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# How Does Climate Influence Speciation?

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ABSTRACT: Variation in climatic conditions over space and time is thought to be an important driver of speciation. However, the role of climate has not been explored in the theoretical literature on speciation, and the theory underlying empirical studies of climate and speciation has come largely from informal, verbal models. In this study, we develop a quantitative model to test a relatively new but theoretically untested model of speciation (speciation via niche conservatism) and to examine the climatic conditions under which speciation via niche conservatism and speciation via niche divergence are most plausible. Our results have three broad implications for the study of speciation: (1) ecological similarity over time (niche conservatism) can be an important part of speciation, despite the traditional emphasis on ecological divergence, (2) long-term directional climate change promotes speciation via niche conservatism for species with low climatic-niche lability, whereas climatic oscillations promote speciation via niche divergence for species with high climatic-niche lability, and (3) population extinction can be a key component of speciation.

*Keywords:* climate, model, niche conservatism, niche evolution, speciation, theory.

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## Introduction

The responses of organisms to variation in climate (over both space and time) are thought to be important drivers of speciation. For example, the influence of climate on rates and patterns of speciation has been hypothesized to underlie global patterns of biodiversity, particularly the high richness of tropical regions (e.g., Mittelbach et al. 2007). Quaternary climatic oscillations may also have an important role in speciation, but this has been controversial (e.g., Jansson and Dynesius 2002; Barnosky 2005; Lovette 2005; Hoskin et al. 2011). However, the role of climate in speciation is largely unexplored in the theoretical speciation literature (e.g., Turelli et al. 2001; Coyne and Orr 2004). Thus, the current literature relating speciation and climate consists largely of empirical tests of informal verbal models.

These verbal models suggest that climate may drive speciation through at least the two mechanisms of niche divergence and niche conservatism. First, when different populations of a species occupy different habitats, the different climatic conditions they inhabit may impose divergent selection that drives the evolution of reproductive isolation between them, as suggested by hypotheses of "ecological speciation" (Schluter 2001, 2009; Rundle and Nosil 2005) or "gradient speciation" (Moritz et al. 2000). Under this mechanism, climatic-niche divergence is necessary for the two incipient species to occupy different habitats. These incipient species may be reproductively isolated simply because one species cannot occur in the habitat of the other. Alternatively, reproductive isolation may evolve as a pleiotropic effect of niche divergence.

Second, under the hypothesis of speciation via niche conservatism (Wiens 2004), differences in climate over space serve as a barrier to dispersal between allopatric populations. Under this scenario, incipient species on either side of a barrier of unsuitable habitat fail to adapt to climatic conditions there because they maintain similar climatic tolerances over time (i.e., niche conservatism). Once they are geographically isolated because of niche conservatism, these allopatric populations may then evolve intrinsic reproductive isolation through various mechanisms, including (1) pleiotropic effects as a by-product of divergence in traits unrelated to climate, (2) divergent adaptations to similar environmental conditions, and (3) epistatic interactions between genes whose fixation in different populations does not require ecological niche divergence (e.g., fixation via genetic drift). The idea that geographic isolation involves the separation of suitable habitats by unsuitable habitats is certainly not new (e.g., Mayr 1963), but allopatric speciation has only recently been hypothesized to be associated with climatic-niche conservatism (Wiens 2004).

A burgeoning number of empirical studies have now

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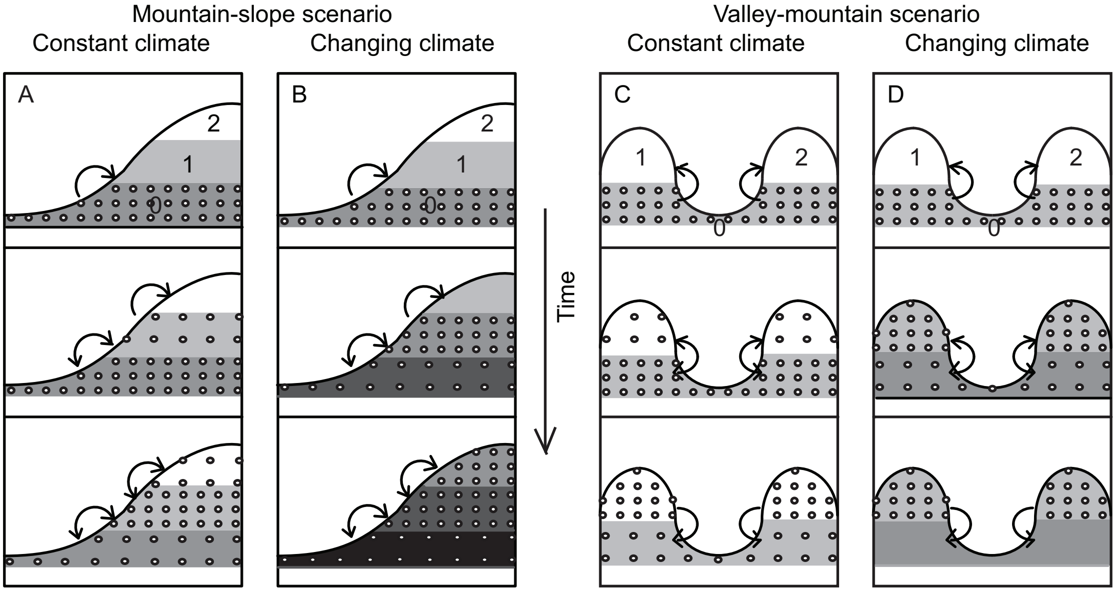

