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Will Sympatric Speciation Fail due to Stochastic Competitive Exclusion?

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ABSTRACT: Sympatric speciation requires coexistence of the newly formed species. If divergence proceeds by small mutational steps, the new species utilize almost the same resources initially, and full speciation may be impeded by competitive exclusion in stochastic environments. We investigate this primarily ecological problem of sympatric speciation by studying the population dynamics of a diverging asexual population in a fluctuating environment. Correlation between species responses to environmental fluctuation is assumed to decrease with distance in trait space. Rapidly declining correlation in combination with high environmental variability may delay full speciation or even render it impossible. Stochastic extinctions impeding speciation are most likely when correlation decays faster than competition, for example, when demographic stochasticity is strong or when divergence is not accompanied by niche separation, such as in speciation driven entirely by sexual selection. Our general theoretical results show an interesting connection between short-term ecological dynamics and long-term, large-scale evolution.

Keywords: sympatric speciation, adaptive dynamics, stochastic population dynamics, extinction risk, competitive exclusion.

Speciation is a fundamental evolutionary process that biologists have described with a number of complementary as well as competing theories. Speciation in sympatry, that is, in the same geographic area, is an appealing yet problematic possibility (Dieckmann et al. 2004; Gavrillets 2004). Theories set out to describe this mode of speciation have to overcome two fundamental difficulties (Coyne and Orr 2004). First, they have to explain how a population can split into two despite the continuous production of intermediate offspring due to recombination, that is, account

for the emergence of reproductive isolation. Second, the diverging lineages must be able to coexist in sympatry during and after the speciation process.

The first problem has been the focus of many investigations. A well-known example is the model by Dieckmann and Doebeli (1999), in which disruptive selection driven by competition for resources leads to evolution of assortative mating, which in turn results in reproductive isolation. Their model has ignited a lively debate and given rise to several studies indicating that conditions for sympatric speciation to occur may be restricted (Gourbiere 2004; Gavrillets 2005; Polechova and Barton 2005; but see also Doebeli and Dieckmann 2005; Doebeli et al. 2005). The main part of the criticism concerns whether reproductive isolation will appear when different aspects are taken into consideration, for example, costs of assortative mating (Gavrillets 2004; Polechova and Barton 2005; Bürger and Schneider 2006), lower and presumably more realistic mutation rates (Waxman and Gavrillets 2005), mating disadvantage for rare phenotypes (Gourbiere 2004), and increased number of loci (Bürger and Schneider 2006).

The second problem, coexistence, has a more ecological nature and has received less attention, at least in current discussions. It is connected to the competitive exclusion principle, which states that coexistence of two species is impossible without differentiation of their realized niches (Begon et al. 1996). If the species are reared together in the same environment, the weaker competitor is doomed to extinction. In a deterministic competition model, such as the standard Lotka-Volterra equations, the slightest niche differentiation is sufficient for coexistence. In nature, however, growth rates of populations are not deterministic but depend on stochastic fluctuations in the biotic and abiotic environments. A variable environment will make competitive exclusion less predictable (e.g., a competitor that is stronger on average may occasionally become extinct) and turn into a question of probabilities. Further, since all species will be subject to a certain risk of extinction, such a “stochastic” variant of the competitive exclusion principle will also be gradual; species will have higher or lower probabilities of extinction depending on how much their niches overlap. In particular, it follows that species that have overlapping niches and are able to coexist

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in a stable environment will be subject to a nonnegligible extinction risk in a stochastic environment (May and MacArthur 1972; Turelli 1978). More recent theoretical work on population dynamics in competitive communities has shown the importance of the interplay between intra- and interspecific competition, environmental variance, and environmental correlation for the variance of population densities (Ives et al. 1999). Populations with a large niche overlap are likely to respond in similar ways to environmental variability, which yields a positive correlation between the two populations' growth rates. As an example, when a shared resource becomes scarce as a result of extreme weather conditions, both populations will suffer and decrease in numbers. It can be shown that a positive environmental correlation between competing populations decreases the variance in the density of each single population, especially when interspecific competition is high (Ives et al. 1999). A low environmental correlation, on the other hand, yields a high variance and hence a high risk of extinction, provided that the overall environmental variance is high.

