Sympatric ecological divergence with coevolution of niche preference

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Abstract

Are there phases of speciation? Reinforcement, the increase of assortative mating driven by selection against unfit hybrids, is conditional on pre-existing divergence. Yet, for ecological divergence to precede the evolution of assortment, strict symmetries between fitnesses in niches must hold, and/or there must be low gene flow between the nascent species. It has thus been argued that conditions favouring sympatric speciation are rarely met in nature. Indeed, we show that under disruptive selection, violating symmetries in niche sizes and increasing convexity of the trade-off in selection between the niches (i.e. increasing the “disruptivness” of selection) quickly leads to loss of genetic variation, instead of evolution of specialists. Furthermore, increasing the number of loci encoding the diverging trait and the rate of recombination between them further narrows the region of the parameter space where polymorphism is maintained. Yet, introducing assortment based on niche recognition substantially broadens the parameter space within which polymorphism is maintained. We conclude that in order for sympatric ecological divergence to occur, niche preference must co-evolve from the very beginning of the divergence process. Even if populations come into secondary contact, having diverged in isolation, assortment substantially broadens the conditions for coexistence in sympatry.

Introduction

Darwin observed that many closely related species occupied the same habitat. However, he considered the sympatric origin of species by ecological divergence due to an advantage of specialists over generalists rather unlikely [1]. Since then, the contribution of sympatric speciation to observed biodiversity has remained controversial [2–5]. Speciation in a well-mixed, panmictic population is difficult for two main reasons. First, gene flow and recombination oppose divergence in polygenic traits as well as preventing reinforcement (the build-up of associations between the loci contributing to pre- and post-zygotic isolation; [6,7]. Second, the diverging types must be able to coexist. It is often thought that ecological divergence must precede the evolution of mating assortment (Maynard-Smith 1966), as assortment is reinforced by selection against maladapted hybrids. However, this order of events is not necessary: Assortment can precede divergence, or co-evolve with ecological loci. It is the combined effect of assortment and ecological divergence which contributes to the isolation of the nascent species [9–11]. Yet, in contrast to ecological selection, the loss of fitness due to missed heterospecific matings is typically compensated by an increase in conspecific matings. This stabilises polymorphism at the loci determining assortment and can protect polymorphism at other loci diverging under natural selection.

Habitat choice is an important source of assortment when mating occurs locally. Host-specific mating is prevalent in nature, as in phytophagous insects (reviewed in [12]). Habitat fidelity based on a preference for the hatching site is common for birds [13], another group rich in sympatric species. In general, habitat choice can be based on learned characteristics of the hatching site, on specific preference loci, or on an association with another (ecological) phenotype. The first two drove the classic sympatric speciation process in the experiment by Rice and Salt [14], where fruit flies learned to choose based on phototaxis and chemotaxis. In this experiment, 60 mated females from each of two extreme habitats founded the next generation. Severe disruptive selection on multiple traits in a fairly large population, coupled with independent regulation within equally sized niches, led to nearly complete reproductive isolation over 30 generations. Effectively, behavioural allopatry evolved (c.f. [8]). Further divergence in other traits, both selective and neutral, could have followed. While the plausibility of sympatric speciation is undisputed, how common can it really be? Selection is rarely that severe in nature, and even if niches are independently regulated, they will very rarely be perfectly symmetric.

A recognition and preference for the correct habitat is a common example of assortment by association with another phenotype. While preference for food source is omnipresent, trade-offs in specialization of the sympatric-species-rich phytophagous insects have been hard to find, triggering a substantial controversy [15,16]. Yet, trade-offs must be reasonably common – otherwise, all habitats would be colonised by one generalist species. Indeed, trade-offs have often been recovered when life-time fitness and/or performance of F1 hybrids on both hosts is assessed [17–21].

Here we use mathematical modelling to investigate how genetically encoded preferences for the most favourable habitat facilitate sympatric speciation by ecological divergence. We assume that there is a convex trade-off in a polygenic trait, leading to disruptive selection such that generalists have a lower mean fitness than specialists. Assortment arises via preference for the correct niche. Because regulation is independent within niches (soft selection, [22]), frequency of a type well adapted to its niche rises faster when this type is rare than when it is common. This protects the polymorphism in the ecological loci (coexistence of the specialists) via negative frequency-dependence [22].