**Figure 1:** Schematic illustrations of the mountain-slope scenario (*A*, *B*) and the valley-mountain scenario (*C*, *D*), given both constant and changing climate. In all the scenarios, the ancestral population initially occupies the lowland habitat (habitat 0) and colonizes the montane habitats (habitats 1 and 2). Darker habitats have higher temperatures. Dotted habitats are inhabited by the species. Populations with denser dots are more fit in their habitats and have higher population densities. Temperature is temporally constant in *A* and *C* and increases over time in *B* and *D*. Arrows indicate directions of dispersal of individuals. In *A* and *B*, colonization of new climatic zones and adaptation to those different zones potentially lead to speciation via niche divergence. In *D*, the initially lowland species colonizes montane regions as climate warms and lowland regions become inhospitable (because of failure to adapt to these conditions), eventually leading to geographic isolation of the montane populations and allopatric speciation via niche conservatism.

addressed these two possible speciation mechanisms, mostly on the basis of comparisons of the climatic distributions of sister species (e.g., Peterson et al. 1999; Kozak and Wiens 2006, 2007; Raxworthy et al. 2007; Warren et al. 2008; Hua and Wiens 2010; McCormack et al. 2010; Cadena et al. 2012). These studies have collectively found evidence supporting both mechanisms. However, it remains highly unclear why speciation seems to occur through climatic-niche conservatism in some cases and through niche divergence in others.

Numerous mathematical models have been developed to examine how disruptive selection imposed by habitat differences (e.g., Endler 1977; Barton 1999) or biological interactions (e.g., Doebeli and Dieckmann 2000, 2003; Mizera and Meszéna 2003) may lead to reproductive isolation among populations (see the extensive review by Gavrilets [2004]). This body of work is very useful for understanding speciation through niche divergence. In fact, any model that considers local adaptation could potentially be relevant for understanding how climatic differences between habitats relate to speciation via niche divergence. However, no studies have focused on speciation via niche conservatism, nor have any tried to understand both speciation mechanisms under the same framework. Therefore, we still know little about the processes of speciation via climatic-niche conservatism and its plausibility relative to speciation via climatic-niche divergence.

In this study, we develop a numerical model to test the plausibility of these two basic verbal models of how climate drives speciation (niche conservatism and niche divergence). Specifically, we ask: under what conditions of climatic variation (over both space and time) is one speciation mechanism more plausible than the other? The model includes the geographic distribution of populations in different habitats as well as the evolution of a trait reflecting the climatic niche and the evolution of postzygotic (hybrid viability) and premating isolation between populations.

## Methods

### *Climatic Background*

Our model starts with three habitats of a species (habitats 0, 1, and 2; fig. 1). These habitats differ on one axis of the multivariate climatic niche (e.g., temperature) and take the values $\hat{z}_0$, $\hat{z}_1$, and $\hat{z}_2$. We assume that most climatic variation occurs between rather than within habitats. For example, the three habitats could represent different forest types that occur at different elevations and experience very different climatic regimes (e.g., oak vs. pine vs. fir forest). Initially, only one of the three habitats is populated by the species. Over time, the ancestral population may invade adjacent habitats, and reproductive incompatibility may then accumulate among populations in different habitats. We assume that a trait (e.g., physiological tolerance to temperature) influences individual fitness under the given climatic-niche axis. We refer to this trait as the "climatic trait" hereafter. The climatic-trait values follow a normal distribution in the ancestral population. The trait distribution initially has a mean equal to the climatic value of the ancestral habitat, and its genetic variation ($V_{\mathrm{LE}}$) is at linkage equilibrium. Higher levels of genetic variation correspond to higher heritability for the climatic trait and thus more rapid response to selection (e.g., Bulmer 1980). Therefore, we use $V_{\mathrm{LE}}$ to measure how conserved the species is on the climatic-niche axis.

We first examine how spatial variation in climate influences speciation by assuming spatially variable but temporally constant climate. We then examine how temporal variation in climate influences speciation by assuming two patterns of climate change over time. Under the first pattern, climate changes at a constant rate $b$ in the same direction until the initially inhospitable habitat becomes suitable for the species (see fig. 1). Under the second pattern, climate oscillates as a sine wave. The sine wave has an amplitude equal to half the maximum difference in climatic conditions across the three habitats. The frequency equals $b/(2 \times \text{amplitude})$, where $b$ is the rate of directional climate change. The sine wave takes the same amount of time as the directional pattern of climate change does to make the initially inhospitable habitat suitable for the species. Thus, the two temporal patterns are roughly comparable.

We focus on two types of spatial variation in climate, which we call the "mountain-slope" scenario and the "valley-mountain" scenario. Under the mountain-slope scenario, the three habitats occur at different elevations along a mountain slope and the ancestral population occupies the lowland habitat (habitat 0; fig. 1*A*, 1*B*). Under a constant climate over time (fig. 1*A*), the ancestral population colonizes the high montane habitat (habitat 2) by first adapting to the midelevation habitat (habitat 1). Under a changing (warming) climate (fig. 1*B*), climatic-niche divergence occurs when the lowland population adapts to increasing temperature at the same time as the warming climate helps the species to colonize higher elevations. Under this spatial variation in climate, climatic-niche divergence is essential to population expansion along the mountain slope and therefore to speciation.

Under the valley-mountain scenario, the three habitats are a series of lowland and montane habitats, where the "middle" habitat (habitat 0) is in lowlands and the two "end" habitats (habitats 1 and 2) are in montane regions and have the same climatic conditions (fig. 1*C*, 1*D*). The ancestral population again occupies the lowland habitat. Given a warming climate (fig. 1*D*), the lowland habitat becomes less suitable and the montane habitats more suitable over time. The lowland population may then become extinct if the species fails to adapt to higher temperatures, which leads to geographic isolation and eventual speciation of the montane populations. Under this pattern of spatial and temporal variation in climate, population expansion into different mountaintops is facilitated by climate change and climatic-niche conservatism is essential to speciation by causing geographic isolation (i.e., species cannot adapt quickly enough to the warming climate in the valley). Under a constant climate (fig. 1*C*), climatic-niche evolution is necessary for the species to colonize montane habitats. The lowland population may also become maladapted to lowland temperatures over time, if gene flow from montane populations swamps stabilizing selection on the lowland population. Therefore, it is unclear which speciation mechanism contributes more to speciation under these constant climatic conditions, if at all.

