

Neutral Biogeography and the Evolution of Climatic Niches

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ABSTRACT: Recent debate on whether climatic niches are conserved through time has focused on how phylogenetic niche conservatism can be measured by deviations from a Brownian motion model of evolutionary change. However, there has been no evaluation of this methodological approach. In particular, the fact that climatic niches are usually obtained from distribution data and are thus heavily influenced by biogeographic factors has largely been overlooked. Our main objective here was to test whether patterns of climatic niche evolution that are frequently observed might arise from neutral dynamics rather than from adaptive scenarios. We developed a model inspired by neutral biodiversity theory, where individuals disperse, compete, and undergo speciation independently of climate. We then sampled the climatic niches of species according to their geographic position and showed that even when species evolve independently of climate, their niches can nonetheless exhibit evolutionary patterns strongly differing from Brownian motion. Indeed, climatic niche evolution is better captured by a model of punctuated evolution with constraints due to landscape boundaries, two features that are traditionally interpreted as evidence for selective processes acting on the niche. We therefore suggest that deviation from Brownian motion alone should not be used as evidence for phylogenetic niche conservatism but that information on phenotypic traits directly linked to physiology is required to demonstrate that climatic niches have been conserved through time.

Keywords: comparative analysis, neutral biodiversity theory, phylogenetic niche conservatism, Ornstein-Uhlenbeck process, punctuated equilibrium.

Introduction

Phylogenetic niche conservatism (PNC), the tendency for species and clades to retain ancestral niche attributes across large temporal scales, is a surprisingly controversial issue (Losos 2008; Wiens et al. 2010). In particular, the evolution of species' climatic niches has implications for understanding a wide range of questions in evolutionary biology, including the origin of broad-scale diversity patterns (Buckley et al. 2010), the drivers of speciation (Kozak et

al. 2008), invasive species niche shifts (Petitpierre et al. 2012), and the response of species and communities to climate change (Lavergne et al. 2010). Despite intensive research during the last decades, the conditions that have triggered or impeded climatic niche evolution remain hotly debated, with a major disagreement on how observed macroevolutionary patterns of species niches should be compared to neutral expectations (Losos 2008; Wiens et al. 2010).

Most common approaches aimed at investigating PNC share several basic premises and assumptions. Climatic niches are often measured as species' mean position over continuous environmental gradients (e.g., Hof et al. 2010; Pyron and Burbrink 2012). This choice is usually made because it enables climatic niches to be characterized in a broad sense without the practical difficulty to obtain physiological estimates of climatic tolerance for a large number of species (but see Kellermann et al. 2012). However, climatic niches measured this way are emergent properties at the species level (Vrba and Gould 1986), a product of the interaction between individual physiology and extrinsic factors including biotic interactions and dispersal limitation (Soberón 2007). This has led some authors to argue that climatic niches do not evolve by descent with modification and thus should not be analyzed in a phylogenetic context (Grandcolas et al. 2011). The strength of PNC is then usually assessed by comparison to a Brownian motion (BM) model of evolution as the neutral expectation. Under BM, traits are inherited from a common ancestor but diverge gradually over time independently according to a continuous random walk. BM is used to mimic genetic drift or selection in a variable environment (Edwards and Cavalli-Sforza 1964; Felsenstein 1985). Different approaches to the study of PNC examine different deviations from BM: (i) phylogenetic signal measures the tendency for closely related species to resemble each other more or less than expected under BM and (ii) model comparisons that contrast the fit of the BM model to alternative models evaluate evidence for selective constraints on niche evolution (Wiens et al. 2010). Here we question the underlying

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assumption that BM provides an appropriate neutral expectation for climatic niches.

To our knowledge, there has been no rigorous assessment of the major assumptions underlying tests of PNC outlined above. Here, we attempt a first step toward bridging this gap and evaluate whether, in the absence of any influence of climate on individual survival and reproduction, wrong conclusions can be made concerning PNC when assuming a neutral BM model. In particular, we test whether patterns of punctuationalism or constraints on climatic niche evolution could result from neutral dynamics that are independent of climate. Spatially explicit simulations of the neutral biodiversity theory (NBT; Hubbell 2001) are well suited for this purpose since they explicitly include the processes of speciation, migration, and competition but do not make any assumption on the model of niche evolution. Specifically, NBT assumes performance equivalence between individuals in terms of speciation, migration, and competitive ability regardless of species identity. NBT also models ecological drift via a simple limitation of the carrying capacity of local communities. For these reasons, NBT provides a useful link between biogeographic and ecological processes, as illustrated in macroevolutionary studies of range size heritability (Mouillot and Gaston 2007) and phylogenetic tree shape (Davies et al. 2011).

In this article, we confront the traditional neutral model in macroevolution (BM) with an alternative neutral biogeographic model (NBT) of climatic niche evolution. Specifically, using an absurdum argument where our simulated climatic niches do not result from adaptive processes but rather from purely neutral spatial dynamics, we ask the following questions: (1) Do climatic niches exhibit phylogenetic signal when they arise via neutral spatial dynamics? (2) Is gradualism a reasonable neutral expectation for the evolution of climatic niches on geological time-scales? and (3) Can constraints on climatic niche diversification arise simply through bounded geographic space?

To address these questions, we simulate clades evolving under NBT, in which dynamics are independent from climate. We first examine whether such models generate macroevolutionary patterns resembling those produced by BM, that is, strong phylogenetic signal and gradualism. We then compare the fit of NBT models to alternative macroevolutionary models (i.e., stabilizing selection and punctuated evolution) to describe more in detail the process of niche evolution expected from a neutral biogeographic scenario of species diversification and range dynamics. Finally, we show that assuming an incorrect model of niche evolution, and in particular wrongly assuming BM, can lead to spurious conclusions in analyses of trait-climate relationships.

