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Abstract

Although verbal theories of speciation consider landscape changes, ecological speciation is usually modeled in a fixed geographical arrangement. Yet landscape changes occur, at different spatio-temporal scales, due to geological, climatic or ecological processes, and these changes result in repeated divisions and reconnections of populations. We examine the effect of such landscape dynamics on speciation. We use a stochastic, sexual population model with polygenic inheritance, embedded in a landscape dynamics model (allopatry-sympatry oscillations). We show that, under stabilizing selection, allopatry easily generates diversity, but species coexistence is evolutionarily unsustainable. Allopatry produces refuges whose persistence depends on the characteristic time scales of the landscape dynamics. Under disruptive selection, assuming that sympatric speciation is impossible due to Mendelian inheritance, allopatry is necessary for ecological differentiation. The completion of reproductive isolation, by reinforcement, then requires several sympatric phases. These results demonstrate that the succession of past, current and future geographical arrangements considerably influence the speciation process.

Keywords: Landscape dynamics; Ecological speciation; Allopatry; Sympatry; Secondary contact; Reinforcement; Dynamic metapopulation

1 Introduction

Ecological speciation — the evolution of reproductive isolation as a consequence of divergent selection based on ecological mechanisms (Schluter, 2001) — can occur in any geographical arrangement, allopatry, parapatry or sympatry. Allopatric and parapatric speciation have been well accepted for years as plausible modes of speciation. Thanks to the recent accumulation of theoretical models and of empirical evidence, sympatric speciation now seems to be accepted as possible at least (Turelli et al., 2001; Via, 2001; Bolnick & Fitzpatrick, 2007). A debate about its frequency is nevertheless still going on (see e.g. Bolnick & Fitzpatrick, 2007; Fitzpatrick et al., 2009). Some authors (e.g. Fitzpatrick et al., 2008, 2009) argue that classifying speciation events into distinct classes (allopatric, parapatric or sympatric) is unrealistic and potentially misleading. However, the geographic arrangement of speciation candidates remains informative since this selects the possible mechanisms leading to speciation (Rundle & Nosil, 2005; Bolnick & Fitzpatrick, 2007). For example, divergent selection between different environments can drive speciation in allopatry, as opposed to sympatry where all individuals necessarily experience the same environment. On the contrary, ecological interactions between the individuals of a sympatric population, such as competition, can generate reproductive isolation in sympatry, as opposed to allopatry where individuals in different locations do not interact.

It is rather surprising that almost all models of speciation focus on a single geographical arrangement (Fitzpatrick et al., 2009), given that standard verbal models of speciation take into account both allopatry and sympatry (Rundle & Nosil, 2005). Ample empirical evidence shows that speciation is often initiated in allopatry and completed in sympatry (e.g. Taylor & McPhail, 2000; Feder et al., 2003; Jordal et al., 2006; Xie et al., 2007; Grant & Grant, 2009), or conversely (e.g. Baack, 2004; Stuessy et al., 2004). The succession of different geographical arrangements seems to be of particular importance in adaptive radiations (Rundell & Price, 2009). In addition, even if ecological speciation can be initiated (i.e. the evolution of weak reproductive isolation and of weak ecological divergence) within only tens of generations (Hendry et al., 2007), divergent selection alone often fails to complete speciation on such a time scale (Nosil et al., 2009). As a result, complete ecological speciation (i.e. the evolution of persistent reproductive isolation) can require a significant time during which several biogeographical changes are likely to influence the speciation process (Bolnick & Fitzpatrick, 2007; Fitzpatrick et al., 2008).

Dynamic landscapes, here defined as the repeated alternation of allopatry and sympatry of populations (Aguilée et al., 2009), are indeed common at different spatio-temporal scales. For example, the connections between populations may vary due to glaciations and postglacial secondary contacts (Hewitt, 2000; Young et al., 2002; Zhang et al., 2008). Geological processes (e.g. volcanic events) as well as climatic variations can cause sea level changes, resulting in separations or fusions of islands (Cook, 2008; Esselstyn et al., 2009). Similarly, persistent fluctuations of water level causing fragmentation and fusion of lakes are thought to have influenced the radiation of cichlid fishes in the Great African Lakes (Owen et al., 1990; Arnegard et al., 1999; Stiassny & Meyer, 1999; Young et al., 2009). At a different spatio-temporal scale, populations can oscillate between allopatry and sympatry due to the establishment of new colonies by dispersal and their later fusion (DeHeer & Kamble, 2008; Vasquez & Silverman, 2008). Landscapes are also rapidly changed by contemporary fragmentation and reconstruction of habitats due to human activities (Davies et al., 2006). Note that the spatio-temporal scales of landscape dynamics and the nature of the geographical arrangements of populations are relative to their population dynamics and to their evolutionary dynamics.

In the present paper, we address the following question: how do dynamic landscapes, in contrast to static landscape, affect ecological speciation? A well documented related question concerns the effect on speciation of secondary contact, i.e. the transition from allopatry to sympatry. Secondary contact can have two opposite effects (Servedio & Kirkpatrick, 1997; Noor, 1999; Servedio & Noor, 2003). First, it allows gene flow between differentiated populations, which homogenizes genotypes and impedes speciation. Second, hybrids produced by differentiated individuals can have a reduced fitness: reinforcement can then potentially complete speciation. Diversity generated in allopatry can thus be maintained or lost at secondary contact, essentially depending on the rate of interbreeding and on how much the fitness of hybrids is reduced compared to their parents (Kirkpatrick, 2000; Servedio & Noor, 2003). The success of speciation at secondary contact also depends on the mechanisms of reinforcement. Consequently, the duration of the allopatric state preceding secondary contact may be crucial. For example, hybrids produced at secondary contact can have a reduced fitness due to genetic incompatibilities between individuals from different former allopatric populations (Orr, 1995), and when hybrids are unviable, post-zygotic reproductive isolation is complete. Reinforcement reducing hybrid production is then called intrinsic. Such genetic incompatibilities take long to evolve (Orr & Orr, 1996), so that intrinsic reinforcement is expected at secondary contact only after a long geographical isolation period. Alternatively, hybrids can have a reduced fitness because of ecological interactions (e.g. hybrids are phenotypically intermediate to their parents and consequently worse competitors than their parents). In this case, reinforcement is called extrinsic and can lead to pre-zygotic reproductive isolation, often much more quickly than the genetic incompatibilities do, for example via the evolution of assortative mating (Servedio & Noor, 2003). In such a case, reinforcement is driven by disruptive selection, selecting for positive assortative mating which is either directly related to the ecological trait responsible for the reduced fitness of hybrids ("one-allele" mechanism), or related to a non-ecological, linked and possibly sexual trait ("two-alleles" mechanism) (Felsenstein, 1981; Doebeli & Dieckmann, 2005).

These results on secondary contact are not sufficient to fully answer the question because the whole process is heavily dependent on the time scales of allopatric stages before and after secondary contact. For example, ecological divergence is often assumed to be at equilibrium at secondary contact, whereas the duration of allopatry before secondary contact can be too short for that. Similarly, secondary contact is usually assumed to last long enough to let the population reach an equilibrium state (either failed or permanent speciation), whereas a new landscape change could prevent the population from reaching this equilibrium. Moreover, the effect of successive secondary contacts has not been investigated. This paper examines under which conditions landscape dynamics allow (i) the formation of diversity and (ii) its maintenance (or not) until ecological speciation is complete and persistent. We aim to characterize the likelihood, time scale and predominant underlying mechanisms for each of these two points.

2 Model

In order to address these questions, our model is built upon the following four guiding assumptions. First, as a first analysis of the effect of landscape dynamics, the landscape dynamics should be as simple as possible: we assume that the landscape oscillates between an undivided state (sympatry) and a divided state with two subpopulations (allopatry). Second, as the outcome of secondary contact is expected to depend on the fitness landscape, the model should allow us to explore different fitness landscapes. We thus choose a model where, the population trait evolves to a singular point (Geritz et al.,

1998) where, depending on parameter values, it then evolves under either stabilizing or disruptive selection. Third, we assume that diversification can only occur between allopatric populations. This is done by generating different environmental conditions for allopatric populations. Sympatric diversification is made unlikely by assuming that phenotypic traits are determined by many independently segregating loci, with small allelic effects. Such genetic constraints are known to impede sympatric divergence (Waxman & Gavrilets, 2005). Fourth, reproductive isolation should be allowed to evolve. To this end, we allow for the evolution of assortative mating based on a one-allele mechanism. Post-zygotic reproductive isolation, for example due to genetic incompatibilities, is assumed to take longer to evolve than the time scales we will consider (Orr & Orr, 1996) and is thus not incorporated into the model.

2.1 Ecological model

This section describes the population dynamics and evolution in one subpopulation, either the only subpopulation when the landscape is in a sympatric state, or either of the two subpopulations when the landscape is in an allopatric state. The dependence of the parameters on the landscape structure is detailed in Section 2.2.

Consumer-resource dynamics

We use a stochastic, individually based model inspired by the models of Claessen et al. (2007, 2008). The consumer population consists of $n(t)$ discrete individuals. Individuals of the subpopulation under scrutiny compete with each other for two different resources. Each individual i is characterized by an evolving phenotypic trait u_i determining its resource utilization strategy (see Table 1 for a summary of the notation). This ecological trait represents a degree of specialisation where $u_i = 0.5$ represents a generalist strategy, $u_i = 1$ and $u_i = 0$ represent complete specialisation on resource 1 or 2, respectively. It operates through e.g. morphological adaptations influencing the ability to feed on each resource. We assume a power-law trade-off (e.g. Egas et al., 2004; Spichtig & Kawecki, 2004) between the exploitation of the two different resources, specified by a parameter z. The fitness $W(u_i)$ of individual i is a linear combination of performance on either resource:

$$W(u_i) = \beta(u_i) - d = F_1 u_i^z + F_2(1 - u_i)^z - d \tag{1}$$

where $\beta(u_i)$ is the birth rate of individual i, d is the constant per-capita death rate, and F_1 and F_2 are the densities of resources 1 and 2 available for the subpopulation under scrutiny. The shape of the trade-off depends on the parameter z. When $0 < z < 1$ (resp. $z > 1$), the trade-off is weak (resp. strong) (e.g. Egas et al., 2004; Spichtig & Kawecki, 2004): the population is predicted to evolve by directional selection to a singular strategy u^* where it then experiences stabilizing (resp. disruptive) selection (Rueffler et al., 2004). When $z = 1$, the trade-off is linear; at a singular strategy u^*, $F_1 = F_2$ and the selection gradient is flat (i.e. no selection).

Assuming that resources follow semi-chemostat dynamics, the densities of resources can be expressed as

$$\begin{cases} F_1 = K_1/[1 + \frac{1}{V}\sum_{i=1}^{n(t)} u_i^z] \\ F_2 = K_2/[1 + \frac{1}{V}\sum_{i=1}^{n(t)} (1 - u_i)^z] \end{cases} \tag{2}$$

where K_1 (resp. K_2) is the maximum density of resource 1 (resp. 2) available for the subpopulation under scrutiny and V is a scaling parameter allowing us to set the consumer

Table 1: Notation and numerical values

Evolving trait	Definition	Interpretation
u_i	Ecological trait of individual i	$u_i = 0.5$: generalist strategy $u_i \neq 0.5$: specialist strategy
α_i	Mating trait of individual i	$\alpha_i = 0$: random mating $\alpha_i > 0$: assortative mating $\alpha_i < 0$: disassortative mating
Parameter	**Definition**	**Range of values explored**
z	Power-law trade-off parameter	$0.2 \leq z \leq 2$
d	Per-capita death rate	$d = 0.1$
L_j	Number of diploid loci coding trait j	$L_j = 6$ ($L_j = 1$, $L_j = 12$)
μ_j	Trait j per-locus mutation probability	$10^{-9} \leq \mu_j \leq 10^{-1}$
σ_j^2	Phenotypic variance of trait j	$10^{-6} \leq \sigma_j^2 \leq 0.5$
K_j	Maximum density of resource j available in sympatry	$K_1 = K_2 = 1$
V	Population size scaling parameter in sympatry	$10 \leq V \leq 100$
h	Asymmetry of the two resource distributions in allopatry	$1.1 \leq h \leq 25$
p	Asymmetry of the two subpopulation sizes in allopatry	$0.5 \leq p \leq 0.95$
T_a	Duration of allopatric phases	$10 \leq T_a \leq 10^6$ generations
T_s	Duration of sympatric phases	$10 \leq T_s \leq 10^6$ generations
T_r	Duration of partial secondary contact phases	$0 \leq T_r \leq 10^5$ generations
r	Hybridization probability during the partial secondary contact window	$10^{-6} \leq r \leq 0.25$
δ_i	Dilution rate of resource i (see Appendix A)	$\delta_1 = \delta_2 = 1$

population size relative to the maximum density of resources (see Appendix A for the derivation of Eq. 2). Such resource dynamics pertain to, for example, systems of size-selective fish foraging on zooplankton (Persson et al., 1998).