In addition, we also examine alternate scenarios in which the ancestral habitat has a different location on the niche gradient. First, we examine speciation under the mountain-slope scenario when the ancestral population occupies the middle habitat (i.e., habitat 1 in fig. 1*A*). Second, we examine speciation under the valley-mountain scenario when the ancestral population occupies an end, montane habitat (e.g., habitat 1 in fig. 1*C*, 1*D*).

Given these different patterns of climatic variation over space and time, we modeled speciation processes for each set of conditions by numerically approximating changes in four properties of each population. These properties are (1) population size ($N$), (2) the mean ($z$) and variance ($V$) of the climatic trait, (3) hybrid viability between individuals from different populations ($D$), and (4) the mating probability between individuals from different populations ($D_{\mathrm{s}}$). Hybrid viability and mating probability are then used to estimate the plausibility of speciation. In each generation, two gametes can produce a fertile adult if they survive gametic selection (related to $D$) and if their offspring survive phenotypic selection related to climate (related to $z$ and $V$). After the offspring become adults, a proportion of adults ($m$) migrate to adjacent habitats. After migration, mating occurs, along with sexual selection (related to $D_{\mathrm{s}}$). In the following sections, we describe in detail how we model each of these four properties.

### Population Size

To estimate population size ($N$), we start with the differential equation for population growth, using population 1 as an example: $dN_1/dt = \bar{w}_1(t)N_1(t)$, where $\bar{w}_1(t)$ denotes the average fitness of individuals in population 1. Assuming that individual fitness under the climatic conditions of a habitat does not influence the strength of competition between individuals within and among populations, we can write $\bar{w}_1(t)$ as

$$\bar{w}_1(t) = \bar{r}_1(t) - \frac{\bar{r}_1(t)}{C}[N_1(t) + N_{01}(t) + N_{21}(t)] - \frac{[\hat{z}_1 - z_1(t)]^2}{2V_s} - \frac{V_1(t)}{2V_s}.$$

The first term, $\bar{r}_1(t)$, denotes the intrinsic growth rate of population 1, which is associated with reproductive success within and among populations (see appendix, available online). The second term gives the total amount of competition for population 1 in its habitat, where $C$ denotes the carrying capacity for individuals with the optimum climatic-trait value of the habitat; $N_{01}(t)$ and $N_{21}(t)$ are the numbers of migrants from populations 0 and 2 to where population 1 occurs. The last two terms represent the stabilizing selection on the climatic trait (mean $z_1(t)$ and variance $V_1(t)$) around the optimum that equals the climatic value of the habitat $\hat{z}_1$, where $V_s$ measures the strength of selection, with larger values corresponding to weaker selection. We then use the Beverton-Holt equation (Beverton and Holt 1957) to approximate discrete population growth over nonoverlapping generations.

### Climatic-Niche Evolution

Following standard quantitative genetic theory (Bulmer 1980), we assume that the climatic trait is approximately normally distributed before and after selection. This assumption holds even under disruptive selection, if the trait is affected by many loci with small and additive effects (Turelli and Barton 1994). The mean and variance of the trait after selection become

$$z_1(t+1) = z_1(t) + [\hat{z}_1 - z_1(t)]\frac{V_{g1}(t)}{V_1(t) + V_s}$$

and

$$V_{g1}(t+1) = V_{g1}(t) - \frac{V_{g1}^2(t)}{V_1(t) + V_s},$$

respectively (Bulmer 1980), where $V_{g1}(t)$ is the additive genetic variance and $V_1(t) = V_{g1}(t) + V_e$, where $V_e$ denotes environmental variance. The mean and additive genetic variance after migration become

$$z_1^*(t+1) = z_1(t+1) + m_{e01}[z_0(t+1) - z_1(t+1)] + m_{e21}[z_2(t+1) - z_1(t+1)]$$

and

$$V_{g1}^*(t+1) = V_{g1}(t+1) + (1 - m_{e21} - m_{e01}) \times \{m_{e01}[z_0(t+1) - z_1(t+1)]^2 + m_{e21}[z_2(t+1) - z_1(t+1)]^2\},$$

respectively (Bulmer 1980), where $m_{e01}$ and $m_{e21}$ are the effective migration rates from populations 0 and 2, respectively, to population 1. The variance after reproduction further becomes

$$V_1^*(t+1) = \left(1 - \frac{1}{2N_{e1}}\right)\left[\frac{1}{2}V_{g1}^*(t+1) + \frac{1}{2}V_{LE}\right] + V_e$$

(Bulmer 1980), where $V_{LE}$ is the genetic variance at linkage equilibrium and $N_{e1}$ is the effective population size of population 1. We describe the estimation of the effective migration rate and effective population size in the appendix.

### Hybrid Dysfunction

The evolution of hybrid dysfunction is commonly attributed to the accumulation of incompatible gene interactions between gametes (the Dobzhansky-Muller model; Dobzhansky 1936; Muller 1942; Matute et al. 2010; Moyle and Nakazato 2010). Therefore, we assume that a set of loci is associated with hybrid dysfunction and that each mutation on these hybrid-dysfunction loci has a complementary mutation on a different locus. These complementary mutations build genetic backgrounds that resemble the adaptive-ridge metaphor under the Dobzhansky-Muller model. For example, if there is a hybrid-dysfunction locus with two alleles, *A* and *a*, and allele *b* is the complementary mutation for the allele *a*, then gametes with allele *A* are compatible with gametes with allele *a* only under the genetic background with allele *b*. Consequently, the number of incompatible genes (variable *D*) between two gametes is the number of mutations on hybrid-dysfunction loci in one gamete that do not have complementary mutations in the other gamete. Following Gavrilets (1999), we assume that two gametes can produce viable and fecund offspring only if the number of incompatible genes between them is no more than *K* loci. We modified the model of Gavrilets (1999) to be more in line with the Dobzhansky-Muller model because Gavrilets assumed reproductive incompatibility as a result of heterozygous disadvantage within a locus rather than as deleterious epistatic interactions among alleles on different loci. Details of the model are included in the appendix.