Model Presentation

Death, Migration, and Reproduction

To simulate the evolution of a clade in geographic space, we developed a model that includes the processes of speciation and migration, derived from NBT. We modeled clade diversification in a “continent” represented as a rectangular lattice with hard boundaries. The continent was 51×21 pixels and thus stretched more in latitude than in longitude. Each pixel in the lattice had a finite carrying capacity set to 20 individuals, leading to competition for space and hence ecological drift. Simulations were initiated with an empty lattice except for the central pixel, which was at carrying capacity with individuals of the ancestral species. Simulations then followed Davies et al. (2011): at each time step, an individual was randomly chosen in the landscape; it either speciated with probability b (per capita speciation rate; see below for speciation modes) or died and was replaced by the offspring of another individual. This new individual, irrespective of species identity, could either be from the same pixel or from the eight neighboring pixels with probability m (migration rate). Because we did not assume all pixels were at carrying capacity at the beginning of the simulations, we thus created a reproductive advantage for individuals in close proximity to empty slots. Simulations were terminated after 10^8 individual replacements, which roughly corresponded to 4,500 generations. Metacommunities were then recorded (fig. 1), and phylogenetic trees for extant species were reconstructed using the recorded history of speciation events.

Speciation

We modeled two different modes of speciation, both sharing the basic assumption that more abundant species have a greater chance to speciate (Hubbell 2001). For the sake of simplicity and computational tractability, speciation occurred instantaneously in our simulations.

1. We first modeled a modified version of point mutation speciation (Hubbell 2001): when a randomly chosen individual within a pixel underwent speciation, a random fraction of conspecifics occurring in the same pixel were delineated as the new species (following Davies et al. 2011). In this version of point mutation, one of the two daughter species has low abundance and occupies only one location, which can be anywhere in the ancestral range. Speciation via polyploidization (Abbott et al. 2013) is probably the mode of speciation that is best embodied by point mutation.

2. Despite the recent accommodation of more realistic models of speciation (e.g., Rosindell et al. 2010; Desjardins-Proulx and Gravel 2012), NBT still lacks an explicit treatment of vicariance. To overcome this limitation and

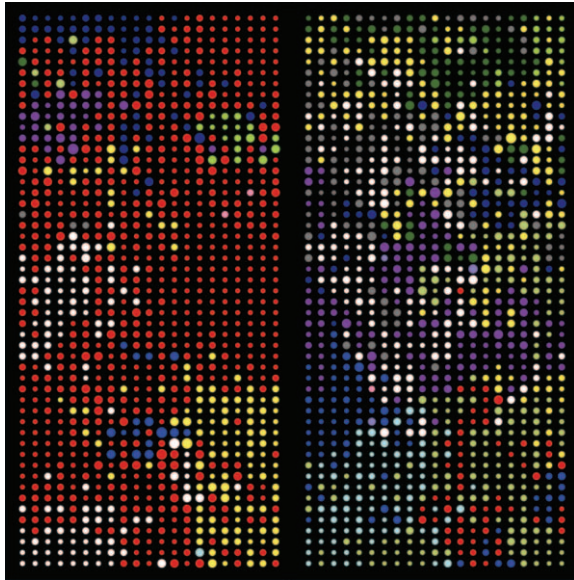


Figure 1: Snapshots of two metacommunities after 4,500 generations. Each local community is represented by a filled circle colored according to the most abundant species; circle size is proportional to local species richness. *Left*, simulation under point mutation speciation, with $m = 0.07$ and $b = 1.3E-5$ (16 species). A few species are very abundant, while all others are rare. *Right*, simulation under the vicariance model, with $m = 0.13$ and $b = 4.1E-7$ (14 species). Abundances are more even between species.

to keep the simulation model tractable, we proposed an alternative speciation mode that is based on the vicariance model developed by Pigot et al. (2010; see also Davies et al. 2005). In this speciation mode, a geographic barrier is assumed to bisect the species range, splitting the target species into two. To match the philosophy of previous spatial NBT models, we specified that the geographical barrier would run through the local pixel where an individual had been randomly selected to undergo speciation. The orientation of the barrier was then randomly chosen, and only the species of the selected individual was subdivided. We chose this strategy because it better captures the contingency of speciation events where barriers are more or less permeable to different species and are rarely constant through time (e.g., Lavergne et al. 2013).

Species' Climatic Niches

We first modeled a single climatic variable as a function of latitude, so that within each pixel climate was given by latitude + ε , where ε is a random normal deviate (in the simulations presented in the main text, ε has a standard deviation of 2, and latitude ranges from -25 to $+25$, but we verified that the size of the random deviate, the center of the gradient, and its slope do not qualitatively influence

our conclusions; see app. B; apps. A–G available online). Although this latitudinal dependence is rather strong, it was meant to broadly mirror the distribution of temperatures at continental scale. In a second step, we used mean annual temperature maps from six mountainous regions of the world. This provided examples of real landscapes that include both a latitudinal dependency and a strong spatial aggregation of climate (detailed methods in app. B). Climate had no impact on the simulations (i.e., it did not influence individual performance), but at the end of each run, the climatic niche of each species was calculated as the mean climate over the pixels where the species was present, as usually done from atlas data in comparative analyses (e.g., Hof et al. 2010; Barnagaud et al. 2012; Pyron and Burbrink 2012).

Our simulations model the evolution of species ranges via migration and biotic interactions (included in the model as carrying capacity) and provide a dynamic neutral model of species climatic niches. Under such a scenario, actual niche changes may be small and thus do not call for the evolution of physiological tolerances or require assumptions regarding individual performance differences across the underlying climatic gradient. We suggest that our simulations might match to a scenario in which fundamental niches are generally broad, encompassing all climates found in the landscape, and thus provide a useful neutral model for the evolution of climatic niches. In this framework, the term “evolution” is used in a weak sense, since change in the climatic niche is a product of migration, speciation, and ecological drift.

