

Phylogenetic niche conservatism and the evolutionary basis of ecological speciation

R. Alexander Pyron^{1,*}, Gabriel C. Costa², Michael A. Patten^{3,4} and Frank T. Burbrink^{5,6}

¹*Department of Biological Sciences, The George Washington University, 2023 G Street NW, Washington, DC 20052, U.S.A.*

²*Departamento de Ecologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Campus Universitário Lagoa Nova, Natal, 59072-970, Rio Grande do Norte Brazil*

³*Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, OK 73019, U.S.A.*

⁴*Department of Biology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019, U.S.A.*

⁵*Department of Biology, The Graduate School and University Center, The City University of New York, 365 5th Avenue, New York, NY 10016, U.S.A.*

⁶*Department of Biology, The College of Staten Island, The City University of New York, 2800 Victory Boulevard, Staten Island, NY 10314, U.S.A.*

ABSTRACT

Phylogenetic niche conservatism (PNC) typically refers to the tendency of closely related species to be more similar to each other in terms of niche than they are to more distant relatives. This has been implicated as a potential driving force in speciation and other species-richness patterns, such as latitudinal gradients. However, PNC has not been very well defined in most previous studies. Is it a pattern or a process? What are the underlying endogenous (e.g. genetic) and exogenous (e.g. ecological) factors that cause niches to be conserved? What degree of similarity is necessary to qualify as PNC? Is it possible for the evolutionary processes causing niches to be conserved to also result in niche divergence in different habitats? Here, we revisit these questions, codifying a theoretical and operational definition of PNC as a mechanistic evolutionary process resulting from several factors. We frame this both from a macroevolutionary and population-genetic perspective. We discuss how different axes of physical (e.g. geographic) and environmental (e.g. climatic) heterogeneity interact with the fundamental process of PNC to produce different outcomes of ecological speciation. We also review tests for PNC, and suggest ways that these could be improved or better utilized in future studies. Ultimately, PNC as a process has a well-defined mechanistic basis in organisms, and future studies investigating ecological speciation would be well served to consider this, and frame hypothesis testing in terms of the processes and expected patterns described herein. The process of PNC may lead to patterns where niches are conserved (more similar than expected), constrained (divergent within a limited subset of available niches), or divergent (less similar than expected), based on degree of phylogenetic relatedness between species.

Key words: phylogenetic niche conservatism, ecological speciation, allopatry, niche divergence, canalization, evolutionary constraint.

CONTENTS

I. Introduction	1249
II. The pattern and process of PNC	1251
(1) PNC as a process	1251
(2) PNC as a pattern	1255
(a) Low physical and environmental heterogeneity	1255
(b) Low physical heterogeneity and high environmental heterogeneity	1255
(c) High physical heterogeneity and low environmental heterogeneity	1255
(d) High physical and environmental heterogeneity	1255
(e) Summary	1256

* Address for correspondence (Tel: 202-994-6616; E-mail: rpyron@colubroid.org).

(3) Genetic variation and niche divergence	1256
(4) Tests for PNC	1257
III. Future directions	1258
IV. Conclusions	1259
V. Acknowledgements	1259
VI. References	1260

I. INTRODUCTION

Phylogenetic niche conservatism (PNC; Harvey & Pagel, 1991) is typically defined as the tendency for lineages to retain ancestral ecological characteristics over time (Holt & Gaines, 1992; Ricklefs & Latham, 1992; Peterson, Soberon & Sanchez-Cordero, 1999; Prinzing, 2001; Wiens & Graham, 2005). It is the notion that some biological process constrains niche divergence between closely related species, and therefore constrains populations from expanding into new niches (Losos, 2008a). Recent work highlights the significance of PNC as an important principle in several areas of ecology and evolution (Wiens *et al.*, 2010; Peterson, 2011a; Condamine *et al.*, 2012; Stegen, Ferriere & Enquist, 2012). For example, PNC may explain species-richness patterns, including latitudinal gradients and community diversity (Ricklefs & Latham, 1992; Wiens *et al.*, 2007; Pyron & Burbrink, 2009a; Buckley *et al.*, 2010; Stevens, 2011; Wiens, Pyron & Moen, 2011; Rosser *et al.*, 2012). The presence of PNC is also a key (but often unacknowledged) assumption in many forms of species distribution modelling (Elith & Leathwick, 2009; Peterson, 2011b). Understanding PNC may help predict the impact of climate change on adaptation to novel environments as niches shift through time and space (Sinervo *et al.*, 2010; Roberts & Hamann, 2012).

The focus of this review is to distinguish between the pattern and process of PNC as it relates to speciation. Confusingly, the term PNC is often used to describe both a pattern of high niche similarity in related species, and a process comprising the evolutionary mechanisms responsible for that similarity (Losos, 2008a,b; Wiens, 2008). As a measurement of this pattern (high-similarity ecological niches between related species), a simple null model of Brownian Motion evolution produces a phylogenetic signal of closely related species having more similar traits than distantly related species (Revell, Harmon & Collar, 2008). Thus, a main question is how similar do niches need to be to qualify as conserved (the pattern of PNC)?

By contrast, if PNC is a process (a biological mechanism promoting active retention of niche characteristics *via* selection), then how do the mechanisms responsible for this similarity promote speciation by constraining niche evolution? What patterns do this process generate, and what patterns do processes which are categorized as 'niche conservatism' generate? We recognize that all niche-related traits will be divergent in some ways and conserved in others. The geography of speciation and the mechanisms of evolutionary heritability ensure that there will be at least some similarity between newly diverged species. We thus wish to

examine explicitly the interaction between niche evolution and speciation to ask: 'how do evolutionary processes that conserve niche-related traits affect ecological patterns of lineage divergence?'

The 'niche' is defined as the set of conditions in which a population can persist (Grinnell, 1917; Hutchinson, 1957). Detailed definitions and discussions of the meaning of the niche have been reviewed extensively elsewhere (Chase & Leibold, 2003; Soberón, 2007; Soberón & Nakamura, 2009). At a basic level, niches can be divided into two broad categories depending on the characteristics of variables being analysed (Hutchinson, 1978). The Grinnellian niche is defined by the set of broad-scale environmental conditions (scenopoetic variables) a species requires to survive (temperature, precipitation, etc.). The Eltonian niche (Soberón, 2007), on the other hand, is defined by resource needs and fine-scale biotic interactions (bionomic variables). In theory, PNC concepts can apply to both kinds of niche. Traits affecting biotic interactions like co-existence or mate choice (Maan & Seehausen, 2011; HilleRisLambers *et al.*, 2012) may also be conserved by selection, but this brings in the added dimension of complexity of interactions among species. In discussion of ecological speciation, the Grinnellian niche is often more tractable in empirical studies (Peterson, 2011b), and that is what we focus on here.

Species may not fill their entire available niche space (the occupancy of the niche) due to dispersal limits, interactions with other species, or chance events (Hutchinson, 1957; Pulliam, 2000; Hurlbert & White, 2007). The niche space a species actually occupies is then a subset of the conditions it is capable of physiologically tolerating (Fig. 1). Indeed, this is often a very small subset of the conditions species can inhabit, as demonstrated in studies that show changes from native niches in recently introduced invasive species (Broennimann *et al.*, 2007; Rödder & Lötters, 2009; Gallagher *et al.*, 2010; Schulte *et al.*, 2012; Liu *et al.*, 2014) and the results of reciprocal-transplant experiments (Hargreaves, Samis & Eckert, 2014). To characterize ecological niches completely, precise information on physiological limits (scenopoetic) and resource-use interactions (bionomic) is necessary. Given the difficulty of obtaining these data, most studies involving Grinnellian niches rely on measurement of climatic variables from observations of occupied niche space (Peterson & Vieglais, 2001; Peterson, 2003; Pearson & Dawson, 2003; Kozak, Graham & Wiens, 2008; Soberón & Nakamura, 2009).

We suggest further that it will be helpful, at least in the context of this discussion, to examine the environmental conditions within the geographical context where species

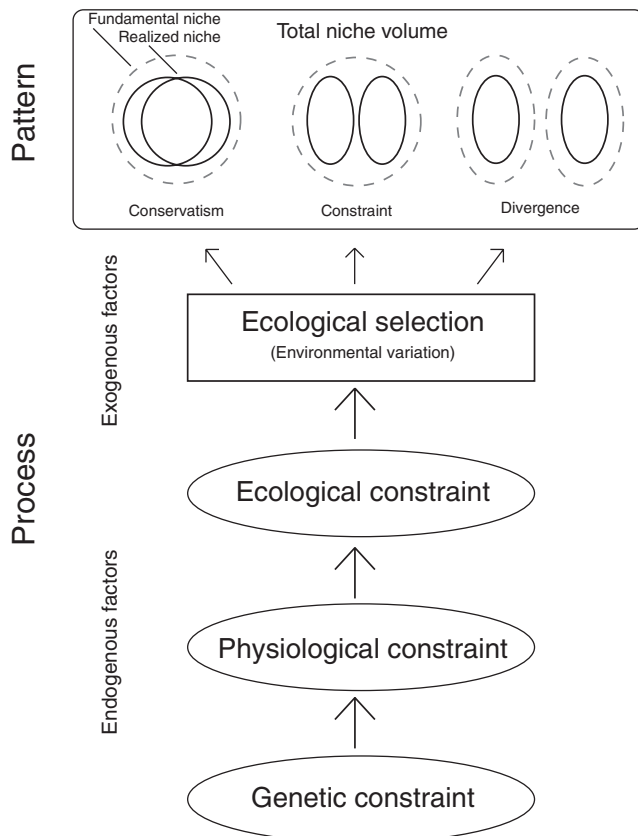


Fig. 1. Illustration of the evolutionary origin and ecological consequences of phylogenetic niche conservatism (PNC), from endogenous factors of constraint on phenotypes to the exogenous factors of ecological selection. This leads to the primary patterns of PNC, including conservatism, constraint, and divergence in niches between species.

occur (Warren, Glor & Turelli, 2008; Glor & Warren, 2011; Broennimann *et al.*, 2012): the potential range of environmental conditions which species are actually capable of occupying (Fig. 1). For example, the whole set of conditions a species is physiologically capable of tolerating may include temperatures that do not occur on the landmass inhabited by that species; there is thus a local and global set of suitable environmental conditions (Peterson, 2011a). Therefore, the niche space the species occupies will be a subset of the local conditions (Fig. 1). This was discussed by previous authors (Peterson, 2011a), referred to as a 'movement' axis which limits occupancy of the potential distribution comprising the intersection between the abiotic and biotic niches.