The review of Presgraves (2010) on the genetic basis of hybrid dysfunction suggests that the evolution of hybrid dysfunction often involves neutral (e.g., duplicated genes) or deleterious (e.g., selfish genes) mutations. Those mutations may also have pleiotropic effects on adaptation to novel environments (e.g., Lee et al. 2008) or have tight physical linkage to genes under natural selection (e.g., Via 2009). Therefore, we assume two scenarios of mutations on hybrid dysfunction loci. Under one scenario (hereafter the "non–magic trait" scenario), mutations on a fixed number of hybrid dysfunction loci are selfish genes and mutations on all the other hybrid dysfunction loci are neutral except for their deleterious effect on reproductive incompatibility. Under this scenario, climatic-niche divergence and conservatism influence speciation mainly by influencing the geographic distributions of populations and consequently the level of gene flow between populations. The other scenario (hereafter the "magic-trait" scenario) is similar, except that a fixed number of hybrid-dysfunction loci are not selfish genes but instead are genes with pleiotropic effects on adaptation to novel climatic conditions. Under this scenario, climatic-niche evolution influences speciation not only by influencing the geographic distributions of populations but also by directly influencing the fixation rates of hybrid dysfunction loci.

### *Mate Choice*

Besides hybrid dysfunction and geographic isolation, populations may also become reproductively isolated if individuals from different populations do not mate when they meet. We model the evolution of mate choice in the same way as for hybrid dysfunction, by making an analogy between mutations on hybrid-dysfunction loci and a set of male traits and their corresponding female preferences and complementary mutations. We assume that two individuals do not mate if the male fails to display more than $K_s$ male traits that are preferred by the female. The number of these male traits is denoted as variable $D_s$. In the set of male traits and female preferences, we assume that each male trait and the corresponding female preference are determined by a single separate locus. Similar to the case of hybrid-dysfunction loci, we also assume two scenarios for mutations on male traits. Under the non–magic trait scenario, we assume a fixed number of male traits for which females initially have no preference. Mutations on these male traits should not affect mating success and are therefore neutral. The other male traits are assumed to be already preferred by females. Thus, mutations on these male traits should suffer a selective disadvantage because the mutant male has a trait that is not preferred by any existing females in the population. Under the magic-trait scenario, mutations on a fixed number of male traits are not neutral but arise as the pleiotropic effect of adaptation to novel climatic conditions (i.e., magic traits; Servedio et al. 2011). Details on modeling mate choice are included in the appendix.

### *Speciation Criterion*

Based on the biological species concept (widely used in speciation theory; Coyne and Orr 2004), incipient species are considered distinct species if they are intrinsically reproductively isolated. Using this criterion, one can consider speciation to have been achieved if the product of hybrid viability (a function of variables $D$ and $K$; see appendix) and the intrinsic mating probability (a function of variables $D_s$ and $K_s$; see appendix) between individuals from the two incipient species equals 0 (i.e., all hybrids are inviable and/or the probability of two individuals mating is 0). Nevertheless, reproductive isolation is not an all-or-none phenomenon, and hybridization between otherwise distinct species is commonly observed in nature (Coyne and Orr 2004). Therefore, we also include a scale bar indicating the probability that individuals from the two end populations will successfully produce offspring. This probability equals the product of hybrid viability and intrinsic mating probability. We focus on speciation between populations in the two end habitats because (1) the population in the middle habitat tends to have low reproductive success because it hybridizes with both populations in the end habitats, and (2) the middle population is of less interest, especially for speciation via niche conservatism, where population 0 is located in the barrier between populations 1 and 2.

### *Parameter Values*

To examine how spatial variation in climate influences speciation, we set the climatic value in the ancestral habitat (see fig. 1) to 0 and the climatic values in the other habitats to random values from a uniform distribution on the climatic-niche axis. Species have either a low degree of niche lability, with genetic variation in the climatic trait at linkage equilibrium ($V_{LE}$) equal to 0.01, or a high degree of niche lability, with $V_{LE} = 0.9$. To examine how temporal variation in climate influences speciation, we report representative results with initial values of $\hat{z}_1 = -10$ (or $-15$), $\hat{z}_0 = 0$, and $\hat{z}_2 = -10$ (or $-15$) units on the climatic-niche axis for the mountain-valley scenario (fig. 1*C*, 1*D*) and values of $\hat{z}_2 = -15$ (or $-20$), $\hat{z}_1 = -7.5$ (or $-10$), and $\hat{z}_0 = 0$ units for the mountain-slope scenario (fig. 1*A*, 1*B*). The rate of climate change is set to a value between 0 and 1 unit on the climatic-niche axis per generation.

For the non–magic trait scenario, we arbitrarily set 100 hybrid-dysfunction loci to be selfish genes and 100 male