In contrast to previous models [8,23], we consider a polygenic trait under ecological divergence, and focus on assortment via preference for the niche the individual is best adapted to. The assortment allele can therefore be seen as a type of a 'modifier-allele' [8], realized via niche choice. It represents a 'one-allele model' [7], where recombination cannot break down the allele-specific association with the choice-locus. Thereby, the constraints on symmetries, which render sympatric speciation implausible, are relaxed (c.f. [7,24]). Yet, in our model, assortment is only possible if the population diverges in its ecological loci. We focus on the co-evolution of assortment by niche choice and ecological polymorphism in the diverging populations.

How do two nascent species evolve towards coexistence? Coexistence during divergence in sympatry is often overlooked in speciation models, side-lined by focus on growth of associations between and within polygenic traits, assuming symmetries are protected [11]. It is far from obvious if divergence and coexistence in sympatry is more difficult than partial divergence in allopatry or broad parapatry, followed by sympatry as assortment evolves, reducing production of unfit hybrids. When neutral divergence does not lead to a sufficient niche separation then (similarly to instant assortment by chromosomal variations; [25]) coexistence will not be possible. Yet, coexistence in sympatry is essential: without it, every speciation in sympatry or parapatry would lead to a subdivision of the existing range – and through time, species' ranges would become ever smaller.

Methods and results

Model

Since we focus on the effects of disruptive selection on sympatric divergence, we use a haploid biallelic version of Levene's [26] model with mating within niches, which is more favourable to speciation. In the lifecycle of the model, individuals with non-overlapping generations are – in the basic model without assortment -- randomly distributed into two niches, where selection acts. Alleles of the first type (capital letters) are beneficial in one niche and alleles of the second type (small letters) in the other niche. The individuals who survive mate within the niches and then each niche contributes to a common pool proportionally to its size. From the common pool, individuals are again randomly distributed into the two niches.

For further analysis, it is convenient to define fitness of the genotypes to be between zero and one. The presence of an allele which is deleterious in niche γ reduces the fitness of its carrier by selection coefficient s_{γ}, which is equal for all loci. The epistatic coefficient ϵ determines how much the intermediate generalist (*ab*) genotypes are disadvantaged relative to the specialist (*AB*) genotypes (for $\epsilon < 0$) and is defined as the deviation from additivity of deleterious alleles in each niche if more than one of these alleles is present. Here we are assuming a special kind of symmetric epistasis, which acts among alleles deleterious in one niche and also those in the other niche.

Analytical solutions for polymorphic equilibria of our model are generally imposible to find. Instead, we have analysed the instability of the two monomorphic equilibria for allele frequencies in ecological and niche preference loci at 1 and 0. We assume that an equilibrium polymorphic at the ecological loci exists between them. This approach was used by Levene [26], Prout [27] and Hoekstra et al. [28]. Gliddon and Strobeck [29] analysed the haploid multilocus analogue of Levene's (1953) model and proved that conditions for instability of the monomorphic equilibria are also necessary and sufficient conditions for stability of the unique polymorphic equilibrium. Although this conclusion may not be valid in the presence of epistasis and is not in general valid when assortment is present, it still allows us to estimate the stability of the polymorphic equilibrium for the ecological loci in the full model for most of the parameter range. The stability is then tested numerically. We discuss a small parameter region where the local equilibrium also depends on the initial conditions. Depending on the initial allele frequencies, the system evolves either to a polymorphic equilibrium in the ecological loci, or to another equilibrium where ecological loci are fixed and the locus for assortment is polymorphic.