By any of these definitions, the niche will inevitably bear some similarity from ancestor to descendant through time, and related species often have similar ecological profiles (Losos, 2008a), which has been noted by numerous authors for over 150 years (reviewed by Wiens & Graham, 2005). Given that PNC can occur at some strength across multiple phylogenetic scales, we would expect that even when multiple closely related species are bound within a single clade-level fundamental niche, they may still be free to vary more

widely within it (Holt, 2009), which we refer to as 'niche constraint' rather than conservatism (Fig. 1). In the broad sense, the aquatic niche of fish has been conserved for hundreds of millions of years, but this tells us nothing about the finer-scale processes that lead to ecological speciation in African rift-lake cichlids that occur in lakes only a few million years old (Seehausen, 2006).

If traits are not under strong selection, then PNC (as a pattern of niche similarity) may arise simply *via* 'evolutionary inertia,' and divergence in niches and traits from drift. This may be particularly true if the timescale for divergence by drift is longer than that for the origin of the species under investigation, as in rapid evolutionary radiations where speciation occurs because of selection on a non-ecological trait such as sexually selected phenotypes (Wagner, Harmon & Seehausen, 2012). Thus, most discussions of PNC invoke evolutionary mechanisms beyond inertia and drift for how traits, and more specifically, ecological niches and climatic traits might be conserved through time (Blomberg & Garland, 2002; Losos, 2008a).

Conservatism can be observed in any trait, although PNC is usually interpreted as the similarity of ecological niches in related species over recent evolutionary timescales (Ricklefs & Latham, 1992; Peterson *et al.*, 1999). Generally, PNC could occur at any phylogenetic scale (Hadly, Spaeth & Li, 2009; Holt, 2009), but it is typically examined in terms of species and speciation processes (Wiens, 2004). When conservatism of ecological niches results in allopatric divergence in ecologically similar patches of geographically distant habitat, PNC is thought to be a major mechanism of speciation. Thus, species will track their ancestral niches spatially, resulting in interrupted gene flow between populations that have been separated geographically (Peterson *et al.*, 1999; Wiens, 2004; Kozak & Wiens, 2006; Peterson & Nyari, 2008; Pyron & Burbrink, 2009b; McCormack, Zellmer & Knowles, 2010).

We are also interested in the less-obvious role of PNC in ecological speciation, defined as the separation of lineages as a result of ecologically mediated divergent selection on standing genetic variation in populations (Schluter, 2001; Nosil, Harmon & Seehausen, 2009; Schluter & Conte, 2009). Ecological differentiation among related species is common, occurring significantly in 74% of surveyed cases in a recent review (Sexton, Hangartner & Hoffmann, 2014). The absolute case of ecological speciation is one in which lineages do not experience ecological selection for stasis in their current niche, PNC therefore does not occur, and species immediately track changing environments. Thus, populations in different areas experiencing ecological shifts in different directions or of different magnitudes are quickly separated geographically, leading to rapid ecological divergence and speciation.

Nevertheless, PNC may influence ecological speciation in changing ecological environments if species track favourable ecological niches through time that slowly diverge from the ancestral niche (Ackerly, 2003; Kozak & Wiens, 2006). Such a process of local adaptation is posited as a key cause of subspecific differentiation (Belliere *et al.*, 2000). In a

changing environment, any force (e.g. stabilizing selection, genetic canalization) that promotes retention of ancestral niche characteristics (i.e. PNC) may actually enhance niche divergence due to increased adaptation to the local environment that most closely resembles the ancestral niche (i.e. the available niche with the highest fitness). If two allopatric populations experience different available ecological conditions, the closest analogue of the ancestral niche may be different for the two populations. Thus, the process of PNC may lead them to adapt to what are ultimately divergent ecological niches (Warren *et al.*, 2008).

This becomes evident when one considers that it is not the ‘ancestral’ niche *per se* that is being retained, but the instantaneous niche (see Section II.1). Thus, if populations are experiencing rapid ecological change, selection for stasis in their current niche (PNC) may actually result in more rapid niche divergence as the availability of the current niche is consistently shifting away from the ancestral niche (Figs 1–4). If two allopatric populations experience different environmental conditions, the closest analogue of the ancestral niche may be different in the different environments. As a result, the two populations will experience different paths of tracking the ‘ancestral’ niche (i.e. the ‘instantaneous’ niche), and therefore could present a pattern of niche divergence when compared to each other and the ancestral condition.

The patterns (ecological similarity) and processes (ecological constraint) typically defined as PNC may arise at different phylogenetic scales for entirely different reasons and under entirely different conditions. Distinguishing between PNC as a pattern and process (and the mechanisms responsible) is crucial for evaluating historical evolutionary scenarios (Wiens *et al.*, 2010). In order for PNC to be considered a process driving observed patterns (Losos, 2008a), one must show higher similarity than expected from null models of drift, as might be expected under a model of ecological speciation in the absence of PNC.

Several mechanisms have been proposed for the maintenance of this similarity (PNC as a process), including stabilizing selection, where individuals preserving ancestral niche properties are favoured (Holt & Barfield, 2008), gene flow swamping local adaptation where introgression from one part of a species range to another may prevent adaptations in niche traits to new habitats (Sexton *et al.*, 2009), pleiotropic constraints on adaptation where a gene that allows niche expansion is linked with a gene that reduces fitness (Etterson & Shaw, 2001), and lack of standing genetic variation (Wiens & Graham, 2005; Saltz & Nuzhdin, 2014). Any of these may lead to failure to adapt (Futuyma, 2010), causing lineages to maintain the status quo in their ecological niches, and a tendency for sister species to inhabit highly similar ecological niches. The process of ecological constraint is a primary driver of PNC as an evolutionary mechanism. At the species level, the tendency to maintain a given niche (Tingley *et al.*, 2009) may lead to allopatric divergence if a population is divided among multiple ecologically similar refugia due to PNC (Wiens, 2004).

This tendency for stasis could be thought of as an extension of the idea of canalization, the suppression of phenotypic variation (Wagner, Booth & Bagheri, 1997). Thus, adaptive phenotypes for a given range of novel climatic conditions may be limited either by a lack of genetic potential for evolvability, or by limited plasticity of the ecologically relevant characters. We expand on this model in a population-genetic framework below. However, this model would seem to predict a relationship between the rate of climatic-niche evolution and niche breadth, which has not been found by some authors (Fisher-Reid, Kozak & Wiens, 2012).

Finally, interpreting the pattern of PNC solely as the tendency for closely related species to exhibit similar climatic niches may obscure important mechanisms by which the process of PNC may promote speciation. Recent empirical and theoretical work has focused on the mechanisms by which speciation processes vary given different amounts of ecological and geographic heterogeneity (Kozak & Wiens, 2007; Connor *et al.*, 2010; Hua & Wiens, 2010; Pyron & Burbrink, 2010; Anacker & Strauss, 2014). Importantly, ecological niches are not coupled among independent lineages (i.e. the niche of one species does not generally depend on the niche of another species) and in many cases, PNC may promote the retention of a single ancestral niche in related species if it is equally available to them. However, lineages that experience divergent ecological selection may nonetheless experience the process of PNC, leading each lineage to retain its current niches through time, meaning that the set of lineages ultimately end up in different niches. Thus, an evolutionary process of PNC may lead to allopatric speciation bearing the pattern of niche divergence (Fig. 1) when the current niche of species begins to differ from the ancestor.

Given these ambiguities in the definition, delimitation, and interpretation of PNC, we aim to address three primary questions: (i) what is PNC (as a pattern and process); (ii) how do we identify and test for it; and (iii) how is PNC related to ecological speciation across populations? By attempting to clarify these issues, we hope to provide a more stable framework for future researchers investigating ecological speciation.

II. THE PATTERN AND PROCESS OF PNC

(1) PNC as a process

The terms ‘niche conservatism’ and ‘phylogenetic signal’ are often applied to multiple, potentially independent phenomena (Revell *et al.*, 2008), including both processes and patterns, and occasionally in a contradictory manner (Wiens & Graham, 2005; Losos, 2008a,b; Wiens, 2008). We suggest that it is also important that any definition refer to ‘lineages’ rather than species (though we are primarily interested in speciation), as any process of PNC is not limited to a particular phylogenetic scale. In the context of speciation, PNC acts on local populations to produce

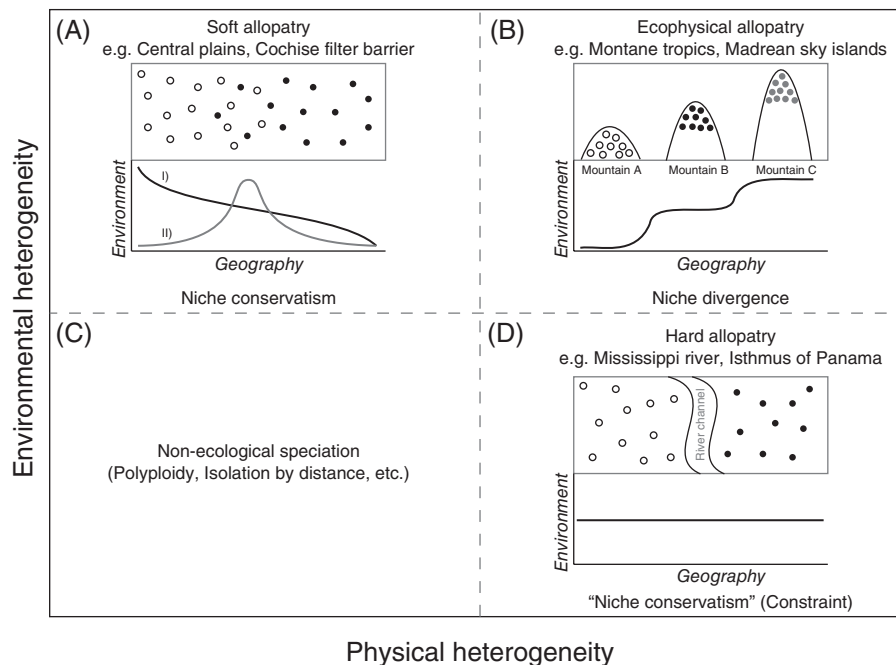


Fig. 2. Illustration of the factors that can influence speciation *via* phylogenetic niche conservatism (PNC), including axes of physical and environmental heterogeneity. Speciation events occurring at different points along these axes may result in different patterns as described above the graphs, including conservatism (A), constraint (C, D), and divergence (B) in niches between species. In (A), curve I represents an environmental variable that changes slowly from a high to low value, with populations adapted to either extreme meeting in the middle. Curve II represents two ecologically similar areas separated by an intervening higher value for a given environmental variable, with two similarly adapted populations nearing the edge of their range limits in that area.

multiple species. We suggest that the local population is thus the fundamental unit of PNC for speciation (with the individual being the unit on which evolutionary forces act), but the impact of PNC is crucial for interpreting subsequent patterns of community assembly, regional diversity, and biogeography at higher levels across the phylogeny (Ackerly, 2003; Wiens & Graham, 2005; Donoghue, 2008; Peterson, 2011a; Crisp & Cook, 2012).

