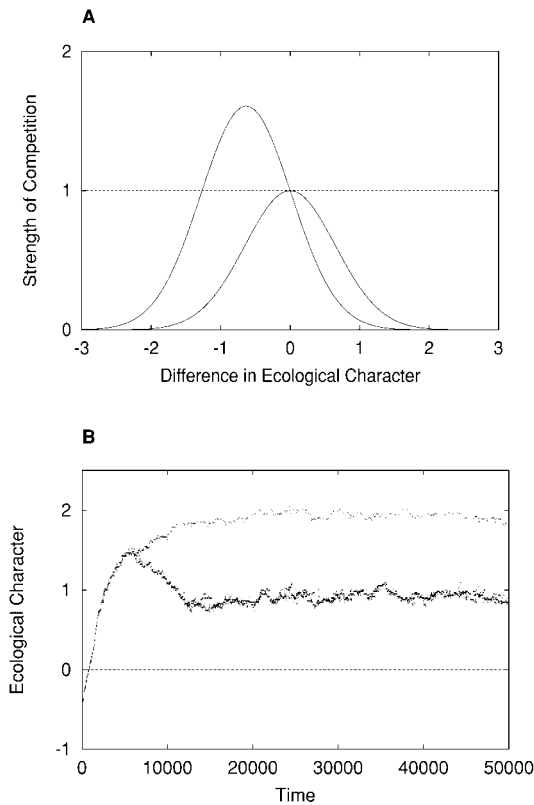
Figure 1: Asexual resource competition and evolutionary branching. *A*, Strength of competition as a function of phenotypic difference between competitors. Symmetric competition is described by the function $\alpha(x - y)$ (see text) with $\beta = 0$. An example of asymmetric competition is shown for $\beta = 1.5$. In both cases, σ_α is set to 0.65. *B*, Evolutionary dynamics with the asymmetric competition function shown in *A*. The distribution of character values (shown by scales of gray: *black* = highest frequency, *white* = absence) first converges toward the ecological character's evolutionary branching point. Since higher values of the ecological character confer an advantage under asymmetric competition, branching occurs at a phenotype that is larger than the one with maximal resources, $x_0 = 0$. At the branching point, directional selection turns into disruptive selection, which splits the character distribution into two phenotypic clusters. The two resulting branches differ in their population size: the upper branch, which is farther away from the carrying capacity's maximum, consists of fewer individuals, although its individuals possess a competitive advantage over those in the lower branch. Parameters: $r = 1$, $K_0 = 1,000$, $\sigma_K = 1$, $\sigma_\alpha = 0.65$, $\beta = 1.5$, $x_0 = 0$.

asymmetric competition would, for example, occur when overlaps in resource utilization between different phenotypes are asymmetric but vanish with increasing phenotypic distance.

For both symmetric and asymmetric competition, the effective density $N_{eff}(x, t)$ is obtained as a weighted sum over all densities $N(x, t)$:

$$N_{\text{eff}}(x, t) = \int \alpha(x - x')N(x', t)dx'. \tag{3}$$

To determine the invasion fitness $f(y, x)$ of a rare mutant y in a resident population that is monomorphic for the character value x, we assume that mutants invade sufficiently rarely, so that residents are always at (or very close to) their ecological equilibrium $K(x)$ when new mutants appear. Since the mutant is initially rare, its own density is negligible compared to that of the resident, and hence the effective density that the mutant experiences is simply the resident density $K(x)$ weighted by the strength of competition $\alpha(y - x)$ between the mutant and the resident. Thus, in the initial phase of the invasion when the mutant is rare, the population dynamics of the mutant are given by

$$\frac{dN(y, t)}{dt} = rN(y, t)\left[1 - \frac{\alpha(y - x)K(x)}{K(y)}\right]. \tag{4}$$

The invasion fitness of the mutant is its long-term per capita growth rate when rare (Metz et al. 1992; Dieckmann 1994; Rand et al. 1994; Dieckmann and Law 1996; Metz et al. 1996), hence the invasion fitness of the mutant y in the resident x is

$$f(y, x) = r\left[1 - \frac{\alpha(y - x)K(x)}{K(y)}\right]. \tag{5}$$

To determine the evolutionary dynamics, one calculates the derivative of $f(y, x)$ with respect to y and evaluates it at the resident value x. Thus, the crucial quantity is the selection gradient:

$$g(x) = \left.\frac{\partial f(y, x)}{\partial y}\right|_{y=x}. \tag{6}$$

If $g(x) > 0$, then invasion fitness increases for mutants with higher trait values than the resident, while invasion fitness decreases for mutants with lower trait values. Since $f(x, x) = 0$ by necessity (i.e., the resident neither grows nor declines in its own equilibrium population), this means that mutants with higher trait values can invade, that is, are favored by natural selection, while mutants with lower trait values are selected against. Analogous statements in the opposite direction hold for $g(x) < 0$. Thus, as long as $g(x) \neq 0$, selection is directional. For the evolutionary dynamics, those values x^* are important for which $g(x^*) = 0$. These trait values are called "evolutionarily singular" (Metz et al. 1996; Geritz et al. 1998). A

singular value x^* is an attractor for the evolutionary dynamics if and only if

$$\frac{dg(x)}{dx}\bigg|_{x=x^*} < 0, \tag{7}$$

for, in that case, $g(x) < 0$ for $x > x^*$ and $g(x) > 0$ for $x < x^*$; hence, lower trait values are favored when the resident is larger than x^* and higher trait values are favored when the resident is smaller than the singular value x^*. Singular points that are not attractors are of little practical interest since, even starting with resident populations that are very close to such a point, evolution will drive the trait away from the singular point. A critical issue to realize, however, is that there are two different types of evolutionary attractors.

This can be seen by considering the second derivative of the invasion fitness at the evolutionary attractor x^*. If $[\partial^2 f(y, x^*)]/\partial y^2|_{y=x^*} < 0$, then the point x^* is a fitness maximum with respect to the mutant trait value y (recall that $[\partial f(y, x^*)]/\partial y|_{y=x^*} = g(x^*) = 0$, since we assume that x^* is a singular point). The evolutionary attractor x^* is, therefore, stable against invasion of neighboring phenotypes; that is, it is an evolutionarily stable strategy (ESS).

If x^* is an ESS, selection first drives the population toward x^* and then comes to a halt; that is, x^* is an evolutionary equilibrium, also called a "continuously stable strategy" (CSS; Eshel 1983). A very different scenario occurs when

$$\frac{\partial^2 f(y, x^*)}{\partial y^2}\bigg|_{y=x^*} > 0. \tag{8}$$

In this case, evolution still drives the population toward x^* since we assumed the singular point x^* to be an evolutionary attractor. However, once at x^*, the population is actually located at a fitness minimum and therefore experiences disruptive selection. As a consequence, evolutionary branching can occur; that is, the population can split into two different and diverging phenotypic clusters (Metz et al. 1996; Geritz et al. 1997, 1998).

Metz et al. (1996), Dieckmann and Doebeli (1999), and Kisdi (1999) have shown that evolution toward a fitness minimum, and hence evolutionary branching, is a generic phenomenon in models for resource competition similar to the ones described above. To complement this theory, we use equation (2) above for the function $\alpha(x - y)$ describing the frequency dependence in the competitive interactions, and we take the resource distribution to be of Gaussian form with a maximum at some intermediate phenotype x_0:

$$K(x) = K_0 \exp\left[\frac{-(x - x_0)^2}{2\sigma_K^2}\right]. \tag{9}$$

We then calculate $g(x)$, equation (6), from equations (4) and (5), as

$$g(x) = -r\left[\alpha'(0) - \frac{K'(x)}{K(x)}\right]$$

$$= -r\left(\frac{x - x_0}{\sigma_K^2} - \beta\right). \tag{10}$$

It follows that $g(x^*) = 0$ for $x^* = x_0 + \beta\sigma_K^2$. Note that the singular point is always larger than the trait value maximizing the carrying capacity. The derivative of $g(x)$ at the singular point x^* is

$$\frac{dg(x)}{dx}\bigg|_{x=x^*} = -\frac{r}{\sigma_K^2} < 0. \tag{11}$$

Hence, x^* always is an evolutionary attractor. In addition, straightforward calculations reveal that condition (8) becomes

$$\frac{\partial^2 f(y, x^*)}{\partial y^2}\bigg|_{y=x^*} = r\left(\frac{1}{\sigma_\alpha^2} - \frac{1}{\sigma_K^2}\right) > 0. \tag{12}$$

This condition is satisfied, and hence x^* is a fitness minimum, if

$$\sigma_\alpha < \sigma_K. \tag{13}$$

Thus, for a given width σ_K of the resource distribution, the singular point x^* is a branching point, that is, an evolutionarily attracting fitness minimum, if the parameter σ_α is small enough. Since σ_α measures the strength of the frequency dependence in the competitive interactions, this implies that, in the model considered, asymmetric competition leads to evolutionary branching whenever the frequency dependence is strong enough. (Note that this result is also true if competition is symmetric; i.e., if $\beta = 0$; see Dieckmann and Doebeli 1999.) An example of the corresponding evolutionary dynamics is shown in figure 1B. (This figure is based on an individual-based model, the details of which are described in app. A.) Starting with small phenotypic values, the evolutionary dynamics show a steady increase in the trait value until the system reaches the branching point. Because larger phenotypes have an intrinsic advantage, branching occurs at a phenotypic value that is larger than the value that maximizes the car-

rying capacity. After branching, the phenotype in one branch continues to increase, while in the other branch it decreases again. Note that the population size is different in the two branches, with the branch that consists of larger individuals and is located farther away from the optimal carrying capacity having fewer individuals. For a more thorough treatment and additional examples of evolutionary branching under symmetric and asymmetric competition, see Dieckmann and Doebeli (1999) and Kisdi (1999).

Evolutionary Branching in Coevolutionary Models for Mutualisms

The classical models for studying processes of diversification are based on competition (MacArthur and Levins 1967), and other types of ecological interactions have received less attention. In the next two sections, we therefore examine evolutionary branching in models for mutualism and for predator-prey interactions. In the models considered, coevolutionary dynamics of quantitative characters in two separate species are driven by interspecific ecological interactions. The mathematics of adaptive dynamics in two-species models are more involved than in their one-species counterparts (Abrams et al. 1993; Dieckmann and Law 1996; Marrow et al. 1996; Matessi and Di Pasquale 1996; Metz et al. 1996; Leimar 2000). However, conditions for evolutionary branching are analogous to those for the one-species models: frequency-dependent selection results in convergence to an evolutionary attractor on which either one or both species find themselves at fitness minima. Accordingly, evolutionary branching can occur in only one species, in both species simultaneously, or in both species sequentially (see below).

In this section, we extend standard Lotka-Volterra models for mutualisms to coevolutionary models in which quantitative characters affect the strength of mutualistic interactions. Simple models of mutualistic dynamics (see, e.g., Vandermeer and Boucher 1978) arise in a very similar way from one-species models as do two-species competition models, namely by adding a second density-dependent term to per capita growth rates in the basic Lotka-Volterra equation for one species:

$$\frac{dN_1(t)}{dt} = r_1 N_1(t)\left[1 - \frac{N_1(t)}{K_1} + a_{12} N_2(t)\right],$$

$$\frac{dN_2(t)}{dt} = r_2 N_2(t)\left[1 - \frac{N_2(t)}{K_2} + a_{21} N_1(t)\right]. \quad (14)$$

Here a_{12} and a_{21} are positive real numbers describing the strength of mutualistic support that the two species pro-

vide to each other. Vandermeer and Boucher (1975) have studied the ecological dynamics of system (14) (for an extension see Bever 1999), but we are not aware of extensions of this system to situations where the interaction coefficients a_{ij} are determined by evolving quantitative characters in the two species. Such an extension can be formulated based on the theory of mutualism developed in Kiester et al. (1984), who analyzed coevolution in mutualistic systems using the quantitative genetics framework of Lande (1982). They considered a pair of mutualistic species, for example, a flowering plant and its insect pollinator, in which quantitative characters, for example, related to flower morphology and to feeding apparatus, determine the level of mutualistic support. Specifically, let x_1 and x_2 denote the characters in the two species, and let $p_1(x_1)$ and $p_2(x_2)$ be the phenotype distributions in the two species. In other words, the frequency of individuals with phenotypes in the interval $(x_1, x_1 + dx_1)$ in species 1 is $p_1(x_1)dx_1$ and similarly for $p_2(x_2)$. Following Kiester et al. (1984), we assume that the support $\alpha_{12}(x_1 - x_2)$ that a species-1 individual with phenotype x_1 receives from a species-2 individual with phenotype x_2 is given by

$$a_{12}\frac{\alpha(x_1 - x_2)}{\int \alpha(x_1' - x_2)p_1(x_1')dx_1'}, \quad (15)$$

where $\alpha(x_1 - x_2) = \exp\left[-(x_1 - x_2)^2/2\sigma_\alpha^2\right]$, and where a_{12} is a positive constant. This expression takes into account that the total amount of support provided to species-1 individuals by any one species-2 individual is limited and equal to a_{12} and that this total amount is distributed among species-1 individuals according to the weights $\alpha(x_1 - x_2)$. Thus, individuals of species 2 do not vary in their total amount of support given to species-1 individuals. Instead, they vary in how the support is distributed among species-1 individuals according to differences in character values. The support $\alpha_{21}(x_2 - x_1)$ provided by species-1 individuals with phenotype x_1 to species-2 individuals with phenotype x_2 is obtained in an analogous way as

$$a_{21}\frac{\alpha(x_2 - x_1)}{\int \alpha(x_2' - x_1)p_2(x_2')dx_2'}, \quad (16)$$

where a_{21} is the total amount of support provided by species-1 individuals. The rationale behind expressions (15) and (16) is applicable to many mutualistic species pairs, as is explained in detail in Kiester et al. (1984). Here, we combine their approach with the classical models of Vandermeer and Boucher (1978), equation (14) above.

