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# The Effect of Population Size and Recombination on Delayed Evolution of Polymorphism and Speciation in Sexual Populations

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ABSTRACT: Recent theory suggests that absolute population size may qualitatively influence the outcome of evolution under disruptive selection in asexual populations. Large populations are predicted to undergo rapid evolutionary branching; however, in small populations, the waiting time to branching increases steeply with decreasing abundance, and below a critical size, the population remains monomorphic indefinitely. Here, we (1) extend the theory to sexual populations and (2) confront its predictions with empirical data, testing statistically whether lake size affects the level of resource polymorphism in arctic char (*Salvelinus alpinus*) in 22 lakes of different sizes. For a given level of recombination, our model predicts qualitatively similar relations between population size and time to evolutionary branching (either speciation or evolution of genetic polymorphism) as the asexual model, while recombination further increases the delay to branching. The loss of polymorphism at certain loci, an inherent aspect of multilocus-trait evolution, may increase the delay to speciation, resulting in stable genetic polymorphism without speciation. The empirical analysis demonstrates that the occurrence of resource

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polymorphism depends on both lake size and the number of coexisting fish species. For a given number of coexisting species, the level of polymorphism increases significantly with lake size, thus confirming our model prediction.

Populations with small absolute population size exhibit larger stochastic fluctuations caused by the randomness of demographic events than larger populations (Desharnais et al. 2006). In the hypothetical case of two populations in two lakes that differ only in their volume, the population in the smaller lake is therefore more likely to become extinct despite its average population density (number per m³) being the same as the population in the bigger lake. Populations with small absolute population size are also subject to higher levels of genetic drift. Recent theoretical results have shown that absolute population size, by determining the level of these effects, may qualitatively influence the outcome of evolutionary dynamics. On the one hand, the direction of evolution in populations subject to demographic stochasticity may differ from the expectation based on a deterministic model (Proulx and Day 2001; Cadet et al. 2003; Parvinen et al. 2003). On the other hand, in asexual populations under disruptive selection, demographic stochasticity is predicted to interfere with the process of evolutionary branching (Claessen et al. 2007). Large populations are predicted to undergo rapid evolutionary branching. However, in small populations, the waiting time to branching increases very steeply with decreasing population size, and below a critical size, the population is predicted to remain monomorphic indefinitely. The two processes that have been proposed to explain this delay in evolutionary splitting are genetic drift and the high risk of extinction of incipient branches (Claessen et al. 2007).

An open question is whether these results, and in particular delayed evolutionary branching, carry over to sex-

ual populations and hence to the dynamics of speciation (in the sense of reproductive isolation) or the evolution of genetic polymorphism. The process of evolutionary branching was originally described for purely phenotypic models (Geritz et al. 1997). The underlying genetics were implicitly or explicitly assumed to correspond to clonal reproduction, that is, the absence of diploidy, recombination, multilocus dynamics, and so forth. The strength of such asexual models is to elucidate the link between ecological dynamics and fitness and to discover which ecological processes can create conditions that favor evolutionary branching. Extensions of such models that include simple, sexual genetics have demonstrated that the role of genetics is nontrivial. First, sexual populations may respond to disruptive selection by finding other "solutions" than splitting into two daughter populations—for example, the evolution of genetic polymorphism (Kisdi and Geritz 1999) or of sexual dimorphism (Bolnick and Doebeli 2003). In the latter case, the ecological roles of males and females diverge to fill the ecological niches generating the disruptive selection. In both cases, the population remains panmictic. Second, sexual reproduction is expected to make evolutionary branching difficult through the continuous formation of intermediate hybrid genotypes that prevent the splitting of the population. Dieckmann and Doebeli (1999) have shown that evolutionary branching may yet occur in sexual models if the model allows for the evolution of assortative mating. Under disruptive selection, assortative mating is favored and may thus be expected to evolve once the population has reached an evolutionary branching point (EBP). Third, in the case of multilocus traits, interactions between loci may result in unexpected dynamical patterns, such as polymorphism formation and collapse, that influence the predicted evolutionary trajectory and the resulting level of polymorphism (Kopp and Hermisson 2006; van Doorn and Dieckmann 2006). These patterns emerge from the collective dynamics of multiple alleles at multiple loci under frequency-dependent disruptive selection. Due to the added complexities related to sexual reproduction and the associated possibility of multilocus genetics, it is not clear a priori that results from asexual population models carry over to sexual populations.

In this article, we extend the model of Claessen et al. (2007) by taking into account sexual reproduction. This allows us to assess whether the phenomenon of delayed evolutionary branching is robust to the occurrence of segregation, recombination, and multilocus evolution. In our model, evolutionary branching can result in either a protected polymorphism in a panmictic population (i.e., dimorphism at some or all the loci) or speciation (i.e., dimorphism at all loci followed by sorting of genotypes and reproductive isolation of purely homozygous genotypes).

We can thus study the effect of small population size on the evolution of genetic polymorphism and on speciation.

The extended model will allow us to confront model predictions with data on sexual species. In particular, freshwater fish species offer interesting opportunities for testing the theory of adaptive dynamics due to the frequent but variable occurrence of resource polymorphism (Skúlason and Snorrason 2004). Such polymorphisms often include a pelagic morphotype feeding mainly on zooplankton and a benthic morphotype feeding mainly on macroinvertebrates (Smith and Skúlason 1996; Skúlason and Snorrason 2004). Examples are sticklebacks, whitefish pumpkinseed, and bluegill sunfishes (Andersson et al. 2007). We focus on arctic char (*Salvelinus alpinus*), for which the degree of polymorphism varies between one and four morphotypes per lake (Alekseyev et al. 2002; Adams et al. 2003; Skúlason and Snorrason 2004). The explanation for the frequent but variable polymorphism in freshwater fish species is still a matter of debate and may differ for different lake systems. A current hypothesis is that resource polymorphism is an early stage of an ongoing speciation process (Lavin and McPhail 1986; Schluter 1996; Skúlason and Snorrason 2004; Knudsen et al. 2006). Different morphotypes may have allopatric origins, but once in sympatry through repeated invasion, they remain polymorphic due to disruptive selection that results from ecological interactions, such as competition for food (Svärdson 1979; Nyman et al. 1981; Schluter and McPhail 1993; Rundle and Schluter 2004). Alternatively, the morphotypes may originate sympatrically as a consequence of adaptive sympatric speciation. Evidence for sympatric (within-lake) origin of arctic char morphotypes stems from both genetic (Gíslason et al. 1999) and morphological studies (Alekseyev et al. 2002). In both scenarios, disruptive selection is an essential force driving and maintaining the sympatric divergence and coexistence of morphotypes.

The goals of this article are (i) to extend the theory on delayed evolutionary branching to sexual populations and (ii) to confront the model prediction with empirical data. Part 1 of the article is theoretical and is a study of the implications of sexual reproduction for the phenomenon of delayed evolutionary branching. Part 2 is an empirical test of the main prediction based on this theory, using data on the level of resource polymorphism in arctic char (*S. alpinus*) populations in 22 lakes of different sizes. Under the hypothesis of a sympatric origin of the morphotypes, our theory predicts a positive relation between lake size and the occurrence and level of polymorphism, whether in the form of genetic polymorphism or reproductively isolated subpopulations.

## Part 1: Theory

The theory is developed in the framework of adaptive dynamics. The basic assumption of this theory is that evolution takes place in a dynamic fitness landscape in which fitness is the outcome of density- and/or frequency-dependent ecological interactions between individuals (Metz et al. 1992). The theory shows that in such a dynamic fitness landscape, "upward" movement, resulting from directional selection, can take an evolving population to a fitness minimum (Eshel 1983), often referred to as an "evolutionary branching point" (Geritz et al. 1997). At the EBP, selection turns disruptive, and the population may branch into two sympatrically diverging subpopulations (Metz et al. 1992; Geritz et al. 1997; Dieckmann and Doebeli 1999), a genetic polymorphism (Kisdi and Geritz 1999), or a sexual dimorphism (Bolnick and Doebeli 2003).

We study evolutionary branching in a simple model of one consumer and two resource populations. The resources are assumed to occur in two distinct habitats, and so the consumers spend a certain fraction of their time in each habitat. We focus on the evolution of this time allocation, that is, of the relative utilization of either resource. The model is loosely based on the ecology of lake fish such as arctic char (*Salvelinus alpinus*), perch (*Perca fluviatilis*) and sticklebacks (*Gasterosteus aculeatus*). Such species often have access to two resources in different habitats: zooplankton in the pelagic habitat and macroinvertebrates in the benthic habitat. The evolutionary trait can be interpreted as either the fraction of the lifetime in each habitat (in the case of an ontogenetic niche shift) or the daily time fraction in each habitat.