This note treats the coexistence problem of sympatric speciation and particularly how environmental fluctuations influence the process. We view this primarily as an ecological question where genetic details and exactly how reproductive isolation is achieved is of secondary importance. We will therefore confine the study to evolving asexual populations characterized by a single continuous quantitative trait as an approximation for more detailed models with, for example, sexual reproduction and complex genetic structures, where selection affects many loci with possible interactions. We will show that the risk of extinction just after speciation depends on how quickly environmental correlation declines during divergence in trait space and on the variance of the environmental fluctuations. If correlation declines faster than interspecific competition, speciation will not occur or will at least be delayed. This result emphasizes the importance of taking ecological processes such as population dynamics and extinctions into account when studying the evolution of interacting species.

A Scenario for Competition-Driven Sympatric Speciation

Many specific models have been proposed to explain sympatric speciation (e.g., Rosenzweig 1977; Udovic 1980; van Doorn et al. 1998; Gavrillets and Waxman 2002). A typical scenario is one where competition causes disruptive selection on an ecological trait (Christiansen and Loeschke 1980; Dieckmann and Doebeli 1999). Such a situation may arise if intraspecific competition is intense and mutant offspring differing from the main population experience

reduced competition, conferring a fitness advantage. The disruptive selection readily increases genetic variance within the population and may lead to a stable polymorphism. If reproductive isolation between morphs is achieved through evolution of assortative mating, the former single population has been replaced by two new populations that continue to evolve as new species, diverging in trait space. The rate with which competition declines with distance in trait space is important for the speed and probability of sympatric speciation; if competition between populations declines quickly, mutants will benefit from higher fitness advantages and disruptive selection will be stronger (Doebeli and Dieckmann 2000).

We have chosen the same ecological model as in an article by Dieckmann and Doebeli (1999), where competition for different resource types gives rise to a density-dependent disruptive selection. The competition coefficient α is a declining function of the distance D in trait space between competing individuals:

$$\alpha = e^{-D^2/2\sigma_\alpha^2}.$$

Identical individuals will have $\alpha = 1$ corresponding to intraspecific competition, and the rate of decline is controlled by the parameter σ_α , which can be interpreted as niche width.

To incorporate a stochastic environment in this model, we assume environmental fluctuations affect population growth in such a way that population growth rates deviate randomly from the deterministic, density-dependent prediction. More precisely, we assume these random deviations are additive on a log scale, a common assumption in population modeling and ecological time series analysis (e.g., Royama 1981; Turchin and Taylor 1992; Bjørnstad et al. 1995; Ives et al. 1999). Populations with identical traits can be expected to respond to environmental fluctuations in a similar way; that is, we expect a high-correlation ρ between their respective deviations from the deterministic growth rate. The more ecologically different they are, the smaller we expect this correlation to be. In other words, the environmental correlation between species will decrease with distance D in trait space, and just as with the competition coefficient, we assume the decline follows a Gaussian relationship:

$$\rho = e^{-D^2/2\sigma_\rho^2}.$$

Ecologically equivalent populations ($D = 0$) will hence have fully correlated responses ($\rho = 1$), and the rate of decline will be controlled by σ_ρ . A high (low) σ_ρ corresponds to slowly (quickly) declining correlations. The appropriate rate of correlation decline can be different for different organisms and environments. Finally, the am-

plitude of the environmental fluctuations was set by its standard deviation σ_e . A complete model description is given in the appendix in the online edition of the *American Naturalist*.

Extinction Risk during Sympatric Speciation

We studied the population dynamics during competition-driven trait divergence with the aid of stochastic simulations as well as a more general but approximate mathematical analysis (see appendix for details). First, we simulated sympatric speciation with two different rates of decline in environmental correlation, that is, two different values of σ_p . The initial population consisted of individuals with trait value zero subject to frequency-dependent disruptive selection. Figure 1 shows how individual trait values split into clusters and the population dynamics corresponding to these clusters. When there is one cluster, the distribution of the total population size is shown, and when there are two, only the distribution of the population size corresponding to the lower branch is shown, since the dynamics of the upper one is similar. Immediately after a split, the population sizes are reduced to roughly half the original size. In the scenario with slowly decaying environmental correlation (fig. 1A, 1C), the reduction in population size is accompanied by a reduction, in absolute magnitude, of the fluctuations as well. Thus, there is little risk of extinction after branching, and divergence occurs readily. When environmental correlation decays quickly, the first diverging lineage becomes extinct and only the second branching attempt is successful (fig. 1B). During the initial stages of the second branching, the populations fluctuate wildly, but after some time, competition α decreases as the trait values diverge, causing fluctuations to decline (fig. 1D). In both cases, the population sizes increase toward the end of the simulations because of decreased competition.