For populations that are monomorphic for character values x_1 and x_2, respectively, the ecological dynamics are given by

$$\frac{dN_1(x_1, t)}{dt} = r_1 N_1(x_1, t)$$

$$\times \left[1 - \frac{N_1(x_1, t)}{K_1(x_1)} + a_{12} N_2(x_2, t)\right],$$

$$\frac{dN_2(x_2, t)}{dt} = r_2 N_2(x_2, t) \qquad (17)$$

$$\times \left[1 - \frac{N_2(x_2, t)}{K_2(x_2)} + a_{21} N_1(x_1, t)\right].$$

Here, $N_1(x_1, t)$ and $N_2(x_2, t)$ are the population sizes of the monomorphic populations of species 1 and 2 at time t, and we again assume that individuals do not vary within species in their intrinsic growth rates but that, owing to variation in resource availability, there is within-species variation in the carrying capacities $K_1(x_1)$ and $K_2(x_2)$. These functions are assumed to be of of the form $K_1(x) = K_{11} + K_{12} N(x_{10}, \sigma_{K_1}, x)$ for species 1 and $K_2(x) = K_{21} + K_{22} N(x_{20}, \sigma_{K_2}, x)$ for species 2, where the $N(x_{i0}, \sigma_{K_i}, x)$ are Gaussian functions of the variable x with maximum at $x = x_{i0}$ and variance equal to σ_{K_i}. The parameters K_{i1} represent a uniform background level of resources. Note that the maxima x_{10} and x_{20} of the two resource distributions will generally occur at different character values in the two species.

As in the previous section, we assume a separation of ecological and evolutionary timescales in order to analyze the coevolutionary dynamics of the two traits x_1 and x_2. That is, we start from monomorphic resident populations at their ecological equilibrium and then determine the fate of rare mutants as they arise in both species. For certain choices of parameters a_{12} and a_{21}, the ecological system (14) does not converge toward an equilibrium (Vandermeer and Boucher 1978), and instead, population sizes increase without bounds. Here we restrict our attention to those biologically feasible cases in which the monomorphic residents reach a stable equilibrium.

The equilibrium population sizes of such resident populations are functions $N_1^*(x_1, x_2)$ and $N_2^*(x_1, x_2)$ of the resident character values x_1, x_2 in both species and can be calculated from (17) by setting right-hand sides equal to 0. Given these values, the dynamics of a rare mutant y_1 in species 1 are given by

$$\frac{dN_1(y_1, t)}{dt} = r_1 N_1(y_1, t) \left[1 - \frac{N_1^*(x_1, x_2)}{K_1(y_1)}\right.$$

$$\left. + a_{12} \frac{\alpha(y_1 - x_2)}{\alpha(x_1 - x_2)} N_2^*(x_1, x_2)\right]. \qquad (18)$$

Here the support given to species-1 individuals with character value y_1 by species-2 individuals with character value x_2 is calculated from equation (15) using the fact that the mutant y_1 is very rare initially, so that the phenotype distribution $p_1(x_1')$ in species 1 is concentrated at the resident phenotype x_1, $\int \alpha(x_1' - x_2) p_1(x_1') dx_1' = \alpha(x_1 - x_2)$. Thus, the initial per capita growth rate of a rare species-1 mutant y_1 in the resident (x_1, x_2)-population, that is, the invasion fitness $f_1(y_1, x_1, x_2)$, is given by

$$f_1(y_1, x_1, x_2) = r_1 \left[1 - \frac{N_1^*(x_1, x_2)}{K_1(y_1)}\right.$$

$$\left. + a_{12} \frac{\alpha(y_1 - x_2)}{\alpha(x_1 - x_2)} N_2^*(x_1, x_2)\right]. \qquad (19)$$

Analogously, the invasion fitness of a rare species-2 mutant y_2 in the resident (x_1, x_2) population is

$$f_2(y_2, x_1, x_2) = r_2 \left[1 - \frac{N_2^*(x_1, x_2)}{K_2(y_2)}\right.$$

$$\left. + a_{21} \frac{\alpha(y_2 - x_1)}{\alpha(x_2 - x_1)} N_1^*(x_1, x_2)\right]. \qquad (20)$$

The evolutionary dynamics of this system are determined by evaluating the derivatives of the invasion fitness functions with respect to the mutant trait value at the respective resident values, that is, by

$$g_1(x_1, x_2) = \left.\frac{\partial f_1(y_1, x_1, x_2)}{\partial y_1}\right|_{y_1 = x_1} \qquad (21)$$

and by

$$g_2(x_1, x_2) = \left.\frac{\partial f_2(y_2, x_1, x_2)}{\partial y_2}\right|_{y_2 = x_2}. \qquad (22)$$

In analogy with the one-dimensional system considered in the previous section, the singular points of the two-dimensional coevolutionary system studied here are resident values x_1^*, x_2^* such that $g_1(x_1^*, x_2^*) = g_2(x_1^*, x_2^*) = 0$ (Dieckmann and Law 1996; Metz et al. 1996; Geritz et al. 1998; Leimar 2000). Whereas in one-dimensional systems singular points are either attractors or repellors for the evolutionary dynamics, two-dimensional systems offer more possibilities, including saddle points (Dieckmann and Law 1996; Leimar 2000) and cyclic evolutionary dynamics (Dieckmann et al. 1995; Marrow et al. 1996). In appendix B, we indicate how to determine the evolutionary
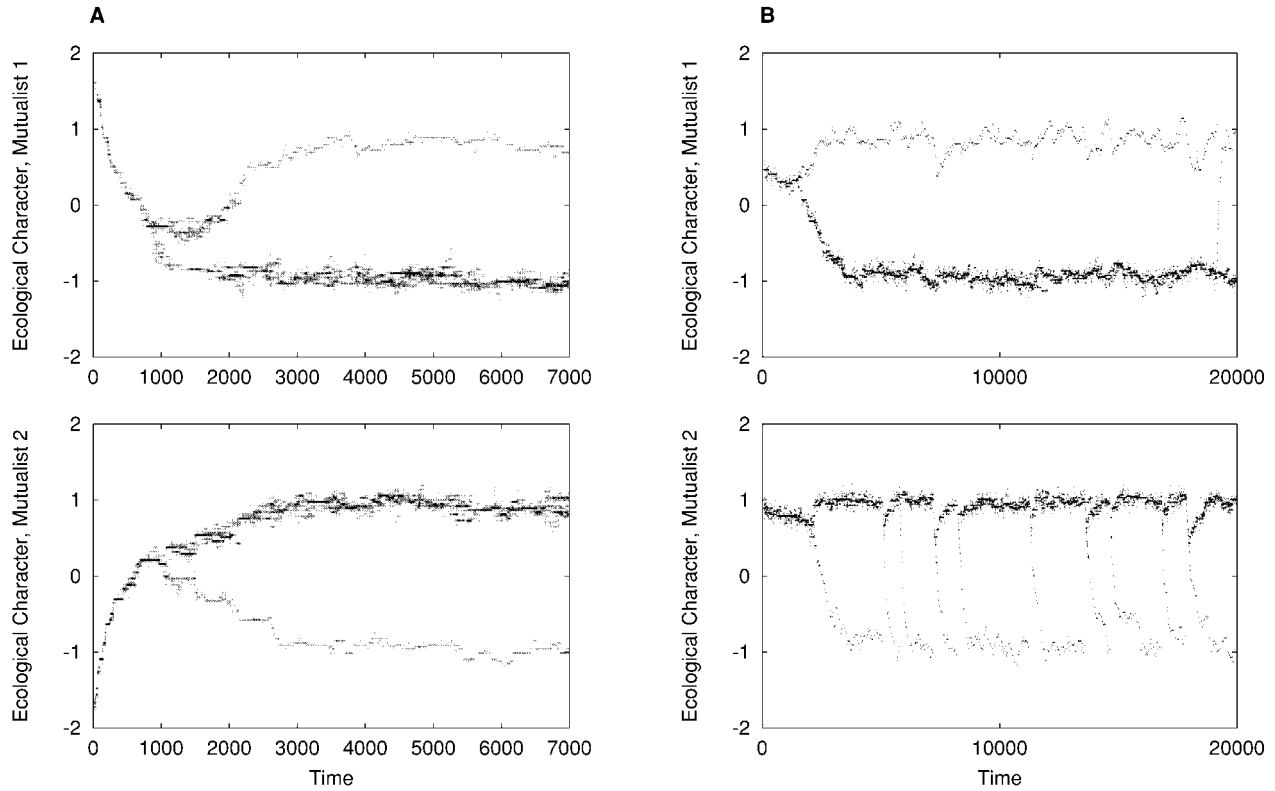
Figure 2: Asexual coevolutionary dynamics of mutualistic interactions. *A*, Simultaneous evolutionary branching in two symmetric mutualistic species leads to two asymmetric pairs of mutually specialized populations. In each pair, one branch is close to its resource optimum (high abundance), while the other (low abundance) mainly exploits its mutualistic partner. Parameters: $r_1 = r_2 = 1$, $K_1(x_1) = K_{11} + K_{12} \exp\left[-(x_1 - x_{10})^2/2\sigma_{K_1}\right]$, $K_2(x_2) = K_{21} + K_{22} \exp\left[-(x_2 - x_{20})^2/2\sigma_{K_2}\right]$, $K_{11} = K_{21} = 300$, $K_{12} = K_{22} = 400$, $x_{10} = -1$, $x_{20} = 1$, $\sigma_{K_1} = \sigma_{K_2} = 1.0$, $a_{12} = a_{21} = 0.00016$, $\alpha(x_1 - x_2) = \exp\left[-(x_1 - x_2)^2/2\sigma_\alpha^2\right]$, $\sigma_\alpha = 0.4$, $\mu_1 = \mu_2 = 0.01$, $\sigma_{M_1} = \sigma_{M_2} = 0.05$. *B*, Primary evolutionary branching in one of two asymmetric mutualistic species results in repeated secondary evolutionary branching and extinction in the partner species. After the two branches of the first mutualist are established, subsequent branching occurs in the second mutualist. This causes one of the resulting secondary branches to evolve to exploit the highly abundant branch of its mutualistic partner. This adaptation requires a large departure from the second species' resource optimum, upon which the newly established branch goes extinct again, triggering a continual cyclic sequence of repeated branching and extinction in the second mutualist. Parameters are the same as in *A*, except for $K_{11} = K_{21} = 50$, $K_{12} = K_{22} = 200$, $\sigma_{K_1} = 0.8$, $\sigma_{K_2} = 0.55$, $a_{12} = a_{21} = 0.001$, $\sigma_\alpha = 0.3$.

stability properties of a singular point (x_1^*, x_2^*). We are interested in singular points that are evolutionary attractors, and we wish to determine the conditions under which those evolutionary attractors are also fitness minima for either one or both of the trait values x_1^* and x_2^*. That is, we are looking for evolutionary attractors (x_1^*, x_2^*) for which the invasion fitness functions have a minimum with respect to the mutant trait values:

$$\left.\frac{\partial^2 f_1(y_1, x_1^*, x_2^*)}{\partial y_1^2}\right|_{y_1 = x_1^*} > 0, \qquad (23)$$

$$\left.\frac{\partial^2 f_2(y_2, x_1^*, x_2^*)}{\partial y_2^2}\right|_{y_2 = x_2^*} > 0. \qquad (24)$$

If either one or both of these conditions are satisfied at an evolutionary attractor, then the evolutionary dynamics will first converge to the singular point (x_1^*, x_2^*), after which evolutionary branching will occur in one or both species (see app. B). It is not our aim here to give an exhaustive classification of all the possibilities of coevolutionary dynamics in our model for mutualism (although this would seem to be a worthwhile and interesting endeavor). Instead, we confine ourselves to pointing out that, again, evolutionary branching is a generic feature of this model and proceed by describing general conditions under which branching occurs.