Ecological divergence at a polygenic trait

Ecological divergence is often driven by disruptive selection acting on polygenic traits. Therefore, we first set out to analyse how increasing the number of loci (from two to three) influences the ability of the model to maintain polymorphism under disruptive selection. In particular, we focus on violation of symmetries in niche proportions, which are defined as $c_{\mathrm{I}} = 1 - c_{\mathrm{II}}$. Fitnesses of the individual genotypes for the two- and three-locus model are defined in Table 1A and Table 1B, respectively. In order to be able to compare the two- and three-locus models, we normalise the strength of selection and epistasis in the three-locus model such that the mean fitness at a Hardy-Weinberg equilibrium remains the same ($s_{\gamma,\mathrm{3loci}} = \frac{2}{3} s_{\gamma,\mathrm{2loci}}$ and $\epsilon_{\gamma,\mathrm{3loci}} = \frac{1}{3}\epsilon_{\gamma,\mathrm{2loci}}$, $\gamma = \{\mathrm{I}, \mathrm{II}\}$ for niche I and II, respectively). This normalisation assures the same convexity of the trade-off, therefore the same strength of disruptive selection. For simplicity, we assume all pairwise epistasic effets have the same value, and neglect higher-order interactions between alleles.

A

genotype	niche I	niche II
AB	$1-2s_{\mathrm{I}}-\epsilon$	1
aB, Ab	$1-s_{\mathrm{I}}$	$1-s_{\mathrm{II}}$
ab	1	$1-2s_{\mathrm{II}}-\epsilon$

B

genotype	niche I	niche II
ABC	$1-3s_{\mathrm{I}}-3\epsilon$	1
ABc, AbC, aBC	$1-2s_{\mathrm{I}}-\epsilon$	$1-s_{\mathrm{II}}$
Abc, aBc, abC	$1-s_{\mathrm{I}}$	$1-2s_{\mathrm{II}}-\epsilon$
abc	1	$1-3s_{\mathrm{II}}-3\epsilon$

***Table 1**. A. Two-locus model without niche preference. B. Three-locus model without niche preference. Fitnesses of individual genotypes. s_I is the selection coefficient for niche specific deleterious alleles in niche I, s_{II} is selection coefficient for niche specific deleterious alleles in niche II and ϵ and is the epistatic coefficient which is defined as the deviation from additivity of the two deleterious alleles present in a genotype together. We only consider $\epsilon < 0$ as it generates a convex trade-off and hence disruptive selection.*

First, we show that the region of parameter space where polymorphism is maintained is highly sensitive to violation of symmetry in niche proportions, c, even if loci are completely linked. Also, increasing convexity of the trade-off (i.e., more negative ϵ, more disruptive selection) further reduces the parameter space with maintained polymorphism (Fig. 1A). When the loci are freely recombining (r=0.5), there is also no difference with respect to increasing the number of loci. In both the two- and the three-locus cases the regions of parameter space with maintained polymorphism are shifted towards very strong selection (Fig. 1C). When recombination between loci is low (r=0.01, i.e., 1cM), the regions of parameter space with maintained polymorphism shift closer towards those of the free recombination regime in the three-locus model than in the two-locus model, as in the three-locus case the per-locus strength of selection is lower (Fig. 1B). Interestingly, there is a threshold for recombination rate, above which the parameter space is independent of the number of loci. Below we provide the analytical expressions for the boundaries of the stable regions, and the recombination threshold.

In both models with normalized selection and $\epsilon = 0$ a polymorphic equilibrium is stable if

$$\frac{1-2s}{2-2s} < c < \frac{1}{2-2s}.$$

In the case with no recombination (Fig. 1A) and $\epsilon < 0$, polymorphism is maintained if

$$\frac{2s+\epsilon-1}{2s+\epsilon-2} < c < \frac{1}{2-\epsilon-2s},$$

and with free recombination (Fig. 1C) if

$$\frac{s(1-2s-\epsilon)}{(1-s)(2s+\epsilon)} < c < \frac{s+\epsilon}{(1-s)(2s+\epsilon)}.$$

These conditions hold for the two-locus model for recombination rates $r > \frac{-\epsilon}{1-s-\epsilon}$. If recombination rate is low ($0 < r < \frac{-\epsilon}{1-s-\epsilon}$; Fig. 1B), the conditions above do not hold anymore and maintenance of polymorphism is determined by

$$\frac{(1-2s-\epsilon)(2s+\epsilon(1-r)+r(1-2s))}{(1-r)(4(1-s)s+2\epsilon(1-2s)-\epsilon^2)} < c < \frac{2s+\epsilon-r}{(1-r)(4(1-s)s+2\epsilon(1-2s)-\epsilon^2)}.$$

Since the equations describing the conditions for the three-locus model with low recombination and all other models presented from this point on exceed the width of a page, we confine them to the Supplementary materials.