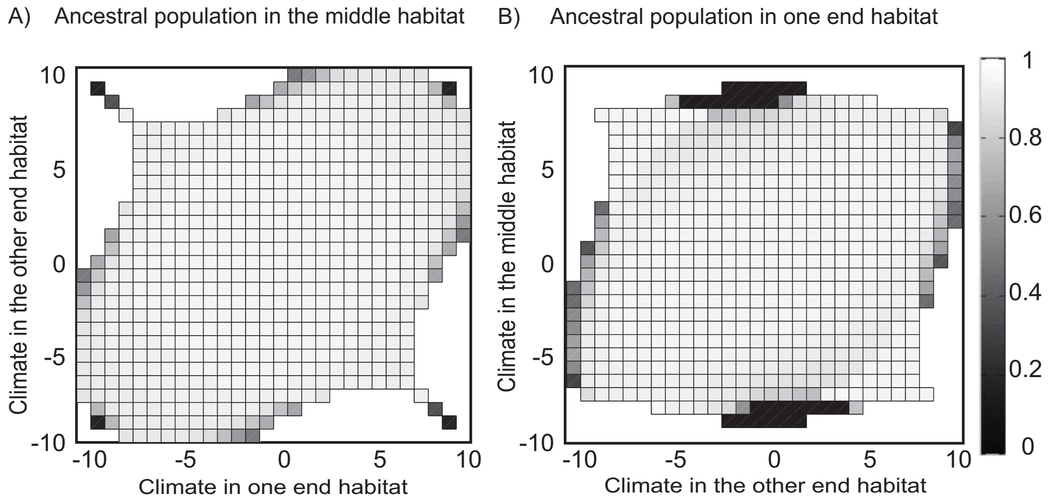

**Figure 2:** Speciation when climate varies over space but not over time. The scale bar represents the probability that individuals from the two end habitats will produce fertile offspring, with 0 indicating complete reproductive isolation between populations (i.e., speciation occurs in black cells), 1 indicating complete reproductive compatibility between populations, and darker colors indicating greater intrinsic reproductive isolation. Empty areas (no squares) indicate that the ancestral population failed to colonize the adjacent habitat. The climatic value in the ancestral habitat is set to 0 in both graphs. In *A*, the ancestral population occurred in the middle habitat, and in *B* it occurred in one of the two end habitats. Speciation (black cells) occurs under two main sets of conditions that are similar to the valley-mountain and mountain-slope scenarios illustrated in figure 1.

traits to be neutral. For the magic-trait scenario, we set 200 hybrid-dysfunction loci and 200 male traits to be associated with climatic-niche evolution, with 100 mutations having positive effects and the other 100 having negative effects on the values of the climatic trait. These numbers are assumed so that roughly equal numbers of nonmagic and magic traits are involved during speciation. Therefore, if speciation turns out to be more likely under one scenario, it is not because there are more loci included in that scenario. Under both scenarios, mutation rates on hybrid-dysfunction loci and male traits are set to $10^{-7}$ per locus per generation (a reasonable mutation rate in eukaryotes; Baer et al. 2007), and their complementary mutation rate is set to $10^{-5}$ (assuming multiple potential sites for complementary mutations). The total mutation rate on hybrid-dysfunction loci, as well as male traits, is set to 0.01. We arbitrarily assume that two gametes produce inviable offspring if the number of incompatible genes between them is more than 20 loci and that two individuals are intrinsically isolated if they have more than 20 mismatches between male traits and female preferences (i.e., $K = K_s = 20$). The physical migration rate ($m$) between populations is 1% of the individuals in the population per generation. For each parameter combination, we iterate the numerical model for $10^5$ generations. Preliminary analyses showed that all values become stable after $10^5$ generations.

## Results

In general, model results under the magic-trait scenario (appendix) and the non–magic trait scenario (figs. 2–4) are similar, and we present them together. Under constant climate over time but variable climate over space, no speciation occurred for species with high niche lability (data not shown). Instead, a single species occurred across all three habitats. For species with low niche lability, speciation was possible under two main sets of conditions (figs. 2, A1; figs. A1–A4 are available online): (1) when climatic conditions in the two end habitats were very similar to each other but differed from those of the middle habitat (similar to the valley-mountain scenario) and (2) when the climate at one end habitat was similar to that of the middle habitat but different from that of the other end habitat (similar to the mountain-slope scenario). Under both of these sets of climatic conditions, the ancestral population did not become locally extinct but was just able to colonize the end habitats and persist in a small population size, potentially representing "peripatric" speciation driven by climatic-niche divergence (Coyne and Orr 2004).

Directional variation in climate over time had contrasting effects on speciation via climatic-niche conservatism versus speciation via climatic-niche divergence (figs. 3, A2). Directional climate change (warming) promoted spe-