Reproductive isolation

We model pre-zygotic reproductive isolation by assuming that the population is sexual and that each individual i is characterized by a mating trait α_i. At each birth event, the individual i chosen to reproduce randomly encounters a sexual partner j among the individuals of the opposite sex in the subpopulation under scrutiny. The pair mates (or not) depending on the mating trait α_i of individual i and the difference $\Delta = u_i - u_j$ between the ecological traits of the two individuals (one-allele mechanism). Individual i mates with the chosen partner j with probability

$$q = \begin{cases} (1 - \frac{1}{2}\exp{[-\alpha_i^2]})\exp{[-\frac{\Delta^2}{2s_i^2}]} & \text{if } \alpha_i > 0 \\ 0.5 & \text{if } \alpha_i = 0 \\ 1 - (1 - \frac{1}{2}\exp{[-\alpha_i^2]})\exp{[-\frac{\Delta^2}{2s_i^2}]} & \text{if } \alpha_i < 0 \end{cases} \quad (3)$$

where $s_i = 1/(20\alpha_i^2)$. This Gaussian mating function has the minimal biological realism required: it is a continuous function in α_i, individual i has no preference when $\alpha_i = 0$ and mates assortatively (resp. disassortatively) when $\alpha_i > 0$ (resp. $\alpha_i < 0$), and choosiness increases when $|\alpha_i|$ increases. We will first analyze our model with α_i fixed and identical for all individuals, then we will allow this trait to evolve. In the first case, using a fixed, positive, large enough α_i simulates assortative mating based on the ecological trait or some other pre-zygotic reproductive isolation mechanism satisfying Eq. (3), such as temporal isolation or pollinator isolation (Coyne & Orr, 2004). In the second case, we model the evolution of exclusively (dis-)assortative mating based on the ecological trait.

When individual i rejects partner j, another partner is randomly chosen and the process repeats until mating succeeds, or until individual i has rejected 50 potential partners. This represents a very small cost of (dis-)assortativeness: Schneider & Bürger (2006) and Kopp & Hermisson (2008) showed that giving up mating after rejecting just ten potential partners has a very low cost.

Inheritance rules

The genetic architecture and inheritance rules are based on Claessen et al. (2008). Trait j (j being either the ecological trait u or the mating trait α) is determined by L_j diploid, additive loci on autosomal chromosomes. We assume neither environmental effects, nor epistasis, nor dominance effects. Each allele can take any real value (restricted to $[0, 1]$ for the ecological trait). The value of the phenotypic trait j is the mean of the $2L_j$ alleles determining this trait.

We assume independent segregation of each locus; at each locus, one offspring allele is randomly chosen from maternal and paternal alleles. We also assume $L_j = 6$, so that each allele has a limited effect on the value of the phenotypic trait. Because of these assumptions, when selection is disruptive, sympatric evolutionary diversification is severely delayed (Claessen et al., 2008) and is not expected to happen on the time scales we investigate.

At birth, the offspring's sex is determined randomly assuming a balanced sex-ratio. Mutation occurs at each locus determining trait j with probability μ_j. The mutant allele value is drawn from a normal distribution (truncated between $[0, 1]$ for trait u) with mean equal to the parental allele value and with standard deviation $\sigma_j\sqrt{2L_j}$. This mutation size at the allele level results in a variance σ_j^2 at the trait j level, regardless of the number of loci L_j (van Doorn et al., 2004).

2.2 Landscape model

Environmental conditions

In allopatry, the population consists of two isolated subpopulations (i.e. without migration between them), referred to as the "first" and "second" subpopulation. Parameters related to the first and second allopatric subpopulations are differentiated by a superscript $^{(1)}$ and $^{(2)}$ respectively; parameters related to the single subpopulation when the landscape is in a sympatric state are indicated without superscript.

In sympatry, we assume that the maximum densities of both resources are the same, i.e. $K_1 = K_2$. By contrast, in allopatry, we assume that the two subpopulations face different environmental conditions so that allopatric subpopulations are expected to diverge with respect to their ecological trait. This is done by assuming an asymmetrical distribution of the resources in the two patches: resource 1 is $h > 1$ times more abundant in the first patch than in the second one, whereas resource 2 is h times more abundant in the second patch than in the first one. The maximum densities of resources in the allopatric patches are defined by

$$\begin{cases} K_1^{(1)} = hK_1^{(2)} \\ K_1 = pK_1^{(1)} + (1-p)K_1^{(2)} \end{cases} \text{and} \begin{cases} K_2^{(2)} = hK_2^{(1)} \\ K_2 = pK_2^{(1)} + (1-p)K_2^{(2)} \end{cases} \tag{4}$$

(see Appendix B for the derivation of Eq. 4). Parameter p allows us to set the relative sizes of allopatric subpopulations: the further from 0.5, the more asymmetrical the sizes of the allopatric subpopulations. The scaling parameters for the allopatric subpopulation sizes are expressed accordingly: $V^{(1)} = pV$ and $V^{(2)} = (1-p)V$.

Because we assume $K_1 = K_2$, the singular strategy in sympatry corresponds to the generalist strategy $u^* = 0.5$. Because resource 1 is more abundant in the first patch than in the second patch in allopatry, and conversely for resource 2, the singular strategies $u^{*(1)}$ and $u^{*(2)}$ in allopatry correspond to two more specialized strategies: $u^{*(1)} > 0.5$ and $u^{*(2)} < 0.5$ respectively. Note that the nature of singular strategies does not depend on the geographic arrangement: under a weak (resp. strong) trade-off, populations at singular strategies experience stabilizing (resp. disruptive) selection both in sympatry and in allopatry. Appendix C gives the detailed adaptive dynamics analysis of the model.

Landscape dynamics

We first investigate the effect of a secondary contact, that is, a one-off landscape change from allopatry to sympatry. Later, we assume that the landscape oscillates between sympatry and allopatry.

Allopatric phases last T_a generations. At fragmentation of the landscape, each individual ends up in the first subpopulation with probability p and in the second subpopulation with probability $1-p$. Sympatric phases last T_s generations. During the T_r first generations of sympatric phases ($T_r < T_s$), we assume a reduced mating probability between individuals from different former allopatric subpopulations, in this way mimicking a "window of partial secondary contact". This assumption allows us to slow down the process of hybridization at secondary contact.

During the window of partial secondary contact, although all individuals have access to the same resources (sympatric state), as a result of their specialization on different resources in allopatry we expect that individuals from a given former allopatric patch reach a contact zone and meet individuals from the other former allopatric patch less often than they meet individuals from their own former patch. Hybrids born in the contact zone are assumed to tend to remain in the contact zone (as do e.g. hybrids of *Corvus corone* and *C. cornix*, (Saino, 1992)), and thus to meet individuals from each former allopatric patch less often than they meet other hybrids.

We model such partial secondary contact as follows. The model assumptions are those used for the sympatric state (in particular resource abundance and competition for resources), except that, at each birth event, the set of potential sexual partners of the individual chosen to reproduce is a randomly drawn fraction of the population of the opposite sex. For an individual from a given former allopatric patch, this fraction consists of individuals from the same former allopatric patch with probability 1, and of individuals from the other former allopatric patch with probability r ($0 \leq r < 1$) per individual. For a hybrid, this fraction consists of hybrids with probability 1, and of individuals from each former allopatric patch with probability r per individual. Note that such modelling of the window of partial secondary contact does not explicitly take into account the spatially-explicit modelling of a contact zone.

2.3 Numerical simulations

The stochastic model described above is simulated using a birth and death process in continuous time. We used the Gillespie (1977) algorithm. We pick the time until the next event from an exponential distribution with mean equal to $1/(\sum_{i=1}^{n(t)}(\beta(u_i)+d))$, i.e. the inverse of the total rate at which events occur. The occurring event is randomly chosen proportionally to the rate of each possible event (birth or death).

The weak trade-off case is analyzed using a fixed mating trait; the strong trade-off case is first analyzed using a fixed mating trait, then this trait is allowed to evolve. The model with a fixed mating trait is simulated by initializing the allele value of the L_α diploid loci of all individuals to the same value and by setting the mutation rate μ_α to 0.

We measure time in generations: the generation time is equal to one time unit of the simulation real time divided by the constant death rate d. Our numerical simulations use a high mutation rate, $\mu_u = 0.01$ (and $\mu_\alpha = 0.01$ when the mating trait is allowed to evolve), because this considerably speeds up the process we wish to study. We show in Appendix D that using a smaller mutation rate does not change the results, except in terms of time scales: the speed of trait evolution is expected to be proportional to the mutation rate. In order to minimise the underestimation of time scales, we used a low phenotypic variance of new mutants, $\sigma_u = 0.02$ (and $\sigma_\alpha = 0.02$ when the mating trait is allowed to evolve), when using a high mutation rate (the speed of trait evolution is also expected to be proportional to the phenotypic variance of new mutants).

All figures show either specific time series, or means over 50 replications of a simulation (or more replications when indicated as such). In the latter case, we present in the figures the 95% confidence intervals of the estimated means over the replicates.

3 Results

3.1 Weak trade-off case

Under a weak trade-off between the use of the two resources, we expect from the model definition that the mean ecological trait evolves to — and remains at — a generalist strategy in sympatry. In allopatry, the two subpopulations are expected to evolve to two different specialized strategies, i.e. allopatry is expected to generate diversity. We checked this expected behaviour of the model before analyzing the effect of landscape dynamics (not shown).

Secondary contact

At secondary contact, i.e. the transition from allopatry to sympatry, diversity generated in allopatry may be lost. Fig. 1 shows that when individuals that are specialized on different resources are not reproductively isolated (fixed mating trait $\alpha < 0.5$), diversity collapses immediately after secondary contact. Their offspring have indeed a generalist strategy: under a weak trade-off ($z = 0.4$ in Fig. 1), selection is stabilizing, so that generalists have a higher fitness than specialists. Intermediate types thus are selected for and rapidly invade the population. Positive assortative mating increases the frequency of extreme phenotypes which are selected against because they depart from the generalist strategy. Assortative mating is thus not expected to evolve at secondary contact under a weak trade-off (see Appendix D, Fig. D1 and Table D1, and e.g. Slatkin, 1979; Dieckmann & Doebeli, 1999; Schneider & Bürger, 2006). Some other mechanisms, not depending on mate choice but depending on the ecological trait could nevertheless lead to reproductive isolation in allopatry. Temporal isolation and pollinator isolation are such other mechanisms (Coyne & Orr, 2004).

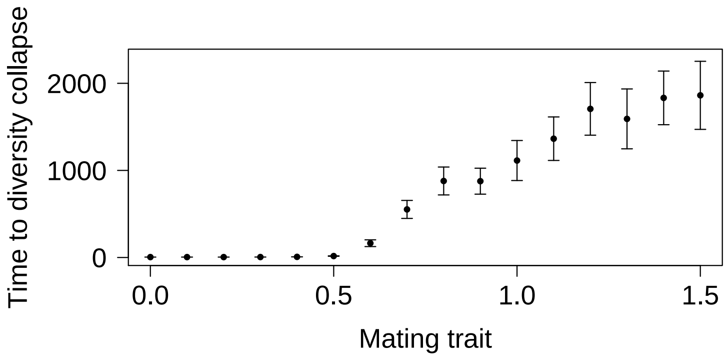

Figure 1: Mean time from the start of secondary contact to the loss of ecological diversity. We consider that diversity (generated by an allopatric phase of $T_a = 20,000$ generations) has collapsed when all individuals have the same ecological strategy (taking into account the phenotypic variance). The x-axis shows the fixed mating trait α. There is no window of partial secondary contact ($T_r = 0$). Whiskers represent the 95% confidence intervals of the estimated means over the simulation replicates. Other parameter values: $p = 0.5$, $h = 5$, $V = 35$ ($n(t) \approx 675$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 0.45$, $L_u = 6$, $\mu_u = 0.01$, $\sigma_u = 0.02$.

Next, we analyze the effect of secondary contact assuming that during the allopatric stage, one or several mechanisms lead to the appearance of pre-zygotic reproductive isolation (simulated by assuming a fixed, positive α_i). In this case, Fig. 1 (fixed $\alpha > 1$) shows that diversity in the ecological trait is nevertheless lost after some time. Indeed, the two differentiated species can ecologically coexist at secondary contact since they occupy two different ecological niches, but directional selection acts on their ecological traits, so that they converge towards the same generalist strategy. Typical evolutionary trajectories of the ecological trait shown in Appendix D (Fig. D2) illustrate that one of the two species almost always goes extinct before reaching the generalist strategy. When converging to the generalist strategy, the ecological niches of the two species become more similar. Because of stochasticity in the evolutionary trajectories of the pair of species, one of them reaches the generalist strategy before the other one. The generalist species is slightly better adapted than the other, which consequenlty goes extinct by competitive exclusion. In brief, the coexistence of two species is thus ecologically possible at secondary contact, but evolutionarily unsustainable.