Parameter Choice

To generate robust estimates of the relative importance of speciation mode, migration rate, and per capita speciation rate, we performed 2,500 simulations for each speciation mode. Because simulations were uninformative when only one species was present at the end of the run, we retained only simulations with final species richness >1 , generating 1,402 replicates for point mutation and 2,210 replicates for vicariance. For computational tractability, values of speciation rate were selected following preliminary analyses so as to produce trees with fewer than 1,000 species. Speciation rate was typically an order of magnitude higher in point mutation (values uniformly drawn between $2E^{-6}$ and $2E^{-4}$ speciation events/individual) than in the vicariance scenario ($2E^{-7}$ – $2E^{-5}$) due to higher chance of extinction by ecological drift. For both speciation modes, we varied migration rates uniformly between 0 and 1.

In the simulations we present, the maximum number of individuals in the landscape was 21,420, and the number of generations over which the history of the clade was followed was less than 5,000. As in all such models, these

parameters are highly unrealistic if they were to be compared with real metacommunity sizes (Ricklefs 2003) or to timescales necessary to complete many speciation events. Indeed, simulations considering more realistic values would require several centuries of processing time, and analytical solutions or coalescent techniques have not yet been developed for the modeled speciation modes. We therefore derive analytical expressions for niche evolution in the next section to further explore parameter space and gain a better understanding of model behavior.

Evolution of Climatic Niches during Anagenesis

In our simulations, the evolution of the climatic niche during anagenesis is a succession of two steps: death of an individual and birth of a new individual (with migration). In the absence of boundaries (i.e., before domain boundaries have been reached) it is straightforward to show that the expected value of the niche (after either of these two steps) remains unchanged (detailed calculations in app. A): $E[\text{niche}(t + dt)] = \text{niche}(t)$.

The niche thus follows a succession of random steps with no direction bias. The expected variance of these random steps can be obtained separately for each step (detailed calculations in app. A):

$$\begin{aligned} & \text{Var}_{\text{death}} [\text{niche}(t + dt) - \text{niche}(t)] \\ &= \frac{1}{K \times L \times l} \times \frac{N(t)}{[N(t) - 1]^2} \times \text{Var}(\text{CLIM}_i(t)), \\ & \text{Var}_{\text{reproduction}} [\text{niche}(t + dt) - \text{niche}(t)] \\ &= \frac{1}{K \times L \times l} \times \frac{N(t)}{[N(t) + 1]^2} \\ & \times [\text{Var}(\text{CLIM}_i(t)) + (1 - f) \times m], \end{aligned}$$

where $N(t)$ is the number of individuals in the focal species at time t , each of them experiencing climate $\text{CLIM}_i(t)$; m is the migration rate, and f is the proportion of migration events in the same latitudinal band ($f = 1/4$ in our case, where migration between each of the eight neighboring pixels is equally likely; see app. A). Term K is the carrying capacity in one pixel, and L and l are the dimensions of the landscape. The variance of individual positions can be interpreted as the breadth of the species' niche (see app. A for a more detailed discussion). Therefore, during anagenesis and before the boundaries of the landscape have been reached, the mean niche of a species moves according to a succession of random steps with no trend. This random walk, however, is different from Brownian motion since its variance is not constant over time but depends on the population size and niche breadth of the species. Importantly, migration is not the only contributor to niche

change: large niche breadths and small population sizes also speed up niche evolution.

The above calculations hold only when the species is unbounded; when individuals approach the edge of the domain, a trend toward the middle of the landscape will appear. Such constraints are of course more important when the migration rate is high, since individuals will reach the boundaries of the landscape sooner. Given that in our simulations one generation corresponds to $K \times L \times l$ individual replacements, $1/(K \times L \times l)$ can be interpreted as the basic unit of time dt . Hence, increasing any of these three parameters would not modify model behavior but only increase the number of iterations one has to wait before seeing the effect of landscape boundaries. Furthermore, simulating anisotropic migration (included here as a tendency to migrate more easily in the same latitudinal band than toward higher or lower latitudes) would not modify model behavior but just reduce the effective migration rate, $(1 - f) \times m$ (see app. A). We are thus confident that the simulations we present cover a sufficiently broad range of scenarios of speciation and migration to be representative of model behavior for more realistic values of K , L , and l , as well as for scenarios of anisotropic migration. Because we could not treat the effects of landscape boundaries and speciation analytically, we explored their effects using comparative analysis.

Macroevolutionary Analysis of Simulation Outcomes

Comparison to Macroevolutionary Models

As a first attempt to describe the patterns of niche evolution produced by our simulations, we calculated two indexes commonly used in comparative analyses: Pagel's λ and κ parameters (Pagel 1994, 1999), which quantify departures from BM. First, λ was used to assess phylogenetic signal. It has been shown to be one of the best measures of phylogenetic signal since it can detect deviations from BM under a wide range of evolutionary models (Münkemüller et al. 2012). Pagel's λ is a multiplicative parameter affecting the phylogenetic covariances between the tips of the tree, and it equals 1 when signal is equal to that expected under BM. At the other extreme, $\lambda = 0$ indicates no signal, such that phylogenetic distances between species do not correlate with niche differences. Support for $\lambda = 0$ in our simulations might indicate (but not demonstrate) that climatic niches are independent from phylogeny (Grandcolas et al. 2011). Second, Pagel's κ was used to measure punctuationism (Gould and Eldredge 1977) in niche evolution. This parameter exponentially stretches or compresses branch lengths of the tree in order to test whether topology is a better predictor of interspecific niche differences than branch lengths. When κ equals

0, evolution is independent from the branch lengths, indicating punctuated evolution. When κ equals unity, a model of gradual evolution is supported, as expected under Brownian motion.