Studies have shown that a consumer population exploiting two distinct resource populations can evolve to an EBP and hence potentially speciate into two specialists or give rise to a genetic polymorphism (e.g., Kisdi and Geritz 1999; Day 2000; Claessen and Dieckmann 2002; Rueffler et al. 2006). The condition for evolutionary branching in such models is that the generalist strategy exploiting both resources has a lower fitness than mutant strategies with a slightly higher degree of specialization in either direction. In other words, the shape of the trade-off between performance in the two habitats determines the outcome of the evolutionary dynamics. When fitness is a linear combination of performance in two habitats (as is the case here), evolutionary branching is expected if the trade-off is "strong" (convex). An evolutionarily stable generalist is expected if the trade-off is "weak" (concave) or "neutral" (linear; Rueffler et al. 2006).

Strong trade-offs may result from various biological mechanisms, including diet-induced changes in foraging capacity (Claessen et al. 2007). This mechanism can be understood intuitively as follows. Consider the energy gain obtained from two resources that occur in two different habitats. The total gain equals search rate × resource density × time spent in the habitat. Time splitting between the habitats amounts to a neutral trade-off because the gain from each habitat is a linear function of the time spent in the habitat. If, in addition, the search rate increases with the time spent in a habitat, the trade-off becomes strong (convex). A positive dependence of foraging ability on foraging time may result when foraging on a certain prey type (or habitat) induces physiological changes, for example, morphological adaptation. For a number of fish species, it has been demonstrated that diet influences individual development and morphology, resulting in increased habitat-specific foraging capacity (Robinson and Wilson 1995; Day and McPhail 1996; Andersson 2003; Andersson et al. 2005).

## The Model: The Individual Level

Our deterministic model is the same as the one presented in Claessen et al. (2007), while our stochastic model is a multilocus, diploid, sexual version of the single-locus, asexual model presented in that article. Below, we outline the model with a focus on the details of sexual reproduction and inheritance; additional details of the deterministic model, parameter values, and the simulation procedure can be found in Claessen et al. (2007).

### Phenotype and Genotype

We assume that consumers have a phenotype, denoted by $u$, that is the fraction of time they spend foraging on resource 1, while they spend the remaining fraction $(1 - u)$ foraging on resource 2 (as discussed above). We assume that the value of $u$ is determined additively (no dominance or epistasis) by $L$ diploid loci. Each allele may have a value between 0 and 1, and the phenotype is determined as the mean of all alleles:

$$u = \frac{1}{2L} \sum_{k=1}^{L} (x_k + y_k), \tag{1}$$

where $x_k$ and $y_k$ are the values of the two alleles at locus $k$.

### Assortative Mating

For simplicity, we assume a fixed level of assortative mating. An alternative approach is to allow for the evolution of assortativeness as an independent evolutionary trait; studies have demonstrated that under conditions of disruptive selection, assortativeness is favored by natural or sexual selection (Dieckmann and Doebeli 1999; van

Doorn et al. 2004), but this is outside the scope of our study (but see app. B).

We model assortative mating as follows. For an individual $i$, a candidate partner $j$ is selected randomly from the population of the opposite sex. The phenotypic difference between the two individuals is computed as $d = \text{abs}(u_i - u_j)$. The candidate is rejected with probability

$$q = \begin{cases} 0 & \text{if } d < 0.5 - (0.5/S), \\ 1 & \text{if } d > 0.5 + (0.5/S), \\ S(d - 0.5) + 0.5 & \text{otherwise.} \end{cases} \quad (2)$$

Figure 1 shows the relation between the phenotypic difference between two potential partners and the probability of partner rejection. With $S = 0$, mating is random, while a value of $S > 0$ implies that the probability of rejecting a randomly selected partner increases with the phenotypic distance $d$ between the individuals. A value of $S > 1$ results in reproductive isolation between individuals at the extremes of the phenotype space and is hence required for speciation to be possible. Our standard value of $S = 2$ results in complete rejection of candidates at a large phenotypic distance ($q = 1$ if $d > 0.75$), thus allowing for reproductive isolation. In simulations, a mating event is canceled if after 100 attempts no suitable partner has been found (this amounts to a small cost of assortativeness but happens extremely rarely in our simulations).

### Inheritance

We assume there are $L$ loci on a single pair of homologous, autosomal chromosomes. At reproduction, a gamete is defined by randomly drawing one of the two homologous chromosomes. We allow for recombination by assuming that between any two adjacent loci, crossing over occurs with a probability $p_C$. We thus assume the loci are equidistantly distributed on the chromosome. By tuning the parameter $p_C$, we can control the level of recombination, from no recombination at all ($p_C = 0$) to independent segregation ($p_C = 0.5$). In the case of $p_C = 0.5$, the loci behave as if they were each located on a separate chromosome. In the case of $p_C = 0$, all the loci together behave like a single locus. With $p_C = 0$ and $S = 0$, we obtain results analogous to Kisdi and Geritz (1999), that is, evolutionary branching of a single locus in a panmictic sexual population that results in a stable genetic polymorphism.

### Mutations

At birth, mutations occur with frequency $p_M$ per allele. The allele's trait value is then drawn from a truncated normal distribution with standard deviation $\sigma(2L)^{1/2}$
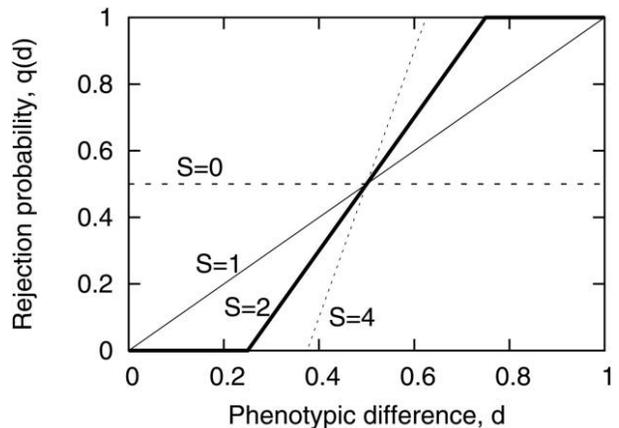


**Figure 1:** Rejection probability $q(d)$ (eq. [2]) as a function of the difference in ecological trait value $d = \text{abs}(u_1 - u_2)$ between two randomly selected potential mates, for values of $S$ equal to 0, 1, 2, and 4. The parameter $S$ determines the strength of assortative mating.

around the value of the parental allele. This mutation size at the allele level results in a variance of $\sigma^2$ at the trait level, independently of $L$ (van Doorn et al. 2004). If the drawn value is below 0 or above 1, it is replaced by 0 or 1, respectively.

Our assumption of several loci, each of them with a continuum of the possible alleles, differs from the perhaps more standard assumption that a quantitative character is determined by the cumulative effect of many biallelic, or few-allelic, loci (e.g., Dieckmann and Doebeli 1999). Our assumption is, however, the most straightforward extension of our previous model to multiple diploid loci and hence allows for a direct comparison.

*Vital rates.* We assume a constant death rate $\mu$. The per capita birth rate $\beta(u)$ is assumed to be proportional to the consumption rate, which in turn is assumed to be proportional to the resource densities ($F_1(t)$, $F_2(t)$), the search rates in each habitat ($A_1(u)$, $A_2(u)$), and the time spent in each habitat:

$$\beta(u) = F_1(t)A_1(u)u + F_2(t)A_2(u)(1 - u). \quad (3)$$

The search rates are functions of the fraction of time spent in each habitat:

$$A_1(u) = a_1 + b_1u, \quad (4)$$

$$A_2(u) = a_2 + b_2u. \quad (5)$$

These functions represent our assumption of diet-induced changes in foraging capacity. For arctic char, it has been demonstrated that exposure of juveniles during ontogeny to either zooplankton prey, macroinvertebrate prey, or a

mixture of both influences the foraging performance at the end of the experiment (associated with a morphological effect; Andersson 2003). Their results can be stated this way: the search rate on zooplankton increases with the time spent in the pelagic habitat, while the search rate on macroinvertebrates is unaffected. If the pelagic is habitat 1, this can be modeled as $b_1 > 0$ and $b_2 = 0$.

## The Model: Population Level

### Deterministic Model

For the deterministic model, we assume that all alleles are identical, in which case the dynamics of alleles and hence sexual reproduction can be ignored. Our deterministic model of the population dynamics is given by

$$\frac{dN}{dt} = (\beta(u) - \mu)N(t), \tag{6}$$

$$\frac{dF_1}{dt} = \delta_1(K_1 - F_1(t)) - F_1(t)N(t)A_1(u)u, \tag{7}$$

$$\frac{dF_2}{dt} = \delta_2(K_2 - F_2(t)) - F_2(t)N(t)A_2(u)(1 - u), \tag{8}$$

where $N(t)$ is the consumer population density and $F_1(t)$ and $F_2(t)$ are the densities of its two resource populations. The resources are assumed to have no direct interaction with each other and to follow semichemostat dynamics, which has been argued to appropriately describe resource dynamics in systems of size-selective fish foraging on zooplankton (Persson et al. 1998). Parameters $\delta_i$ and $K_i$ are the renewal rate and maximum density of resource $i$.