The speed of diversity loss strongly depends on the asymmetry of the sizes of the subpopulations in allopatry (parameter p). At secondary contact, the more different their relative population sizes, the faster one of them goes extinct (Fig. 2). Moreover, the population which goes extinct is most of the time the smallest of the two subpopulations (see typical evolutionary trajectories in Appendix D, Fig. D2). Two reasons explain this result. First, the speed of evolution of a population to the generalist strategy is proportional to its abundance (everything else being equal). The smaller subpopulation thus converges slower to the generalist strategy than the larger one. The smallest subpopulation becomes more maladapted in comparison to the other one, which competitively excludes it more easily. The second reason is a by-product of the model construction: resource abundances in allopatry are defined so that the relative abundance of the two resources is more asymmetrical in the small patch than in the large patch (Eq. 4). Consequently, the level of specialization of the smaller subpopulation in allopatry is higher than that of the larger one. Thus, for the same reason, converging to the generalist strategy takes more time for the smaller subpopulation, which risks exclusion by the better adapted, larger subpopulation.

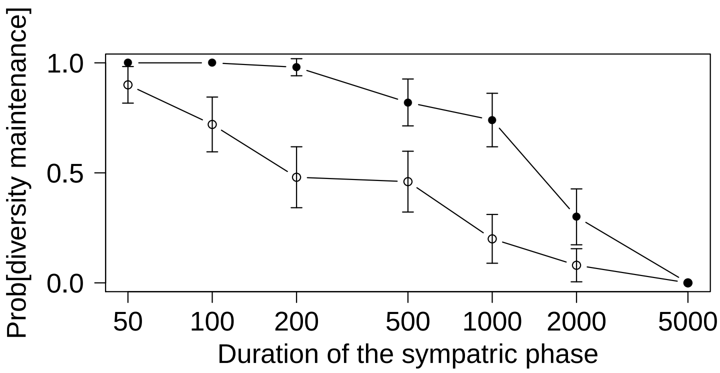

Figure 2: Coexistence probability of the two former allopatric subpopulations after a sympatric phase of fixed duration T_s, as function of this duration. Filled circles: $p = 0.5$, open circles: $p = 0.7$. Subpopulations are assumed to be reproductively isolated (fixed mating trait, $\alpha = 1$), and there is no window of partial secondary contact ($T_r = 0$). Whiskers represent the 95% confidence intervals of the estimated probabilities over the simulation replicates. Other parameter values: $h = 5$, $V = 50$ ($n(t) \approx 940$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 0.45$, $L_u = 6$, $\mu_u = 0.01$, $\sigma_u = 0.02$. Diversity is generated by an allopatric phase of $T_a = 20,000$ generations.

Sympatry-allopatry oscillations

Assuming full landscape dynamics, i.e. oscillations between sympatry and allopatry, the end of a secondary contact is the beginning of an allopatric phase. The latter makes the two subpopulations diverge. Therefore, if subpopulations still coexist at the end of sympatry, their persistence is guaranteed until the next secondary contact. Fig. 2 shows the probability that two species derived from former allopatric subpopulations still coexist after a sympatric phase of fixed duration. With the parameter values used in Fig. 2, the probability of diversity maintenance is higher than the probability of diversity loss for at least 1000 generations in sympatry. Consequently, landscape dynamics could maintain diversity if sympatric phases are short enough. The coexistence of two species, while evolutionarily unsustainable in a fixed, sympatric landscape, becomes possible in a dynamic landscape. Appendix D (Fig. D3) shows typical evolutionary trajectories where diversity is maintained in the long term thanks to landscape dynamics and typical evolutionary trajectories where it is not.

The characteristics of landscape dynamics allowing speciation and its maintenance depend on the parameters of the environment and of the population dynamics. When allopatric patches are more different in terms of their resource abundances (larger h), subpopulations are more specialized at secondary contact. Fig. 3 shows that sympatry can then last a longer time without diversity loss since the convergence to the generalist strategy takes longer. When the population size is small, the stochasticity of the evolutionary trajectory of the pair of species converging to the generalist strategy is high. One of the species is then likely to rapidly become significantly closer to the generalist strategy than the other which then becomes extinct. When population size is small, sympatry should thus be shortlived to avoid diversity loss (Fig. 3). The speed of trait evolution is expected to vary along with the strength of selection. Fig. 3 shows that for weaker selection, sympatry can accordingly last longer without diversity loss (see also Appendix D, Fig. D4). Note that our numerical results may underestimate the time scale at which the system maintains diversity since we use a high mutation rate on the ecological trait ($\mu_u = 0.01$). We have checked that mutation rates several orders smaller do not change our results, except with respect to absolute time scales (see Appendix D, Fig. D5).

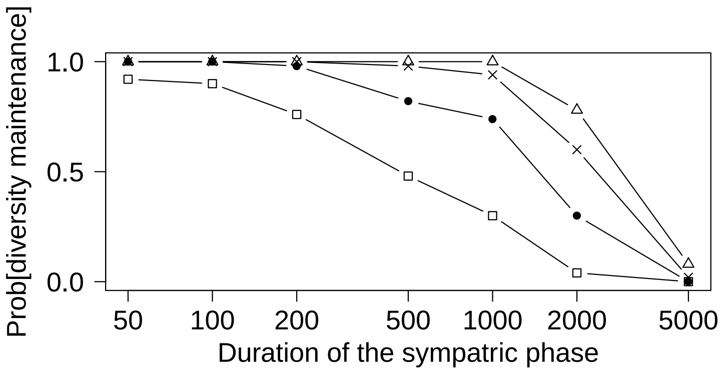

Figure 3: Replication of Fig. 2. Filled circles are the same as in Fig. 2. Other points correspond to simulations with the same parameter values, except $h = 10$ for crosses (more asymmetrical distributions of resources), $V = 25$ ($n(t) \approx 470$) for squares (smaller population size) and $z = 0.65$ for triangles (weaker selection). Confidence intervals are not plotted to ease reading; they are similar in magnitude to those in Fig. 2.

Under a weak trade-off, speciation is impossible in a static, sympatric landscape. Landscape dynamics generate and maintain speciation under four conditions. First, the allopatric phases must be long enough to allow subpopulations to diverge significantly. Second, reproductive isolation must have evolved in allopatry and must be maintained. Third, the sympatric phases must be shorter than the time needed for the species to co-evolve to the same generalist strategy. Last, allopatry must divide the population into two subpopulations whose abundances are of similar sizes. Ecological speciation and its maintenance in a dynamic landscape is thus possible, but it occurs under more restrictive conditions than purely allopatric speciation.

3.2 Strong trade-off case

Under a strong trade-off between the use of the two resources, we expect from the model definition that, in sympatry, the mean ecological trait evolves to a generalist strategy. In allopatry, the two subpopulations are expected to evolve to two different specialized strategies. We checked this expected behaviour of the model before analyzing the effect of landscape dynamics (not shown). In addition, sympatric evolutionary diversification is not expected to happen on the time scale we investigate: we checked this with simulations lasting 10^6 generations (see Appendix D, Fig. D6).

Secondary contact

Simulations with a fixed mating trait reveal a sharp transition in the maintenance of diversity at secondary contact: diversity generated in allopatry is maintained in the long term after secondary contact only when the mating trait of the population is above a threshold α_{lim} (Fig. 4, strong trade-off generated with $z = 1.6$). This threshold is the boundary between interbreeding and reproductive isolation of individuals specialized on different resources. Its value thus depends on the ecological divergence of individuals in allopatry: the higher the divergence at equilibrium, the lower the threshold (Fig. 4).

Hybrids produced at secondary contact by specialists have a generalist strategy. Under a strong trade-off, selection is disruptive: hybrids thus have a lower fitness than

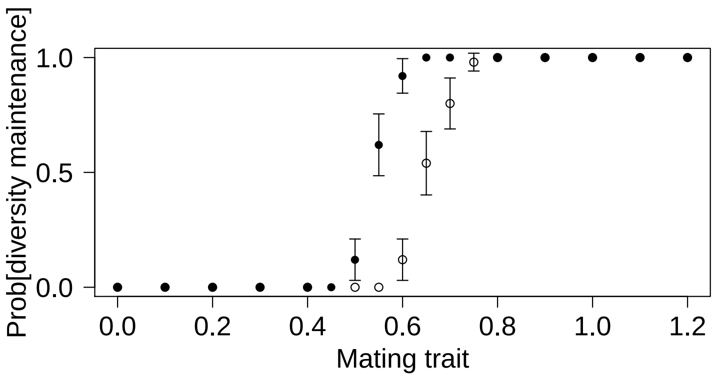

Figure 4: Probability that the two former allopatric subpopulations still coexist after a sympatric phase of fixed duration ($T_s = 10,000$) vs fixed mating trait α. There is no window of partial secondary contact ($T_r = 0$). Open circles: $h = 2$, resulting in an asymptotic divergence between allopatric subpopulations of specialists $\Delta \approx 0.46$. The threshold value of the mating trait (see text) is $\alpha_{\text{lim}} \approx 0.65$. The mating probability between differentiated individuals with a mating trait $\alpha_{\text{lim}} = 0.65$ is almost zero ($q \approx 0.00035$, Eq. 3). Filled circles: $h = 2.7$, resulting in $\Delta \approx 0.76$. The threshold is $\alpha_{\text{lim}} \approx 0.55$, which gives a mating probability $q \approx 0.00002$. Whiskers represent the 95% confidence intervals of the estimated probabilities over the simulation replicates. Other parameter values: $p = 0.5$, $V = 35$ ($n(t) \approx 675$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 1.6$, $L_u = 6$, $\mu_u = 0.01$, $\sigma_u = 0.02$. Diversity is generated by an allopatric phase of $T_a = 20,000$ generations (we checked by inspecting time series that 20,000 generations is enough to reach the maximal allopatric divergence).

specialists and should be selected against. In other words, allowing α to evolve, we expect reinforcement to increase α after secondary contact. However, assuming an instantaneous well mixed secondary contact (no window of partial secondary contact, $T_r = 0$), hybrids replace the population in only a few generations (< 10 generations) for a wide range of parameters (see Appendix D, Table D2). In addition, the mean assortative trait of the population remains very close to 0 before all specialists are replaced by generalist hybrids. Hybrids are only weakly disadvantaged: their birth rate is only a few percent lower than that of specialists, e.g. 10% with $z = 1.8$ and maximal ecological differentiation between specialists. Reinforcement is then weak because this hybrid disadvantage is too small compared to the speed of hybrid production: under random mating ($\alpha = 0$), in each generation, at least half the offspring of each specialist are hybrids.

Fig. 5 (right panel) shows that assuming a window of partial secondary contact increases the speciation probability. This is because during the window of partial secondary contact, the production of hybrids by specialists is limited, so that reinforcement has enough time to act, then increasing the mating trait of the population. The longer the duration of the window of partial secondary contact, the longer reinforcement acts, and the higher the mating trait of the population, until it levels off for long windows of partial secondary contact (Fig. 5, left panel). When the mating trait reaches a higher value than the threshold α_{lim}, speciation is successful, otherwise it is not. After one secondary contact, the probability of successful speciation remains rather small (< 0.2, Fig. 5, right panel). As long as a hybrid population persists, it can still grow and replace the population of specialists: the production of generalist hybrids by specialists is reduced, but the production of generalists by hybrids is not. Consequently, if assortative mating does not evolve on a short time scale at secondary contact, the hybrid population is likely to replace the population of specialists before the end of the window of partial secondary contact. Reinforcement is then no longer efficient and speciation is likely to fail. As a result, the probability of speciation remains small, and increasing the duration of partial secondary contact to very high (unrealistic) values does not make speciation more likely (Fig. 5, right panel). Note that the probability of speciation depends on the strength of selection at secondary contact: when disruptive selection is weak, speciation never occurs, and the stronger selection, the higher the probability of speciation (Appendix D, Fig. D7).