Phylogenetic signal has been widely used in the literature to measure PNC (e.g., Hof et al. 2010; Olalla-Tarraga et al. 2011); however, there is growing evidence that phylogenetic signal per se does not give any insight into the underlying processes driving niche evolution (Revell et al. 2008). Therefore, to explore further the process of niche evolution, we compared the fit of alternative macroevolutionary models to our simulated data (Wiens et al. 2010). We evaluated five alternative macroevolutionary models using Akaike's Information Criterion corrected for small sample sizes (AICc): (1) BM; (2) the κ model (KAPPA; Pagel 1994), which adds some degree of punctuationism to BM; (3) an Ornstein-Uhlenbeck process (OU; Hansen 1997), where species are subject to BM but also to selection toward a common optimum; (4) OU with strict punctuationism (OUp), where all branch lengths in the tree are set to unity; and finally, (5) white noise (WN), a non-phylogenetic model where all niches are drawn from a normal distribution regardless of shared ancestry between species. These macroevolutionary models do not form an exhaustive list but allow us to evaluate three alternative hypotheses. First, support for WN would indicate that phylogenetic relationships do not explain niche differences between species, consistent with extremely fast and recent niche diversification. Second, if KAPPA or OUp have a good fit to the data, a model of punctuated evolution would be supported. Third, support for OU or OUp would show constraints on niche evolution.

Potential Biases in the Analysis of Trait-Climate Relationships

To evaluate the impacts of mis-specifying the model of niche evolution, we use additional trait simulations to explore potential biases in studies trying to find biological correlates of climatic niches. First, we verified that OUp is discernible from BM and OU and that parameters (rate of evolution σ^2 and selection strength α) were correctly estimated (see app. E). We then asked how mis-specifying the underlying model of climatic niche evolution might affect conclusions regarding correlation estimates. Using the phylogenetic trees obtained from each NBT simulation, (i) we simulated the evolution of another niche-related trait (Y) evolving independently from the climatic niche under an OUp model ($\sigma^2 = 1$, $0.05 \leq \alpha \leq 0.9$) and estimated the correlation (Type I error) between this trait and the observed climatic niche from the NBT simulations using phylogenetic generalized least squares (Grafen 1989) assuming the various models of evolution specified above

(OUp, BM, OU, KAPPA, WN, and Pagel's λ); and (ii) we simulated a second niche-related trait as $Y = \text{niche} + \varepsilon$, where ε evolved under an OUp model, and here examined Type II error by fitting the same set of comparative models.

All analyses were run in R (R Development Core Team 2012), using packages ape (Paradis et al. 2004), caper (<http://cran.r-project.org/web/packages/caper>), geiger (Harmon et al. 2008), and phytools (Revell 2012).

Results

The two modes of speciation yielded slightly different biogeographic patterns (fig. 1). Under point mutation, many very rare species were produced (on average the least abundant species occupied 1.3 pixels out of 1,071 in the landscape), and the resulting phylogenetic trees were highly unbalanced (see app. G). In contrast, vicariance produced fewer rare species (the least abundant occupied on average 5.9 pixels), leading to more balanced phylogenetic trees (see app. G). However, phylogenetic tree shape did not seem to influence strongly our results: although phylogenetic signal was positively correlated with imbalance, this explained only little variance across simulations ($R^2 = 0.24$ for point mutation and $R^2 = 0.09$ for vicariance). In nearly all simulations (3,603 out of 3,612), the metacommunity was at carrying capacity by the end of the simulation, meaning that the boundaries of the landscape had been reached and that each local community was saturated with individuals. The number of extant species ranged between 2 and 952, with mean = 107.8, depending on birth rate and speciation mode.

Patterns of Climatic Niche Evolution

Simulations yielded values of phylogenetic signal in climatic niche ranging from $\lambda = 0$ (no signal) to $\lambda = 1$ (equal to BM expectations), covering the range of values reported in empirical studies (app. C). Both speciation modes showed the same qualitative pattern: phylogenetic signal was moderate for low rates of both birth and migration, generally increasing with birth rate and decreasing with migration rate (table 1).

Under both modes of speciation, climatic niche evolution tended to be largely punctual ($\kappa_{\text{mean}} = 0.32 \pm 0.16$ for point mutation and $\kappa_{\text{mean}} = 0.23 \pm 0.12$ for vicariance), suggesting niche stasis along branches of the tree and fast niche evolution during cladogenesis. This pattern is well illustrated by the traitgrams in figure 2, which show shifts in climatic niches occurring at speciation.

Table 1: Dependency of phylogenetic signal on migration and speciation rates

	Point mutation	Vicariance
Intercept	.69 ($P < 2E-16$)	.87 ($P < 2E-16$)
Migration rate	-.83 ($P < 2E-16$)	-.98 ($P < 2E-16$)
Speciation rate	2.16E3 ($P < 2E-16$)	1.26E4 ($P < 2E-16$)
Migration \times speciation	548 ($P = .26$)	2.64E4 ($P < 2E-16$)
Number of simulations	1,402	2,210
Adjusted R^2	.49	.63

Note: For both speciation modes, we explored the effect of model parameters (migration, speciation rates, and their interaction) using a linear model. The number of simulations for each model and the goodness-of-fit of the model are also reported. Note that values of speciation rate were 10 times smaller for vicariance than for point mutation, which explains the 10-fold differences in the coefficients between the two models. Models with quadratic terms were also fitted but were rejected due to higher Akaike Information Criterion scores.