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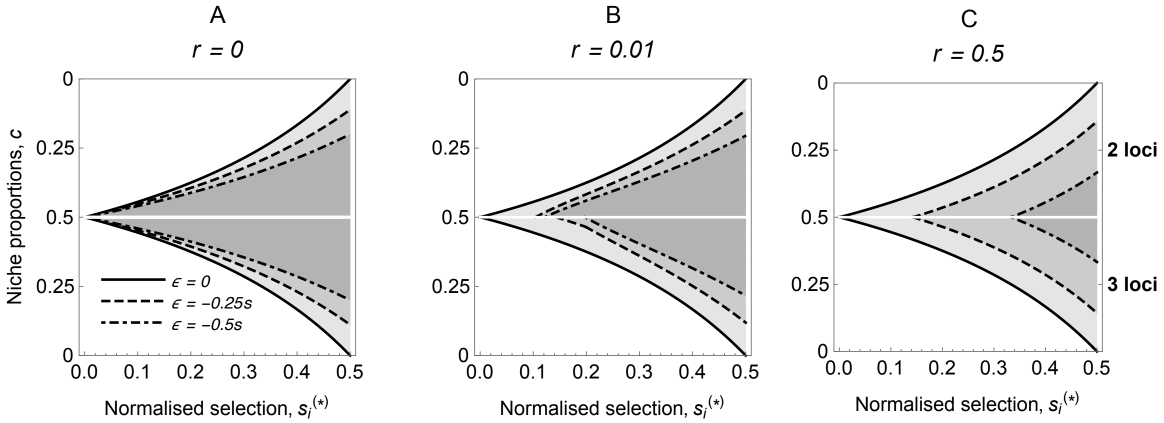

Figure 1. Range of niche proportions where polymorphism is maintained: where ecological divergence towards two specialists is stable. The upper half of the graphs show conditions for the two-locus model, the lower half for the three-locus model. On the x-axis is the normalized strength of selection (symmetric across loci) and on the y-axis are niche proportions. A polymorphic equilibrium is achieved for the parameter combinations of s^* and c between the black curves and the white axis at $c = 0.5$ (shaded). Note that we are showing only one half of the parameter space for each model as the conditions are symmetrical. Therefore, every condition at a value of c has its symmetric counterpart at $1 - c$. The outer solid curves represent linear trade-offs ($\epsilon = 0$), the dashed curves are for ($\epsilon = -0.25s$), and the dash-dotted curves for ($\epsilon = -0.5s$). A) No recombination; B) Low recombination ($\mathrm{r} = 0.01$), and C) Free recombination ($\mathrm{r} = 0.5$).

Ecological divergence with niche choice

Next, we analyse how the presence of a niche preference allele influences the sensitivity of polymorphism to violation of symmetry in niche proportions.

We assume that habitat choice depends both on the presence of a choosy (modifier) allele *M* and the phenotype under natural divergent selection. For the individuals with wildtype modifier allele '*m*', there is no bias in selecting niches. When the modifier allele is '*M*', choice depends on the selected loci in the following manner: intermediate generalist genotypes (*Ab*, *aB*) disperse to both niches with equal probability, and specialist genotypes (*AB, ab*) choose with probability $1+\alpha$ the niche which they are adapted to, and with probability $1-\alpha$ the niche where they are maladapted. Since in our model mating occurs within niches, this translates into a direct modification of fitnesses of the individual genotypes, as defined in Table 2.

genotype	niche I	niche II
ABM	$(1-2s_{\mathrm{I}}-\epsilon)(1-\alpha)$	$1+\alpha$
ABm	$(1-2s_{\mathrm{I}}-\epsilon)$	1
$\mathrm{Abm}, \mathrm{AbM}, \mathrm{aBm}, \mathrm{aBM}$	$1-s_{\mathrm{I}}$	$1-s_{\mathrm{II}}$
abm	1	$(1-2s_{\mathrm{II}}-\epsilon)$
abM	$1+\alpha$	$(1-2s_{\mathrm{II}}-\epsilon)(1-\alpha)$