The key difference between the two scenarios is the magnitude of the fluctuations after the splitting of the lineages. With slowly decaying correlation, fluctuations are moderate, but with quickly decaying correlation, the population sizes vary a lot and often reach levels near zero, that is, close to extinction. An analysis of the linearized population dynamics just after speciation generalizes this conclusion to all of parameter space where a deterministically stable coexistence is possible (see appendix). A slowly decaying environmental correlation (a large σ_p) makes the populations fluctuate largely in synchrony, such that a decline in one of the populations is often accompanied by a corresponding decline in the other. In such cases, both intra- and interspecific competition decrease simultaneously, generating a rapid return toward equilibrium for both populations, small population fluctuations,

and consequently, small extinction risks. If, on the other hand, environmental correlation decays quickly in trait space (σ_p is small), then environmental fluctuations of newly formed species are little correlated, and population fluctuations will be less synchronous. Accordingly, one population can be small while the other is still abundant, which delays the return to equilibrium and makes possible further stochastic decline of the smaller population. A weakly correlated, or even uncorrelated, environment thus generates more violent population fluctuations and a high risk of extinction. Broad niche widths amplify this effect by intensifying competition.

In order to determine how different rates of decay of environmental correlation and levels of environmental fluctuations affect speciation, we repeated the simulations while varying σ_p and σ_e . Figure 2 shows mean number of generations until speciation under no (*horizontal dashed line*), low (*thin solid line*), and strong (*thick solid line*) environmental fluctuations at different values of σ_p (for criterion of speciation and other details, see appendix). Time to speciation for low environmental fluctuations is similar to that without fluctuations and without discernible differences between quickly and slowly decaying correlation (fig. 2). For strong environmental fluctuations, however, the mean time to speciation increases at low values of σ_p , that is, when environmental correlation declines quickly in trait space. This occurs for $\sigma_p < \sigma_e$, that is, when correlation decreases more quickly than competition (left of the vertical dashed line in fig. 2). At $\sigma_p \approx 0.1$, time to speciation is approximately doubled, and for the lowest value (point *a* in fig. 2), all simulations lasted until the maximal allowed time, 10^6 generations; that is, we did not record a single speciation event in any of the simulations. When inspecting these simulations, we observed that branches were rarely formed, indicating that coexistence was so rarely attained as to not even allow for the initial branching, even though the single branch fluctuated over time when invading genotypes replaced each other.

Discussion

We have studied the coexistence problem of sympatric speciation to see whether complete speciation may fail due to intense competition between newly formed branches in fluctuating environments. We have shown, both by simulations and an analytical approach, that it is a plausible outcome in some cases and that environmental variability may impede or delay branching (fig. 2). Stochastic competitive exclusion was observed in two different ways—either one of the newly formed branches became extinct before it was sufficiently separated from the other branch (fig. 1B) or coexistence was so hard to obtain that even