We first consider a symmetric case, in which the mutual support is equal for both species (i.e., $a_{12} = a_{21}$), and in which the two species only differ in the location of the maxima of their resource distributions. Then, if these max-

ima are far enough apart, evolutionary branching is likely to occur. This can be understood as follows. If the resource distributions have different maxima, say $x_{10} < x_{20}$, then there is an evolutionarily singular point (x_1^*, x_2^*) that lies symmetrically between these maxima, that is, such that $x_{10} < x_1^* < x_2^* < x_{20}$ and such that the distance to their respective resource maxima is the same in both species (app. B). Such a configuration results from a trade-off between being close to the own resource maximum and being close to the phenotype of the other species in order to benefit from its mutualistic support. With increasing distance between the two resource maxima, the distance between the singular values x_1^* and x_2^* constituting a symmetric singular point increases as well. Intuitively speaking, an increasing distance between the resource distributions increases the strain on the evolutionary compromise between the two species. If this strain is large enough, and if the symmetric singular point is an evolutanry attractor (for techinical details, see app. B), then simultaneous evolutionary branching in both species occurs, an example of which is shown in figure 2*A*.

The evolutionary outcome resulting from branching is interesting: branching leads to two species pairs, in each of which one of the species is close to its resource optimum and provides a large amount of mutualistic support to the other species in the pair, which in turn is far away from its resource optimum and therefore can give only little support. Thus, in each of the two original species, branching leads to one mutualistic branch, which is close to its resource optimum, and one "exploitative branch," which is far from its resource optimum, and each branch interacts mainly with its respective opposite in the other species. In this way, an initially symmetric configuration, with each species being at equal distance from its resource optimum and giving equal amounts of support to its partner, evolves into two asymmetric species pairs, in each of which one species essentially only survives because of the mutualistic support from the other species.

These results are robust in the sense that introducing asymmetries in the system will not qualitatively change them. With large asymmetries, however, new phenomena such as repetitive evolutionary branching can be observed. An example is shown in figure 2*B*. Here the evolutionarily attracting singular point (x_1^*, x_2^*) is a fitness minimum for only one of the two species and, therefore, branching first occurs only in that species. Subsequently, the evolving dimorphism also induces evolutionary branching in the second species because emergence of the two branches in the first species leads to disruptive selection for mutualistic support in the second species. The two branches in the second species, however, do not persist indefinitely, and, instead, the branch that is far away from its resource optimum eventually goes extinct. The remaining branch then again undergoes secondary branching, which leads to a repeating, cyclic pattern of speciation and extinction in this lineage. That frequency-dependent ecological interactions can lead to adaptation-driven extinctions has been observed before (see, e.g., Dieckmann et al. 1995).

Evolutionary Branching in Coevolutionary Predator-Prey Models

To complete our survey of evolutionary branching under different fundamental types of ecological interactions, we study coevolution in predator-prey systems. For this purpose, we use an extension of classical Lotka-Volterra predator-prey models, similar to the ones used in Dieckmann at al. (1995) and in Brown and Vincent (1992; see also Doebeli 1997). Brown and Vincent (1992) already concluded that frequency-dependent predation could lead to coexistence of multiple predator and prey species at evolutionary stable states. However, their approach differs in at least two ways from the predator-prey models described below: first, they did not study the actual mechanisms by which multiple species would arise (i.e., speciation), and, second, they included frequency-dependent competition among the prey as an additional diversifying agent.

Here we assume that the interaction parameter describing predation efficiency depends on two quantitative characters, one in the prey and the other in the predator. These characters are scaled such that the interactions are the stronger the more similar prey and predator characters are. If x_1 denotes the character in the prey and x_2 that in the predator, the predation efficiency of a predator with phenotype x_2 on prey individuals with phenotype x_1 is

$$\alpha(x_1 - x_2) = \alpha_0 \exp\left[\frac{-(x_1 - x_2)^2}{2\sigma_\alpha^2}\right]. \qquad (25)$$

As a consequence, the ecological dynamics of monomorphic prey and predator populations with trait values x_1 and x_2 are given by

$$\frac{dN_1(x_1, t)}{dt} = rN_1(x_1, t)$$

$$\times \left[1 - \frac{N_1(x_1, t)}{K(x_1)}\right.$$

$$\left. - \alpha(x_1 - x_2)N_2(x_2, t)\right], \qquad (26)$$

$$\frac{dN_2(x_2, t)}{dt} = N_2(x_2, t)$$

$$\times [-d + c\alpha(x_1 - x_2)N_1(x_1, t)].$$

Here, $N_1(x_1, t)$ is the size at time t of the prey population monomorphic for x_1, $N_2(x_2, t)$ is the size of the predator population monomorphic for x_2, and r, d, and c are positive rate constants describing, respectively, the intrinsic growth rate of the prey, the death rate of the predator, and the conversion efficiency of captured prey into predator offspring. For simplicity, we assume that these parameters are not influenced by the quantitative characters x_1 and x_2. However, we again assume that resource availability for the prey varies with the quantitative character x_1 such that the resource distribution function $K(x_1)$ is of Gaussian form $N(x_0, \sigma_K)$ with a maximum at x_0. Note, however, that we do not assume frequency dependence in the competitive interactions among the prey.

Yet, the existence of the predator system imposes frequency-dependent selection on the prey because common prey phenotypes have the disadvantage that the predator phenotype that preys upon them most efficiently is thriving. We show that this frequency dependence can easily lead to evolutionary branching in the prey. To see this, we again calculate the growth rate of rare mutants in both prey and predator while assuming that the resident phenotypes are at their ecological equilibria, $N_1^*(x_1, x_2)$ and $N_2^*(x_1, x_2)$, which can easily be calculated by setting the right-hand sides of (26) to 0. The population dynamics of a rare prey mutant y_1 in the resident population is given by

$$\frac{dN_1(y_1, t)}{dt} = rN_1(y_1, t)\left[1 - \frac{N_1^*(x_1, x_2)}{K(y_1)}\right.$$

$$\left. - \alpha(y_1 - x_2)N_2^*(x_1, x_2)\right], \quad (27)$$

so that the invasion fitness becomes

$$f_1(y_1, x_1, x_2) = r\left[1 - \frac{N_1^*(x_1, x_2)}{K(y_1)}\right.$$

$$\left. - \alpha(y_1 - x_2)N_2^*(x_1, x_2)\right]. \quad (28)$$

Similarly, the dynamics of a rare predator mutant y_2 is given by

$$\frac{dN_2(y_2, t)}{dt} = N_2(y_2, t)[-d + c\alpha(x_1 - y_2)N_1^*(x_1, x_2)], \quad (29)$$

so that the invasion fitness for the predator becomes

$$f_2(y_2, x_1, x_2) = -d + c\alpha(x_1 - y_2)N_1^*(x_1, x_2). \quad (30)$$

As in the previous models, the quantities that determine the monomorphic evolutionary dynamics of the system are the selection gradients, that is, the derivatives of the invasion fitness functions with respect to mutant phenotypes, evaluated at the resident values:

$$g_1(x_1, x_2) = \left.\frac{\partial f_1(y_1, x_1, x_2)}{\partial y_1}\right|_{y_1 = x_1}$$

$$= r\frac{N_1^*(x_1, x_2)K'(x_1)}{K^2(x_1)} \quad (31)$$

$$- r\alpha'(x_1 - x_2)N_2^*(x_1, x_2),$$

$$g_2(x_1, x_2) = \left.\frac{\partial f_2(y_2, x_1, x_2)}{\partial y_2}\right|_{y_2 = x_2}$$

$$= -d + c\alpha'(x_1 - x_2)N_1^*(x_1, x_2). \quad (32)$$

The quantities $g_1(x_1, x_2)$ and $g_2(x_1, x_2)$, together with the rate constants for the mutation processes in the two species, determine the coevolutionary dynamics (app. B). Singular points of this system are points (x_1^*, x_2^*) with $g_1(x_1^*, x_2^*) = g_2(x_1^*, x_2^*) = 0$. Their stability is determined as described in appendix B. It is intuitively clear (and easy to see analytically from eqq. [31] and [32]) that the only singular point in this system is $x_1^* = x_2^* = x_0$. If this point is an evolutionary attractor, the prey character will evolve to the optimum of the resource distribution, and the predator will evolve to maximize its predation efficiency. It is also intuitively clear that for a given prey character, it is best for the predator to have the same character value as

Figure 3: Asexual coevolutionary dynamics of predator-prey interactions. *A*, Evolutionary branching only in the prey. While the ecological character in the prey converges (with oscillations) to a fitness minimum, leading to branching in the prey character, the resulting branches do not move far enough apart to induce secondary branching in the predator. Parameters: $r = d = 1$, $c = 2$, $\alpha_0 = 0.001$, $K(x_1) = K_0 \exp[-(x_1 - x_0)^2/2\sigma_K]$, $K_0 = 2,000$, $x_0 = 0$, $\sigma_K = 0.27$, $\alpha(x_1 - x_2) = \exp[-(x_1 - x_2)^2/2\sigma_\alpha^2]$, $\sigma_\alpha = 0.23$, $\mu_1 = \mu_2 = 0.01$, $\sigma_{M_1} = \sigma_{M_2} = 0.05$. *B*, Secondary evolutionary branching in the predator. In this case, the prey branches diverge sufficiently for the predator to experience a fitness minimum, resulting in secondary branching in the predator character. Parameters are the same as in *A*, except for $\sigma_K = 0.7$, $\sigma_\alpha = 0.4$. *C*, Evolutionary cycling of predator-prey interactions. Under identical ecological conditions, changes in mutation rates can dramatically affect outcomes of asexual coevolution. In the case shown here, the prey evolves so fast relative to the predator that it always evades the predator's adaptation, instead of being caught at a fitness minimum and undergoing evolutionary branching. Parameters are the same as in *B*, except for $\mu_2 = 0.002$.

A

B

C
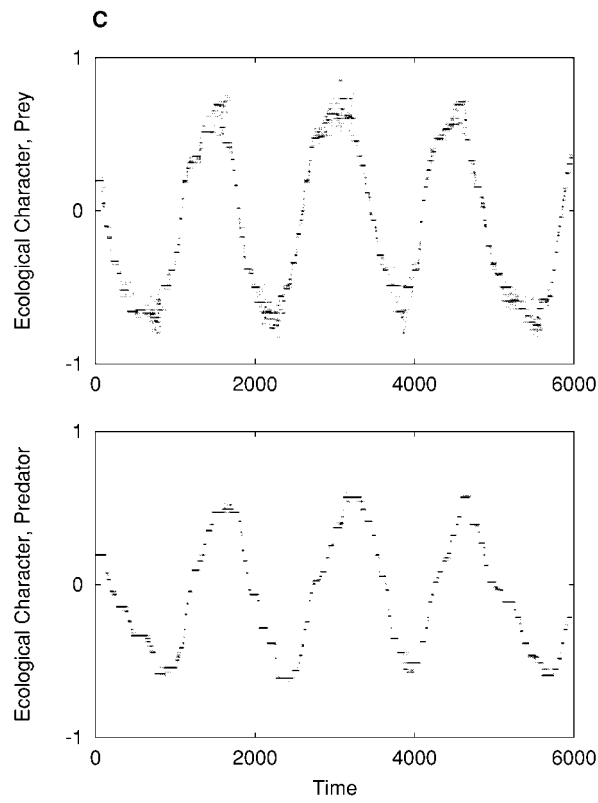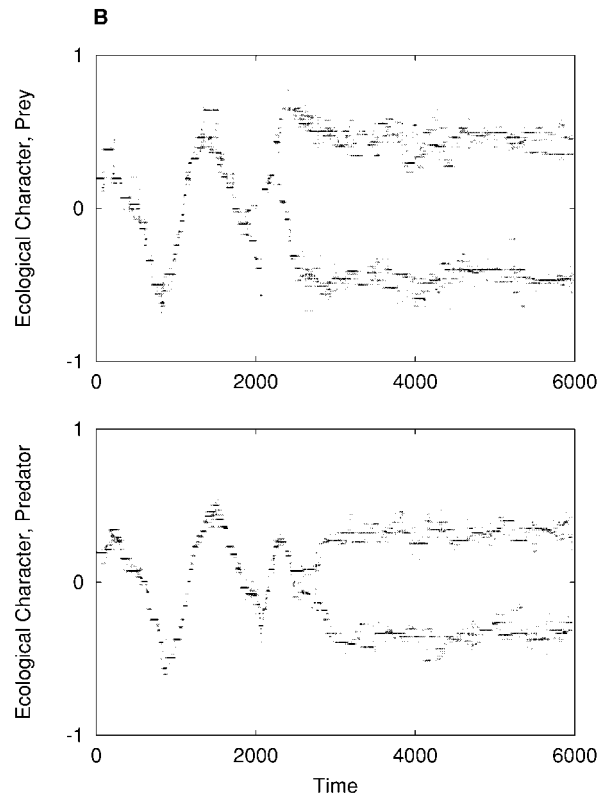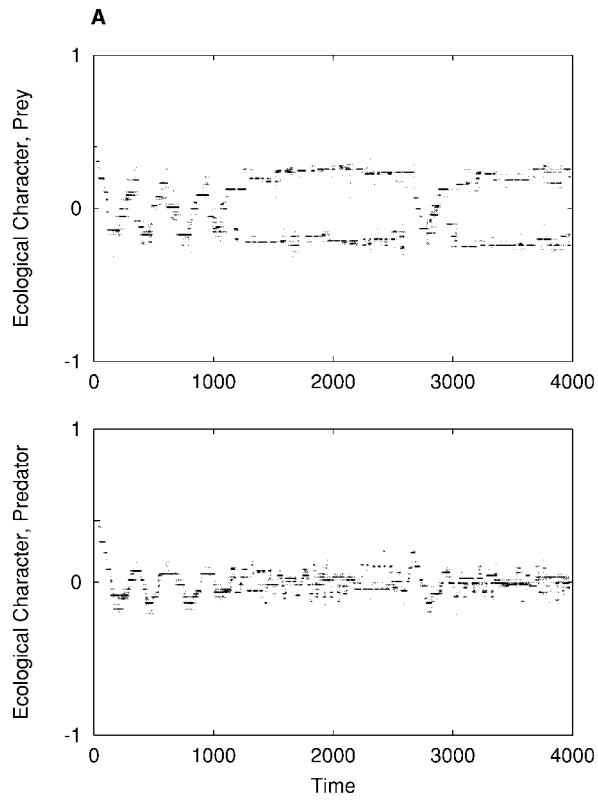
the prey to maximize its predation efficiency. This implies that the singular point (x_0, x_0) will always be a fitness maximum for the predator and, hence, can never be a branching point for the predator character.