Process of Climatic Niche Evolution

The process of niche evolution did not strongly depend on the mode and rate of speciation but was highly influenced by migration rate. For both speciation modes, Brownian motion was often the worst-fit model (app. D, $\Delta AIC_c > 11$ in comparison with all other models on average over all simulations). Overall, models including some degree of punctuationalism had a better fit to the data (app. D; $\Delta AIC_{c_{BM-KAPPA}} = 118.4$ and $\Delta AIC_{c_{OU-OUp}} = 36.07$, on average). KAPPA was the best model for low migration rates (fig. 3), but when migration was higher, constraints on niche evolution were detected and an Ornstein-Uhlenbeck model with strict punctuationalism (OU_p) had the best fit (fig. 3; see also fig. 2B). The strength of selection estimated in the OU_p model (α) increased with migration rate ($P < 2E^{-16}$ for both speciation modes). In simulations where OU_p had the best fit, α ranged from $2E^{-9}$ to 1.26 (mean = 0.31) for point mutation and from 0.06 to 0.91 (mean = 0.32) for the vicariance model (although these values might be underestimated due to extinction; see app. E). A nonphylogenetic model (white noise) was sometimes preferred for very low birth rates and high migration (fig. 3), which generally produced trees with fewer than 10 species.

When using real climatic landscapes from six mountainous regions of the world, results supported even more strongly the OU_p model, which appeared to have the best fit even for low migration rates (fig. B2; figs. B1–B4, D1, E1, E2, F1 available online).

Potential Biases in the Analysis of Trait-Climate Relationships

Type I error in tests of the correlation between the two niche-related traits (Y and the niche from our simulations) were high (>30%) when either the BM or an OU model was assumed to describe the evolution of the residuals of this relationship (table 2). In contrast, specifying the true

evolutionary model under which residuals evolved, OU_p, dramatically reduced Type I errors (table 2). Transforming the phylogenetic covariances matrix using the maximum likelihood estimate of Pagel's λ also improved Type I errors, but perhaps most surprisingly, even a model of no phylogenetic structure (i.e., WN) was vastly superior to both the BM and OU models. Type II error was very low (0.3%) when using the correct OU_p model, whereas for all other evolutionary models, the true correlation between Y and the niche very often remained undetected (Type II error rate >20% for all other models).

Discussion

Phylogenetically informed comparative analyses are increasingly being used to investigate the evolution of climatic niches, yet there has been little appreciation that common measures such as the mean position of species across a climatic gradient might arise from purely neutral biogeographic processes. The role of biogeography has thus been largely overlooked in the literature on niche evolution and conservatism (but see Freckleton and Jetz 2009). Here, we show that a simple neutral model of biogeography, in which species spread and speciate independently of climate, can generate varying patterns of climatic niche evolution, depending on speciation mode, migration rate, and speciation rate. Our analysis reveals several major features of climatic niche evolution relevant for comparative analysis and the study of PNC. These results caution against the overuse of traditional phylogenetic signal metrics and macroevolutionary tests assuming BM as the neutral expectation to investigate climatic niche evolution.

Migration Rate and Phylogenetic Signal in Climatic Niches

Phylogenetic signal remains a commonly used measure in macroevolutionary studies of climatic niche evolution