We also suggest that it is important to conceive of PNC not as the retention of the ancestral niche, but of the instantaneous niche. There is no direct link to any specific ‘ancestral’ niche in a lineage (i.e. a specific time in the past); a given population comprises a discrete set of individuals with a shared niche to which they are adapted as an emergent property of the group (Rabosky & McCune, 2010), given the genetic and phenotypic variation present at a given time. The process of PNC is the tendency for that set of individuals, in the face of ecological variation, to track its current niche geographically, as closely as possible within the range of standing genetic variation (the alternative being extinction). Factors that govern the process of PNC only act on the immediate niche of a given set of individuals that form a local population. Thus, lineages will tend to maintain their current, rather than their ‘ancestral,’ niche through time, due to the action of PNC as an evolutionary process.

This is the factor that allows PNC as a process (selection for stasis in a current niche) to potentially lead to niche divergence in heterogeneous or rapidly shifting habitats,

as populations move rather than adapt (Fig. 4). It is thus actually PNC that causes populations to become allopatrically separated. Were they to adapt fully or partially to changing environments, geographic separation would be minimized, and the selection for ecological speciation would be reduced (Figs 2 and 3). Thus, the primary driver of ecological speciation, the separation of populations in ecologically disjunct geographic areas, can in many ways be interpreted as the result of PNC. This is not to say that PNC drives all patterns of speciation, but rather that certain underlying evolutionary processes may result in a broad range of patterns.

Why does PNC as an evolutionary process occur? How might these processes affect our interpretation of ecological speciation? Considering the potential factors that influence niche evolution leads to the recognition of a set of endogenous and exogenous influences leading to retention of niche characteristics through time (Figs 1–3). As noted above, previous authors have invoked four mechanisms by which instantaneous niches could be retained through time: stabilizing selection, gene flow swamping local adaptations, pleiotropic effects constraining adaptation, and lack of genetic variation. This covers much of what we term the endogenous factors that lead to PNC. These endogenous factors are those specific to the local population, and are hierarchically arranged based on their underlying cause (Fig. 1).

The ultimate root cause of PNC is genetic constraint (Futuyma, 2010); all adaptations to any ecological niche are

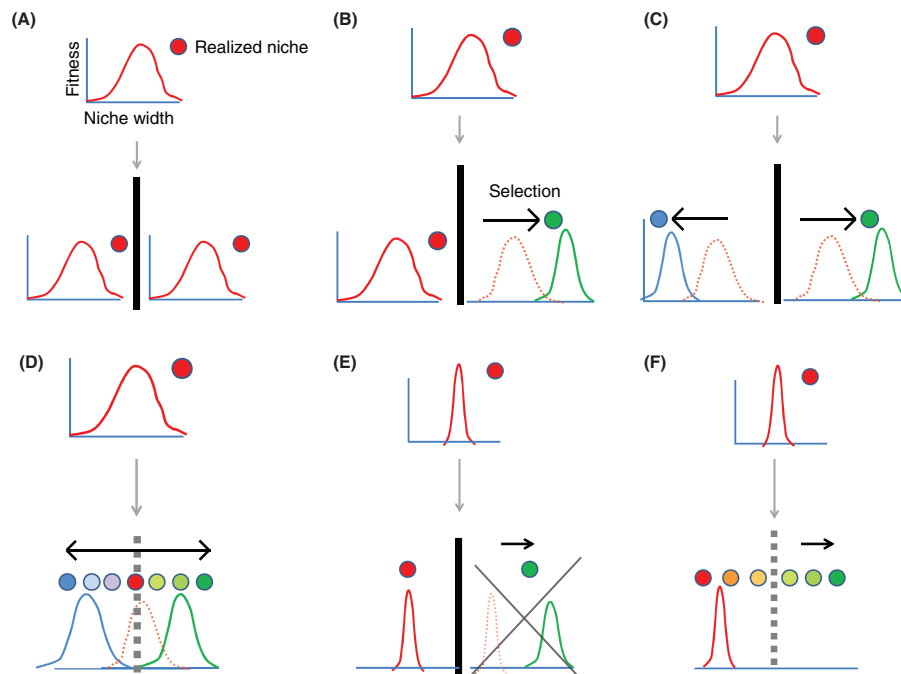


Fig. 3. Formulating the process of phylogenetic niche conservatism (PNC) in terms of standing genetic variation of the population, as measured *via* niche width. The red curve (see online version for colour) shows the initial niche width of the ancestral population (A–F), which is centered at the fitness peak (red) in the environment, and is fairly broad, including a wide range of slightly suboptimal phenotypes near the margin. The second panel of each part of the figure shows that population separated by a physical (black) or ecological (grey dotted) barrier. Selection (indicated by an arrow) can then shift towards different optima (colours), if phenotypes adapted to those optima were already present in the ancestral population. If they were not (narrow ancestral population), then the population will either go extinct (E), or remain in the ancestral niche (F). Note that (A), (E), and (F), would all qualify as a pattern of ‘niche conservatism,’ while (B), (C), and (D) would typically be interpreted as ‘niche divergence.’

predicated on the existence of genetic variation sufficient for the evolution of traits necessary to persist in that niche. Similarly, physiological or developmental constraints, even in the presence of sufficient genetic variation, may limit adaptation or the expression of various traits (Beldade, Koops & Brakefield, 2002). Finally, ecological constraints, such as the impacts of biotic interactions (Hatchwell & Komdeur, 2000), or ecological limitations on dispersal and gene flow that prevent or swamp adaptation (Kirkpatrick & Barton, 1997), may lead to the retention of current niche characteristics. These have been referred to as the ‘easier to move than to evolve’ principle (Donoghue, 2008). These are also the primary mechanistic factors by which PNC as a process would arise in natural populations, as adaptation to novel environmental conditions lags behind the pace of ecological change, resulting in a selective advantage for individuals maintaining the closest analogue of the current niche.

This process could also be viewed from the perspective of extinction as the operative force (Waldron, 2010). Populations exceeding their habitable niche go extinct due to selection on individuals (Kirkpatrick & Barton, 1997). Thus, the greatest selective advantage is derived from inhabiting the niche with the largest area supporting the largest population size. Ecological pressures subdividing this niche inherently decrease area and population size, increasing the probability

of stochastic extinction of the resulting lineages. This is compounded by ecological selection arising if the niches are shifting away from their ancestral values (Warren *et al.*, 2008; Pyron & Burbrink, 2009b). This would also require rates of climatic-niche evolution to exceed the magnitude of the combined extinction pressures resulting from smaller geographic areas, smaller population sizes, and ecological selection. Such a scenario has been suggested as a major driver of speciation, particularly in montane habitats, where increased rates of climatic-niche evolution are associated with increased diversification rates (Kozak & Wiens, 2010a). This could occur both due to decreased extinction (due to a larger environmental space available for populations), and increased speciation (due to increased rates of population subdivision).

The exogenous factors that lead to PNC as a process are thus the broad category of mechanisms collected under the umbrella of selection arising from ecological variation, including both environmental and geographic heterogeneity, in the physical environment of a local population. In the absence of ecological variation, all species would occupy similar niches by default. Taking constant ecological change as given, such that the optimal habitat for a species varies continually and geographically, several outcomes are possible (Fig. 2), and the ‘move, adapt, or die’ maxim can be invoked (Fig. 3).

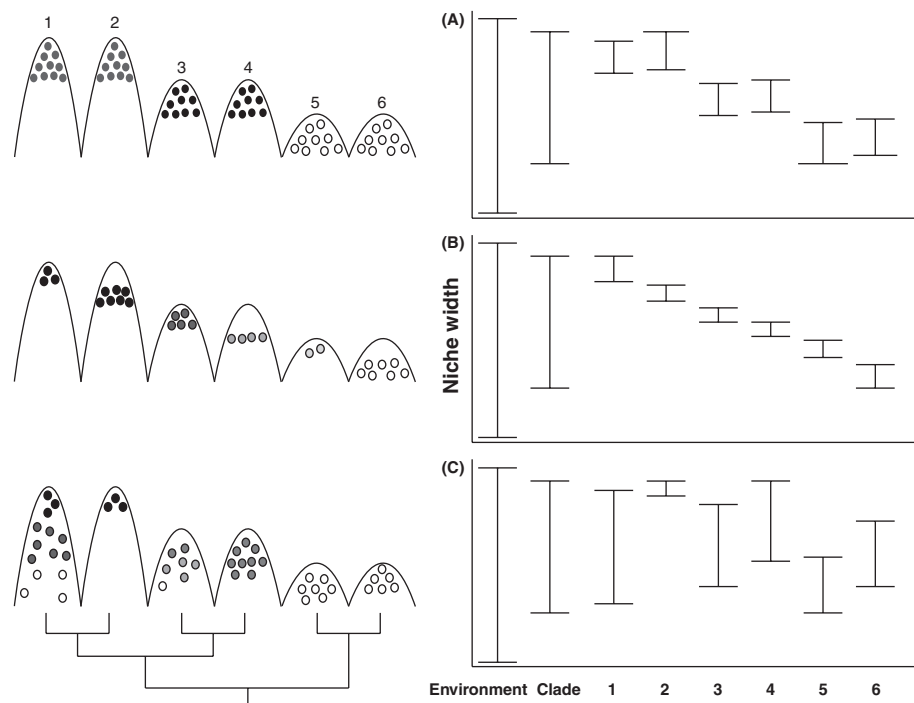


Fig. 4. Conceptual illustration of phylogenetic distributions of niches and tests for phylogenetic niche conservatism (PNC). The niche breadth of the clade (all species combined) can be calculated as a subset of the total variation that is present in the environment. Then one can ask whether sister-species pairs are more similar than expected (A) or more divergent than expected (B) under a null model of drift, which would produce random divergence between species (C). The scenario illustrated here combines high levels of physical heterogeneity (the heights of the mountains) and environmental heterogeneity (the climate on the mountains, illustrated by the colour of the populations). The phylogeny in the lower left illustrates the relationships between the populations on the different mountains, illustrating the niche divergences.

If environmental changes occur too rapidly for adaptation to overcome organismal constraints, then populations will go extinct, failing to adapt to the new conditions (Futuyma, 2010; Waldron, 2010). If an analogue of the current niche of a species is available and geographically proximate, the path of least resistance dictated by the endogenous constraints is the maintenance of that niche *via* geographic migration (or dispersal) to new regions (i.e. it is easier to move than to adapt). This is the classical view of speciation *via* PNC (Wiens, 2004).

