How does climate influence speciation: theoretical and empirical perspectives

A Dissertation Presented

by

Xia Hua

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Ecology and Evolution

Stony Brook University

December 2012

Stony Brook University
The Graduate School

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Abstract of the Dissertation

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Many people are now familiar with the idea that climate change can cause extinction. Here, I show how climate change may also lead to the origin of new species. I explore two major aspects of how climate influences speciation. First, variation in climatic conditions over space and time can be a direct driver of speciation, via two mechanisms. Climate may drive allopatric speciation when a geographic barrier that consists of suboptimal climatic conditions for a species divides the species range and climatic niche conservatism of the species limits its adaptation to the climatic conditions, preventing gene flow between the two incipient sister species (speciation via climatic niche conservatism). Climate may also drive gradient speciation by imposing divergent selection across a strong climatic gradient. The subsequent climatic niche divergence may then lead to restricted gene flow and reproductive isolation between two incipient sister species that inhabit different climatic conditions (speciation via climatic niche divergence). The second aspect that I explore is how the level of elevational climatic stratification may affect the range of climatic conditions that a species can tolerate, potentially leading to more limited dispersal of the species between different climatic conditions at different elevations and thus promoting speciation. In my dissertation, I examine these two aspects of climate and speciation from both theoretical and empirical perspectives. Specifically, I develop the first mathematical models to examine: (1) the relative plausibility of speciation via climatic niche conservatism and speciation via climatic niche divergence; (2) the conditions under which climatic stratification affects the evolution of a species' climatic niche breadth. I also conduct an empirical study on latitudinal variation in speciation mechanisms in anurans globally. There is a strong latitudinal gradient in climatic stratification, with greater climatic zonation in the tropics. I examine whether this latitudinal variation in climatic stratification leads to latitudinal variation in species' climatic niche breadths and therefore a latitudinal gradient in the relative plausibility of speciation via climatic niche conservatism versus climatic niche divergence.

Dedication

To my parents, Zhengxiang Hua and Qingchun Xia.

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Acknowledgements

My foremost appreciation goes to my advisor, Dr. John J. Wiens. Through John's mentorship, I find the research area that I truly want to dedicate myself to and I have become a better scientist that I ever could have imagined. I also thank my committee, Dr. Douglas J. Futuyma, Dr. F. James Rohlf, and Dr. Maria R. Servedio for their supports and constructive comments and suggestions. In particular, Doug has greatly helped me with developing evolutionary theories and Jim led me to the wonderful world of statistics and mathematics.

I appreciate all the faculties and staff in Ecology and Eolution for their help and support, without which I never could have come this far. Special thanks to Dr. John R. True and Shian-Ren Liou for treating me like family, to Dr. Fumio Aoki for helping me with C programming, and to Dr. Shu-Dan Yeh, Dr. Jin Gao, and many other friands in the department for letting me love my life.

And finally, to my parents, Zhengxiang Hua and Qingchun Xia. Thank you for everything.

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Introduction

Many people are now familiar with the idea that climate change can cause extinction and anthropogenic climate change is predicted to be a major cause of species extinctions in the next 100 years (e.g., Dawson et al. 2001; Thomas et al. 2004; Pereira et al. 2010; Hof et al. 2011; Cahill et al. 2012). As the opposite side of extinction, speciation has also been hypothesized to be associated with variation in climatic conditions over space and time (e.g. Jansson and Dynesius 2002; Mittelbach et al. 2007; Kozak and Wiens 2010). Climate may influence speciation through at least two aspects. First, the responses of organisms to variation in climate (i.e. climatic niche evolution) can be important drivers of speciation (e.g. Moritz et al. 2000; Wiens 2004). Second, climate may also influence the climatic niches of a species and therefore its climatic niche evolution.

Verbal models have suggested two mechanisms linking climatic niche evolution and speciation. 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. Under this scenario, climate drives "ecological speciation" (Rundle and Nosil 2005; Schluter 2001, 2009) or "gradient speciation" (Moritz et al. 2000). Second, differences in climate over space might serve as an effective barrier to dispersal between allopatric populations, such that incipient species on either side have lower fitness in this barrier of unsuitable habitat and fail to adapt to climatic conditions there (Wiens 2004). These allopatric species may then diverge in response to other climatic or non-climatic factors and evolve intrinsic reproductive isolation. Under this scenario, speciation is driven by the species's failure to adapt to the climatic conditons in the barrier (i.e. speciation via climatic niche conservatism (Wiens 2004), also related to "refugial speciation" (Moritz et al. 2000)). Empirical studies have collectively found evidence supporting both mechanisms, but it remains unclear as to why speciation seems to occur through climatic niche conservatism in some cases and via niche divergence in others.

A good example for how climate may influence the climatic niches of a species (and therefore its climatic niche evolution and speciation) is Janzen (1967)'s hypothesis of "why mountain passes are higher in the tropics". Janzen (1967) hypothesized that the limited seasonal temperature variation in the tropics reduces overlap in thermal regimes between low and high elevations. The greater temperature stratification across elevational gradients in the tropics then makes a tropical species more likely to be evolutionarily adapted to a narrower range of temperature than a species in temperate regions, potentially making mountain passes in the tropics more effective dispersal barriers (hence "higher"). If true, the limited dispersal between different elevations may promote gradient speciation along mountain slopes in the tropics (e.g. Moritz et al. 2000), leading to a potential latitudinal pattern in the relative importance of climatic niche conservatism and niche divergence in speciation, with niche conservatism being more common in temperature areas and niche divergence more prevalent in the tropics (Kozak and Wiens 2007).

In my dissertation, I first present an empirical study in chapter 1 to test whether there is latitudinal variation in the relative importance of climatic niche conservatism and climatic niche divergence in speciation, using frogs as a model system. I then develop the first mathematical model in chapter 2 to examine the relationships between climatic niche evolution and speciation. Specifically, I examine relative plausibility of speciation via climatic niche conservatism and speciation via climatic niche divergence under different climatic variation over both space and time. In chapter 3, I develop the first mathematical model for Janzen's hypothesis to examine why and under what conditions tropical species evolve narrower ranges of temperature tolerance and narrower elevational ranges.

References

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, et al. 2012. How does climate change cause extinction? Proc. R. Soc. B. (published online).

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58.

Hof, C., M. B. Araujo, W. Jetz, and C. Rahbek. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480:516–519.

Jansson, R., and M. Dynesius. 2002. The fate of clades in a world of recurrent climatic change: milankovitch oscillations and evolution. Annual Review of Ecology and Systematics 33:741–777.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101:233–249.

Kozak, K. H., and J. J. Wiens. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. Proceedings of the Royal Society B: Biological Sciences 274:2995–3003.

Kozak, K. H., and J. J. Wiens. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. Ecol. Lett. 13:1378–1389.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10:315–331.

Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annual Review of Ecology and Systematics 31:533–563.

Pereira, H. M., P. W. Leadley, V. Proenca, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarrés, M. b. Araújo, et al. 2010. Scenarios for global biodiversity in the 21st century. Science 330:1496–1501.

Rundle, H. D., and P. Nosil. 2005. Ecological speciation. Ecology Letters 8:336–352.

Schluter, D. 2001. Ecology and the origin of species. Trends in Ecology & Evolution 16:372–380.

Schluter, D. 2009. Evidence for ecological speciation and its alternative. Science 323:737–741.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Wiens, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197.

Chapter 1

Latitudinal variation in speciation mechanisms in frogs

Introduction

It is widely understood that geography is a critical aspect of speciation (e.g., allopatric, parapatric, and sympatric modes; Futuyma 1998; Coyne and Orr 2004), and that speciation may have a strong ecological component (see numerous recent papers on "ecological speciation"; e.g., Schluter 2001; 2009; Ogden and Thorpe 2002; Nosil et al. 2005; Rundle and Nosil 2005). However, the ecological basis for different geographic modes, particularly allopatric speciation, has not been as widely studied. For example, despite the general consensus that the allopatric mode seems to be the most common (e.g., Futuyma 1998; Barraclough and Vogler 2000; Coyne and Orr 2004; Phillimore et al. 2008), there is relatively little research on what ecological factors cause sister species to become geographically isolated from each other (e.g., Wiens 2004a, b).

The ecological niche is a crucial concept when considering the geographic ranges of species (Lomolino et al. 2006), and therefore, the geography of speciation. The fundamental ecological niche of a species determines the biotic and abiotic conditions where the species is able to persist and spread (Hutchinson 1957). There are two general models for speciation in terms of the niche: niche conservatism and niche divergence. Niche conservatism is the maintenance of ecological similarity within species or clades over time (e.g., Peterson et al. 1999; Wiens and Graham 2005). Niche conservatism may be an important driver of allopatric speciation, as it may be the initial cause of geographic isolation between two incipient species (e.g., Wiens 2004a, b; Kozak and Wiens 2006). A species may be split into two descendant species when a geographic barrier that consists of suboptimal environmental conditions for the species divides the species range, and niche conservatism limits adaptation to the ecological conditions at the geographic barrier, preventing gene flow between the two sets of populations (Wiens 2004a). For example, many sister species that are endemic to montane habitats on adjacent mountain ranges presumably originated from an ancestral species that was more widely distributed in the lowlands during periods of cooler climate, and are now confined to higher elevations by climate change. These species presumably became geographically isolated because they were unable to adapt to climatic conditions in the lowlands separating their geographic ranges (Wiens 2004a, b; Wiens and Graham 2005; Kozak and Wiens 2006). This mechanism is also referred to as refuge speciation (Moritz et al. 2000). This model predicts that recently evolved sister species will occur in similar but allopatric habitats, which are separated by less similar habitat in between (Fig. 1.1A). This same basic model could apply to many different types of ecological barriers (Wiens 2004a,b), from the trivial (e.g., terrestrial species separated by oceans) to the more subtle (e.g., xeric-adapted species separated by mesic habitats, stream species separated by rivers).

Under the second model, new species may originate as populations adapt to new niches, through the process of niche divergence. Niche divergence is potentially important for both allopatric and parapatric speciation. For allopatric speciation, species may become allopatric through niche conservatism and subsequently diverge ecologically from their ancestral species' niches in allopatry, limiting any further gene flow between them. Under this model, environmental conditions in each sister species' geographic range are unsuitable for the other species, as is the area in between their ranges, even though the habitats of sister species could still be more similar to each other than they are to the barrier habitat that separates them (Fig. 1.1B). Similarly, species may become allopatric via factors other than climatic niche conservatism, and subsequent niche divergence may then limit further gene flow between them. Under this mechanism, we expect that allopatric sister species would occur in environments that are no more similar to each other than they are to the environment separating their geographic ranges (Fig. 1.1C). Thus, comparing habitats where species occur to where they do not occur is a critical aspect of distinguishing whether niche conservatism is involved in the initial isolation of species, even if the niches of sister species have diverged considerably (Wiens and Graham 2005). It is important to note that these two models of allopatric speciation refer to somewhat different portions of the speciation process: niche conservatism pertains to the initial isolation and origin of lineages, whereas niche divergence pertains to the subsequent divergence of lineages that are already allopatric.

For parapatric speciation, niche divergence may be a common mechanism underlying the initial origin of parapatric lineages (Futuyma 1998; Coyne and Orr 2004). Under this model, incipient species experience divergent selection across a strong environmental gradient (referred to as gradient speciation in Moritz et al. 2000), such as high and low elevation populations along a mountain slope. Adaptation to these different environments eventually leads to restricted gene flow and reproductive isolation between the populations that inhabit them (Coyne and Orr 2004). This model predicts that newly evolved sister species will be parapatrically distributed and occupy adjacent but distinct environments (Moritz et al. 2000).

Recent studies have begun to explore the relative importance of niche divergence and niche conservatism in speciation, particularly using GIS-based environmental data sets. However, these studies have found highly divergent results. For example, some studies have found evidence for speciation by niche conservatism in temperate montane regions (e.g., Kozak and Wiens 2006) and in the tropics (e.g., Peterson et al. 1999; Peterson and Nyári 2007). Others have found evidence for speciation by niche divergence along climatic gradients in the tropics (e.g., Graham et al. 2004; Kozak and Wiens 2007; Raxworthy et al. 2007), as well as a strong association between genetic distances and divergence in the ecological niche in temperate regions (e.g., Rissler and Apodaca 2007; but see Kozak and Wiens 2006; Stockman and Bond 2007).

Kozak and Wiens (2007) suggested that there might be a latitudinal pattern in the relative importance of niche divergence and niche conservatism in speciation, with niche conservatism being more common in temperate areas and niche divergence more prevalent in the tropics (also predicted by Moritz et al. 2000). By comparing climatic data from 16 temperate sister-species pairs and 14 tropical sister-species pairs in the salamander family Plethodontidae, they found that temperate sister species tend to occupy similar climatic niches (which are very different from the intervening “absence” locations) and that tropical sister species tend to occur at different elevations and in different climatic zones. Kozak and Wiens (2007) related this geographic pattern to Janzen's (1967) hypothesis of "why mountain passes are higher in the tropics." Janzen (1967) suggested that more limited temperature seasonality in the tropics selects for organism that are narrowly adapted to a given elevational band, potentially leading to more limited dispersal between different elevations in the tropics. If true, this pattern may promote gradient speciation along mountain slopes in the tropics (e.g., Moritz et al. 2000; Kozak and Wiens 2007), leading to a higher frequency of parapatric speciation and niche divergence in the tropics. Such differences in speciation mechanisms might also be important in explaining why there are more species in the tropics for so many groups of organisms. Indeed, tropical plethodontids have higher rates of diversification than temperate salamander clades (Wiens 2007), and the species richness of plethodontids in tropical Middle America is nearly twice that in temperate North America (even though plethodontids seem to have originated in the temperate zone and spread to the tropics relatively recently). If the results found in plethodontid salamanders apply widely to other groups of organisms, these latitudinal differences in climatic zonation may be important for explaining both variation in mechanisms of speciation across studies and global-scale patterns of species richness.

In the present study, we test whether there is latitudinal variation in speciation mechanisms related to climate, using frogs as a model system. We focus on frogs because they are the sister group to salamanders and may show complementary patterns. We select 79 sister species pairs from across the world and across the phylogeny of frogs. For the first time, we compare the relative frequencies of allopatric, parapatric (or partially sympatric), and sympatric distributions of sister species in the tropics versus the temperate zone. We then test for latitudinal variation in elevational and climatic overlap between sister species. We also evaluate the relative importance of allopatric speciation via niche conservatism versus niche divergence in relation to latitude. In contrast to the results of Kozak and Wiens (2007) for salamanders, we find no tendency for tropical frog species to show greater divergence (or less overlap) in their elevational or climatic distributions than temperate species. Although our results are consistent with Janzen's (1967) hypothesis that tropical species occupy narrower climatic regimes than temperate species, we show that the relationships between climate, latitude, and speciation are not straightforward, and may even be clade-specific.

Materials and Methods

Given that our methods are lengthy and somewhat complex, we provide a summary and overview in a flow chart (Fig. 1.2). Our description of methods follows the order in the numbered boxes in the flow chart, starting with the identification of sister species.

Identification of sister species

We examined recently published phylogenetic analyses across all major frog clades, and identified 79 useable pairs of sister species (see Table S1.1). Although dozens of frog phylogenies have been published recently that collectively include hundreds of species, we only included sister-species pairs from phylogenetic studies in which all described species in their genera or species groups were included. This restriction greatly limited the number of species pairs, but was necessary to ensure (as much as possible) that included species pairs are actually sister species. However, we acknowledge the possibility that undescribed or extinct species might still interdigitate among these species in some cases (although relatively short branch lengths for many species suggest that they are relatively recent, and that there may have been too little time for undiscovered or extinct species to have arisen along these branches). To evaluate whether taxon sampling in a given study was sufficiently complete, we used the summary of taxonomy from Frost's (2008) database. When a phylogeny with adequate taxon sampling was available, we only used sister-species pairs if the stem uniting them had a likelihood or parsimony bootstrap value >50%, or a Bayesian posterior probability > 0.50 (but 88.6% of the 79 species pairs have a bootstrap value >70% or a posterior probability >0.90). In the few cases where there were conflicts among different phylogenies from different datasets (e.g., different genes), we used the phylogeny based on the combined data, if possible. Otherwise, we used the relationships supported by the majority of phylogenies based on different datasets.

Among the phylogenetic analyses we used, phylogenies for the families Eleutherodactylidae (sensu Frost 2008), Hylidae (sensu Frost 2008), and Ranidae (sensu Wiens et al. 2009) are relatively complete. Over 60% (26.6 % from Eleutherodactylidae, 30.4% from Hylidae, 5.1% from Ranidae) of the sister-species pairs we used are from these families. However, these are also among the three largest families of frogs (collectively including ~33%

of all frog species) and they collectively span nearly the entire geographic range of all frog species combined (Amphibiaweb 2009).

Species distribution and speciation modes

We used the species distribution maps from the Global Amphibian Assessment (GAA hereafter; IUCN 2009). The GAA provides a recent estimate of geographic ranges for almost all amphibian species, based on minimum area polygons (IUCN 2009). We acknowledge that such maps are not necessarily without error. However, any errors in these maps should only be relevant to our study if they influence the inferred geographic overlap of sister species. Further, most of our analyses are based on elevational distribution patterns and climatic data (from specific localities), and do not depend directly on these maps. For 14 species without distribution maps available from the GAA, we developed maps in ARCGIS version 8.3 (ESRI, Redland, CA), based on maps and relevant descriptions from the original literature.

We first classified each species pair as being allopatric, parapatric (or partially sympatric), or sympatric, and then compared the frequency of each pattern in tropical versus temperate regions. We defined the tropics as the region between 23.5˚ S and 23.5˚ N latitude, the same angle as the tilt of the Earth's axis, and a standard geographic definition for the tropics. A sister-species pair was considered to occur in the tropics if its latitudinal mid-point (the average of the maximum and minimum latitudes of both sister species) falls within this latitudinal zone. Species pairs were considered allopatric when there was no geographic overlap between them, and a geographic gap or barrier (i.e. one species pair is separated by the Mississippi River) separated their localities. Pairs were considered sympatric if one species' range was entirely within the range of its sister species. Initially, we intended to have a category for parapatrically distributed species to represent this important geographic mode of speciation. However, we found no species pairs with distributions that were truly abutting, only ones that were allopatric, fully sympatric, or partially sympatric. We therefore created an intermediate, "partial sympatry" category for distributions that were partially overlapping.

Using these criteria described above, we classified all species pairs as either tropical or temperate and as either allopatric, partially sympatric, or sympatric. We then compared the frequency of each geographic pattern in each region using the 2×3 G-test with William's correction (Sokal and Rohlf 1995; Fig. 1.2; flow chart step 3).

Elevational and climatic data

In order to test the hypothesis that elevational overlap of sister species decreases at lower latitudes, we determined the elevational overlap for all 79 species pairs. We obtained the elevational ranges of most species from the summary provided for each species in the GAA (IUCN 2009). For species without elevational data in the GAA, we extracted data on elevational distribution from georeferenced specimen localities (see below for methods) and obtained the elevational range by subtracting the minimum elevation from the maximum elevation (Fig. 1.2;

step 4a). The degree of elevational overlap between sister species was calculated using the following formula (Fig. 1.2; step 4b):

Elevational overlap = $0.5(O/R_A+O/R_B)$,

where R_A and R_B are the elevational ranges of species A and B, and O is the absolute elevational overlap of R_A and R_B. This formula is different from the one used in Kozak and Wiens (2007), where the degree of overlap was calculated by dividing the elevational overlap by the elevational range of the species with the smaller elevational range. For their formula, an index of 1.0 describes both sympatric sister species and allopatric sister species distributed over identical elevational ranges (none of the sister species included in Kozak and Wiens (2007) are sympatric). In our study, 12 out of 79 pairs are sympatric sister species, in which one species has a narrower elevational range then the other, whereas allopatric sister species usually share a similar elevational range. Given this difference, our index should be a better estimation of elevational overlap between sister species.

To quantify and compare the climatic distribution of sister species at different latitudes, we first obtained climatic data from each included species using GIS-based environmental layers from georeferenced specimen localities. Specimen localities were obtained from museum collections by searching the HerpNet (www.herpnet.org) database (which includes locality data for all species represented in dozens of U.S. and foreign collections) and from the original literature. Pseudacris locality data were gathered from Lemmon et al. (2007), in which specimen localities were georeferenced by those authors. For species whose specimen localities were not georeferenced by the original collectors, we georeferenced the localities ourselves. Localities were only used that were within 1 km of a georeferenced landmark (e.g., 1 km from a village). All georeferenced localities were then checked against the species distribution maps (e.g., from IUCN 2009 or the original literature). Localities far away from the mapped ranges were eliminated as being potentially erroneous. Although we began with a large number of potential species pairs, we only included pairs if there were at least five useable georeferenced specimen localities for each species (to provide an adequate description of the climatic distribution). We also eliminated species whose available georeferenced localities were highly localized compared to the overall geographic distribution of the species, such that the available climatic data might not match the species' overall climatic distribution. We eventually mapped a total of 2,591 georeferenced specimen localities for 28 carefully selected sister-species pairs (see Tables S1.2 and S1.3 for a listing of species and their data).

For each locality, we extracted elevation and climatic variables from the WORLDCLIM database with 1 km2 spatial resolution (Hijmans et al. 2005), using ARCGIS version 8.3. To quantify the temperature ranges of each species (Fig. 1.2; step 4a), we extracted the maximum temperature of the warmest month (Bio 5) and the minimum temperature of the coldest month (Bio 6) for each locality. The temperature range of the species is the difference between its maximum observed value of Bio 5 and minimum value of Bio 6. To quantify the temperature overlap between sister species, we first extracted the maximum and minimum temperature for each month across all of a species' localities. We then calculated the temperature range of a species for each month as the difference between the maximum and minimum temperatures. Finally, the degree of temperature overlap between sister species was calculated using the same formula in Kozak and Wiens (2007) as follows (Fig. 1.2; step 4b):

$$\text{Temperature overlap} = \sum_{i=1}^{12} 0.5(O_i/R_{Ai}+O_i/R_{Bi}),$$

where R_{Ai} and R_{Bi} are the temperature ranges of species A and B for month i, and O_i is the absolute overlap of R_{Ai} and R_{Bi}. We also calculated the degree of temperature overlap by the same formula as the one used for elevational overlap in order to account for the possibility that sister species differ somewhat in which months are coldest and warmest within their geograhic ranges.

The overall climatic distribution of a species was characterized using 19 climatic variables derived from monthly temperature and precipitation values in the WORLDCLIM database (Hijmans et al. 2005). For each species, we extracted the maximum and minimum values of each variable across all of the species' localities, and calculated the species' range for each climatic variable as difference between the maximum and the minimum values (Fig. 1.2; step 4a). The overall climatic range of a species, therefore, is a vector of 19 derived variables (data for each species listed in Table S1.2). Similarly, we calculated the overlap of each climatic variable between sister species by the same formula as the one used for elevational overlap (Fig. 1.2; step 4b). The overall climatic overlap between two sister species is a vector of another 19 derived variables (see Table S1.3). To account for the potential redundancy among the 19 variables, a Principal Components Analysis (PCA) was run for each matrix (19 variables with 28 sister-species pairs) of climatic ranges and climatic overlap (see the section below on statistical analysis), using S-PLUS version 6 (Insightful Corporation 2001). The first several principal components (PCs) that cumulatively account for over 95% of the variation were used in the following statistic analyses (see below).

We also tested the hypothesis that niche conservatism causes populations to become isolated as they track suitable climatic conditions over time (Fig. 1.2; step 5a). We calculated separately (1) the climatic distance (see below for methods) between allopatric sister species, and (2) the climatic distance between each species of the sister-species pair and locations in the gap between their geographic ranges (i.e., "absence localities" where neither species occurs). Among the 28 species pairs with adequate climatic data, there were 9 allopatric species pairs (i.e., no geographic overlap between sister species' geographic ranges, and a geographic gap separating their ranges). To obtain climatic data for absence locations, we first drew a maximum convex polygon in the most narrow part of the gap between the geographical ranges of the two sister species (i.e., the place where their ranges most closely approach each other). We then randomly generated pseudoabsence locations within this polygon. The number of pseudoabsence locations was set to be equal to the average of the number of sampling localities for both species of the sister-species pair. Data for all 19 climatic variables were then extracted from each absence location.

To quantify the climatic distances, we first performed a PCA on the correlation matrix of the 19 climatic variables extracted from the localities of each species in a sister-species pair and their corresponding absence locations. Due to the limited number of localities for some species, we selected the first several PCs by the Kaiser criterion (Kaiser 1960). Using this criterion, we included fewer PCs than using an arbitrary threshold of the PCs that explain 95% of the variance, but still included PCs that account for at least 80% of the variance for all the allopatric sister-species pairs. For a given sister-species pair (species A and species B, for example), we calculated Mahalanobis distances using the selected PCs, first between species A and species B, then between species A and absence locations, and then between species B and absence locations. To test whether the distance between species A and B is significantly smaller than that between species A and absence locations (the same procedure is applied to species B), we pooled and reshuffled the localities of species B and the absence locations 1,000 times using PopTools version 3.0.6 (www.cse.csiro.au/poptools). In each replicate, we recalculated the Mahalanobis distances between species A and B, and between species A and absence locations. The difference between these two Mahalanobis distances (Dm hereafter) for species A is then calculated using the following formula:

D_m = (distance between species A and absence locations - distance between species A and B)/distance between species A and B.

If fewer than 5% of the 1000 randomizations had a difference larger than the observed one, we considered the result to be significant support for the potential importance of niche conservatism in explaining their allopatric distributions (i.e., the climatic distributions of sister species are more similar to each other than they are to the intervening absence localities). Similarly, if more than 95% of the 1000 randomizations had a difference larger than the observed one, the climatic distributions of sister species are more different from each other than they are from the absence localities. This could be the result of niche divergence between sister species or possibly spatial autocorrelation (i.e., a species has more similar climatic distribution to the absence localities than to its sister species because it occurs geographically closer to the absence localities).

Warren et al. (2008) proposed a promising statistical test to address whether species climatic niches are conserved over evolutionary time scales. However, we did not use their test in the present study, for two main reasons. First, the statistics used in their test are based on probabilities of occurrence estimated from niche modeling, instead of directly analyzing climatic data or presence/absence data. Since the accuracy of niche modeling depends on many factors (see discussion in Warren et al. (2008)), this may introduce unnecessary biases to the final results as opposed to directly using climatic data. Second, their test does not include the absence locations (between the ranges of allopatric sister species) in the test of niche conservatism. Theoretically, we could extend the test by performing niche modeling based on absence localities and comparing the similarity indices used in Warren et al. (2008) between sister species and between species and their absence locations. However basing niche modeling on absence localities could be problematic, especially considering that the absence localities in our study are randomly sampled within somewhat arbitrarily defined gap areas between the ranges of sister species.

We consider a significantly large D_m as potential evidence for niche conservatism in allopatric speciation. However this test alone cannot distinguish between the model of allopatric speciation via niche conservatism and niche conservatism followed by major niche divergence, because it does not address whether the geographic range of one species is climatically suitable for its sister species, or whether the intervening absence locations are suitable. To distinguish these two models, we estimated the spatial patterns of predicted climatic suitability of the 9 pairs of allopatric sister species using ecological niche modeling, as implemented in Maxent version 3.2 (Phillips et al. 2006). The combination of the Dm test with ecological niche modeling allows us to potentially distinguish among several possible speciation scenarios involving niche conservatism and/or niche divergence (Fig. 1.1).

Under the scenario of speciation via niche conservatism, we expect each species niche model to predict its occurence in a substantial portion of its sister species' geographic range, but not in the intervening gap area that separates where they are found today (Fig. 1.1A). In addition, the D_m for each species is expected to be significantly larger than its null distribution. In contrast, under the scenario of speciation via niche divergence, we expect that niche modeling will show that each species' geographic range is climatically unsuitable for its sister species, as is the intervening gap between their ranges. In addition, when D_m is significantly larger than its null distribution for both species, the model of speciation via niche divergence may have involved an initial isolation by niche conservatism (Fig. 1.1B). However, when D_m is not significantly larger than its null distribution, the model of speciation may involve an initial isolation by either niche conservatism or by other factors not included in this study (Fig. 1.1C). Although it is hard to rule out the role of niche conservatism in initiating allopatry, under this model, niche divergence maintains the allopatric distribution between sister species.

Theoretically, if species' niches are fully conserved during the speciation process, we expect a species to predict 100% of its sister species' localities as suitable. In contrast, when species' niches are completely divergent after an initial isolation, we expect a species to predict 0% of its sister species' localities as suitable. However, many factors may cause the results to deviate from these expectations somewhat (e.g., differences in sampling or species range sizes).

To test if sister species distributions were significantly more suitable than the intervening absence locations (Fig. 1.2; step 5b), we mapped the georeferenced localities of each species and their absence localities onto the Maxent predictive map of its sister species, and extracted the occurence probabilities for each locality. For each species, we conducted a one-sided Wilcoxon rank-sum test between the distribution of occurrence probabilities for its sister species and the distribution of occurrence probabilities for the absence localities (most distributions significantly differ from normal distribution as indicated by the Kolmogorov-Smirnov test). Under the model of niche conservatism, we expect a species to predict its sister species' presence localities with significantly greater probability then the absence localities. Under the model of niche divergence, we expect probabilities for the sister species to be no greater than for the absence localities. This general approach follows that of Kozak and Wiens (2006). However, these differences in probabilities do not directly address if a species should be able to survive in a substantial portion of its sister species' range. In order to address this (Fig. 1.2; step 5c), we calculated for each species the proportion of its sister species' localities and the absence localities that were predicted as climatically suitable (see below for details). We considered a species to fail to predict the geographic range of its sister species, or the gap area that separates their ranges, when < 30% of its sister species' localities or the absence localities were predicted as suitable. Although this threshold is arbitrary, we found that use of alternate thresholds gave similar overall results.

In general, we expect the Wilcoxon test and the proportion of predicted localities to be concordant. However, to be conservative, we only considered a species pair as supporting niche conservatism if, for both species: (a) D_m values were significantly large, (b) the Wilcoxon test was significant, (c) >30 % of the sister species' localities were predicted as suitable and (d) < 30% of the absence localities were predicted as suitable.

It is important to note that the three scenarios above assume that the current allopatric distributions of sister species are maintained by climatic factors, so that species should not be predicted to occur in the "gap" area between their geographic ranges using ecological niche modeling. When a species' predicted distribution includes > 30% of the absence localities, we assumed that factors other than climate are presumably involved in determining the current allopatric distributions of sister species. Under this scenario, the climatic similarity of species (and similarity to gap locations) may not be relevant to speciation (Fig. 1.1D).

Sometimes, two sister species may have asymmetric results, potentially indicating different speciation scenarios for each species. For example, if allopatric speciation is completed by niche divergence, but the current distribution of one species is limited by factors other than climate, we might expect this species to support the scenario that involves factors other than climate, while its sister species supports the scenario of niche divergence. To account for these asymmetric results, we assigned each sister species separately into one of the four possible speciation scenarios, instead of treating a sister species pair as a unit.

We estimated a species' climatic niche envelope based on its georeferenced localities, using the default modeling parameters in Maxent and environmental layers with 1 km^2 grid resolution for 7 climatic variables selected from the WORLDCLIM database. These variables are: Bio2, mean diurnal temperature range; Bio5, maximum temperature of the warmest month; Bio6, minimum temperature of the coldest month; Bio9, mean temperature of the driest quarter; Bio15, precipitation seasonality; Bio17, precipitation of the driest quarter; and Bio18, precipitation of the warmest quarter. Each variable was selected to represent a group of highly correlated variables in which the selected variable is most likely to set the range limits of anuran species (e.g., we selected maximum temperature rather than mean temperature). Groups of variables were identified by Pearson-product correlation analysis of the 19 bioclimatic variables in SPSS version 11.5 (SPSS, Chicago, IL), and variables were grouped if their $r \geq 0.70$. To decide the background area used in niche modeling, we first divided the 9 sister-species pairs into four large-scale geographic regions: northern South America, Mexico-Central America, North America, and Western Australia. We then drew a rough polygon for each region that included all its species pairs' distribution ranges. This polygon was then used as the background area for each species pair in its corresponding region and the background data (data that represents the range of environmental conditions in the modeled region) were drawn randomly from the background area. These analyses confirm that the models for all the species in their corresponding regions have AUC values (the probability that a tested locality has a higher rank of presence than a randomly chosen background site; Phillips et al. 2006) larger than 0.75 and are thus considered useful (Elith 2002). We presented results using logistic values (the default output value in Maxent version 3.2; it gives an estimate between 0 and 1 of the probability of presence) and generated binary prediction maps of presence-absence for each species using an arbitrary threshold of 0.3 (grid value is absence if its logistic value < 0.3). We chose this threshold because for most species, it appears to include adequate grids that cover the actual geographic range of the species under estimation, but yields few predicted presence locations outside the range. However, this threshold also captures the qualitatively similar pattern of climatic suitability outside the range as those produced using higher threshold values (for example, a species that is predicted to occur in its' sister specie's geographic range when using a threshold higher than 0.3 is still predicted to occur in that area when using the threshold of 0.3).

Statistical analysis

To test for regional differences in species' elevational ranges and temperature ranges (as predicted by Janzen's hypothesis), we performed linear regressions, in which elevational range and temperature range were regressed separately on the latitudinal mid-point of each species' distribution (Fig. 1.2; step 4a). However, since limited sampling of a species' localities might lead to underestimation of its temperature range, we also performed a multiple regression analysis with the number of georeferenced localities per species and species' latitudinal mid-point as the independent variables. Unless otherwise noted, all analyses were carried out using S-PLUS, version 6 (Insightful Corporation 2001).