### Stochastic Model

For small populations we need to incorporate demographic stochasticity. We denote the number of consumer individuals by the integer number $n(t)$. The density of consumers $N(t)$ is then obtained as $N(t) = n(t)/V$, where $V$ is the lake volume. Very large systems (i.e., $V \to \infty$) have so many individuals that discrete events at the level of individuals (i.e., births and deaths) each have very small effects. The changes in the population density $N(t)$ are then well approximated by the deterministic model (eqq. [6]–[8]). For small systems, however, these discrete events cannot be ignored. The deterministic model can still be used to find the long-term average densities $\tilde{N}$, $\tilde{F}_1$, and $\tilde{F}_2$, which correspond to the equilibrium of equations (6)–(8) (unpublished data), but the actual values will deviate from these values due to demographic stochasticity. All else being equal, the variability around the expected steady state increases if $V$ decreases; according to the scaling rule

for demographic stochasticity (Desharnais et al. 2006), the coefficient of variation (CV) of population size $n$ is expected to scale in this way: $CV(n) \propto n^{-0.5}$ (or, equivalently, $CV(n) \propto V^{-0.5}$).

The consumer individuals are characterized by their trait value $u_i$, with $i = 1, \ldots, n(t)$. The number of individuals changes through discrete birth and death events. The rate at which birth and death events occur depends on the number of individuals, their individual birth rates $\beta(u_i)$, and the death rate $\mu$. We use an individual-based, discrete-event simulation model (i.e., a birth-death process in continuous time) to describe the population dynamics (Claessen et al. 2007). The stochastic model was coded in the C programming language, using algorithms for individual-based discrete-event simulation that were written by U. Dieckmann (Claessen and Dieckmann 2002).

Compared with the population of consumers, the resources (zooplankton and macroinvertebrates) are much more numerous, with smaller body sizes and shorter generation times. We therefore choose to model their dynamics with ordinary differential equations analogous to equations (7) and (8). In simulations, we assume that the resources are in quasi-steady state with the current consumer population (Claessen et al. 2007). In the absence of polymorphism, the individual-based model defined this way is fully analogous to the deterministic model. In the limit of $V \to \infty$, the dynamics of $n(t)/V$ and the resource densities converge to equations (6)–(8).

## Model Results

First, we discuss two illustrative example runs of the stochastic model. Second, we present a systematic and quantitative analysis of the effect of lake volume and recombination on the predicted time to speciation. All the simulations presented below start from a monomorphic resident population with a trait $u$ somewhere between 0 and 1. Generically, the adaptive dynamics then consist of two phases. In the first phase, the ecological equilibrium of the current resident population and its two resources is characterized by an imbalance: due to its biased trait value ($u \neq u^*$), the consumer overexploits one resource and leaves the other one relatively abundant (Claessen and Dieckmann 2002; Claessen et al. 2007). Mutants that spend more time in the underexploited niche can invade (directional selection). The average trait, denoted by $\hat{u}$, thus evolves gradually toward the singular point $u^*$, at which the consumer's intake rates in the two habitats are balanced and the directional selection vanishes. Evolution in the second phase depends on the trade-off between gain from the two habitats, that is, $uA_1(u)\tilde{F}_1$ versus $(1 - u)A_2(u)\tilde{F}_2$, where $\tilde{F}_1$ and $\tilde{F}_2$ are the equilibrium resource densities. In the case of a "weak" trade-off (e.g., if the

**(a)**



**(b)**
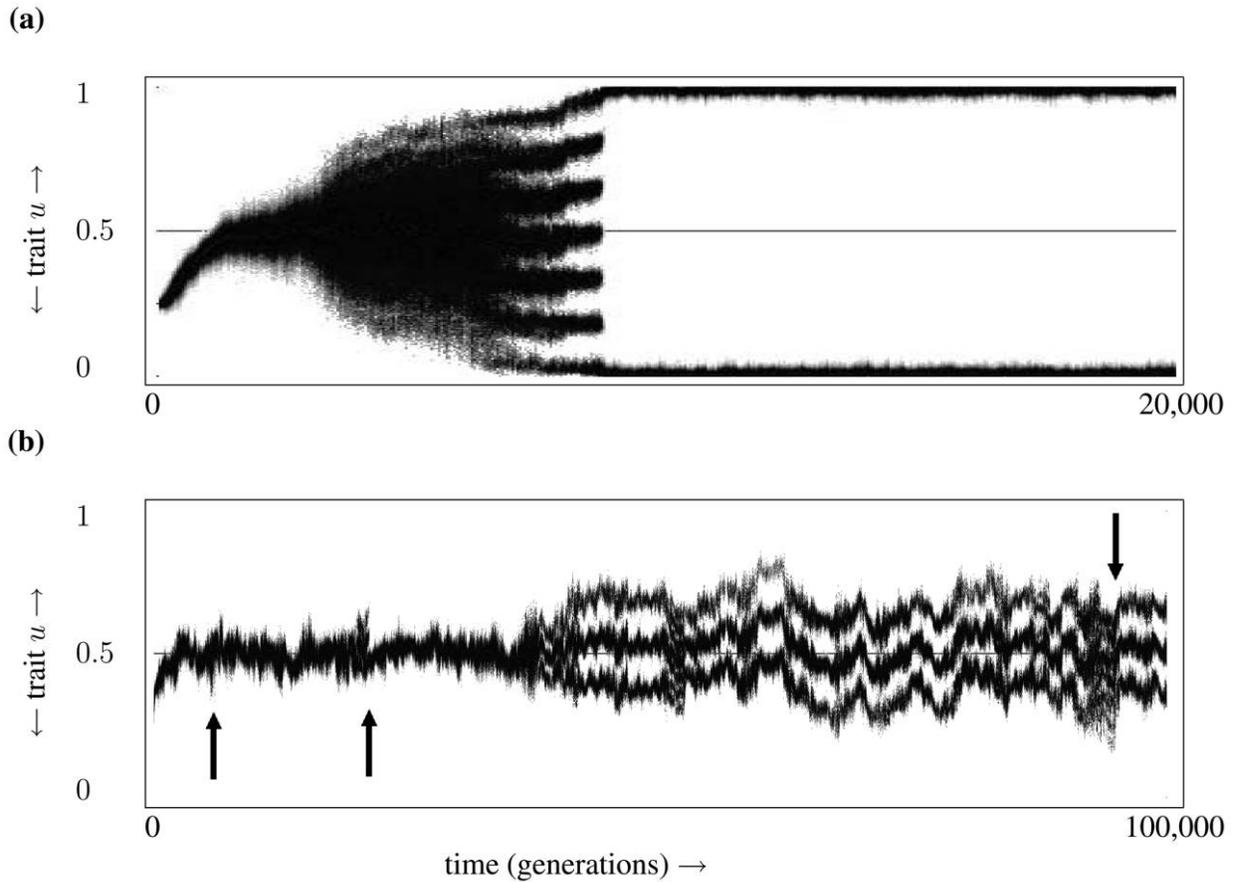


**Figure 2:** Examples of adaptive dynamics with three loci ($L = 3$) in two lake volumes. Depicted is the phenotypic trait distribution $n(u)$ at time $t$ (note different scaling of $X$-axis in $a$ and $b$). $a$, Lake volume $V = 200$: all loci branch on reaching the evolutionary branching point ($u^* = 0.5$). Seven phenotypes appear once the alleles have evolved into discrete clusters. Assortative mating results in speciation (reproductive isolation) after $\approx 8,800$ generations. $b$, Lake volume $V = 30$: branching is delayed; note the average phenotype drifting around $u^*$ and unsuccessful branching events (*arrows*). Branching results in a polymorphism of three phenotypes caused by a stable dimorphism at a single locus. Parameters: $S = 2$, $p_C = 0.1$, $p_M = 0.01$, $\sigma = 0.01$, $a_1 = 0$, $a_2 = 2$, $b_1 = 2$, $b_2 = -2$.

habitat-specific search rates decrease with the time spent in the habitats—a very unlikely case), selection is stabilizing, and the population will remain stable at this point. The trait value $u^*$ is then a continuously stable strategy (CSS, similar to an evolutionarily stable strategy; Eshel 1983). In the case of a "strong" trade-off (e.g., the habitat-specific search rates increase with the time spent in the habitats), selection is disruptive. The trait value $u^*$ is then an evolutionary branching point, and the population is predicted to branch into two diverging subpopulations (Geritz et al. 1997).