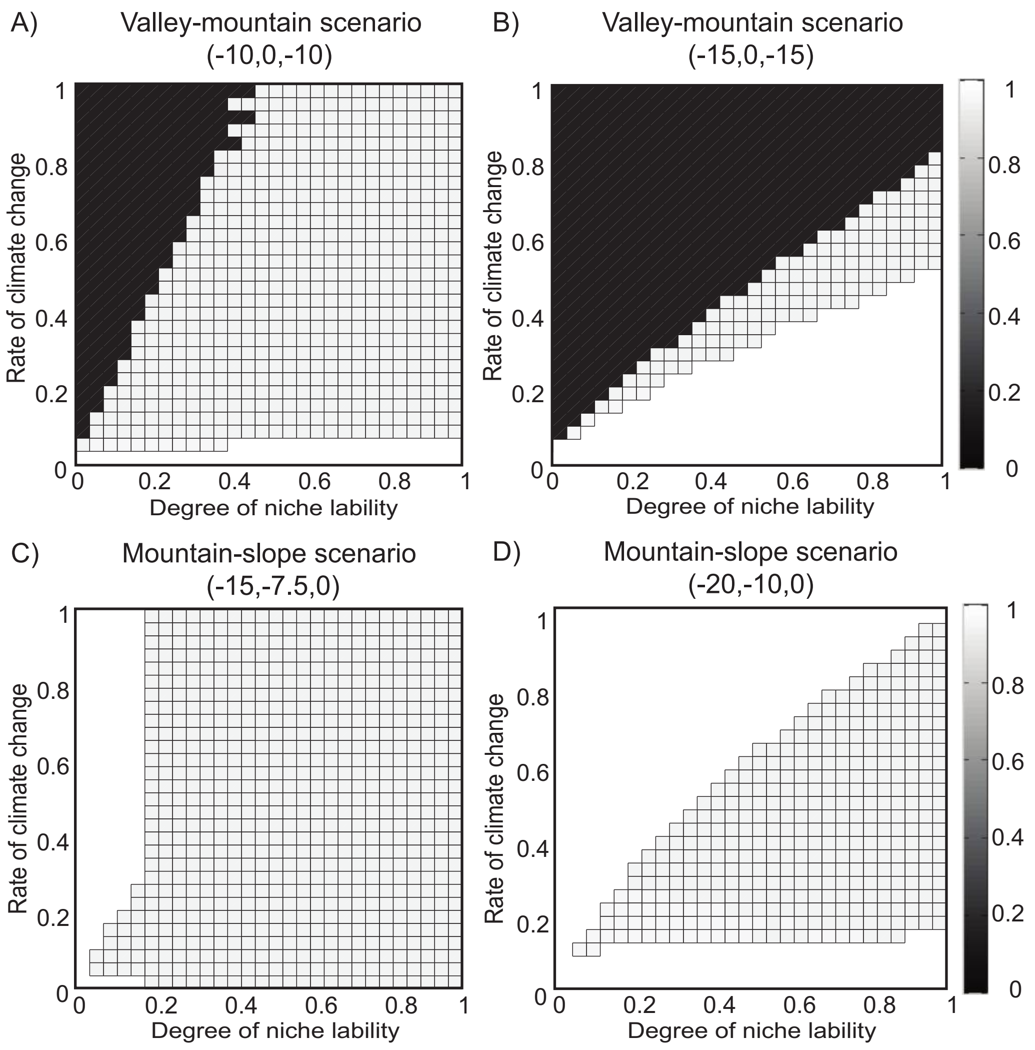

**Figure 3:** Speciation under directional climate change (warming) over time. Graphs show the conditions under which speciation occurs under the valley-mountain scenario (where niche conservatism is potentially important for speciation; *A*, *B*) and the mountain-slope scenario (where niche divergence is potentially important for speciation; *C*, *D*). These conditions are the rates of directional climate change and different levels of niche lability. The scale bar represents the probability that individuals from the two end habitats will produce fertile offspring. Empty areas (no squares) indicate that the ancestral population failed to colonize the adjacent habitat. Speciation occurs in black cells, which also indicate conditions under which the ancestral population becomes extinct during the speciation process.

ciation under the valley-mountain scenario and the non–magic trait scenario (fig. 3*A*, 3*B*), especially for species with low niche lability. The conditions under which speciation occurred under the valley-mountain scenario (black cells in fig. 3*A*, 3*B*) are when the population in the middle habitat (i.e., the lowland population in fig. 1*D*) became locally extinct, indicating that climatic-niche conservatism drove speciation by causing geographic isolation. In contrast, no speciation occurred under the mountain-slope scenario (fig. 3*C*, 3*D*), where climatic-niche divergence was involved. Interestingly, when mutations underlying reproductive incompatibility were the pleiotropic effects of climatic-niche evolution (magic-trait scenario), populations in the two end habitats were not intrinsically reproductively isolated, although they were geographically isolated (fig. A2).

Climatic oscillations over time also had contrasting effects on speciation via climatic-niche conservatism versus speciation via climatic-niche divergence (figs. 4, A3). Climatic oscillations promoted speciation under the mountain-slope scenario (figs. 4*C*, 4*D*, A3) and therefore speciation via climatic-niche divergence. Speciation occurred when a species was just able to persist in all three habitats along a mountain slope through climatic oscillations (figs.