Table 2. *Fitnesses of individual genotypes modified by niche choice parameter* α. s_I *is the selection coefficient for niche specific deleterious alleles in niche I,* s_{II} *is selection coefficient for niche specific deleterious alleles in niche II and* ϵ *and is the epistatic coefficient which is defined as the deviation from additivity of the two deleterious alleles present in a genotype together. We only consider* $\epsilon < 0$ *as it generates convex trade-offs and hence disruptive selection. Genotype Abc goes to niche I with a probability increased by the factor* α *and to niche II decreased by* α*. Similarly, genotype ABC preferentially goes to niche II instead of niche I.*

In the presence of niche preference, the parameter space where polymorphism is maintained broadens (Fig. 2). As allele *M* is beneficial for both specialist genotypes (*AB* and *ab*), it quickly goes to fixation when polymorphisms for the other two loci are maintained – hence, two specialists coexist. This holds in the case of complete linkage (Fig. 2A) and low recombination (Fig. 2B). In the scenario with free recombination, maintenance of polymorphism at the ecological loci depends on the initial frequencies of alleles *A, B* and *M* in the population. The weaker the selection against the maladapted genotypes, s_i, the more sensitive the model is to initial conditions, as indicated by the fading grey colour in the lower left part of Fig. 2C. Within this region, depending on the initial allele frequencies, either the preference allele M goes to fixation and protects polymorphism in the other loci, or the ecological loci go to fixation and allele M remains polymorphic and converges to its equilibrium frequency $\frac{1\pm 2c}{\alpha}$. We further numerically evaluate this sensitivity to initial conditions in Supplementary material Fig S1.

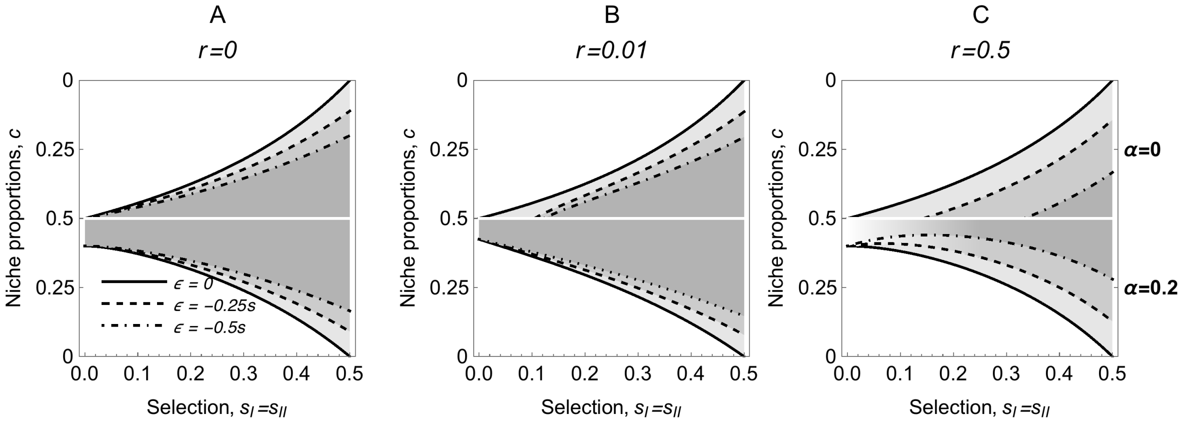

Figure 2. Range of niche proportions where polymorphism is maintained under coevolution of assortment with ecological divergence. The upper half of the graphs show conditions for the two-locus model without niche preference, the lower half for the three-locus model where two loci encode ecologically diverging loci and the third locus a preference allele *M* with niche preference $\alpha = 0.2$. On the x-axis is the strength of selection and on the y-axis are niche proportions. A polymorphic equilibrium is achieved for the parameter combinations of s and c between the black curves and the white axis at $c = 0.5$ (shaded). Note that we are showing only one half of the parameter space for each model as the conditions are symmetrical. Therefore, every condition at a value of c has its symmetric counterpart at $1 - c$. The outer solid curves represent linear trade-offs ($\epsilon = 0$), the dashed curves are for ($\epsilon = -0.25s$), and the dash-dotted curves for ($\epsilon = -0.5s$). A) No recombination; B) Low recombination ($\mathrm{r} = 0.01$), and C) Free recombination ($\mathrm{r} = 0.5$).