However, the singular point will be a branching point for the prey character as soon as the frequency dependence given by the function $\alpha(x_1 - x_2)$ is strong enough (app. B). In other words, for fixed values of the other parameters in the system, evolutionary branching in the prey character occurs when the predation efficiency decreases sufficiently fast with increasing distance between prey and predator characters. An example of evolutionary branching in the prey is shown in figure 3A. In the example shown, the predator does not undergo evolutionary branching. As a consequence of branching in the prey, the predator therefore becomes a generalist with a lower predation efficiency on each of the two emerging prey species than it had on the single prey species that existed before branching.

Evolutionary branching in the prey can sometimes induce secondary branching in the predator. When the prey character splits into two clusters, one might, at first glance, expect that it would always be best for the predator to undergo such a split as well. However, whether this happens depends on the details of the system: predator individuals having character values deviating from the intermediate between the two prey branches have the advantage of being closer to one of the two branches, but at the same time they have the disadvantage of being farther away from the other one. As is shown in appendix B, it is the distance of the two prey branches from the intermediate singular point x_0 that determines whether or not branching in the prey induces secondary branching in the predator. This is exemplified in figure 3B, for which parameters are the same as in figure 3A, except for increased widths of the resource distribution and the predation efficiency. This allows the two phenotypic branches in the prey to diverge farther and hence to induce secondary branching in the predator. In this case, the outcome of the evolutionary process are two prey species, each being exploited by a specialist predator, as opposed to the generalist predator emerging with a narrower resource distribution for the prey (fig. 3A).

To end this section, we give an example of how a change in the relative evolutionary speed, resulting from different mutation rates in the two species, can critically affect the adaptive dynamics. In the system shown in figure 3C, everything is the same as in figure 3B, except that now the mutation rate in the predator is five times lower than the mutation rate in the prey. This destabilizes the singular point (x_0, x_0), as described in appendix B: instead of convergence to the singular point, the coevolutionary adaptive dynamics now show sustained evolutionary cycling. Thus, the evolution in the predator-prey system gives rise to a cyclic type of arms race. This scenario has been extensively studied by Dieckmann et al. (1995; see also Abrams and Matsuda 1996; Doebeli 1997).

Evolutionary Branching in Sexual Populations

So far we have considered clonally reproducing populations. That is, the quantitative characters of offspring were identical to those of their parents, except for changes resulting from mutations. While such a theory is applicable to simple organisms, it clearly requires incorporation of population genetics in order to serve as a basis for understanding evolution in sexual populations. In this section, we describe ways of including multilocus genetics into models of adaptive dynamics, and we identify some of the conditions under which branching can occur in sexual populations. In particular, we show that evolutionary branching can easily arise in sexual species if mating is assortative with respect to traits determining the ecological interactions. The evolution of assortative mating therefore is a crucial issue, which we address by assuming that assortativeness is also a quantitative trait. We show that under branching conditions selection favors genotypes that mate assortatively, which leads to evolutionary branching in initially randomly mating sexual populations.

To introduce population genetics into our ecological models, we assume that the quantitative characters determining ecological interactions in these models are genetically determined by many equivalent, additive, diploid and diallelic loci with free recombination. This assumption is easily implemented into individual-based models, as described in appendix A. Examining parameter values that ensure evolutionary branching in the corresponding asexual models, simulations of the individual-based sexual models readily reveal that evolutionary branching cannot occur in sexual populations if mating is random (fig. 4A). This is intuitively clear, for random mating produces intermediate offspring phenotypes from extreme parent phenotypes and therefore results in the continual production of intermediate phenotypes from two incipient branches. This prevents the branches from developing into distinct phenotypic clusters.

However, the situation drastically changes if mating is assortative rather than random. To model this case, we assume that the probability of mating between individuals with similar ecological characters is relatively higher than the probability of mating between individuals with dissimilar ecological characters. Such a situation would, for example, arise if mating is assortative with respect to body size and if body size at the same time has a strong effect on the ecological interactions, conditions that appear to be satisfied in many species (Schluter and Nagel 1995). Another example is given by quantitative characters that
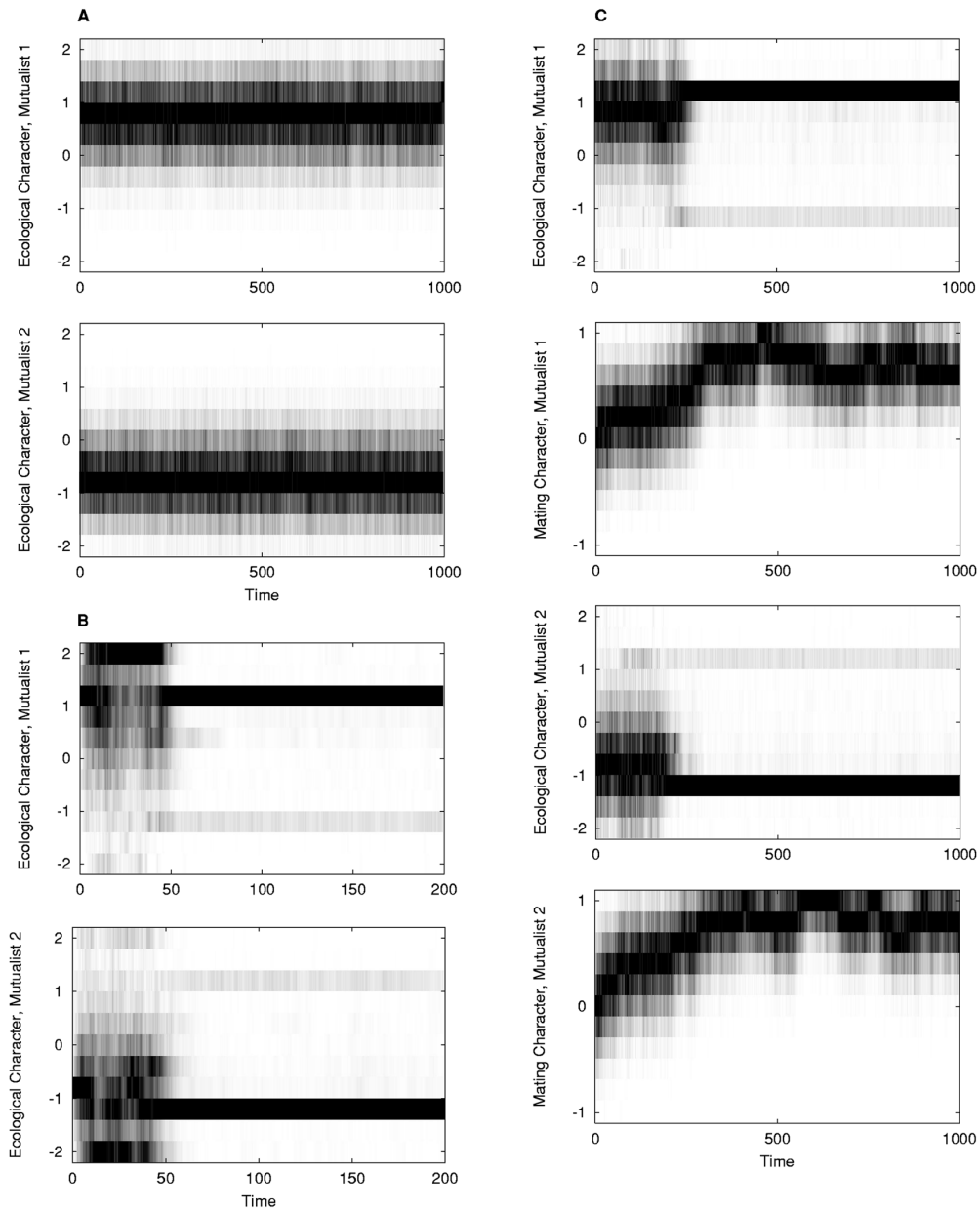
Figure 4: Sexual coevolutionary dynamics of mutualistic interactions. *A*, Coevolution under random mating. Without assortative mating, the two sexually reproducing mutualistic species cannot undergo evolutionary branching: the continual generation of intermediate offspring characters prevents any bimodality in character values to persist. *B*, Coevolution under fixed assortative mating. Given a sufficiently high, yet fixed, degree of assortativeness ($\sigma_{\text{mate}} = 1/20$), each of the two sexually reproducing mutualistic species rapidly splits into two reproductively isolated branches. *C*, Coevolution under evolving degrees of assortative/disassortative mating. When allowing for adaptation in the degree of assortativeness (*second and fourth panel*), disruptive selection at the fitness minima favors the evolution of assortative mating, thus enabling evolutionary branching in the two sexually reproducing mutualistic species (*first and third panel*). Ecological characters and mating characters are determined by five diploid loci; other parameters are the same as in figure 2*A*.

control diet preferences: often individuals mate where they feed so that mating probabilities increase with similarity of feeding preferences, as is the case, for example, for the apple maggot fly (Feder et al. 1988).

To be specific, we assume that the probability of mating between two individuals with ecological character values x and y is proportional to

$$\exp\left[\frac{-(x-y)^2}{2\sigma_{mate}^2}\right], \tag{33}$$

where the parameter σ_{mate} determines the degree of assortativeness: if σ_{mate} is small, mating is strongly assortative, and if $\sigma_{mate} = \infty$, mating is random. In a randomly mating population, the probability of mating between phenotypes x and y is $p(x)p(y)$, where $p(x)$ and $p(y)$ are the frequencies of the two phenotypes. In a population with assortative mating, however, the probability of mating between phenotypes x and y is proportional to $\exp\left[-(x-y)^2/2\sigma_{mate}^2\right]p(x)p(y)$, with a proportionality factor arising from a normalization ensuring that, as with random mating, the total probability of mating equals 1 for all phenotypes. (This may not be a realistic assumption for all systems: when assortative mating has a large cost extreme phenotypes may have a disadvantage. However, we expect our results to be robust against introducing small to moderate costs of assortative mating.)

With this setup, evolutionary branching occurs in sexual populations if mating is sufficiently assortative. An example is shown in figure 4*B*, for which we have implemented the genetic assumptions in the model for the evolution of mutualism described in "Evolutionary Branching in Coevolutionary Models for Mutualism." The ecological parameters for this figure are the same as those used for figure 2*A*, which shows simultaneous branching in two asexual mutualistic species. In figure 4*A*, mating is random, and branching does not occur in either species. In figure 4*B*, however, mating is assortative with respect to the quantitative characters determining the mutualistic interaction, and evolutionary branching again occurs simultaneously in both species. In other words, each species splits into two distinct phenotypic and genotypic clusters. Note that because mating is assortative with respect to the phenotypes forming the clusters, these clusters eventually are almost completely reproductively isolated, so that there is very little gene flow between them. Similar observations hold for our models for resource competition and for predator-prey interactions: under branching conditions in the clonal versions, evolutionary branching occurs in the sexual multilocus versions of these models if assortative mating with respect to the characters determining the ecological interactions is strong enough.

The remaining question is why mating should be assortative in the first place. To investigate this, we regard the degree of assortativeness itself as a quantitative character that is determined by many loci. This allows us to study the evolution of assortative mating in initially randomly mating populations. To exert no bias on the evolution of mating preference, we also allow for the possibility of disassortative mating in our individual-based models, that is, for the possibility that mating probabilities increase with the distance between ecological characters of partners. Thus, individuals having an intermediate mating character mate randomly, while individuals having character values toward one extreme of the mating character's range mate disassortatively and individuals with values toward the other extreme mate assortatively, that is, preferentially with ecologically similar partners (fig. 5).