In general, the relation between $V$ and absolute population size $n$ depends on $u$, or more precisely, on the distribution of $u$. Note, however, that we have chosen all parameter combinations used in this article so the EBP is at $u = 0.5$ and the equilibrium population size of a monomorphic population with $\hat{u} = 0.5$ equals $n = 18V$.

### Two Illustrative Examples

In the following, we use parameter values for which the singular point $u^*$ is an evolutionary branching point (i.e., $b_1/(a_1 + b_1) > b_2/a_2$; Claessen et al. 2007). For simplicity, we use parameters that correspond to a symmetric trade-off ($b_2 = -b_1$, $a_2 = a_1 + b_1$). Assuming symmetric resource parameter values ($r_1 = r_2$, $K_1 = K_2$), the EBP is then at $u^* = 0.5$. Qualitatively similar results have been obtained with asymmetric parameter combinations (data not shown). We assume $S = 2$ (but see app. A).

Figure 2$a$ demonstrates the two phases of adaptive dy-

namics for a diploid population in which trait $u$ is determined by three loci in a relatively big lake ($V = 200$). The inital condition of the simulation is 10 individuals, of which all (six) alleles equal 0.25. The population quickly grows to about 3,200 individuals, which is a stable equilibrium for these parameter and trait values. The population responds to the directional selection by converging to the predicted EBP ($u = 0.5$). The average population size at $\hat{u} = 0.5$ equals $18V = 3,600$ individuals. At the EBP, disruptive selection causes increasing genetic variability. During this period, all three loci undergo evolutionary branching. At each locus, two alleles appear that diverge toward the values $\approx 0$ and $\approx 1$, respectively (not shown). Initially, this phase is characterized by a continuous phenotypic distribution (fig. 2a) caused by variability in the degree of divergence between loci. Once the alleles approach their final values at all loci, discrete phenotypes appear. With $k$ dimorphic loci, the number of phenotypes equals $2k + 1$ (seven phenotypes in the example; fig. 2a). While extreme phenotypes have superior fitness due to the strong trade-off, the intermediate phenotypes are produced through segregation and crossing over. Speciation, defined as the emergence of two reproductively isolated subpopulations, can occur once the homogeneous chromosomes [0, 0, 0] and [1, 1, 1] appear in the population. The homozygotic genotypes [0, 0, 0] + [0, 0, 0] and [1, 1, 1] + [1, 1, 1], corresponding to phenotypes $u = 0$ and $u = 1$, respectively, have superior fitness to the intermediate ones, owing to the strong trade-off. In combination with assortative mating, this fitness advantage allows the homozygotes to outcompete the intermediate genotypes, while the production of new hybrids is prevented by assortative mating. In figure 2a, speciation occurs around $t = 8,800$ generations, resulting in two specialized and reproductively isolated populations.

Figure 2b shows the adaptive dynamics in a smaller lake ($V = 30$). The population quickly converges to the EBP, but no successful branching occurs until $t \approx 45,000$. The average population size at $\hat{u} = 0.5$ equals $18V = 900$ individuals. The subsequent coexistence of three phenotypes indicates a dimorphism at a single locus only. Despite considerable drift of the branches, the single-locus dimorphism appears stable and persists for more than $t \approx 50,000$ generations. Two effects of small population size can be recognized that have been identified as causes of delayed evolutionary branching. First, before branching, the average trait wobbles around the predicted EBP (random genetic drift), resulting in prolonged periods with directional rather than disruptive selection. Second, incipient branches frequently become extinct (*arrows*, fig. 2b). The figure thus illustrates, for a sexual population, that evolutionary branching is delayed in small populations, as shown by Claessen et al. [2007] for asexual populations.

The figure also illustrates aspects that are unique to sexual reproduction and multilocus evolution. First, speciation depends on the evolutionary branching of all loci, and thus, for multilocus traits, the delay is expected to be longer than for single-locus traits. This is illustrated in figure 2b, where successful branching of one locus is followed by a long delay (with considerable genetic drift) until the next branching event, which is followed by the extinction of an incipient branch (*third arrow*). Second, in sexual populations, phenotypic variation can evolve without speciation, in the form of a genetic polymorphism at one or more loci (fig. 2b). The population remains panmictic, while the polymorphism is maintained by sustained disruptive selection. The homozygotic types are specialists, while the heterozygotes are generalists. The latter have inferior fitness and are maintained in the population exclusively due to the Mendelian hybrid formation. Such a stable genetic polymorphism can occur even if a dimorphism has evolved at all loci. That is, the prespeciation phase (e.g., the seven coexisting phenotypes in fig. 2a) can last forever if the sorting of alleles into homogeneous chromosomes does not happen, which may be due to weak disruptive selection or to strong recombination (see "Trade-off curvature" in the following subsection).

### Effect of Model Parameters on the Speciation Delay

*Lake size.* To investigate systematically the effect of lake size, we run 20 simulations of $10^7$ generations, for a range of values of $V$ and starting with 10 individuals of which all alleles have value 0.1, that is, $x_k = y_k = 0.1$ for all $k$. For each run, the approach time $t_A$ is noted (defined as the time elapsed until the mean of the phenotype distribution is close to the singular point, i.e., $\hat{u} > 0.95u^*$). Speciation is defined as the moment that two discrete, reproductively isolated clusters of individuals have formed (cf. fig. 2a). The time of speciation is denoted by $t_S$. The algorithm used is analogous to the one used for evolutionary branching in Claessen et al. 2007. The delay to speciation, denoted by $\Delta_S$, is defined as the time elapsed between approaching $u^*$ and the moment of speciation: $\Delta_S = t_S - t_A$.

For the case of three loci with two different settings of the mutation parameters, figure 3a, 3b shows that the delay to speciation is very sensitive to $V$. There appears to be a minimum lake size below which speciation does not occur and above which $\Delta_S$ decreases steeply with $V$ until an asymptotic minimum delay has been reached. The approach time $t_A$ decreases much less steeply with $V$. We find the same pattern for different values of the mutation rate $p_M$ and mutation width $\sigma$ (fig. 3a, 3b). Qualitatively, this result does not depend on the chosen number of loci or the specific level of crossing over (see "Recombination and
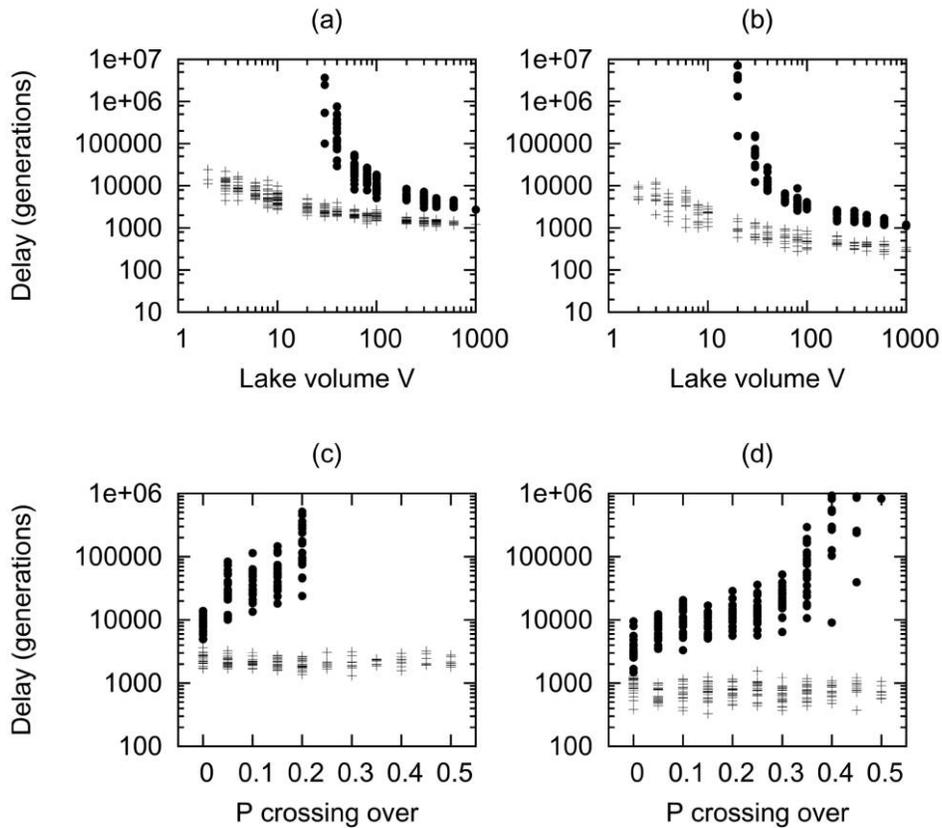
**Figure 3:** Delay to speciation depending on lake volume $V$ ($a$, $b$) or the crossing-over probability $p_C$ ($c$, $d$), with three loci ($L = 3$). For each simulation, the delay to approach $u^*$ ($t_A$; *plus symbols*) and the delay to speciation ($\Delta_S$; *filled circles*) are plotted. Parameters: $a_1 = 0$, $a_2 = 2$, $b_1 = 2$, $b_2 = -2$. $a$, $p_C = 0.1$, $p_M = 0.01$, $\sigma = 0.01$. $b$, $p_C = 0.1$, $p_M = 0.001$, $\sigma = 0.05$. $c$, $V = 50$, $p_M = 0.01$, $\sigma = 0.01$. $d$, $V = 50$, $p_M = 0.001$, $\sigma = 0.05$. Note the equilibrium population size of a monomorphic population with $\hat{u} = 0.5$ equals $n = 18V$; that is, $n \approx 900$ for $V = 50$, as in $c$ and $d$.

number of loci"). These results show that our earlier results on delayed evolutionary branching in asexual populations (Claessen et al. 2007) extend to speciation in sexual populations.