To test for regional differences in elevational overlap and temperature overlap between sister species (Fig. 1.2; step 4b), we regressed the degree of elevational overlap and temperature overlap separately on the sister-species pair's latitudinal mid-point (see above). However, sister species with a larger area of overlap in their spatial distribution may tend to have larger elevational and temperature overlap as well. In addition, uneven sampling effort along the latitudinal gradient (i.e., less sampling in the tropics) could also introduce bias in the estimation of elevational and temperature overlap. To account for the effects of area overlap and sample size, we performed a multiple regression analysis in which the area of geographic range overlap between sister species, the number of localities sampled per sister-species pair, and the sister-species pair's latitudinal mid-point were the independent variables. The area of geographic range overlap between sister species was calculated using IDRISI version 14.0 (Eastman 2003) with 30 second resolution.

Similarly, to test for regional differences in overall climatic ranges (Fig. 1.2; step 4a) and climatic overlap between sister species (Fig. 1.2; step 4b), we regressed the matrix of climatic ranges on the lattudinal mid-point of each species' distribution, and the matrix of climatic overlap on the latitudinal mid-point of both sister species' distribution using multivariate regression by the General Linear Method (GLM). A PCA was run for each matrix prior to the regressions and the selected PCs (see above) were used to generate new matrices in the following regressions. However, lower rank PCs that explain less variation but have a strong relationship with the independent variable might bias the overall relationship between the set of dependent variables and the independent variables. To examine the robustness of our results to this potential bias, we did several additional regressions using fewer PCs (if seven PCs were originally included, we ran additional regressions based on PC1, then PC1 and PC2, etc.) and compared the results. We also did multivariate multiple regressions that included the area of overlap between sister species and the number of localities sampled per sister-species pair in the set of independent variables.

All the residuals in the above regressions were first tested for normality by the Kolmogorov-Smirnov test. When data significantly departed from normality, the Robust MM regression method (Yohai and Zamar 1998) was used for the univariate regressions. This method is robust to violation of the assumption of normality, but is more efficient than traditional nonparametric regressions (Insightful Corporation 2001). For multivariate analyses, variables were normal-score transformed prior to the analyses.

Results

The frequency of allopatric: partially sympatric: sympatric distribution modes is 42: 25: 12 across a total of 79 sister-species pairs of anurans. The frequency for temperate frogs is 16: 8: 3 out of 27 sister-species pairs. The frequency for tropical frogs is 26: 17: 9 out of 52 sister-species pairs. The 2×3 G-test indicates no significant differences between the tropical and temperate regions ($G_{adj} = 0.34$, $P = 0.84$, $df = 2$). In the category of partial sympatry, 7 out of 25 sister species have geographic overlap < 20% of the area of the sister species with smaller distribution, indicating that few species have ranges that approach expectations for parapatric species.

As predicted by Janzen's (1967) hypothesis, the extents of species' temperature ranges are positively related to latitude ($F_{1, 53} = 10.36$, $P < 0.0001$; Fig. 3B). This relationship remains significant even after controlling for sample size, which has a significant influence on the relationship between temperature ranges and latitude ($F_{1, 53} = 3.88$, $P = 0.0003$). In contrast, there is no significant relationship between species' elevational ranges and latitude ($F_{1, 156} = -1.24$, $P = 0.22$; Fig. 1.3A). These results are consistent with those of Kozak and Wiens (2007).

However, contrary to the evolutionary predictions derived from Janzen's hypothesis (and the results of Kozak and Wiens 2007), we found no evidence that the extent of elevational overlap ($F_{1, 77} = 0.94$, $P = 0.35$; Fig. 1.4A) or temperature overlap ($F_{1, 24} = -0.36$, $P = 0.72$; Fig. 1.4C) between sister species were higher as latitude increased. Temperature overlap also has no significant relationship with latitude when calculated by the same formula as the one used for elevational overlap ($F_{1,26} = -0.91$, $P = 0.37$). Neither sample size ($F_{1,\,13} = 0.00$, $P = 1.00$) nor area of overlap ($F_{1,\,13} = 0.00$, $P = 1.00$) has a significant influence on the relationship between temperature overlap and latitude. Similarly, area of overlap has no influence on the relationship between elevational overlap and latitude ($F_{1,\,33} = 1.26$, $P = 0.22$). Sister species produced by allopatric speciation via niche conservatism may have high niche overlap, which might obscure any latitudinal pattern in gradient speciation. However, a regression analysis that excludes allopatric sister species also indicated no linear relationship between either elevational overlap and latitude ($F_{1,\,33} = 0.75$, $P = 0.46$; Fig. 1.4B) or between temperature overlap and latitude ($F_{1,\,13} = -0.00$, $P = 1.00$; Fig. 1.4D). These different results of the two studies cannot be explained by the use of different indices of elevational overlap. Our index estimates a lower degree of overlap between sympatric sister species than the index used in Kozak and Wiens (2007), and there are more sympatric sister species in the tropics than in the temperate zone. Thus, the use of our index makes it even easier to detect a positive relationship between elevational overlap and latitude, as found in Kozak and Wiens (2007).

The overall climatic range of a species increases significantly as one goes from the tropics to the poles (regression coefficient for PC1 = 0.050, which explains 49.5% climatic variance among species; $F_{7,\,47} = 18.59$, $P < 0.0001$). Results of additional regressions indicate that this significant result is not caused by lower rank PCs that explain less variation but have strong relationships with the independent variable (all $P < 0.0001$; Table 1.1). In contrast, the degree of overall climatic overlap between sister species does not show a significant tendency to increase as latitude increases ($F_{10, 15} = 2.48$, $P = 0.055$). Instead, additional regressions with fewer PCs show a significant trend in the opposite direction (i.e., climatic overlap is higher in tropical species). In particular, the regression coefficient for PC1 equals -0.026 ($P = 0.0076$), which explains 39.1% climatic variance among species (Table 1.1). Regressions that exclude allopatric sister species indicated no linear relationship between climatic overlap and latitude ($F_{7, 7} = 1.31$, $P = 0.366$; Table 1.1).

Considering the results of both niche modeling (Table 1.2; see also Figure S1.1) and D_m estimation (Table 1.2), we tentatively assigned 18 species in the 9 allopatric species pairs (with adequate climatic data) into one of four possible speciation scenarios (Fig. S1.1). The results show little unambiguous evidence for speciation through niche conservatism, in either tropical or temperate species pairs. Only one species, *Engystomops pustulosus*, has results consistent with scenario B, a scenario that involves both niche conservatism and niche divergence. Results from 10 species support scenario C, which involves significant niche divergence with no evidence for niche conservatism. The remaining 7 species (of 18 total) support scenario D, indicating that factors other than climate are involved in determining the current allopatric distributions of sister species.

To test for potential regional differences in the extent of niche divergence during allopatric speciation, we also regressed the climatic overlap between these allopatric sister species on the latitudinal mid-point of their distributions using GLM. The results show that allopatric sister species in lower latitudes do not have a significantly higher degrees of climatic overlap ($F_{5,2} = 2.30$, $P = 0.330$; Table 1.1), although such a trend is nearly significant when only using PC1, which explains 35.3% of the variance among species pairs (regression coefficient = -0.154, $P = 0.066$).

Discussion

In this study, we test for latitudinal differences in the relative importance of niche conservatism and niche divergence in speciation, using frogs as a model system. In general, our results support Janzen's (1967) hypothesis that tropical species have narrower climatic ranges. However, our results do not support the hypothesis that these narrower climatic ranges lead to a greater tendency for speciation through elevational and climatic divergence in the tropics, in contrast to recent results from salamanders (Kozak and Wiens 2007). Instead, some of our results suggest that sister species may be more climatically similar to each other in the tropics (Table 1.1). To our knowledge, these two amphibian studies represent the first attempts to systematically test for latitudinal differences in speciation mechanisms related to climatic distributions (i.e., niche conservatism vs. divergence), although they come to quite different conclusions. We also present possibly the first test for latitudinal differences in geographic modes of speciation (or at least, geographic distribution of sister species). Our results suggest that there is no significant difference in the frequency of different speciation modes between tropical and temperate regions.

Our major results are as follow. First, as predicted by Janzen's hypothesis, we found that anuran species inhabit significantly wider climatic regimes as one goes from the tropics to the pole, based on data from 158 species. However, the elevational ranges of species do not show the same pattern of increasing width with latitude, a surprising result also found by Kozak and Wiens (2007; but see McCain (2009) for more extensive analyses of this particular question). Second, there is no evidence that anuran sister species occurring in lower latitude exhibit less overlap in their elevational and climatic ranges (based on data from 79 and 28 species pairs, respectively). In fact, some analyses even show significant evidence for the opposite trend (i.e., tropical species pairs tend to be climatically more similar to each other than temperate pairs). Taken together, these two results suggest that species in lower latitudes, although having narrower climatic regimes, do not show greater propensity for divergent speciation along environmental gradients. Finally, our analyses of 9 allopatric pairs suggest that climatic niche conservatism may not be commonly important in allopatric speciation for anurans. We find no species pairs that unambiguously support this scenario. Instead, niche divergence and factors other than climate seem to determine the current distributions of allopatric sister species. But we find no evidence that tropical allopatric species pairs show greater niche divergence than temperate pairs. However, these latter results on niche conservatism and divergence are based on only 9 allopatric sister-species pairs, and so should be taken with appropriate caution. In the sections that follow, we discuss the major assumptions of our analyses and the implications of our results for studies of parapatric speciation and patterns of species richness.

Major assumptions

Our analyses rest on several assumptions. However it is important to note that our methods are similar to those of Kozak and Wiens (2007), and so we make very similar assumptions. Thus, even if the geographic and elevational patterns that we analyze do not fully address the causes of speciation, the biogeographic patterns found in frogs are still very different from those found in salamanders. One notable difference between our methods and those of Kozak and Wiens (2007) is that we only included species pairs in which both species were represented by at least five localities (for climatic data). However, Kozak and Wiens (2007) concluded that the different patterns in tropical and temperate species pairs were not explained by different sample sizes in tropical and temperate species pairs.

First, we assume that the 79 species sampled are representative of overall patterns in frogs, and not some unusual subset of taxa. Our sampling of species pairs (see Table S1.1) includes taxa in both the New World and Old World, the primitive and advanced frogs, and in the two major clades of advanced anurans (Hyloidea, Ranoidea). Our phylogenetic and geographic sampling for frogs is more diverse than that of Kozak and Wiens (2007) for salamanders, although most tropical salamanders occur in only one clade (Bolitoglossinae) in one geographic region (Middle America).

Second, we assume that the current geographic distributions of sister species reflect their original geographic modes of speciation. However, many factors can drive significant post-speciational range shifts that increase or decrease species' geographic overlap (e.g., Futuyma 1998; Barraclough and Vogler 2000; Losos and Glor 2003). Most importantly, the sister species in the "partial sympatry" category in our study could be the result of secondary contact between allopatric species or changes in distributions after parapatric and sympatric speciation. However, even though there may be some shifts in distribution after speciation, our results from analyses of geographic overlap, elevational overlap, and climatic distribution are all concordant. These analyses all suggest that there is no greater propensity for parapatric speciation along environmental and elevational gradients in the tropics.

Similarly, it is possible that post-speciational climatic changes may influence our analyses of niche conservatism and divergence. For example, environmental changes after speciation might cause the geographic area separating the ranges of two allopatric species to become less hospitable over time, leading to inflated values of D_m and overestimated support for niche conservatism. However, our analyses do not rely on D_m values alone as a test of niche conservatism. Perhaps more importantly, our results showed little evidence for allopatric speciation through niche conservatism in the 9 allopatric species pairs that we examined, suggesting that such inflation was not important in our study.

Third, we assume that there is some relationship between the climatic distribution of species (based on environmental data from known localities) and their climatic tolerances. For example, when sister species occur in very different climatic regimes, we assume that one species could not tolerate the climatic conditions experienced by the other, such that the climatic distributions may serve to isolate them from gene flow. Similarly, if the absence localities separating members of an allopatric species pair are very different from the presence localities, we assume that these differences may serve as a barrier to dispersal and gene flow between species. In partial support of this assumption, Kozak and Wiens (2007) showed a general relationship between the climatic distribution of selected salamander species and their body temperatures in the field. However, we acknowledge that this does not directly address physiological tolerances per se. Thus, the climatic distributions that we analyze here could overestimate the actual climatic tolerance range of a species, especially given that some amphibians have effective thermoregulatory behaviors and can hibernate or migrate to avoid extreme temperatures (Zug et al. 2001).

Further, species distributions may also be influenced by biotic interactions, rather than by climate alone (Lomolino et al. 2006). For example, Heyer (1967) showed that herpetofaunal distributions correlated with particular vegetation zones that create necessary microhabitats. Competition between closely related species may also set limits to species ranges, potentially resulting in parapatric distributions between sister species (e.g., Twomey et al. 2008). Consequently, the observed climatic-regime width could underestimate the climatic tolerance range of a species. Although it would be useful to have more data on the roles of physiological tolerances and biotic interactions on species distributions in frogs, our results do not suggest that there are obvious latitudinal differences in their geographic and climatic patterns of speciation to be explained. Finally, our own results suggest that climatic factors may not be universally important in setting geographic range limits in frogs (at least for the 9 pairs we studied in detail).

We also acknowledge that the factors limiting geographic distributions are only one of many aspects of speciation (Coyne and Orr 2004). Other intrinsic isolating mechanisms may be important, especially for initiating parapatric or sympatric speciation (Turelli et al. 2001) and maintaining the reproductive isolation of allopatric lineages that have become partially sympatric. For example, reproductive isolation based on calls has been recorded for allopatric, parapatric, and sympatric sister species of frogs (e.g., Littlejohn 1965; Fouquette 1975; Loftus-Hills and Littlejohn 1992). There is now growing evidence that the evolution of male calls and female preferences are important drivers of speciation in frogs. For example, Hoskin et al. (2005) showed that premating isolation caused by natural selection against hybridization drove both rapid parapatric speciation and rapid allopatric speciation in treefrogs (Hylidae: *Litoria*) in Australia. Similarly, Boul et al. (2007) showed that divergent sexual selection on female preferences and male calls drove premating isolation and speciation in Amazonian frogs (*Physalaemus/Engystomops*).

Parapatric speciation along environmental gradients

Our results from anurans do not support the hypothesis that parapatric speciation along environmental gradients is more frequent in the tropics (e.g., Moritz et al. 2000; Kozak and Wiens 2007). This hypothesis is derived partly from Janzen's (1967) observation that tropical species have narrower climatic regimes due to limited temperature seasonality, which may lead to narrower elevational ranges and greater opportunities for parapatric speciation along mountain slopes. Our results partially support Janzen's hypothesis by showing that species in lower latitudes occupy narrower climatic regimes (Fig. 1.1). However, we found no tendency for greater elevational or climatic divergence between species pairs in the tropics (and some evidence for the opposite trend; Table 1.1), as would be predicted under a model of parapatric speciation along environmental gradients.

The prediction of a higher frequency of parapatric speciation and niche divergence in the tropics is based on two assumptions following from Janzen's (1967) hypothesis. First, more limited temperature seasonality in the tropics should select for organism that are tightly adapted to a narrow elevational band. Second, tropical species should also evolve limited thermal acclimation, leading to limited dispersal between different elevations (Ghalambor et al. 2006). In fact, we find that tropical species do not have significantly narrower elevational ranges (see also Kozak and Wiens 2007; but see McCain 2009), and tropical sister species do not show less elevational and climatic overlap along elevational gradients. Thus, one of the reasons why we do not support the prediction of more gradient speciation in the tropic is because the elevational distribution patterns we observed do not support this prediction from Janzen's hypothesis. In fact, our finding that species in lower latitudes occupy narrower climatic regimes simply supports the assumption of less climatic seasonality in the tropics, rather than supporting any direct effects of limited seasonality on the relationship between elevation, climate, latitude and speciation.

Overall, our results suggest that parapatric speciation along environmental gradients may be uncommon or absent among the 79 frog species pairs that we sampled, regardless of whether they are tropical or temperate. Perhaps the best evidence for parapatric speciation is the finding that sister species have abutting distributions with no obvious geographic barriers in between. However, we found no species pairs with such a distribution pattern, only species distributions that are allopatric, sympatric, or partially sympatric. In theory, some species might have speciated parapatrically and then become partially sympatric, however only 7 out of 25 species pairs in the "partial sympatry" group have overlap < 20%, an arbitrary threshold that has been used as evidence for parapatric speciation in previous studies (e.g., Lynch 1989). Moreover, if sister species speciated parapatrically along environmental gradients that limited their dispersal, then we would not expect any overlap in their geographic ranges after speciation (assuming that the environmental gradient that caused them to speciate is still present).

Speciation patterns and patterns of species richness

Latitiudinal differences in speciation mechanisms might potentially contribute to the latitudinal diversity gradient, if different speciation mechanisms influence the rate of speciation.

Anurans and plethodontid salamanders both seem to be ancestrally temperate, and have dispersed into the tropics subsequently, and both have high species richness in the tropics (Wiens 2007). Wiens (2007) attributed this pattern to differential diversification rates along the latitudinal gradient. Indeed, he found that diversification rates in both amphibian groups increased significantly with decreasing latitude (but in frogs, this only pertains to the largest time scales, not within diverse, primarily tropical families; Wiens et al. 2006, 2009). Higher diversification rates may be caused by either higher speciation rates or lower extinction rates, and distinguishing the relative contribution of these two factors is relatively difficult (e.g., Ricklefs 2007). In fact, higher diversification rates in tropical amphibian clades may be due to higher extinction rates in the temperate zone rather than faster tropical speciation rates (Wiens 2007).

Many factors have been proposed that might promote faster speciation in tropical faunas (e.g., Willig et al. 2003; Mittelbach et al. 2007). Although climatic stratification in the tropics does not seem to drive widespread speciation along climatic gradients in tropical frogs (based on our results), climatic stratification could also make allopatric speciation via niche conservatism more effective (Ghalambor et al. 2006). However, our findings also show that climatic niche conservatism may not be widely important in allopatric speciation in anurans. Instead, niche divergence and factors other than climate may be more important in determining the current distributions of allopatric sister species in frogs (at least for the 9 species pairs we studied in detail). Most importantly, our results do not support the idea that speciation mechanisms are fundamentally different between tropical and temperate regions. Thus, our results provide little basis for predicting that speciation rates should be higher in tropical frogs, a finding echoed in analyses of diversification rates across latitudes in species-rich frog clades (e.g., Wiens et al. 2006, 2009) and across amphibians (Wiens 2007). Overall, our study shows different latitudinal trends in speciation mechanisms in frogs and in salamanders, suggesting that the relationships between climatic zonation, speciation mechanisms, and species richness are not straightforward.

References

AmphibiaWeb: Information on amphibian biology and conservation. [web application]. 2009. Berkeley, California: AmphibiaWeb. Available: http://amphibiaweb.org/. (Accessed: Jun 4, 2009).

Barraclough, T. G., and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. Am. Nat. 155:419–434.

Boul, K. E., W. C. Funk, C. R. Darst, D. C. Cannatella, and M. J. Ryan. 2007. Sexual selection drives speciation in an Amazonian frog. Proc. R. Soc. Lond. B 274:399–406.

Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, MA. .

Eastman, R. 2003. Idrisi Kilimanjaro manual and tutorial. Worchester: Clark Labs, Clark University.

Elith, J. 2002. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. In *Quantitative methods for conservation biology* (Ferson, S. and Burgman, M., eds) pp. 39–58, Springer.

Fouquette, M. J. 1975. Speciation in chorus frogs. I. reproductive character displacement in the *Pseudacris nigrita* complex. Syst. Zool. 24:16–23.

Frost, D. R. 2008. Amphibian Species of the World: an Online Reference. American Museum of Natural History, New York, USA. Available at http://research.amnh.org/herpetology/amphibia. Accessed September, 2008.

Futuyma, D. J. 1998. Evolutionary biology. 3rd ed. Sinauer Associates, Sunderland, MA.

Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integr. Comp. Biol. 46:5–17.

Graham, C. H., S. R. Ron, J. C. Santos, C. J. Schneider, and C. Moritz. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution 58:1781–1793.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25:1965–1978.

Heyer, R. W. 1967. A herpetofaunal study of an ecological transect through the Cordillera de Tilarán, Costa Rica. Copeia 1967:259–271.

Hoskin, C. J., M. Higgie, K. R. McDonald, and C. Moritz. 2005. Reinforcement drives rapid allopatric speciation. Nature 437:1353–1356.

Hutchinson, G. E. 1957. A Treatise on Limnology. Vol. 1. John Wiley & Sons, New York. 1015 pp.

Insightful Corporation. 2001. S-Plus 6 for Windows: Guide to Statistics. Vol. 1. Insightful Corporation, Seattle, WA.

IUCN 2009. *IUCN Red List of Threatened Species. Version 2009.1.* Available at http://www.iucnredlist.org. Accessed on September, 2008.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101:233–249.

Kaiser, H. F. 1960. The application of electronic computers to factor analysis. Educ. Psychol. Meas. 20:141–151.

Kozak, K. H., and J. J. Wiens. 2006. Does niche conservatism promote speciation? A case study in North American salamanders. Evolution 60:2604–2621.

Kozak, K. H., and J. J. Wiens. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. Proc. R. Soc. Lond. B 274:2995–3003.

Lemmon, E. M., A. R. Lemmon, J. T. Collins, J. A. Lee-Yaw, and D. C. Cannatella. 2007. Phylogeny-based delimitation of species boundaries and contact zones in the trilling chorus frogs (*Pseudacris*). Mol. Phylogenet. Evol. 44:1068–1082.

Littlejohn, M. J. 1965. Premating isolation in the *Hyla ewingi* complex (Anura, Hylidae). Evolution 19:234–243.

Loftus-Hills, J. J., and M. J. Littlejohn. 1992. Reinforcement and reproductive character displacement in *Gastrophryne carolinensis* and *G. olivacea* (Anura, Microhylidae)–a reexamination. Evolution 46:896–906.

Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. Biogeography, 3rd Edition. Sinauer Associates, Sunderland, MA.

Losos, J. B., and R. E. Glor. 2003. Phylogenetic comparative methods and the geography of speciation. Trends Ecol. Evol. 18:220–227.

Lynch, J. D. 1989. The gauge of speciation: on the frequencies of modes of speciation. In *Speciation and Its Consequences* (Otte, D. and Endler, J. A., eds) pp. 527–553, Sinauer Associates.

McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. Ecol. Lett. 12:550–560.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. Ecol. Lett. 10:315–331.

Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annu. Rev. Ecol. Syst. 31:533–563.

Nosil, P., T. H. Vines, and D. J. Funk. 2005. Perspective: Reproductive isolation caused by natural selection against immigrants using divergent environments. Evolution 59:705–719.

Ogden, R., and R. S. Thorpe. 2002. Molecular evidence for ecological speciation in tropical habitats. Proc. Natl. Acad. Sci. USA 99:13612–13615.

Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Peterson, A. T. and A. S. Nyári. 2007. Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, *Schiffornis* sp., in the Neotropics. Evolution 62:173–183.

Phillimore, A. B., C. D. Orme, G. H. Thomas, T. M. Blackburn, P. M. Bennett, K. J. Gaston, and I. P. F. Owens. 2008. Sympatric speciation in birds is rare: insights from range data and simulations. Am. Nat. 171:646–657.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190:231–259.

Raxworthy, C. J., C. M. Ingram, N. Rabibisoa, and R. G. Pearson. 2007. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. Syst. Biol. 56:907–923.

Ricklefs, R. E. 2007. Estimating diversification rates from phylogenetic information. Trends Ecol. Evol. 22:601–610.

Rissler, L. J., and J. J. Apodaca. 2007. Adding more ecology into species delimitation: ecological niche models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). Syst. Biol. 56:924–942.

Rundle, H. D., and P. Nosil. 2005. Ecological speciation. Ecol. Lett. 8: 336–352.

Schluter, D. 2001. Ecology and the origin of species. Trends Ecol. Evol. 16:372–380.

Schluter, D. 2009. Evidence for ecological speciation and its alternative. Science 323:737–741.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Co., New York.

Stockman, A. K., and J. E. Bond. 2007. Delimiting cohesion species: extreme population structuring and the role of ecological interchangeability. Mol. Ecol. 16:3374–3392.

Turelli, M., N. H. Barton, and J. A. Coyne. 2001. Theory and speciation. Trends Ecol. Evol. 16:330–343.

Twomey, E., V. Morales, and K. Summers. 2008. Evaluating condition-specific and asymmetric competition in a species-distribution context. Oikos 117:1175–1184.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883.

Wiens, J. J. 2004a. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197.

Wiens, J. J. 2004b. What is speciation and how should we study it? Am. Nat. 163:914–923.

Wiens, J. J. 2007. Global patterns of diversification and species richness in amphibians. Am. Nat.170:S86–S106.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36:519–539.

Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. Am. Nat. 168:579-596.

Wiens, J. J., J. Sukumaran, R. A. Pyron, and R. M. Brown. 2009. Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). Evolution 63:1217–1231.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annu. Rev. Ecol. Evol. Syst. 34:273–309.

Yohai, V. J., and R. H. Zamar. 1998. Optimal locally robust M-estimates of regression. J. Statist. Plann. Inference 64:309–323.

Zug, G. R., L. J. Vitt, and J. P. Caldwell. 2001. Herpetology: an introductory biology of amphibians and reptiles. 2nd ed. Academic Press, New York.

Table 1.1. Regression coefficients (β) and *P*-values for the multivariate regressions of sister species' climatic overlap on the latitudinal midpoint of the pair, using different numbers of principal components (PCs) for climatic data. PCs are used in the order of the amount of variance that each explains. In each row, for example, when the number of PCs is two, the *P*-value is the statistical significance for the multivariate regression using PC1 and PC2, and β is the independent regression coefficient for PC2.

Num. of PCs	Climatic range		Climatic overlap (all species pairs)		Climatic overlap (no allopatric pairs)		Climatic overlap (allopatric pairs)	
	β	*P*	β	*P*	β	*P*	β	*P*
1	0.050	<0.0001	-0.026	0.0076	-0.013	0.3617	-0.154	0.0665
2	-0.148	<0.0001	0.016	0.0195	-0.006	0.5594	0.018	0.2869
3	0.022	<0.0001	0.001	0.0516	0.007	0.5721	-0.036	0.3700
4	-0.014	<0.0001	0.000	0.1083	-0.008	0.5771	-0.012	0.5432
5	0.000	<0.0001	-0.001	0.1929	0.005	0.1403	-0.040	0.3303
6	-0.001	<0.0001	0.008	0.0068	0.001	0.2376	--	--
7	-0.010	<0.0001	-0.002	0.0146	0.000	0.3661	--	--
8	--	--	-0.002	0.0162	--	--	--	--
9	--	--	0.001	0.0296	--	--	--	--
10	--	--	-0.001	0.0550	--	--	--	--

Table 1.2. Results of niche modeling and D_m (P-value) estimation for each species in the 9 allopatric sister-species pairs. Positive D_m with P-value ≤ 0.05 indicates that sister species occupy climatic niches that are significantly more similar to each other than they are to the absence localities that separate them. Negative D_m with P-value ≥ 0.95 indicates that sister species occupy climatic niches that are significantly less similar to each other than they are to the intervening absence localities. The P-value in the Wilcoxon rank-sum test represents the probability that a species predicts its sister species' localities with greater probability then the absence localities (significantly greater when P-value ≥ 0.95). The proportion of suitable sister species localities and absence localities are estimated based on niche modeling for a given species using 7 climatic variables (see Supplementary Figure 1). Categories of speciation scenarios correspond to letters in Fig. 1. Species are classified into scenarios based on the combination of niche modeling and *Dm* values.

Sister species	D_m (P-value)	P-value in Wilcoxon rank-sum test	Proportion of suitable sister species localities	Proportion of suitable absence localities	Scenario
Engystomops petersi	-0.101 (0.703)	0.016	0.38	0.65	D
E. pustulosus	0.781 (0.013)	0.688	0.23	0.05	B
Phyllobates vittatus	-0.569 (0.982)	0.999	0.20	0	C
P. lugubris	0.028 (0.535)	0.170	0	0	C
Agalychnis annae	0.134 (0.254)	0.092	0.08	0.14	C
A. moreletii	-0.572 (1.000)	0.999	0.81	0.36	D
Tlalocohyla picta	-0.254 (0.879)	<0.001	0	0	C
T. smithii	-0.425 (0.907)	0.001	0	0.22	C
Rana tarahumarae	-0.256 (0.977)	0.141	0.17	0.38	D
R. pustulosa	-0.541 (0.994)	0.004	0.25	0.88	D
Arenophryne rotunda	-0.415 (0.912)	0.003	0.20	1.00	D
A. xiphorhyncha	-0.644 (1.000)	0.036	0.75	1.00	D

Bufo californicus	-0.269 (1.000)	<0.001	0	0	C
B. microscaphus	-0.230 (0.996)	<0.001	0	0	C
Pseudacris brimleyi	-0.074 (0.538)	0.002	0.16	0.60	D
P. brachyphona	-0.313 (0.995)	0.004	0.13	0.25	C
Ascaphus montanus	-0.422 (1.000)	0.003	0.08	0.11	C
A. truei	0.068 (0.606)	0.960	0	0	C

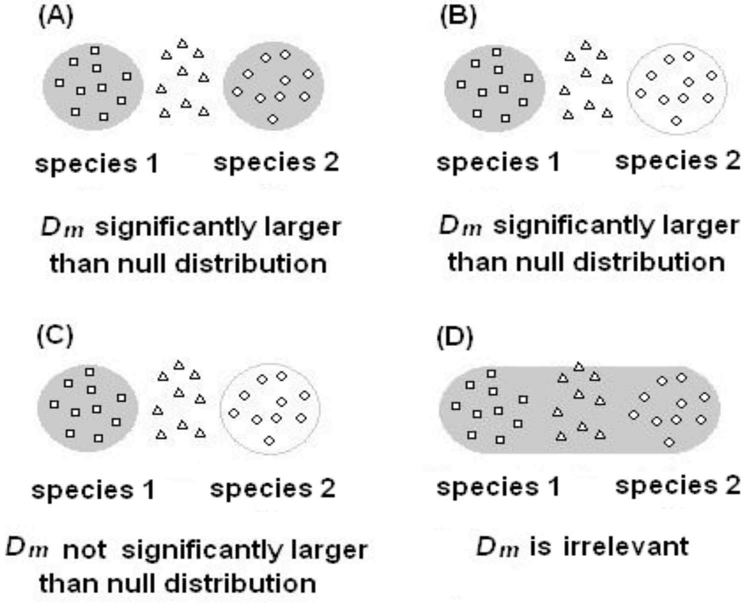


Figure 1.1. Hypothetical example illustrating four potential outcomes of niche modeling and D_m estimation, with their implications for speciation mechanisms. Significantly positive values of D_m indicate that the climatic distributions of sister species are more similar to each other than they are to the intervening absence localities. Squares represent the observed localities of species 1. Circles represent the observed localities of its sister species, species 2. Triangles represent locations where both species are known to be absent. The shading represents the spatial distribution of climatically suitable habitat for species 1 based on ecological niche modeling. In all four cases, we assume results based on species 1 are similar to those based on species 2 (but see Materials and Methods for discussion of potentially asymmetric outcomes). (A) Species 1 is predicted to occur in its sister species' geographic range, but not in the intervening gap area. D_m for the species is significantly larger than its null distribution. This pattern suggests that niche conservatism initiates the isolation between sister species and maintains their current allopatric distributions, given that results are similar for species 2. (B) Species 1 is not predicted to occur in either its sister species' geographic range or in the intervening gap region. D_m is significantly larger than its null distribution. This pattern (assuming similar results in species 2) suggests that niche conservatism initiates the geographic isolation between sister species and subsequent niche divergence prevents further gene flow between them. (C) Species 1 is not predicted to occur in either its sister species' geographic range or in the intervening gap, but D_m is not significantly larger than the null distribution. This pattern suggests that factors other than climatic niche conservatism may have initiated the geographic isolation of these species and that subsequent niche divergence prevents further gene flow. (D) Species 1 is predicted to occur both in its sister species' geographic range and in the intervening gap between their ranges. This pattern suggests that the current allopatric distributions of sister species are determined by factors other than climate, and so the climatic similarity of species (and similarity to gap locations) may not be relevant to speciation.

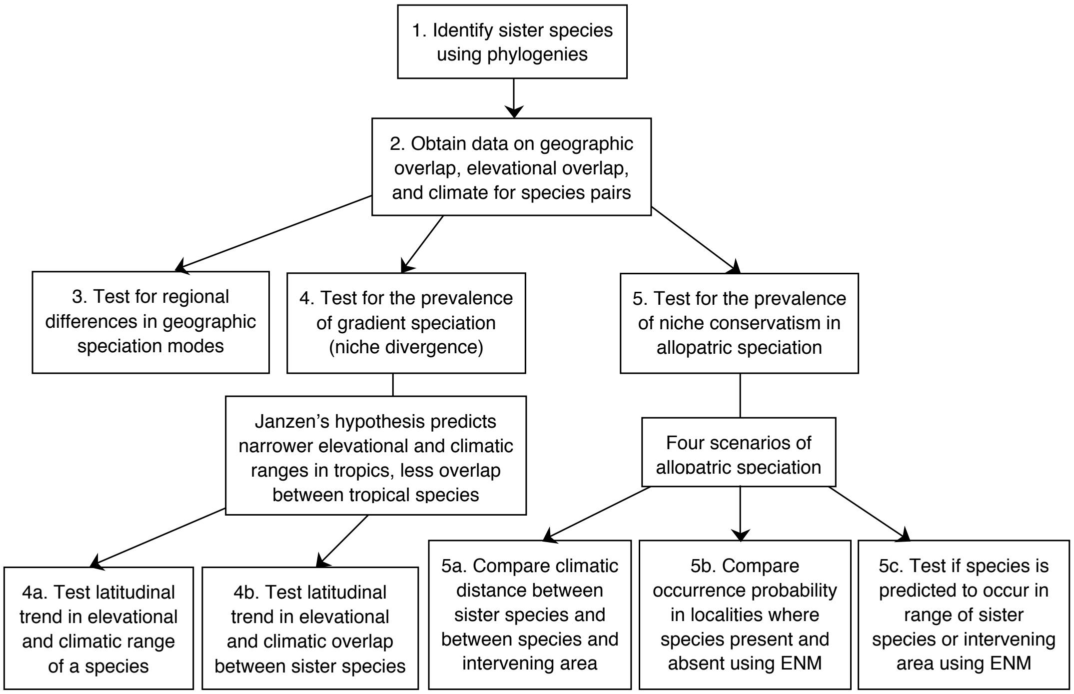


Figure 1.2. A flow chart summarizing the methods used in this study. ENM represents ecological niche modeling.