Increase of assortment

Once such a niche preference modifier allele gets fixed in a population, it not only inflates the parameter space where polymorphism is maintained but it also always favours fixation of another modifier allele, which then reinforces the divergent process. In order to analyse such an increase of assortment, we again redefined fitnesses of the genotypes as in shown in Table 3. The fitnesses of the specialist genotypes (*AB* and *ab*) are now defined such that the niche preference allele *M* from the previous model is fixed in the population. Therefore, both specialist genotypes have their probability of going to the right niche increased by α_1. The third locus can now be polymorphic for another modifier allele, which further increases the probability of going to the right niche by α_2. In Fig. 3 we show how the parameter space where polymorphism is maintained further broadens in the presence of another modifier allele, increasing the assortment.

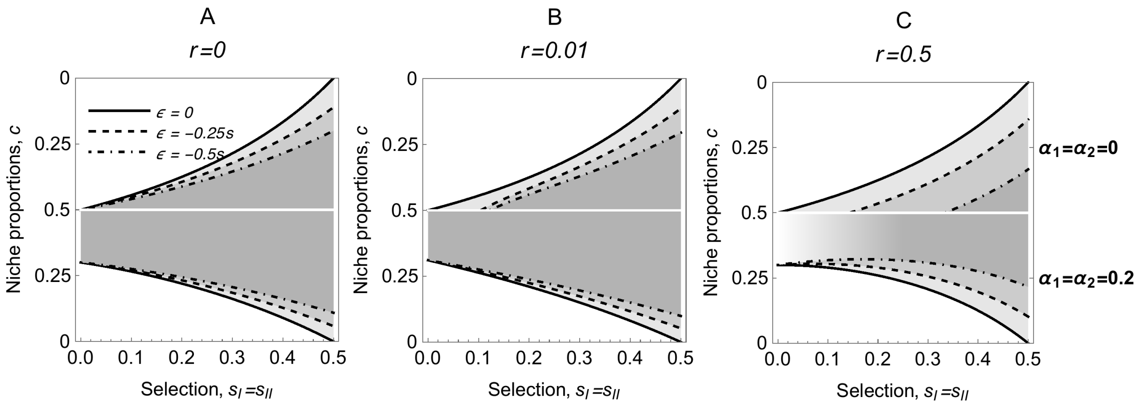

Figure 3. Range of niche proportions where polymorphism is maintained when assortment further increases. The upper half of the graphs shows conditions for the two-locus model without assortment, the lower half for the three-locus model where two loci encode ecologically diverging loci with already fixed niche preference $\alpha_1 = 0.2$, and the third locus a preference allele M_2 with niche preference $\alpha_2 = 0.2$. On the x-axis is the strength of selection and on the y-axis are niche proportions. A polymorphic equilibrium is achieved for the parameter combinations of s and c between the black curves and the white axis at $c = 0.5$ (shaded). Note that we are showing only one half of the parameter space for each model as the conditions are symmetrical. Therefore, every condition at a value of c has its symmetric counterpart at $1 - c$. The outer solid curves represent linear trade-off ($\epsilon = 0$), the dashed curves are for ($\epsilon = -0.25s$), and the dash-dotted curves for ($\epsilon = -0.5s$). A) No recombination; B) Low recombination ($r = 0.01$), and C) Free recombination ($r = 0.5$).

genotype	niche I	niche II
ABM_2	$(1 - 2s_I - \epsilon)(1 - \alpha_1 - \alpha_2)$	$1 + \alpha_1 + \alpha_2$
ABm_2	$(1 - 2s_I - \epsilon)(1 - \alpha_1)$	$1 + \alpha_1$
$AbM_2, aBM_2, Abm_2, aBm_2$	$1 - s_I$	$1 - s_{II}$
abm_2	$1 + \alpha_1$	$(1 - 2s_{II} - \epsilon)(1 - \alpha_1)$
abM_2	$1 + \alpha_1 + \alpha_2$	$(1 - 2s_{II} - \epsilon)(1 - \alpha_1 - \alpha_2)$