Genetic polymorphisms may evolve long before eventual speciation (fig. 2$b$). To complete the analysis of the effect of lake size, we record in each simulation the first time, denoted by $t_P$, that the alleles $x_i = 0$ and $y_i = 1$ coexist in the population at any locus $i$. For example, $t_P = 42,871$ generations in figure 2$b$, just after the moment where three distinct phenotypes appear. The relation of $t_P$ with lake size is depicted in figure 4. The figure confirms that in general, genetic polymorphism evolves long before speciation. In intermediately sized systems (e.g., $V = 30$), the population may become polymorphic fairly quickly but remain polymorphic almost indefinitely without actually speciating into reproductively isolated populations.

*Recombination and number of loci.* For the case of three

loci with two different settings of the mutation parameters, figure 3$c$, 3$d$ shows that the delay to speciation increases at an accelerating rate with the probability of recombination. Increased crossing over tends to destroy the homogeneous chromosomes ($[0, 0, 0]$ and $[1, 1, 1]$) and hence decreases the probability that these genotypes come to dominate the population. The approach time $t_A$, on the other hand, is insensitive to $p_C$. We find the same pattern for different values of the mutation rate $p_M$ and mutation width $\sigma$ (fig. 3$c$, 3$d$).

The effect of sexual reproduction on speciation is expected to depend on both the recombination probability $p_C$ and the number of loci $L$. First, the chance of crossing over increases with both $p_C$ and the number of loci. Second, in a polymorphic population, the frequency of extreme phenotypes decreases with $L$. Third, speciation requires the evolution of polymorphism at all loci, which may take longer with more loci. To quantify the combined effect of crossing over and the number of loci, 20 simu-
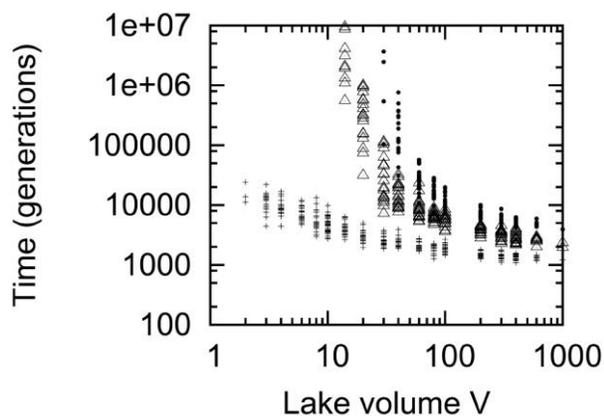
**Figure 4:** Time to genetic polymorphism, depending on lake volume *V*. Data and parameters as in figure 3*a*. For each simulation run, the time at which a complete polymorphism at one locus arises ($t_P$; *triangles*) is indicated. For reference, the approach time ($t_A$; *plus symbols*) and the time at speciation ($t_S$; *filled circles*) are also plotted. Note the equilibrium population size of a monomorphic population with $\hat{u} = 0.5$ equals $n = 18V$.

lations of 20,000 generations were run for each combination of $p_C$ and $L$ and for four different lake volumes. For each parameter combination, the frequency of speciation was noted (fig. 5). The figure shows that increasing either one of these two parameters can impede speciation, even if the system size *V* is large. Only in simulations with up to three loci is speciation frequently observed. Figure 5 also shows that the qualitative effect of *L* and $p_C$ is independent of lake volume, although the frequency of speciation depends on lake volume. By contrast, the evolution of polymorphism is not significantly affected by the crossing-over probability (fig. A2*c*).

*Trade-off curvature.* The strategic (simplified) nature of our model does not allow for a close parameterization to the ecology of a specific empirical case such as the arctic char. Yet certain qualitative consequences of parameterization can be assessed with the model. In particular, the parameterization of the trade-off between search rates in the two habitats may influence the results. Here, we concentrate on the effect of the curvature of the trade-off, which influences the curvature of the fitness function at the EBP (i.e., assuming a monomorphic resident population with trait $u = u^*$). A stronger, positive curvature of the trade-off function (and hence of the fitness function) corresponds to stronger disruptive selection and is expected to promote evolutionary branching. A flatter function is expected to result in longer delays.

In order to assess the effect of curvature, we use six different trade-offs by tuning the parameters of the search rate functions (eqq. [4], [5]). The different trade-offs are

assumed to be symmetric (i.e., $b_2 = -b_1$ and $a_2 = a_1 + b_1$) and are defined such that $A_1(u)$ and $A_2(u)$ intersect at the point $A_1(0.5) = A_2(0.5) = 1$. At the EBP, the ecological equilibrium ($N^*, F_1^*, F_2^*$) is then the same for all trade-offs, the only difference being the curvature of the fitness function. Defining fitness as the per capita growth rate, $w(u) = \beta(u) - \mu$, the curvature of the fitness function is $\partial^2 w(u)/\partial u^2 = 2b_1F_1^* - 2b_2F_2^*$. The trade-offs are specified by the parameter pair ($a_1, b_1$), equal to (0, 2), (0.2, 1.6), (0.4, 1.2), (0.6, 0.8), (0.8, 0.4), and (1.0, 0), respectively. Given the other parameter values, the curvature at the EBP then equals 0.8, 0.64, 0.48, 0.32, 0.16, and 0, respectively. Note the trade-off ($a_1, b_1$), equal to (0, 2), corresponds to the one used in the other figures.
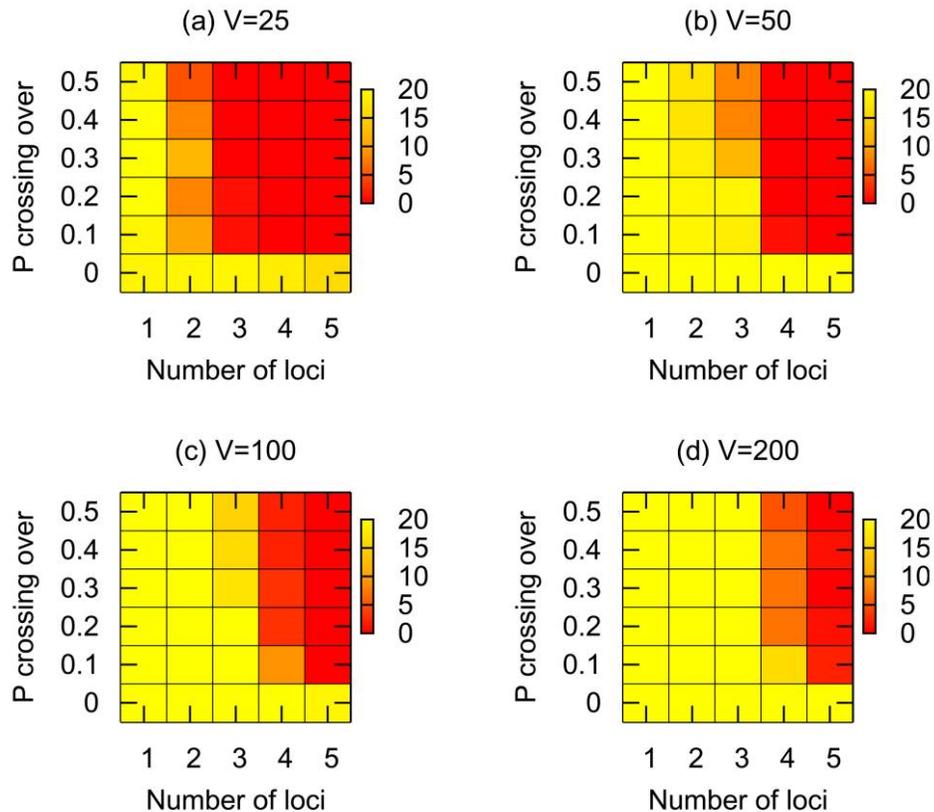
We run 30 simulations of 20,000 generations for each trade-off, with $L = 3$ and $p_C = 0.1$. We find a strong effect of curvature on the delay to speciation because speciation is observed only with the highest curvature (0.8). A more subtle effect of curvature is revealed by observing the highest level of polymorphism (number of dimorphic loci; i.e., with alleles 0 and 1) attained during a simulation, which can be estimated from the number of discrete coexisting phenotypes, as explained above. Figure 6 shows that the level of polymorphism increases with the curvature of the fitness function. With a relatively strong curvature of 0.64, we find stable dimorphism in all three loci in all 30 simulations but no speciation. Apparently, the fitness differences are not sufficient for the fully homozygous to oust the hybrids. With intermediate curvature, we find dimorphism in either two or three loci (0.48) or in either one or two loci (0.32). With the linear trade-off (0 curvature), we find incipient branching resulting in a single dimorphic locus in two out of 30 runs. However, the dimorphisms last only briefly.