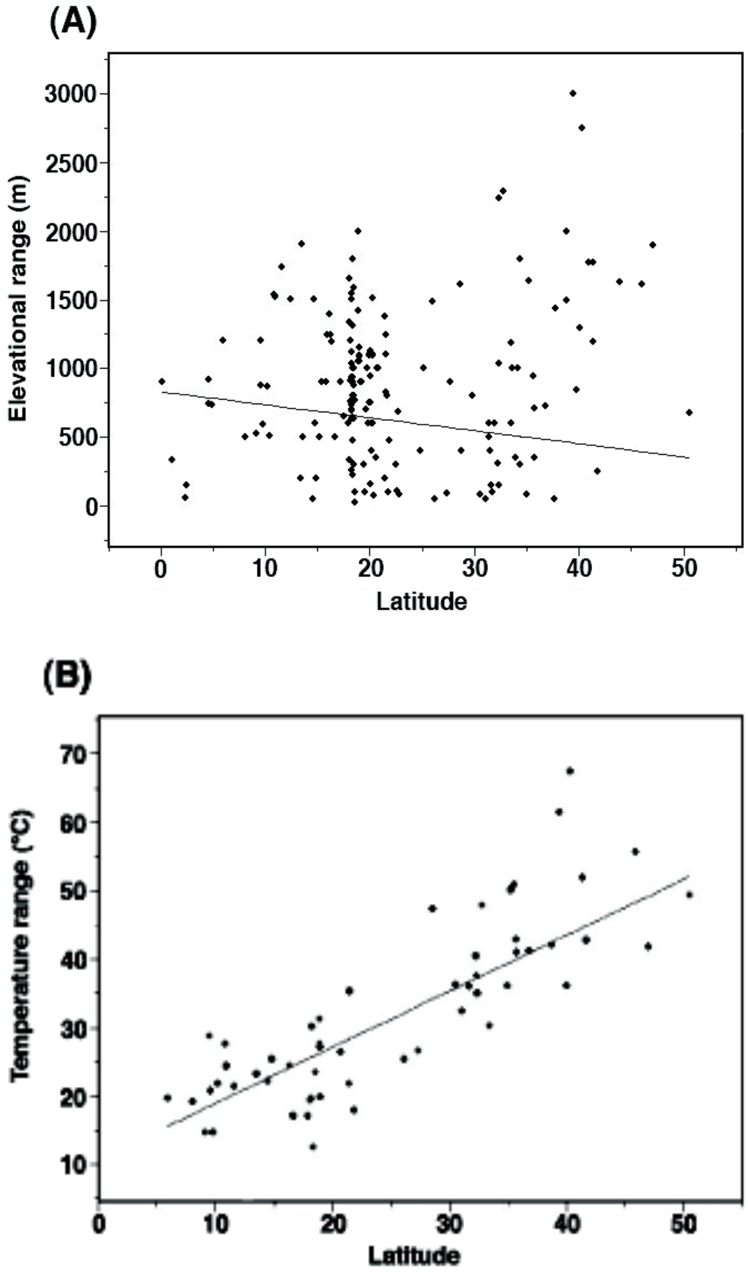
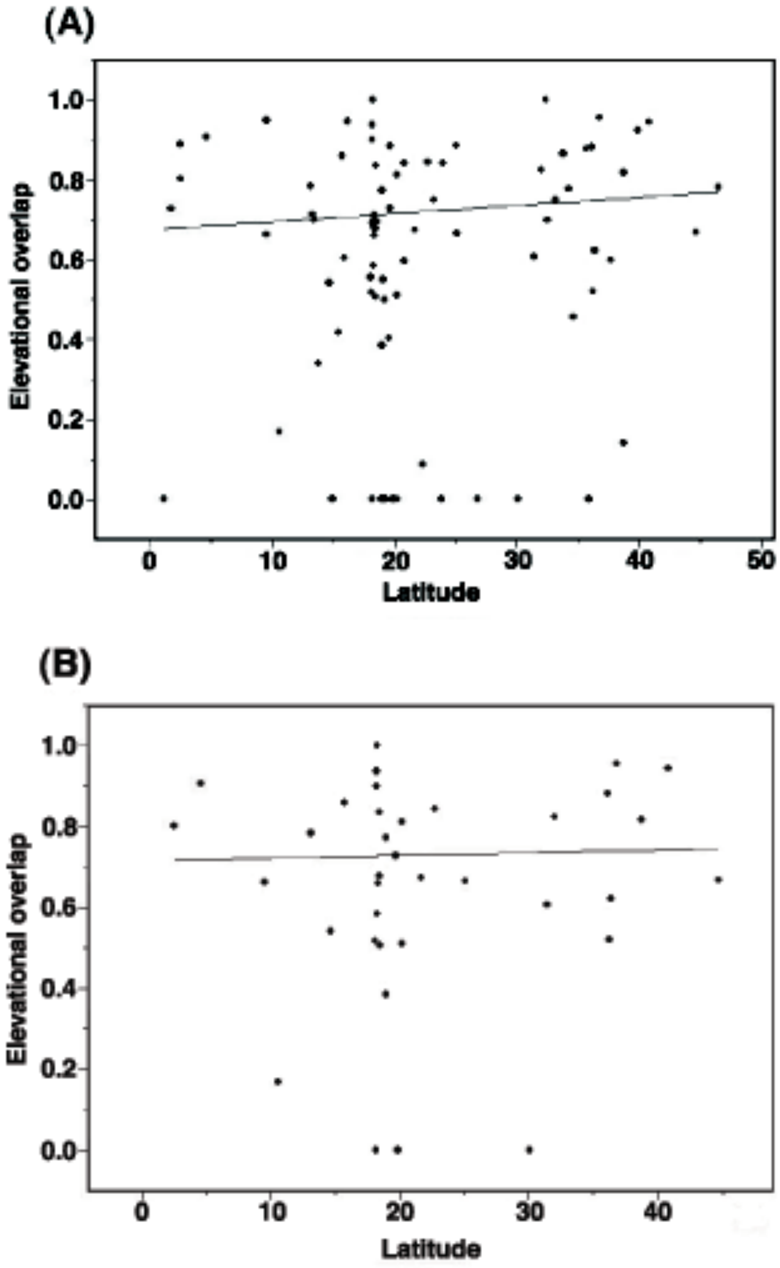


Figure 1.3. Regressions of species' elevational range (A) and temperature range (B) on the latitudinal midpoint of the species range, using the Robust MM method. (A) There is no relationship between species' elevational range and latitude ($t_{156} = -1.24$, $P = 0.22$). (B) Species' temperature ranges are positively related to latitude ($t_{53} = 10.36$, $P < 0.0001$).


(A)
Elevational overlap
1.0
0.8
0.6
0.4
0.2
0.0
Latitude
0
10
20
30
40
50
(B)
Elevational overlap
1.0
0.8
0.6
0.4
0.2
0.0
Latitude
0
10
20
30
40

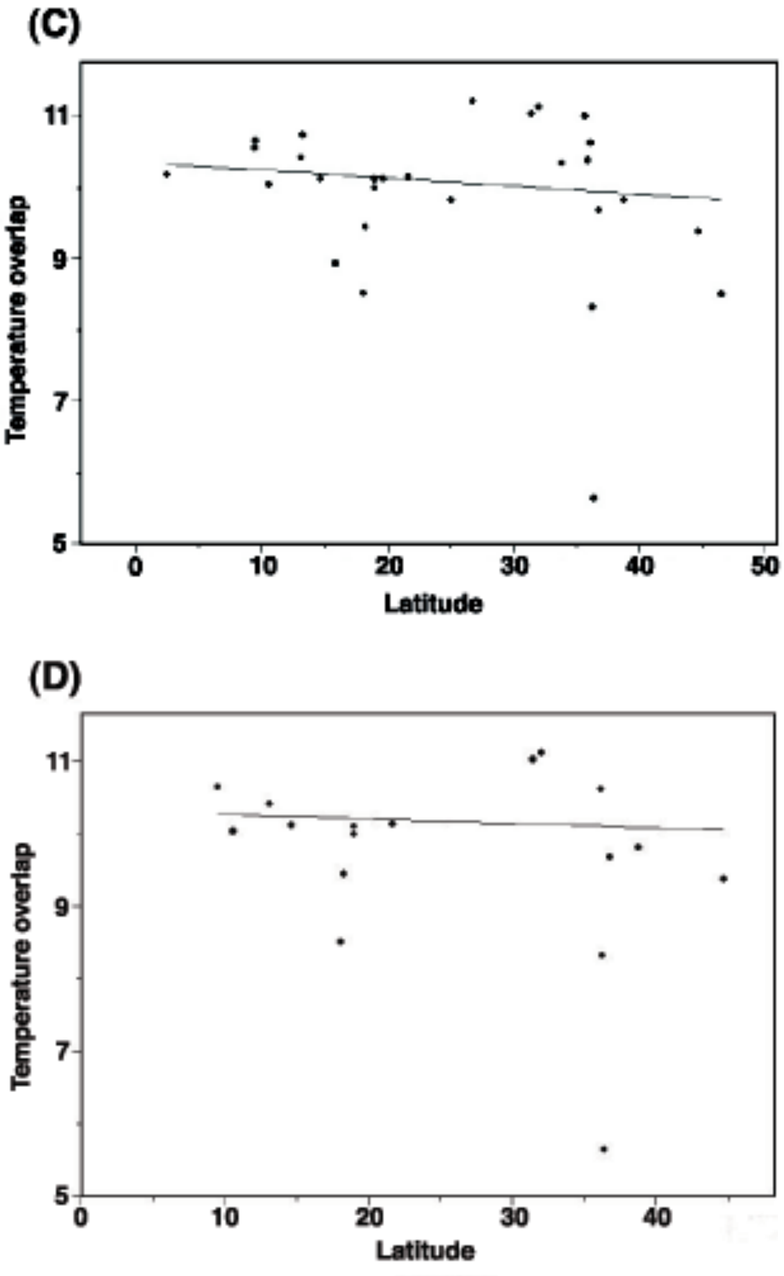


Figure 1.4. Regressions of sister species' elevational overlap (A, B) and temperature overlap (C, D) on the latitudinal midpoint of the species pair, using the Robust MM method. A and C are regressions including all the sister species (*n* = 79 and *n* = 28, respectively). B and D are regressions that exclude allopatric sister species (*n* = 35 and *n* = 17, respectively). There is no significant relationship between elevational overlap and latitude (A: $t_{77} = 0.94$, $P = 0.35$; B: $t_{33} = 0.75$, $P = 0.46$), nor between temperature overlap and latitude (C: $t_{24} = -0.36$, $P = 0.72$; D: $t_{13} = 0.00$, $P = 1.00$).

Appendices

Table S1.1. The 79 species included in analyses of geographic mode and elevational distribution, along with their distribution patterns, latitudinal mid-points, maximum and minimum elevations, and elevational overlaps, and the literature sources that suggest they are sister species.

Family	Species (and literature source)	Distribution	Latitudinal mid-point	Max. elevation	Min. elevation	Elev. overlap
Alytidae	*Discoglossus sardus* [30]	Allopatric	40.9	1770	0	0.92
	D. pictus		38.8	1500	0	
	Alytes muletensis [12]	Allopatric	39.7	850	10	0.14
	A. dickhilleni		37.7	2140	700	
Bufonidae	*Bufo californicus* [15]	Allopatric	32.3	2240	0	0.87
	B. microscaphus		35.3	2000	365	
Dendrobatidae	*Phyllobates vittatus* [18,25]	Allopatric	9.2	550	20	0.95
	P. lugubris		9.8	601	10	
Eleutherodactylidae	*Eleutherodactylus poolei* [8]	Allopatric	19.5	650	550	0
	E. minutus		18.9	2300	879	
	E. leberi [8]	Allopatric	20.4	465	394	0
	E. melacara		20.1	1974	845	
	E. fowleri [8]	Allopatric	18.3	1303	1045	0.70
	E. lamprotes		18.4	1455	818	
	E. montanus [8]	Partially sympatric	19.0	2424	1270	0.39
	E. patriciae		18.9	3050	2000	

E. schwartzi [8]	Partially sympatric	18.4	227	0	0.58
E. coqui		18.1	1338	0	
E. portoricensis [8]	Sympatric	18.2	1182	273	0.94
E. wightmanae		18.2	1189	150	
E. hedricki [8]	Partially sympatric	18.2	1152	455	0
E. cochranae		18.1	335	0	
E. martinicensis [8]	Sympatric	15.9	1250	0	0.86
E. amplinympha		15.4	1200	300	
E. pinchoni [8]	Partially sympatric	16.2	1250	0	0.95
E. barlagnei		16.2	1400	0	
E. chlorophenax [8]	Partially sympatric	18.4	1290	990	0.66
E. nortoni		18.3	1515	576	
E. glaucoreius [8]	Allopatric	18.1	1650	0	0.69
E. cundalli		18.2	635	0	
E. rivularis [8]	Allopatric	20.0	240	80	0.60
E. riparius		21.5	830	0	
E. cuneatus [8]	Partially sympatric	20.3	1515	0	0.81
E. turquinensis		20.0	1400	455	
E. darlingtoni [8]	Allopatric	18.4	2200	1720	0.71
E. leoncei		18.3	2303	1182	
E. armstrongi [8]	Partially sympatric	18.2	1697	152	0.52
E. alcoae		17.9	600	0	

	E. limbatus [8]	Allopatric	21.5	1150	50	0.84
	E. jaumei		20.0	950	200	
	E. dimidiatus [8]	Sympatric	21.4	1375	0	0.67
	E. emiliae		21.9	830	350	
	E. oxyrhyncus [8]	Partially sympatric	18.4	1212	333	0.84
	E. apostates		18.4	1640	333	
	E. glandulifer [8]	Sympatric	18.4	1886	300	0.51
	E. sciagraphus		18.5	1081	1060	
	E. ventrilineatus [8]	Sympatric	18.4	2340	1700	0.68
	E. brevirostris		18.4	2375	575	
	E. symingtoni [8]	Partially sympatric	22.8	155	70	0.84
	E. zeus		22.6	182	75	
Hylidae	*Acris blanchardi* [4]	Allopatric	35.6	945	0	0.88
	A. crepitans		35.7	714	0	
	Agalychnis annae [7]	Allopatric	32.8	1650	780	0.71
	A. moreletii		39.4	1500	300	
	A. spurrelli [7]	Partially sympatric	41.4	750	15	0.80
	A. litodryas		31.1	1000	100	
	Aplastodiscus cochranae [26]	Sympatric	37.6	800	500	0.67
	A. perviridis		35.0	1200	300	
	Hyla cinerea [10]	Sympatric	36.8	148	0	0.82
	H. gratiosa		40.4	109	13	

Hyloscirtus. armatus [7]	Allopatric	32.4	2500	1000	0
H. charazani		30.6	3200	2700	
Litoria. aurea [1]	Partially sympatric	32.3	1184	0	0.96
L. raniformis		41.7	1300	0	
L. moorei [1]	Allopatric	35.8	600	0	1
L. cyclorhyncha		18.6	600	0	
Osteopilus dominicensis [13]	Partially sympatric	20.7	2000	0	0.77
O. pulchrilineatus		32.3	1091	0	
O. brunneus [13]	Sympatric	31.7	1500	0	0.90
O. crucialis		-14.7	1200	0	
O. mariannae [13]	Sympatric	-15.2	880	120	1
O. wilderi		-22.5	880	120	
Pseudacris cadaverina [11,26]	Sympatric	-27.7	2290	0	0.88
P. regilla		-31.4	3000	0	
P. crucifer [11,26]	Partially sympatric	-28.8	1196	0	0.52
P. ocutlaris		-33.5	52	0	
P. streckeri [11,26]	Allopatric	-40.1	252	98	0.46
P. illinoensis		-31.4	135	80	
P. brimleyi [11,26]	Allopatric	-33.4	83	0	0
P. brachyphona		18.2	812	88	
P. maculata [11,26]	Partially sympatric	13.5	2845	98	0.62
P. clarkii		8.1	1033	0	

	P. nigrita [11,26]	Partially sympatric	10.9	88	0	0.61
	P. fouguettei		17.1	310	5	
	P. triseriata [11,26]	Partially sympatric	10.4	364	114	0.82
	P. feriarum		26.0	353	1	
	Pseudis minuta [5]	Partially sympatric	21.7	500	0	0
	P. cardosoi		18.9	1200	800	
	Smilisca fodiens [20]	Allopatric	19.0	1490	0	0
	S.. dentata		18.2	1900	1800	
	Smilisca sila [20]	Partially sympatric	18.2	500	0	0.66
	S. sordida		18.3	1525	0	
	S. cyanosticta [20]	Allopatric	18.2	1200	300	0.34
	S. puma		10.2	520	15	
	Tlalocohyla picta [21]	Allopatric	16.3	770	0	0.89
	T. smithii		4.9	1000	0	
	Anotheca spinosa [20]	Allopatric	13.5	2000	95	0.61
	Triprion petasatus		18.2	740	0	
Hyperoliidae	*Heterixalus variabilis* [28]	Allopatric	-13.3	200	0	0.70
	H. andrakata		-13.6	500	0	
	H. betsileo [28]	Allopatric	-20.0	1600	500	0.40
	H. carbonei		-19.1	900	0	
	H. luteostriatus [28]	Allopatric	-18.4	800	0	0

	H. rutenbergi		-19.5	1500	1200	
	H. alboguttatus [28]	Allopatric	-21.6	800	0	0.75
	H. boettgeri		-24.8	400	0	
Leiopelmatidae	*Ascaphus montanus* [14]	Allopatric	46.0	2156	541	0.78
	A. truei		47.1	1904	9	
Leiuperidae	*Engystomops guayaco* [17]	Allopatric	-2.4	92	32	0
	E. coloradorum		0.1	1000	100	
	E. montubio [17]	Allopatric	-1.0	330	0	0.73
	E. randi		-2.4	150	0	
	E. petersi [17]	Allopatric	-5.9	1200	0	0.89
	E. pustulosus		10.9	1540	0	
Limnodynastidae	*Limnodynastes ornatus* [19]	Allopatric	-22.7	684	0	0.84
	L. spenceri		-25.2	1000	0	
	L. depressus [19]	Allopatric	-14.8	200	0	0.09
	L. fletcheri		-29.8	980	172	
Mantellidae	*Blommersia domerguei* [6]	Partially sympatric	-18.4	2000	900	0.51
	B. blommersae		-18.5	1200	800	
	B. kely [6]	Allopatric	-17.5	1600	1000	0.50
	B. sarotra		-20.6	1200	900	
	Mantella crocea [24]	Allopatric	-15.9	1057	800	0.69
	M. milotympanum		-20.2	1000	900	
	M. pulchra [24]	Allopatric	-20.2	950	300	0.55

	M. madagascariensis		-20.1	1050	700	
	M. nigricans [24]	Allopatric	-19.8	1000	100	0.56
	M. baroni		-18.5	1200	600	
Microhylidae	*Plethodontohyla ocellata* [29]	Partially sympatric	-18.3	900	0	0
	P. brevipes		-21.4	1100	900	
	P. mihanika [29]	Partially sympatric	-19.7	1500	500	0.73
	P. inguinalis		-19.6	1100	400	
Myobatrachidae	*Arenophryne rotunda* [3]	Allopatric	-14.5	62	11	0
	A. xiphorhyncha		-14.8	194	105	
	Crinia remota [16]	Partially sympatric	-34.3	50	0	0.54
	C. bilingua		-32.0	600	0	
	C. subinsignifera [16]	Allopatric	-31.5	300	0	0.75
	C. pseudinsignifera		-33.6	600	0	
	C. riparia [16]	Allopatric	-26.1	600	200	0.70
	C. signifera		-27.4	1000	0	
Pelobatidae	*Pelobates cultripes* [23]	Allopatric	41.4	1770	0	0.60
	P. varaldii		34.0	350	0	
	P. syriacus [23]	Partially sympatric	38.8	2000	0	0.67
	P. fuscus		50.6	675	0	
Pelodytidae	*Pelodytes ibericus* [23]	Partially sympatric	37.7	1450	0	0.94

	P. punctatus		43.9	1630	0	
Pyxicephalidae	*Arthroleptella villiersi*[2]	Allopatric	-34.4	1800	0	0.78
	A. lightfooti		-34.1	1000	0	
Ranidae	*Clinotarsus alticola*[27]	Allopatric	18.4	1000	0	0.42
	C. curtipes		12.4	2000	500	
	Rana tarahumarae[9]	Allopatric	28.6	1000	0	0.89
	R. pustulosa		21.5	2000	500	
	R. vibicaria[9]	Partially sympatric	9.5	2700	1500	0.17
	R. warszewitschii		11.6	1740	0	
	R. vaillanti[9]	Sympatric	9.6	880	0	0.78
	R. juliani		16.7	600	100	
Sooglossidae	*Sooglossus sechellensis*[22]	Sympatric	-4.6	984	240	0.91
	S. thomasseti		-4.6	994	80	

Supplementary Literature Cited:

1. Burns, E. L., and D. M. Crayn. 2006. Phylogenetics and evolution of bell frogs (*Litoria aurea* species-group, Anura: Hylidae) based on mitochondrial *ND4* sequences. Molecular Phylogenetics and Evolution 39:573–579.
2. Dawood, A., and E. M. Stam. 2006. The taxonomic status of the monotypic frog genus *Anhydrophryne* Hewitt from South Africa: a molecular perspective. South African Journal of Science 102:249–253.
3. Edwards, D. 2007. Biogeography and speciation of a direct developing frog from the coastal arid zone of Western Australia. Molecular Phylogenetics and Evolution 45:494–505.
4. Gamble, T., P. B. Berendzen, H. B. Shaffer, D. E. Starkey, and A. M. Simons. 2008. Species limits and phylogeography of North American cricket frogs (*Acris*: Hylidae). Molecular Phylogenetics and Evolution 48:112–125.

5. Garda, A. A., and D. C. Cannatella. 2007. Phylogeny and biogeography of paradoxical frogs (Anura, Hylidae, Pseudae) inferred from 12S and 16S mitochondrial DNA. Molecular Phylogenetics and Evolution 44:104−114.
6. Glaw, F. and M. Vences. 2002. A new sibling species of the Anuran subgenus *Blommersia* from Madagascar (Amphibia: Mantellidae: *Mantidactylus*) and its molecular phylogenetic relationships. Herpetological Journal 12:11−20.
7. Gomez-Mestre, I., J. J. Wiens, and K. M. Warkentin. 2008. Evolution of adaptive plasticity: risk-sensitive hatching in Neotropical leaf-breeding treefrogs. Ecological Monographs 78:205−224.
8. Hedges, S. B., W. E. Duellman, and M. P. Heinicke. 2008. New World direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation. Zootaxa 1737:1–182.
9. Hillis, D. M. and T. P. Wilcox. 2005. Phylogeny of the New World true frogs (*Rana*). Molecular Phylogenetics and Evolution 34:299−314.
10. Hua, X., C. Fu, J. Li, A. Nieto Montes de Oca, and J. J. Wiens. 2009. A revised phylogeny of holarctic treefrogs (genus *Hyla*) based on nuclear and mitochondrial DNA sequences. Herpetologica (in press).
11. Lemmon, E. M., A. R. Lemmon, J. T. Collins, J. A. Lee-Yaw, and D. C. Cannatella. 2007. Phylogeny-based delimitation of species boundaries and contact zones in the trilling chorus frogs (*Pseudacris*). Molecular Phylogenetics and Evolution 44:1068−1082.
12. Martínez-Solano, I., H. A. Goncalves, J. W. Arntzen, and M. García-París. 2004. Phylogenetic relationships and biogeography of midwife toads (Discoglossidae: *Alytes*). Journal of Biogeography 31:603−618.
13. Moen, D. S., and J. J. Wiens. 2009. Phylogenetic evidence for competitively driven divergence: body-size evolution in Caribbean treefrogs (Hylidae: *Osteopilus*). Evolution 63:195−214.
14. Nielson, M., K. Lohman, and J. Sullivan. 2001. Phylogeography of the tailed frog *(Ascaphus truei*): implications for the biogeography of the Pacific Northwest. Evolution 55(1):147−160.
15. Pauly, G. B., D. M. Hillis, and D. C. Cannatella. 2004. The history of a Nearctic colonization: molecular phylogenetics and biogeography of the Nearctic toads (*Bufo*). Evolution 58(11):2517−2535.
16. Read, K., J. S. Keogh, I. A. W. Scott, J. D. Roberts, and P. Doughty. 2001. Molecular phylogeny of the Australian frog *genera Crinia*, *Geocrinia*, and allied taxa (Anura: Myobatrachidae). Molecular Phylogenetics and Evolution 21:294−308.
17. Ron, S. R., J. C. Santos, and D. C. Cannatella. 2006. Phylogeny of the túngara frog genus *Engystomops* (= *Physalaemus pustulosus* species group; Anura: Leptodactylidae). Molecular Phylogenetics and Evolution 39:392−403.
18. Santos, J. C., L. A. Coloma, and D. C. Cannatella. 2003. Multiple, recurring origins of aposematism and diet specialization in poison frogs. PNAS 100:12792−12797.

19. Schäuble, C. S., C. Moritz, and R. W. Slade. 2000. A molecular phylogeny for the frog genus *Limnodynastes* (Anura: Myobatrachidae). Molecular Phylogenetics and Evolution 16:379–391.
20. Smith, S. A., S. Arif, A. Nieto Montes de Oca, and J. J. Wiens. 2007. A phylogenetic hot spot for evolutionary novelty in Middle American treefrogs. Evolution 61:2075–2085.
21. Smith, S. A., A. Nieto Montes de Oca, T. W. Reeder, and J. J. Wiens. 2007. A phylogenetic perspective on elevational species richness patterns in Middle American treefrogs: why so few species in lowland tropical rainforests? Evolution 61:1188–1207.
22. Van der Meijden, A., R. Boistel, J. Gerlach, A. Ohler, M. Vences, and A. Meyer. 2007. Molecular phylogenetics evidence for paraphyly of the genus *Sooglossus*, with the description of a new genus of Seychellean frogs. Biological Journal of the Linnean Society 91:347–359.
23. Veith, M., L. Fromhage, J. Kosuch, and M. Vences. 2006. Historical biogeography of Western Palaearctic pelobatid and pelodytid frogs: a molecular phylogenetic perspective. Contribution to Zoology 75:109–120.
24. Vences, M., Y. Chiari, L. Raharivololoniaina, and A. Meyer. 2004. High mitochondrial diversity within and among populations of Malagasy poison frogs. Molecular Phylogenetics and Evolution 30:295–307.
25. Widmer, A., S. Lötters, and K. H. Jungfer. 2000. A molecular phylogenetic analysis of the neotropical dart-poison frog genus *Phylloates* (Amphibia: Dendrobatidae). Naturwissenschaften 87:559–562.
26. Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in Hylid frogs: treefrog trees unearth the roots of high tropical diversity. The American Naturalist 168:579–596.
27. Wiens, J. J., J. Sukumaran, R. A. Pyron, and R. M. Brown. 2009. Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). Evolution 63:1217–1231..
28. Wollenberg, K. C., F. Glaw, A. Meyer, and M. Vences. 2007. Molecular phylogeny of Malagasy reed frogs, *Heterixalus*, and the relative performance of bioacoustics and color-patterns for resolving their systematics. Molecular Phylogenetics and Evolution 45:14–22.
29. Wollenberg, K. C., D. R. Vieites, A. van der Meijden, F. Glaw, D. C. Cannatella, and M. Vences. 2008. Patterns of endemism and species richness in Malagasy cophyline frogs support a key role of mountainous areas for speciation. Evolution 62:1890–1907.
30. Zangari, F., R. Cimmaruta, and G. Nascetti. 2006. Genetic relationships of the western Mediterranean painted frogs based on allozymes and mitochondrial markers: evolutionay and taxonomic inferences (Amphibia, Anura, Discoglossidae). Biological Journal of the Linnean Society 87:525–536.

Table S1.2. The 28 sister-species pairs used in climatic analyses, including the ranges of values of each species for each of the 19 variables (maximum – minimum), sample size (georeferenced localities per species), temperature ranges, and additional literature resources for localities (all others are from museum localities from HerpNet). The 19 climatic variables are: Bio1, annual mean temperature; Bio2, mean diurnal temperature range; Bio3, isothermality ((Bio2/Bio7)*100); Bio4, temperature seasonality (standard deviation of monthly temperate * 100); Bio5, maximum temperature of the warmest month; Bio6, minimum temperature of the coldest month; Bio7, temperature annual range (Bio5-Bio6); Bio8, mean temperature of wettest quarter; Bio9, mean temperature of the driest quarter; Bio10, mean temperature of warmest quarter; Bio11, mean temperature of coldest quarter; Bio12, annual precipitation; Bio13, precipitation of wettest month; Bio14, precipitation of driest month; Bio15, precipitation seasonality (coefficient of variation); Bio16, precipitation of wettest quarter; Bio17, precipitation of the driest quarter; Bio18, precipitation of the warmest quarter; and Bio19,precipitation of coldest quarter.