If the current niche is unavailable, adaptation to the closest analogue (niche divergence) is the next path of least resistance (Pyron & Burbrink, 2010). This is ecological speciation, broadly speaking (Rundle & Nosil, 2005). If there were no ecological selection, and adaptation to the changing niches was limited only by standing genetic variation, there would be low phylogenetic signal in occupied ecological niches (Revell *et al.*, 2008). However, if PNC is acting on lineages to remain in the closest analogue of the ancestral niche, this will both promote and limit niche divergence (Figs 1, 2 and 3D). This pattern of divergence along niche gradients with nonetheless high similarity of sister species seems to be relatively common empirically (Graham *et al.*, 2004; Pyron & Burbrink, 2009b; McCormack *et al.*, 2010; Glor & Warren, 2011).

Thus, the process of PNC is the sum of effects of endogenous organismal constraints and ecological variation

(both environmental and geographic) that lead local populations to persist in their current niche, with the net effect of selection against adaptation to novel niches. This interpretation is fairly straightforward and consistent with the definitions of most previous authors (Harvey & Pagel, 1991; Wiens & Graham, 2005; Losos, 2008a). As mentioned above, the action of PNC to promote retention of the current niche by a population can lead to the radically different patterns of high similarity, random variation, and significant divergence in niche among species (Fig. 2). It is thus desirable to quantify the potential pattern-based outcomes of PNC, with regard to the environmental and geographic setting of speciation (Figs 2 and 3).

To reiterate, we contend that it is crucial to define PNC in terms of both lineages, rather than species, and in terms of the current, rather than the ancestral niche. An important outcome of this definition, which has been overlooked by most recent literature, is that patterns produced by the process of PNC vary dramatically. A hypothesis of PNC-mediated speciation is thus one that implies a concrete mechanism for the evolutionary direction of ancestral–descendant populations through ecological-niche space. Any such hypothesis must be framed as an explicit test, and evaluated using analytical methods (e.g. Warren *et al.*, 2008). Crucially, a hypothesized evolutionary mechanism for each specific instance of PNC (e.g. stabilizing selection) is needed.

(2) PNC as a pattern

Confusingly, most literature on speciation invoking PNC as a mechanism also refers to niches of species as being ‘conserved’ and those species (or their ecological characteristics) as exhibiting PNC (Peterson *et al.*, 1999; Pyron & Burbrink, 2009b; Crisp & Cook, 2012). This is true for niches that fit simple null models of drift relative to the phylogeny as well as those that are more similar than expected given the phylogenetic relatedness of the species (Holt, 2009). As noted above, such similarity might occur as a result of at least four mechanisms. Alternatively, those species that are less similar than expected under given models of phylogenetic niche evolution are typically taken to represent niche divergence (Warren *et al.*, 2008; Glor & Warren, 2011). Thus, the process and expected patterns of PNC become conflated in discussions of ecological speciation. Given the framework outlined above, we can delineate at least some of the expected outcomes of PNC as an evolutionary process in the context of speciation.

Previous authors have focused on the potential patterns of speciation *via* PNC (Lindeman, 2000; Graham *et al.*, 2004; Wiens, 2004; Costa *et al.*, 2008; Simard *et al.*, 2009; McCormack *et al.*, 2010; Pyron & Burbrink, 2010; Svensson, 2012). However, a full consideration of the geographic and ecological contexts in which speciation may arise *via* PNC requires considering additional axes of environmental variation, which suggests several discrete patterns (Fig. 2). The primary axes along which allopatric separation may occur are physical heterogeneity (topography, etc.) and ecological heterogeneity (temperature, precipitation, etc.), either of which may promote speciation (Coyne & Orr, 2004). This yields at least four distinct avenues (Fig. 2) *via* which PNC as a process (instantaneous niche retention) might promote speciation (PNC as a pattern), resulting either in niche divergence or niche conservatism.

(a) Low physical and environmental heterogeneity

In this case (Fig. 2C), PNC will not act strongly to promote population divergence, and speciation must occur either by intrinsic mechanisms (e.g. autopolyploidy) or non-ecological extrinsic mechanisms, such as isolation-by-distance, host-shifting (for symbiotic species), or sexual selection (Coyne & Orr, 2004). In this context, we would expect ecological differences between species to be proportional to their phylogenetic distance under null models of drift (Losos, 2008a; Pearman *et al.*, 2008), as PNC has not driven either conservatism or divergence in niche relative to congeners.

(b) Low physical heterogeneity and high environmental heterogeneity

This scenario (Fig. 2A) has been referred to as ‘soft allopatry’ or ‘soft vicariance’ by some authors (Hickerson & Meyer, 2008; Pyron & Burbrink, 2010). In this case, PNC drives parapatry along ecological gradients or across ecological disruptions in the relative absence of geographic barriers to

dispersal (Wiens, 2004). This can yield ‘leaky’ contact zones between species or populations, as the forces separating them at their interface are relatively weak, depending on the strength of the ecological differences in their respective habitats. Evidence for this pattern of speciation, putatively resulting from PNC, seems to be relatively common (Gee, 2004; Hickerson & Meyer, 2008). In this case, species experiencing PNC as a local process in their current niche may undergo niche divergence as a result of PNC, a somewhat counterintuitive result. As described above, this would result when PNC is acting in the opposite direction to ecological selection while environments are changing, leading to adaptation for a niche that resembles, but is distinct from, the ancestral niche. This would lead to divergent niches among related species with strong phylogenetic signal in the clade as a whole (Fig. 4).

(c) High physical heterogeneity and low environmental heterogeneity

This scenario (Fig. 2D) has been referred to as ‘hard allopatry’ by some authors (Hickerson & Meyer, 2008; Pyron & Burbrink, 2010). If physical barriers to gene flow (e.g. a river through an open plain, or an isthmus separating two oceans) disrupt an ecologically homogeneous habitat, then ecological selection may be relatively unimportant for driving speciation, as geographic barriers limit gene flow. Thus PNC as a process may not be important for separating populations, even if those populations are all still adapted to similar habitats and exhibit ‘PNC’ as a pattern as a result of stabilizing selection to maintain their existing ecological niches in different geographic areas (Wiens, 2004), separated by a physical barrier to dispersal. Such a process is thought to be a major driver of phylogeographic diversity in many regions, particularly around rivers (Pellegrino *et al.*, 2005; Soltis *et al.*, 2006; Jackson & Austin, 2010; Pyron & Burbrink, 2010).

(d) High physical and environmental heterogeneity

When both geographic and ecological variation is high (Fig. 2B), the two processes described above (hard and soft allopatry) may interact synergistically to promote rapid divergence between populations (‘species pumps’), such as in tropical montane regions (Janzen, 1967; Brehm, Colwell & Kluge, 2007; Smith *et al.*, 2007; Bryant *et al.*, 2008; Kozak & Wiens, 2010b). In such areas, any geographic distance also results in environmental distance, promoting niche divergence, while the combined topographic variation and ecological distance reduces dispersal and, therefore, gene flow between adjacent populations (Gascon *et al.*, 2000; Gehring *et al.*, 2012). Lineages may thus exhibit either niche divergence or conservatism as a result of PNC driving continued adaptation to local niches. These effects may be intensified by climatic shifts (Haffer, 1969), particularly in temperate regions (Hewitt, 1996; Dynesius & Jansson, 2000).

Why are these populations not simply moving up and down the mountains (Fig. 4), and maintaining stasis within a climatic band, as might be expected under strong PNC?

First, for lower mountains, land area is simply not available (Rahbek, 1997; Wiens, 2004), and populations must adapt or die, as no further movement is possible (at least not upward). Second, the continual processes of drift and local adaptation will lead populations to diverge over time away from the shared ancestral niche, as each population tracks its instantaneous niche. Thus, since PNC is not absolute retention of a given ancestral niche (say, the mid elevations of the mountains), selection for the current niche of each individual population will lead to a mosaic of populations at different elevations on different mountains. As we argue, this can yield the pattern of ecological speciation and niche divergence among populations, due to the short-term action of PNC for each population to remain in its current niche, even as the current niche of each population diverges from the ancestral niche. Ancestral similarity may degrade rapidly in regions such as this, even when selection for ancestral similarity from PNC drove initial divergence.

(e) Summary

When referring to empirical patterns in the distribution of ecological niches among ancestral–descendant species, we suggest that future authors take care not to describe similar niches as a ‘pattern’ of ‘PNC.’ The term ‘PNC’ should be restricted to the evolutionary processes guiding the movement of ancestral–descendant populations through ecological niche space, which could ultimately generate several distinct outcomes. Discussion of the empirical patterns should be framed in reference to the similarity or dissimilarity of observed niches, with reference to an explicit mechanistic hypothesis of PNC purported to be responsible for those patterns. This could include one of the four scenarios discussed above, or any novel hypothesis of ecological history. As noted above, we do not intend to suggest that PNC is responsible for all patterns of ecological speciation, or a catch-all for any associated processes. However, evolutionary mechanisms of endogenous constraint against adaptation and the exogenous forces of selection for ecological stasis can yield multiple, potentially overlapping patterns that may not have previously been intuitive.

(3) Genetic variation and niche divergence

One aspect that has not received as much attention is the role of standing genetic variation in the population (Fig. 3) as the fundamental material of PNC (Wiens & Graham, 2005; Futuyma, 2010; Crisp & Cook, 2012). For simplicity’s sake, we will assume that the niche breadth exhibited by a species (the amplitude of conditions occupied by the species) is equal to its genetic variation, although in practice this is unlikely to be true. Considering the extremes, the conditions occupied by the species may be similar to the total niche volume (Fig. 1), in which case speciation will always exhibit the signature of conserved niches, as the niches of the resulting species will always be highly similar (Holt, 2009). Alternately, species with extremely narrow niche-breadths (e.g. microendemics) will tend to exhibit proportionally

greater niche differences following speciation (Graham *et al.*, 2004; Carnicer *et al.*, 2012). This leads to the problem touched on earlier, that even when PNC as a process acts to promote ecological speciation, the resulting species may exhibit a pattern of niche divergence (Fig. 2). The degree to which this is true is likely to be inversely proportional to the niche breadths of the original lineages (Figs 1 and 3).

We can now consider the various process- and pattern-based outcomes of PNC given genetic variation, environmental heterogeneity, and ecological selection (Fig. 3). In the case of a population with a wide niche-breadth that is divided by a barrier to dispersal (Fig. 3A), the resulting lineages may merely occupy the same realized niche in allopatric populations (i.e. see Section II.2c). If populations are simply on opposite sides of a barrier (such as a river) dividing an ecologically homogeneous area, then the resulting species may bear the pattern of PNC (high niche similarity) due to stabilizing selection being directly responsible for that similarity. By contrast, if populations occupy different geographic regions with similar niches separated by ecologically heterogeneous habitats (Sections II.2b, c), this has been considered evidence for PNC driving allopatric speciation *via* ecologically mediated selection (Peterson *et al.*, 1999; Wiens, 2004).