Close inspection of the dynamics at the allele level shows that with low curvature, branching occurs initially at all the loci but that polymorphism is subsequently lost at some or all loci (data not shown). This usually occurs during the initial period of phenotypic divergence, that is, before the appearance of the $2k + 1$ discrete phenotypes. The subsequent reduced polymorphism is very stable, such as the single-locus dimorphisms observed in figure 2*b*.

### Part 2: An Empirical Test

#### *Material and Methods*

Table 1 was modified from Alekseyev et al. (1998, 1999, 2002) and supplemented with new information about additional lakes (S. Alekseyev, personal communication). The table shows data on 22 lakes in Transbaikalia, Russia. Lake volume was estimated as the product of maximum length, maximum width, and maximum depth of the lake.

**Figure 5:** Frequency of speciation in 20 runs of 20,000 generations, for four different lake sizes. For each combination of the number of loci and the crossing-over probability, the color indicates the number of simulations (out of 20) in which speciation occurred. $S = 2$, $p_M = 0.001$, $\sigma = 0.05$.

The number of char types was counted as the total number of morphotypes ever found. For the analysis, the independent factors were $\log(1 + x)$ transformed (where $x$ is the number of other fish species or lake volume).

We used ordinal logistic regression (SPSS v12.0.1) in order to test for relationships between lake volume, number of other species, and number of char morphs. First, we analyzed the relation between the number of char forms versus lake volume. Second, since the number of other species present can negatively affect the chance that new char morphs develop (as fewer niches remain unexploited when more species are present), we analyzed the relation between the number of char morphs versus the number of other species present in the lake. Third, we included both factors simultaneously in the analysis, with the number of char morphs as dependent and the number of other species present and lake volume as independent factors.

## Results of Data Analysis

The number of char morphs does not show a significant relationship with lake volume only (pseudo-$R^2 = 0.13$, $P = .21$) or with only the number of other species present (pseudo-$R^2 = 0.03$, $P = .71$). Lake volume and the number of other species together, however, have a significant effect on the number of char morphs (pseudo-$R^2 = 0.66$, $P < .001$). The number of other species has a negative effect (Wald statistic $= -9.9$, $P = .010$), while lake volume has a positive effect (Wald statistic $= 2.8$, $P = .009$) on the number of char morphs.

## Discussion

With a simple model, we have shown that our previous results (Claessen et al. 2007) extend to sexually reproducing populations: evolutionary branching (resulting in ei-
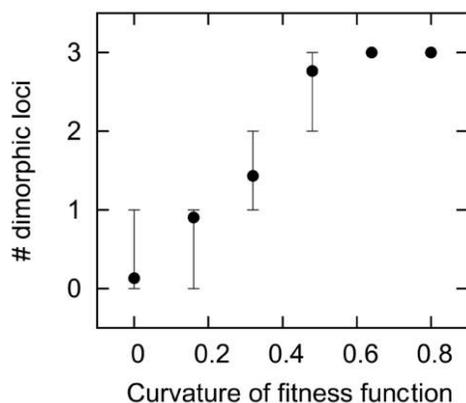
**Figure 6:** Maximum number (out of $L = 3$) of dimorphic loci, that is, with alleles 0 and 1 present, observed in simulations of 20,000 generations, as a function of the curvature of the fitness function (evaluated at the evolutionary branching point). *Dots* = averages in 30 simulations. Error bars indicate the lowest and highest observations. Speciation occurred in all simulations with the highest curvature (0.8, the same as fig. 2a) but in none of the others. For search rate parameters, see text. Other parameters: $V = 200$, $S = 2$, $p_M = 0.01$, $\sigma = 0.01$.

ther speciation or a stable genetic polymorphism) is delayed in small populations due to the effects of demographic stochasticity. We have also shown that the delay to speciation increases with higher levels of recombination, with more loci, and with lower curvature of the fitness function. The evolution of polymorphism, however, is unaffected by the level of crossing over. In addition, we have shown that the process of speciation can stagnate in a state of genetic polymorphism in systems of intermediate size or with a low curvature of the fitness function.

The two mechanisms that were identified in our previous article as causes of the delay to evolutionary branching (i.e., genetic drift and extinction of incipient branches) operate in sexual populations as well. In addition, dynamical processes at the allele level may add to the delay in sexual populations. We have observed partial loss of allele dimorphism, resulting in dimorphism at a few loci or a single locus only. The observed high stability of such reduced genetic polymorphism may further impede the processes of speciation when speciation requires dimorphisms at all loci, such as in our model.

The formation and subsequent collapse of polymorphisms in multilocus trait evolution has recently been analyzed in detail by van Doorn and Dieckmann (2006). Their description of different phases of formation and collapse of polymorphisms closely matches the dynamics observed in our model. With a deterministic approximation of the evolutionary dynamics at the allele level based on the canonical equation of adaptive dynamics,

they show that the loss of polymorphism in all but one locus can be expected even in very large populations. A similar result has been found by Kopp and Hermisson (2006), who showed that frequency-dependent, disruptive selection favors such concentration of genetic variation at one or a few loci. We have shown that the level of stable polymorphism depends on the strength of disruptive selection and on the system volume. Only with sufficient curvature and in sufficiently large lakes do we find multiple polymorphism that allows for speciation. With weaker curvature or in smaller lakes, the population genetic structure tends to get "trapped" in a collapsed polymorphism. Because the strength of disruptive selection is smaller in such partially polymorphic populations than in monomorphic populations at the EBP (Kopp and Hermisson 2006), this process is likely to increase the delay to speciation.

Dieckmann and Doebeli (1999) highlight a positive effect of stochasticity on evolutionary branching. In their model, as in ours, speciation cannot occur until a linkage disequilibrium arises in the population. The disequilibrium results from recombination and drift and hence depends critically on demographic stochasticity. Stochasticity is hence indispensable for sympatric speciation, yet too much stochasticity impedes branching because of the reasons mentioned above.

## Comparison with Data on Arctic Char

Quantitatively, our results depend on model parameters, including the number of loci, the level of recombination, mutation probability, and the size of mutation steps (fig. 3a, 3b; see also Claessen et al. 2007). Without knowledge of these parameter values, it is not possible to pinpoint a lower limit of absolute population size below which branching is expected to be delayed or impossible. We can, however, make two qualitative predictions. First, in a given species, resource polymorphism (whether the result of speciation or a genetic polymorphism) is more likely to occur in large lakes than in small lakes, since absolute population size is expected to be proportional to lake size (Sondergaard et al. 2005). Second, given that the morphological trait underlying the resource polymorphism is most likely a multilocus trait (Skúlason and Snorrason 2004), our model further predicts that the extent of reproductive isolation in observed cases of resource polymorphisms depends on lake size, with complete reproductive isolation and hence speciation underlying the resource polymorphism in large lakes, while in intermediate lakes the resource polymorphism is more likely to be a genetic polymorphism in a panmictic population (fig. 4).