Species (and additional references)	Bio 1	Bio 2	Bio 3	Bio 4	Bio 5	Bio 6	Bio 7	Bio 8	Bio 9	Bio 10	Bio 11
Bufo californicus	90	42	17	3815	125	72	136	95	135	95	95
Bufo microscaphus	110	35	12	2721	135	93	80	270	123	131	100
Acris blanchardi	139	69	17	5363	78	214	172	182	350	81	210
Acris crepitans	110	32	14	3146	52	158	121	225	248	68	154
Pseudacris cadaverina	169	71	16	4321	196	132	184	300	190	183	155
Pseudacris regilla	252	127	34	6769	289	294	274	408	271	271	288
Pseudacris crucifer	156	61	20	5053	97	228	168	253	364	108	224
Pseudacris ocularis	55	34	16	3108	17	107	111	12	45	14	94
Pseudacris brimleyi[1]	35	29	8	1178	29	42	28	26	40	19	50
Pseudacris brachyphona[1]	73	21	9	1916	61	90	60	169	238	62	93
Pseudacris maculata[1]	230	106	26	6601	174	289	137	210	429	164	299
Pseudacris clarkii[1]	43	46	7	3103	29	98	125	41	105	17	80
Pseudacris nigrita[1]	79	37	14	3639	34	129	121	166	101	29	125
Pseudacris fouguettei[1]	58	25	11	2782	19	101	109	167	233	27	92
Pseudacris triseriata[1]	73	43	11	1260	62	62	31	93	250	60	85
Pseudacris feriarum[1]	91	40	14	3037	44	120	88	218	238	55	126
Hyla cinerea	105	48	23	4892	65	165	141	183	267	50	168
Hyla gratiosa	65	25	15	2874	28	96	79	161	101	27	102
Triprion petasatus	14	50	12	402	45	23	62	22	30	18	6
Anotheca spinosa	78	43	19	1419	69	112	68	78	95	75	88
Smilisca sila	59	49	7	354	64	67	53	57	61	61	59
Smilisca sordida	109	34	17	752	129	108	42	103	120	115	109

Agalychnis annae	103	17	10	293	106	103	20	93	108	109	100
Agalychnis moreletii	87	69	23	1638	109	96	72	91	92	87	95
Ascaphus montanus	75	48	16	7147	84	196	181	261	325	90	168
Ascaphus truei	98	88	25	4246	165	117	186	106	115	111	109
Engystomops petersi	60	36	19	715	67	76	77	59	63	63	62
Engystomops pustulosus	117	53	17	1015	133	116	83	105	129	118	122
Crinia remota	42	46	8	1308	53	68	86	33	53	38	56
Crinia bilingua	26	35	7	1744	52	50	80	34	27	34	35
Arenophryne rotunda [2]	5	23	3	585	20	14	34	9	30	7	9
Arenophryne xiphorhyncha [2]	11	5	1	399	16	4	14	7	15	15	6
Rana vibicaria	177	26	9	260	184	175	29	170	189	182	177
Rana warszewitschii	84	43	20	733	93	90	42	89	94	91	83
Eleutherodactylus armstrongi	156	28	6	304	150	168	33	153	162	153	160
Eleutherodactylus alcoae	17	23	5	444	25	27	34	19	19	19	18
Eleutherodactylus schwartzi	26	6	4	97	25	30	7	25	23	26	27
Eleutherodactylus coqui	61	30	9	182	71	59	26	60	62	60	62
Eleutherodactylus dimidiatus	70	30	9	675	82	60	37	69	69	70	69
Eleutherodactylus emiliae	24	6	3	62	27	24	5	27	25	24	25
Eleutherodactylus montanus	112	22	5	190	119	100	19	119	113	108	113
Eleutherodactylus patriciae	154	25	7	238	155	162	19	146	152	157	152
Litoria aurea	130	67	21	4007	75	205	170	167	165	93	172
Litoria raniformis	110	47	8	2457	156	85	107	153	195	141	78
Osteopilus dominicensis	109	50	9	629	109	129	57	117	124	112	110
Osteopilus pulchrilineatus	64	14	8	264	67	65	20	66	68	61	67
Pelobates syriacus	129	52	20	4193	56	184	142	162	225	79	184
Pelobates fuscus	78	34	13	6588	96	180	209	95	127	81	161
Phyllobates vittatus	7	6	4	51	5	7	4	7	6	7	6
phyllobates lugubris	33	20	6	313	31	35	22	28	36	36	31

Rana tarahumarae	135	50	12	2586	83	165	85	104	93	100	157
Rana pustulosa	124	40	12	1523	152	107	47	92	130	122	140
Rana vaillanti	42	61	31	1624	71	74	92	51	57	44	59
Rana juliani	49	10	7	483	40	53	27	49	47	47	51
Tlalocohyla picta	99	36	8	557	86	102	50	90	110	97	101
Tlalocohyla smithii	64	50	15	1937	61	76	69	66	77	61	73

Species (and additional references)	Bio 12	Bio 13	Bio 14	Bio 15	Bio 16	Bio 17	Bio 18	Bio 19	Sample size	Temp. range
Bufo californicus	489	105	3	37	273	23	117	274	19	376
Bufo microscaphus	512	80	12	27	191	55	160	145	101	501
Acris blanchardi	1192	119	86	49	286	287	309	373	8	509
Acris crepitans	699	97	61	29	291	182	232	242	20	429
Pseudacris cadaverina	743	135	7	57	399	59	112	384	47	478
Pseudacris regilla	3653	555	163	111	1354	567	583	1033	10	614
Pseudacris crucifer	1022	103	103	36	274	318	277	399	26	519
Pseudacris ocularis	228	95	29	47	270	113	260	212	19	324
Pseudacris brimleyi [1]	192	42	20	11	114	27	116	37	25	361
Pseudacris brachyphona [1]	538	67	34	9	160	125	90	230	6	412
Pseudacris maculata [1]	784	95	57	56	240	179	263	202	15	674
Pseudacris clarkii [1]	252	72	28	29	97	71	58	51	62	350
Pseudacris nigrita [1]	489	86	38	28	252	139	222	224	5	362
Pseudacris fouguettei [1]	724	46	70	22	132	208	209	328	53	405
Pseudacris triseriata [1]	499	55	40	14	136	133	78	216	39	428
Pseudacris feriarum [1]	627	115	42	22	286	117	292	252	810	410
Hyla cinerea	780	118	59	56	353	199	436	294	31	405
Hyla gratiosa	501	73	37	28	196	144	221	65	27	360
Triprion petasatus	1049	144	40	25	285	139	319	389	16	196
Anotheca spinosa	2775	302	155	52	690	517	306	1121	53	232
Smilisca sila	1057	159	69	21	370	227	363	726	49	191
Smilisca sordida	2889	503	172	66	1115	613	795	1336	11	244
Agalychnis annae	2355	179	143	51	592	496	769	705	47	218
Agalychnis moreletii	3966	694	136	52	1709	444	855	1085	15	245
Ascaphus montanus	795	99	33	78	285	124	78	337	11	557
Ascaphus truei	2564	423	56	24	1139	200	1118	1118	6	418

Engystomops petersi	2513	221	289	58	614	893	842	1059	10	196
Engystomops pustulosus	3324	601	79	61	1411	275	476	1484	5	276
Crinia remota	980	203	35	45	575	118	470	144	78	222
Crinia bilingua	957	242	2	9	623	11	439	11	81	254
Arenophryne rotunda[2]	55	23	1	13	48	2	10	49	58	254
Arenophryne xiphorhyncha[2]	125	23	2	5	64	8	4	67	26	266
Rana vibicaria	2676	248	169	51	740	582	947	950	9	288
Rana warszewitschii	2527	311	157	57	776	547	720	918	18	214
Eleutherodactylus armstrongi	1068	176	27	10	403	81	433	67	13	301
Eleutherodactylus alcoae	652	92	21	4	264	61	207	62	8	171
Eleutherodactylus schwartzi	174	19	8	4	50	42	109	84	15	125
Eleutherodactylus coqui	2184	201	104	30	607	391	672	391	25	194
Eleutherodactylus dimidiatus	819	121	82	34	298	254	426	355	26	218
Eleutherodactylus emiliae	302	18	9	5	105	51	101	51	7	179
Eleutherodactylus montanus	919	161	38	7	331	109	269	101	9	271
Eleutherodactylus patriciae	758	116	41	23	278	117	264	120	11	313
Litoria aurea	1488	236	47	42	648	160	726	232	23	303
Litoria raniformis	929	128	46	30	346	150	169	358	9	361
Osteopilus dominicensis	1769	277	93	50	642	289	542	550	8	276
Osteopilus pulchrilineatus	220	114	48	32	239	137	229	204	64	198
Pelobates syriacus	1131	220	40	99	559	127	172	312	15	421
Pelobates fuscus	636	76	38	16	203	143	166	151	23	493
Phyllobates vittatus	909	169	44	7	400	141	149	448	28	147
phyllobates lugubris	1991	253	84	7	650	261	392	655	5	147
Rana tarahumarae	437	147	7	58	368	20	337	48	7	473
Rana pustulosa	322	122	9	26	230	42	482	156	5	353
Rana vaillanti	4021	474	189	76	1266	700	1153	1665	28	207
Rana juliani	1096	170	18	6	416	95	488	211	16	171
Tlalocohyla picta	1614	340	67	38	968	217	473	757	6	235
Tlalocohyla smithii	633	193	3	20	589	16	964	39	6	265

Supplementary Literature Cited:

1. Lemmon, E. M., A. R. Lemmon, J. T. Collins, J. A. Lee-Yaw, and D. C. Cannatella. 2007. Phylogeny-based delimitation of species boundaries and contact zones in the trilling chorus frogs (*Pseudacris*). Molecular Phylogenetics and Evolution 44:1068−1082.
2. Edwards, D. 2007. Biogeography and speciation of a direct developing frog from the coastal arid zone of Western Australia. Molecular Phylogenetics and Evolution 45:494−505.

Table S1.3. The 28 sister-species pairs used in the climatic analyses, included along with the latitudinal midpoint of the species pair (the average of the latitudinal midpoints of the two species), temperature overlap, geographic area overlap, and overlap in values for each of the 19 climatic variables. The formula for calculating overlap in species values is described in the Materials and Methods.

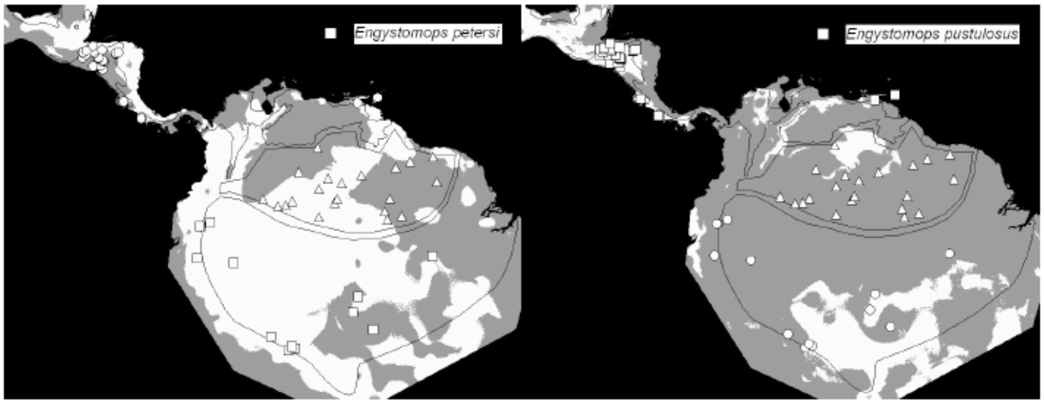
Species	Latitude midpoint	Temp. overlap	Area overlap	Bio 1	Bio 2	Bio 3	Bio 4	Bio 5	Bio 6	Bio 7
Bufo californicus, B. microscaphus	33.81	10.34	0	0.91	0.50	0.21	0.03	0.64	0.25	0.10
Acris blanchardi, A. crepitans	35.67	11.00	0	0.90	0.73	0.91	0.78	0.69	0.87	0.75
Pseudacris regilla, P. cadaverina	36.12	10.62	0.43	0.84	0.78	0.74	0.82	0.84	0.72	0.84
Pseudacris crucifer, P. ocutlaris	36.24	8.32	0.44	0.20	0.78	0.45	0.22	0.59	0.23	0.35
Pseudacris brimleyi, P. brachyphona	35.91	10.38	0	0.66	0.70	0.94	0.66	0.69	0.65	0.73
Pseudacris maculata, P. clarkii	36.37	5.64	0.05	0.00	0.65	0.63	0.10	0.34	0.00	0.00
Pseudacris nigrita, P. fouguettei	31.41	11.03	0.02	0.78	0.77	0.89	0.52	0.29	0.62	0.49
Pseudacris triseriata, P. feriarum	38.75	9.82	0.11	0.44	0.77	0.41	0.31	0.60	0.38	0.41
Hyla cinerea, H. gratiosa	32.01	11.12	0.66	0.81	0.76	0.83	0.79	0.72	0.79	0.78
Triprion petasatus, A. spinosa	15.86	8.93	0	0.59	0.78	0.27	0.61	0.31	0.60	0.74
Smilisca sila, S. sordida	9.50	10.65	0.09	0.77	0.85	0.71	0.52	0.75	0.76	0.85
Agalychnis annae, A. moreletii	13.26	10.74	0	0.92	0.62	0.65	0.59	0.75	0.97	0.58
Ascaphus montanus, A. truei	46.52	8.50	0	0.47	0.77	0.31	0.00	0.75	0.11	0.04
Engystomops petersi, E. pustulosus	2.46	10.18	0	0.76	0.84	0.72	0.54	0.75	0.73	0.96
Crinia remota, C. bilingua	14.64	10.12	0.01	0.16	0.70	0.67	0.72	0.38	0.87	0.63
Arenophryne rotunda, A. xiphorhyncha	26.76	11.21	0	0.00	0.00	0.00	0.52	0.73	0.00	0.30

Rana vibicaria, R. warszewitschii	10.57	10.04	0.40	0.74	0.80	0.73	0.68	0.67	0.76	0.64
Eleutherodactylus armstrongi, E. alcoae	18.08	8.51	0.16	0.46	0.91	0.92	0.84	0.26	0.52	0.93
Eleutherodactylus schwartzi, E. coqui	18.26	9.45	0.20	0.44	0.00	0.00	0.77	0.68	0.05	0.00
Eleutherodactylus dimidiatus, E. emiliae	21.66	10.14	0.50	0.67	0.60	0.44	0.55	0.66	0.70	0.57
Eleutherodactylus montanus, E. patriciae	18.96	10.00	0.51	0.63	0.85	0.69	0.56	0.65	0.61	0.95
Litoria aurea, L. raniformis	36.78	9.68	0.19	0.50	0.74	0.52	0.59	0.74	0.50	0.60
Osteopilus dominicnsis, O. pulchrilineatus	18.96	10.11	0.72	0.79	0.64	0.71	0.71	0.81	0.75	0.68
Pelobates syriacus, P. fuscus	44.68	9.38	0.03	0.51	0.83	0.44	0.47	0.76	0.58	0.69
Phyllobates vittatus, P. lugubris	9.49	10.55	0	0.61	0.00	0.83	0.58	0.00	0.60	0.00
Rana tarahumarae, R. pustulosa	25.04	9.82	0	0.82	0.00	0.00	0.00	0.73	0.39	0.00
Rana vaillanti, R. juliani	13.11	10.42	0.50	0.64	0.58	0.61	0.63	0.59	0.78	0.65
Tlalocohyla picta, T. smithii	19.65	10.12	0	0.66	0.12	0.77	0.64	0.24	0.87	0.33

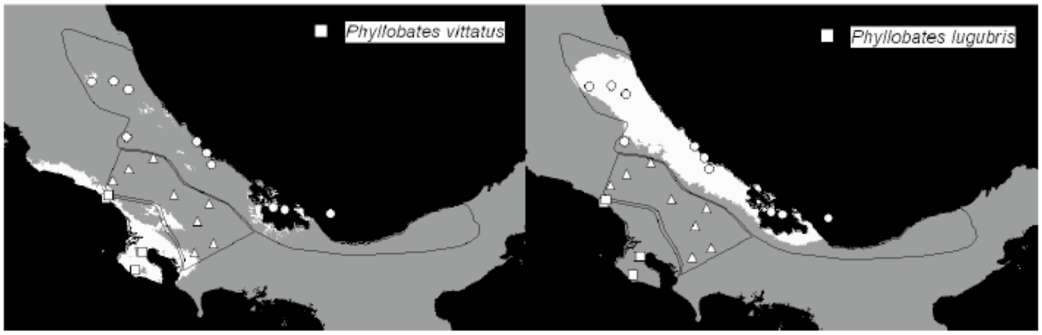
Bio 8	Bio 9	Bio 10	Bio 11	Bio 12	Bio 13	Bio 14	Bio 15	Bio 16	Bio 17	Bio 18	Bio 19
0.68	0.87	0.64	0.46	0.93	0.75	0.21	0.00	0.69	0.40	0.74	0.55
0.88	0.85	0.77	0.87	0.50	0.71	0.50	0.66	0.49	0.48	0.56	0.56
0.87	0.85	0.84	0.77	0.60	0.62	0.52	0.76	0.65	0.55	0.60	0.69
0.35	0.56	0.32	0.20	0.61	0.63	0.64	0.59	0.57	0.68	0.53	0.77
0.00	0.58	0.58	0.65	0.68	0.81	0.79	0.71	0.86	0.61	0.39	0.58
0.10	0.49	0.00	0.00	0.66	0.61	0.75	0.76	0.70	0.70	0.61	0.63
0.99	0.72	0.89	0.68	0.84	0.75	0.77	0.81	0.68	0.83	0.46	0.84
0.71	0.86	0.58	0.37	0.61	0.59	0.46	0.82	0.50	0.59	0.36	0.67

0.94	0.69	0.77	0.80	0.74	0.81	0.81	0.75	0.78	0.81	0.75	0.61
0.26	0.66	0.38	0.53	0.11	0.11	0.60	0.74	0.00	0.43	0.69	0.58
0.78	0.75	0.77	0.77	0.68	0.66	0.70	0.66	0.67	0.69	0.73	0.77
0.83	0.93	0.90	0.94	0.80	0.63	0.93	0.56	0.67	0.90	0.95	0.82
0.70	0.38	0.73	0.08	0.14	0.00	0.77	0.65	0.00	0.71	0.00	0.00
0.78	0.74	0.77	0.74	0.84	0.68	0.58	0.64	0.72	0.55	0.78	0.86
0.18	0.73	0.14	0.70	0.67	0.70	0.26	0.60	0.69	0.55	0.30	0.54
0.00	0.75	0.73	0.00	0.00	0.22	0.00	0.69	0.24	0.00	0.70	0.07
0.70	0.75	0.75	0.73	0.82	0.90	0.92	0.95	0.81	0.95	0.67	0.98
0.36	0.56	0.36	0.53	0.35	0.37	0.68	0.53	0.37	0.66	0.30	0.51
0.60	0.36	0.44	0.43	0.54	0.17	0.54	0.57	0.54	0.55	0.35	0.61
0.70	0.68	0.67	0.68	0.67	0.57	0.55	0.57	0.54	0.60	0.46	0.57
0.60	0.64	0.63	0.64	0.79	0.85	0.96	0.56	0.81	0.97	0.77	0.92
0.56	0.92	0.72	0.38	0.60	0.59	0.73	0.86	0.58	0.72	0.47	0.82
0.78	0.77	0.77	0.80	0.56	0.71	0.76	0.82	0.69	0.74	0.71	0.69
0.71	0.19	0.79	0.50	0.63	0.45	0.69	0.58	0.48	0.62	0.56	0.63
0.63	0.58	0.60	0.50	0.68	0.00	0.00	0.00	0.00	0.00	0.69	0.50
0.66	0.86	0.85	0.56	0.00	0.00	0.89	0.72	0.00	0.74	0.71	0.65
0.82	0.72	0.75	0.60	0.64	0.68	0.55	0.54	0.66	0.57	0.71	0.56
0.56	0.81	0.64	0.61	0.24	0.78	0.00	0.00	0.80	0.00	0.75	0.00

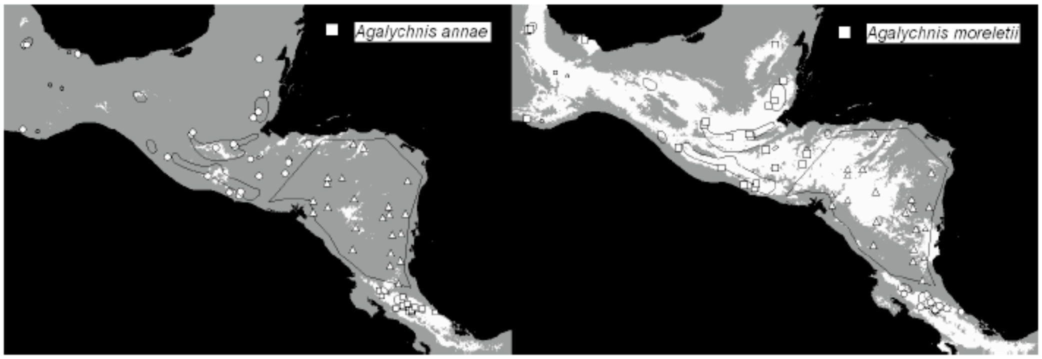
(A) *Engystomops petersi* & *E. pustulosus*



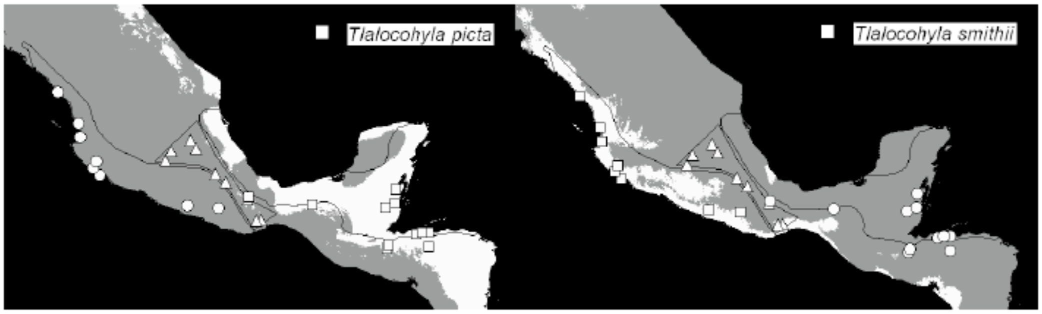
(B) *Phyllobates vittatus* & *P. lugubris*



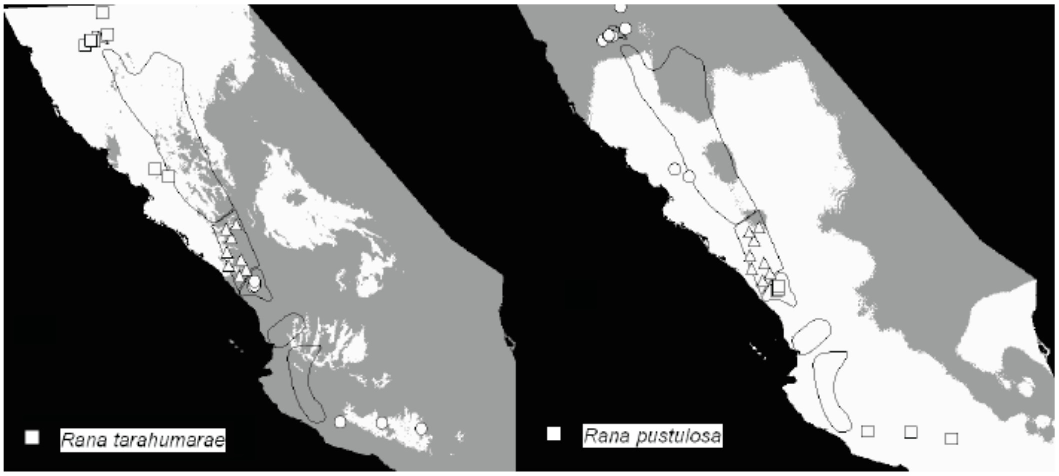
(C) *Agalychnis annae* & *A. moreletii*



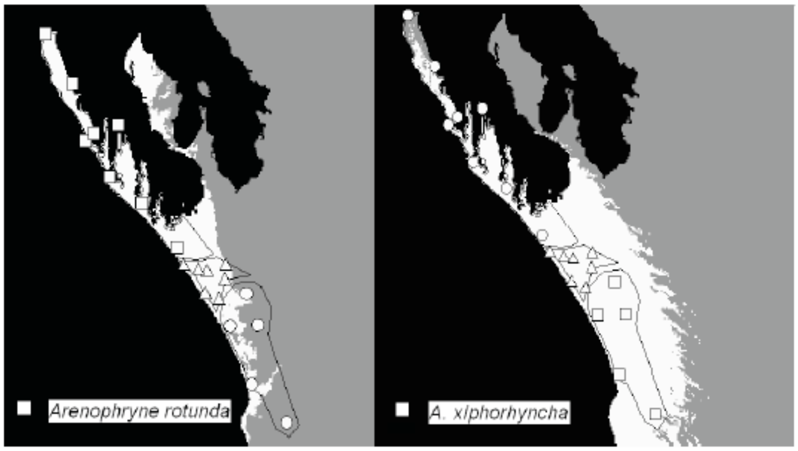
(D) *Tlalocohyla picta* & *T. smithii*



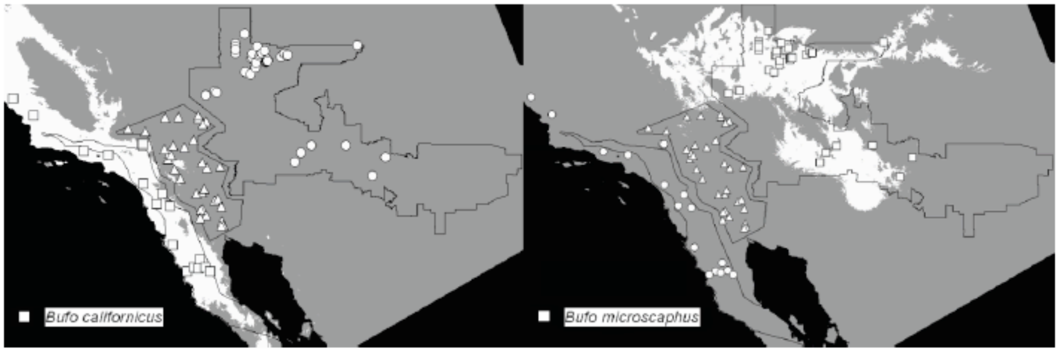
(E) *Rana tarahumarae* & *R. pustulosa*



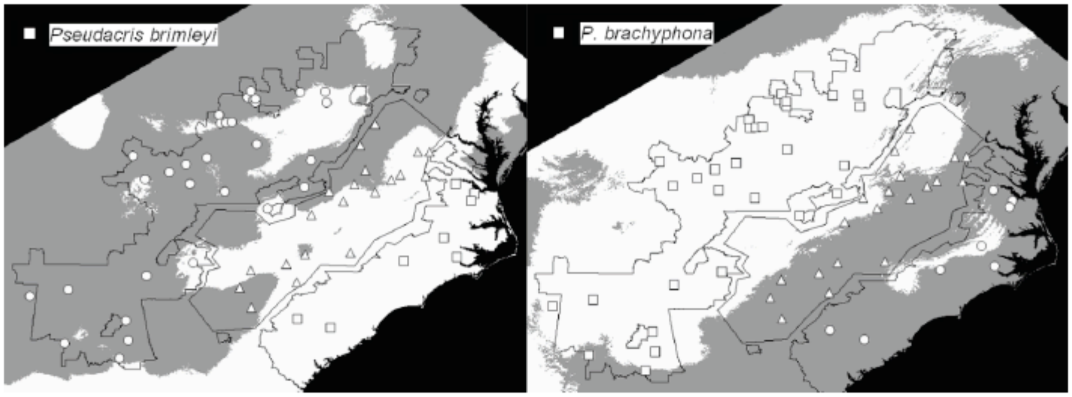
(F) *Arenophryne rotunda* & *A. xiphorhyncha*



(G) *Bufo californicus* & *B. microscaphus*



(H) *Pseudacris brimleyi* & *P. brachyphona*



(I) *Ascaphus montanus* & *A. truei*

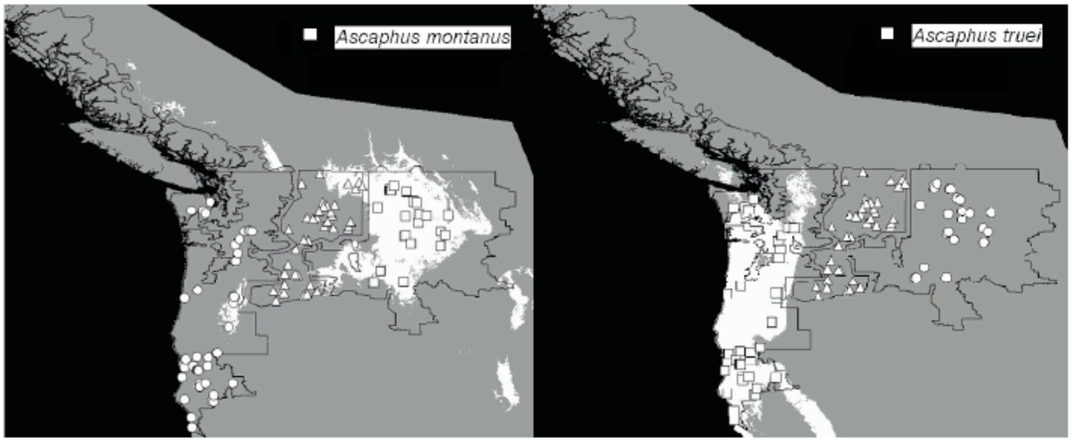


Figure S1.1. Predicted geographic distributions for each species of the 9 selected allopatric sister species pairs, based on ecological niche modeling. Squares represent the georeferenced localities of the species for which a niche model is being estimated. The polygon surrounding the squares is the known geographic range of that species (e.g., based on the GAA; IUCN 2009). Circles represent the georeferenced localities of its sister species, with the surrounding polygon indicating its geographic range. Triangles represent locations where both species should be absent, based on their known geographic ranges. The polygon surrounds the triangles is the "gap" area between the geographical ranges of the two sister species (see methods). The white area represents the spatial distribution of climatically suitable habitats for the species for which a niche model is being estimated, whereas the gray area represents the spatial distribution of climatically unsuitable habitats. The black area is not included in the niche modeling. The general geographic area for each map is as follows: (A) northern South America, (B) Central America, (C) MesoAmerica, (D) MesoAmerica, (E) Mexico, (F) Western Australia, (G) southwestern North America, (H) eastern U.S., and (I) northwestern North America.

Chapter 2

How does climate influence speciation?

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 influence 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 is largely unexplored in the theoretical literature on speciation (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 two mechanisms. 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. Under this scenario, climate drives “ecological speciation” (Rundle and Nosil 2005; Schluter 2001, 2009) or “gradient speciation” (Moritz et al. 2000). Speciation driven by this mechanism is thought to result in parapatrically distributed sister species that have divergent climatic niches (e.g. Moritz et al. 2000; Kozak and Wiens 2007).

Second, differences in climate over space might serve as an effective barrier to dispersal between allopatric populations, such that incipient species on either side have lower fitness in this barrier of unsuitable habitat and fail to adapt to climatic conditions there (Wiens 2004). These allopatric species may then diverge in response to other climatic or non-climatic factors and evolve intrinsic reproductive isolation. Speciation driven by this mechanism should result in allopatric sister species with similar climatic niches, separated by a barrier with very different climatic conditions (i.e. speciation via climatic niche conservatism (Wiens 2004), also related to "refugial speciation" (Moritz et al. 2000)). The idea that geographic isolation involves the separation of suitable habitats by unsuitable habitats is certainly not new (e.g., Mayr 1963), but the ecological and evolutionary basis for allopatry is only recently hypothesized to be associated with the ability of a species to evolve its niches (Wiens 2004).

Speciation via climatic niche conservatism and speciation via climatic niche divergence can be seen as two ends of a continuum of the tendency of a species to evolve its climatic niche to the climatic conditions where the species inhabits (related to "niche conservatism" (Wiens and Graham 2005)). Whether its climatic niche is conserved or labile may depend on the intrinsic degree of niche lability of the species and the extrinsic forces of natural selection, such as the geographic and temporal variation in the climatic conditions of the species' habitats (Wiens and Graham 2005). A species may be intrinsically niche conserved if it lacks genetic variation in the appropriate traits that are related to climatic niche evolution (e.g., the lack of mutations to develop freezing tolerance) or these traits may have pleiotropic effects that are antagonistic to the direction of selection exerted by the climatic conditions (e.g., Jenkins and Hoffman 1999; Etterson and Shaw 2001).

Speciation via climatic niche conservatism may be the dominant speciation mechanism for a species that is intrinsically niche conserved because the species remains maladapted to unsuitable habitats, which restricts gene flow between populations in suitable habitats if they are geographically separated by an unsuitable habitat. These allopatric populations may then accumulate reproductive incompatibility as a result of genetic drift or a by-product of niche divergence in other climatic or non-climatic factors. If the populations also lack appropriate mutations that are related to the evolution of those niches, then speciation between them is purely driven by climatic niche conservatism that leads to populations in allopatry and the subsequent evolution of reproductive isolation between them via genetic drift.

In contrast, speciation via climatic niche divergence may be the dominant speciation mechanism for a species that is intrinsically niche labile because the species may rapidly adapted to an initially unsuitable habitat, so that the unsuitable habitat is not likely to serve as a dispersal barrier that is essential for speciation via climatic niche conservatism. Meanwhile, mutations that cause reproductive incompatibility between populations can be fixed rapidly if they are genetically correlated with mutations underlying the adaptation of populations to difference climatic conditions in their habitats.

A burgeoning number of empirical studies have now addressed these two possible speciation mechanisms, based mostly on 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. Some studies have also tried to explore the linkage between species niche lability and the relative plausibility of the two speciation mechanisms (Kozak and Wiens 2007; Hua and Wiens 2010). However, it remains highly unclear as to why speciation seems to occur through climatic niche conservatism in some cases and via 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 to understand speciation through niche divergence. In fact, any model that considers local adaptation could be modeling “climate”. Our study is also based on several previous models (Pease and Lande 1989; Gavrilets 1999; Case and Taper 2000). 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. Furthermore, we know little about how climatic variation over time may influence speciation via niche divergence, because the literature on how habitat differences drive speciation is mostly based on static habitats over time.

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 vs. 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? How do those conditions depend on the intrinsic niche lability of a species?

Methods

Climatic Background

Our model starts with three habitats of a species (habitats 0, 1, and 2; Fig. 2.1). These habitats differ on one axis of the multivariate climatic niche (e.g. temperature), and take the values $\hat{z}_0$, $\hat{z}_1$, $\hat{z}_2$. 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 which 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 tolerances 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_{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_{LE} as a measurement of the intrinsic degree of climatic niche lability of the species.

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 (see Fig. 2.1) becomes suitable for the species. 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 is equal to $b/(2\times\text{amplitude})$, 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: mountain-slope scenario and valley-mountain scenario. Under the mountain-slope scenario, the three habitats occur at different elevations along a mountain slope and in which the ancestral population occupies the lowland habitat (habitat 0; Fig. 2.1A,B). Under constant climate over time (Fig. 2.1A), the ancestral population colonizes the high montane habitat (habitat 2) by first adapting to the mid-elevation habitat (habitat 1). Under changing (warming) climate (Fig. 2.1B), climatic niche divergence occurs when the lowland population adapts to increasing temperature at the same time as warming climate helps the species to colonize to 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 (Fig. 2.1C,D). The ancestral population again occupies the lowland habitat. Under warming climate (Fig. 2.1D), the lowland habitat becomes less suitable and the montane habitats more suitable over time. The lowland population may then go extinct if the species fails to adapt to higher temperatures, which should lead to geographic isolation and eventual speciation of the montane populations. Under this spatial and temporal variation in climate, population expansion into different mountaintops is facilitated by climate change and climatic niche conservatism may be essential to speciation by causing population isolation.

Nevertheless, under constant climate (Fig. 2.1C), climatic-niche evolution is necessary for the species to colonize montane habitats. Depending on the migration rate and niche lability of the species, the lowland population may become less adapted to lowland temperatures over time, if there is (a) gene flow from montane populations that swamps stabilizing selection and leads maladaptation of lowland populations, or (b) reproductive incompatibility develops between montane and lowland populations, which produces hybrids with low fitness. In these cases, the species' failure to maintain well-adapted populations in the lowlands results in allopatric montane sister species with similar climatic niches.

In addition, we also examine alternate scenarios in which the ancestral habitat has a different location on the niche gradient. First, we examine speciation via niche divergence under the scenario that the ancestral population occupies the middle habitat (i.e. habitat 1 in Fig. 2.1A). Second, we examine speciation via niche conservatism under the scenario that the ancestral population occupies an end habitat (e.g. habitat 1 in Fig. 2.1C).

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) the degree of gametic incompatibility (or hybrid dysfunction for individuals from other populations; D); and (4) mating probability between individuals (D_s). The degree of gametic incompatibility and the 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, m proportion of adults migrate to adjacent habitats. After migration, mating occurs along with sexual selection (related to D_s). In the following sections, we describe in detail how we model each of these four properties (population size, climatic niche evolution, hybrid dysfunction, mate choice).

Population Size

To estimate population size (N), we start with the differential equation of population growth, using population 1 as an example: $dN_1/dt = \overline{w}_1(t)N_1(t)$, where $\overline{w}_1(t)$ 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 $\overline{w}_1(t)$ as:

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

The first term $\overline{r}_1(t)$ denotes the intrinsic growth rate of population 1 that is independent of its climatic niche but associated with reproductive success within and among populations (see the section below on reproductive success). The second term gives the total amount of competition on population 1 in its habitat, where C denotes the carrying capacity for individuals with optimum climatic trait value of the habitat; $N_{01}(t)$ and $N_{21}(t)$ are the number migrants from population 0 and population 2 to habitat 1 (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 non-overlapping 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 (Bulmer 1980):

$$\begin{aligned} z_1(t+1) &= z_1(t) + [\hat{z}_1 - z_1(t)]V_{g1}(t)/[V_1(t)+V_s] \\ V_{g1}(t+1) &= V_{g1}(t) - V_{g1}^2(t)/[V_1(t)+V_s] \end{aligned},$$

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

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

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

$$V_1^*(t+1) = (1 - \tfrac{1}{2N_{e_1}})[\tfrac{1}{2}V_{g1}^*(t+1) + \tfrac{1}{2}V_{LE}] + V_e,$$

where V_{LE} is the genetic variance at linkage equilibrium and N_{e1} is the effective population size of population 1. Effective migration rate and effective population size are associated with reproductive success between populations, thus we describe the estimation of them in the section on reproductive success.