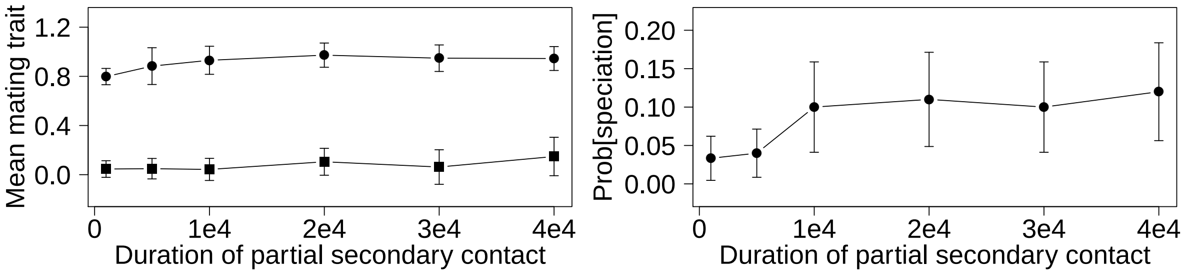

Figure 5: Mean assortative trait in simulations leading to speciation after secondary contact (left panel, circles), mean assortative trait in simulations where speciation failed (left panel, squares) and probability of speciation (right panel). The x-axis shows the duration of the partial secondary contact phase (T_r). The success or failure of speciation is assessed 10,000 generations after the end of the window of partial secondary ($T_s = T_r + 10,000$). Whiskers represent the 95% confidence intervals of the estimated means and probabilities over the simulation replicates. Other parameter values: $p = 0.5$, $h = 2$, $V = 35$ ($n(t) \approx 675$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 1.6$, $L_u = L_\alpha = 6$, $\mu_u = \mu_\alpha = 0.01$, $\sigma_u = \sigma_\alpha = 0.02$, $r = 0.005$. Diversity is generated by an allopatric phase of $T_a = 20,000$ generations. With these parameter values, the threshold value of the mating trait is $\alpha_{\lim} \approx 0.65$ (Fig. 4). Points for $T_r = 1,000$ and $T_r = 5,000$ were computed over 150 simulation replications, other points were computed over 100 simulation replications.

Sympatry-allopatry oscillations

Despite the impediments to speciation after one secondary contact, persistent ecological speciation is a likely outcome of recurrent landscape dynamics: Fig. 6 (right panels) shows that the probability of speciation after six allopatry-sympatry oscillations is higher than 0.45 (vs 0.2 after one oscillation). At each secondary contact, positive assortative mating is selected. Assuming a negligible cost to assortativeness as we do here, there is neither selection for nor against assortative mating during allopatric phases. After enough allopatry-sympatry oscillation, assortative mating is thus likely to be higher than the threshold $\alpha_{\lim}$ allowing successful speciation. In other words, oscillation between allopatry and sympatry allows several reinforcement "shots", increasing the likelihood of speciation. Note that the likelihood of speciation is determined by the total duration of reinforcement, which is not equivalent to the total duration of partial secondary contact. As explained above, generalist hybrids can replace the population of specialists before the end of a window of partial secondary contact, stopping reinforcement. Consequently, many short windows of partial secondary contact due to allopatry-sympatry oscillations lead more efficiently to speciation than a few long windows of partial secondary contact (Fig. 6, top panels versus bottom panels). We have checked that using smaller mutation rates than the mutation rate used in Fig. 6 ($\mu_u = \mu_a = 0.01$) does not change our results, except in terms of absolute time scales (see Appendix D, Fig. D8).

Once ecological differentiation and speciation have occurred, further landscape changes affect populations but not the total level of diversity (see typical evolutionary trajectory in Appendix D, Fig. D9). In sympatry, disruptive selection maintains ecological divergence and a high value of the mating trait. In allopatry, both species can coexist in each patch, but one species may go extinct. The species specialized on the less abundant

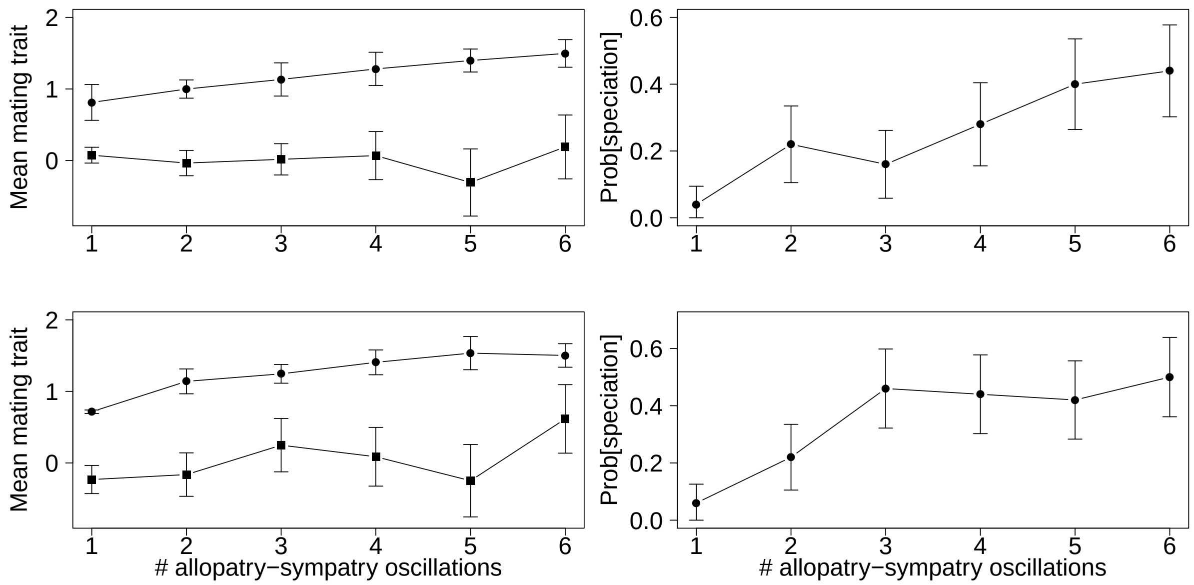

Figure 6: Replications of Fig. 5 with the number of allopatry-sympatry oscillations on the x-axis. Top panels: short windows of partial secondary contact ($T_r = 1,000$). Bottom panels: long windows of partial secondary contact ($T_r = 20,000$). Other parameter values: identical to Fig. 5, resulting at a threshold value of the mating trait is $\alpha_{\text{lim}} \approx 0.65$ (Fig. 4). After only two allopatry-sympatry oscillations with short windows of partial secondary contact (thus, the total duration of partial secondary contact is 2,000 generations), the probability of speciation is 0.22. This value is already higher than the probability of speciation after a single window of partial secondary contact of 20,000 generations (probability of speciation in this case: 0.06).

resource has indeed a small population size, so that it may become extinct by demographic stochasticity. Nevertheless, looking at the whole metapopulation, both species persist.

In a static, allopatric landscape, a population can become ecologically differentiated, but pre-zygotic reproductive isolation between geographically isolated subpopulations may not be selected for. In a static, sympatric landscape, a population may be stuck at a fitness minimum because of genetic constraints. An equilibrium state with two specialist species exists, but it is unattainable. In a dynamic landscape, a first landscape change allows such a population to diverge ecologically. A second landscape change allows the evolution of reproductive isolation. Eventually, the two species equilibrium may be attained, and this is more likely after several landscape changes which increase assortative mating sequentially. In conclusion, under a strong trade-off landscape dynamics can facilitate ecological speciation, a state which may be unattainable in a static, allopatric or sympatric, landscape.

4 Discussion

Under stabilizing selection (resulting in our model from a weak trade-off between the use of the two resources), speciation can occur in allopatry, but the coexistence of the two new species is evolutionary unsustainable in a sympatric landscape (i.e. after secondary contact). We showed that landscape dynamics (allopatry-sympatry oscillations) may facilitate their long-term coexistence. In particular, landscape dynamics preserve allopatric speciation given certain characteristic time scales (long allopatry, short sympatry). Also, the maintenance of speciation is facilitated by similarly sized subpopulations upon secondary contact. Under disruptive selection (resulting from a strong trade-off between the use of the two resources), landscape dynamics generate diversity more readily than a fixed, sympatric landscape can: a shift from sympatry to allopatry stops gene flow, allowing ecological divergence that may be impossible in sympatry due to genetic constraints. When a mechanism allowing extrinsic ecological reinforcement to occur at secondary contact exists (e.g. a temporarily reduced meeting probability between ecologically differentiated individuals), speciation is also more likely than in a static, allopatric landscape. Landscape dynamics facilitate the evolution of reproductive isolation between ecologically differentiated subpopulations by offering many opportunities (i.e. at each secondary contact) for reinforcement to be successful.

Standard, verbal scenarios of speciation usually hypothesize that speciation is initiated in allopatry and completed in sympatry, or conversely (Rundle & Nosil, 2005). Accordingly, different authors have pointed out the necessity to take into account the temporal dimension of speciation in models because of likely shifts in the geographical arrangement during the process (e.g. Schluter, 2001; Rundle & Nosil, 2005; Bolnick & Fitzpatrick, 2007; Fitzpatrick et al., 2008). Despite these claims and ample empirical evidence supporting them (e.g. Taylor & McPhail, 2000; Feder et al., 2003; Baack, 2004; Stuessy et al., 2004; Jordal et al., 2006; Xie et al., 2007; Grant & Grant, 2009; Rundell & Price, 2009), almost all models of speciation focus on a single geographical arrangement. Initial ecological and evolutionary conditions are assumed, as well as the evolution of the population in the considered geographical arrangement. Our results show how constraining these assumptions are: past and future geographical arrangements are likely to considerably alter the likelihood of speciation, as well as its long-term maintenance.

Given the way we derived the resource distributions (Appendix B), our model implicitely assumes that individuals are not limited in their intrinsic migration capabilities. Allopatry corresponds to an extrinsic constraint geographically isolating two patches holding two different principal resources. Sympatry corresponds to two patches with unlimited migration between them, justifying the assumption of two resources of the same abundance. Migration is however a life-history trait subject to evolution (e.g. Roff, 1990). We could thus have considered a model with oscillations between allopatry and parapatry (with two patches holding two different principal resources) and evolving migration. In this case, under stabilizing selection (weak trade-off case), migration may be selected against at secondary contact because, after specialisation in allopatry, migrants are poorly adapted in the patch they reach (Maynard Smith, 1966; Balkau & Feldman, 1973). This would result in permanent (intrinsic) geographical isolation, allowing both specialists to persist in the long term. In addition, if reproductive isolation is not yet complete at secondary contact, a sufficiently low migration rate between subpopulations may induce their genetic divergence and possibly speciation (e.g. Felsenstein, 1981; Kirkpatrick & Ravigné, 2002; Gavrilets, 2004). Still considering stabilizing selection, specialisation may be selected against if migration remains high (Maynard Smith, 1966; Balkau & Feldman, 1973). Weakly specialised individuals should not be too poorly adapted in either habitat to persist. These two alternative strategies (low dispersal, high specialisation and high dispersal, low specialisation) might also coexist, and even appear by evolutionary branching (Mathias et al., 2001). When selection is disruptive in each patch (strong trade-off case), the two different specialists are selected for in each patch. The results assuming allopatry-parapatry oscillations would thus be the same as those reported in the Results section assuming allopatry-sympatry oscillations.

4.1 Landscape dynamics and speciation under stabilizing selection

Under a weak trade-off, diversity can be maintained at a secondary contact if reproductive isolation has evolved in allopatry and is maintained (i.e. if allopatric speciation has occurred). In our model with an evolving mating trait, reproductive isolation is equivalent to assortative mating between ecologically differentiated individuals. Under a weak trade-off, assortative mating is selected neither in allopatry nor at secondary contact. Because our model does not allow for the evolution of assortative mating based on an ecological trait, we have assumed that reproductive isolation evolves during allopatric stages in order to be able to study the consequences of secondary contact. Making this assumption does not weaken our results because some other mechanisms, not included in our model, could lead to pre-zygotic reproductive isolation in allopatry or at secondary contact. Assuming a fixed positive mating trait at secondary contact allows for such mechanisms. For our conclusions to remain valid, such mechanisms must allow the evolution of strong pre-zygotic reproductive isolation on a short time scale and must satisfy Eq. (3) which describes a one-allele mechanism (mating probabilities directly depend on similarity on an ecological trait). These mechanisms may be e.g. temporal or pollinator reproductive isolation (Coyne & Orr, 2004). Eq. (3) may also be used for two-alleles mechanisms (mating probabilities depend on similarity on a marker trait linked to the ecological trait) when the maker trait is not genetically coded, but determined by parental imprinting (culturally inherited). In this case, recombination does indeed not break the linkage between the ecological trait and the marker trait (note that other mechanisms, such as drift of the marker trait, may nevertheless break the linkage in the long term; Eq. (3) may thus be satisfied only on a short time scale). For example, in Darwin's finches, each ecotype sings a specific song, and mating is mainly based on similarity on song which is culturally inherited (Grant & Grant, 1996). Founder effects on song when populations become allopatric or at secondary contact may generate strong pre-zygotic reproductive isolation. An example in the medium ground finches on the Daphne Major island (Galápagos islands) was recently reported by Grant & Grant (2009): in 1981, an immigrant finch with an unusually large beak (ecological trait) and an unusual song (marker trait) arrived on the island; only seven generations after this founder event, the descendents of the immigrant were strongly reproductively isolated from the resident medium ground finches who have a smaller beak and sing a different song.