The basic result emerging from our individual-based simulations is that, under branching conditions, positive assortative mating is selectively favored and typically evolves to a degree that allows for evolutionary branching. That is, given parameter values that ensure branching in the corresponding asexual model, mating evolves from being random to a degree of assortativeness that enables branching in sexual populations. For the case of symmetric competition, this is described in more detail in Dieckmann and Doebeli (1999). Here, we give examples for the evo-
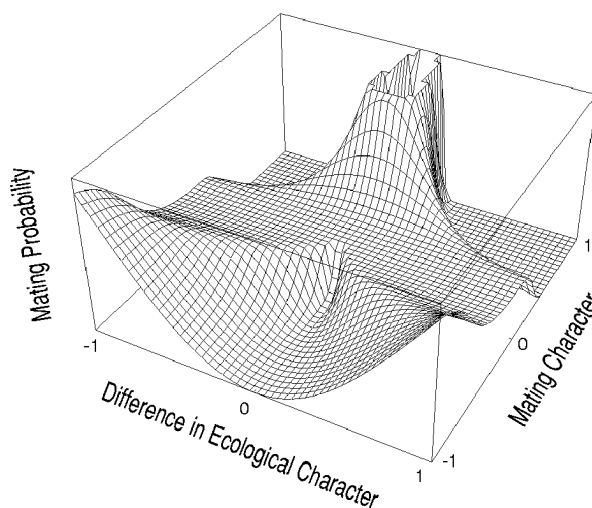

Figure 5: Character-dependent degrees of assortative/disassortative mating. Mating probabilities as determined by mating character and difference in ecological characters between mates. If the mating character in a focal individual is close to +1 (only plus alleles at mating loci), it has a high probability of mating only with similar individuals. If its mating character is close to −1 (only minus alleles), it is more likely to mate with dissimilar individuals. Intermediate mating characters (close to 0) correspond to random mating.
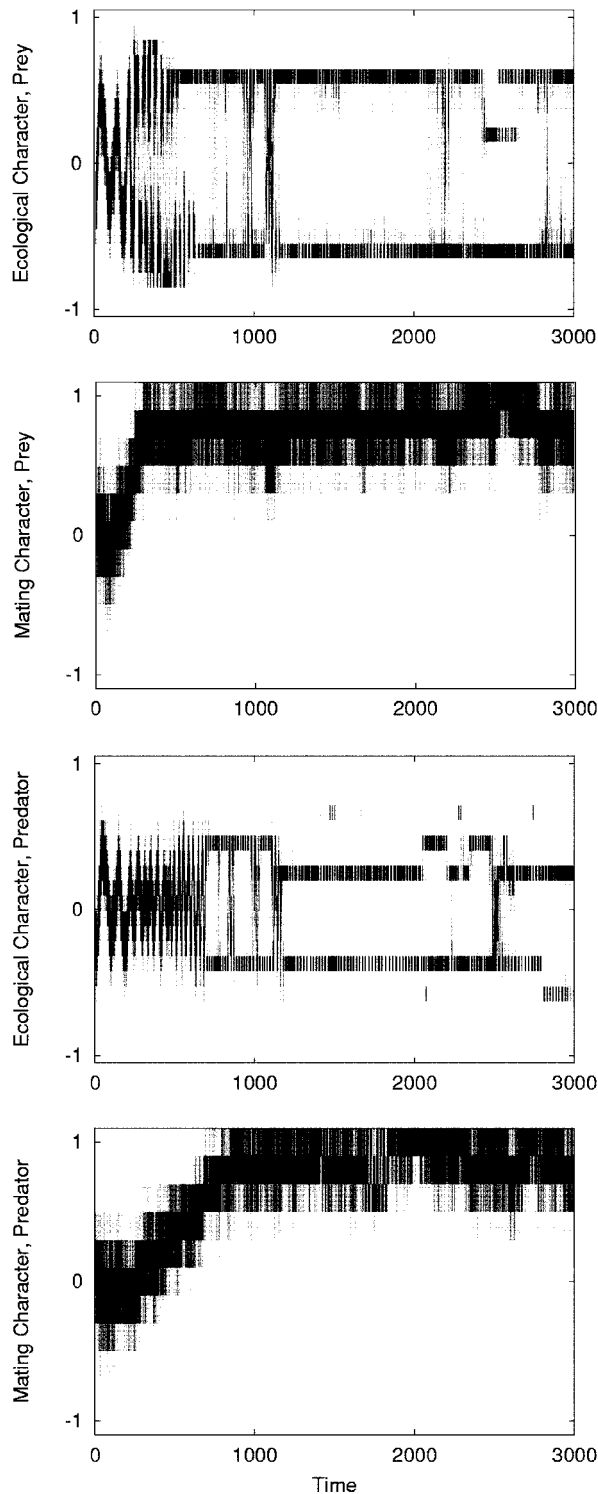
lution of assortative mating and subsequent evolutionary branching in the sexual mutualistic model (fig. 4C) and in the sexual predator-prey model (fig. 6).

Our extensive numerical simulations indicate that for the models considered in this article, parameter requirements for the evolution of assortative mating, and hence for evolutionary branching in sexual populations, are not significantly more restrictive than the conditions for branching in the corresponding clonal models. The reason why assortative mating evolves under branching conditions is rather straightforward. At the branching point, the population is trapped at a fitness minimum if mating is random (fig. 4A). Assortative mating is a mechanism that allows for evolutionary branching and hence for a departure from the fitness minimum because it prevents the generation of intermediate offspring phenotypes from extreme parent phenotypes. Because their offspring are less likely to have a phenotype corresponding to the fitness minimum, individuals that mate assortatively are favored by natural selection. Once assortative mating has evolved, evolutionary branching can occur in sexual populations. In conclusion, when multilocus genetics and the evolution of assortative mating are incorporated into ecological models, adaptive dynamics leading to evolutionary branching offers a unifying framework for studying and understanding sympatric speciation.

Discussion

Evolutionary branching is a type of adaptive dynamics that naturally occurs in phenotypic evolutionary models involving frequency-dependent selection (Metz et al. 1996; Geritz et al. 1998). It consists of two phases: first, there is convergence in phenotype space to an evolutionarily attracting fitness minimum, and then the population splits into two diverging phenotypic clusters. In this article, we have shown that this evolutionary phenomenon readily occurs in a range of basic models in which evolutionary dynamics are driven by different types of ecological interactions. Symmetric and

Figure 6: Sexual coevolutionary dynamics of predator-prey interactions. Coevolution under evolving degrees of assortative/disassortative mating in sexual predator and prey populations leads to primary and secondary evolutionary branching. Initially, the prey character converges (with oscillations) toward the fitness minimum at its resource optimum (*first panel*). There, the degree of assortativeness is evolutionarily adjusted to high values (*second panel*). Under these conditions, primary evolutionary branching occurs in the prey (*first panel*). This induces a fitness minimum for the predator, leading to increased levels of assortativeness in this species (*fourth panel*), and subsequently allowing for secondary evolutionary branching in the predator (*third panel*). Ecological characters are determined by 10 diploid loci, mating characters by five diploid loci; other parameters are the same as in figure 3B.

asymmetric resource competition, mutualistic interactions, and predator-prey interactions can all lead to evolutionary branching, which is therefore a general and robust feature of adaptive dynamics.

Evolutionary branching is a mechanism that can explain speciation in asexual populations. By including population genetics into the underlying ecological models, it becomes an integrating paradigm for studying sympatric speciation in sexual populations. To illustrate this finding we have assumed that the quantitative characters that determine ecological interactions are controlled by many loci, and we have investigated the evolution of assortative mating in our models. The results show that, because of the evolution of positive assortative mating with respect to the characters determining ecological interactions, evolutionary branching also generically arises in models for sexual populations, in which it can lead to sympatric speciation.

Previous Models for Sympatric Speciation

One of the main differences between our approach and previous work is that in the framework presented here disruptive selection is not an externally imposed assumption, as is the case in the majority of earlier models, where some form of habitat difference is usually needed to generate disruptive selection (e.g., Maynard Smith 1966; Udovic 1980; Felsenstein 1981; Johnson et al. 1996; Kawecki 1996). In such models, the maintenance of a polymorphism for the phenotypes favored in the different habitats (a prerequisite for the evolution of reproductive isolation) is problematic. By contrast, in the framework of adaptive dynamics, the emergence of disruptive selection is an intrinsic process: disruptive selection dynamically arises from the underlying ecological interactions in such a way that the conditions for the evolution and maintenance of a polymorphism, that is, for evolutionary branching, are automatically satisfied. The basic insight is that this is a generic phenomenon. (It should be noted that evolutionary branching in traits determining habitat specialization also readily occurs in multiple-habitat models; see Geritz et al. 1998.)

Two approaches similar to our theory were previously put forward by Seger (1985) and by Kondrashov (1986; Kondrashov and Kondrashov 1999). In Seger (1985) frequency-dependent resource competition could generate a mismatch between the phenotype distribution and the resource distribution, the consequences of which were explored by means of a simple genetic model leading to the conclusion that overdispersed resources are needed for sympatric speciation. Seger (1985) modeled assortative mating as a discrete rather than as a continuous trait, which may have contributed to the fact that unimodal (binomial) resource distributions did not favor speciation

in his model. Nevertheless, if his model is put into the framework of adaptive dynamics, his results can be reformulated in terms of conditions for evolutionary branching points. From the perspective of population genetics, Kondrashov's studies of sympatric speciation (Kondrashov 1986; Kondrashov and Mina 1986; Kondrashov and Kondrashov 1999) are more similar to ours, although these authors did not use an ecological embedding that would generate the selection regimes. Instead, an unspecified mechanism is assumed to favor marginal phenotypes at all times. Moreover, these authors did not model the degree of assortative mating as a quantitative trait. Our results can be viewed as an extension and generalization of these previous results, suggesting that, in theory, sympatric speciation is a common evolutionary process.

The model that comes closest to this one—because it is a precursor—is Doebeli (1996). This article shows that frequency-dependent competition for unimodally distributed resources can lead to sympatric speciation if mating is assortative, and that assortative mating should evolve continuously toward a degree inducing speciation. It used a deterministic multilocus genetic model for the ecological traits but did not consider genetics for assortative mating. It also did not put results into the framework of adaptive dynamics and evolutionary branching and therefore did not highlight the obtained results as a special case of a general phenomenon.

Felsenstein (1981), who used a model of the type involving habitat differences to generate disruptiveness, classified models for sympatric speciation into two groups: the "one-allele" models, in which the same alleles need to be substituted in the subpopulations forming the two incipient branches in order to achieve divergence and reproductive isolation, and the "two-allele" models, in which different alleles must be substituted in the two incipient species. Felsenstein (1981) noted that sympatric speciation occurs relatively easily in one-allele models but is much harder to obtain in two-allele models. The models presented here would all be classified as one-allele models because in our models evolutionary branching occurs in sexual populations if assortative mating evolves in both incipient branches; that is, if the alleles coding for stronger assortativeness are substituted in both branches. To make the genetic theory more general, one therefore wants to consider models in which assortative mating is not based on the characters that determine ecological interactions but instead on selectively neutral marker traits. In this case, evolution of assortative mating is not sufficient anymore to induce speciation under branching conditions. In addition, a linkage disequilibrium between loci coding for the marker trait on the one hand and for the ecological character on the other is required. This implies that different marker alleles must be substituted in the two in-

cipient branches: this scenario thus corresponds to the two-allele models of Felsenstein (1981). The reason why speciation is more difficult when mating is based on a marker trait is that recombination between the marker loci and the loci determining the ecological character prevents the buildup of a linkage disequilibrium between the marker trait and the ecological trait. As Felsenstein (1981) pointed out, deterministic models predict that sympatric speciation is unlikely under these conditions (see also Seger 1985).

However, a rather different picture emerges when stochastic, individual-based models are employed. In Dieckmann and Doebeli (1999), we have shown that, once demographic stochasticity and resulting genetic drift are included in the description, evolutionary branching is a robust phenomenon in sexual populations even when assortative mating is based on a neutral marker trait. The reason is that genetic drift that is due to demographic stochasticity leads to small and genetically localized linkage disequilibria. These local and temporary disequilibria select for assortative mating, which in turn magnifies the local disequilibria into a global and stable linkage disequilibrium between marker trait and ecological character, allowing for evolutionary branching. Thus, symmetry breaking that is due to genetic drift can trigger evolutionary branching in sexual populations, despite the opposing force of recombination. We have described this phenomenon in detail in Dieckmann and Doebeli (1999) for the case of symmetric resource competition, and similar observations are expected to hold for the coevolutionary models described in this article. This establishes a strong link between our theory and models for sympatric speciation based on sexual selection (Lande 1982). That assortative mating based on marker traits can lead to evolutionary branching and sympatric speciation in our ecological models means that the evolution of sexually selected traits might strongly promote phenotypic cluster formation and divergence if sexually selected characters become correlated with characters affecting ecological interactions. Recent results of Kondrashov and Shpak (1998) indicate that sympatric speciation is unlikely without such a correlation, that is, with assortative mating based on a selectively neutral trait alone. Notice that a wide range of potential marker traits coexist in typical organisms. For branching to occur in sexual populations, only one of these needs to latch on to the ecologically relevant character. The likelihood for such an event is further enhanced by the existence of spatial phenotypic heterogeneity and by the occurrence of cryptic speciation (Metz et al. 1996): fleeting patterns of cryptic variation may become "frozen" at a branching point.