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 each mutation on these hybrid dysfunction loci has a complementary mutation on a different locus. These complementary mutations build the 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*/*a* and allele *b* is the complementary mutation for the allele *a*, then only under the genetic background with allele *b*, gametes with allele *A* are compatible with gametes with allele *a*. 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 (1999) assumed reproductive incompatibility as a result of heterozygous disadvantage within a locus rather than deleterious epistatic interactions among alleles on different loci. Using population 1 as an example, the average probability of gametes from population 1 producing fertile and viable offspring is:

$$W_1 = \frac{\Gamma(K - k_1 + 1, D_1 - k_1)}{\Gamma(K - k_1 + 1)},$$

where D_1 is the average number of incompatible genes between gametes in population 1 and k_1 is the number of the incompatible genes that are fixed in population 1. Similarly, the average probability of gametes from different populations (e.g. population 1 and population 2) producing fertile and variable offspring is:

$$W_{12} = \frac{\Gamma(K - k_{12} + 1, D_{12} - k_{12})}{\Gamma(K - k_{12} + 1)},$$

where D_{12} is the average number of incompatible genes between population 1 and population 2; k_{12} is the number of the incompatible genes that are fixed in both populations.

Following Gavrilets (1999), the expected change in D_1 and D_{12} per generation is:

$$\Delta D_1 = -s_1(D_1 - k_1) + 2u + 2m_{e01}(D_{01} - D_1) + 2m_{e21}(D_{12} - D_1) - \tfrac{D_1 - k_1}{2N_{e1}}$$
$$\Delta D_{12} = -\tfrac{s_1 + s_2}{2}(D_{12} - k_{12}) + 2u + 2m_{e21}(D_2 - D_{12}) + 2m_{e12}(D_1 - D_{12}),$$

where the first term describes decrease in D_1 and D_{12} as a result of selection against low-fit genotypes (i.e., genotypes with large number of incompatible genes), with

$s_1 = \frac{\partial \ln W_1}{\partial D_1} = \frac{e^{-(D_1 - k_1)}(D_1 - k_1)^{(K - k_1)}}{\Gamma(K - k_1 + 1, D_1 - k_1)}$ being the selection coefficient against incompatible genes in population 1 (s_2 for population 2). The second term describes increase in D_1 and D_{12} as a result of new mutations on hybrid dysfunction loci occurring in one generation, with u being the total mutation rate on the hybrid dysfunction loci. The next two terms describe changes in D_1 and D_{12}

as a result of gene flow between populations. The last term in the equation for ΔD_1 describes decrease in D_1 as a result of genetic drift.

In the equations for the expected change in D_1 and D_{12} per generation, k_1 (the number of the incompatible genes that are fixed in population 1) is modeled as:

$k_1 = L_1 + L_{01} + L_{21} - l_1 - l_{01} - l_{21}$, with L_1 denoting the number of mutations on the hybrid dysfunction loci that arise in population 1 and get fixed in population 1, L_{01} and L_{21} denoting the number of mutations that get fixed in population 1 but arise in population 0 and population 2, and l_1, l_{01}, l_{21} denoting the number of the L_1, L_{01}, L_{21} mutations whose complementary mutations also get fixed in population 1. Using the same notation, k_{12} (the number of the incompatible genes that are fixed in both populations) is modeled as:

$k_{12} = L_1 + L_2 - l_{12} - l_{21} + \max\{L_{01}, L_{02}\} - \min\{l_{01}, l_{02}\}$.

We follow the method of Lynch & Abegg (2010) to approximate changes in the number of fixed mutations (L_1, L_{01}, L_{21}) and their complementary mutations (l_1, l_{01}, l_{21}) over the course of a generation. 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 different environments (e.g., Lee et al. 2008) or have tight physical linkage to genes under divergent selection (e.g., Via 2009). Therefore, we assume two scenarios of mutations on hybrid dysfunction loci. Under one scenario (climate independent scenario hereafter), mutations on a fixed number of 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 evolution influences speciation mainly by influencing the geographic distributions of populations and consequently the level of gene flow between populations as well as the level of genetic drift within population. The other scenario (climate dependent scenario hereafter) is similar except that mutations on the fixed number of loci are not selfish genes but have pleiotropic effects on adaptation to different climatic conditions. Under this scenario, climatic niche evolution influences speciation not only by influencing the geographic distributions of populations, but also directly influencing the fixation rates of hybrid dysfunction loci.

Using population 1 as an example, changes in the fixation rate of selfish genes are (Lynch & Abegg 2010):

$$\Delta L_1 = vR_1 2^{-4N_{e1}(m_{e01}+m_{e21})},\ R_1 = 2N_1\frac{1-e^{-2(d-s_1)}}{1-e^{-4N_{e_1}(d-s_1)}}$$

where v is the mutation rate of the selfish genes and d is the intensity of meiotic drive for the selfish genes. Changes in the fixation rate of their complementary mutations are (Lynch & Abegg 2010):

$$\Delta l_1 = \left[\frac{1}{\Delta L_1} + \frac{1}{v_c R_{c1} 2^{-4N_{e1}(m_{e01}+m_{e21})}}\right]^{-1}\ R_{c1} = 2N_1\frac{1-e^{-2s_{c1}}}{1-e^{-4N_{e_1}s_{c1}}},\ ,$$

where v_c is the mutation rate of a complementary mutation, s_{c1} is selective advantage of carrying a complimentary mutation. Using similar arguments, changes in the fixation rate in population 1 of mutations arising in population 0 are:

$$\Delta L_{01} = \begin{cases} (L_{02} - L_{01})(1 - e^{-(m_{e01} + m_{21})R_1 (e/2)^{4N_{e1}(m_{e01}+m_{e21})}}) + (L_0 - L_{02})(1 - e^{-(m_{e01} - m_{e21})R_1 (e/2)^{4N_{e1}(m_{e01}-m_{e21})}}) & (L_{02} > L_{01}, m_{e01} > m_{e21}) \\ (L_{02} - L_{01})(1 - e^{-(m_{e01} + m_{e21})R_1 (e/2)^{4N_{e1}(m_{e01}+m_{e21})}}) & (L_{02} > L_{01}, m_{e01} < m_{e21}) \\ (L_0 - L_{01})(1 - e^{-(m_{e01} - m_{e21})R_1 (e/2)^{4N_{e1}(m_{e01}-m_{e21})}}) & (L_{02} < L_{01}, m_{e01} > m_{e21}) \\ 0 & (L_{02} < L_{01}, m_{e01} < m_{e21}) \end{cases}$$

$$\Delta l_{01}^{-1} = \begin{cases} \frac{1}{\Delta L_{01}} + [(l_{02} - l_{01})(1 - e^{-(m_{e01} + m_{e21})R_{c1} (e/2)^{4N_{e1}(m_{e01}+m_{e21})}}) + (l_0 - l_{02})(1 - e^{-(m_{e01} - m_{e21})R_{c1} (e/2)^{4N_{e1}(m_{e01}-m_{e21})}})]^{-1} & (l_{02} > l_{01}, m_{e01} > m_{e21}) \\ \frac{1}{\Delta L_{01}} + [(l_{02} - l_{01})(1 - e^{-(m_{e01} + m_{e21})R_{c1} (e/2)^{4N_{e1}(m_{e01}+m_{e21})}})]^{-1} & (l_{02} > l_{01}, m_{e01} < m_{e21}) \\ \frac{1}{\Delta L_{01}} + [(l_0 - l_{01})(1 - e^{-(m_{e01} - m_{e21})R_{c1} (e/2)^{4N_{e1}(m_{e01}-m_{e21})}})]^{-1} & (l_{02} < l_{01}, m_{e01} > m_{e21}) \\ 0 & (l_{02} < l_{01}, m_{e01} < m_{e21}) \end{cases}$$

Solutions for nearly neutral mutations are similar to those for selfish genes, except that $R_1 = 2N_1 \frac{1 - e^{2s_1}}{1 - e^{4N_{e1} s_1}}$ and the fixation of mutation on hybrid dysfunction loci can be accelerated if its complementary mutations arise prior to its fixation (Lynch & Abegg 2010). After accounting for these differences, the term in the square brackets in Δl_{01}^{-1} becomes:

$$\begin{cases} (l_{02} - l_{01})(1 - e^{-(m_{e01} + m_{e21})(e/2)^{4N_{e1}(m_{e01}+m_{e21})}(R_{c1} + (m_{e01} + m_{e21})N_1 / Ne_1)}) + (l_0 - l_{02})(1 - e^{-(m_{e01} - m_{e21})(e/2)^{4N_{e1}(m_{e01}-m_{e21})}(R_{c1} + (m_{e01} - m_{e21})N_1 / N_{e1})}) & (l_{02} > l_{01}, m_{e01} > m_{e21}) \\ (l_{02} - l_{01})(1 - e^{-(m_{e01} + m_{e21})(e/2)^{4N_{e1}(m_{e01}+m_{e21})}(R_{c1} + (m_{e01} + m_{e21})N_1 / N_{e1})}) & (l_{02} > l_{01}, m_{e01} < m_{e21}) \\ (l_0 - l_{01})(1 - e^{-(m_{e01} - m_{e21})(e/2)^{4N_{e1}(m_{e01}-m_{e21})}(R_{c1} + (m_{e01} - m_{e21})N_1 / N_{e1})}) & (l_{02} < l_{01}, m_{e01} > m_{e21}) \\ (L_{02} - l_{01})(1 - e^{-(m_{e21} - m_{e01})^2 (e/2)^{4N_{e1}(m_{e21}-m_{e01})} N_1 / N_{e1}}) & (L_{02} < l_{01}, m_{e01} < m_{e21}) \end{cases}$$

Solutions for mutations that have pleiotripic effects on adaptation to different climatic conditions are also similar to those for selfish genes, except that the intensity of meiotic drive (*d*) is replaced by the selection advantage (s_{LA}) of the mutations in local climatic conditions. Because the climatic niche of a species is modeled as a quantitative trait, the selective coefficient of a single mutation on one of the loci that determine the climatic niche is modeled as, using population 1 as an example: $s_{LA}(t) = A \frac{\hat{z}_1 - z_1(t)}{V_s + V_1(t)}$, where *A* is the effect size of the mutation that describes the amount by which individuals carrying the mutation deviate from the population average climatic niche z_1 (Kimura and Crow 1978; Chevin and Hospital 2008). Since the climatic niche of the ancestral population is initially set to zero, we follow the number of fixed mutations that either make the climatic niche more positive or more negative. For example, if the local climatic condition $\hat{z} < 0$, mutations with negative effects should be selected over those with positive effects. We arbitrarily assume that mutations on each locus have equal effect size A=0.1.

Mate Choice

Besides hybrid dysfunction, populations may also become reproductively isolated if individuals from different populations do not mate. We model the evolution of mate choice as done for hybrid dysfunction, by making an analogy between a set of male traits and mutations on hybrid dysfunction loci and between female preference and complementary mutations. Using population 1 as an example, the average mating probability between individuals in population 1 is $W_{s1} = \frac{\Gamma(K_s - k_{s1} + 1, D_{s1} - k_{s1})}{\Gamma(K_s - k_{s1} + 1)}$, where D_{s1} is the average number of traits a male carries that are not preferred by females in population 1; k_{s1} is the number of such traits that are fixed in population 1; two individuals will mate only if the number of such traits is no more than K_s. When different male traits become fixed in different populations, the females' preference for the male trait of their own population becomes advantageous (to avoid low-fit hybrid progeny from matings between individuals of different populations; see section below on Reproductive Success).

In the set of male traits and female preferences, we assume that each male trait and female preference for the male trait are each determined by a single separate locus. Similar to hybrid dysfunction loci, we also assume two scenarios of mutations on male traits. Under one scenario (climate independent 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 trait loci should suffer a selective disadvantage $S_{s1} = \frac{e^{-(D_{s1}-k_{s1})}(D_{s1}-k_{s1})^{(K_s-k_{s1})}}{\Gamma(K_s-k_{s1}+1, D_{s1}-k_{s1})}$ because the mutant male has a trait that is not preferred by any existing females in the population. Under the other scenario (climate dependent scenario), mutations on the fixed number of male traits are not neutral but arise as the pleiotropic effect of adaptation to different climatic conditions (i.e., the classic magic traits; Servedio et al. 2011).

Solutions for male traits are similar to those for the mutations on hybrid dysfunction loci, except that $R_1 = \frac{N_1}{N_{e1}}$ for the neutral male traits under the climate independent scenario and, using population 1 as an example, s_1 (the selection coefficient against incompatible genes) is replaced by s_{s1} (the selection coefficient against mutant male traits); s_{c1} (the selective advantage of carrying a complimentary mutation) is replaced by s_{sc1} (the selective advantage of developing female preferences for male traits in the same population in order to avoid mating with individuals from different populations that produces low-fit hybrids; see the section on reproductive success).

Reproductive Success

An individual can reproduce if it finds a mate with compatible gametes. For mathematical simplicity, we assume that females mate once and males mate multiple times in their life spans. Using habitat 1 as an example, the number of matings between individuals that are both from population 1 is $n_1 = \frac{W_{s1}N_1^2}{2(W_{s1}N_1 + W_{s01}N_{01} + W_{s12}N_{12})}$; the number of matings between population 1 and population 0 is $n_0 = \frac{W_{s01}N_{01}N_1}{2(W_{s1}N_1 + W_{s01}N_{01} + W_{s12}N_{12})} + \frac{W_{s01}N_{01}N_1}{2(W_{s0}N_{01} + W_{s01}N_1)}$ and so is the number of matings between population 1 and population 2 (n_2).

Consequently, the average growth rate of population 1 is $\bar{r}_1 = r_{\max}\frac{W_1n_1 + W_{01}n_0 + W_{12}n_2}{n_1 + n_0 + n_2}$ with $r_{\max}$ denoting the maximum intrinsic growth rate (i.e. when both probability of mating and probability of producing viable offspring equals to 1). The effective migration rate from population 0 to population 1 is $m_{e01} = \frac{W_{01}n_0}{2(W_1n_1 + W_{01}n_0 + W_{12}n_2)}$ and so is the effective migration rate from population 2 to population 1 (m_{e02}; with corresponding changes in notations). The effective population size of population 1 is

$$N_{e1} = \frac{\bar{r}_1(n_1 + n_0 + n_2)[\bar{r}_1(n_1 + n_0 + n_2) - 1]}{W_1r_{\max}n_1(W_1r_{\max} - 1) + W_{01}r_{\max}n_0(W_{01}r_{\max} - 1) + W_{12}r_{\max}n_2(W_{12}r_{\max} - 1)}.$$

When a complementary mutation for hybrid dysfunction arises, it increases population growth rate by increasing the reproductive success between individuals from the same population. Thus, the mutation has a selective advantage:

$S_{c1} = \frac{\partial \ln \bar{r}_1}{\partial W_1}\frac{\partial W_1}{\partial D_1} = \frac{n_1}{W_1n_1 + W_{01}n_0 + W_{12}n_2}\frac{e^{-(D_1-k_1)}(D_1 - k_1)^{K-k_1}}{\Gamma(K - k_1 + 1)}$. When a female preference arises, it increases population growth rate by increasing the mating probability between individuals from the same population relative to the mating probability between different populations. Thus the female preference has a selective advantage:

$$S_{sc1} = \frac{\partial \ln \bar{r}_1}{\partial W_{s1}} \frac{\partial W_{s1}}{\partial D_{s1}} = \frac{n_1}{W_{s1}} \frac{e^{-(D_{s1}-k_{s1})}(D_{s1}-k_{s1})^{K_s-k_{s1}}}{\Gamma(K_s-k_{s1}+1)} [\frac{2W_1W_{s1}N_1+(W_1+W_{01})W_{s01}N_{01}+(W_1+W_{21})W_{s12}N_{21}}{W_1n_1+W_{01}n_0+W_{12}n_2} - \frac{2W_{s1}N_1+2W_{s01}N_{01}+2W_{s12}N_{21}}{n_1+n_0+n_2}]$$

Speciation Criterion

Based on the biological species concept (which is 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 (W_{12}) and the intrinsic mating probability between individuals from the two incipient species (W_{s12}) equals to zero. Nevertheless, reproductive isolation is not an all-or-none phenomenon and hybridization between species is commonly observed in nature (Coyne and Orr 2004). Speciation occurring under the limited parameter space examined in the present study does not guarantee that it will occur under other parameter values. Therefore, besides setting cut-off on the number of incompatible genes between two gametes that leads to complete inviable offsprings or zero mating probability (see the section on parameter values). We also include a scale bar, values on which are the probability of individuals from different populations to successfully produce offspring. This probability equals the product of hybrid viability (W_{12}) and intrinsic mating probability (W_{s12}).

We focus on speciation between populations in the 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; (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 between -10 and 10. Species either have low degree of niche lability with genetic variation (V_{LE}) of the climatic trait at linkage equilibrium equal to 0.01 or have high degree of niche lability with $V_{LE} = 0.9$. To examine how temporal variation in climate influences speciation, we use a wide range of values for the initial climatic conditions in each habitat and report representative results with $\hat{z}_1$=-10 (or -15), $\hat{z}_0$ =0, $\hat{z}_2$=-10 (or -15) for mountain-valley scenario (fig. 1*C*,*D*) and $\hat{z}_0$=-15 (or -20), $\hat{z}_1$=-7.5 (or -10), $\hat{z}_2$=0 for mountain-slope scenario (fig. 1*A*,*B*). Rate of climate change is set to vary between 0 and 1 unit on the axis of climatic niche per generation. Values for V_{LE} is set to vary between 0 and 1, a range that includes previously reported intraspecific variation in trait values related to climatic tolerance (e.g. Gilchrist and Huey 1999; Gibert and Huey 2001). We arbitrarily set 100 loci of mutations on hybrid dysfunction loci to be selfish genes and 100 mutations on neutral male traits under the climate independent scenario. We also set 200 loci of mutations on hybrid dysfunction loci and on male traits to be associated with climatic niche divergence (with 100 loci having positive effects and 100 loci having negative effects on the values of the climatic trait) under the climate dependent scenario. Under both scenarios, mutation rate on those loci is set to 10^{-7} per locus per generation and their complementary mutation rate (v_c) is set to 10^{-5}. The total mutation rate on hybrid dysfunction loci as well as male traits (u) is set to 0.01. We assume that two gametes produce inviable offspring if the number of incompatible genes between them is more than 20 loci and two individuals do not mate intrinsically if they have more than 20 mismatches between male traits and female preferences (i.e., $K = K_s = 20$). Values of other parameters are: $r_{\max} = 4$, $C = 1000$, $V_s = 10$, $m = 0.01$. 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 climate dependent scenario (Fig. S2.1-2.3) and climate independent scenario (Fig. 2.2-2.4) for the composition of mutations underlying reproductive incompatibility between populations are surprisingly similar. 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 can occur under a set of conditions (Fig. 2.2; Fig. S2.1): 1) when climatic conditions in the two end habitats were very similar to each other but differed from the middle habitat; 2) when the climate at one end habitat was similar to the middle habitat but very different from the other end habitat. Under these climate conditions, the ancestral population did not go locally extinct but was barely able to colonize the end habitats and persisted in a small population size, potentially representing "peripatric" speciation (Coyne and Orr 2004).

Directional variation in climate over time had contrasting effects on speciation under the valley-mountain scenario and the mountain-slope scenario (Fig. 2.3; Fig. S2.2). Directional climate change promoted speciation under the valley-mountain scenario (Fig. 2.3A,B), especially for species with low niche lability and when climate change was rapid. The conditions under which speciation occurred under the valley-mountain scenario (black cells in Fig. 2.3A,B) are when the population in the middle habitat (i.e. the lowland population in Fig. 2.1D) went locally extinct. In contrast, no speciation occurred under the mountain-slope scenario (Fig. 2.3C,D). Interestingly, when mutations underlying reproductive incompatibility are the pleiotripic effects of climatic niche evolution (the climate dependent scenario), populations in the two end habitats were not intrinsically reproductively isolated, although they were geographically isolated (Fig. S2.2; see Discussion section).

Climatic oscillations over time also had contrasting effects on speciation under the valley-mountain scenario and the mountain-slope scenario (Fig. 2.4). In contrast to directional climate change, climatic oscillations promoted speciation under the mountain-slope scenario (Fig. 2.4C,D). Speciation occurred when a species was barely able to persist in all the three habitats along a mountain slope through climatic oscillations (Fig. 2.4C,D; Fig. S2.4). In contrast, climatic oscillations did not promote speciation under the valley-mountain scenario

(Fig. 2.4A,B). For species with low niche lability and when climate oscillations were frequent, species did not establish constant populations in the two end habitats, where local extinction and recolonization events continually occurred during climatic oscillations (Fig. S2.4). Under these conditions, reproductive incomparability cannot 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 vs. niche divergence). Our results show that speciation via niche conservatism is theoretically plausible, and illustrate the conditions where speciation via niche conservatism and 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 vs. 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; Via 2002; Rundle and Nosil 2005; Schluter 2009). Here, to our knowledge, we explored for the first time 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 and under a valley-mountain scenario of spatial variation in climate, speciation between populations on two mountaintops occurred when the ancestral population in the intermediate lowland habitat went locally extinct, which was most likely for species with low climatic niche lability (Fig. 2.2A,B). With the barrier to gene flow, complete reproductive isolation can evolve between populations if there are mutations underlying reproductive incompatibility being selfish genes (maybe other types of non-deleterious mutations that are not modeled in this study; e.g., mutations on duplicated genes; Presgrave 2010). Intriguingly, the two populations are not intrinsically reproductively isolated when mutations underlying reproductive incompatibility are the pleiotropic effects of climatic niche evolution (Fig. S2.2). This is presumably because the barrier of unsuitable habitat is effective only to niche-conserved species and niche-conserved species tend to track its climatic niche tightly up or down hills, leaving little chance for climatic niche evolution. It is important to note that the above result is based on the assumption that the two mountaintops have the same climatic conditions under the valley-mountain scenario. 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 the geographic isolation between populations on different mountaintops and the latter promoting the evolution of reproductive isolation between them as the pleiotropic effects of adaptations to different climatic conditions.

Taken together, speciation via climatic niche conservatism should be the predominant speciation mechanism for niche-conserved species under directional climate change and a spatial variation in climate that resembles the valley-mountain scenario.

In contrast to speciation via niche conservatism, we find that speciation via climatic niche divergence may be the predominant speciation mechanism for species with low niche lability under constant climate over time (Fig. 2.2), and for species with high niche lability under a mountain-slope scenario of spatial variation in climate when climate oscillates (Fig. 2.4). Under these conditions, climatic niche divergence is necessary for the species to persist in all the three habitats during speciation process. Nonetheless, speciation didn't occur if the adaptation to local climatic conditions is too rapid or if local adaptation is more rapid than climate changes (Fig. 2.4).

Surely, the above results depend on the relative prevalence of different genetic bases of reproductive isolation. At one extreme where all the mutations underlying reproductive incomparability are the pleiotropic effects of climatic niche evolution, intrinsic reproductive isolation between populations should only evolve when populations are niche diverged. At the other extreme where no mutations are the pleiotropic effects of niche evolution, climate should influence speciation only by affecting the geographic distributions of populations. In the present study, we arbitrarily assume roughly equal number of mutations being the pleiotropic effects of climatic niche evolution (climate dependent scenario) or not (climate independent scenario). We find that the conditions under which speciation via niche divergence occurred are very similar under the two scenarios (Fig. 2.2, 2.4 and Fig. S2.1, S2.3). This result may indicate that climate influences speciation mainly by influencing the geographic distributions of populations rather than directly influencing the fixation rate of mutations underlying reproductive isolation between populations.

We acknowledge that we only modeled two scenarios for the genetic basis of reproductive incompatibility between populations, i.e., reproductive incompatibility is the result of new mutations that are incompatible with their genetic backgrounds and may (climate dependent scenario) or may not (climate independent scenario) be the pleiotropic effects of adaptation to different 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 adapted to different pollinators (e.g., Schemske and Bradshaw 1999), or in habitat preferences (e.g, Rice and Salt 1990). If the evolution of reproductive isolation involves these automatic magic traits, then niche divergence undoubtedly drives speciation by directly influencing the fixation rate of mutations underlying reproductive isolation.

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 (~0.01–2.6 Ma) is characterized by cyclical glacial-interglacial climatic oscillations (Zachos et al. 2001). Our study leads to two testable predictions: (1) ecologically similar sister species are more likely to have originated in the Tertiary (during particular periods of directional climate change); (2) ecologically divergent sister species are more likely to have originated in the Quaternary (although both periods may have species that evolved via both processes). These predictions can be readily tested by comparisons of the climatic distributions of sister species (e.g. using GIS-based methods) and estimates of their divergence dates (e.g. using molecular dating methods). These predictions may also help explain the conflicting results of previous empirical studies on niche conservatism vs. niche divergence (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).

There has been considerable debate about the role of Pleistocene climatic changes in driving speciation (e.g. in birds; 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 reproductive 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 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., population in habitat 0 in Fig. 2.1). Specifically, under directional climate change, speciation via niche conservatism is plausible when the ancestral, intermediate population goes extinct (Fig. 2.3A.B). Under climatic oscillations, speciation via niche divergence is plausible when the ancestral population is barely able to persist (Fig. 2.4C,D). This latter pattern seems to occur because climatic oscillations cause fluctuations in population size. Small population size is under strong genetic drift, thus favors fixation of hybrid dysfunction mutations that tend to be selected against due to their deleterious effects on reproductive compatibility. In contrast, 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.

The tight association between speciation and population persistence implies that speciation and extinction are not always independent processes. We find that climatic factors that hasten local extinction may also increase speciation by promoting speciation via niche conservatism under directional climate change. Under climatic oscillations, extreme climatic conditions may drive local extinction in some species, but also increase population fluctuation in some other species and therefore promoting speciation via niche divergence. Both of these two processes may lead to a positive relationship between speciation and extinction. We know of one study (Weir and Schluter 2007) that has shown evidence for a positive correlation between speciation and extinction rates along latitudinal gradients in birds and mammals with both rates higher in temperate regions, but it is unclear if this pattern is related to the climatically-driven processes described here. Given the current threat of climate change to biodiversity (and past mass extinction events), it is tempting to assume that climate change leads solely to extinction and not speciation. Our results suggest that directional climate change might also lead to speciation, and that local extinctions actually facilitate this process.

Model Assumptions and Future Research

Our study builds on several previous models, including that of Pease and Lande (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: (1) it incorporates various aspects of speciation, from the initial range expansion to the establishment of reproductive isolation among populations; (2) it incorporates various genetic bases of reproductive isolation; and (3) it provides a new numerical approach to study speciation under a spatially explicit environment.

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). Furthermore, species distributions may be determined only indirectly by climate, if at all (e.g. climate influences vegetation which influences prey distributions, and the distribution of prey influences the distribution of the species of interest; 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 only include three habitat types in our model, with climatic variation assumed to be 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 loci (e.g. Nagylaki 1975) underlying reproductive isolation.

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

Summary

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 predominating speciation mechanism under some realistic conditions (e.g. directional climate change). This finding leads to testable predictions for empirical speciation studies, and may help explain the seemingly contradictory findings of previous empirically studies. Remarkably, 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 influence speciation from a theoretical perspective.

References

Barnosky, A. D. 2005. Effects of Quaternary climatic change on speciation in mammals. Journal of Mammalian Evolution 12:247–264.

Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. Annual Review of Ecology, Evolution, and Systematics 16:113–148.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. *In* Fishery Investigations Series II, Vol. 19. Ministry of Agriculture, Fisheries and Food, London.

Brooks, C. B., and S. C. Griffith. 2010. Mate choice. Pages 416–434 *in* D. Westneat, and C. Fox, ed. Evolutionary behavioral ecology. Oxford University Press, Oxford.

Bulmer, M. G. 1980. The mathematical theory of quantitative genetics. Clarendon Press, Oxford.

Cadena, C. D., K. H. Kozak, J. P. Gómez, J. L. Parra, C. M. McCain, R. C. K. Bowie, A. C. Carnaval, C. Moritz, C. Rahbek, T. E. Roberts, N. J. Sanders, C. J. Schneider, J. VanDerWal, K. R. Zamudio, and C. H. Graham. 2012. Latitude, elevational climatic zonation and speciation in New World vertebrates. Proceedings of the Royal Society B: Biological Sciences 279:194–201.

Case, T. J., and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. American Naturalist 155:583–605.

Chevin, L. and F. Hospital. 2008. Selective sweep at a quantitative trait locus in the presence of background genetic variation. Genetics 180:1645–1660.

Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, MA.

Davis, M. B., and R. G. Shaw. 2001. Range shift and adaptive responses to Quaternary climate change. Science 292:673–679.

Dobzhansky, T. 1936. Studies on hybrid sterility. II. Localization of sterility factors in *Drosophila pseudoobscura* hybrids. Genetics 21:113–135.

Doebeli, M., and U. Dieckmann. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. American Naturalist 156:S77–S101.

Doebeli, M., and U. Dieckmann. 2003. Speciation along environmental gradients. Nature 421:259–264.

Endler, J. A. 1977. Geographic variation, speciation and clines. Princeton University Press, Princeton.

Etterson, J. R. and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. Science 294:151–154.

Gavrilets, S. 1999. A dynamical theory of speciation on holey adaptive landscapes. American Naturalist 154:1–22.

Gavrilets, S. 2004. Fitness landscapes and the origin of species. Princeton University Press, Princeton.

Gross, S. J., and T. D. Price. 2000. Determinants of the northern and southern range limits of a warbler. Journal of Biogeography 27:869–878.

Hill, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339.

Hoffman, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Hoskin, C. J., M. Tonione, M. Higgie, J. B. MacKenzie, S. E. Williams, J. VanDerWal, and C. Moritz. 2011. Persistence in peripheral refugia promotes phenotypic divergence and speciation in a rainforest frog. American Naturalist 178:561–578.

Hua, X., and J. J. Wiens. 2010. Latitutudinal variation in speciation mechanisms in frogs. Evolution 64:429–443.

Jansson, R., and M. Dynesius. 2002. The fate of clades in a world of recurrent climatic change: milankovitch oscillations and evolution. Annual Review of Ecology and Systematics 33:741–777.

Jenkins, N.L. and A. A. Hoffman. 1999. Limits to the southern border of *Drosophila serrata:* cold resistance, heritability, and trade-offs. Evolution 53:1823–1834.

Johnson, N. K., and C. Cicero. 2004. New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. Evolution 58:1122–1130.

Kimura M. and J. F. Crow. 1978. Effect of overall phenotypic selection on genetic change at individual loci. Proceedings of the National Academy of Sciences of the United States of America 75:6168–6171.

Kozak, K. H., and J. J. Wiens. 2006. Does niche conservatism promote speciation? A case study in North American salamanders. Evolution 60:2604–2621.

Kozak, K. H., and J. J. Wiens. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. Proceedings of the Royal Society B: Biological Sciences 274:2995–3003.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

Lee, H. Y., J. Y. Chou, L. Cheong, N. H. Chang, S. Y. Yang, and J. Y. Leu. 2008. Incompatibility of nuclear and mitochondrial genomes causes hybrid sterility between two yeast species. Cell 135:1065–1073.

Lovette, I. J. 2005. Glacial cycles and the tempo of avian speciation. Trends in Ecology & Evolution 20:57–59.

Lowry, D. B., R. C. Rockwood, and J. H. Willis. 2008. Ecological reproductive isolation of coast and inland races of *Minulus guttatus*. Evolution 62:2196–2214.

Lynch, M., and A. Abegg. 2010. The rate of establishment of complex adaptations. Molecular Biology and Evolution 27:1404–1414.

Matute, D. R., I. A. Butler, D. A. Turissini, and J. A. Coyne. 2010. A test of the snowball theory for the rate of evolution of hybrid incompatibilities. Science 329:1518–1521.

Mayer, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Mass.

McCormack, J. E., A. J. Zellmer, and L. L. Knowles. 2010. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation? Insights from tests with niche models. Evolution 64:1231-1244

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A. McDade, M. A. McPeek, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J. M. Sobel, and M. Turelli. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10:315–331.

Mizera, F., and G. Meszéna. 2003. Spatial niche packing, character displacement and adaptive speciation along an environmental gradient. Evolutionary Ecology Research 5:1–20.

Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annual Review of Ecology and Systematics 31:533–563.

Moyle, L. C., and T. Nakazato. 2010. Hybrid incompatibility 'snowballs' between *Solanum* species. Science 329:1521–1523.

Muller, H. J. 1942. Isolating mechanisms, evolution and temperature. Biological Symposia 6:71–125.

Nagylaki, T. 1975. Conditions for the existence of clines. Genetics 80:595–615.

Nosil, P. 2012. Ecological speciation. Oxford University Press, Oxford.

Orr, M. R., and T. B. Smith. 1998. Ecology and speciation. Trends in Ecology & Evolution 13:502–506.

Pease, C. M., and R. Lande, R. 1989. A model of population growth, dispersal and evolution in a changing environment. Ecology 70:1657–1664.

Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Presgraves, D. C. 2010. The molecular evolutionary basis of species formation. Nature Reviews Genetics 11:175–180.

Raxworthy, C. J., C. M. Ingram, N. Rabibisoa, and R. G. Pearson. 2007. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. Systematic Biology 56:907–923.

Rice, W. R. and G. W. Salt. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions – experimental evidence. Evolution 44:1140–1152.

Rundle, H. D., and P. Nosil. 2005. Ecological speciation. Ecology Letters 8:336–352.

Schemske, D. W. and H. D. Bradshaw. 1999. Pollinator preference and the evolution of floral traits in monkeyflowers (Mimulus). Proceedings of the National Academy of Sciences of the United States of America 96:11910-11915.