Assuming a weak trade-off, we showed that the coexistence of two ecologically differentiated species is ecologically possible at secondary contact, but evolutionarily unsustainable. Our results highlight the conditions necessary to maintain diversity in sympatry for a long time: large allopatric divergence, weak stabilizing selection, little genetic drift. Our model assumes that the abundances of the two resources are the same (or at least similar) in sympatry; this assumption facilitates the persistence of species at secondary contact. Without this assumption, the population would evolve to a specialist strategy despite being in sympatry. Consequently, the sets of strategies allowing for an ecological coexistence of the two species would not be symmetrical with respect to the singular strategy in sympatry. Extinction of one of the species in sympatry would thus be more rapid.

Some other model studies have concluded that after an allopatric speciation event, species can ecologically coexist at secondary contact (i.e. no competitive exclusion), but that their coexistence is evolutionarily unsustainable. For example, Mougi & Nishimura (2007) showed that a trade-off on life-history traits not directly related to competition can lead to evolutionarily unsustainable coexistence. As in our model, this result is strengthened by the fact that one subpopulation evolving faster than another drives the latter to rapid extinction. They conclude that evolutionary coexistence is unlikely to occur. We agree with this conclusion, assuming a static, sympatric landscape (and stabilizing selection). As we previously argued, however, landscape dynamics may be common and long-term coexistence could thus be more likely than suggested by previous models.

4.2 Landscape dynamics and speciation under disruptive selection

Under disruptive selection in sympatry (strong trade-off case), we showed that landscape dynamics allow ecological divergence, i.e. allow the population to escape from a fitness minimum. Populations may find other solutions to escape from a fitness minimum (Rueffler et al., 2006), including: evolutionary branching (Geritz et al., 1998; Dieckmann & Doebeli, 1999), the evolution of sexual dimorphism (Bolnick & Doebeli, 2003; van Dooren et al., 2004), the evolution of genetic polymorphism (Kisdi & Geritz, 1999; van Doorn & Dieckmann, 2006; Claessen et al., 2008), the evolution of dominance which allows the emergence of specialists (van Dooren, 1999; Peischl & Bürger, 2008; Durinx & van Dooren, 2009; Peischl & Schneider, 2010), and the migration of a reproductively isolated population leading to character displacement (Aguilée et al., 2011).

The scenario of ecological speciation we proposed differs from adaptive speciation (in which speciation is an adaptative response to frequency-dependent biological interactions generating disruptive selection (Dieckmann et al., 2004)): our scenario of speciation indeed requires both allopatric and sympatric phases whereas adaptive speciation necessarily occurs in sympatry only. In our scenario, a dynamic landscape allows an escape from a fitness minimum, whereas a static landscape would have fixed the population at the minimum. This situation can happen mainly for two reasons. First, as we have assumed, a population can stay at a fitness minimum without being able to split into two branches (as with evolutionary branching) because of genetic constraints (free recombination and polygenic inheritance with small allelic effects) (Waxman & Gavrilets, 2005). Second, a population can be locked on a fitness minimum because of small population size (Claessen et al., 2007, 2008; Johansson et al., 2010). Evolutionary branching can indeed be strongly delayed by demographic stochasticity which affects small populations with sizes similar to those occurring in our simulations (usually ≤ 1000 individuals). By relaxing the genetic constraints and with increased population sizes, sympatric evolutionary branching would become possible. Because, once speciation has occurred, landscape dynamics have no effect on the total level of diversity, the effect of landscape dynamics would then be undetectable (unless the level of ecological differentiation is not the same in sympatry and allopatry, which is not the case in our model).

Two of our model assumptions facilitate the evolution of assortative mating. First, we assumed that the mating trait evolves via a one-allele mechanism, i.e. the assortative mating level is directly related to the ecological trait. Such an ecological trait is sometimes called a "magic trait" (e.g. Gavrilets, 2004): this hypothesis indeed facilitates the evolution of assortative mating (Felsenstein, 1981; Dieckmann & Doebeli, 1999; Servedio, 2000). This assumption has long been debated in the literature and seems now accepted as possible (e.g. Kirkpatrick & Ravigné, 2002; Servedio et al., 2011). Moreover, some authors (Schneider & Bürger, 2006; Kopp & Hermisson, 2008) demonstrated that the evolution of positive assortative mating is difficult with a high cost of being choosy. Because we consider only a small cost to (dis-)assortative mating, we probably overestimate the ease of its evolution compared to natural populations.

We have focused our analysis of the evolution of the mating trait on phases of disruptive selection on the ecological trait. The mating trait may also evolve during phases of directional selection on the ecological trait. Our focus is relevant because in our model, selection on the ecological trait is directional from a landscape change to the moment the population reaches its new singular strategy, and the mating trait changes very weakly during these phases (Figure D9). Further analysis would nevertheless be helpful to precisely investigate selective pressures on the mating trait when selection on the ecological trait is directional.

We have shown that reinforcement is inefficient when assuming a well mixed fusion of the allopatric subpopulations at secondary contact. Due to the homogenizing effect of gene flow, full sympatry is indeed known as the environment most hostile to reinforcement (Felsenstein, 1981; Liou & Price, 1994; Servedio & Kirkpatrick, 1997; Kirkpatrick, 2000; Kirkpatrick & Ravigné, 2002). A mechanism allowing reinforcement to be efficient at secondary contact is thus necessary. Here, we propose a window of partial secondary contact, i.e. a temporary reduction of the meeting probability between specialist individuals. We argue that any other assumption generating reinforcement at secondary contacts would have led to the same results. The probability of speciation is ultimately determined by the total time during which reinforcement is efficient. Because reinforcement may fail to lead to speciation even under suitable initial conditions (in particular a large ecological divergence at secondary contact), landscape dynamics facilitate speciation by repetitively generating these suitable initial conditions. Consequently, for a similar duration of possible reinforcement, allopatry-sympatry oscillations lead more easily to speciation than a one-off secondary contact. Note also that, when reinforcement is efficient because of a reduced introgression rate, we found an optimal introgression rate (see Appendix D, Fig. D10). Kirkpatrick (2001) who proposed another model with reinforcement on an ecological basis, also found that reinforcement is possible only under this restrictive assumption (despite important differences with our model: Kirkpatrick's model assumes e.g. haploid individuals, a fixed phenotypic variance and that hybrids mate with only one of the ancestral subpopulations).

4.3 Empirical data on speciation under landscape dynamics

An array of empirical studies support the outcomes of our model. We first discuss examples where allopatry first generates diversity but then sympatry causes its collapse. Next we show examples where allopatry generates diversity and sympatry maintains part of it, followed by cases resulting in complete and persistent speciation. Finally, we discuss possible signatures of landscape dynamics in present day empirical data.

A study by Gow et al. (2006) on three-spined sticklebacks (*Gasterosteus aculeatus*) in Paxton Lake (Texada Island, Canada) showed oscillations of diversity correlated to landscape dynamics. Due to the adaptation to different habitats within the same lake, sticklebacks were differentiated into limnetic and benthic morphs and were geographically isolated in these habitats until the late 1950s. Then, human disturbance reduced the differences between the habitats of the lake. This landscape change from an allopatric-like state to a sympatric-like state increased the hybridization rate, despite hybrids having a reduced fitness, leading to a strong diversity reduction. Sticklebacks were indeed not reproductively isolated by assortative mating. Disturbance stopped in the 1970s, environmental conditions were then close to initial ones, i.e. differentiated habitats were restored, and sticklebacks have differentiated again: a transition from sympatry to allopatry regenerated the lost diversity. This empirical example illustrates a feature of our model: allopatry easily generates diversity, but in the absence of previously evolved reproductive isolation, the maintenance of incipient species at secondary contact is far from certain, even under disruptive selection. Seehausen et al. (2008a) reviewed other examples of diversity reduction due to hybridization. This is usually associated with a very fast loss of environmental heterogeneity, i.e. secondary contact without reduced introgression. Empirical data reveal that this process occurs very quickly. Accordingly, with the removal of reproductive isolation, our results predict diversity collapse in a few generations at such a secondary contact for cases of both stabilizing and disruptive selection.

Esselstyn et al. (2009) analyzed the effect of landscape dynamics on Southeast Asian shrews (*Crocidura*). During the Miocene-Pliocene, volcanic uplift produced many new islands in Southeast Asia, and during the Pleistocene, repeated sea level fluctuations have temporarily connected islands. These landscape dynamics have constantly produced new available ecological niches, but the present diversity is less than the number of ecological niches that have probably been produced. In this example, allopatric phases are indeed likely to have been long enough (on the order of thousands of generations) to produce strongly differentiated populations. However, sympatric phases are likely to have been equally long. Our results show that two populations that come into sympatry are expected to persist on such a long time scale only under disruptive selection (and assuming that reproductive isolation has evolved in allopatry; without reproductive isolation, coexistence is impossible regardless of the shape of the fitness landscape). Given the possible high number of secondary contacts and the fact that stabilizing selection may also have been at work, it is unlikely that all populations that have differentiated in allopatry still exist nowadays. Data analyses of Esselstyn et al. (2009) reached this same conclusion. The effect of similar geological and climatic processes (volcanic events and sea level fluctuations) have been analyzed by Cook (2008) in the Atlantic Madeiran archipelago. She reached similar conclusions: the high diversity of Madeiran land snails is likely to result from numerous geological and climatic changes, mainly because of many allopatric divergence opportunities.

Young et al. (2009) analyzed the diversity of mbuna cichlid fishes in lake Malawi in relation to landscape dynamics: water level fluctuations repeatedly divided and reconnected entire communities during some hundreds of years. Cichlid fishes usually mate assortatively, according to their body colors, which is correlated to their ecological behaviour (Seehausen & van Alphen, 1998; Seehausen et al., 2008b; Egger et al., 2010). Based on the analysis of a matrix of pair-wise interaction coefficients for native and transplanted mbuna cichlid species, Young et al. (2009) suggested that the total diversity increased by community splitting, facilitating allopatric divergence, and that the local diversity also increased, at secondary contacts, by bringing reproductively isolated differentiated fishes back together. In this example, sympatric phases are likely to have lasted only a few dozens of generations and, assuming high enough assortative mating, our results show that coexistence in sympatry may indeed be possible on this time scale under both stabilizing and disruptive selection. Young et al. (2009) conclude that landscape dynamics may be the main mechanism responsible for the adaptive radiation of mbuna cichlid fishes of lake Malawi, a radiation which produced hundreds of species.

The different outcomes of our model depend on specific conditions, in particular the time scales of the landscape dynamics. In order to quantitatively test theoretical predictions of models featuring landscape dynamics, it would be valuable to develop methods allowing us to detect historical landscape dynamics from present day empirical data. We give two examples of signatures of landscape dynamics which may be found in data. First, past allopatric phases should make coalescent gene trees strongly deviate from expected unstructured coalescent trees. In particular, as computed in Aguilée et al. (2009), the mean coalescence time of two uniformly sampled neutral genes in a sympatric population can take significantly different values, depending on whether one assumes a past allopatric phase or not. Assuming several past fusions and fissions of populations, these coalescence times are expected to reach unusually high values (see also Jesus et al., 2006). The characterization of the whole shape of the gene tree with landscape dynamics is a particularly challenging task. Second, landscape dynamics could result in different genealogies for different genes, because different genes would coalesce at different sympatric phases, possibly generating incomplete lineage sorting. Quantifying the effect of given landscape dynamics models on these discrepancies would allow us to infer past hybridization periods as well as allopatric phases from genetic data.

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Appendices

A Derivation of resource density (Eq. 2)

For simplicity, let us assume that the densities of resources 1 and 2, $f_1(t)$ and $f_2(t)$ respectively, follow semi-chemostat dynamics. Then, the consumer-resource dynamics is described by

$$\begin{cases} \dfrac{\mathrm{d}n(t)}{\mathrm{d}t} = \sum_{i=1}^{n(t)} \left[f_1(t)u_i^z + f_2(t)(1-u_i)^z - d\right] \\ \dfrac{\mathrm{d}f_1(t)}{\mathrm{d}t} = \delta_1[K_1 - f_1(t)] - \dfrac{f_1(t)}{v}\sum_{i=1}^{n(t)} u_i^z \\ \dfrac{\mathrm{d}f_2(t)}{\mathrm{d}t} = \delta_2[K_2 - f_2(t)] - \dfrac{f_2(t)}{v}\sum_{i=1}^{n(t)} (1-u_i)^z \end{cases} . \tag{A1}$$

The consumer population size is $n(t)$, u_i is the ecological strategy of individual i, z is the trade-off parameter and d is the constant per-capita death rate. K_1 (resp. K_2) is the maximum density of resource 1 (resp. 2) and δ_1 (resp. δ_2) is the dilution rate of resource 1 (resp. 2). The renewal rate of resource j is thus $\delta_j K_j$. Parameter v is a scaling parameter setting the per-individual consumption rate relative to the maximum resource densities.