In regions undergoing rapid ecological change, the ancestral niche may persist in one part of the range while conditions on the other side of the barrier may shift rapidly (Fig. 3B). Thus, even though the descendent populations track the instantaneous niche, this niche may shift rapidly, resulting in the process of PNC again yielding a pattern of niche divergence (Section II.2d). In highly heterogeneous environments such as tropical mountain ranges (Fig. 2), both populations may experience such pressures, resulting in none of the descendant species resembling the ancestral niche (Fig. 3C). Similar patterns may occur for a population occurring along an ecological gradient with less dispersal limitation (Fig. 3D), such as a filter barrier (Pyron & Burbrink, 2010; Cicero & Koo, 2012; Zink, 2014), where disruptive ecological selection may result in allopatric speciation, although the resulting species have different niches than the ancestor. By contrast, if niche width of the ancestor is narrow, selection resulting from different ecological conditions on one side of a barrier may result in the extirpation of that population (Fig. 3E), while selection across an ecological gradient may simply result in a single population that does not move (Fig. 3F).

As noted earlier, this bears some resemblance to the population-genetic model for canalization, wherein phenotypic variation is suppressed by either environmental or genetic factors (Wagner *et al.*, 1997). Environmental canalization can be thought of either as the inverse of phenotypic plasticity, where characters are insensitive to environmental variation, or as the reduction in environmental variance by a quantitative trait. Genetic canalization results from the insensitivity of a character to epistatic mutations. Under stabilizing selection, both result in reduced phenotypic variance around the optimum phenotype.

Under this model, genetic variation may be higher than the niche breadth of the organism, but this is not expressed phenotypically.

In the context of ecologically relevant traits, this provides a population-level mechanism for PNC integrating several of the factors mentioned previously. Genetic canalization in particular may allow for the accumulation of cryptic genetic variation (Wagner *et al.*, 1997), allowing for divergence when niches shift. However, there is little apparent relationship between rates of climatic-niche evolution and climatic-niche breadth (Fisher-Reid *et al.*, 2012), suggesting that the relationship between observed variation (as measured by niche breadth) and ability to adapt (as measured by rate) is not linear. Determining the association between observed variation and underlying genetic variation in ecologically relevant traits (i.e. degree of canalization) will likely be important for pinpointing the environmental and genetic causes of PNC.

(4) Tests for PNC

The final major consideration is how we can test for PNC (Losos, 2008a,b; Wiens, 2008; Wiens *et al.*, 2010). This is again a matter of scale and perspective regarding the hypotheses and processes we are interested in; the aquatic niche of fish is clearly conserved, but this pattern tells us little about speciation of cichlids in African rift lakes. The question of how we can test for PNC has been debated extensively (Wiens *et al.*, 2010), and we review the available options and describe some alternative possibilities. The original tests involved model fitting for continuous traits on a phylogeny, which can be applicable across scales. Key models include Brownian motion (BM; genetic drift), Ornstein–Uhlenbeck (OU; stabilizing selection), and white noise (WN; no phylogenetic signal). Fit of BM or OU over WN is evidence that evolutionary factors are involved in determining the distribution of trait values among species, although care is needed when interpreting this as a result of evolutionary processes (Revell *et al.*, 2008; Harmon *et al.*, 2010). The ‘*k*’ statistic (Blomberg, Garland & Ives, 2003) compares the observed distribution of species to that expected under a simulated BM model using the phylogeny, allowing one to determine if the empirical similarity is greater or less than expected.

Some authors have suggested that similarity beyond that expected *via* BM is needed for evidence of PNC (Losos, 2008a), although as noted here and elsewhere even a BM drift model can produce some of the expected patterns from ‘PNC’ (Wiens *et al.*, 2010). Strong fit of an OU model provides evidence that some factors constrain niche divergence around an evolutionary optimum, but additional evidence would be needed to interpret this as evidence for a driver of speciation (Beaulieu *et al.*, 2012). However, such strong evidence for stabilizing selection could be taken as evidence that PNC is acting as a process, given that divergence from the optimum is constrained (or canalized). Furthermore, the actual elements of the niche examined could differ widely considering the traits examined. For instance, we could imagine that some

biotic aspect of niche such as diet changes much more rapidly between species than expected under a BM model of evolution, when compared to some aspect of abiotic niche such as temperature, which might evolve much slower than predicted under a BM model. This could also vary given the local composition of competitors in different populations (Chesson & Huntly, 1997).

Tests for PNC may also hinge on rates of evolution. Previous authors described methods in which various clades could be compared in terms of the rate of a continuous trait (O’Meara *et al.*, 2006), which can be interpreted as evidence for PNC (Wiens *et al.*, 2010). Recently, a test has been introduced for comparing the rates of two or more characters on a single phylogeny (Adams, 2013), which can be used as a test for PNC, comparing the rates of normalized trait values of niche evolution compared to a non-climatic trait (e.g. colour pattern), if that trait is decoupled from speciation dynamics (Adams *et al.*, 2009; Burbrink *et al.*, 2012). Other alternatives include simulation-based approaches, where summary statistics such as range-size distributions are generated under various models of PNC-based scenarios, and matched to the observed data (Rangel, Diniz-Filho & Colwell, 2007). Other empirical tests involve fine-scale study of range-shifts through time using recent (Tingley *et al.*, 2009; Hadley *et al.*, 2013) or palaeontological (Eldredge *et al.*, 2005; Stigall, 2012) data, comparing the amounts of niche *versus* geographic divergence through time. Another approach is to examine invasive species to determine the magnitude of niche shifts, which seem to be rare, suggesting that at least short-term conservatism of niches is common (Petitpierre *et al.*, 2012; Liu *et al.*, 2014).

A conceptually different set of tests applies to the niche of species as measured (or modelled) through their distribution (Elith *et al.*, 2006). Given ecological niche models for a set of species, we can then assess variation among them with respect to each other, and the available niche volume where they occur (Pearson & Dawson, 2003). Recently proposed approaches randomly resample presence localities of species to test whether the observed ecological niche models vary significantly from (i) each other, (ii) the ‘background’ niche in which they occur, or (iii) an intervening biogeographic area (Warren *et al.*, 2008; Glor & Warren, 2011). These tests can be used to assess PNC among related species in adjacent areas, and to assess ecological divergence across landscapes (Pyron & Burbrink, 2009b; McCormack *et al.*, 2010; Glor & Warren, 2011; Broennimann *et al.*, 2012).

There are conceptually similar tests based on distribution models (Fig. 4) for the effects of PNC in sister-species pairs in small geographic areas (such as montane regions), based on the climatic envelopes of species (Evans *et al.*, 2009; Quintero & Wiens, 2013). Given a measure of climatic niche (e.g. temperature and precipitation), we can randomly sample from the total geographic area available to the species, and calculate the total niche volume in the region. Given sampled presence localities, we can also calculate the climatic breadth of the clade and the individual species (*sensu* Holt, 2009), which can be compared to the total niche volume (Fig. 4).

The niche differences between sister-species pairs can then be calculated, and compared to a simulated distribution under a given model such as BM or OU on the phylogeny. If sister-species pairs are more similar (Fig. 4A) or less similar (Fig. 4B) than expected under null models (Fig. 4C), this would be indicative of PNC due to stabilizing or directional ecological selection, respectively, driving speciation. This is similar in many ways to both '*k*' (Blomberg *et al.*, 2003) and the phylogenetic ANOVA (Garland *et al.*, 1993), but allows a more specific test of ecological similarity among species. This would allow a more precise discrimination between the patterns of PNC described above, in relation to ecological speciation.

Finally, recent authors (Pillar & Duarte, 2010) suggested a test for PNC in the context of community assemblage, where, given a path model that has environment (E) impacting phylogeny (P) which in turn affects traits (T) [$E \rightarrow P \rightarrow T$], it is then expected that a causal relationship between E and T exists only through P. Therefore, the partial correlational relationship between E and T must be null when controlling for P for PNC to be valid. By contrast, PNC will not occur if both E and P affect T [$E \rightarrow T \leftarrow P$] and there the correlation between P and E must be null when controlling for T. Using this model for grassland communities with environment and ecologically important plant traits, they concluded that PNC is unlikely to have occurred. Such an approach may be particularly powerful, as it integrates information on the phylogeny, traits, and ecological attributes across multiple species and communities, and can thus give multiple perspectives on the relative amounts of conservatism and divergence of niches among species across the tree. A number of such approaches have recently been introduced in statistical packages (Debastiani & Pillar, 2012; Ulrich *et al.*, 2012), although evidence seems to be mixed in terms of how important PNC is for community assembly, depending on the lability of traits involved in co-existence (Araya *et al.*, 2012; Yang *et al.*, 2012), and the interaction between competition and environment (Chesson & Huntly, 1997).

In general, however, researchers need to be aware of the fundamental limitations of traditional tests for PNC using standard phylogenetic comparative methods and simplistic models such as BM. As noted above, numerous distinct evolutionary processes can produce similar signatures of 'phylogenetic signal' under BM, limiting power to discriminate among them (Revell *et al.*, 2008). In the particular context of speciation, climate is always spatially structured, and speciation (even ecological speciation) nearly always has a geographic component (Hubbell, 2001; Coyne & Orr, 2004; Nosil *et al.*, 2009; Boucher *et al.*, 2014). Purely neutral processes can produce variation in climatic niches that does not reflect any selective process (Hubbell, 2001; Boucher *et al.*, 2014).

Furthermore, simulations suggest that speciation processes of niche evolution are not adequately modeled by BM, and that strong support can be found for BM or OU models even when selection is absent, leading to 'artificial' support for PNC (Boucher *et al.*, 2014). As species reach the 'edge' of climatic variability in a given region, they

will tend to revert to the mean, giving the signature of a selective force towards a central tendency. Thus, model support alone cannot be considered support for PNC in the absence of corroborating evidence of physiological tolerances or quantitative genetic variation.

III. FUTURE DIRECTIONS

There are numerous areas for improvement in our understanding of PNC as a process and of the pattern of conserved niches, particularly as it relates to ecological speciation. We have assumed that the realized niche breadth of species corresponds to the amount of standing genetic variation in the population (Fig. 3), but this is unlikely to be true in practice. Understanding the genetic and physiological limits of species (and associated canalization) compared to their realized niche will give us greater insight into both the potential role of PNC in driving ecological speciation, as well as the clade-level niche and PNC at deeper phylogenetic scales (Holt, 2009). Integration of global information system (GIS)-based data (Kozak *et al.*, 2008) may allow us to test for more fine-scale processes in recent times (Kidd & Ritchie, 2006; Tingley *et al.*, 2009). Furthermore, increasing integration of palaeontological data (such as palynological or palaeolimnetic series) will help examine niche evolution and conservatism over time (Maguire & Stigall, 2008; Holland & Zaffos, 2011).