The first prediction is confirmed by our analysis of empirical data on arctic char polymorphism in 22 lakes in Transbaikalia that showed that, indeed, the number of

**Table 1:** Data on 22 lakes in Transbaikalia (Russia) with the number of arctic char morphotypes and the number of other fish species found in each lake

| Lake | Volume (km³) | No. other species | No. char morphs | Source |
|---|---|---|---|---|
| Frolikha | 3.6 | 10 | 1 | Alekseyev et al. 1999 and references therein |
| Nomama | .1 | 5 | 2 | Alekseyev et al. 1999 and references therein |
| Ogiendo-1* | .008 | 2 | 2 | Alekseyev et al. 1998, 2002; and S. Alekseyev, pers. comm. |
| Ogiendo-3* | .003 | 3 | 1 | Alekseyev et al. 1999 and references therein |
| Kudushkit* | .005 | 0 | 3 | Alekseyev et al. 1999 and references therein |
| Soli | .27 | 3 | 3 | Alekseyev et al. 1998, 2002; and S. Alekseyev, pers. comm. |
| Irbo | .13 | 4 | 2 | Alekseyev et al. 1999 and references therein |
| Padorinskoe | .0024 | 1 | 2 | Alekseyev et al. 1999 and references therein |
| Davatchanda* | .0055 | 2 | 2 | Alekseyev et al. 1999 and references therein |
| Krestaki-1* | .013 | 0 | 3 | Alekseyev et al. 1999 and references therein |
| Bol'shoi Namarakit | .98 | 4 | 3 | Alekseyev et al. 1999 and references therein |
| Dzhelo | .011 | 2 | 2 | Alekseyev et al. 1998, 2002; and S. Alekseyev, pers. comm. |
| Leprindokan | .42 | 8 | 2 | Alekseyev et al. 1999 and references therein |
| Bol'shoe Leprindo | 2.1 | 11 | 2 | Alekseyev et al. 1999 and references therein |
| Gol'tsovo* | .004 | 0 | 3 | Alekseyev et al. 1999 and references therein |
| Davatchan | .28 | 5 | 3 | Alekseyev et al. 1999 and references therein |
| Severonichatskoe* | .01 | 3 | 2 | Alekseyev et al. 1998, 2002; and S. Alekseyev, pers. comm. |
| Kiryalta-3* | .01 | 3 | 2 | Alekseyev et al. 1998, 2002; and S. Alekseyev, pers. comm. |
| Kiryalta-4 | .07 | 3 | 2 | Alekseyev et al. 1999 and references therein |
| Kamkanda | .06 | 3 | 3 | Alekseyev et al. 1998, 2002; and S. Alekseyev, pers. comm. |
| Lesha* | .0004 | 1 | 1 | Alekseyev et al. 1999 and references therein |
| Tokko | .03 | 1 | 3 | Alekseyev et al. 1999 and references therein |

Note: Lakes with names not specified in topographic maps are marked with an asterisk. Numbers following the names of the lakes correspond to the number of the lake in a chain of lakes located in the upper reaches of the same river, starting from the upper one. See text for estimation of volume.

morphotypes is positively related to lake size. In addition, the data analysis revealed a negative relation with the number of other fish species present. We hypothesize that the presence of other species may reduce the likelihood of evolutionary branching in two ways. First, additional species reduce the availability of niches and hence limit the maximum level of diversification. The presence of another fish species in one of the available niches reduces the resource associated with that niche and hence changes the curvature of the fitness function, resulting in directional selection toward specialization in the other niche. This idea could be investigated theoretically by extending the model analysis to multiple species, but from general theory we already know that the number of resources is an upper limit to the level of diversity (including the other species) that can evolve (Tilman 1982; Meszéna and Metz 1999). Second, the presence of a predator species would not affect the relative abundance of the two resources but rather reduce the population size of the focal species. Our results suggest that a predator thus decreases the likelihood of evolutionary branching in its prey by reducing its absolute population size. This suggests that higher-dimensional environments (e.g., taking into account the interactions with competing and predatory fish) may modulate the rela-

tionship that the model has revealed; in both cases, evolutionary branching is inhibited by the presence of other species. A negative relation between the number of other species and the number of morphotypes is, however, consistent with our hypothesis of a sympatric origin of the morphotypes, depending on lake size.

It should be stressed, however, that alternative hypotheses may lead to the same prediction. First, if the probability of invasion of a lake increases with lake size, the hypothesis of multiple invasions of lakes by allopatrically diverged morphotypes would lead to the observed correlation between lake size and diversity. Second, it can be argued that larger lakes are likely to harbor more available niches or habitats and may therefore support higher levels of diversity. The data (table 1) therefore cannot differentiate between these hypotheses. However, analysis of meristic data from a subset of these lakes suggests that different sympatric morphotypes are more closely related than allopatric populations of the same morphotype, thus supporting a sympatric origin of morphotypes (Alekseyev et al. 2002). This observation seems to rule out the invasion hypothesis but leaves the second alternative hypothesis intact.

*Adaptive Dynamics: Theory and Data*

Mathematical models of ecological systems that can give rise to evolutionary branching, such as our model, abound in the literature and cover various ecological interactions such as resource competition, predation, interference competition, mutualism, parasitism, and competition for mates (Geritz et al. 2004 and references therein). Yet a largely unexplored aspect of adaptive dynamics theory is the confrontation of its predictions with empirical evidence. The recent volume edited by Dieckmann et al. (2004) makes an effort in this direction. It contains examples of systems in which important assumptions of the models of adaptive dynamics are fulfilled, such as mechanisms that give rise to frequency-dependent selection and mechanisms of assortative mating. Microbial systems have a large potential for rigorously testing theoretical predictions of adaptive dynamics (Travisano 2004), as demonstrated by Friesen et al. (2004). Indirect evidence for validation of the theory can be obtained from phylogeographic data, because certain patterns that are hard to explain assuming allopatric speciation are easily explained with sympatric speciation (e.g., monophyletic fish species in crater lakes; Schliewen et al. 1994; Tautz 2004). We view our study as a contribution in this direction. We identified an abiotic, eco-logical factor (lake size) that modifies the likelihood of evolutionary branching. The advantage of varying an abiotic factor such as lake size is that it does not coevolve with the life history under consideration. Our model predictions allow for straightforward testing with empirical data as demonstrated above, although not all alternative hypotheses can be ruled out. We argue that prediction and verification of such patterns of variation in evolutionary outcomes over ecological gradients constitutes a promising approach in exposing theory to empirical scrutiny. In this context, it is interesting to note that gradients in other factors that influence absolute population size, such as productivity, may equally influence evolutionary branching.

## APPENDIX A

### The Effect of Assortative Mating ($S$) on Polymorphism and Speciation

The strength of assortative mating is determined by the parameter $S$ (eq. [2]). To investigate the robustness of our results to the value of $S$, we have run a large number of additional simulations for constructing plots such as figure 5 for different values of $S$. Figure A1 thus shows the frequency of speciation in 20 simulations of 20,000 generations for each combination of $p_C$ and $L$ for a fixed lake size of $V = 50$. As expected, the figure shows that with random mating ($S = 0$) and weak assortative mating ($S = 1$), speciation does not occur (within 20,000 generations), while with strong assortative mating ($S = 2$ and $S = 4$) speciation is possible. Note that figure A1$c$ corresponds to figure 5$b$.