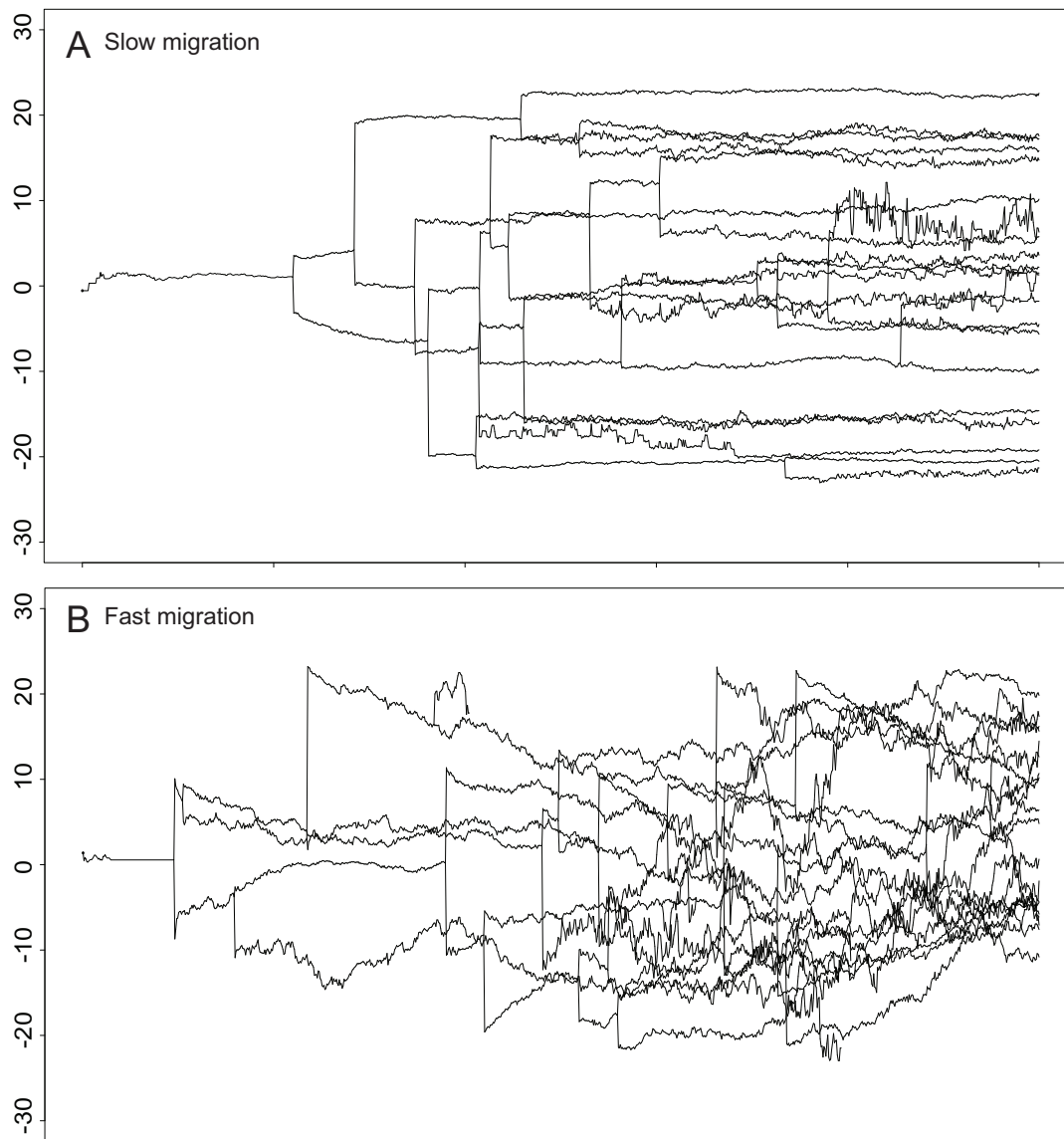


Figure 2: Evolution of the mean climatic niche in the vicariance model. Each traitgram (time on the X-axis, mean climatic niche on the Y-axis) illustrates the temporal process of climatic niche evolution during $2.5E^7$ steps in simulations under the vicariance model. *A*, For low migration rates (here $m = 0.01$), almost all evolution happens at speciation. *B*, For high migration rates (here $m = 0.9$), niche shifts also occur at speciation, but mean niches tend to be pulled back toward the average climate of the landscape.

(e.g., Hof et al. 2010; Olalla-Tarraga et al. 2011) in spite of recent warnings concerning its interpretation in the context of niche conservatism (Revell et al. 2008). In particular, low signal is often interpreted as evidence for rapid evolution (e.g., Losos 2008). Here, we have demonstrated that even under a neutral model of biogeography, phylogenetic signal in climatic niches can take a wide range of values. Nonetheless, we show that signal is related to evolutionary processes. In our simulations, migration strongly decreases phylogenetic signal under both speci-

ation modes examined here. We also found that phylogenetic signal increased with the per capita speciation rate, likely reflecting the shorter time available for migration between speciation events and perhaps also the higher power of λ on large trees (Münkemüller et al. 2012).

Therefore, we suggest that the phylogenetic signal in climatic niches observed in empirical studies could reflect more the history of species migration rather than the mode of evolution of physiological traits related to climatic tolerances. Empirical observations support this view both in

mammals (Freckleton and Jetz 2009) and birds, where clades of sedentary birds have been shown to exhibit much higher phylogenetic signal in many climatic variables than clades composed of migratory species (Jetz et al. 2008; app. C).

Geographic Speciation Leads to Punctuated Niche Evolution

The two speciation modes examined in our model result in daughter species inheriting different geographic distributions at speciation. Under point mutation, one of the two daughter species is restricted to only one location whereas its sister often has a larger range, while in the vicariance model both daughter species have by definition nonoverlapping ranges immediately after speciation. This range disjunction between sister species directly translates into a difference in their mean climatic niches (fig. 2). Whatever the spatial distribution of climate, model comparisons favored a punctuated mode of niche evolution over gradualist models, such as BM, which are typically assumed in most phylogenetic comparative methods (fig. B2, app. D). Even though our simulations are simplistic,

Table 2: Detection of correlated evolution under the OUp model

	WN (%)	BM (%)	λ (%)	KAPPA (%)	OU (%)	OUp (%)
Type I error rate	4.8	46.0	5.2	8.4	30.5	5.6
Type II error rate	37.2	21.4	30.2	20.6	24.8	.3

Note: Five different macroevolutionary models classically used in comparative analyses were confronted to the OUp model to test a relation between a trait Y and the niche. First, Y was simulated to be independent of the niche values but following an OUp model, and the Type I error rate was assessed by recording the percentage of simulations where a false correlation was detected at the 5% level. Similarly, Type II error rates were estimated as the proportion of existing correlations that remained undetected at the 5% level when Y was simulated to be linearly correlated to niche values assuming an OUp model of evolution for the residuals. See “Comparison to Macroevolutionary Models” for definitions.

we believe that this conclusion tends to be generally true. Indeed, empirical and theoretical studies support the idea that speciation often involves some degree of geographic isolation (Coyne and Orr 2004), even in cases where speciation is ecological (Nosil 2012). Given that climate always exhibits a strong spatial structure, we suggest that speciation will almost always produce sister species with different mean climatic niches. However, this initial diver-