Empirical Evidence for Sympatric Speciation

Evidence for the sympatric origin of many species groups is accumulating rapidly in recent years. Strong support comes from phylogenetic reconstruction studies based on genetic analyses, for example, in cichlids (Meyer et al. 1993; Schliewen et al. 1994), and it is increasingly recognized that extent populations show large degrees of population subdivision, which may often be the raw material for processes of speciation. Relevant studies (e.g., Boursot et al. 1996; De Leon et al. 1997) may reveal cases of incipient speciation that can be investigated experimentally, for example, in light of the theory presented here. This seems to be promising because there already are a few cases in which our theory agrees particularly well with empirical insights about the mechanisms of speciation. For example, a recent study of incipient speciation in a pair of cichlid morphs in a crater lake in Cameroon by U. Schliewen, K. Rassmann, and D. Tautz (unpublished manuscript) argues that competition for resources and size-assortative mating are responsible for reproductive isolation between two monophyletic morphs that only differ in size. More generally, sympatric speciation driven by niche separation due to resource competition is an attractive explanation for the radiation of the monophyletic cichlids in large lakes in Africa. Recent studies by Seehausen et al. (1997) show that sexually selected traits are used for maintaining species boundaries, which seems to correspond well with the extension of our theory to the evolution of assortative mating based on marker traits that are correlated with ecological characteristics (Dieckmann and Doebeli 1999).

Another example where our theory would seem to be applicable are sticklebacks in the lakes of British Columbia (Schluter and McPhail 1992; Schluter 1994; Taylor and McPhail 1999). Although it is not clear at present whether the two forms that exist in some lakes, a large benthic one and a small limnetic one, arose sympatrically, there is evidence from experimental research (Schluter 1994; Nagel and Schluter 1998; Rundle and Schluter 1998) as well as from phylogenetic studies (Taylor and McPhail 1999) that supports this hypothesis. In these species, body size is an ecologically important trait, and studies of assortative mating (Nagel and Schluter 1998; Rundle and Schluter 1998) match with the theoretical prediction that size assortative mating could have led to a sympatric split into a large and a small form as a result of competition for resources.

Further empirical evidence for sympatric speciation via evolutionary branching comes from studies on organisms such as intertidal snails (Johannesson et al. 1995), *Anolis* lizards (Losos et al. 1998), and senecio trees (Knox and Palmer 1995), in which resource competition is likely to have been a major driving force of speciation. Evolutionary

branching due to resource competition may also help explain the much discussed speciation events in Darwin's finches, a group that, because of the biogeography of the Galápagos islands, is regarded as a stronghold for allopatric speciation theory. In fact, it is known that size-assortative mating is common in these birds and that body size, and in particular beak size, strongly influences their diet (Grant et al. 1985). While these birds are a classical study system for ecological character displacement (e.g., Schluter et al. 1985; Schluter 1988), the possibility of sympatric speciation has not been a major focus of interest, and it may be worthwhile to reconsider even this apparently long-resolved case of allopatric speciation in the light of evolutionary branching.

There are also cases of radiation and divergence in mutualistic and predator-prey systems for which our models may help unravel the underlying mechanisms. For example, Kiester et al. (1984) argue that the exceptional diversity of orchids may be due to coevolution with orchid bees, and our model for facultative mutualism could provide a theoretical basis for understanding speciation in this group of species. Another example comes from carnations in Middle Europe, whose diversity matches the diversity of their pollinators. It is believed that coevolutionary interactions dominate these mutualistic systems (A. Erhardt, personal communication), and it is likely that many more examples of adaptive speciation due to mutualistic interactions are revealed once mutualisms are investigated more rigorously from the perspective of ecologically driven radiations (see Pellmyr and Leebens-Mack 2000, in this issue).

When viewed from the predator's perspective, predator-prey interactions lead to familiar resource competition, but for the prey a different type of selection pressure emerges, termed "apparent competition" by Holt (1977), under which prey compete for predator-free phenotype space. Recently, it has been emphasized that apparent competition may be a strong diversifying force (Brown and Vincent 1992; Abrams 2000, in this issue), and our theory shows that apparent competition can lead to sympatric speciation through evolutionary branching in the prey. Empirical support for this comes for instance from mollusks, where it has been argued that the great diversity of ornamentation in some groups is due to evolutionary responses to predation (e.g., Van Damme and Pickford 1995; Stone 1998; Leighton 1999). Another example comes from sticklebacks, where it has been proposed that predation is important for the evolution of divergent body shapes (Walker 1997). Finally, Chown and Smith (1993) suggested that size-selective predation by mice, in combination with size-assortative mating, is causing sympatric speciation in sub-Antarctic weevils, a scenario that corresponds well with

the models presented in "Evolutionary Branching in Sexual Populations."

In sum, there appear to exist many case studies supporting a theory of sympatric speciation and radiation driven by ecological interactions, as presented in this article. However, evidence for sympatric speciation from field research and from experimental studies involving relatively large organisms with long generation times such as fish will almost always be circumstantial to some extent (the example of Schliewen et al., unpublished manuscript, mentioned above provides a convincing exception). A promising alternative for empirically testing the theory of evolutionary branching may be found in experimental evolution of microorganisms. Recent work by Rainey and Travisano (1998; Travisano and Rainey 2000, in this issue) shows that sympatric divergence can be induced in bacteria by placing them in a novel, heterogeneous environment. It would appear that such approaches could be developed into direct tests of evolutionary branching by experimentally generating the ecological conditions and interactions predicted by the theory to induce adaptive speciation. Such experiments could greatly advance our knowledge about one of the central problems in biology: understanding the processes that lead to the origin of new species.

APPENDIX A

Description of the Individual-Based Models

In this appendix, we summarize the algorithmic procedures underlying the simulation results presented in this article. For the individual-based asexual simulations, we follow the polymorphic stochastic model developed in Dieckmann (1994) and employed in Dieckmann et al. (1995) and Dieckmann and Doebeli (1999). In this model, individuals in an ecological community can belong to different species and can possess distinct phenotypes. At any given time, each individual can reproduce or die according to stochastic rates that can depend on the abundance and phenotypic composition of all species in the community. When an individual gives birth, its offspring will either inherit the parent's phenotype or undergo a mutation that results in a random displacement between offspring and parent phenotype.

For the evolutionary models of symmetric and asymmetric intraspecific competition ("Evolutionary Branching

in Models for Symmetric and Asymmetric Competition"), the community comprises a single species. The distribution of phenotypes x at time t is described by $n(x, t)$. From this, the phenotypic frequency distribution $p(x, t)$, used in equations (15) and (16), is obtained as $p(x, t) = n(x, t)/\int n(x', t)dx'$. The stochastic per capita rates for birth and death of an individual with phenotype x at time t are then given by

$$b(x, n) = r,$$

$$d(x, n) = r\frac{1}{K(x)}\int \alpha(x - x')n(x', t)dx' \quad (A1)$$

$$= r\frac{N_{\text{eff}}(x, t)}{K(x)}.$$

Mutations in offspring phenotypes occur with probability μ. For a parent phenotype x, mutated offspring phenotypes are chosen according to a Gaussian distribution $N(x, \sigma_M)$ with mean x and variance σ_M^2.

For the coevolutionary models of interspecific mutualisms ("Evolutionary Branching in Coevolutionary Models for Mutualisms"), the stochastic per capita birth and death rates in the two mutualistic species are set to

$$b_1(x_1, n_1, n_2) = r_1\left[1 + a_{12}\right.$$
$$\left. \times \int \frac{\alpha(x_1 - x_2)\int n_1(x_1')dx_1'}{\int \alpha(x_1' - x_2)n_1(x_1')dx_1'}\right.$$
$$\left. \times n_2(x_2)dx_2\right], \quad (A2)$$

$$d_1(x_1, n_1, n_2) = r_1\frac{1}{K_1(x_1)}\int n_1(x_1')dx_1',$$

and to

$$b_2(x_2, n_1, n_2) = r_2\left[1 + a_{21}\right.$$
$$\left. \times \int \frac{\alpha(x_2 - x_1)\int n_2(x_2')dx_2'}{\int \alpha(x_2' - x_1)n_2(x_2')dx_2'}\right.$$
$$\left. \times n_1(x_1)dx_1\right] \quad (A3)$$

$$d_2(x_2, n_1, n_2) = r_2\frac{1}{K_2(x_2)}\int n_2(x_2')dx_2'.$$

As for the single-species models, mutation probabilities for two-species models are determined by μ_1 and μ_2, and mutation distributions around parent phenotypes are given by $N(x_1, \sigma_{M_1})$ and $N(x_2, \sigma_{M_2})$.

For the coevolutionary predator-prey models ("Evolutionary Branching in Coevolutionary Predator-Prey Models"), per capita birth and death rates for the prey are

$$b_1(x_1, n_1, n_2) = r,$$

$$d_1(x_1, n_1, n_2) = r\left[\frac{1}{K(x_1)}\right.$$
$$\left. \times \int n_1(x_1')dx_1' \quad (A4)\right.$$
$$\left. + \int \alpha(x_1 - x_2)n_2(x_2)dx_2\right],$$

and for the predator

$$b_2(x_2, n_1, n_2) = c\int \alpha(x_1 - x_2)n_1(x_1)dx_1,$$
$$d_2(x_2, n_1, n_2) = d. \quad (A5)$$

For the individual-based sexual simulations, we generalize the genetic model introduced by Dieckmann and Doebeli (1999) to coevolutionary dynamics. In this extended model, individuals in an ecological community can belong to different species and can possess distinct genotypes. The stochastic per capita rates for birth and death are affected by the abundance and phenotypic composition of all species in the community in the same way as in the asexual models.

However, in the sexual models, phenotypic diversity is no longer only generated by mutations but now also arises from the recombination of genotypes. Each individual carries two diploid sets of diallelic loci (with alleles plus and minus), one set determining the ecological phenotype, the other set affecting mate choice. Loci have equivalent and additive phenotypic effects and recombine freely. Under these assumptions, five diploid loci, for example, can code for 11 equidistant phenotypic values. The ecological character is chosen to range from -1 to $+1$ for the predator-prey system and from -2 to $+2$ for the system of mutualists. The mating character always assumes values between -1 and $+1$ and is given by the difference between the number of plus and minus alleles at the mating loci divided by the total number of mating alleles.

An individual with ecological character x and mating character m reproduces by chosing a partner with ecological character x' depending on the difference $x' - x$. The

probability distribution for this choice is depicted in figure 5. For $m > 0$, mating is assortative with mating probabilities following a Gaussian function $N(x, \sigma_{\text{mate}})$ with $\sigma_{\text{mate}} = 1/20m^2$. For $m = 0$, mating is random. For $m < 0$, mating is disassortative with mating probabilities following a Gaussian function $1 - N(x, \sigma_{\text{mate}})$ with $\sigma_{\text{mate}} = 1/m^2$. In order to avoid a bias against marginal phenotypes in the population, mating probabilities are normalized, so that their sum over all potential partners is 1 for all ecological phenotypes. Upon reproduction, one offspring allele at each diploid locus is chosen randomly from the two alleles at the corresponding homologous locus of the first parent and the other allele from those of the second parent. With a small probability ($\mu = 0.001$), a mutation occurs in the inherited alleles and reverses their value.

APPENDIX B

Coevolutionary Adaptive Dynamics of Two Traits in Two Species

We briefly review some properties of the dynamical systems describing the coevolution of two quantitative traits in two species. Let x_1 and x_2 denote the current resident values of the two traits in species 1 and 2, respectively, and let y_1 and y_2 denote trait values of rare mutants appearing in the populations. Then the fate of these mutants is determined by the invasion fitness functions $f_1(y_1, x_1, x_2)$ and $f_2(y_2, x_1, x_2)$. The quantities that determine the direction of gradual evolutionary change are the selection gradients

$$g_1(x_1, x_2) = \frac{\partial f_1(y_1, x_1, x_2)}{\partial y_1}\bigg|_{y_1 = x_1},$$

$$g_2(x_1, x_2) = \frac{\partial f_2(y_2, x_1, x_2)}{\partial y_2}\bigg|_{y_2 = x_2}. \tag{B1}$$

More precisely, if mutations are sufficiently rare and sufficiently small the adaptive dynamics of the trait vector

$$\begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$$

is given by

$$\frac{d}{dt}\begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{bmatrix} m_1(x_1)g_1(x_1, x_2) \\ m_2(x_2)g_2(x_1, x_2) \end{bmatrix}. \tag{B2}$$

Here $m_1(x_1)$ and $m_2(x_2)$ are quantities describing how the

mutational process that governs evolution in the two traits (and affects the rates and the distributions at which new mutations occur) influences the speed of evolution.