There are several questions that could be answered in future studies relating to PNC that have not been thoroughly addressed previously. The first set has to do with the accumulation of niche divergence over time. What is the shape of the relationship between time-since-speciation and niche divergence between sister-species pairs? A flat relationship might indicate that PNC is not a consistent driver of speciation in a given group. By contrast, we might expect a negative linear relationship under a null model of BM niche divergence. A slope significantly less than 1 might indicate that tracking niche similarity was driving speciation, the traditional interpretation of PNC-mediated ecological speciation (Wiens, 2004). A slope much greater than 1, or an exponentially decreasing amount of similarity, might indicate heavy levels of niche divergence in heterogeneous habitats driving speciation (Graham *et al.*, 2004; Pyron & Burbrink, 2009b). Latitudinal variation in such mechanisms has been shown to be important in some groups, such as salamanders (Kozak & Wiens, 2007), but not others, such as frogs (Hua & Wiens, 2010).

More explicit characterization is needed for testing hypotheses of PNC as it relates to ecological speciation, rather than simply attributing allopatric divergence to PNC *sensu lato*. We have outlined several of the major tests above, including model fitting, ecological-niche modelling, geographic simulations, and novel methods based on sister-species divergence and community assembly. For future studies, outlining the mechanisms by which PNC could have initiated speciation and the expected outcomes under

different historical scenarios, are needed to test hypotheses fully. In general, we suggest that ecological speciation *via* PNC is likely to be a common null model (Wiens, 2004), based on the generally observed tendency for species to track their niche geographically (Tingley *et al.*, 2009), an observation that has led to ecological species concepts (Van Valen, 1976). However, this may produce multiple distinct patterns (Figs 2 and 4) that could be termed PNC, and which need to be enumerated beforehand. Ultimately, we believe a clearer understanding of the origin and outcome of PNC can help simplify and extend our conception of speciation *via* ecological selection, and foster a more complete synthesis of ecology and evolutionary biology, as well as phylogeography and historical biogeography.

Thus, for a study attempting to elucidate the ecological mechanisms of speciation in a group, several pieces are needed when considering the potential occurrence and influence of PNC. As we have shown, PNC can act more broadly than has been considered by most recent authors (e.g. causing niche divergence). At minimum, researchers should consider several points. First, are species more similar or more divergent than expected under a null model of diversification (Losos, 2008a), particularly when compared to the group as a whole (Holt, 2009)? This establishes conservatism, constraint, or divergence (Fig. 1) as a pattern with respect to the available niche volume (Warren *et al.*, 2008). Second, what is the degree of physical and ecological heterogeneity in the focal region (Fig. 2), from which the process of PNC can be inferred (Pyrón & Burbrink, 2010)? Third, what is the phylogeographic history of the constituent lineages with respect to ecological niches and geographic location (Lemmon & Lemmon, 2008; Knowles & Alvarado-Serrano, 2010)? These elements combined give a cohesive historical framework for the interplay between the evolutionary processes of niche evolution and ecological speciation, interpreted relative to observable patterns of climatic-niche variability.

IV. CONCLUSIONS

(1) The endogenous factors of genetic, physiological and ecological constraints limit the ability of individuals, and thus populations, to adapt rapidly to changing environmental conditions. The selective forces resulting from ecological variation experienced by populations thus result in the tendency of populations to maintain their current niche through time. We argue that this is the true underlying process of PNC (Fig. 1). Within a total ecosystem niche volume (i.e. the environmental background), this can result in several potential patterns (Figs 1–4).

(2) First is niche divergence: two populations maintaining their current niche (driven by PNC) may nonetheless end up in drastically different niches if the ecological trajectories of their local environments differ to a sufficient degree (Figs 2 and 4). For instance, a population in a rapidly aridifying desert will rapidly diverge in niche from a sister species in a

temperate environment that is becoming more mesic if both experience PNC in their respective niches.

(3) Second, the fundamental niche of a species or group of related species may be relatively fixed, but taxa may differ in their realizations of that fundamental niche, a process we term niche constraint (Holt, 2009). This may give the appearance of niche divergence, when niches are in reality more similar than might be expected given the phylogeny, due to PNC.

(4) Third is that of high overlap in realized niche between species that are evolutionarily divergent enough for large ecological differences to be expected (Fig. 1). If certain habitats are particularly suitable for populations, then selection for that niche may persist for relatively long periods of evolutionary time, leading to greater-than-expected similarity.

(5) The latter pattern is the only one typically referred to as ‘PNC’ (Wiens, 2004, 2008; Losos, 2008a,b). However, all three patterns (niche divergence, niche constraint, and niche conservatism) may result from the same underlying process of niche conservatism, which results from the endogenous factors we have enumerated (Fig. 1). The process of PNC may promote ecological speciation along axes of both physical and environmental heterogeneity, yielding any of the three patterns listed above. We suggest, as do other recent authors (Wiens & Graham, 2005), that testing for the presence of this ‘pattern of PNC’ is not the key question of interest for ecology and evolutionary biology, as the tendency of related species to be similar is a foregone conclusion.

(6) Instead, we suggest that observed patterns in ecological speciation be considered in terms of an underlying mechanism of PNC generating multiple potential patterns, including that of ‘niche conservatism.’ However, PNC as a process may also yield niche divergence, as well as intermediate patterns (Figs 1 and 2). Distinguishing between these based on phylogenetic signal may be difficult (Revell *et al.*, 2008), but the ecophysiological roots of allopatric speciation can likely be classified in most cases into one of the four general categories we have outlined, driven by the single underlying process of PNC, and exhibiting patterns along a continuum from conservatism to divergence in ecological niche, both fundamental and realized. By distinguishing between PNC as a process and a pattern, we can more easily understand ecological speciation.

V. ACKNOWLEDGEMENTS

This research was funded in part by U.S. NSF grants DBI-0905765 and DEB-1441719 to R.A.P., U.S. NSF Grant DEB 1257926 to F.T.B., and CNPq grants 302776/2012-5 and 563352/2010-8 to G.C.C. We thank J. Kelly for early development of some of these ideas, and W. Foster and one anonymous reviewer for comments on earlier versions.