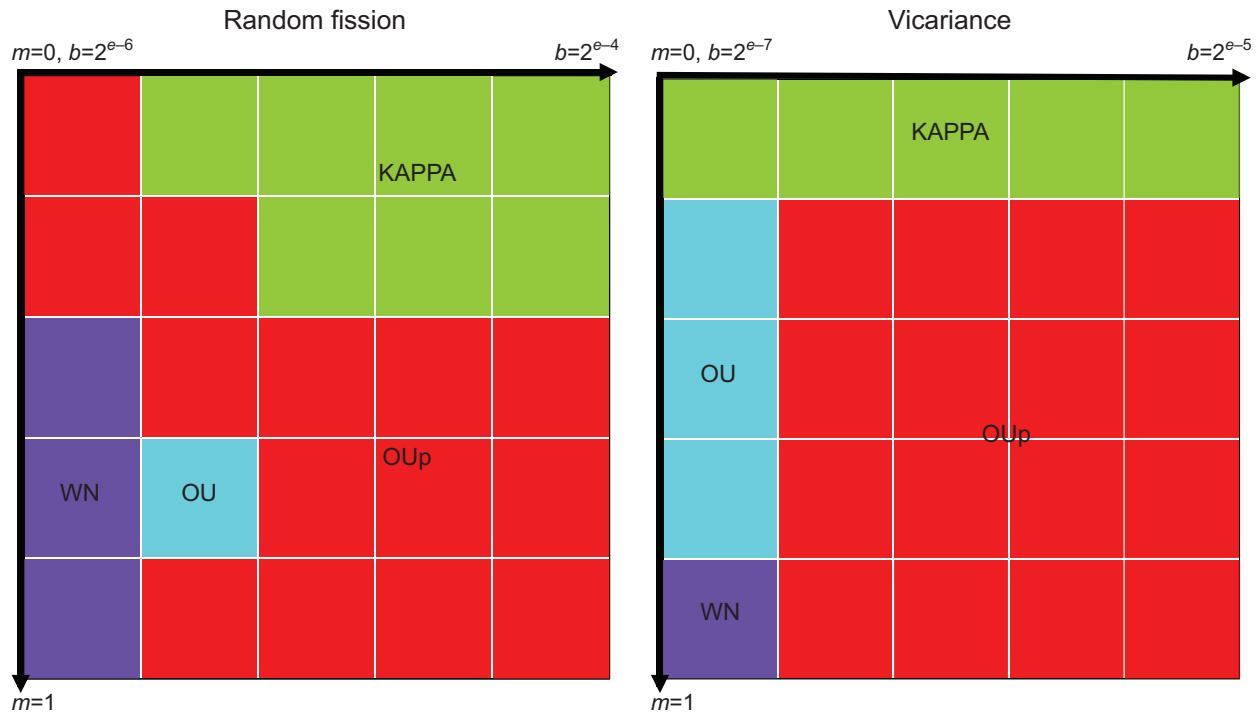


Figure 3: Comparison of NBT models to macroevolutionary models. For both speciation modes, the parameter values for migration and speciation rate are divided in five equal classes. In each of the 25 resulting cells, the model with the highest corrected Akaike Information Criterion weight on average over all simulations with the corresponding parameters is represented. See appendix D (available online) for boxplots illustrating model comparison in each corner of the parameter space. Data underlying figure 3 are deposited in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.nf591> (Boucher et al. 2013).

gence implies no evolutionary change in physiology or ecology, it could simply be a by-product of geographic separation. Punctuated evolution of climatic niches has indeed already been detected in alpine plants of the genus *Androsace* (Boucher et al. 2012), and niche shifts have been triggered by speciation following long-distance dispersal in the genus *Hordeum* (Jakob et al. 2010). Our results imply that evidence for punctuated evolution of climatic niches should not be directly interpreted as evidence for rapid evolution of physiological tolerances and even less as support for divergent selection on climatic attributes driving speciation. Indeed, physiological tolerances may remain unchanged even in the presence of apparent rapid change in the climatic niche.

Landscape Boundaries Create “Artifactual” Niche Conservatism

When comparing alternative models of niche evolution we found strong support for models that include a constraint (either OU or OUp) when migration was high. Under this scenario, regardless of the speciation mode, individuals move fast and therefore soon reach the borders of the landscape. This scenario approximates bounded Brownian motion and leads the mean climatic niches of species to be pulled back to the mean climate of the continent, thus producing outcomes similar to expectations of an OU process (Revell et al. 2008). Although our simulations are not able to represent the actual size and age of empirical meta-communities, we expect that OU models will be favored when the landscape is small, the clade is old, and the migration rate is high (see app. A for more details). Furthermore, even when climate was not simulated according to a latitudinal gradient but rather taken from real, spatially autocorrelated landscapes, OU and OUp had still the best fit, even for relatively low migration rates. The OU process was initially applied to macroevolution to model adaptive evolution toward a given selective optima (Hansen 1997; Butler and King 2004) and is often interpreted as evidence for PNC (Wiens et al. 2010). However, our simulations favor an OU model even in the absence of selection. We follow Crisp and Cook (2012) in considering that such processes represent indirect causes that lead to “artifactual” PNC, that is, conservatism that is not a consequence of demo-genetic processes (Holt 1996).

To illustrate this point, we ran comparative analyses on *Diprotodontia*, a mammalian order that is restricted to Australia and Tasmania (app. F). We found that the best model depicting the phylogenetic patterns of their climatic niches was OUp. This case study demonstrates that BM can be easily rejected. Previously, we might have considered rejection of the BM model sufficient to conclude support for physiological constraints in *Diprotodontia* (i.e.,

niche conservatism), our simulations illustrate that this would be erroneous since the insular history of this clade alone could have created this pattern. Caution should then be taken when interpreting support for OU models for climatic niches in the absence of clear biological evidence for physiological constraints on species niches or stabilizing selection on some key ecological attributes. Indeed, it has already been shown that parameter estimates in OU models are often incompatible with the underlying quantitative genetic model of stabilizing selection (Revell et al. 2008; Harmon et al. 2010), and in addition, our study shows that similar patterns can arise through the migration of individuals in a bounded landscape with competition for space.

Which Model to Choose for Climatic Niche Evolution?

Our results indicate that BM does not appropriately describe patterns of climatic niche evolution under a neutral model of biogeography because it fails to capture the punctuated and bounded nature of niche evolution. This limitation may be important because BM is often used in comparative studies either a priori as the default evolutionary model (e.g., Barnagaud et al. 2012; Pyron and Burbrink 2012) or because its few parameters make it likely to be favored over more complex models when the data contain insufficient information (Boettiger et al. 2012). In particular, assuming BM as the underlying model of niche evolution may lead to inflated Type I and Type II errors in tests of correlations between climate-related traits (table 2). Our results suggest that a punctuated and/or bounded evolutionary model (i.e., OUp) might be more appropriate than BM for describing neutral climatic niche evolution and that such models should be routinely included in comparative studies of niche evolution.