Expression (B2) has been derived in Dieckmann (1994) and in Dieckmann and Law (1996), to which we refer for a much more detailed and general discussion of this so-called canonical equation of adaptive dynamics (see also Leimar 2000). The singular points of the evolutionary dynamics given by (B2) are those points (x_1^*, x_2^*) in trait space for which both selection gradients vanish, $g_1(x_1^*, x_2^*) = g_2(x_1^*, x_2^*) = 0$. Whether a singular point is an evolutionary attractor or not can be seen from the Jacobian $\mathbf{J}(x_1^*, x_2^*)$ of the dynamical system (B2) at the singular point (x_1^*, x_2^*) (see Marrow et al. 1996; Leimar 2000):

$$\mathbf{J}(x_1^*, x_2^*) = \begin{bmatrix} m_1(x_1^*)\dfrac{\partial g_1}{\partial x_1}(x_1^*, x_2^*) & m_1(x_1^*)\dfrac{\partial g_1}{\partial x_2}(x_1^*, x_2^*) \\ m_2(x_2^*)\dfrac{\partial g_2}{\partial x_1}(x_1^*, x_2^*) & m_2(x_2^*)\dfrac{\partial g_2}{\partial x_2}(x_1^*, x_2^*) \end{bmatrix}. \tag{B3}$$

The singular point (x_1^*, x_2^*) is an evolutionary attractor if and only if the Jacobian $\mathbf{J}(x_1^*, x_2^*)$ has eigenvalues with negative real parts. Note that the stability of a singular point depends on the constants $m_1(x_1^*)$ and $m_2(x_2^*)$, characterizing the mutation process: for given selection gradients $g_1(x_1, x_2)$ and $g_2(x_1, x_2)$ a singular point may be an attractor for some values of $m_1(x_1^*)$ and $m_2(x_2^*)$ but not for others (Marrow et al. 1996; see also Abrams and Matsuda 1996).

Just as in one-dimensional (i.e., in single-trait, single-species) adaptive dynamics, a singular point that is an attractor for system (B2) may not represent the endpoint of the evolutionary process if one or both species find themselves at a fitness minimum at the singular point. The conditions for fitness minima at the singular point are simply that the invasion fitness has a minimum with respect to the mutant trait values,

$$\frac{\partial^2 f_1}{\partial y_1^2}(y_1, x_1^*, x_2^*)\bigg|_{y_1 = x_1^*} > 0, \tag{B4}$$

$$\frac{\partial^2 f_2}{\partial y_2^2}(y_2, x_1^*, x_2^*)\bigg|_{y_2 = x_2^*} > 0. \tag{B5}$$

Note that

$$g_1(x_1^*, x_2^*) = \frac{\partial f_1}{\partial y_1}(y_1, x_1^*, x_2^*)\Big|_{y_1 = x_1^*} = 0,$$

$$g_2(x_1^*, x_2^*) = \frac{\partial f_2}{\partial y_2}(y_2, x_1^*, x_2^*)\Big|_{y_2 = x_2^*} = 0,$$

for any singular point. In one-dimensional adaptive dynamics, a fitness minimum at an attracting singular point is sufficient for evolutionary branching (Geritz et al. 1998). In higher-dimensional adaptive dynamics, this need not be true anymore. For example, in adaptive dynamics of two correlated traits in a single species, convergent stable fitness minima alone need not generate evolutionary branching (U. Dieckmann, personal observation). However, in all the cases considered in this article, it can be shown that, if one (or both) of the species are at a fitness minimum at an attracting singular point, then evolutionary branching occurs in one (or both) species. This simplification relative to two-dimensional adaptive dynamics in a single species occurs because, in our coevolutionary models, the two traits are necessarily uncorrelated since they belong to differerent species. A timescale separation argument then shows that, at the singular point, each species' resident phenotype can be considered as a parameter for the evolutionary dynamics of the other species, which in effect reduces the two-dimensional problem at the singular point to the one-dimensional case, where convergence to fitness minima is sufficient for branching.

To understand evolutionary branching in the adaptive dynamics of mutualism defined by system (17) in "Evolutionary Branching in Coevolutionary Models for Mutualism," we first have to find trait combinations (x_1^*, x_2^*) for which the selection gradients vanish and then check the conditions for stability from (B3) and for branching from (B4). The selection gradients are

$$g_1(x_1, x_2) = \frac{\partial f_1(y_1, x_1, x_2)}{\partial y_1}\bigg|_{y_1 = x_1}$$

$$= \frac{r_1 N_1^* K_1'(x_1)}{K_1^2(x_1)} + \frac{r_1 \alpha'(x_1 - x_2)}{\alpha(x_1 - x_2)} a_{12} N_2^*,$$

$$g_2(x_1, x_2) = \frac{\partial f_2(y_2, x_1, x_2)}{\partial y_2}\bigg|_{y_2 = x_2} \tag{B6}$$

$$= \frac{r_2 N_2^* K_2'(x_2)}{K_2^2(x_1)} + \frac{r_2 \alpha'(x_2 - x_1)}{\alpha(x_2 - x_1)} a_{21} N_1^*,$$

where $N_1^* = N_1^*(x_1, x_2)$ and $N_2^* = N_2^*(x_1, x_2)$ are the ecological equilibrium points of system (17).

We briefly discuss the symmetric case, in which the only ecological difference between the two mutualistic species is the position of the maxima of the resource distribution. In this case, there is always a singular point (x_1^*, x_2^*) that lies symmetrically around the midpoint between the two resource maxima x_{10} and x_{20} and satisfies $x_{10} < x_1^* < x_2^* < x_{20}$. This symmetric singular point may or may not be an evolutionary attractor. For example, the symmetric singular point may lose its stability through a pitchfork bifurcation, during which two new asymmetric and convergent stable singular points are borne. Numerical simulations indicate that, if the symmetric singular point is the only singularity and if the mutational functions $m_1(x_1)$ and $m_2(x_2)$ are the same, then this point is always an evolutionary attractor. To see whether such a singular point is an evolutionary branching point, we calculate the second derivatives of the invasion fitness functions, equations (19) and (20), at the singular point:

$$\frac{\partial^2 f_1(y_1, x_1^*, x_2^*)}{\partial y_1^2}\bigg|_{y_1 = x_1^*} = \frac{r_1 N_1^* K_1''(x_1^*)}{K_1^2(x_1^*)}$$

$$- \frac{2 r_1 N_1^* K_1'^2(x_1^*)}{K_1^3(x_1^*)}$$

$$+ \frac{r_1 \alpha''(x_1^* - x_2^*)}{\alpha(x_1^* - x_2^*)} a_{12} N_2^*,$$

$$\frac{\partial^2 f_2(y_2, x_1^*, x_2^*)}{\partial y_2^2}\bigg|_{y_2 = x_2^*} = \frac{r_2 N_2^* K_2''(x_2^*)}{K_2^2(x_2^*)} \tag{B7}$$

$$- \frac{2 r_2 N_2^* K_2'^2(x_2^*)}{K_2^3(x_2^*)}$$

$$+ \frac{r_2 \alpha''(x_2^* - x_1^*)}{\alpha(x_1^* - x_2^*)} a_{21} N_1^*.$$

Two factors tend to make these expressions positive: first, x_1^* and x_2^* must lie far enough away from their respective resource optimum, that is, beyond the inflection points of the corresponding resource distributions, so that $K_1''(x_1^*) > 0$ and $K_2''(x_2^*) > 0$, and, second, x_1^* and x_2^* should be far enough apart from each other, so that the distance $x_1^* - x_2^*$ lies beyond the inflection point of the function α, so that $\alpha''(x_1^* - x_2^*) > 0$. These conditions can be met by increasing the distance between the maxima of the resource distributions, which is equivalent to decreasing the widths of the resource distributions and the width of the mutualistic interaction function α. It is easy to do this in such a way that the symmetric singular point does not lose its stability. Consequently, it is easy to allow for si-

multaneous evolutionary branching in this system (see fig. 2A).

Finally, we discuss the adaptive dynamics in the predator-prey system (26). It follows from the expression for the selection gradient in the predator, equation (32), that a singular point (x_1^*, x_2^*) must satisfy $\alpha'(x_1^* - x_2^*) = 0$. We therefore must have $x_1^* - x_2^* = 0$; that is, $x_1^* = x_2^*$. It then follows from the selection gradient in the prey that $K'(x_1^*) = 0$ for the singular prey character x_1^*, hence $x_1^* = x_0$, so that the singular point occurs at the maximum of the resource distribution. Straightforward calculations reveal that the Jacobian matrix at the singular point is given by

$$\mathbf{J}(x_0, x_0) = \begin{bmatrix} m_1 r(N_1^* K''(x_0)/K^2(x_0) - \alpha''(0)N_2^*) & m_1 r\alpha''(0)N_2^* \\ -m_2 c\alpha''(0)N_1^* & m_2 c\alpha''(0)N_1^* \end{bmatrix},$$

(B8)

where N_1^* and N_2^* are the ecological equilibrium sizes of populations monomorphic for the singular character values (x_0, x_0), and where $m_1 = m_1(x_0)$ and $m_2 = m_2(x_0)$ are the mutational parameters at the singular point. Using the functional form for the predation efficiency α, equation (25), and for the resource distribution K, equation (9), and calculating the equilibrium populations sizes N_1^* and N_2^* using $x_1 = x_2 = x_0$ in equation (26), one obtains

$$\mathbf{J}(x_0, x_0) = \begin{bmatrix} \dfrac{m_1 r}{c\alpha_0 K_0} \times \left(\dfrac{c\alpha_0 K_0 - d}{\sigma_\alpha^2} - \dfrac{d}{\sigma_K^2} \right) & -\dfrac{m_1 r(c\alpha_0 K_0 - d)}{c\alpha_0 K_0 \sigma_\alpha^2} \\ \dfrac{m_2 d}{\sigma_\alpha^2} & -\dfrac{m_2 d}{\sigma_\alpha^2} \end{bmatrix}.$$

(B9)

Both eigenvalues of the Jacobian matrix $\mathbf{J}(x_0, x_0)$ have negative real parts if the determinant of $\mathbf{J}(x_0, x_0)$ is positive and its trace is negative. The determinant of $\mathbf{J}(x_0, x_0)$ is equal to $(d^2 m_1 m_2 r)/(c\alpha_0 K_0 \sigma_\alpha^2 \sigma_K^2)$ and hence is always positive. The trace is the sum of the diagonal elements and may be positive or negative. In this situation, the diagonal elements of the Jacobian matrix are, up to the constants m_1 and m_2, respectively, equal to the second derivatives of the invasion fitness functions with respect to the mutant traits, evaluated at the singular point:

$$\left. \frac{\partial^2 f_1}{\partial y_1^2}(y_1, x_0, x_0) \right|_{y_1 = x_0} = \frac{\partial g_1}{\partial x_1}(x_0, x_0)$$

$$= \frac{r}{c\alpha_0 K_0} \left(\frac{c\alpha_0 K_0 - d}{\sigma_\alpha^2} - \frac{d}{\sigma_K^2} \right), \quad \text{(B10)}$$

$$\left. \frac{\partial^2 f_2}{\partial y_2^2}(y_2, x_0, x_0) \right|_{y_2 = x_0} = \frac{\partial g_2}{\partial y_2}(x_0, x_0) = -\frac{m_2 d}{\sigma_\alpha^2}. \quad \text{(B11)}$$

In particular, the singular point is never a branching point for the predator because $(\partial^2 f_2/\partial y_2^2)(y_2, x_0, x_0)|_{y_2=x_0}$ is always negative. Thus, to obtain attraction to the singular point and subsequent evolutionary branching, the upper diagonal element of the Jacobian matrix $\mathbf{J}(x_0, x_0)$ must be positive, which would make the singular point a fitness minimum for the prey, whereas adding the negative lower diagonal element must give a negative number, ensuring that the singular point is an attractor. These conditions are easy to meet. For example, setting $m_1 = m_2$ and $r = d = 1$, it follows that the trace of the Jacobian is negative, and provided that $c\alpha_0 K_0 > d$, the upper diagonal element will be positive as soon as σ_α is small enough.