Assuming that resource dynamics are fast compared to consumer dynamics ($\delta_j \gg d$), resource density can be considered to be in quasi-steady state with the current consumer population. This quasi-steady state is given by the solutions F_1 and F_2 to the equations $\mathrm{d}f_1(t)/\mathrm{d}t = 0$ and $\mathrm{d}f_2(t)/\mathrm{d}t = 0$ respectively (Claessen et al., 2007):

$$\begin{cases} F_1 = K_1/[1 + \frac{1}{\delta_1 v}\sum_{i=1}^{n(t)} u_i^z] \\ F_2 = K_2/[1 + \frac{1}{\delta_2 v}\sum_{i=1}^{n(t)} (1-u_i)^z] \end{cases} .$$

Assuming that the dilution rates are constant and equal to 1 ($\delta_1 = \delta_2 = 1$), we can redefine the scaling parameter as $V = \delta_1 v = \delta_2 v$, which gives Eq. 2.

B Derivation of the maximum densities of resources in allopatry (Eq. 4)

First, assume that individuals are uniformly distributed along a spatial continuum between spatial locations 0 and 1. Then, assume that the maximal abundance of each resource follows a linear gradient along this continuum (Fig. B1, top panels). Also assume that an unbridgeable geographical barrier appears at location p as the landscape switches from sympatry to allopatry ($0 < p < 1$). Now, simplify space considering that all individuals and resources in the same range (i.e. either on the left or on the right of spatial location p) constitute a homogeneous patch. The resource amount in each patch can then be taken as the average of the resource gradient on this patch (Fig. B1, bottom panels). The parameter p is here defined as a spatial location. This spatial location also sets the fraction of the total amount of resources available in each allopatric patch. This parameter thus controls the relative sizes of the two allopatric consumer subpopulations.

Instead of writing the resource amounts in each patch as a function of the slope and intercept of the underlying gradients, we can write them as a function of an asymmetry parameter h defined such that $K_1^{(1)} = hK_1^{(2)}$ and $K_2^{(2)} = hK_2^{(1)}$, which gives Eq. 4.

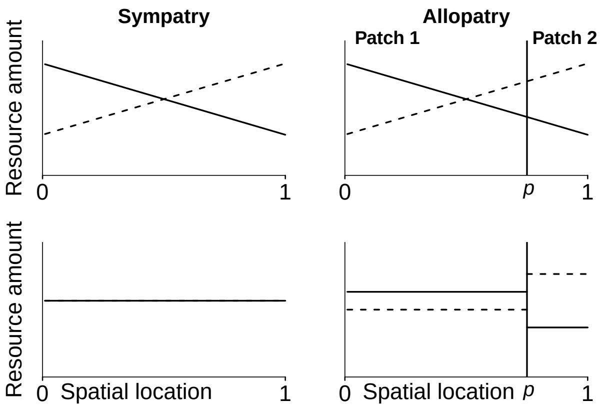

Figure B1: Solid (resp. dashed) lines indicate the amount of resource 1 (resp. resource 2) as a function of the spatial location. Top panels show the resources gradients. Bottom panels show their simplification. Left (resp. right) panels indicate the situation in sympatry (resp. allopatry). Fragmentation occurs at spatial location p.

C Adaptive dynamics of the model

We use a standard method for model analysis in adaptive dynamics: we first make predictions with a simplified, unrealistic but mathematically tractable model (described in this appendix), then we test them with more realistic assumptions using simulations (described in the main text). For details about the adaptive dynamics method, we refer the reader to Metz et al. (1996) and Geritz et al. (1998).

Following Claessen et al. (2007), we can approximate the stochastic ecological model described in the main text by a deterministic one assuming a monomorphic, large population, i.e. all individuals have the same ecological trait u and $V \to \infty$. The density of individuals is $N(t) = n(t)/V$. Then, the consumer-resource dynamics described by Eq. A1 become

$$\begin{cases} \dfrac{\mathrm{d}N(t)}{\mathrm{d}t} = (f_1(t)u^z + f_2(t)(1-u)^z - d)N(t) \\ \dfrac{\mathrm{d}f_1(t)}{\mathrm{d}t} = \delta_1(K_1 - f_1(t)) - f_1(t)N(t)u^z \\ \dfrac{\mathrm{d}f_2(t)}{\mathrm{d}t} = \delta_2(K_2 - f_2(t)) - f_2(t)N(t)(1-u)^z \end{cases} . \tag{C1}$$

Let us assume a rare mutant with an ecological trait u' in the resident population, supposed to be at its ecological equilibrium. The (per-capita) initial growth rate of this mutant $s(u', u)$, called the invasion fitness, is

$$s(u', u) = \frac{1}{N'(t)} \frac{\mathrm{d}N'(t)}{\mathrm{d}t} = f_1(t)u'^z + f_2(t)(1-u')^z - d$$

where $f_1(t)$ and $f_2(t)$ are defined by Eq. C1 (i.e. the impact of the mutant on resources abundance is negligible). The adaptive dynamics framework predicts that the mutant invades the resident population if and only if its invasion fitness is positive, i.e. $s(u', u) > 0$ (Metz et al., 1996).

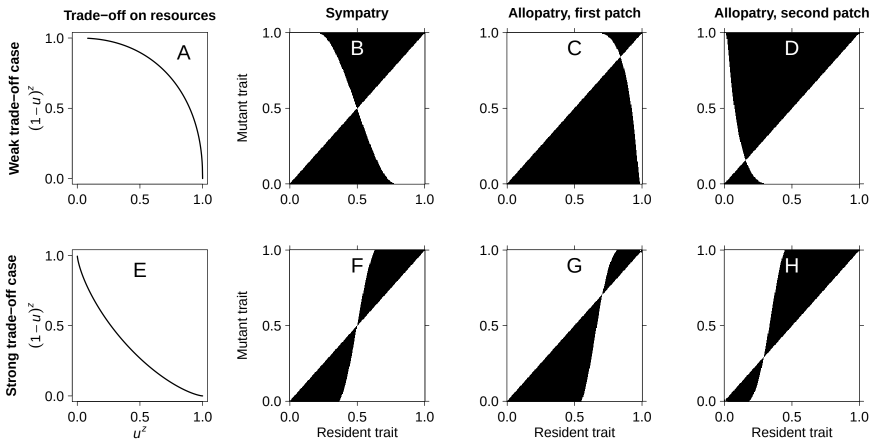

Figure C1: Panels A and E: power-law trade-off between the use of the two resources (Eq. 1) in a monomorphic population with a trait u. Top panels correspond to a weak trade-off ($z = 0.45$), bottom panels illustrate a strong trade-off ($z = 1.4$). Panels B-D and F-H: pairwise-invasibility plots (PIPs). White (resp. black) areas indicate positive (resp. negative) invasion fitness of a rare mutant in a resident population at its ecological equilibrium. Panels B and F show PIPs for one undivided population (landscape in sympatric state), panels C and G show PIPs for the subpopulation in the first patch in allopatry, and panels D and H show PIPs for the subpopulation in the second patch in allopatry. In the case of a weak (resp. strong) trade-off, singular points are CSS (resp. EBP). Singular points in sympatry correspond to a generalist strategy ($u^* = 0.5$) for both weak and strong trade-off cases. In allopatry, the nature of singular points is not changed, but they correspond to opposite specialist strategies in the two patches ($u^{*(1)} > 0.5$ and $u^{*(2)} < 0.5$). Other parameter values: $p = 0.5$, $V = 20$, $K_1 = K_2 = 1$, $d = 0.1$, $\delta_1 = \delta_2 = 1$, top panels: $h = 5$, bottom panels: $h = 2$.

Based on this rule, pairwise-invasibility plots (PIPs, Metz et al., 1996) allow us to predict the evolutionary trajectory of a population. A PIP shows the sign of the invasion fitness of a rare mutant in a resident population at its ecological equilibrium. The x-axis is the trait of the resident population, the y-axis is the trait of a rare mutant (Fig. C1). For a given resident population trait, each possible mutant (i.e. along a vertical line) has either a positive invasion fitness, and may invade the population, or a negative invasion fitness, and will go extinct. An isolated, large asexual population is assumed to evolve by the successive substitutions of the monomorphic resident population by slightly different mutants with positive fitness.

Singular strategies are points where the mutant invasion gradient vanishes. The geometry of PIPs allows us to distinguish between two kinds of singular points that are convergent stable. First, "continuously stable strategies" (CSSs): the invasion fitness of all mutants in a resident population at a CSS is negative, so that they cannot invade the resident population. In other words, stabilizing selection is at work. Singular points are CSSs when the trade-off is weak, i.e. when $0 < z < 1$ (Fig. C1, top panels). Second, "evolutionary branching points" (EBPs): the invasion fitness of all mutants in a resident population at an EBP is positive, so that they all can invade the population. The population then experiences disruptive selection. Singular points are EBPs when the trade-off is strong, i.e. when $z > 1$ (Fig. C1, bottom panels). At an EBP, an isolated large asexual population is expected to split into two subpopulations specialized on each of the two resources, a phenomenon called "evolutionary branching". As explained in the main text, although possible with its deterministic approximation, this mechanism of sympatric evolutionary branching is unlikely with the stochastic model we used in simulations.

D Additional results and illustrations

Weak trade-off case

Under a weak trade-off, assortative mating is expected to be selected neither in allopatry nor at secondary contact (e.g. Slatkin, 1979; Dieckmann & Doebeli, 1999; Schneider & Bürger, 2006). Positive assortative mating indeed increases the frequency of extreme phenotypes departing from the singular strategy reached by the population after a landscape change (generalist strategy in sympatry, specialized strategy in allopatry). Because selection is stabilizing at the singular strategy, such extreme phenotypes are selected against. Figure D1 shows a typical evolutionary trajectory of the ecological and mating traits when the mating trait is allowed to evolve: the mating trait mainly drifts over time, and at secondary contact, former allopatric subpopulations are not reproductively isolated by assortative mating so that diversity is not maintained. We observed a pattern consistent with drift of the mating trait in almost all the simulation replications we checked. For different parameter values combinations, Table D1 shows that the mating trait remains on average close to 0 (random mating) after one allopatric phase followed by secondary contact, and that reproductive isolation due to assortative mating evolves neither in allopatry nor at secondary contact.

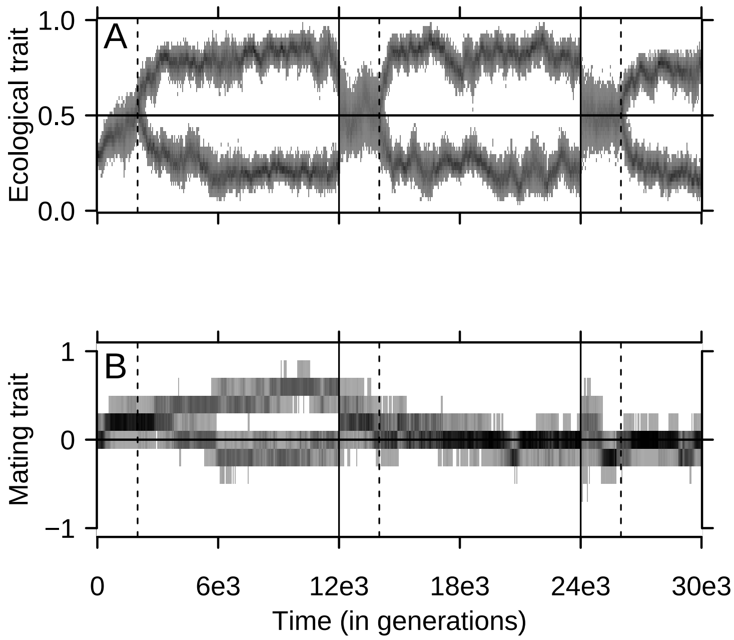

Figure D1: Typical evolutionary trajectories of the ecological trait (panel A) and of the mating trait of the population (panel B) over time under a weak trade-off when the mating trait is allowed to evolve. Population density is indicated by the level of gray. Vertical dashed lines indicate shifts of the landscape from sympatry to allopatry, vertical solid lines indicate shifts from allopatry to sympatry (without window of partial secondary contact, $T_r = 0$). Parameter values: $p = 0.5$, $h = 5$, $V = 50$ ($n(t) \approx 940$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 0.45$, $L_u = 6$, $\mu_u = \mu_\alpha = 0.01$, $\sigma_u = \sigma_\alpha = 0.02$, $T_a = 10,000$, $T_s = 2,000$.