Table 3. *Fitnesses of individual genotypes modified by fixed niche choice parameter α_1 and a polymorphic allele M_2, which encodes increased preference by α_2 for better niche. s_I is the selection coefficient for niche specific deleterious alleles in niche I, s_{II} is selection coefficient for niche specific deleterious alleles in niche II and ϵ and is the epistatic coefficient which is defined as the deviation from additivity of the two deleterious alleles present in a genotype together. We only consider $\epsilon < 0$ as it generates convex trade-off and hence disruptive selection. Genotype abM_2 goes to niche I with a probability increased by the factor α_2 and to niche II decreased by α_2. Similarly, genotype ABM_2 preferentially goes to niche II instead of niche I.*

When selection is weak and recombination large, the stability of the ecological polymorphism depends on the initial allele frequencies and disequilibria (Fig. 2C, 3C). However, for most of the parameter space, the conditions for stability of the ecological polymorphism hold no matter whether or not the initial population is in Hardy-Weinberg linkage equilibrium. Then, even if the initial population consists only of the two specialist genotypes, the conditions presented above must be fulfilled so that ecological polymorphism is maintained.

Discussion

Maintenance of polymorphism and the plausibility of sympatric speciation are some of the most persistent questions in evolutionary biology. An arguable assumption frequently made in many sympatric speciation models is their restriction to one or rarely several loci, whereas ecological adaptation of a population often involves a gradual change in a polygenic trait [30]. An obvious reason for this common restriction is the analytical difficulty of such models, especially if additional evolutionary forces such as epistasis and nonlinear trade-off between viabilities are included. Notably, the multilocus version of Levene's model – with a trade-off in adaptation to two different niches – has been analysed [31,32] but no epistasis was allowed. An exception is Barton's [33] analyses of adaptation in a quantitative trait under a convex trade-off. He assumed the symmetries in allele frequencies were maintained under disruptive and negative frequency dependent selection [34]. Yet, when niches are not perfectly symmetric, independent regulation within niches does not always generate sufficient negative frequency-dependence to stabilise ecological polymorphism.

In order for specialists to be favoured over generalists, trade-off in fitness between niches must be convex. When adaptation occurs in a polygenic trait, this implies less-than-additive epistasis and/or heterozygote disadvantage. Yet, most early models of sympatric speciation focused on maintenance of polymorphism at a single diploid locus under heterozygote advantage, and on coupling of such polymorphism with a locus for assortment [8,23,28]. Felsenstein [7] analysed coupling of two loci under an ecological trade-off with an independent self-recognising locus for assortment concluded that assortment can only increase for linear or concave trade-offs. With negative epistasis (convex trade-off), polymorphism was not maintained and assortment could not evolve ([7] , p. 130). It has been recognised that asymmetry in niche proportions significantly influences the ability of these models to maintain genetic polymorphism – and that symmetric selection and concave trade-offs in fitness make such maintenance easier (citations above). Curiously, Barton [33] showed that assortment can readily increase in a population under a convex trade-off,, provided the starting genetic variance is large enough. However, that model assumed symmetric niches, and that symmetry in allelic frequencies is maintained by frequency-dependent selection (hypergeometric model, [34]).

We show that specialists can readily evolve even when the trade-off in fitness between niches is convex, provided that polymorphism is stabilised by assortment arising from a preference for the ''correct'' niche (to which the individual is better adapted). Similarly, assortment via niche-recognition stabilises polymorphism in divergent populations under secondary contact (replacing the assortment which arose by geographic isolation). In the absence of any form of assortment reflecting adaptation, the conditions for divergence under disruptive selection are far from realistic, as they require specific and perfect symmetries [4]. We argue that such niche recognition and preference is widespread across all life forms. Even plants' roots have growth oriented towards nutrient-rich parts of the rhizosphere [35], motile unicelular organisms, including even bacteria, can move towards their preferred food source by chemotaxis [36,37] and among (in)vertebrates it is generally known that they can recognise and choose their preferred food or habitat. Therefore, this pre-existing ability to recognise the preferred niche may in fact "hijack" arising ecological divergence, protect it, and even further reinforce the newly arising reproductive isolation by strengthening the assortment.

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