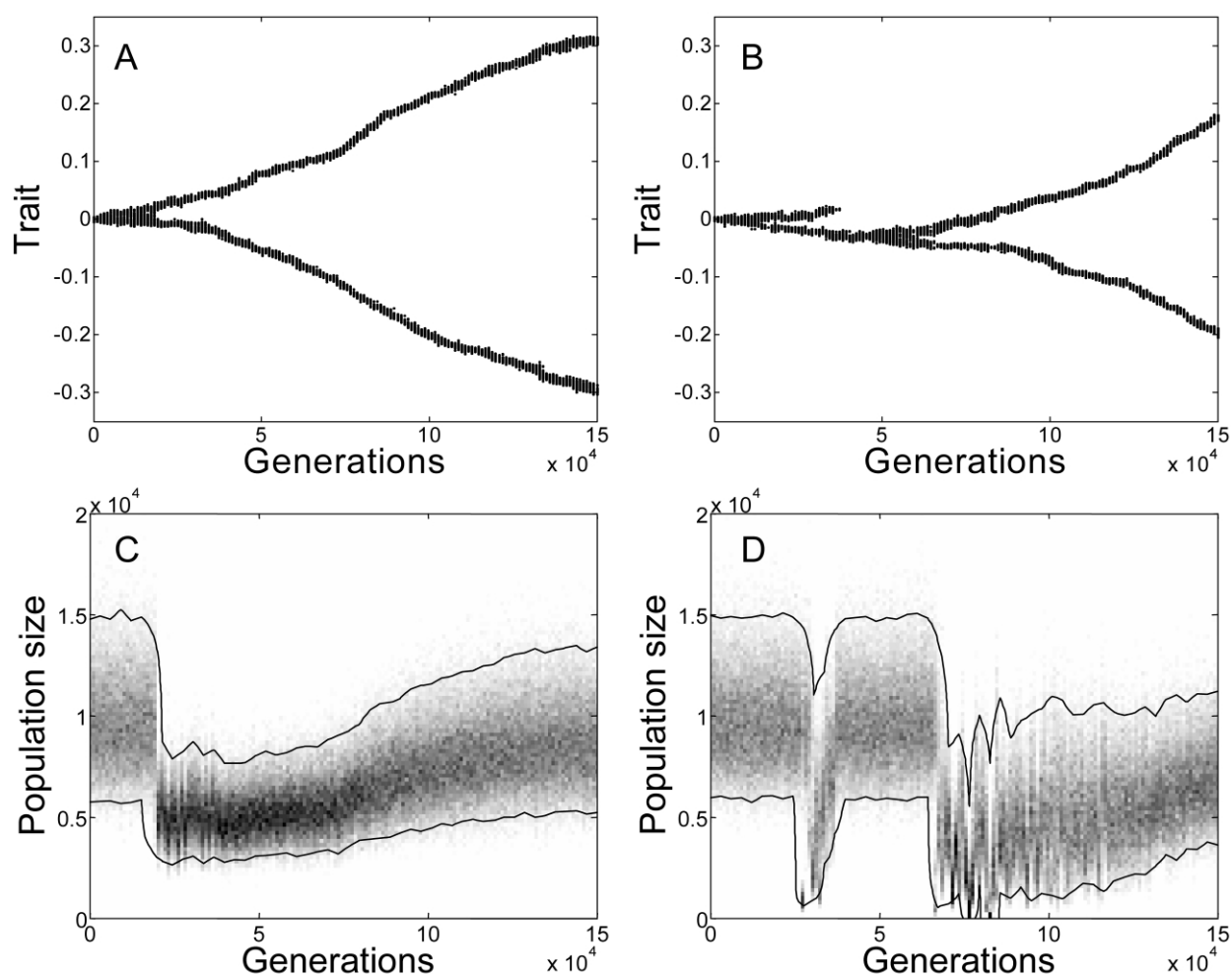


Figure 1: Population dynamics during speciation. *A, B*, Trait values of existing populations over time. Dots represent the genotype values sampled every 1,000 generations. The correlation parameter σ_e was set to 1 in *A* and to 0.1 in *B*. *C, D*, Population size distributions in the course of evolution accumulated over periods of 1,000 time steps. The distribution of the lower branch is shown together with two solid lines indicating 95% interval of the sampled population sizes. A higher (lower) frequency is indicated with a darker (lighter) shade of gray. The distribution in *C* (*D*) corresponds to the simulation in *A* (*B*).

initial branching was impossible. According to our results, delay or failure of complete sympatric speciation can be expected when environmental fluctuations are strong in combination with quickly declining environmental correlation (fig. 2). This is in harmony with the result from Ives et al. (1999), that high environmental correlation makes competing species vary more in concert and reduces their variability. Time series analysis of population data shows that environmental stochasticity is often strong (e.g., Turchin and Taylor 1992; Bjørnstad et al. 1995; Sæther et al. 1998), making these scenarios plausible. We find it interesting that environmental correlation is of importance

not only for the population dynamics but also for the evolutionary outcome.