Next, the weak trade-off case is analyzed assuming that some other mechanisms than assortative mating have generated reproductive isolation in allopatry, which is equivalent

Parameter	Assortativeness when $T_r = 0$	Assortativeness when $T_r = 5,000$ generations
Default	-0.024 ± 0.512	-0.044 ± 0.466
$V = 100$ ($n(t) \approx 1900$)	0.043 ± 0.473	0.061 ± 0.401
$z = 0.65$	-0.051 ± 0.526	0.119 ± 0.531
$h = 10$	-0.017 ± 0.487	0.141 ± 0.455

Table D1: Mean mating trait $\pm$ its standard deviation after one allopatric phase followed by secondary contact, starting from random mating. The first column "Assortativeness" gives the results without window of partial secondary contact; the second one assumes a window of partial secondary contact of $T_r = 5,000$ generations and $r = 0.005$. Default parameter values are $T_a = 20,000$, $T_s = 10,000 + T_r$, $p = 0.5$, $h = 5$, $V = 50$ ($n(t) \approx 940$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 0.45$, $L_u = L_\alpha = 6$, $\mu_u = \mu_\alpha = 0.01$, $\sigma_u = \sigma_\alpha = 0.02$. Each line in the table gives the results with the default parameter values, except for the indicated parameter change. In all simulation replications reported in this table, hybrids have started to be produced from the first generation after secondary contact (with or without window of partial secondary contact): reproductive isolation did thus not evolve in allopatry. In all replications, there was only one lineage after the end of the sympatric phase and this was a lineage of hybrids: reproductive isolation did thus not evolve at secondary contact.

in our model to assume a fixed, large enough, positive mating trait. Such other mechanism could be e.g. temporal repoductive isolation or pollinator reproductive isolation (Coyne & Orr, 2004).

Under a weak trade-off, assuming that specialist subpopulations are reproductively isolated, directional selection acts on the ecological trait of both subpopulations at secondary contact. Both species converge towards the same generalist strategy but one of them almost always goes extinct before reaching the generalist strategy. Typical evolutionary trajectories of the ecological trait of such species are shown in a trait evolution plot (TEP, Geritz et al., 1998) in Fig. D2. A TEP delineates regions where pairs of traits can mutually invade each other. The x-axis is the trait of one subpopulation, the y-axis is the trait of the other subpopulation. Two subpopulations whose ecological traits define a point in the mutually invasible area of the TEP can ecologically coexist. Outside these coexistence regions of the TEP, one of the subpopulations is expected to go extinct.

When both species have approximately the same size at secondary contact (Fig. D2, black trajectory), both species converge to the generalist strategy at the same speed. Extinction of one of the species occurs when their ecological strategies are very close to the generalist strategy. Indeed, the closer both species are to the generalist strategy, the narrower the ecological coexistence area, and the more likely stochasticity in the evolutionary trajectory makes the pair of species to leave the coexistence region.

When the population sizes are different at secondary contact (Fig. D2, gray trajectory), the smaller subpopulation converges slower to the generalist strategy than the larger subpopulation. In other words, the evolutionary trajectory of the ecological traits of these subpopulations in the TEP points to the edge of the coexistence area corresponding to the extinction boundary of the smaller subpopulation. The smaller subpopulation thus goes extinct before reaching the generalist strategy. In addition, because of the asymmetry of the resource distributions in allopatry (Eq. 4), the expected level of specialization of the smaller subpopulation is higher than the expected level of specialization of the other one. Consequently, converging to the generalist strategy takes more time for the smaller subpopulation: the evolutionary trajectory of the ecological traits in the TEP is thus expected to cross the extinction boundary of the smaller subpopulation before the

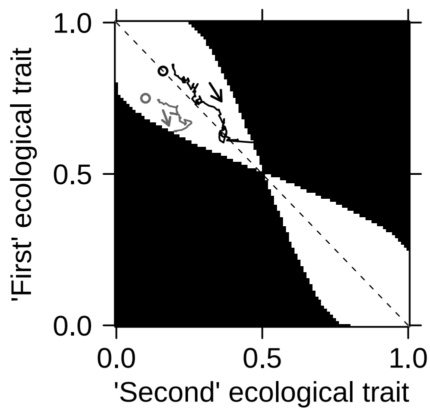

Figure D2: Trait evolution plot (TEP): white areas define regions where two subpopulations can ecologically coexist. Trajectories in the TEP are drawn from secondary contact to the extinction of one of the two subpopulations derived from the former allopatric patches. The axes indicate the mean ecological trait of these two subpopulations. The two subpopulations are reproductively isolated (fixed mating trait, $\alpha = 1$). There is no window of partial secondary contact ($T_r = 0$). Black trajectory: $p = 0.5$, gray trajectory: $p = 0.7$. In this latter case, the size of the subpopulations are different: about 580 individuals in the first subpopulation and 360 for the second. Circles indicate where trajectories should start assuming that allopatric subpopulations are exactly on their singular point at the time of secondary contact. Arrows indicate the direction of each trajectory. The border on which the gray trajectory ends corresponds to the extinction boundary of the second subpopulation, i.e. the smallest of the two subpopulations. Other parameter values: $h = 5$, $V = 50$ ($n(t) \approx 940$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 0.45$, $L_u = 6$, $\mu_u = 0.01$, $\sigma_u = 0.02$. Diversity is generated by an allopatric phase of $T_a = 20,000$ generations.

smaller subpopulation reaches the generalist strategy.

Fig. D3 (panel A) shows a typical evolutionary trajectory where landscape dynamics maintain diversity in the long term. Diversity is maintained in the long term when sympatric phases are shorter than the time needed for the subpopulations to converge to the generalist strategy. If sympatric phases are long, one specialist goes extinct at each secondary contact, but is regenerated at each allopatric phase from the remaining population (Fig. D3, panel B). If population sizes are too asymmetrical, the small population repeatedly goes extinct, but is regenerated at each allopatric phase (Fig. D3, panel C).

Fig. D4 shows the effect of the trade-off parameter z on the probability of coexistance of the two former allopatric subpopulations after a sympatric state of fixed duration. For z between 0 and 1, the trade-off is weak, and the closer to 1, the weaker the strength of selection. Fig. D4 shows that the weaker selection, the higher the coexistance probability of the former allopatric subpopulations. The speed of trait evolution to the generalist strategy indeed varies in the same way as the strength of selection.

Our numerical results use a high mutation rate on the ecological trait ($\mu_u = 0.01$), so that time scales may be underestimated. Results in Figure D5 show that the magnitude of the mutation rate alters only the absolute time scale of our results (the evolution of the ecological trait is slower). We checked on a few simulations that the behaviour of the model is not changed for mutation rate lower than 0.0001 (the smallest mutation rate we tested is $\mu_u = 10^{-9}$).

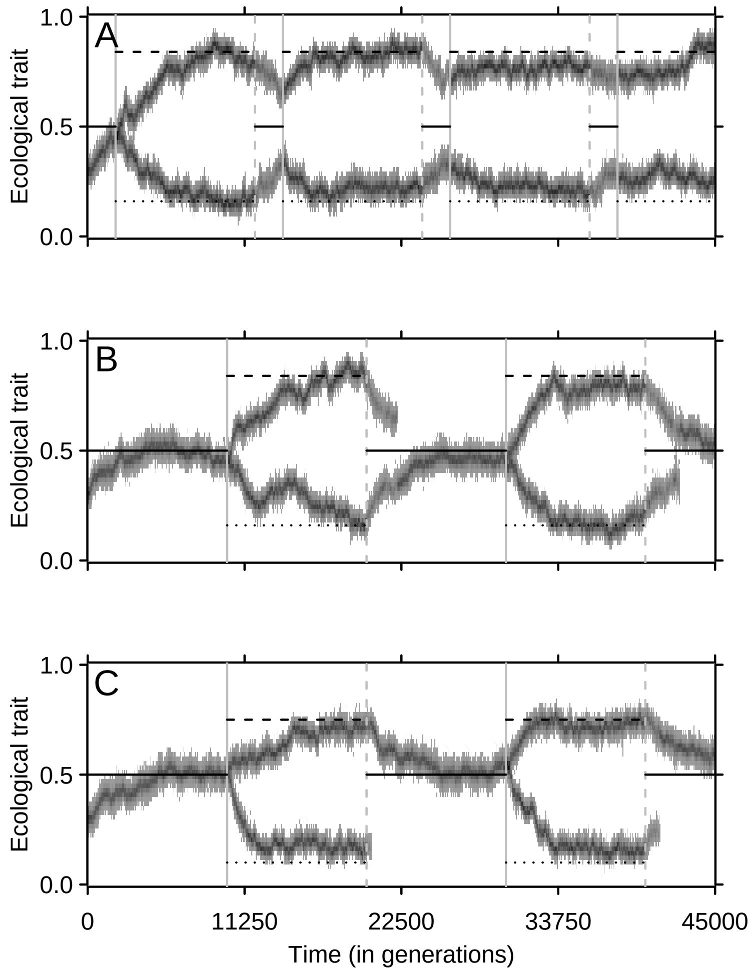

Figure D3: Typical evolutionary trajectories of the ecological trait over time under a weak trade-off. Population density is indicated by the level of gray. Black horizontal lines indicate the values of convergent singular points in sympatry (solid lines), in the first patch in allopatry (dashed lines) and in the second patch in allopatry (dotted lines). Vertical gray lines indicate shifts of the landscape from sympatry to allopatry (solid lines) and conversely (dashed lines). The two subpopulations are reproductively isolated (fixed mating trait, $\alpha = 1$), there is no window of partial secondary contact ($T_r = 0$). Panel A: symmetrical population sizes in allopatry ($p = 0.5$), long allopatric phases but short sympatric phases ($T_a = 10,000$ and $T_s = 2,000$). Differentiated populations coexist in the long-term. Panel B: symmetrical population sizes in allopatry ($p = 0.5$) and long allopatric and sympatric phases ($T_a = 10,000$, $T_s = 10,000$). One of the subpopulations goes extinct in sympatry when their ecological traits are too similar. Panel C: asymmetrical population sizes in allopatry ($p = 0.7$), with $T_a = 10,000$ and $T_s = 10,000$. The second subpopulation in allopatry (converging to the singular point represented by a dotted line) is the smallest and rapidly goes extinct at secondary contact. Other parameter values: $h = 5$, $V = 50$ ($n(t) \approx 940$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 0.45$, $L_u = 6$, $\mu_u = 0.01$, $\sigma_u = 0.02$.

Strong trade-off case

Under a strong trade-off, we checked that sympatric evolutionary branching does not happen by running very long simulations (10^6 generations) for a population of about 675 sympatric individuals ($V = 35$). Inspecting time series of 50 runs, we observed evolutionary branching neither in a constantly sympatric landscape, nor in each patch of a constantly allopatric landscape (Fig. D6).

Allowing the mating trait to evolve is expected to lead to reinforcement at secondary contact. However, without a window of partial secondary contact ($T_r = 0$), Table D2

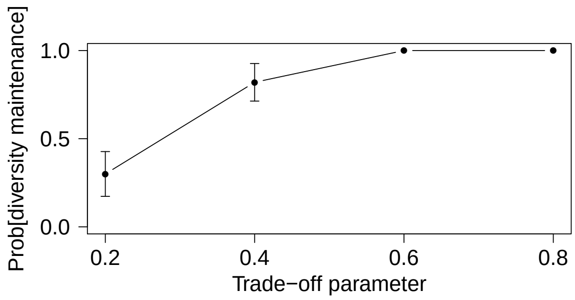

Figure D4: Coexistence probability of the two former allopatric subpopulations after a sympatric phase of fixed duration $T_s = 500$ generations as function of the trade-off parameter z. Subpopulations are assumed to be reproductively isolated (fixed mating trait, $\alpha = 1$), and there is no window of partial secondary contact ($T_r = 0$). Whiskers represent the 95% confidence intervals of the estimated probabilities over the simulation replicates. Other parameter values: $p = 0.5$, $h = 5$, $V = 50$ ($n(t) \approx 940$), $K_1 = K_2 = 1$, $d = 0.1$, $L_u = 6$, $\mu_u = 0.01$, $\sigma_u = 0.02$. Diversity is generated by an allopatric phase of $T_a = 20,000$ generations.