Schluter, D. 2001. Ecology and the origin of species. Trends in Ecology & Evolution 16:372–380.

Schluter, D. 2009. Evidence for ecological speciation and its alternative. Science 323:737–741.

Servedio, M. R., G. S. Van Doorn, M. Kopp, A. M. Frame, and P. Nosil. 2011. Magic traits in speciation: ‘magic’ but not rare? Trends in Ecology & Evolution 26:389–397.

Servedio, M. R. and M. Kopp. 2011. Sexual selection and magic traits in speciation with gene flow. Current Zoology 58:510–516.

Turelli, M., N. H. Barton, and J. A. Coyne. 2001. Theory and speciation. Trends in Ecology & Evolution 16:330–343.

Turelli, M., and N. H. Barton. 1994. Genetic and statistical analyses of strong selection on polygenic traits: what, me normal? Genetics 138:913–941.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883.

Weir, J. T., and D. Schluter. 2004. Ice sheets promote speciation in boreal birds. Proceedings of the Royal Society B: Biological Sciences 271:1881–1887.

Weir, J. T., and D. Schluter. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. Science 315:1574–1576.

Wiens, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197.

Wiens, J. J. and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36:519–539.

Via, S. 2002. The ecological genetics of speciation. American Naturalist 159:S1–S7.

Via, S. 2009. Natural selection in action during speciation. Proceedings of the National Academy of Sciences of the United States of America 106:9939–9946.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.

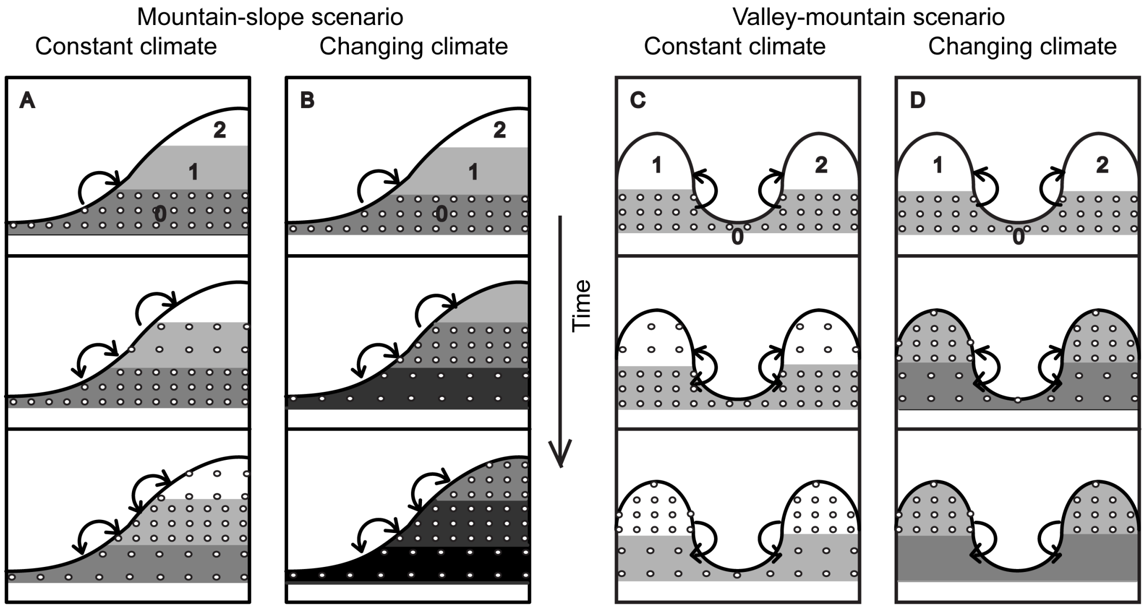


Figure 2.1. Schematic illustrations of Mountain-slope scenario (A and B) and Valley-mountain scenario (C and D), given both constant and changing climate. In all the scenarios, the ancestral population initially occupies the lowland habitat (habitat 0) and colonizes the montane habitats (habitats 1 and 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 plots A and C, and temporally increasing in plots B and D. Arrows indicate directions of dispersal of individuals.

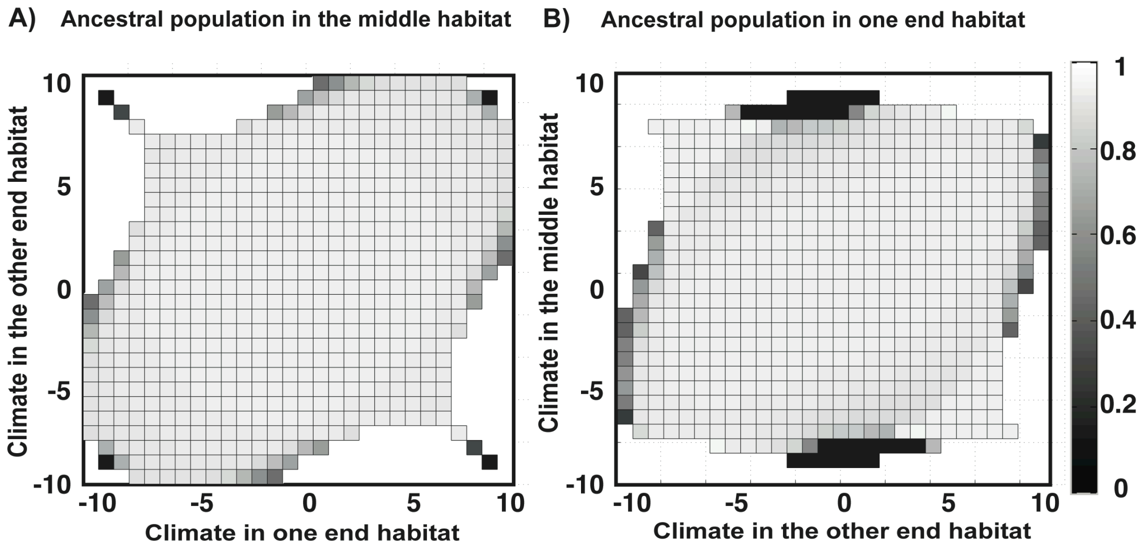


Figure 2.2. Speciation under temporally constant and spatial variant climate. Speciation occurs in black cells and individuals from populations in the two end habitats have less probability to produce hybrids in darker cells. Empty areas indicate that the ancestral population failed to colonize the adjacent habitat. The climatic value in the ancestral habitat is set to 0 in the two graphs.

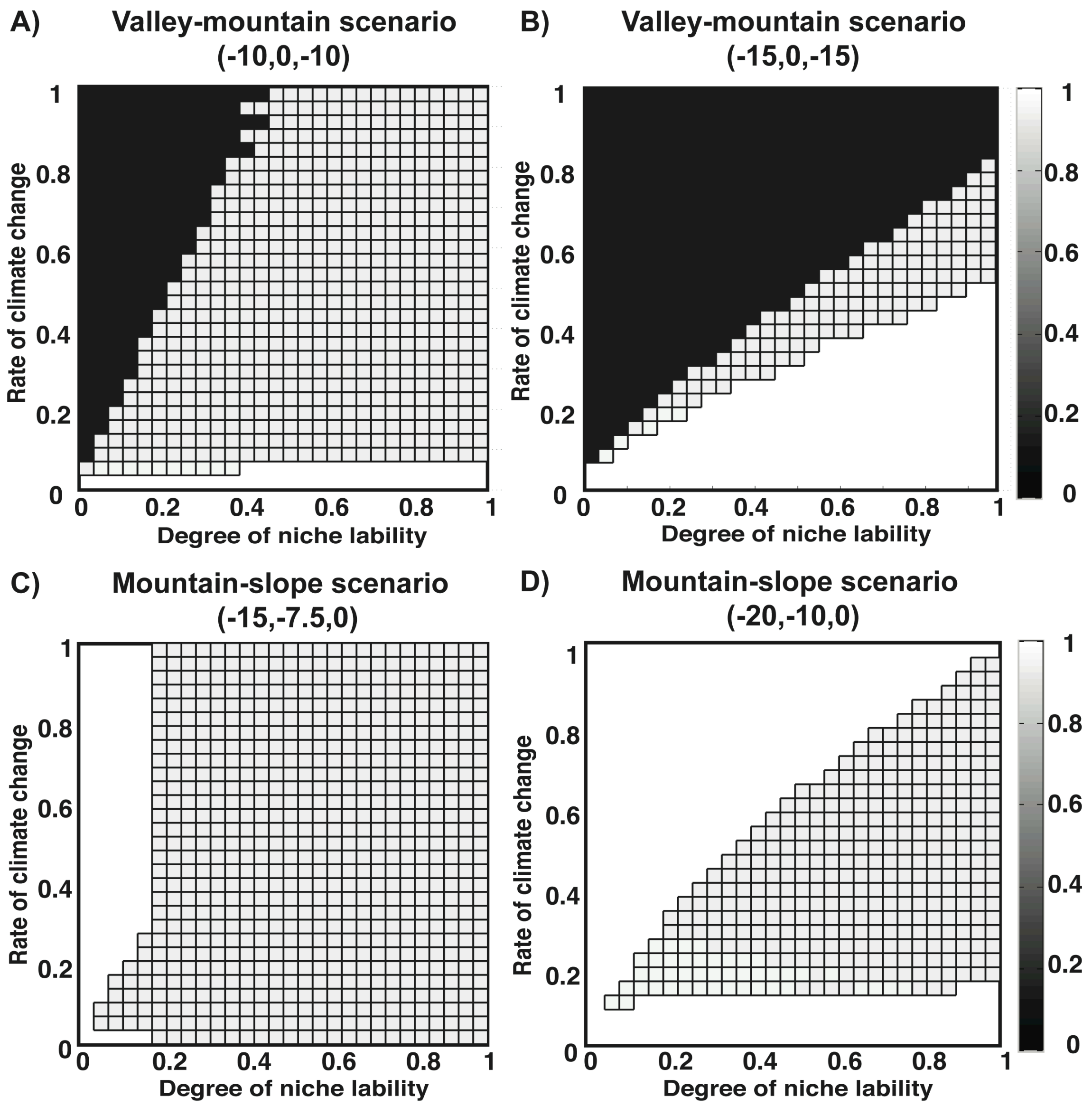


Figure 2.3. Speciation under directional climate change. Graphs show the conditions under which speciation occurs under the valley-mountain scenario (A,B) and the mountain-slope scenario (C,D). These conditions are the rates of directional climate change and the levels of intrinsic niche lability. Empty areas indicate that the ancestral population failed to colonize the adjacent habitat. Speciation occurs in black cells, which happen to be the conditions where the ancestral population goes extinct during the speciation process.

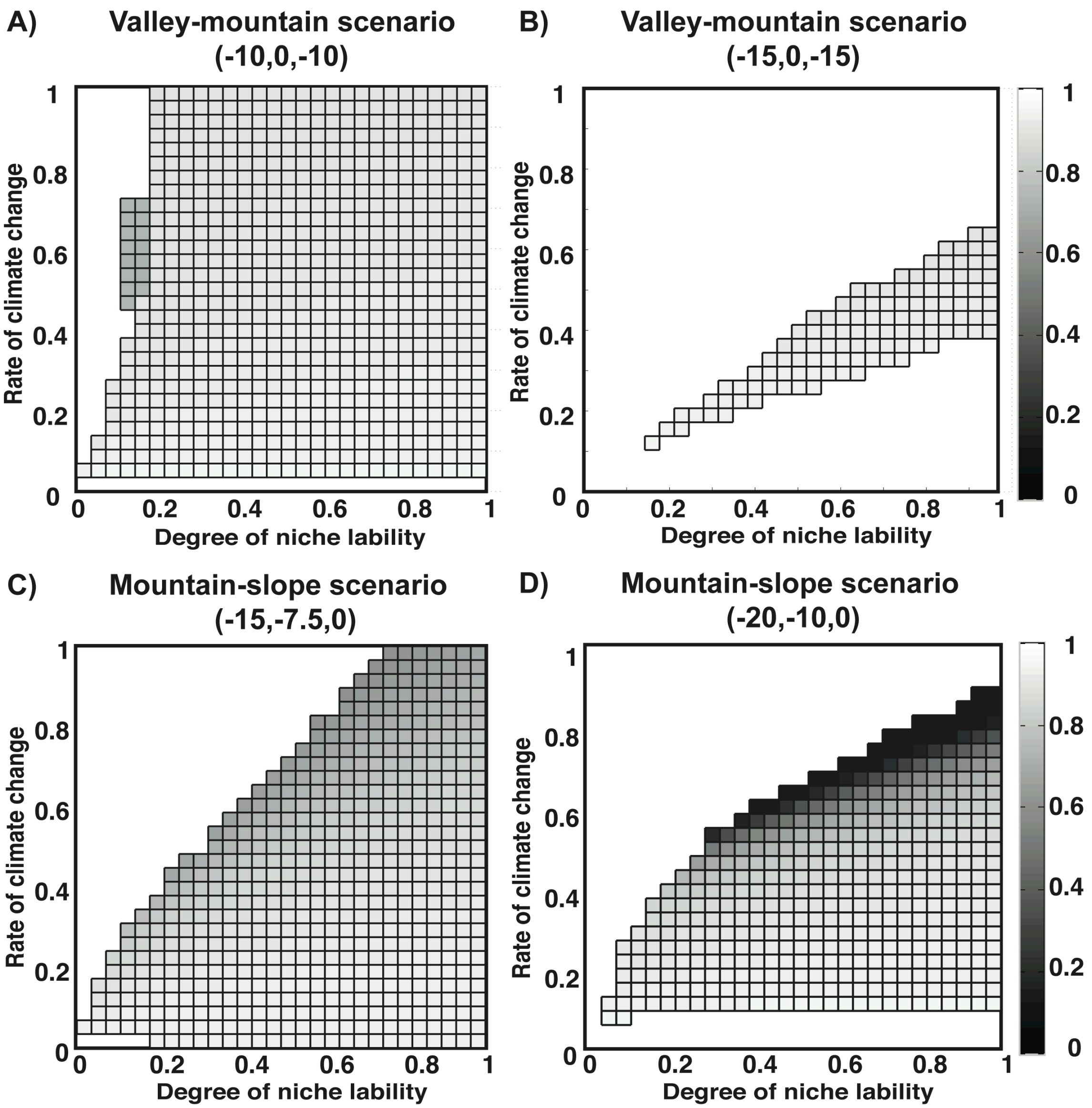


Figure 2.4. Speciation under climatic oscillations. Graphs show the conditions under which speciation occurs under the valley-mountain scenario (A,B) and the mountain-slope scenario (C,D). Empty areas indicate that the species failed to establish constant populations in the two end habitats, where local extinction and recolonization events continually occurred during climatic oscillations. Speciation occurs in black cells, which happen to be the conditions where the species was barely able to persist in all the three habitats along a mountain slope. Individuals from populations in the two end habitats have less probability to produce hybrids in darker cells.

Appendices

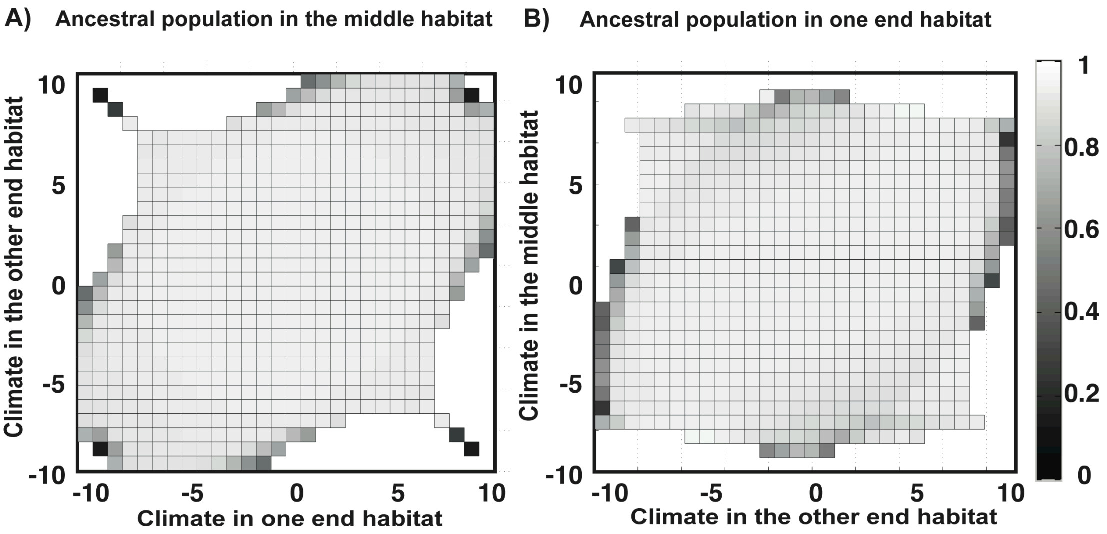


Figure S2.1. Speciation under temporally constant and spatial variant climate. Reproductive incompatibility is assumed to be the pleiotropic effects of climatic niche divergence. Figure legends are the same as Figure 2.2.

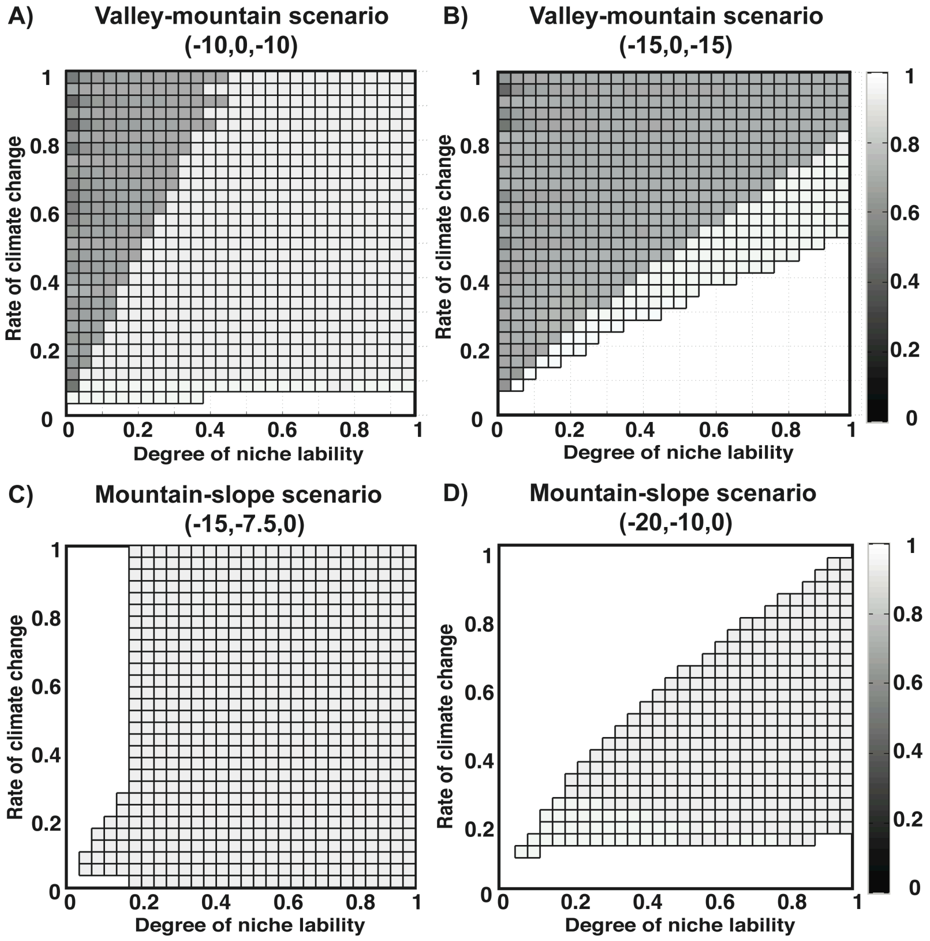


Figure S2.2. Speciation under directional climate changes. Reproductive incompatibility is assumed to be the pleiotropic effects of climatic niche divergence. Figure legends are the same as Figure 2.3.

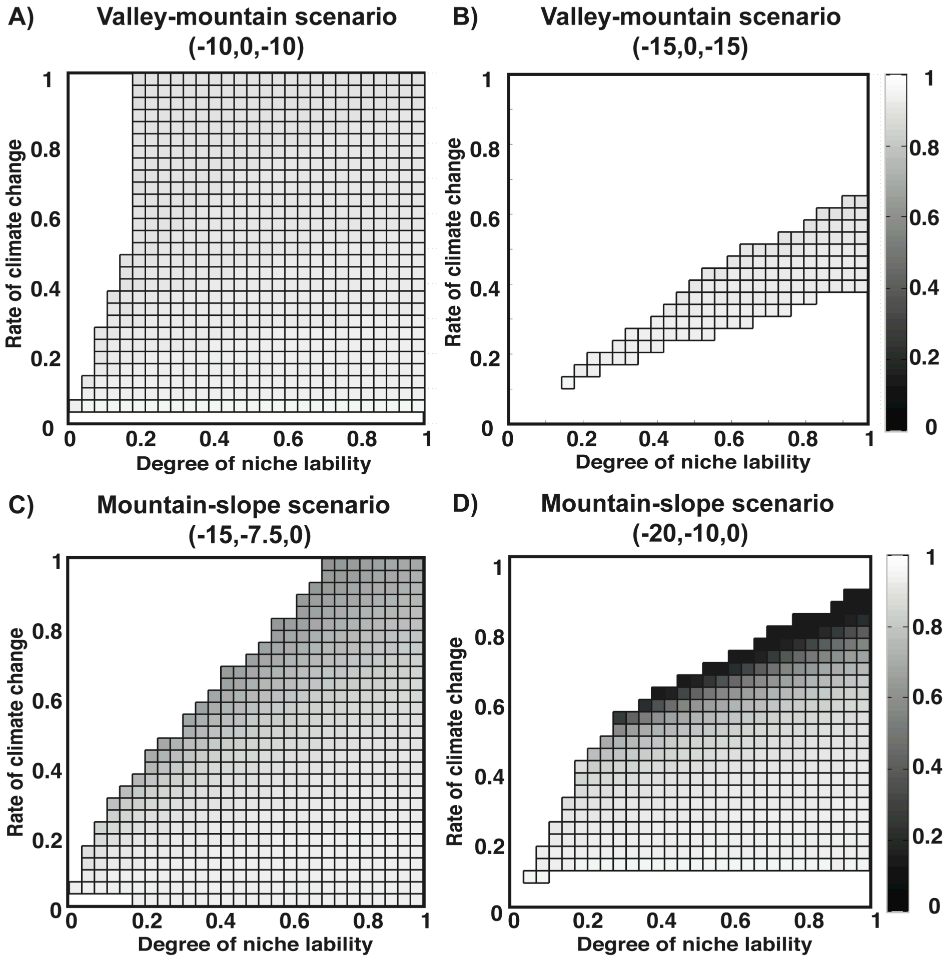


Figure S2.3. Speciation under cyclic climatic oscillations. Reproductive incompatibility is assumed to be the pleiotropic effects of climatic niche divergence. Figure legends are the same as Figure 2.4.

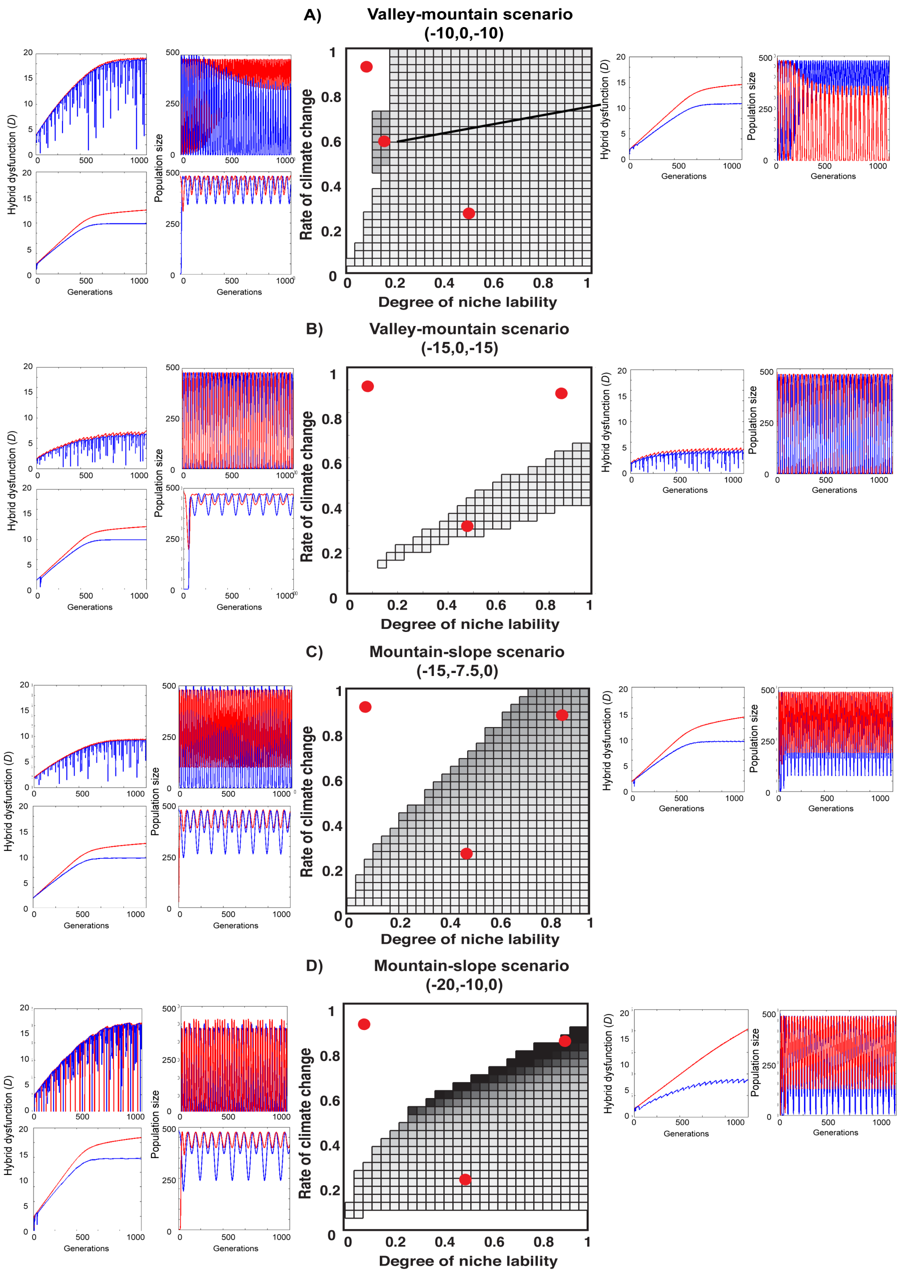


Figure S2.4. Trajectories of population growth and the accumulation of reproductive incompatibility during speciation process under climatic oscillations as shown in Figure 4. Detailed trajectories of population growth (right plots) and the accumulation of hybrid dysfunction (left plots) are included for populations under the conditions where a red dot is pinned to. In plots for hybrid dysfunction, red curves indicate hybrid dysfunction between populations in the end habitats (i.e. habitat 0 and 2 in Fig. 1B and habitat 1 and 2 in Fig. 1D); blue curves indicate gametic incompatibility within those populations. In plots for population growth, red curves are for populations in the middle habitat; blue curves are for populations in the end habitats.

Chapter 3

Why tropical species have narrow ranges: a theoretical exploration of Janzen's hypothesis

Introduction

In 1967, Daniel Janzen published an influential paper titled "Why mountain passes are higher in the tropics". The paper (Janzen 1967) developed a verbal model predicting that the limited seasonal temperature variation in the tropics reduces overlap in thermal regimes between low and high elevations. The greater temperature stratification across elevational gradients in the tropics then makes a tropical species more likely to be acclimated or evolutionarily adapted to a narrower range of temperature than a species in temperate regions. Given this hypothesis, mountain passes should be more effective barriers to dispersal (hence "higher") in the tropics. A corollary of this hypothesis is that tropical species should be distributed in a narrower range of elevations than species in temperate regions. Since the paper was published, Janzen's hypothesis has been invoked to explain many patterns, including differences in how species arise in tropical versus temperature regions (e.g. Ghalambor et al. 2006; Kozak and Wiens 2007), the latitudinal gradient in species diversity (e.g. Mittelbach et al. 2007), and latitudinal patterns in range sizes (i.e. Rapoport's rule; Gaston et al. 1998).

Numerous studies have documented latitudinal patterns in species elevational ranges and temperature tolerances that are consistent with Janzen's hypothesis (review in Ghalambor et al. 2006), but conflicting patterns have also been found. For example, some studies show that tropical species tend to have narrower elevational ranges than temperate species (McCain 2009), whereas others do not (Guralnick 2006; Kozak and Wiens 2007; Hua and Wiens 2010; Cadena et al. 2012). Physiological studies have shown that thermal tolerances of many species increase with increasing latitude (Snyder and Weathers 1975; van Berkum 1988; Addo-Bediako et al. 2000). Some studies show that tropical species tend to occur in narrower ranges of temperature conditions than temperate species (e.g., Kozak and Wiens 2007; Hua and Wiens 2010; Cadena et al. 2012; Quintero and Wiens 2012), but not others (e.g., Guralnick 2006; Fisher-Reid et al. 2012).

In contrast to some empirical studies supporting Janzen's hypothesis, the theoretical underpinnings of Janzen's hypothesis remain unclear. A critical assumption in Janzen's hypothesis is that tropical species "living within the relatively uniform tropical temperature regimes" will be "evolutionarily adapted to a narrower absolute range of temperatures" (Janzen 1967) than species in temperate regions (Ghalambor et al. 2006). Janzen described the assumption as a "reasonable" physiological response to fluctuating temperature, but he did not state explicitly how the physiological response actually works. Classic models (e.g. Levins 1965; Whitlock 1996; Donaldson-Matasci et al. 2008) suggest two population-level processes that may lead to species that have wide thermal tolerances under fluctuating temperature conditions. One is the 'jack-of-all-trades' process (e.g. Lynch and Gabriel 1987), by which a generalist is able to tolerate different environmental conditions at the cost of never reaching peak performance under a specific condition. This process involves a strong trade-off between performance and tolerance range (Lynch and Gabriel 1987). The other is the ‘red-queen’ process (e.g. Whitlock 1996), by which a species that is able to tolerate different environmental conditions may adapt more slowly to any specific condition because the selection for a particular niche-specific trait is not as effective. As a result, the species has lower fitness than a species with a narrow tolerance, especially when there is stable selection for the tolerance to a specific condition (i.e. limited seasonal variation in the environmental conditions). This process does not require a trade-off between performance and tolerance range (Whitlock 1996), but it is not clear how effective the process is in the face of random mating between the two competing groups of individuals.

Based on these classic models, I present the first mathematical model for Janzen’s hypothesis in this study. Specifically, I examined why and under what conditions tropical species evolve narrower temperature tolerances and narrower elevational ranges as the results of population-level processes. To do this, I model the process of continuous population expansion of a species that is distributed along an elevational gradient. During population expansion, I model the evolution of temperature tolerance of the species, which takes into account the above two population-level processes. I also discuss how these population-level processes influence the properties of a species and thus the species-level processes that may in turn lead to narrow elevational ranges and narrow temperature tolerance in tropical species.

To model the evolution of temperature tolerance of a species, I assume that a wide temperature niche breadth in a species can be the result of either large variation in temperature niche locations among individuals (Fig. 3.1A), or each individual having wide thermal tolerance (Fig. 3.1B), or a combination of the two (Lynch and Gabriel 1987). Assuming that the temperature fitness curve of an individual follows a normal distribution, temperature niche location is the mean of the distribution and thermal tolerance is the variance of the distribution (Fig. 3.1). Individuals in different spatial positions adapted to different temperature conditions have different temperature niche locations. Individuals under different level of seasonality may evolve different temperature tolerances as the results of the above two population-level processes (i.e. red queen and jack-of-all trades).

Methods

Climatic Background

The model starts with a population that is initially located at intermediate elevations and subsequently spreads up and down along a mountain slope (the axis x in Fig. 3.1). Temperature changes continuously as a function of distance on the axis *x*, in units of kilometer. Based on the general observation that on average temperature drops about 6°C for every 1 km increase in altitude (Lomolino et al. 2006), I use the function $\Delta Temperature = 6\sin(\alpha)\Delta x$ to approximate the rate of temperature decrease as one goes up a mountain, where sin(α) is the slope of the mountain, thus $\sin(\alpha)\Delta x$ is the maximum elevation of the mountain. Temperature seasonality is assumed to be constant across different elevations (Ghalambor et al. 2006) and is modeled as a sine wave with a one-year period. Important parameters and variables used in the model are listed in Table 3.1 and are referred to throughout the paper.

Temperature niche variables

Based on Lynch and Gabriel (1987), the temperature niche of an individual is described by two variables: temperature niche location and thermal tolerance (see Introduction). The Malthusian fitness of individuals with niche location (z) and tolerance (V_s) at spatial position x at time t is modeled as equation 1. Dropping the (x,t) notation for brevity:

$$w(x,t) = r - \frac{r}{C} n \int_{0}^{\infty} \int_{-\infty}^{\infty} \exp[(V_s - V_s')\lambda] \exp\left[\frac{-(z - z')^2}{4V_u}\right] f(z')dz' f(V_s')dV_s' - \frac{(\theta - z)^2}{2V_s} \qquad [1]$$

The first term r is the absolute fitness of the individuals without the impacts of competition and selection. The second term gives the total impact of intraspecific competition (see below), where C is a carrying capacity that is assumed to be constant over space and time. The last term gives the impact of stabilizing selection on the niche location around the temperature at position x, $\theta(x)$.

In the second term, the function within the integral gives the impact of competition on individuals with niche location (z) and tolerance (V_s) from individuals with niche location (z') and tolerance (V_s'). The competition impact is stronger when competing individuals have more similar niche locations (i.e., $z - z'$ is small). For example, individuals with similar niche locations may have similar strategies to deal with extreme temperature (e.g. finding shelters), thus they are likely to compete for the same type of resources. I assume a constant variance of resource utilization curves (V_u) among individuals, which measures the strength of competition, with larger values corresponding to weaker competition.