Limitations of Our Approach and Future Directions

This study represents a first step toward a more mechanistic approach for the study of PNC, and we are aware of several of its limitations. First, our results strongly supporting a model of punctuated niche evolution reflect our modeling of speciation as an instantaneous process. Although this assumption may be more or less accurate when viewed over geological timescales (Coyne and Orr 2004), simulations considering more subtle and process-informed speciation models (e.g., Desjardins-Proulx and Gravel 2012) would be needed to test the generality of punctationism in niche evolution. Second, a different approach to simulating climate niches needs to be explored. While we have shown that our conclusions are robust to various modifications of the landscape (app. B), our assumptions on fundamental niches were deliberately simplistic. Our

goal here was especially to simulate climatic niche evolution resulting from purely neutral dynamics where realized species' niches are a product of dispersal and competition for space. We assumed that the physiological tolerances of species (i.e., their fundamental niches) were broad enough for individuals to occupy the whole landscape. Analytical results suggest that the pattern of strong punctuationalism and bounded evolution would not be qualitatively modified if fundamental niches were narrower but slowly evolved by diffusion (i.e., progressive adaptation to climates located at the range margins; see app. A). However, this represents just one of many possible scenarios for the evolution of fundamental niches, and we acknowledge that alternative evolutionary models could potentially modify our results. For example, a scenario in which fundamental niches evolve so that each species becomes a strict specialist for a given latitudinal band would give different results, and in this case, migration and ecological drift would not influence the realized niche of species. Simulations in which the fundamental niche also evolves and influences individual fitness, while dispersal and ecological drift determine the realized niche of species, might provide a step toward more realism. However, this would require assumptions on the way fundamental niches evolve, a topic on which very little research has been conducted (but see Kellermann et al. 2012).

We have shown how different processes (e.g., dispersal limitations and stabilizing selection) can lead to similar macroevolutionary patterns (e.g., PNC), thereby confirming previous claims that inferring processes from phylogenetic patterns can be challenging (Losos 2011). The search for potential factors or traits triggering or impeding climatic niche evolution may require additional information on species' ecology and physiology (e.g., including information on life form to study the evolution toward cold niches in *Androsace* plants; Boucher et al. 2012). Fortunately, methods exist to fit flexible models with varying rates of evolution, strengths of selection, and niche optima for different lineages depending on their biological characteristics (Beaulieu et al. 2012).

Conclusion

We do not suggest that the evolution of the climatic niche is solely driven by geographic processes; rather we simply demonstrate that common approaches to studying climatic niche evolution can be affected by the geographic context in which a clade has evolved. Although our simulations may be relatively simplistic, we show that neutral models of biogeography produce very different outcomes than a commonly assumed neutral model of macroevolution (i.e., Brownian motion). We therefore suggest that punctuated and bounded models (e.g., OUp) rather than Brownian

motion should be preferentially assumed as neutral models of climatic niche evolution. Such neutral models might constitute a reasonable first-order approximation for the evolution of realized climatic niches on which more elaborate models could be based. Critically, detecting the imprint of nonneutral ecological and evolutionary processes on the evolution of climatic niches will require additional information, for example, phenotypic traits directly linked to physiological tolerances.

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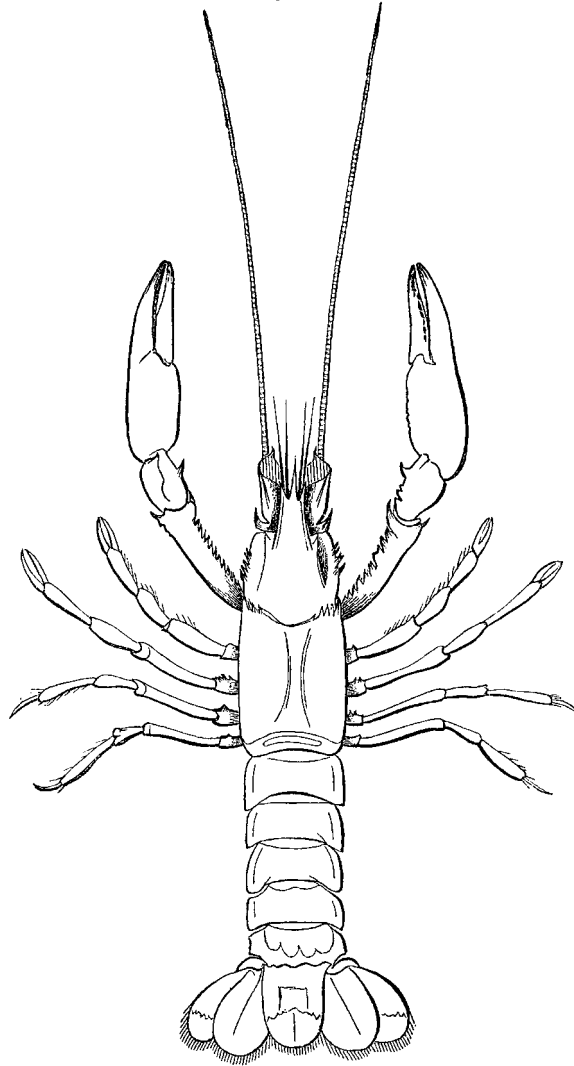
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Fig. 131.



Cambarus pellucidus.

“Next to the blind fish, the blind crawfish attracts the attention of visitors to the cave. This is the *Cambarus pellucidus* (Fig. 131, from Hagen’s monograph of the North American Astacidæ) first described by Dr. Tellkamp. He remarks that ‘the eyes are rudimentary in the adults, but are larger in the young.’” From “The Mammoth Cave and Its Inhabitants” by A. S. Packard Jr. (*The American Naturalist*, 1871, 5:739–761).