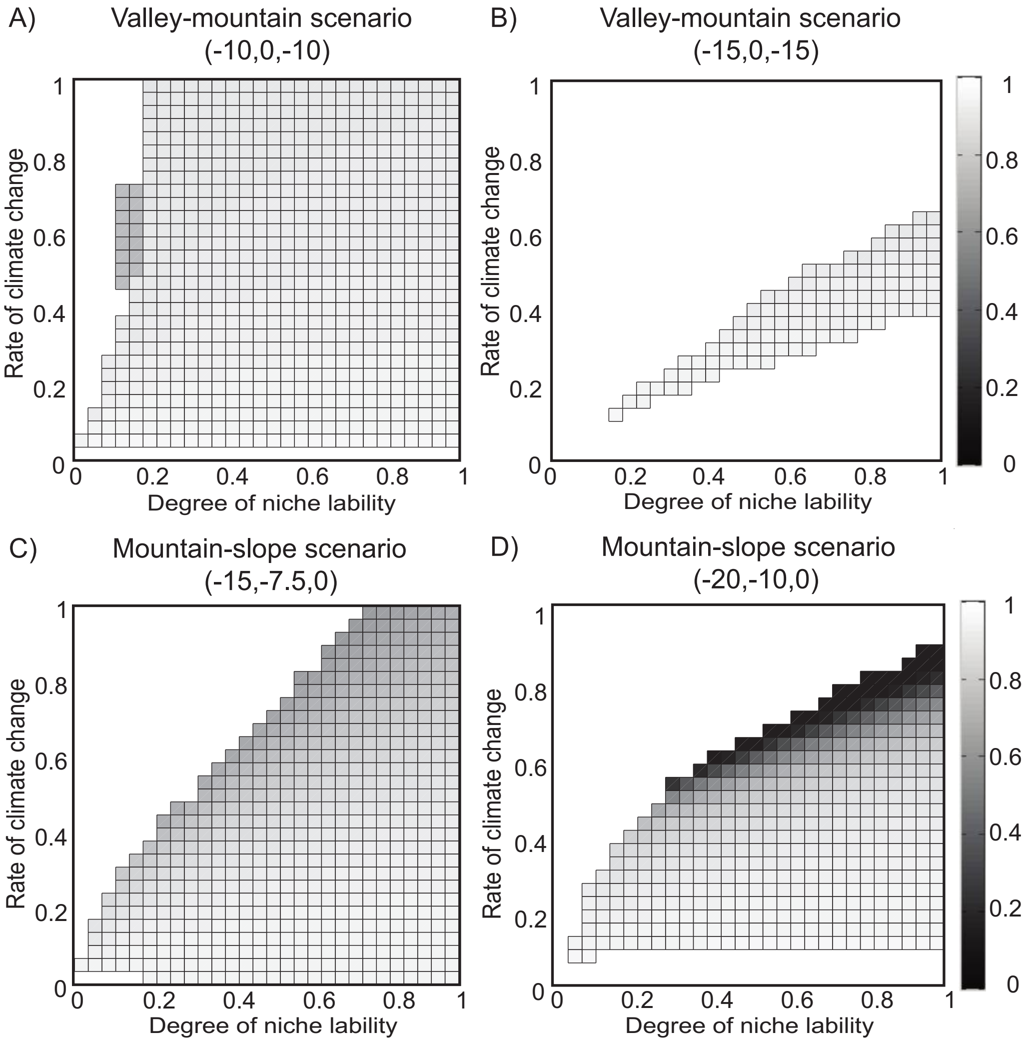

**Figure 4:** Speciation when climate oscillates over time. Graphs show the conditions under which speciation occurs under the valley-mountain scenario (where niche conservatism is potentially important for speciation; *A*, *B*) and the mountain-slope scenario (where niche divergence is potentially important for speciation; *C*, *D*). Empty areas (no squares) indicate that the species failed to establish persistent populations in the two end habitats, where local extinction and recolonization events continually occurred during climatic oscillations. Speciation occurs in black cells, which also indicate conditions where the species was just able to persist in all three habitats along the mountain slope. The scale bar represents the probability that individuals from the two end habitats will produce fertile offspring, with 0 indicating complete reproductive isolation between populations (speciation, black), 1 indicating complete reproductive compatibility between populations, and darker colors indicating greater reproductive isolation.

4*C*, 4*D*, A3, A4). In contrast, climatic oscillations did not promote speciation under the valley-mountain/niche conservatism scenario (figs. 4*A*, 4*B*, A3). When climate oscillations were frequent, species with low niche lability underwent continual local extinction and recolonization events in the two end habitats during climatic oscillations (fig. A4). Under these conditions, reproductive incompatibility was not able to accumulate, and thus no speciation occurred.

## Discussion

Variation in climate is widely considered to be important for speciation, but the details of how climatic variation drives speciation remain poorly understood from a theoretical perspective. Here, we developed a numerical model to test the two basic verbal models of how climate drives speciation, niche conservatism and niche divergence. Our results show that speciation via niche conservatism is theoretically plausible and illustrate the conditions where speciation via niche conservatism and speciation via niche divergence are each most likely. These conditions lead to important predictions for empirical speciation studies. Our results also suggest a counterintuitive relationship between speciation and extinction. We discuss these ideas below.

### *Speciation via Niche Conservatism versus Niche Divergence*

Ever since Darwin, ecology has been thought to potentially play an important role in speciation (Coyne and Orr 2004). However, the literature on "ecology and speciation" has focused almost exclusively on ecological divergence (e.g., Orr and Smith 1998; Schluter 2001, 2009; Via 2002; Rundle and Nosil 2005). Here, we explored a relatively new idea in speciation theory, that the failure of organisms to adapt to different ecological conditions may also drive speciation (Wiens 2004).

We find that under directional climate change over time and a valley-mountain scenario over space, speciation between populations on two mountaintops occurred when the ancestral population in the intermediate lowland habitat became locally extinct, which was most likely for species with low climatic-niche lability (fig. 2*A*, 2*B*). With this climatic barrier to gene flow, complete reproductive isolation was most likely to evolve between populations, given mutations underlying reproductive incompatibility in selfish genes (and possibly other types of nondeleterious mutations, such as mutations on duplicated genes; Presgraves 2010). However, the two montane "end" populations were not intrinsically reproductively isolated when mutations underlying reproductive incompatibility were the pleiotropic effects of climatic-niche evolution (magic-trait scenario; fig. A2). Under this scenario, climatic-niche evolution is limited (i.e., populations shift elevation ranges to track suitable climate rather than adapting to novel conditions), but intrinsic reproductive isolation is tied to climatic-niche evolution. However, this result is based on the assumption that the two mountaintops have similar climatic conditions. In theory, when the two mountaintops have different climatic conditions, speciation can be driven by both climatic-niche conservatism and climatic-niche divergence, with the former leading to geographic isolation between populations and the latter promoting the evolution of reproductive isolation between them (as a pleiotropic effect).

In contrast, speciation via climatic-niche divergence is the predominant speciation mechanism for species with low niche lability under constant climate over time (fig. 2) and for species with high niche lability under a mountain-slope scenario when climate oscillates (fig. 4). Under these two scenarios, climatic-niche divergence is necessary for the species to persist in all three habitats during the speciation process. We also find that the conditions under which speciation via niche divergence occurred were very similar under the non–magic trait and magic-trait scenarios (figs. 2, 4, A1, A3). This result indicates that although climate directly influences the rate of evolution of intrinsic reproductive isolation between populations under the magic-trait scenario, this influence does not outweigh that of climate on the geographic distributions of populations or that of geographic distributions on speciation.

We acknowledge that we modeled only two scenarios for the genetic basis of reproductive isolation: reproductive incompatibility is the result of new mutations that are incompatible with their genetic backgrounds and that may (magic-trait scenario) or may not (non–magic trait scenario) be pleiotropic effects of adaptation to novel climatic conditions. There are other scenarios that have strong empirical evidence. For example, divergence in some traits (automatic magic traits; Servedio et al. 2011) can create immediate reproductive isolation, such as divergence in flowering time (Lowry et al. 2008), in traits related to different pollinators (e.g., Schemske and Bradshaw 1999), or in habitat preferences (e.g., Rice and Salt 1990). If reproductive isolation involves these automatic magic traits, then climatic-niche divergence would drive speciation by directly influencing the fixation rate of mutations underlying reproductive isolation. However, we expect this scenario to give patterns generally similar to those of the "normal" magic-trait scenario that we modeled, especially with regard to conditions favoring speciation via niche conservatism.