Once the prey has branched, selection pressures for the predator change. Due to the symmetry in the system, the two prey branches are at equal distances δ on opposite sides of the singular predator character x_0. It follows that, at time t, the growth rate of a rare mutant predator with character value y_2 is

$$f_2(y_2, \delta, x_0, t) = -d + c\alpha(x_0 + \delta - y_2)\frac{N_1(t)}{2}$$

$$+ c\alpha(x_0 - \delta - y_2)\frac{N_1(t)}{2}, \quad \text{(B12)}$$

where x_0 is the singular predator trait value and $N_1(t)$ is the prey population size at time t. Taking the second derivative with respect to mutant trait value y_2 and evaluating at the resident trait value x_0 reveals whether the predator is located at a fitness minimum after the prey has branched:

$$\left. \frac{\partial^2 f_2(y_2, \delta, x_0, t)}{\partial y_2^2} \right|_{y_2 = x_0} = c\alpha''(\delta)\frac{N_1(t)}{2}$$

$$+ c\alpha''(-\delta)\frac{N_1(t)}{2} \quad \text{(B13)}$$

$$= c\alpha''(\delta)N_1(t),$$

since α is symmetric about the origin. This expression is

positive for all t, and hence the singular point x_0 is a fitness minimum for the predator if δ is large enough, that is, if the two prey branches have moved far enough away from x_0. Once this has happened, the branching in the prey induces secondary branching in the predator (fig. 3*B*).

That a difference in the mutational parameters m_1 and m_2 can greatly affect the adaptive dynamics is shown in figure 3*C*. With m_2 decreased by a factor of 5, the lower diagonal element of the Jacobian matrix $\mathbf{J}(x_0, x_0)$ given in (B8) is not negative enough anymore to outweigh the positive upper diagonal element describing the fitness minimum in the prey. Therefore, the trace of the Jacobian becomes positive, and hence the branching point of figure 3*B* is no longer an attractor for the evolutionary dynamics.

Literature Cited

Abrams, P. A. 1991. The effects of interacting species on predator-prey coevolution. Theoretical Population Biology 39:241–262.

———. 2000. Character shifts of prey species that share predators. American Naturalist 156(suppl.):S000–S000.

Abrams, P. A., and H. Matsuda. 1996. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. Evolutionary Ecology 10:167–186.

Abrams, P. A., H. Matsuda, and Y. Harada. 1993. Evolutionary unstable fitness maxima and stable fitness minima of continuous traits. Evolutionary Ecology 7:465–487.

Bever, J. D. 1999. Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. Ecology Letters 2:52–61.

Boots, M., and Y. Haraguchi. 1999. The evolution of costly resistance in host-parasite systems. American Naturalist 153:359–370.

Boursot, P., W. Din, R. Anand, D. Darviche, B. Dod, F. Von Deimling, G. P. Talwar, and F. Bonhomme. 1996. Origin and radiation of the house mouse: mitochondrial DNA phylogeny. Journal of Evolutionary Biology 9:391–415.

Brown, J. S., and T. L. Vincent. 1992. Organization of predator-prey communities as an evolutionary game. Evolution 46:1269–1283.

Chown, S. L., and V. R. Smith. 1993. Climate change and the short-term impact of feral house mice at the sub-Antarctic Prince Edwards Islands. Oecologia (Berlin) 96:508–516.

Christiansen, F. B. 1991. On conditions for evolutionary stability for a continuously varying character. American Naturalist 138:37–50.

De Leon, F. J. G., L. Chikhi, and F. Bonhomme. 1997. Microsatellite polymorphism and population subdivision in natural populations of European sea bass *Di-* *centrarchus labrax* (Linnaeus, 1758). Molecular Ecology 6:51–62.

Dieckmann, U. 1994. Coevolutionary dynamics of stochastic replicator systems. Reports of the Research Center Juelich 3018

———. 1997. Can adaptive dynamics invade? Trends in Ecology & Evolution 12:128–131.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. Nature (London) 400:354–357.

Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. Journal of Mathematical Biology 34:579–612.

Dieckmann, U., P. Marrow, and R. Law. 1995. Evolutionary cycling in predator-prey interactions: population dynamics and the Red Queen. Journal of Theoretical Biology 176:91–102.

Doebeli, M. 1996. A quantitative genetic competition model for sympatric speciation. Journal of Evolutionary Biology 9:893–909.

———. 1997. Genetic variation and the persistence of predator-prey interactions in the Nicholson-Bailey model. Journal of Theoretical Biology 188:109–120.

Doebeli, M., and G. D. Ruxton. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. Evolution 51:1730–1741.

Eshel, I. 1983. Evolutionary and continuous stability. Journal of Theoretical Biology 103:99–111.

Feder, J. L., C. A. Chilcote, and G. L. Bush. 1988. Genetic differentiation between sympatric host races of the apple maggot fly *Rhagoletis Pomonella*. Nature (London) 336:61–64.

Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? Evolution 35:124–138.

Geritz, S. A. H., J. A. J. Metz, E. Kisdi, G. Meszéna. 1997. The dynamics of adaptation and evolutionary branching. Physical Review Letters 78:2024–2027.

Geritz, S. A. H., E. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12:35–57.

Geritz, S. A. H., E. Van der Meijden, and J. A. J. Metz. 1999. Evolutionary dynamics of seed size and seedling competitive ability. Theoretical Population Biology 55:324–343.

Grant, P. R., I. Abbott, D. Schluter, R. L. Curry, and L. K. Abbott. 1985. Variation in the size and shape of Darwin's finches. Biological Journal of the Linnean Society 25:1–39.

Holt, R. D. 1977. Predation, apparent competition and the

structure of prey communities. Theoretical Population Biology 12:197–229.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145–159.

Johannesson, K., E. Rolan-Alvarez, and A. Ekendahl. 1995. Incipient reproductive isolation between two sympatric morphs of the intertidal snail *Littorina saxatilis*. Evolution 49:1180–1190.

Johnson, P. A., F. C. Hoppenstaedt, J. J. Smith, and G. L. Bush. 1996. Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and non-habitat assortative mating. Evolutionary Ecology 10:187–205.

Kawecki, T. 1996. Sympatric speciation driven by beneficial mutations. Proceedings of the Royal Society of London B, Biological Sciences 263:1515–1520.

Kiester, A. R., R. Lande, and D. W. Schemske. 1984. Models of coevolution and speciation in plants and their pollinators. American Naturalist 124:220–243.

Kisdi, E. 1999. Evolutionary branching under asymmetric competition. Journal of Theoretical Biology 197:149–162.

Kisdi, E., and S. A. H. Geritz. 1999. Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. Evolution 53:993–1008.

Knox, E. B., and J. D. Palmer. 1995. Chloroplast DNA variation and the recent radiation of the giant senecios (*Asteraceae*) on the tall mountains of eastern Africa. Proceedings of the National Academy of Sciences of the USA 92:10349–10353.

Koella, J. C., and M. Doebeli. 1999. Population dynamics and the evolution of virulence in epidemiological models with discrete host generations. Journal of Theoretical Biology 198:461–475.

Kondrashov, A. S. 1986. Multilocus model of sympatric speciation. III. Computer simulations. Theoretical Population Biology 29:1–15.

Kondrashov, A. S., and F. A. Kondrashov. 1999. Interactions among quantitative traits in the course of sympatric speciation. Nature (London) 400:351–354.

Kondrashov, A. S., and M. V. Mina. 1986. Sympatric speciation: when is it possible? Biological Journal of the Linnean Society 27:201–223.

Kondrashov, A. S., and M. Shpak. 1998. On the origin of species by means of assortative mating. Proceedings of the Royal Society of London B, Biological Sciences 265: 2273–2278.

Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology 63:607–615.

Law, R., P. Marrow, and U. Dieckmann. 1997. On evolution under asymmetric competition. Evolutionary Ecology 11:485–501.

Leighton, L. R. 1999. Possible latitudinal predation gradient in middle Paleozoic oceans. Geology 27:47–50.

Leimar, O. 2000. Multidimensional convergence stability and the canonical adaptive dynamics. *In* U. Dickmann and J. A. J. Metz, eds. Elements of adaptive dynamics. Cambridge University Press, Cambridge (in press).

Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science (Washington, D.C.) 279:2115–2118.

Ludwig, D., and S. A. Levin. 1991. Evolutionary stability of plant communities and the maintenance of multiple dispersal types. Theoretical Population Biology 40: 285–307.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. American Naturalist 101:377–385.

Marrow, P., U. Dieckmann, and R. Law. 1996. Evolutionary dynamics of predator-prey systems: an ecological perspective. Journal of Mathematical Biology 34:556–578.

Matessi, C., and C. Di Pasquale. 1996. Long-term evolution of multi-locus traits. Journal of Mathematical Biology 34:613–653.

Maynard Smith, J. 1966. Sympatric speciation. American Naturalist 100:637–650.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Mass.

Meszéna, G., E. Kisdi, U. Dieckmann, S. A. H. Geritz, and J. A. J. Metz. 2000. Evolutionary optimization models and matrix games in the unified perspective of adaptive dynamics. Selection (in press).

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define fitness for general ecological scenarios? Trends in Ecology & Evolution 7:198–202.

Metz, J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. van Heerwaarden. 1996. Pages 183–231 *in* S. J. van Strien and S. M. Verduyn Lunel, eds. Stochastic and spatial structures of dynamical systems. North Holland, Amsterdam.

Meyer, A., T. D. Kocher, P. Basasibwaki, and A. C. Wilson. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. Nature (London) 347:550–553.

Nagel, L., and Schluter D. 1998. Body size, natural selection, and speciation in sticklebacks. Evolution 52: 209–218.

Parvinen, K. 1999. Evolution of migration in a metapopulation. Bulletin of Mathematical Biology 61:531–550.

Pellmyr, O., and J. Leebens-Mack. 2000. Reversal of mutualism as a mechanism for adaptive radiation in yucca moths. American Naturalist 156(suppl.):S000–S000.

Petren, K., B. R. Grant, and P. R. Grant. 1999. A phylogeny of Darwin's finches based on microsatellite DNA length

variation. Proceedings of the Royal Society of London B, Biological Sciences 266:321–329.

Rainey, P. B., and M. Travisano. 1998. Adaptive radiation in a heterogeneous environment. Nature (London) 394: 69–72.

Rand, D. A., H. B. Wilson, and J. M. McGlade. 1994. Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics. Philosophical Transactions of the Royal Society London B, Biological Sciences 1305:261–283.

Rice, W. R., and E. E. Hostert. 1993. Laboratory experiments on speciation: what have we learned in 40 years? Evolution 47:1637–1653.

Rummel, J. D., and J. Roughgarden. 1985. A theory of faunal build-up for competition communities. Evolution 39:1009–1033.

Rundle, H. D., and D. Schluter. 1998. Reinforcement of stickleback mate preferences: sympatry breeds contempt. Evolution 52:200–208.

Schliewen, U. K., D. Tautz, and S. Pääbo. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. Nature (London) 368:629–623.

Schluter, D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. American Naturalist 131:799–824.

———. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. Science (Washington, D.C.) 266:798–801.

Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. American Naturalist 140:85–108.

Schluter, D., and L. M. Nagel. 1995. Parallel speciation by natural selection. American Naturalist 146:292–301.

Schluter, D., T. D. Price, and P. R. Grant. 1985. Ecological character displacement in Darwin's finches. Science (Washington, D.C.) 227:1056–1059.

Seehausen, O., J. J. M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science (Washington, D.C.) 277: 1808–1811.

Seger, J. 1985. Intraspecific resource competition as a cause of sympatric speciation. Pages 43–53 *in* P. J. Greenwood, P. H. Harvey, and M. Slatkin, eds. Evolution: essays in honour of John Maynard Smith. Cambridge University Press, Cambridge.

Stone, H. M. I. 1998. On predator deterrence by pronounced shell ornament in epifaunal bivalves. Palaeontology 41:1051–1068.

Taper, M. L., and T. J. Case. 1992. Coevolution among competitors. Pages 63–111 *in* D. Futuyma and J. Antonivics, eds. Oxford surveys in evolutionary biology. Vol. 8. Oxford University Press, Oxford.

Taylor, E. B., and J. D. McPhail. 1999. Evolutionary history of an adaptive radiation in species pairs of threespine sticklebacks (*Gasterosteus*): insights from mitchondrial DNA. Biological Journal of the Linnean Society 66: 271–291.

Travisano, M., and P. B. Rainey. 2000. Studies of adaptive radiation using model microbial systems. American Naturalist 156(suppl.):S000–S000.

Udovic, D. 1980. Frequency-dependent selection, disruptive selection, and the evolution of reproductive isolation. American Naturalist 116:621–641.

Van Damme, D., and M. Pickford. 1995. The late Cenozoic ampullariidae (mollusca, gastropoda) of the Albertine Rift Valley (Uganda-Zaire). Hydrobiologia 316:1–32.

Vandermeer, J. H., and D. H. Boucher. 1978. Varieties of mutualistic interaction in population models. Journal of Theoretical Biology 74:549–558.

Van Dooren, T. J. M. 1999. The evolutionary ecology of dominance-recessivity. Journal of Theoretical Biology 198:519–532.

Walker, J. A. 1997. Ecological morphology of lacustrine threespine stickleback *Gasterosteus aculeatus* L. (Gasterosteidae) body shape. Biological Journal of the Linnean Society 61:3–50.