Given the importance of environmental correlation for our results, we may ask under what circumstances high or low correlations can be anticipated. The environmental variability in this model can be related to any kind of environmental factor, biotic as well as abiotic, that in some way translates into variation of growth rates. The most common case is probably that environmental correlation declines more slowly than competition because we are dealing with species that were initially closely related and are likely to respond similarly when facing the same en-

vironmental changes. However, for divergence of traits corresponding to differentiation in resource utilization, as studied here, one can expect correlations decaying at rates comparable to the decay of the strength of competition if abundances of different resource types fluctuate independently of each other, at least in the absence of other highly influential environmental fluctuations. Both of these scenarios correspond to correlation decay rates at or to the right of the dashed line in figure 2, that is, where no effect on the process of speciation is expected.

According to our results, situations occur that render sympatric speciation slow or unlikely if environmental correlation decreases more quickly than competition in trait space (fig. 2). It is harder to envision such situations for strict resource competition scenarios, but one could, for example, imagine a competitive community in which the populations are strongly affected by parasites or infectious diseases. If parasites and diseases spread only within species, fluctuations in parasitic load or disease mortality will be uncorrelated between populations. Demographic stochasticity is another source of variation that is totally uncorrelated between populations and hence species. It is not important for large populations, but it can generate large fluctuations in small populations (Lande 1993) and may thus decrease the total correlation between species. In this context, demographic stochasticity can be hard to disentangle from other effects of small population size, such as genetic drift and a decreased number of mutations that will further increase the risk of competitive exclusion by slowing down the divergence and thereby exposing populations to an elevated extinction risk for a longer period. These considerations have consequences for field observations and experiments that attempt to verify theories of sympatric speciation. When searching for suitable environments for this process, researchers may be tempted to look at relatively small habitats, for example, crater lakes (Schliewen et al. 1994) and small post-Pleistocene lakes (Schluter and McPhail 1992), in order to guarantee that the population under study is truly sympatric. However, choosing too small a study area, and hence a small population, may reduce the likelihood of finding an example of sympatric speciation, for the reasons mentioned above. Also, evolutionary branching experiments should include a sufficient number of individuals so that uncorrelated fluctuations due to demographic stochasticity do not affect the evolutionary process.

Sasaki and Ellner (1995) and Ellner and Sasaki (1996) study genetic polymorphism in the neighborhood of a fluctuating fitness optimum. Their scenario resembles the situation after speciation in our model, where the fitness landscape of one species fluctuates depending on the stochastic changes in the trait value and population density of the other species. Fluctuations in the position of a fitness

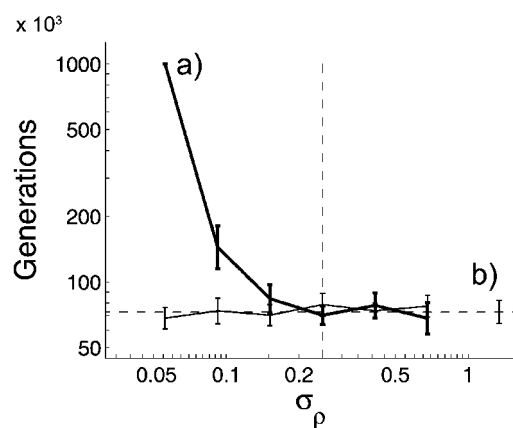


Figure 2: Time to speciation for different environmental correlation decline, σ_ρ . Each data point represents the mean time to speciation from 20 repeated simulations, with error bars corresponding to approximate 95% confidence intervals (except at point *a*, where no speciation was recorded). The thick solid line connects mean time to speciation in scenarios with strongly fluctuating environments ($\sigma_\epsilon = 0.2$), and the thin solid line connects cases with weakly fluctuating environments ($\sigma_\epsilon = 0.05$). Mean time to speciation without environmental fluctuation ($\sigma_\epsilon = 0$) is shown by the horizontal dashed line and the rightmost error bar (*b*). The vertical dashed line indicates the rate of decline of competition, σ_ρ , for all simulations. For further details, see the appendix in the online edition of the *American Naturalist*.