By contrast, figure A2 shows that the evolution of polymorphism is unaffected by the level of assortative mating. As before, the time to polymorphism ($t_p$) is recorded in each simulation as the first time that the alleles $x_i = 0$ and $y_i = 1$ coexist in the population at any locus $i$. Based on figure A2, we can conclude that the evolution of polymorphism is not influenced by $S$ (see also app. B) nor by the crossing over probability $p_C$. Polymorphism evolves more quickly with a higher number of loci $L$, which is due to our model assumption that the size of mutations increases with $L$, in order to keep the phenotypic effect of mutations constant.
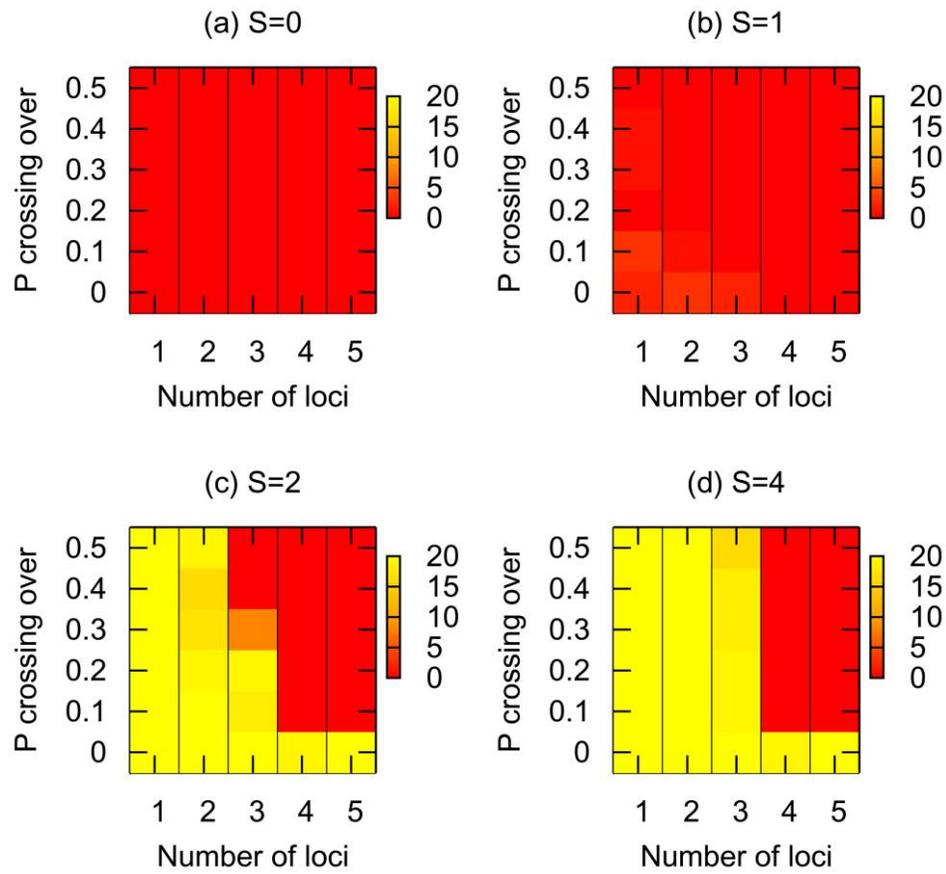
**Figure A1:** Effect of assortative mating (*S*) on the frequency of speciation in 20 runs of 20,000 generations. For each combination of the number of loci and the crossing-over probability, the color indicates the number of simulations (out of 20) in which speciation occurred. $V = 50$, $p_M = 0.001$, $\sigma = 0.05$.
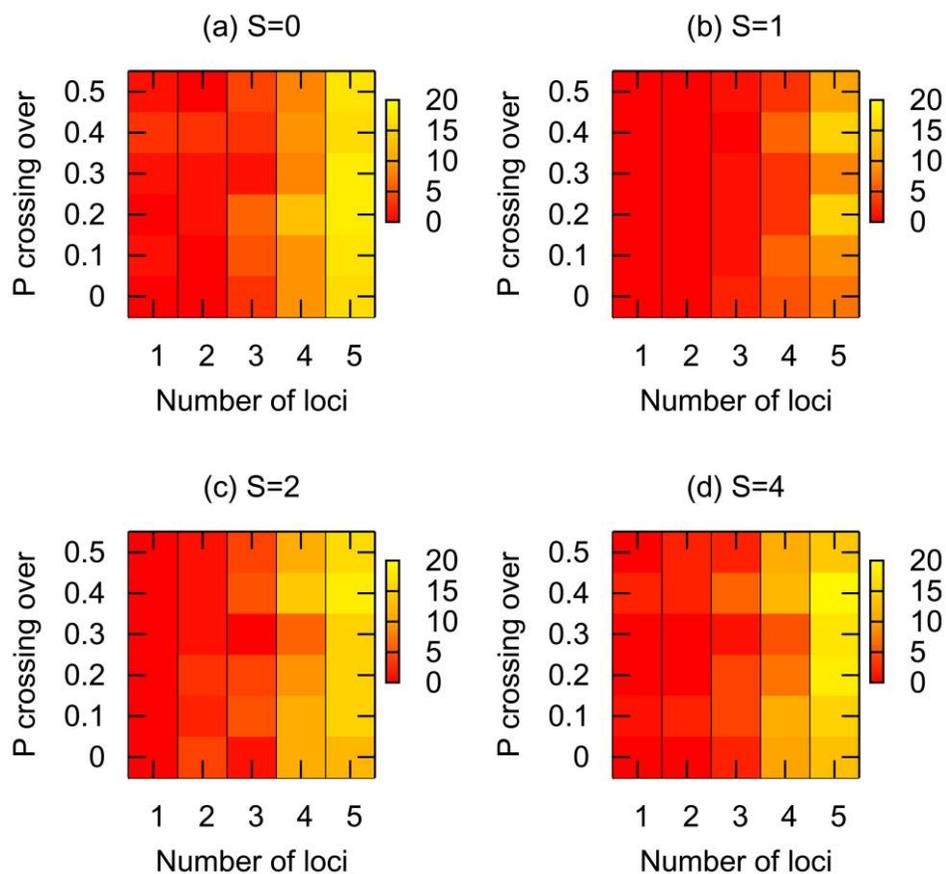
**Figure A2:** Effect of assortative mating ($S$) on the evolution of polymorphism in 20 runs of 20,000 generations. For each combination of the number of loci and the crossing-over probability, the color indicates the number of simulations (out of 20) in which speciation occurred within 1,000 generations. $V = 50$, $p_M = 0.001$, $\sigma = 0.05$.

## APPENDIX B

### Evolution of Assortative Mating (*S*)

Figure B1 shows an example of the simultaneous evolution of the ecological trait $u$ and the mating trait $S$ for a lake volume of $V = 50$ and $L = 3$ loci for the ecological trait. The parameter $S$ is assumed to be determined by a single locus subject to the same mutation rate as the ecological trait. In this run, the allowed range of $S$ has been restricted to between $-2$ and $+2$. The figure shows that after a short delay, evolutionary branching occurs despite mating being random ($S \approx 0$, cf. eq. [2]). Evolution of dimorphism at both loci results in a (still diverging) genetic polymorphism. With two dimorphic loci, say (A, a) and (B, b), with unequal high and low values (i.e., A $\neq$ B, a $\neq$ b), the possible allele combinations result in a total of nine discrete phenotypes (i.e., aabb, Aabb, aaBb, etc.), which are visible in figure B1. However, the emerged polymorphism favors genotypes that mate assortatively, which results in directional selection at the $S$ locus. The trait $S$ converges to its allowed maximum of 2. In this particular run, speciation occurs at around 10,000 generations, when the ecological trait has diverged completely and assortative mating has evolved. Subsequently, drift at the $S$ locus to lower values results in a brief periods of interbreeding, marked by the appearance of intermediate hybrids. An open question is what is the effect of population size on the evolution of assortative mating. Small population size may favor the appearance of the linkage disequilibrium which is required for the evolution of reproductive isolation by assortative mating (Dieckmann and Doebeli 1999).
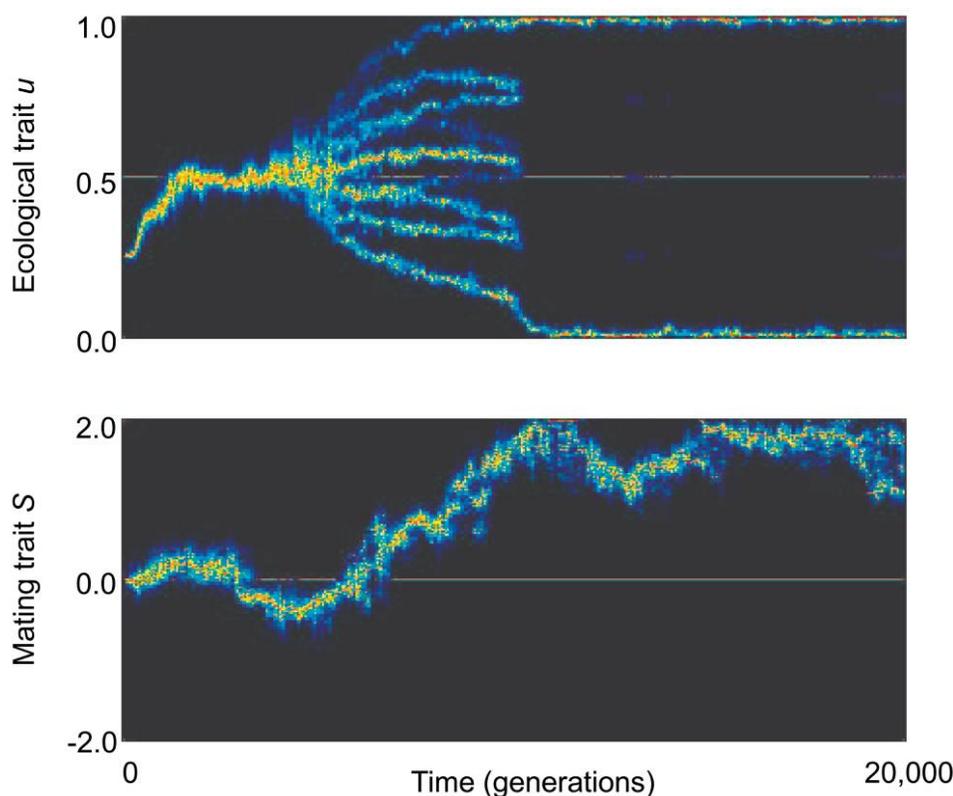
**Figure B1:** Simultaneous evolution of the polygenic ecological trait $u$ (*top*) and the assortative mating trait $S$ (*bottom*), in a single run of 20,000 generations. Parameters: $L = 2$, $V = 50$, $p_C = 0.1$, $p_M = 0.01$, $\sigma = 0.01$, $a_1 = 1$, $a_2 = 2$, $b_1 = 1$, $b_2 = -1$. Density of individuals: black = 0, blue = low, and red = high.

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