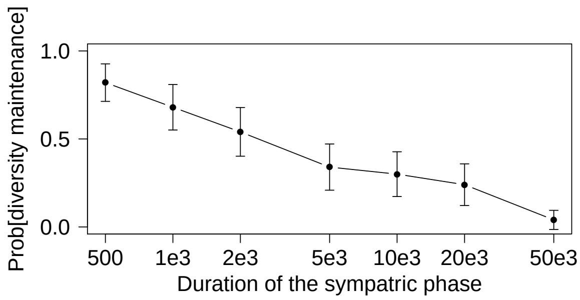

Figure D5: Replication of Fig. 2, filled circles ($p = 0.5$), with a lower mutation rate ($\mu_u = 0.0001$) and a higher phenotypic variance ($\sigma_u = 0.1$). Using longer sympatric phases (x-axis), we observe similar coexistence probabilities of the two former allopatric subpopulations. Note that diversity also takes longer to become established: it was here generated by an allopatric phase of $T_a = 200,000$ generations.

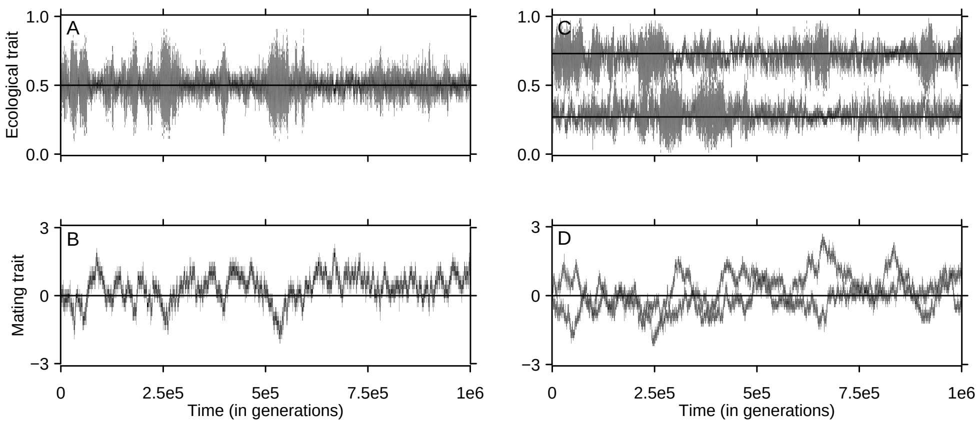

Figure D6: Typical evolutionary trajectories of the ecological trait (panel A) and of the mating trait (panel B) over time under a strong trade-off in sympatry. Panels C and D show a typical evolutionary trajectory of the ecological and mating trait respectively under a strong trade-off in allopatry (the two trajectories of the two allopatric patches are superimposed). Population density is indicated by the level of gray. On top panels, the horizontal lines indicate the singular strategies on which selection is disruptive. Parameter values: $V = 35$ ($n(t) \approx 675$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 1.6$, $L_u = L_\alpha = 6$, $\mu_u = \mu_\alpha = 0.01$, $\sigma_u = 0.02$, $\sigma_\alpha = 0.05$.

shows that hybrids from individuals specialized on different resources replace the population of specialists very rapidly, and that very little positive assortative mating evolves before all specialists are replaced by generalist hybrids, even for parameter values favoring the evolution of assortative mating.

Parameter	Time	Assortativeness
Default	7.68 ± 3.17	-0.0022 ± 0.0300
$V = 100$ ($n(t) \approx 1900$)	8.89 ± 4.28	0.0011 ± 0.0223
$z = 1.8$	7.61 ± 4.15	0.0020 ± 0.0332
$h = 2.7$	9.09 ± 4.16	0.0003 ± 0.0346

Table D2: Evolution of assortativeness starting from random mating at secondary contact. Column "time" indicates the mean duration $\pm$ its standard deviation (in generations) from secondary contact to the replacement of specialists by generalist hybrids. Column "assortativeness" indicates the mean mating trait of the population $\pm$ its standard deviation when generalist hybrids have replaced specialists. There is no window of partial secondary contact ($T_r = 0$). Default parameter values are $p = 0.5$, $h = 1.5$, $V = 35$ ($n(t) \approx 675$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 1.25$, $L_u = L_\alpha = 6$, $\mu_u = \mu_\alpha = 0.01$, $\sigma_u = \sigma_\alpha = 0.02$. Diversity is generated by an allopatric phase of $T_a = 20,000$ generations. Each line in the table gives the results with the default parameter values, except for the indicated parameter change.

Fig. D7 shows the effect of the trade-off parameter z on the probability of speciation after a single window of partial secondary contact. For $z > 1$ the trade-off is strong, and the higher z, the stronger selection. Fig. D7 shows that speciation does not occur when selection is weak ($z \leq 1.3$): the mating trait does not increase enough in this case (as expected from e.g. Matessi et al., 2001). Fig. D7 also shows that, when selection is strong enough to lead to speciation ($z \geq 1.5$), the stronger selection, the higher the probability of speciation. Intermediate hybrids are indeed better selecter against, so that the mean mating trait of the population increases easier above the threshold α_{lim} above which individuals specialized on different resources do not interbreed.

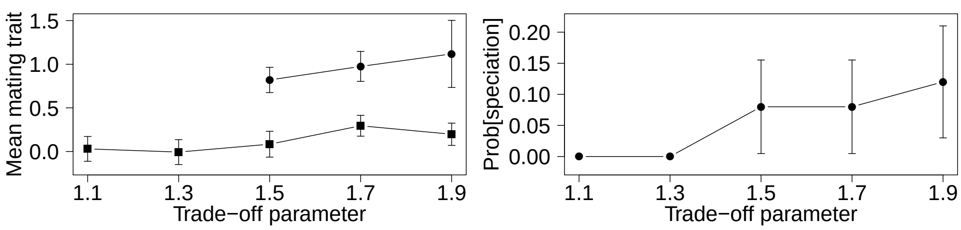

Figure D7: Replication of Fig. 5 with the trade-off parameter z on the x-axis. The success or failure of speciation is assessed 10,000 generations after the end of the window of partial secondary ($T_r = 10,000$, $T_s = T_r + 10,000$). Whiskers represent the 95% confidence intervals of the estimated means and probabilities over the simulation replicates. Other parameter values: $p = 0.5$, $h = 2$, $V = 35$ ($n(t) \approx 675$), $K_1 = K_2 = 1$, $d = 0.1$, $L_u = L_\alpha = 6$, $\mu_u = \mu_\alpha = 0.01$, $\sigma_u = \sigma_\alpha = 0.02$, $r = 0.005$. Diversity is generated by an allopatric phase of $T_a = 20,000$ generations. With these parameter values, the threshold value of the mating trait is $\alpha_{\text{lim}} \approx 0.65$ (Fig. 4).

Our numerical results use a high mutation rate on the ecological and mating traits ($\mu_u = \mu_\alpha = 0.01$), so that time scales may be underestimated. Results in Figure D8 show that the magnitude of the mutation rate alters only the absolute time scale of our results (the evolution of traits is slower). We checked on a few simulations that the behaviour of the model is not changed for mutation rate lower than 0.0001 (the smallest mutation rate we tested is $\mu_u = \mu_\alpha = 10^{-9}$).

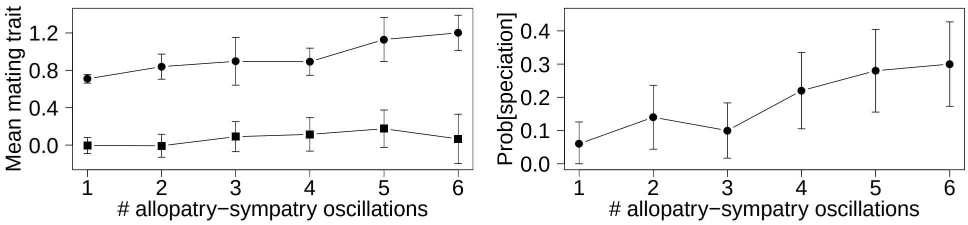

Figure D8: Replication of Fig. 5, top panels, with a lower mutation rate ($\mu_u = \mu_\alpha = 0.0001$) and a higher phenotypic variance ($\sigma_u = \sigma_\alpha = 0.1$). Using longer windows of partial secondary contact ($T_r = 10,000$), we observe similar speciation probabilities.

Once ecological speciation has occurred, disruptive selection maintains it in sympatry, as illustrated in Fig. D9. In allopatry, both species can coexist in each patch. Although the species specialized on the less abundant resource has a small population size and may become extinct, looking at the whole metapopulation, both species persist. Note that in the specific time series shown in Fig. D9, the mating trait slightly increases at each allopatric phase, which helped speciation. Such a pattern was not systematically observed; a more typical pattern of the evolution of the mating trait in allopatry is shown in Figure D6: allopatry has on average no effect on the mating trait.

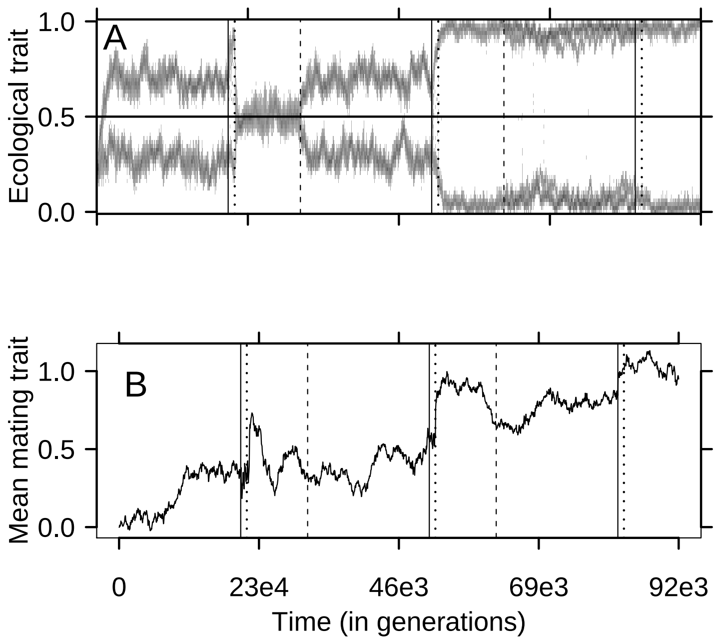

Figure D9: Specific evolutionary trajectories of the ecological trait (panel A) and of the mean mating trait of the population (panel B) over time under a strong trade-off. Population density is indicated by the level of gray. Vertical dashed lines indicate shifts of the landscape from sympatry to allopatry, vertical solid lines indicate shifts from allopatry to sympatry with a window of partial secondary contact, vertical dotted lines indicate the end of the windows of partial secondary contact. Speciation is successful at the second secondary contact and is maintained in both allopatry and sympatry afterwards. Parameter values: $p = 0.5$, $h = 2$, $V = 35$ ($n(t) \approx 675$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 1.6$, $L_u = L_\alpha = 6$, $\mu_u = \mu_\alpha = 0.01$, $\sigma_u = \sigma_\alpha = 0.02$, $r = 0.005$, $T_a = 20,000$, $T_s = 11,000$, $T_r = 1,000$.

Reinforcement is efficient enough at secondary contact only when assuming a window a partial secondary contact, i.e. the production of hybrids by specialists is limited. Fig. D10 shows that reinforcement is efficient for a restrictive range of the meeting probability between differentiated individuals (parameter r). The probability of speciation at secondary contact peaks at $r \approx 0.0005$. For higher r, too many generalist hybrids are produced to prevent them from replacing the population of specialists. For lower r, too few generalist hybrids are produced to select them against efficiently; their frequency mainly evolves under the influence of genetic drift.

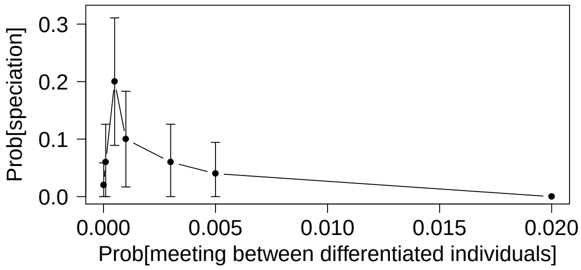

Figure D10: Probability of speciation after one secondary contact against the meeting probability between differentiated individuals (parameter r). Simulations start with an allopatric phase of $T_a = 20,000$ generations generating diversity. Then a secondary contact with a window of partial secondary contact of $T_r = 20,000$ generations occurs. The success or failure of speciation is assessed 10,000 generations after the end of the window of partial secondary contact ($T_s = T_r + 10,000$). Whiskers represent the 95% confidence intervals of the estimated probabilities over the simulation replicates. Other parameter values: $p = 0.5$, $h = 2$, $V = 35$ ($n(t) \approx 675$), $K_1 = K_2 = 1$, $d = 0.1$, $z = 1.6$, $L_u = L_\alpha = 6$, $\mu_u = \mu_\alpha = 0.01$, $\sigma_u = \sigma_\alpha = 0.02$.

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