### *Speciation and Temporal Patterns of Climate Change*

Our study suggests contrasting effects of different patterns of climate change on speciation, with directional climate change promoting speciation via niche conservatism and cyclical climatic oscillations promoting speciation via niche divergence. These results lead to important predictions for empirical studies of climate and speciation. For example, the Tertiary (~65–2.6 Ma) had three major periods of directional climatic warming, followed by long-term climate cooling, whereas the Quaternary (2.6 to ~0.01 Ma) is characterized by cyclical glacial-interglacial climatic oscillations (Zachos et al. 2001). Our study leads to two predictions: (1) ecologically similar sister species are more likely to have originated in the Tertiary (during periods of directional climate change), and (2) ecologically divergent sister species are more likely to have originated in the Quaternary (although ecological divergence may also occur after populations become geographically isolated via niche conservatism). We note that both scenarios could have occurred in both periods and that the different causes of reproductive isolation (e.g., magic trait vs. non–magic trait) may also explain some of the heterogeneity in these patterns.

There has been considerable debate about the role of Pleistocene climatic changes in driving speciation (e.g., in birds; Avise and Walker 1998; Prodon et al. 2002; Johnson and Cicero 2004; Lovette 2005). This debate has mostly focused on the timing of speciation and not on mechanisms (but see Weir and Schluter 2004). Pleistocene climatic changes seemingly led to fragmentation of many species ranges into refugia (presumably via niche conservatism), but it is unclear whether fragmented populations actually became reproductively isolated (e.g., Hoskin et al. 2011). Similarly, our study does not support the idea that Pleistocene climatic oscillations necessarily promoted speciation via niche conservatism. Instead, our results suggest that speciation along climatic gradients (via niche divergence) may predominate among those species that originated and became fully reproductively isolated in the Pleistocene.

### *Speciation and Population Extinction*

Our study also suggests that the plausibility of speciation is tightly associated with the extinction or persistence of the ancestral population (i.e., the population in habitat 0 in fig. 1). Specifically, under directional climate change, speciation via niche conservatism is plausible when the ancestral, intermediate population becomes extinct (fig. 3*A*, 3*B*). Alternatively, under climatic oscillations, speciation via niche divergence is plausible when the ancestral population is barely able to persist (fig. 4*C*, 4*D*). This latter pattern seems to occur because climatic oscillations cause fluctuations in population size. A small population size leads to strong genetic drift, allowing fixation of hybrid-dysfunction mutations that tend to be selected against because of their deleterious effects on reproductive compatibility. In contrast, a large population size favors fixation of beneficial mutations and thus the complementary mutations of those hybrid-dysfunction mutations. These complementary mutations further build up the adaptive ridge, promoting the fixation of hybrid dysfunction mutations.

Our results therefore imply that speciation and extinction are not always independent and that there may be a positive relationship between speciation and extinction. Interestingly, there are some precedents for such a relationship in both the neontological and the paleontological literature (although it is unclear whether these patterns are related to the processes described here). Weir and Schluter (2007) showed a positive correlation between speciation and extinction rates along latitudinal gradients in birds and mammals. Paleontological data for Neotropical plants showed that increased extinction rates during the Late Paleocene–Eocene thermal maximum were coupled with a striking increase in speciation rates (Jaramillo et al. 2010).

### *Model Assumptions and Future Research*

Our study builds on several previous models, including that of Pease et al. (1989) for population growth, the quantitative genetic approach (Bulmer 1980) for climatic-niche evolution, and the model by Gavrilets (1999) for the accumulation of reproductive incompatibility. Our model is different from most previous speciation models in that it (1) incorporates different aspects of speciation, from the initial range expansion to the establishment of reproductive isolation among populations, (2) incorporates different genetic bases of reproductive isolation, and (3) addresses how environmental changes over both space and time drive speciation.

However, as in almost any theoretical study, our study makes several important assumptions, which should be further tested in future studies. First, we assumed a simple relationship between climatic distributions, physiological traits, species distributions, and the evolution of species in response to climatic conditions. In reality, responses to changing climatic conditions over space and time may be very complex (e.g., Davis and Shaw 2001; Hoffman and Sgrò 2011; Cahill et al. 2013). Furthermore, species distributions may be determined only indirectly by climate, if at all (e.g., climate influences vegetation, which influences prey distribution, and prey distribution directly influences the species' range limits; Gross and Price 2000). Our study represents only a simplified starting point for understanding these complex processes, and these complexities should be explored in future studies. For example, one could include one set of traits representing the physiological responses of species to the direct effects of climate and another set of traits for the indirect effects of climate, such as climate-related changes in prey, parasites, or competitors.

Second, we include only three habitat types in our model, with climatic variation assumed to be primarily between habitats rather than within them. In reality, climate may vary continuously within and between broader habitat types. In future studies, a continuous model could be developed. For example, one could estimate population density by diffusion equations (e.g., Pease et al. 1989), model climatic-niche evolution using Lande's (1976) equation (e.g., Case and Taper 2000), and estimate hybrid dysfunction and mating probabilities from the spatial distributions of allele frequencies of relevant loci (e.g., Nagylaki 1975).

Third, as mentioned above, we investigated only two scenarios for the genetic basis of reproductive isolation. In future studies, more scenarios must be considered. These may include automatic magic traits and incompatible genes (and their complementary genes) that arise from standing genetic variation instead of new mutations. It would also be worthwhile to investigate how the relative prevalence of different scenarios may influence speciation. So far, we have only a rough qualitative estimation of their relative prevalence (e.g., Servedio and Kopp 2011; Nosil 2012).

## Conclusions

In this study, we developed a mathematical model to examine how climate influences speciation. Our study provides the first theoretical support for the verbal model of speciation via niche conservatism. We find that speciation via niche conservatism can be the predominant speciation mechanism under some realistic conditions (e.g., directional climate change). This finding leads to testable predictions for empirical speciation research and may help explain the seemingly contradictory findings of previous empirical studies. Our results also show that population extinction can be critically important to speciation. Nevertheless, our study is only a starting point for understanding how climate influences speciation from a theoretical perspective.

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