I assume that the impact of competition is more symmetric when competing individuals have more similar thermal tolerance (i.e., $V_s - V_s'$ is small). This assumption is made to take into account the impact of tradeoffs between the thermal tolerance and the performance under a specific temperature condition (Angilletta et al. 2003). In the same niche location, individuals with wider thermal tolerance tend to be inferior competitors to individuals with narrower thermal tolerance. Parameter λ adjusts the degree of asymmetry in competition as a result of the tradeoff, with larger values corresponding to a stronger tradeoff. Adjusting parameter λ also allows one to examine the relative contribution of the 'jack-of-all-trades' and the 'red-queen' processes (see Introduction) that lead to wide thermal tolerance under high temperature seasonality, as the 'jack-of-all-trades' process requires a strong tradeoff, while the 'red-queen' process does not.

Integrating the competition function over all possible niche locations (z') and tolerances (V_s') within the species at spatial position x at time t gives the total amount of intraspecific competition. I assume that the probability distributions of both niche locations and thermal tolerances (i.e. $f(V_s')$) of individuals that are sampled at position x at time t follow a normal distribution with mean $\bar{z}$ and $\overline{V}_s$, and a constant variance V (Figure 1).

Population Expansion

I assume a species that initially consists of a single population in one location and subsequently expands into new locations along an elevational gradient on which no competing species are present. Based on Case and Taper (2000), the rate of change in population density at spatial position x at time t is modeled as:

$$\frac{\partial n(x,t)}{\partial t} = D\frac{\partial^2 n(x,t)}{\partial^2 x} + n(x,t)\overline{w}(x,t),$$

where D (diffusion coefficient) is the rate of random movement of individuals over space, which for one-dimensional space is the variance of dispersal distance in one time step dt. $\overline{w}(x,t)$ denotes the average Malthusian fitness of individuals occurring at position x at time t, which is the integral of individual fitness $w(x,t)$ over all possible niche locations (z) and tolerance ranges (V_s) within the species, as shown in equation 2.

$$\overline{w}(x,t) = r - \frac{r}{C}ne^{V\lambda^2}\sqrt{\frac{V_u}{V+V_u}} - \left[\frac{(\theta-\overline{z})^2+V}{2}\right]\int_0^\infty V_s^{-1} f(V_s)dV_s \qquad [2]$$

The last integral cannot be evaluated analytically. Therefore, I use the Gauss-Kronrod method (Shampine 2008) implemented in MATLAB (2010a) to numerically approximate the integrals. Note that the integral does not converge when the initial thermal tolerance ($\overline{V}_s$) is very narrow, thus the model does not apply under this condition.

Temperature Niche Evolution

I model the evolution of temperature niche location and the evolution of the thermal tolerance as two genetically independent quantitative traits. Following Case and Taper (2000) with an error corrected (Price and Kirkpatrick 2009; see below), I model the evolution of the mean niche location of individuals occurring at spatial position *x* at time *t* as equation 3.

$$\begin{aligned}\frac{\partial\overline{z}(x,t)}{\partial t} &= D\frac{\partial^2\overline{z}}{\partial^2 x} + 2D\frac{\partial n}{n\partial x}\frac{\partial\overline{z}}{\partial x} \\ &+h^2\left\{r\overline{z} - \frac{r\overline{z}}{C}ne^{V\lambda^2}\sqrt{\frac{V_u}{V+V_u}} - \left[\frac{\overline{z}(\overline{z}-\theta)^2 + 3\overline{z}V}{2} - \theta V\right]\int_0^\infty V_s^{-1}f(V_s)dV_s - \overline{w\overline{z}}\right\}\end{aligned} \qquad [3]$$

The change in mean niche location over time is essentially derived from the classic "breeder's equation" of quantitative genetics (Falconer & MacKay 1996; see Case & Taper 2000 for detailed derivation), where h^2 is the heritability of niche location. The first two terms give the change in mean niche location due to random movement of individuals, with the second term correcting the change for uneven population density over space.

Given the same arguments, the evolution of the mean thermal tolerance of individuals occurring at spatial position *x* at time *t* follows equation 4.

$$\begin{aligned}\frac{\partial\overline{V}_s(x,t)}{\partial t} &= D\frac{\partial^2\overline{V}_s}{\partial^2 x} + 2D\frac{\partial n}{n\partial x}\frac{\partial\overline{V}_s}{\partial x} \\ &+h^2\left\{r\overline{V}_s - \frac{r}{C}ne^{V\lambda^2}(V\lambda + \overline{V}_s)\sqrt{\frac{V_u}{V+V_u}} - \left[\frac{(\theta-\overline{z})^2}{2} + \frac{V}{2}\right] - \overline{w}\overline{V}_s\right\}\end{aligned} \qquad [4]$$

'Jack-of-all-trades' and 'red-queen' processes

How does the current model relate to the 'jack-of-all-trades' and the 'red-queen' processes? The relationship is analytically tractable by focusing on the temperature niche evolution within a single locality *x*. For the evolution of temperature niche location, substituting equation 2 for $\overline{w}$, the term in the curly brackets in equation 3 becomes $(\theta - \overline{z})V\int_0^\infty V_s^{-1} f(V_s)dV_s$. Therefore, the solution for temperature niche location under equilibrium is, intuitively, the temperature conditions in the locality θ. The rate of convergence to the equilibrium depends on the ratio $V/\overline{V}_s$.

For the evolution of the thermal tolerance, substituting equation 2 for $\overline{w}$, the term in the curly brackets in equation 4 becomes $\left[\frac{(\theta - \overline{z})^2 + V}{2}\right]\left[\overline{V}_s\int_0^\infty V_s^{-1} f(V_s)dV_s - 1\right] - \frac{r}{C}ne^{V\lambda^2}V\lambda\sqrt{\frac{V_u}{V + V_u}}$, where the integral is always larger than $1/\overline{V}_s$ and asymptotically approaching $1/\overline{V}_s$ when $\overline{V}_s$ becomes larger (Hall 1979). The first term describes the increase in thermal tolerance in order to minimize decrease in fitness caused by mismatch between temperature niche location and the local temperature conditions ($(\theta - \overline{z})^2$). Since a species with a narrower thermal tolerance adapts to local temperature conditions more rapidly (adaptation rate is proportional to $V/\overline{V}_s$), its thermal tolerance is less likely to increase under less fluctuating temperature conditions. This process resembles the ‘red-queen’ process (Whitlock 1996) and theoretically leads to wide thermal tolerances under high temperature seasonality even if there is no tradeoff between tolerance and performance (i.e. when the second term = 0).

The second term describes the decrease in thermal tolerance as a result of the tradeoff between tolerance and performance. Given a small initial value for $\overline{V}_s$, the thermal tolerance may first increase, depending on the balance between the relative fitness of individuals with the thermal tolerance under a local temperature and their adaptation rate to the local temperature (as suggested by the 'red-queen' process). As $\bar{V}_s$ increases, the first term becomes closer to zero and thus the thermal tolerance decreases until equilibrium. Given a large initial value for $\bar{V}_s$, the thermal tolerance tends to first decrease at a rate equal to $\frac{rh^2}{C} ne^{V\lambda^2} V\lambda\sqrt{\frac{V_u}{V+V_u}}$. As $\bar{V}_s$ decreases, the first term becomes positive, thus the thermal tolerance decreases at a slower rate or even increases until equilibrium, especially under high temperature seasonality. This process resembles the 'jack-of-all-trades' process that also leads to a wide thermal tolerances under high temperature seasonality but requires tradeoff between tolerance and performance.

In general, the analytic properties for the evolution of the thermal tolerance exhibit a potential for multiple equilibria and suggest the importance of the initial state, i.e. the initial thermal tolerance, to the model results. Nevertheless, when taking into account the effects of dispersal, the above differential equations (eqn. 2-4) become analytically intractable, thus a numerical approximation is applied (see below) to examine how these two population-level processes influence the local evolution of temperature niche locations and thermal tolerances.

Numerical Approximation and Parameter Values

Solutions to all the above differential equations are numerically approximated using finite difference method (Morton and Mayers 1994) with the diffusion coefficient $D = 0.1$ km^2, spatial step $\Delta x = 0.1$ km, and time step $\Delta t = 0.01$. These values are chosen to guarantee stable and non-negative solutions in each time step. The finite difference method can be seen as a stepping-stone model with very fine spatial and temporal resolutions. In each time step, about

10% (equal to $\frac{1}{\pi D\Delta t} e^{-\frac{\Delta x^2}{D\Delta t}}$) individuals in a spatial location disperse to the adjacent two locations that is 0.1 km away from it. Therefore, I adjust the number of time steps in a year to incorporate different levels of individual dispersal ability. For example, assuming 100 time steps to be one year, 10% individual will disperse 0.1 km away from where it was 3.65 days ago (assuming 365 days in a year). During the course of a year, the standard deviation of the total dispersal distance of one individual is about 3 kilometer, which appears to be a reasonable dispersal distance for vertebrate animals (e.g. amphibians; Smith and Green 2005). A mountain of 200 spatial steps and slope sin(α) = 0.3 has an elevational spread of about 6,000 m in elevation. This high mountain height is used to eliminate the spatial constraints on species' elevational ranges (McCain 2009). The annual mean temperature difference between the lowlands and the mountaintop is then about 36 °C.

I set the heritability of both niche locations and niche breadth to 0.2 because most fitness related traits have heritabilities less than 0.5 (Mousseau and Roff 1987; Roff and Mousseau 1987) and temperature-related physiological traits (e.g. body temperature or knockdown temperature) seem to have lower heritabilities, around 0.2 (e.g. Sinervo 1990; Gilchrist and Huey 1999). Variance in niche locations and thermal tolerances at a spatial position x at time t is set to vary between 0.1 and 1, a range that includes previously reported intraspecific variation in trait values related to temperature tolerance (e.g. Gilchrist and Huey 1999; Gibert and Huey 2001). The initial value of the mean niche location ($\bar{z}$) is set to equal the temperature at the initial time step and at the initial spatial position of the population. The initial value of mean thermal tolerance ($\overline{V}_s$) is set to vary between 10 and 50 °C^2, which is a reasonable thermal tolerance for vertebrate animals (e.g. amphibians; Snyder and Weathers 1975). The maximum absolute fitness r is set to 4 and carrying capacity (C) is set to 100. These two values are chosen to make sure that the initial population size is large enough to enable population expansion along mountain slopes.

I tested a set of values for parameters V, V_s, V_u and λ in order to examine how the strength of selection, competition, and the performance-tolerance tradeoff influence the evolution of temperature niches. Representative results are under conditions with either high ($V = 1$) or low ($V = 0.1$) niche variance, strong ($V_u = 20$) or weak ($V_u = 100$) competition, strong ($\lambda = 0.1$) or weak ($\lambda = 0.01$) tradeoff, steep ($\sin(\alpha) = 0.3$) or shallow ($\sin(\alpha) = 0.1$) elevational gradient, and strong (annual individual dispersal distance has standard deviation = 3 km) or weak (1.5 km) dispersal ability. Preliminary results suggest the initial thermal tolerance (i.e. the initial value of $\overline{V}_s$) is a critical parameter that has strong interactions with other parameters. Therefore, I examine in detail how this parameter influences species temperature niches and elevational ranges using five values (15, 20, 30, 40, 50 °C^2) for the initial value of $\overline{V}_s$ and under conditions with $V_u = 20$, $\lambda = 0.1$, $\sin(\alpha) = 0.3$, standard deviation of annual individual dispersal distance = 3 km, and with either high ($V = 1$) or low ($V = 0.1$) niche variance. Each parameter combination is iterated for 50000 time steps (i.e., 500 years). The number of iterations is chosen to get roughly stable results in reasonable amount of computational time.

I use three variables to define temperature niche breadth. First, realized temperature niche breadth on the species level (red lines in Fig. 3.2) is the actual range of seasonal temperature conditions where the species occurs over space. It is calculated by the range of temperatures in a set of 500 randomly sampled localities from across the species distribution at different (randomly sampled) points of time during a year. Sampling probability is weighted by the population density over space and time. Standard error of the variable is calculated by 1000 bootstraps. The other two variables are the range of temperature niche locations ($\bar{z}$; black lines in Fig. 3.2) over space and the average thermal tolerance on individual level ($\overline{V}_s$; green lines in Fig. 3.2). The standard error of the two variables is their standard deviation over a year.

Results

Consistent with Janzen's (1967) hypothesis and empirical evidence based on species' climatic distributions (e.g. Kozak and Wiens 2007; Hua and Wiens 2010; Cadena et al. 2012; Quintero and Wiens 2012), results show that a species under higher temperature seasonality tends to have a wider realized temperature niche (red lines in Fig. 3.2). Interestingly, the results suggest that wide realized temperature niche breadths in a species (red line in Fig. 3.2) evolve when each individual of the species has wide thermal tolerance (green lines in Fig. 3.2A,C,F,G; but not in some conditions as described below), rather than different individuals having different temperature niche locations (black line in Fig. 3.2). This result agrees with the empirical evidence that within-locality niche breadths explains most variation in species realized climatic niche breadths, compared to between-locality variation (Quintero and Wiens 2012). In fact, individuals tend to have more similar temperature niche locations (analogous to lower between-locality variation) as temperature seasonality increases (black lines in Fig. 3.2).

However, under some conditions, the species temperature niche breadth increases with increasing seasonality, but individuals do not have wider thermal tolerance under higher seasonality. This occurs when there is strong competition (red vs. green lines in Fig. 3.2D), low niche variance (red vs. green lines in Fig. 3.2E), or weak trade-offs between temperature tolerance and performance when the initial value of thermal tolerance is large (red vs. green lines in Fig. 3.2B). Under these conditions, species can survive high temperature seasonality because individuals have inherited (green line in Fig. 3.2E) or evolved (green lines in Fig. 3.2B,D) wide temperature tolerances. Counter-intuitively, strong competition should favor individuals with narrow thermal tolerances that have better performance than those with wide thermal tolerances; however, strong competition promotes the evolution of wide thermal tolerances, especially under limited temperature seasonality (green line in Fig. 3.2D). This occurs because strong competition acts against stabilizing selection by preventing multiple individuals from evolving similar temperature niche locations around the same local temperature. Individuals with wider thermal tolerances suffer less from the mismatch between their temperature niche locations and local temperature conditions.

As expected by the ‘jack-of-all-trades’ process, a strong tradeoff leads to wide individual thermal tolerances under high temperature seasonality (green line in Fig. 3.2A), while a weak tradeoff favors the evolution of wide thermal tolerances under all levels of seasonality because individuals with wide thermal tolerance are not effectively selected against under a suboptimal temperature when tradeoff is weak (green line in Fig. 3.2B). However, when a species initially has a narrow tolerance, it also tends to evolve a somewhat wider thermal tolerances under high temperature seasonality even when the tradeoff between tolerance and performance is weak (green line in Fig. 3.2C). This result is not expected by the ‘jack-of-all-trades’ process. Instead, it may indicate that individuals with narrower tolerance adapt to local temperature conditions more rapidly under limited temperature seasonality, thus having higher fitness than individuals with wider tolerance (i.e. the ‘red-queen’ process). Note that a species that initially has narrow tolerance fails to persist under very high temperature seasonality (the drop at the amplitude of temperature seasonality equal to 10°C in Fig. 3.2C).

Surprisingly, there were no conditions under which species tend to have wider elevational ranges under higher temperature seasonality (Fig. 3.3A,B). Species with high niche variance are able to expand into all the locations along the elevational gradient (Fig. 3.3A) except if they initially have narrow thermal tolerance (Fig. 3.3A) or weak dispersal ability (not shown in figures), under high seasonality. Species with low niche variance show a large variation in species elevational ranges with different initial values of thermal tolerances (Fig. 3.3B). None of these species have wider elevational ranges under higher seasonality, although they tend to have widest elevatinal ranges under seasonality with amplitude around 4°C (i.e. 8°C between annual temperature extremes at a location), and only species that initially have wide thermal tolerance can sustain high seasonality (Fig. 3.3A,B). The absence of a positive relationship between elevational ranges and temperature seasonality is consistent with some empirical studies in vertebrates (Guralnick 2006; Kozak and Wiens 2007; Hua and Wiens 2010; Cadena et al. 2012). However, this is not consistent with the most comprehensive study on latitudinal variation in vertebrate elevational ranges so far (McCain 2009).

The initial value of the thermal tolerance has contrasting effects on the evolution of temperature niches of species with low niche variance and species with high niche variance (Fig. 3.4). Intuitively, species with low niche variance (Fig. 3.4B,D) should evolve slower in temperature niches than species with high niche variance (Fig. 3.4A,C). These species tend to evolve faster in temperature niche locations if they initially have wide tolerance (i.e. wider range of niche locations of darker lines in Fig. 3.4B), presumably because they can expand into locations with more different temperature conditions along an elevational gradient, and a greater range of temperature conditions creates stronger selection on the evolution of niche locations. In contrast, a species with high niche variance tend to evolve faster in niche locations if they initially have a narrow tolerance (i.e. wider range of niche locations of lighter lines in Fig. 3.4A), because individuals with narrower tolerance have lower fitness in suboptimal temperature conditions and thus are faced with stronger selection on the evolution of niche locations. Note that results for the smallest initial value for thermal tolerance are not shown under limited seasonality in Figure 3.4A,C (lightest lines) because the integral in equation 2 does not converge (see method).

Discussion

Janzen's (1967) hypothesis of "why mountain passes are higher in the tropics" suggested that more limited temperature seasonality in the tropics leads to natural selection for individuals that are narrowly adapted to a small range of temperatures and that this leads to tropical species with narrow elevational ranges. This pattern of narrow temperature and elevational ranges then has many implications for species range sizes (Gaston et al. 1998), speciation (e.g., Kozak and Wiens 2007), species richness (Mittelbach et al. 2007), responses to global warming (e.g., Deutsch et al. 2008; Sheldon et al. 2011), and other topics. The results support two population-level processes ('jack-of-all-trades' process and 'red-queen' process) that may lead to Janzen's (1967) hypothesis regarding the physiological responses of individual thermal tolerance to seasonal temperature variation, but only under the conditions when competition is weak (Fig. 3.2A vs. 3.2D), tradeoffs between tolerance and performance are strong (Fig. 3.2A vs. 3.2B), or species have relatively high niche variance (Fig. 3.2A vs. 2E; Fig. 3.4C,D).

When tradeoff between tolerance and performance is weak, only the 'red-queen' process contributes to wide thermal tolerances under high temperature seasonality. This is weakly supported by the results and under the conditions when species initially tolerate narrow ranges of temperature conditions (Fig. 3.2C).

Surprisingly, the results do not support the hypothesis that the population-level processes leading to narrower individual thermal tolerances within a species lead to a narrower elevational range for the species, although narrower elevational ranges are fundamental to Janzen's hypothesis. In fact, there were no conditions under which species tend to have wider elevational ranges under higher temperature seasonality (Fig. 3.3A,B). A species is most likely to evolve a narrow thermal tolerance under limited temperature seasonality when it has high niche variance and initially tolerates a narrow range of temperatures (2 bottom light green lines in Fig. 3.4C). Under these conditions, the species adapts to local temperature conditions rapidly (i.e. wide range of temperature niche locations; light gray lines in Fig. 3.4A), but it also rapidly evolves a narrow thermal tolerance (light green lines in Fig. 3.4C) under limited temperature seasonality. Under high temperature seasonality, the species adapts to local temperature conditions slowly (i.e. narrow range of temperature niche locations; light gray lines in Fig. 3.4A), but it evolves a wide thermal tolerance. Therefore, under all levels of temperature seasonality, the species, as a whole, is able to persist in a roughly equal range of temperatures along the elevational gradient and thus has a similar elevational range.

Empirical studies also suggest that the relationships between species realized temperature niche breadths and species elevational ranges are not so straightforward. For example, Kozak and Wiens (2007; for salamanders), Hua and Wiens (2010; for frogs), and

Cadena et al. (2012 for vertebrates) tested Janzen's (1967) hypothesis by the range of temperature over the course of a year in the localities where a species was sampled (i.e., hottest temperature minus coldest temperature, averaged across 50 years of climatic data). All the studies found that temperate species inhabit significantly wider temperature ranges (see also Quintero and Wiens 2012), but not significantly wider elevational range (see also Guralnick 2006; for mammals). A possible answer to why species may inhabit wider temperature range, but not wider elevational range under higher temperature seasonality is that species inhabiting wider temperature ranges under higher temperature seasonality do not necessarily indicate the population-level physiological responses to seasonal temperature fluctuations as suggested by Janzen's (1967) hypothesis. The results here show that a species has wider realized temperature niche breadths under higher temperature seasonality even when individuals of the species do not evolve a wider thermal tolerance under limited seasonal temperature variation (red lines vs. green lines in Fig. 3.2B,D,E).

It is important to note that the results of the current study are based on two important simplifying assumptions. First, temperature niche evolution is modeled as two genetically independent quantitative traits: temperature niche location and thermal tolerance range. Both traits are modeled using standard quantitative genetic theory and assumed to be normally distributed with constant niche variance over space and time. Therefore, the model does not include explicit genetic, physiological, or behavioral bases for the evolution of individual temperature niches. An obvious violation of the assumption is that the assumption implicitly sets no limits on the highest and lowest temperature that a species can tolerate, and thus may lead to some biologically unrealistic results. Nevertheless, incorporating truncated normal distribution is mathematically tedious and setting the same limits on temperature tolerance for a species under different level of seasonality may not influence the overall patterns in thermal tolerance along the seasonality gradient.

Here are two more examples that violate the assumption and may influence the results of the current study. One example violates the assumption that temperature niche location and thermal tolerance range are determined by genetically independent loci. A mutation often alters the structure of an enzyme that enhances individual performance at some temperatures but reduces performance at others (Angilletta et al. 2003). If there are duplications of the genes that determine the enzyme structure, than an individual with the mutation on one of the duplications should not only show optimal performance at a different temperature, but also tolerate a wider range of temperatures than individuals without the mutation (Angilletta et al. 2003). Under this scenario, the evolution of wider thermal tolerances becomes the by-product of a species' adaptation to local temperature conditions. Consequently, the selective advantages of rapid local adaptation in individuals with narrow thermal tolerances (as suggested by the 'red-queen' process) become diminished as rapid local adaptation widens the thermal tolerances. The other example involves only handful loci determining the thermal tolerance. Under this scenario, individuals with a single mutation on those loci may have much narrower thermal tolerance than individuals without the mutation. With sufficient variation in niche locations, their increase in fitness due to rapid adaptation to local temperatures can be much larger, making the ‘red-queen’ process more important than indicated in the current study.

Second, the model assumes a species that initially consists of a single population in one location and subsequently expands along a mountain slope with no biotic interactions other than intraspecific competition. Therefore, temperature niches and elevational ranges in the model are only the outcome of population-level processes. Those in nature, however, are presumably the results of complex interplays between species evolutionary history and current population dynamics, between the evolution of species fundamental niches and changing environmental conditions, and between population-level and community-level interactions (e.g. Parmesan et al. 2005; Gaston, 2009; Sexton et al. 2009). This assumption makes results of this study less informative for explaining large-scale empirical patterns in species temperature niches and elevational ranges. For example, the absence of a positive relationship between elevational ranges and temperature seasonality is not consistent with the largest study on latitudinal variation in elevational ranges so far (McCain 2009), which included data on elevational ranges for 7 vertebrate groups. Such a large-scale cross-species study may reveal increasing elevational ranges under higher seasonality because it includes species with very different properties, such as the thermal tolerance of an incipient species (i.e. the initial value of $\overline{V}_s$). Results show that species that initially tolerate narrow ranges of temperatures tend to have narrow elevational ranges (Fig. 3.3A,B). Therefore, one may expect narrower species elevational ranges in the tropics than in the temperature regions if tropical incipient species tend to have narrower thermal tolerance.

Do tropical incipient species have narrower thermal tolerance? Physiological studies show that many tropical species tend to have narrower thermal tolerances (Snyder and Weathers 1975; van Berkum 1988; Addo-Bediako et al. 2000). Present study also elucidates the processes and the conditions under which species tend to evolve narrow thermal tolerances under limited temperature seasonality.

Results further show that species with a narrow initial thermal tolerance tend to adapt rapidly to local temperature conditions and evolve even narrower thermal tolerance under limited temperature seasonality (Fig. 3.4A,C). Therefore, tropical species are likely to consist of several populations, each with different temperature niche locations and a narrow thermal tolerance. These conditions have been hypothesized to promote parapatric speciation along elevational gradients (e.g. Janzen 1967; Ghalambor et al. 2006; Kozak and Wiens 2007) and faster rates of climatic niche evolution have been shown to be associated with higher diversification rates (Kozak and Wiens 2010). Faster evolution in a temperature niche (related to the maximum temperature of the warmest month) has also been found under more limited temperature seasonality, although rates of climatic niche evolution are not generally associated with species climatic niche breaths (Fisher-Reid et al. 2012).

If temperature is important in driving speciation in the tropics, then one may expect a positive cycle in generating increasing elevational ranges and increasing temperature ranges of species with increasing latitude. The cycle may start with the population-level processes that lead to narrow thermal tolerances under limited temperature seasonality or factors other than seasonality, for example, the potential for more biotic interactions in the tropics, given overall higher species richness (Dobzhansky 1950). The narrow thermal tolerances of tropical species may then promote speciation and lead to descendent species with even narrower thermal tolerance. These descendent species initially having narrow thermal tolerance may have more rapid physiological response to limited temperature seasonality, leading to even more chance for speciation. Consequently, this cycle may lead to many tropical species having narrow thermal tolerance then temperature species, and therefore more species with narrower elevational ranges in the tropics.

Summary

Janzen (1967) hypothesized that species may be evolutionarily adapted to a narrower range of temperatures in regions where there is limited seasonal temperature variation (e.g., the tropics) and may then inhabit narrower elevational ranges. Based on modeling of population-level processes, the present study provides theoretical support for Janzen's hypothesis regarding physiological responses of individual thermal tolerance to seasonal temperature variation. However, the results also show that these population-level processes do not necessarily lead to the evolution of species with narrower elevational ranges under more limited temperature seasonality, a pattern also consistent with some empirical studies.

Nevertheless, Janzen’s hypothesis regarding physiological tolerances, if true, may influence the properties of a species and thus the species-level processes (e.g. speciation or extinction) that in turn may lead to narrow elevational ranges and temperature ranges in tropical species. Therefore, it is important to understand how Janzen’s hypothesis influences species-level processes. For example, how do individual thermal tolerances influence speciation and extinction processes? How do speciation and extinction processes, in turn, influence the evolution of species niche breadths and distributional ranges?

References

Addo-Bediako, A., S. L. Chown, and K. J. Gaston, 2000. Thermal tolerance, climatic variability and latitude. Proc. R. Soc. B 267:739–745.

Angilletta Jr, M. J., R. S. Wilson, C. A. Navas and R. S. James. 2003. Tradeoffs and the evolution of thermal reaction norms. Trends Ecol. Evol. 18:234–240.

Bürger, R., and M. Lynch. 1995. Evolution and extinction in a changing environment: a quantitative-genetic analysis. Evolution 49:151–163.

Cadena, C. D., K. H. Kozak, J. P. Gómez, J. L. Parra, C. M. McCain, R. C. K. Bowie, A. C. Carnaval, C. Moritz, C. Rahbek, T. E. Roberts, N. J. Sanders, C. J. Schneider, J. VanDerWal, K. R. Zamudio, and C. H. Graham. 2012. Latitude, elevational climatic zonation and speciation in New World vertebrates. Proc. R. Soc. B 279:194–201.

Case, T. J., and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species’ borders. Am. Nat. 155:583–605.

Cooper, W. S., and R. H. Kaplan. 1982. Adaptive 'coin-flipping': a decision-theoretic examination of natural selection for random individual variation. J. Theor. Biol., 94:135–151.

Deutsch, C. A., J. J., Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. USA 105:6668–6672.

Dobzhansky, T. 1950. Evolution in the tropics. Am. Sci. 38:209–221.

Donaldson-Matasci, M. C., M. Lachmann, and C. T. Bergstrom. 2008. Phenotypic diversity as an adaptation to environmental uncertainty. Evol. Ecol. Res. 10:493–515.

Falconer, D. S., and T. F. C. MacKay. 1996. Introduction to quantitative genetics, 4th edn. Essex, UK: Longman's Green.

Fisher-Reid, M. C., K. H. Kozak, and J. J. Wiens. 2012. How is the rate of climatic-niche evolution related to climatic niche breadth? Evolution (published online).

Gaston, K. J., T. M. Blackburn, and J. I. Spicer. 1998. Rapoport's rule: time for an epitaph? Trends Ecol. Evol. 13:70–74.

Gaston, K. J. 2009. Geographic range limits: achieving synthesis. Proc. R. Soc. B 276: 1395–1406.

Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integr. Comp. Biol. 46:5–17.

Gibert, P., and R. B. Huey 2001. Chill-coma temperature in *Drosophila*: effects of developmental temperature, latitude, and phylogeny. Physiol. Biochem. Zool. 74:429–434.

Gilchrist, G. W., and R. B. Huey. 1999. The direct response of *Drosophila melanogaster* to selection on knockdown temperature. Heredity 83:15–29.

Guralnick, R. 2006. The legacy of past climate and landscape change on species' current experienced climate and elevation ranges across latitude: a multispecies study utilizing mammals in western North America. Global Ecol. Biogeogr. 15:505–518.

Hall, R. L. 1979. Inverse moments for a class of truncated normal distributions. Indian Statist. B 41:66–76.

Hua, X., and J. J. Wiens. 2010. Latitutudinal variation in speciation mechanisms in frogs. Evolution 64:429–443.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101:233–249.

Kozak, K. H., and J. J. Wiens. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. Proc. R. Soc. Lond. B 274:2995–3003.

Kozak, K. H., and J. J. Wiens. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. Ecol. Lett. 13:1378–1389.

Levins, R. 1965. The theory of fitness in a heterogeneous environment. V. Optimal genetic systems. Genetics, 52:891–904.

Lomolino, M., B. Riddle, and J. Brown. 2006. Biogeography, 3rd ed. Sinauer Assoc., Sunderland, Massachusetts.

Lynch, M., and W. Gabriel. 1987. Environniental tolerance. Am. Nat. 129:283–303.

McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. Ecol. Lett. 12:550–560.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. Ecol. Lett. 10:315–331.

Morton, K. W., and D. F. Mayers. 1994. Numerical solution of partial differential equations. Cambridge University Press, Cambridge.

Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. Heredity 59:181–197.

Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, A. T. Peterson, et al. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108:58–75.

Price, T. D., and M. Kirkpatrick. 2009. Evolutionary stable range limits set by interspecific competition. Proc. R. Soc. B 276:1429–1434.

Quintero, I., and J. J. Wiens. 2012. What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. Global Ecology and Biogeography (published online).

Roff, D. A., and T. A. Moousseau. 1987. Quantitative genetics and fitness: lessons from *Drosophila*. Heredity 58:181–197.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annu. Rev. Ecol. Evol. Syst. 40:415–436.

Shampine, L. F. 2008. Vectorized Adaptive Quadrature in MATLAB. J. Comput. Appl. Math. 211:131–140.

Sheldon, K. S., S. Yang, and J. J. Tewksbury. 2011. Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. Ecol. Lett. 14:1191–1200.

Sinervo, B. 1990. Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). Oecologia 83:228–237.

Smith, M. A., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110–128.

Smith, S. A., and J.M. Beaulieu. 2009. Life history influences rates of climatic niche evolution in flowering plants. Proc. R. Soc. Lond. B 276:4345–4352.

Snyder, G. K., and W. W. Weathers. 1975. Temperature adaptations in amphibians. Am. Nat. 109:93–101.

van Berkum, F. H. 1988. Latitudinal patterns of thermal sensitivity of sprint speed in lizards. Am. Nat. 132:327–343.

Whitlock, M. C. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. Am. Nat. 148:S65–S77.

Table 3.1. Major parameters and variables in the model.

Parameter	Description
C	the carrying capacity that is assumed to be constant over space and time
D	the variance of dispersal distance in one time step
h^2	the heritability of both temperature niche location and thermal tolerance
r	the absolute fitness of individuals without the impacts of competition and selection
$\sin(\alpha)$	the slope of a mountain
V	the variance in niche locations and thermal tolerances among individuals from the same location
V_u	the variance of resource utilization curve that measures the strength of competition, with larger values corresponding to weaker competition
λ	the level of tradeoff between tolerance and performance, with larger values corresponding to a stronger tradeoff
$\theta(x,t)$	the temperature condition at a location x and at time t
Variable	**Description**
$n(x,t)$	population density at location x at time t
$\overline{w}(x,t)$	the average Malthusian fitness of individuals at location x at time t
$\overline{V}_s(x,t)$	the average thermal tolerance of individuals at location x at time t
$\overline{z}(x,t)$	the average temperature niche location of individuals at location x at time t

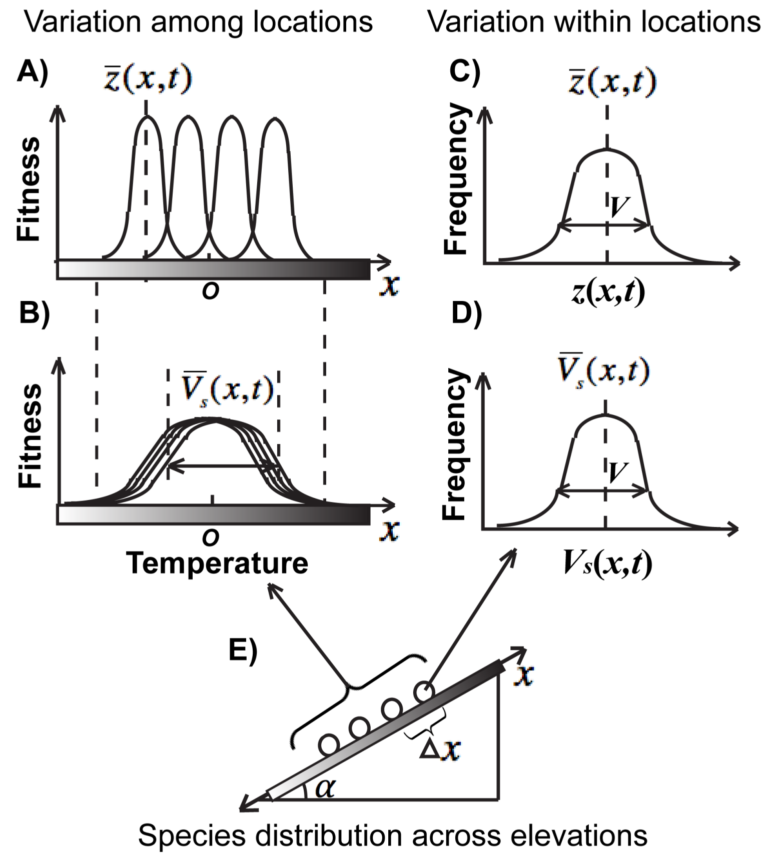


Figure 3.1. Hypothetical examples illustrating the species distribution across elevations (E), variation in temperature niches among individuals from different locations (A,B), and variation in temperature niches among individuals from the same location (C,D). Individuals from four hypothetical locations (E) are sampled from the species distribution to show two possible relationships between temperature niche breadth at the species level versus thermal tolerance at the individual level. (A) All individuals have narrow thermal tolerances but distinct temperature niche locations. Species realized temperature niche breadth is mainly driven by variation in temperature niche locations ($\bar{z}$) among locations. (B) All individuals have wide thermal tolerances but similar niche locations. Species realized temperature niche breadth is driven by thermal tolerances on the individual level ($\overline{V}_s$). Variation among individual temperature niches within each location is assumed to follow a normal distribution with mean $\bar{z}$ (C) and $\overline{V}_s$ (D), and a constant niche variance V.