VI. REFERENCES

- ACKERLY, D. D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* **164**, S165–S184.
- ADAMS, D. C. (2013). Comparing evolutionary rates for different phenotypic traits on a phylogeny using likelihood. *Systematic Biology* **62**, 181–192.
- ADAMS, D. C., BERNIS, C. M., KOZAK, K. H. & WIENS, J. J. (2009). Are rates of species diversification correlated with rates of morphological evolution? *Proceedings of the Royal Society B: Biological Sciences* **276**, 2729–2738.
- ANACKER, B. L. & STRAUSS, S. Y. (2014). The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20132980.
- ARAYA, Y. N., SILVERTOWN, J., GOWING, D. J., MCCONWAY, K. J., LINDER, H. P. & MIDGLEY, G. (2012). Do niche-structured plant communities exhibit phylogenetic conservatism? A test case in an endemic clade. *Journal of Ecology* **100**, 1434–1439.
- BEAULIEU, J. M., JHWUENG, D. C., BOETTIGER, C. & O'MEARA, B. C. (2012). Modeling stabilizing selection: expanding the Ornstein–Uhlenbeck model of adaptive evolution. *Evolution* **66**, 2369–2383.
- BELDADE, P., KOOPS, K. & BRAKEFIELD, P. M. (2002). Developmental constraints versus flexibility in morphological evolution. *Nature* **416**, 844–847.
- BELLIURE, J., SORCI, G., MOLLER, A. P. & CLOBERT, J. (2000). Dispersal distances predict subspecies richness in birds. *Journal of Evolutionary Biology* **13**, 480–487.
- BLOMBERG, S. P. & GARLAND, T. (2002). Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *Journal of Evolutionary Biology* **15**, 899–910.
- BLOMBERG, S. P., GARLAND, T. & IVES, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.
- BOUCHER, F. C., THUILLER, W., DAVIES, T. J. & LAVERGNE, S. (2014). Neutral biogeography and the evolution of climatic niches. *The American Naturalist* **183**, 573–584.
- BREHM, G., COLWELL, R. K. & KLUGE, J. (2007). The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography* **16**, 205–219.
- BROENNIMANN, O., FITZPATRICK, M. C., PEARMAN, P. B., PETITPIERRE, B., PELLISSIER, L., YOCOZ, N. G., THUILLER, W., FORTIN, M. J., RANDIN, C., ZIMMERMANN, N. E., GRAHAM, C. H. & GUIAN, A. (2012). Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* **21**, 481–497.
- BROENNIMANN, O., TREIER, U. A., MULLER-SCHARER, H., THUILLER, W., PETERSON, A. T. & GUIAN, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters* **10**, 701–709.
- BRYANT, J. A., LAMANNA, C., MORLON, H., KERKHOFF, A. J., ENQUIST, B. J. & GREEN, J. L. (2008). Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11505–11511.
- BUCKLEY, L. B., DAVIES, T. J., ACKERLY, D. D., KRAFT, N. J. B., HARRISON, S. P., ANACKER, B. L., CORNELL, H. V., DAMSCHEN, E. I., GRYTNES, J. A., HAWKINS, B. A., MCCAIN, C. M., STEPHENS, P. R. & WIENS, J. J. (2010). Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences* **277**, 2131–2138.
- BURBRINK, F. T., CHEN, X., MYERS, E. A., BRANDLEY, M. C. & PYRON, R. A. (2012). Evidence for determinism in species diversification and contingency in phenotypic evolution during adaptive radiation. *Proceedings of the Royal Society B: Biological Sciences* **279**, 4817–4826.
- CARNICER, J., BROTONS, L., STEFANESCU, C. & PENUELAS, J. (2012). Biogeography of species richness gradients: linking adaptive traits, demography and diversification. *Biological Reviews* **87**, 457–479.
- CHASE, J. M. & LEIBOLD, M. A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago.
- CHESSON, P. & HUNTLY, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* **150**, 519–53.
- CICERO, C. & KOO, M. S. (2012). The role of niche divergence and phenotypic adaptation in promoting lineage diversification in the Sage Sparrow (*Artemisospiza belli*, Aves: Emberizidae). *Biological Journal of the Linnean Society* **107**, 332–354.
- CONDAMINE, F. L., SPERLING, F. A. H., WAHLBERG, N., RASPLUS, J. Y. & KERGOAT, G. J. (2012). What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. *Ecology Letters* **15**, 267–277.
- CONNOR, N., SIKORSKI, J., ROONEY, A. P., KOPAC, S., KOEPEL, A. F., BURGER, A., COLE, S. G., PERRY, E. B., KRIZANG, D. & FIELD, N. C. (2010). Ecology of speciation in the genus *Bacillus*. *Applied and Environmental Microbiology* **76**, 1349–1358.
- COSTA, G. C., WOLFE, C., SHEPARD, D. B., CALDWELL, J. P. & VITT, L. J. (2008). Detecting the influence of climatic variables on species distributions: a test using GIS niche-based models along a steep longitudinal environmental gradient. *Journal of Biogeography* **35**, 637–646.
- COYNE, J. A. & ORR, H. A. (2004). *Speciation*. Sinauer Associates, Sunderland.
- CRISP, M. D. & COOK, L. G. (2012). Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes? *New Phytologist* **196**, 681–694.
- DEBASTIANI, V. J. & PILLAR, V. D. (2012). SYNC-SA-R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. *Bioinformatics* **28**, 2067–2068.
- DONOGHUE, M. J. (2008). A phylogenetic perspective on the distribution of plant diversity. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11549–11555.
- DYNESIUS, M. & JANSSON, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 9115–9120.
- ELDRIDGE, N., THOMPSON, J. N., BRAKEFIELD, P. M., GAVRILETS, S., JABLONSKI, D., JACKSON, J. B. C., LENSKE, R. E., LIEBERMAN, B. S., MCPEEK, M. A. & MILLER, W. (2005). The dynamics of evolutionary stasis. *Paleobiology* **31**, 133–145.
- ELITH, J., GRAHAM, C. H., ANDERSON, R. P., DUDIK, M., FERRIER, S., GUIAN, A., HIJMAN, R. J., HUETTSMANN, F., LEATHWICK, J. R., LEHMANN, A., LI, J., LOHMANN, L. G., LOISELLE, B. A., MANION, G., MORITZ, C., NAKAMURA, M., NAKAZAWA, Y., OVERTON, J. M., PETERSON, A. T., PHILLIPS, S. J., RICHARDSON, K., SCACHETTI-PEREIRA, R., SCHAPIRE, R. E., SOBERON, J., WILLIAMS, S., WISZ, M. S. & ZIMMERMANN, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–151.
- ELITH, J. & LEATHWICK, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**, 677–697.
- ETTERSON, J. R. & SHAW, R. G. (2001). Constraint to adaptive evolution in response to global warming. *Science* **294**, 151–154.
- EVANS, M. E. K., SMITH, S. A., FLYNN, R. S. & DONOGHUE, M. J. (2009). Climate, niche evolution, and diversification of the “bird-cage” evening primroses (Oenothera, Sections Anogra and Kleinia). *American Naturalist* **173**, 225–240.
- FISHER-REID, M. C., KOZAK, K. H. & WIENS, J. J. (2012). How is the rate of climatic-niche evolution related to climatic-niche breadth? *Evolution* **66**, 3836–3851.
- FUTUYMA, D. J. (2010). Evolutionary constraint and ecological consequences. *Evolution* **64**, 1865–1884.
- GALLAGHER, R. V., BEAUMONT, L. J., HUGHES, L. & LEISHMAN, M. R. (2010). Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *Journal of Ecology* **98**, 790–799.
- GARLAND, T., DICKERMAN, A. W., JANIS, C. M. & JONES, J. A. (1993). Phylogenetic analysis of covariance by computer-simulation. *Systematic Biology* **42**, 265–292.
- GASCON, C., MALCOLM, J. R., PATTON, J. L., DA SILVA, M. N. F., BOGART, J. P., LOUGHEED, S. C., PERES, C. A., NECKEL, S. & BOAG, P. T. (2000). Riverine barriers and the geographic distribution of Amazonian species. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 13672–13677.
- GEE, J. M. (2004). Gene flow across a climatic barrier between hybridizing avian species, California and Gambel's quail (*Callipepla californica* and *C. gambeli*). *Evolution* **58**, 1108–1121.
- GEHRING, P. S., PABIJAN, M., RANDRIANIRINA, J. E., GLAW, F. & VENCES, M. (2012). The influence of riverine barriers on phylogeographic patterns of Malagasy reed frogs (*Heterixalus*). *Molecular Phylogenetics and Evolution* **64**, 618–632.
- GLOR, R. E. & WARREN, D. (2011). Testing ecological explanations for biogeographic boundaries. *Evolution* **65**, 673–683.
- GRAHAM, C. H., RON, S. R., SANTOS, J. C., SCHNEIDER, C. J. & MORITZ, C. (2004). Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* **58**, 1781–1793.
- GRINNELL, J. (1917). The niche-relationship of the California thrasher. *Auk* **34**, 427–433.
- HADLEY, K. R., PATERSON, A. M., HALL, R. I. & SMOL, J. P. (2013). Effects of multiple stressors on lakes in south-central Ontario: 15 years of change in lakewater chemistry and sedimentary diatom assemblages. *Aquatic Sciences* **75**, 349–360.
- HADLY, E. A., SPAETH, P. A. & LI, C. (2009). Niche conservatism above the species level. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19707–19714.
- HAFFER, J. (1969). Speciation in Amazonian forest birds. *Science* **165**, 131–137.
- HARGREAVES, A. L., SAMIS, K. E. & ECKERT, C. G. (2014). Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *American Naturalist* **183**, 157–173.
- HARMON, L. J., LOSOS, J. B., DAVIES, T. J., GILLESPIE, R. G., GITTLEMAN, J. L., JENNINGS, W. B., KOZAK, K. H., MCPEEK, M. A., MORENO-ROARK, F., NEAR, T. J., PURVIS, A., RICKLEFS, R. E., SCHLUTER, D., SCHULTE, J. A., SEEHAUSEN, O., SIDLAUSKAS, B. L., TORRES-CARVAJAL, O., WEIR, J. T. & MOOERS, A. O. (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution* **64**, 2385–2396.
- HARVEY, P. H. & PAGEL, M. D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford, New York.
- HATCHWELL, B. J. & KOMDEUR, J. (2000). Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour* **59**, 1079–1086.
- HEWITT, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* **58**, 247–276.