optimum results in growth-rate fluctuations for a given population and can result in positively as well as negatively correlated environments, depending on the difference in trait space between the species (see also Lehman and Tilman 2000). These models hence provide examples of a mechanism by which environmental correlation will decline with distance in trait space. Interestingly, Sasaki and Ellner reach a conclusion opposite to ours, namely, that coexistence of two (and more) morphs is enhanced by increasing the fluctuations in the position of the optimum. The reason for this stems from details in the underlying population model, however. Their model is similar to the lottery models proposed by Chesson and Warner (1981), where strong fitness advantages for small populations and overlapping generations give rise to a storage effect, which allows for coexistence in variable environments but not in nonchanging environments. This is a situation very different from our model, where generations are discrete, there is no such fitness advantage for small populations, and coexistence is obtained in the deterministic case. More importantly, we envision competition for a distribution of resources, a resource landscape rather than a single resource (space). Further, the effect of uncorrelated or even negatively correlated environments differs a lot between the two population dynamic models. In the model of Sasaki and Ellner (1995) and Ellner and Sasaki (1996), weak

or negative correlation increases the fitness advantage for small populations, whereas it leads to larger asynchrony and hence increases the negative impact of competition on a small population in our model. All these differences make a direct comparison between our results difficult. We believe our results to be quite general but conclude that some circumstances, such as a storage effect, may in fact reverse the effects of both environmental variation and correlation.

In scenarios where the divergence leading to sympatric speciation occurs in traits not involved in niche separation, for example, in traits controlling sexual conflicts (Gavrilets and Waxman 2002) or mate choice (van Doorn et al. 1998), there is a more open question of how the rate of decline in environmental correlation relates to decline in resource competition. If divergence is not accompanied by niche differentiation, resource competition α can be expected to remain relatively high, regardless of whether the environmental correlation declines. If for some reason the new daughter species start to respond differently to environmental fluctuations but continue to compete for the same resources, our results imply that extinction risks may become substantial. This is in line with the results of van Doorn et al. (1998), that a certain degree of resource partitioning is necessary to avoid competitive exclusion.

To simplify the model, we did not include explicit genetics or sexual reproduction, both of which are considered by several authors to greatly complicate sympatric speciation and render it improbable (Gavrilets 2005; Polechova and Barton 2005; Waxman and Gavrilets 2005). We nevertheless argue that our main conclusions are still valid when such complications are included. Low environmental correlation simply poses an additional problem that may even further decrease the rate of speciation. The effect would be particularly severe if evolution of assortative mating makes sympatric speciation a slow process, especially since the elevated risk remains for a certain time after the initial splitting (fig. 1). In such cases, it is possible that we have considerably underestimated the expected time to speciation. On the other hand, once reproductive isolation is achieved, the critical period of high extinction risk may be reduced if sexually reproducing species evolve more quickly than asexuals (Crow and Kimura 1965; Maynard Smith 1974; Kim and Orr 2005). With the evidence at hand, we thus cannot make any substantiated predictions about how the mode of reproduction would affect our results quantitatively. Effects of environmental fluctuations on population dynamics during the stage when reproductive isolation is built up are dependent on genetic structure, mechanisms of assortative mating, and more. Once reproductive isolation is achieved, however, the ecological dynamics are similar to those studied in this model, and the only possible difference from the scenario we are

studying would be the rate at which the species diverge. This rate, however, is model dependent, as are the rates of decline in environmental correlation, mutation rates, and so forth. It is an open question whether alternative model assumptions will be more or less affected by the increased extinction risks we have studied, and it is hard to determine exactly where the critical limit lies. Qualitatively, however, this does not change our conclusion that if environmental correlation decays sufficiently quickly compared to interspecific competition, high risks of extinction will impede sympatric speciation.

In conclusion, this study suggests that correlations between population growth fluctuations must be quite low in order to significantly affect the speciation process. This will occur, for instance, if population sizes are small and hence demographic stochasticity is strong, which offers some guidance as to where to find examples of sympatric speciation in nature and for experimental setups. Other cases of low correlation should be possible, however. A more mechanistic modeling of environmental stochasticity could reveal under what circumstances it can be expected, and this would be an interesting aspect to include in future studies. Our results also suggest that if sympatric speciation occurs as a consequence of divergence in traits not leading to niche separation, extinction risks will be considerable. However, if speciation is driven by competition for resources and population fluctuations are driven by variations in the same resources, environmental correlation can be expected to be rather high or intermediate, making this kind of speciation quite robust to environmental fluctuations.

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