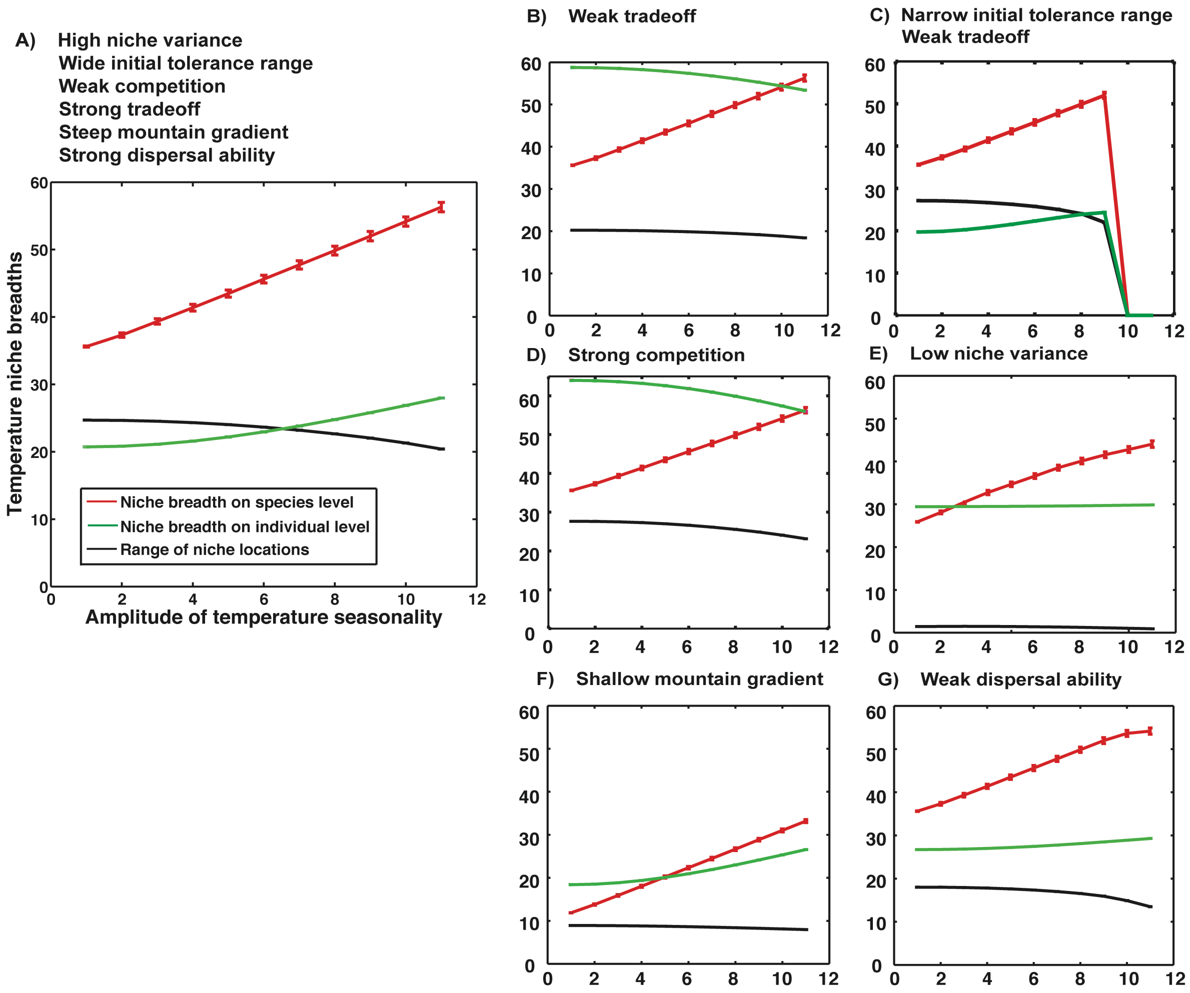


Figure 3.2. The effect of temperature seasonality on species temperature niche breadth. Model conditions are either strong ($\lambda = 0.1$) or weak ($\lambda = 0.01$) trade-off (A vs. B), wide ($V_s = 30$) or narrow ($V_s = 10$) initial value for thermal tolerance (A vs. C), strong ($V_u = 20$) or weak ($V_u = 100$) competition (A vs. D), high ($V = 1$) or low ($V = 0.1$) niche variance (A vs. E), steep ($\sin(\alpha) = 0.3$) or shallow ($\sin(\alpha) = 0.1$) mountain gradient (A vs. F), and strong (annual individual dispersal distance has standard deviation = 3 km) or weak (1.5 km) dispersal ability (A vs. G).

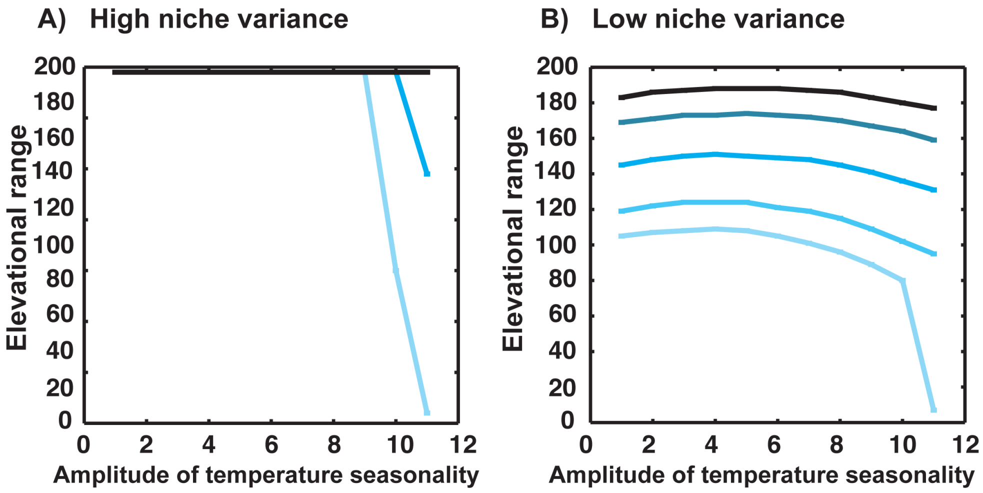


Figure 3.3. The effects of the initial value of the individual thermal tolerance on species' elevational ranges across species with high niche variance (A) and low niche variance (B). The initial value for the thermal tolerance is set to 15, 20, 30, 40, or 50 °C^2, with darker lines for species having wider initial value for the thermal tolerance range.

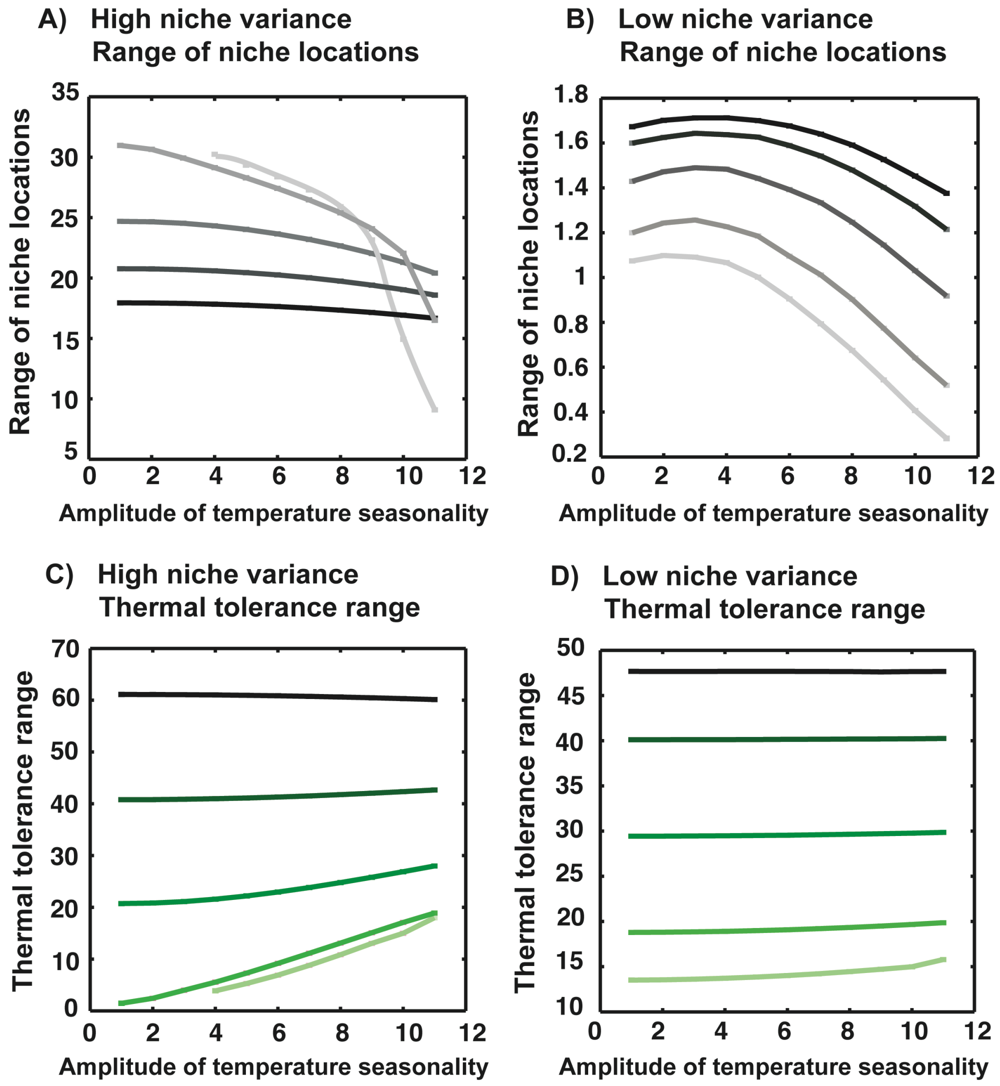


Figure 3.4. The effects of the initial value of the individual thermal tolerance on the range of temperature niche locations (A,B) and individual thermal tolerance (C,D) across species with high niche variance (A,C) and low niche variance (B,D). The initial value for the thermal tolerance is set to 15, 20, 30, 40, or 50 °C^2, with darker lines for species having wider initial value for the thermal tolerance range.

Conclusions

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 (e.g. Janzen 1967; Moritz et al. 2000; Wiens 2004; Kozak and Wiens 2007). Based on these verbal models, my dissertation starts with a simple conceptual map, suggesting potential relationships between climate, climatic niche evolution, and speciation. Climate may first influence the climatic niches of a species and therefore its climatic niche evolution. Climatic niche evolution then determines the responses of organisms to variation in climate over space and time that can be important drivers of speciation.

A good example of the conceptual map starts with Janzen (1967)'s hypothesis. Janzen (1967) suggested that the greater temperature stratification across elevational gradients in the tropics makes a tropical species adapted to a narrower range of temperature than a species in temperate regions, potentially making mountain passes in the tropics more effective dispersal barriers. The limited dispersal between different elevations may then promote gradient speciation along mountain slopes in the tropics (e.g. Moritz et al. 2000), leading to a potential latitudinal pattern in the relative importance of climatic niche conservatism and niche divergence in speciation (Kozak and Wiens 2007).

In chapter 1, we tested for the latitudinal patterns in speciation in the anurans. Using data from up to 79 sister-species pairs, we tested for latitudinal variation in elevational and climatic overlap between sister species, and evaluated the frequency of speciation via niche conservatism versus niche divergence in relation to latitude. In contrast to a previous study on salamanders (Kozak and Wiens 2007), we found no tendency for greater niche divergence in the tropics or for greater niche conservatism in temperate regions. Although our results supported the idea of greater climatic zonation in tropical regions, they show that this climatic pattern does not lead to relationships between climate, climatic niche evolution, and speciation that are as straightforward as suggested by the previous verbal models.

In chapter 2, we developed a quantitative model to test the relatively new but theoretically untested model of speciation, speciation via niche conservatism, and examined the climatic conditions under which speciation via niche conservatism versus 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 essential component of speciation, despite 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.

In chapter 3, I developed a quantitative model to examine why and under what conditions a species tend to evolve narrow climatic tolerance under limited seasonal climatic fluctuations, related to Janzen's hypothesis. Model results support Janzen (1967)'s hypothesis on the physiological responses of individual thermal tolerance to seasonal temperature variation, as the result of two population-level processes: ‘red-queen’ process (Whitlock 1996) and ‘jack-of-all-trades’ process (e.g. Levins 1965). However these population-level processes do not lead to narrower species elevational ranges under more limited temperature seasonality. Instead, I propose that the latitudinal variation in species elevational ranges is the result of speciation rather than the premise of speciation that is suggested by previous verbal models.

These three chapters, together, show more complicated relationships between climate, climatic niche evolution, and speciation than the simple conceptual map we started with. Nevertheless, the studies represent only a simplified starting point for understanding these complex relationships. In reality, responses to climatic conditions over space and time may be even more complex (e.g. Davis and Shaw 2001; Hoffman and Sgrò 2011) and species distributions may be determined only indirectly by climate, if at all (e.g. Gross and Price 2000). These complexities should be explored in future studies.

References

Davis, M. B., and R. G. Shaw. 2001. Range shift and adaptive responses to Quaternary climate change. Science 292:673–679.

Gross, S. J., and T. D. Price. 2000. Determinants of the northern and southern range limits of a warbler. Journal of Biogeography 27:869–878.

Hoffman, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101:233–249.

Kozak, K. H., and J. J. Wiens. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. Proc. R. Soc. Lond. B 274:2995–3003.

Levins, R. 1965. The theory of fitness in a heterogeneous environment. V. Optimal genetic systems. Genetics, 52:891–904.

Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annu. Rev. Ecol. Syst. 31:533–563.

Wiens, J. J. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197.

Whitlock, M. C. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. Am. Nat. 148:S65–S77.

Bibliography

Addo-Bediako, A., S. L. Chown, and K. J. Gaston, 2000. Thermal tolerance, climatic variability and latitude. Proc. R. Soc. B 267:739–745.

AmphibiaWeb: Information on amphibian biology and conservation. [web application]. 2009. Berkeley, California: AmphibiaWeb. Available: http://amphibiaweb.org/. (Accessed: Jun 4, 2009).

Angilletta Jr, M. J., R. S. Wilson, C. A. Navas and R. S. James. 2003. Tradeoffs and the evolution of thermal reaction norms. Trends Ecol. Evol. 18:234–240.

Barnosky, A. D. 2005. Effects of Quaternary climatic change on speciation in mammals. Journal of Mammalian Evolution 12:247–264.

Barraclough, T. G., and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. Am. Nat. 155:419–434.

Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. Annual Review of Ecology, Evolution, and Systematics 16:113–148.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. *In* Fishery Investigations Series II, Vol. 19. Ministry of Agriculture, Fisheries and Food, London.

Boul, K. E., W. C. Funk, C. R. Darst, D. C. Cannatella, and M. J. Ryan. 2007. Sexual selection drives speciation in an Amazonian frog. Proc. R. Soc. Lond. B 274:399–406.

Brooks, C. B., and S. C. Griffith. 2010. Mate choice. Pages 416–434 *in* D. Westneat, and C. Fox, ed. Evolutionary behavioral ecology. Oxford University Press, Oxford.

Bulmer, M. G. 1980. The mathematical theory of quantitative genetics. Clarendon Press, Oxford.

Bürger, R., and M. Lynch. 1995. Evolution and extinction in a changing environment: a quantitative-genetic analysis. Evolution 49:151–163.

Cadena, C. D., K. H. Kozak, J. P. Gómez, J. L. Parra, C. M. McCain, R. C. K. Bowie, A. C. Carnaval, C. Moritz, C. Rahbek, T. E. Roberts, N. J. Sanders, C. J. Schneider, J. VanDerWal, K. R. Zamudio, and C. H. Graham. 2012. Latitude, elevational climatic zonation and speciation in New World vertebrates. Proc. R. Soc. B 279:194–201.

Case, T. J., and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. Am. Nat. 155:583–605.

Chevin, L. and F. Hospital. 2008. Selective sweep at a quantitative trait locus in the presence of background genetic variation. Genetics 180:1645–1660.

Cooper, W. S., and R. H. Kaplan. 1982. Adaptive 'coin-flipping': a decision-theoretic examination of natural selection for random individual variation. J. Theor. Biol., 94:135–151.

Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer Associates, Sunderland, MA.

Davis, M. B., and R. G. Shaw. 2001. Range shift and adaptive responses to Quaternary climate change. Science 292:673–679.

Dawson, T. P., S. T. Jackson, J. I. House, I. C. Prentice, and G. M. Mace. 2011 Beyond predictions: biodiversity conservation in a changing climate. Science 332, 53–58.

Deutsch, C. A., J. J., Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. USA 105:6668–6672.

Dobzhansky, T. 1936. Studies on hybrid sterility. II. Localization of sterility factors in *Drosophila pseudoobscura* hybrids. Genetics 21:113–135.

Dobzhansky, T. 1950. Evolution in the tropics. Am. Sci. 38:209–221.

Donaldson-Matasci, M. C., M. Lachmann, and C. T. Bergstrom. 2008. Phenotypic diversity as an adaptation to environmental uncertainty. Evol. Ecol. Res. 10:493–515.

Doebeli, M., and U. Dieckmann. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. American Naturalist 156:S77–S101.

Doebeli, M., and U. Dieckmann. 2003. Speciation along environmental gradients. Nature 421:259–264.

Eastman, R. 2003. Idrisi Kilimanjaro manual and tutorial. Worchester: Clark Labs, Clark University.

Elith, J. 2002. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. In *Quantitative methods for conservation biology* (Ferson, S. and Burgman, M., eds) pp. 39–58, Springer.

Endler, J. A. 1977. Geographic variation, speciation and clines. Princeton University Press, Princeton.

Etterson, J. R. and R. G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. Science 294:151–154.

Falconer, D. S., and T. F. C. MacKay. 1996. Introduction to quantitative genetics, 4th edn. Essex, UK: Longman's Green.

Fisher-Reid, M. C., K. H. Kozak, and J. J. Wiens. 2012. How is the rate of climatic-niche evolution related to climatic niche breadth? Evolution (published online).

Fouquette, M. J. 1975. Speciation in chorus frogs. I. reproductive character displacement in the *Pseudacris nigrita* complex. Syst. Zool. 24:16–23.

Frost, D. R. 2008. Amphibian Species of the World: an Online Reference. American Museum of Natural History, New York, USA. Available at http://research.amnh.org/herpetology/amphibia. Accessed September, 2008.

Futuyma, D. J. 1998. Evolutionary biology. 3rd ed. Sinauer Associates, Sunderland, MA.

Gaston, K. J., T. M. Blackburn, and J. I. Spicer. 1998. Rapoport's rule: time for an epitaph? Trends Ecol. Evol. 13:70–74.

Gaston, K. J. 2009. Geographic range limits: achieving synthesis. Proc. R. Soc. B 276: 1395–1406.

Gavrilets, S. 1999. A dynamical theory of speciation on holey adaptive landscapes. American Naturalist 154:1–22.

Gavrilets, S. 2004. Fitness landscapes and the origin of species. Princeton University Press, Princeton.

Ghalambor, C. K., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integr. Comp. Biol. 46:5–17.

Gibert, P., and R. B. Huey 2001. Chill‐coma temperature in *Drosophila*: effects of developmental temperature, latitude, and phylogeny. Physiol. Biochem. Zool. 74:429–434.

Gilchrist, G. W., and R. B. Huey. 1999. The direct response of *Drosophila melanogaster* to selection on knockdown temperature. Heredity 83:15–29.

Graham, C. H., S. R. Ron, J. C. Santos, C. J. Schneider, and C. Moritz. 2004. Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution 58:1781–1793.

Gross, S. J., and T. D. Price. 2000. Determinants of the northern and southern range limits of a warbler. Journal of Biogeography 27:869–878.

Guralnick, R. 2006. The legacy of past climate and landscape change on species' current experienced climate and elevation ranges across latitude: a multispecies study utilizing mammals in western North America. Global Ecol. Biogeogr. 15:505–518.

Hall, R. L. 1979. Inverse moments for a class of truncated normal distributions. Indian Statist. B 41:66–76.

Heyer, R. W. 1967. A herpetofaunal study of an ecological transect through the Cordillera de Tilarán, Costa Rica. Copeia 1967:259–271.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25:1965–1978.

Hill, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. Nature 350:337–339.

Hoffman, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. Nature 470:479–485.

Hoskin, C. J., M. Higgie, K. R. McDonald, and C. Moritz. 2005. Reinforcement drives rapid allopatric speciation. Nature 437:1353–1356.

Hoskin, C. J., M. Tonione, M. Higgie, J. B. MacKenzie, S. E. Williams, J. VanDerWal, and C. Moritz. 2011. Persistence in peripheral refugia promotes phenotypic divergence and speciation in a rainforest frog. American Naturalist 178:561–578.

Hua, X., and J. J. Wiens. 2010. Latitutudinal variation in speciation mechanisms in frogs. Evolution 64:429–443.

Hutchinson, G. E. 1957. A Treatise on Limnology. Vol. 1. John Wiley & Sons, New York. 1015 pp.

Insightful Corporation. 2001. S-Plus 6 for Windows: Guide to Statistics. Vol. 1. Insightful Corporation, Seattle, WA.

IUCN 2009. *IUCN Red List of Threatened Species. Version 2009.1.* Available at http://www.iucnredlist.org. Accessed on September, 2008.

Jansson, R., and M. Dynesius. 2002. The fate of clades in a world of recurrent climatic change: milankovitch oscillations and evolution. Annual Review of Ecology and Systematics 33:741–777.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101:233–249.

Jenkins, N.L. and A. A. Hoffman. 1999. Limits to the southern border of *Drosophila serrata:* cold resistance, heritability, and trade-offs. Evolution 53:1823–1834.

Johnson, N. K., and C. Cicero. 2004. New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. Evolution 58:1122–1130.

Kaiser, H. F. 1960. The application of electronic computers to factor analysis. Educ. Psychol. Meas. 20:141–151.

Kimura M. and J. F. Crow. 1978. Effect of overall phenotypic selection on genetic change at individual loci. Proceedings of the National Academy of Sciences of the United States of America 75:6168–6171.

Kozak, K. H., and J. J. Wiens. 2006. Does niche conservatism promote speciation? A case study in North American salamanders. Evolution 60:2604–2621.

Kozak, K. H., and J. J. Wiens. 2007. Climatic zonation drives latitudinal variation in speciation mechanisms. Proc. R. Soc. Lond. B 274:2995–3003.

Kozak, K. H., and J. J. Wiens. 2010. Accelerated rates of climatic-niche evolution underlie rapid species diversification. Ecol. Lett. 13:1378–1389.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

Lee, H. Y., J. Y. Chou, L. Cheong, N. H. Chang, S. Y. Yang, and J. Y. Leu. 2008. Incompatibility of nuclear and mitochondrial genomes causes hybrid sterility between two yeast species. Cell 135:1065–1073.

Lemmon, E. M., A. R. Lemmon, J. T. Collins, J. A. Lee-Yaw, and D. C. Cannatella. 2007. Phylogeny-based delimitation of species boundaries and contact zones in the trilling chorus frogs (*Pseudacris*). Mol. Phylogenet. Evol. 44:1068–1082.

Levins, R. 1965. The theory of fitness in a heterogeneous environment. V. Optimal genetic systems. Genetics, 52:891–904.

Littlejohn, M. J. 1965. Premating isolation in the *Hyla ewingi* complex (Anura, Hylidae). Evolution 19:234–243.

Loftus-Hills, J. J., and M. J. Littlejohn. 1992. Reinforcement and reproductive character displacement in *Gastrophryne carolinensis* and *G. olivacea* (Anura, Microhylidae)–a reexamination. Evolution 46:896–906.

Lomolino, M. V., B. R. Riddle, and J. H. Brown. 2006. Biogeography, 3rd Edition. Sinauer Associates, Sunderland, MA.

Losos, J. B., and R. E. Glor. 2003. Phylogenetic comparative methods and the geography of speciation. Trends Ecol. Evol. 18:220–227.

Lovette, I. J. 2005. Glacial cycles and the tempo of avian speciation. Trends in Ecology & Evolution 20:57–59.

Lowry, D. B., R. C. Rockwood, and J. H. Willis. 2008. Ecological reproductive isolation of coast and inland races of *Minulus guttatus*. Evolution 62:2196–2214.

Lynch, J. D. 1989. The gauge of speciation: on the frequencies of modes of speciation. In *Speciation and Its Consequences* (Otte, D. and Endler, J. A., eds) pp. 527–553, Sinauer Associates.

Lynch, M., and W. Gabriel. 1987. Environniental tolerance. Am. Nat. 129:283–303.

Lynch, M., and A. Abegg. 2010. The rate of establishment of complex adaptations. Molecular Biology and Evolution 27:1404–1414.

Matute, D. R., I. A. Butler, D. A. Turissini, and J. A. Coyne. 2010. A test of the snowball theory for the rate of evolution of hybrid incompatibilities. Science 329:1518–1521.

Mayer, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Mass.

McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. Ecol. Lett. 12:550–560.

McCormack, J. E., A. J. Zellmer, and L. L. Knowles. 2010. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation? Insights from tests with niche models. Evolution 64:1231-1244

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. Ecol. Lett. 10:315–331.

Mizera, F., and G. Meszéna. 2003. Spatial niche packing, character displacement and adaptive speciation along an environmental gradient. Evolutionary Ecology Research 5:1–20.

Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annu. Rev. Ecol. Syst. 31:533–563.

Morton, K. W., and D. F. Mayers. 1994. Numerical solution of partial differential equations. Cambridge University Press, Cambridge.

Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. Heredity 59:181–197.

Moyle, L. C., and T. Nakazato. 2010. Hybrid incompatibility 'snowballs' between *Solanum* species. Science 329:1521–1523.

Muller, H. J. 1942. Isolating mechanisms, evolution and temperature. Biological Symposia 6:71–125.

Nagylaki, T. 1975. Conditions for the existence of clines. Genetics 80:595–615.

Nosil, P. 2012. Ecological speciation. Oxford University Press, Oxford.

Nosil, P., T. H. Vines, and D. J. Funk. 2005. Perspective: Reproductive isolation caused by natural selection against immigrants using divergent environments. Evolution 59:705–719.

Ogden, R., and R. S. Thorpe. 2002. Molecular evidence for ecological speciation in tropical habitats. Proc. Natl. Acad. Sci. USA 99:13612–13615.

Orr, M. R., and T. B. Smith. 1998. Ecology and speciation. Trends in Ecology & Evolution 13:502–506.

Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, A. T. Peterson, et al. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108:58–75.

Pease, C. M., and R. Lande, R. 1989. A model of population growth, dispersal and evolution in a changing environment. Ecology 70:1657–1664.

Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Peterson, A. T. and A. S. Nyári. 2007. Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, *Schiffornis* sp., in the Neotropics. Evolution 62:173–183.

Presgraves, D. C. 2010. The molecular evolutionary basis of species formation. Nature Reviews Genetics 11:175–180.

Price, T. D., and M. Kirkpatrick. 2009. Evolutionary stable range limits set by interspecific competition. Proc. R. Soc. B 276:1429–1434.

Phillimore, A. B., C. D. Orme, G. H. Thomas, T. M. Blackburn, P. M. Bennett, K. J. Gaston, and I. P. F. Owens. 2008. Sympatric speciation in birds is rare: insights from range data and simulations. Am. Nat. 171:646–657.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190:231–259.

Quintero, I., and J. J. Wiens. 2012. What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. Global Ecology and Biogeography (published online).

Raxworthy, C. J., C. M. Ingram, N. Rabibisoa, and R. G. Pearson. 2007. Applications of ecological niche modeling for species delimitation: a review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. Syst. Biol. 56:907–923.

Rice, W. R. and G. W. Salt. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions – experimental evidence. Evolution 44:1140–1152.

Ricklefs, R. E. 2007. Estimating diversification rates from phylogenetic information. Trends Ecol. Evol. 22:601–610.

Rissler, L. J., and J. J. Apodaca. 2007. Adding more ecology into species delimitation: ecological niche models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). Syst. Biol. 56:924–942.

Roff, D. A., and T. A. Moousseau. 1987. Quantitative genetics and fitness: lessons from *Drosophila*. Heredity 58:181–197.

Rundle, H. D., and P. Nosil. 2005. Ecological speciation. Ecol. Lett. 8: 336–352.

Schemske, D. W. and H. D. Bradshaw. 1999. Pollinator preference and the evolution of floral traits in monkeyflowers (Mimulus). Proceedings of the National Academy of Sciences of the United States of America 96:11910-11915.

Schluter, D. 2001. Ecology and the origin of species. Trends Ecol. Evol. 16:372–380.

Schluter, D. 2009. Evidence for ecological speciation and its alternative. Science 323:737–741.

Servedio, M. R., G. S. Van Doorn, M. Kopp, A. M. Frame, and P. Nosil. 2011. Magic traits in speciation: 'magic' but not rare? Trends in Ecology & Evolution 26:389–397.

Servedio, M. R. and M. Kopp. 2011. Sexual selection and magic traits in speciation with gene flow. Current Zoology 58:510–516.

Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. Annu. Rev. Ecol. Evol. Syst. 40:415–436.

Shampine, L. F. 2008. Vectorized Adaptive Quadrature in MATLAB. J. Comput. Appl. Math. 211:131–140.

Sheldon, K. S., S. Yang, and J. J. Tewksbury. 2011. Climate change and community disassembly: impacts of warming on tropical and temperate montane community structure. Ecol. Lett. 14:1191–1200.

Sinervo, B. 1990. Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). Oecologia 83:228–237.

Smith, M. A., and D. M. Green. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110–128.

Smith, S. A., and J.M. Beaulieu. 2009. Life history influences rates of climatic niche evolution in flowering plants. Proc. R. Soc. Lond. B 276:4345–4352.

Snyder, G. K., and W. W. Weathers. 1975. Temperature adaptations in amphibians. Am. Nat. 109:93–101.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Co., New York.

Stockman, A. K., and J. E. Bond. 2007. Delimiting cohesion species: extreme population structuring and the role of ecological interchangeability. Mol. Ecol. 16:3374–3392.

Turelli, M., and N. H. Barton. 1994. Genetic and statistical analyses of strong selection on polygenic traits: what, me normal? Genetics 138:913–941.

Turelli, M., N. H. Barton, and J. A. Coyne. 2001. Theory and speciation. Trends Ecol. Evol. 16:330–343.

Twomey, E., V. Morales, and K. Summers. 2008. Evaluating condition-specific and asymmetric competition in a species-distribution context. Oikos 117:1175–1184.

van Berkum, F. H. 1988. Latitudinal patterns of thermal sensitivity of sprint speed in lizards. Am. Nat. 132:327–343.

Via, S. 2002. The ecological genetics of speciation. American Naturalist 159:S1–S7.

Via, S. 2009. Natural selection in action during speciation. Proceedings of the National Academy of Sciences of the United States of America 106:9939–9946.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883.

Whitlock, M. C. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. Am. Nat. 148:S65–S77.

Weir, J. T., and D. Schluter. 2004. Ice sheets promote speciation in boreal birds. Proceedings of the Royal Society B: Biological Sciences 271:1881–1887.

Weir, J. T., and D. Schluter. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. Science 315:1574–1576.

Wiens, J. J. 2004a. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197.

Wiens, J. J. 2004b. What is speciation and how should we study it? Am. Nat. 163:914–923.

Wiens, J. J. 2007. Global patterns of diversification and species richness in amphibians. Am. Nat.170:S86–S106.

Wiens, J. J., and C. H. Graham. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annu. Rev. Ecol. Evol. Syst. 36:519–539.

Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. Am. Nat. 168:579-596.

Wiens, J. J., J. Sukumaran, R. A. Pyron, and R. M. Brown. 2009. Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). Evolution 63:1217–1231.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annu. Rev. Ecol. Evol. Syst. 34:273–309.

Yohai, V. J., and R. H. Zamar. 1998. Optimal locally robust M-estimates of regression. J. Statist. Plann. Inference 64:309–323.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–693.

Zug, G. R., L. J. Vitt, and J. P. Caldwell. 2001. Herpetology: an introductory biology of amphibians and reptiles. 2nd ed. Academic Press, New York.