- HICKERSON, M. J. & MEYER, C. P. (2008). Testing comparative phylogeographic models of marine vicariance and dispersal using a hierarchical Bayesian approach. *BMC Evolutionary Biology* **8**, 322.
- HILLERISLAMBERS, J., ADLER, P. B., HARPOLE, W. S., LEVINE, J. M. & MAYFIELD, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* **43**, 227–248.
- HOLLAND, S. M. & ZAFFOS, A. (2011). Niche conservatism along an onshore-offshore gradient. *Paleobiology* **37**, 270–286.
- HOLT, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19659–19665.
- HOLT, R. D. & BARFIELD, M. (2008). Habitat selection and niche conservatism. *Israel Journal of Ecology & Evolution* **54**, 295–309.
- HOLT, R. D. & GAINES, M. S. (1992). Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evolutionary Ecology* **6**, 433–447.
- HUA, X. & WIENS, J. J. (2010). Latitudinal variation in speciation mechanisms in frogs. *Evolution* **64**, 429–443.
- HUBBELL, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- HURLBERT, A. H. & WHITE, E. P. (2007). Ecological correlates of geographical range occupancy in North American birds. *Global Ecology and Biogeography* **16**, 764–773.
- HUTCHINSON, G. E. (1957). *A Treatise on Limnology*. Wiley and Sons, New York.
- HUTCHINSON, G. E. (1978). *An Introduction to Population Ecology*. Yale University Press, New Haven.
- JACKSON, N. D. & AUSTIN, C. C. (2010). The combined effects of rivers and refugia generate extreme cryptic fragmentation within the common ground skink (*Scincella lateralis*). *Evolution* **64**, 409–428.
- JANZEN, D. H. (1967). Why mountain passes are higher in the tropics. *American Naturalist* **101**, 233–249.
- KIDD, D. M. & RITCHIE, M. G. (2006). Phylogeographic information systems: putting the geography into phylogeography. *Journal of Biogeography* **33**, 1851–1865.
- KIRKPATRICK, M. & BARTON, N. H. (1997). Evolution of a species' range. *American Naturalist* **150**, 1–23.
- KNOWLES, L. L. & ALVARADO-SERRANO, D. F. (2010). Exploring the population genetic consequences of the colonization process with spatio-temporally explicit models: insights from coupled ecological, demographic and genetic models in montane grasshoppers. *Molecular Ecology* **19**, 3727–3745.
- KOZAK, K. H. & WIENS, J. J. (2006). Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* **60**, 2604–2621.
- KOZAK, K. H. & WIENS, J. J. (2007). Climatic zonation drives latitudinal variation in speciation mechanisms. *Proceedings of the Royal Society B: Biological Sciences* **274**, 2995–3003.
- KOZAK, K. H. & WIENS, J. J. (2010a). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters* **13**, 1378–1389.
- KOZAK, K. H. & WIENS, J. J. (2010b). Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *American Naturalist* **176**, 40–54.
- KOZAK, K. H., GRAHAM, C. H. & WIENS, J. J. (2008). Integrating GIS-based environmental data into evolutionary biology. *Trends in Ecology & Evolution* **23**, 141–148.
- LEMMON, A. R. & LEMMON, E. M. (2008). A likelihood framework for estimating phylogeographic history on a continuous landscape. *Systematic Biology* **57**, 544–561.
- LINDEMAN, P. V. (2000). Resource use of five sympatric turtle species: effects of competition, phylogeny, and morphology. *Canadian Journal of Zoology* **78**, 992–1008.
- LIU, X., LI, X., LIU, Z., TINGLEY, R., KRAUS, F., GUO, Z. & LI, Y. (2014). Congener diversity, topographic heterogeneity and human-assisted dispersal predict spread rates of alien herpetofauna at a global scale. *Ecology Letters* **17**, 821–829.
- LOSOS, J. B. (2008a). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* **11**, 995–1003.
- LOSOS, J. B. (2008b). Rejoinder to Wiens (2008): phylogenetic niche conservatism, its occurrence and importance. *Ecology Letters* **11**, 1005–1007.
- MAAN, M. E. & SEEHAUSEN, O. (2011). Ecology, sexual selection and speciation. *Ecology Letters* **14**, 591–602.
- MAGUIRE, K. C. & STIGALL, A. L. (2008). Paleobiogeography of Miocene Equinae of North America: a phylogenetic biogeographic analysis of the relative roles of climate, vicariance, and dispersal. *Palaeogeography Palaeoclimatology Palaeoecology* **267**, 175–184.
- MCCORMACK, J. E., ZELLMER, A. J. & KNOWLES, L. L. (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.
- NOSIL, P., HARMON, L. J. & SEEHAUSEN, O. (2009). Ecological explanations for (incomplete) speciation. *Trends in Ecology & Evolution* **24**, 145–156.
- O'MEARA, B. C., ANE, C., SANDERSON, M. J. & WAINWRIGHT, P. C. (2006). Testing for different rates of continuous trait evolution using likelihood. *Evolution* **60**, 922–933.
- PEARMAN, P. B., GUIAN, A., BROENNIMANN, O. & RANDIN, C. F. (2008). Niche dynamics in space and time. *Trends in Ecology & Evolution* **23**, 149–158.
- PEARSON, R. G. & DAWSON, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* **12**, 361–371.
- PELLEGRINO, K. C. M., RODRIGUES, M. I., WAITE, A. N., MORANDO, M., YASSUDA, Y. Y. & SITES, J. W. (2005). Phylogeography and species limits in the *Gymnodactylus darwini* complex (Gekkonidae, Squamata): genetic structure coincides with river systems in the Brazilian Atlantic Forest. *Biological Journal of the Linnean Society* **85**, 13–26.
- PETERSON, A. T. (2003). Predicting the geography of species' invasions via ecological niche modeling. *The Quarterly Review of Biology* **78**, 419–433.
- PETERSON, A. T. (2011a). Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography* **38**, 817–827.
- PETERSON, A. T. (2011b). *Ecological Niches and Geographic Distributions*. Princeton University Press, Princeton.
- PETERSON, A. T. & NYARI, A. S. (2008). Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, *Schiffornis* sp., in the Neotropics. *Evolution* **62**, 173–183.
- PETERSON, A. T., SOBERÓN, J. & SÁNCHEZ-CORDERO, V. (1999). Conservatism of ecological niches in evolutionary time. *Science* **285**, 1265–1267.
- PETERSON, A. T. & VIEGLAIS, D. A. (2001). Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. A new approach to ecological niche modeling, based on new tools drawn from biodiversity informatics, is applied to the challenge of predicting potential species' invasions. *BioScience* **51**, 363–371.
- PETITPIERRE, B., KUEFFER, C., BROENNIMANN, O., RANDIN, C., DAEHLER, C. & GUIAN, A. (2012). Climatic niche shifts are rare among terrestrial plant invaders. *Science* **335**, 1344–1348.
- PILLAR, V. D. & DUARTE, L. D. S. (2010). A framework for metacommunity analysis of phylogenetic structure. *Ecology Letters* **13**, 587–596.
- PRINZING, A. (2001). The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **268**, 2383–2389.
- PULLIAM, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters* **3**, 349–361.
- PYRON, R. A. & BURBRINK, F. T. (2009a). Can the tropical conservatism hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lamprodelphini. *Global Ecology and Biogeography* **18**, 406–415.
- PYRON, R. A. & BURBRINK, F. T. (2009b). Lineage diversification in a widespread species: roles for niche divergence and conservatism in the common kingsnake, *Lampropeltis getula*. *Molecular Ecology* **18**, 3443–3457.
- PYRON, R. A. & BURBRINK, F. T. (2010). Hard and soft allopatry: physically and ecologically mediated modes of geographic speciation. *Journal of Biogeography* **37**, 2005–2015.
- QUINTERO, I. & WIENS, J. J. (2013). What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. *Global Ecology and Biogeography* **22**, 422–432.
- RABOSKY, D. L. & MCCUNE, A. R. (2010). Reinventing species selection with molecular phylogenies. *Trends in Ecology & Evolution* **25**, 68–74.
- RAHBEK, C. (1997). The relationship among area, elevation, and regional species richness in neotropical birds. *American Naturalist* **149**, 875–902.
- RANGEL, T. F. L. V. B., DINIZ-FILHO, J. A. F. & COLWELL, R. K. (2007). Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. *American Naturalist* **170**, 602–616.
- REVELL, L. J., HARMON, L. J. & COLLAR, D. C. (2008). Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* **57**, 591–601.
- RICKLEFS, R. E. & LATHAM, R. E. (1992). Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *American Naturalist* **139**, 1305–1321.
- ROBERTS, D. R. & HAMANN, A. (2012). Predicting potential climate change impacts with bioclimate envelope models: a palaeoecological perspective. *Global Ecology and Biogeography* **21**, 121–133.
- RÖDDER, D. & LÖTTERS, S. (2009). Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Global Ecology and Biogeography* **18**, 674–687.
- ROSSER, N., PHILLIMORE, A. B., HUERTAS, B., WILLMOTT, K. R. & MALLET, J. (2012). Testing historical explanations for gradients in species richness in heliconiine butterflies of tropical America. *Biological Journal of the Linnean Society* **105**, 479–497.
- RUNDLE, H. D. & NOSIL, P. (2005). Ecological speciation. *Ecology Letters* **8**, 336–352.
- SALTZ, J. B. & NUZHIDIN, S. V. (2014). Genetic variation in niche construction: implications for development and evolutionary genetics. *Trends in Ecology & Evolution* **29**, 8–14.
- SCHLUTER, D. (2001). Ecology and the origin of species. *Trends in Ecology & Evolution* **16**, 372–380.
- SCHLUTER, D. & CONTE, G. L. (2009). Genetics and ecological speciation. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 9955–9962.

- SCHULTE, U., HOCHKIRCH, A., LÖTTERS, S., RÖDDER, D., SCHWEIGER, S., WEIMANN, T. & VEITH, M. (2012). Cryptic niche conservatism among evolutionary lineages of an invasive lizard. *Global Ecology and Biogeography* **21**, 198–211.
- SEEHAUSEN, O. (2006). African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society B: Biological Sciences* **273**, 1987–1998.
- SEXTON, J. P., HANGARTNER, S. B. & HOFFMANN, A. A. (2014). Genetic isolation by environment or distance: which pattern of gene flow is most common? *Evolution* **68**, 1–15.
- SEXTON, J. P., MCINTYRE, P. J., ANGERT, A. L. & RICE, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* **40**, 415–436.
- SIMARD, F., AYALA, D., KAMDEM, G. C., POMBI, M., ETOUNA, J., OSE, K., FOTSING, J.-M., FONTENILLE, D., BESANSKY, N. J. & COSTANTINI, C. (2009). Ecological niche partitioning between *Anopheles gambiae* molecular forms in Cameroon: the ecological side of speciation. *BMC Ecology* **9**, 17.
- SINERVO, B., MENDEZ-DE-LA-CRUZ, F., MILES, D. B., HEULIN, B., BASTIAANS, E., CRUZ, M. V. S., LARA-RESENDIZ, R., MARTINEZ-MENDEZ, N., CALDERON-ESPINOSA, M. L., MEZA-LAZARO, R. N., GADSDEN, H., AVILA, L. J., MORANDO, M., DE LA RIVA, I. J., SEPULVEDA, P. V., ROCHA, C. F. D., IBARGUENGOTIA, N., PUNTRIANO, C. A., MASSOT, M., LEPETZ, V., OKSANEN, T. A., CHAPPLE, D. G., BAUER, A. M., BRANCH, W. R., CLOBERT, J. & SITES, J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899.
- SMITH, S. A., DE OCA, A. N. M., REEDER, T. W. & WIENS, J. J. (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.
- SOBERÓN, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* **10**, 1115–1211.
- SOBERÓN, J. & NAKAMURA, M. (2009). Niches and distributional areas: concepts, methods, and assumptions (Colloquium Papers). *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19644–19650.
- SOLTIS, D. E., MORRIS, A. B., McLACHLAN, J. S., MANOS, P. S. & SOLTIS, P. S. (2006). Comparative phylogeography of unglaciated eastern North America. *Molecular Ecology* **15**, 4261–4293.
- STEGEN, J. C., FERRIERE, R. & ENQUIST, B. J. (2012). Evolving ecological networks and the emergence of biodiversity patterns across temperature gradients. *Proceedings of the Royal Society B: Biological Sciences* **279**, 1051–1060.
- STEVENS, R. D. (2011). Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. *Proceedings of the Royal Society B: Biological Sciences* **278**, 2528–2536.
- STIGALL, A. L. (2012). Using ecological niche modelling to evaluate niche stability in deep time. *Journal of Biogeography* **39**, 772–781.
- SVENSSON, E. I. (2012). Non-ecological speciation, niche conservatism and thermal adaptation: how are they connected? *Organisms Diversity & Evolution* **12**, 229–240.
- TINGLEY, M. W., MONAHAN, W. B., BEISSINGER, S. R. & MORITZ, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19637–19643.
- ULRICH, W., PIWCZYNSKI, M., MAESTRE, F. T. & GOTELLI, N. J. (2012). Null model tests for niche conservatism, phylogenetic assortment and habitat filtering. *Methods in Ecology and Evolution* **3**, 930–939.
- VAN VALEN, L. (1976). Ecological species, multispecies, and oaks. *Taxon* **25**, 233–239.
- WAGNER, G. P., BOOTH, G. & BAGHERI, H. C. (1997). A population genetic theory of canalization. *Evolution* **51**, 329–347.
- WAGNER, C. E., HARMON, L. J. & SEEHAUSEN, O. (2012). Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* **487**, 366–U124.
- WALDRON, A. (2010). Lineages that cheat death: surviving the squeeze on range size. *Evolution* **64**, 2278–2292.
- WARREN, D. L., GLOR, R. E. & TURELLI, M. (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**, 2868–2883.
- WIENS, J. J. (2004). Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* **58**, 193–197.
- WIENS, J. J. (2008). Commentary on Losos (2008): niche conservatism deja vu. *Ecology Letters* **11**, 1004–1005.
- WIENS, J. J., ACKERLY, D. D., ALLEN, A. P., ANACKER, B. L., BUCKLEY, L. B., CORNELL, H. V., DAMSCHEN, E. I., DAVIES, T. J., GRYTNES, J. A., HARRISON, S. P., HAWKINS, B. A., HOLT, R. D., MCCAIN, C. M. & STEPHENS, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**, 1310–1324.
- WIENS, J. J. & GRAHAM, C. H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* **36**, 519–539.
- WIENS, J. J., PARRA-OLEA, G., GARCIA-PARIS, M. & WAKE, D. B. (2007). Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. *Proceedings of the Royal Society B: Biological Sciences* **274**, 919–928.
- WIENS, J. J., PYRON, R. A. & MOEN, D. S. (2011). Phylogenetic origins of local-scale diversity patterns and the causes of Amazonian megadiversity. *Ecology Letters* **14**, 643–652.
- YANG, Z. L., POWELL, J. R., ZHANG, C. H. & DU, G. Z. (2012). The effect of environmental and phylogenetic drivers on community assembly in an alpine meadow community. *Ecology* **93**, 2321–2328.
- ZINK, R. M. (2014). Homage to Hutchinson, and the role of ecology in lineage divergence and speciation. *Journal of Biogeography* **41**, 999–1006.

(Received 16 December 2013; revised 16 September 2014; accepted 15 October 2014; published online 26 November 2014)