

REVIEW

Phylogenetic comparative approaches for studying niche conservatism

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Abstract

Analyses of phylogenetic niche conservatism (PNC) are becoming increasingly common. However, each analysis makes subtly different assumptions about the evolutionary mechanism that generates patterns of niche conservatism. To understand PNC, analyses should be conducted with reference to a clear underlying model, using appropriate methods. Here, we outline five macroevolutionary models that may underlie patterns of PNC (drift, niche retention, phylogenetic inertia, niche filling/shifting and evolutionary rates) and link these to published phylogenetic comparative methods. For each model, we give recent examples from the literature and suggest how the methods can be practically applied. We hope that this will help clarify the niche conservatism literature and encourage people to think about the evolutionary models underlying niche conservatism in their study group.

Introduction

One of the most basic observations in evolutionary ecology is that closely related species tend to be more similar to each other than to more distantly related ones (Harvey & Pagel, 1991). Thus, close relatives share similarities in their morphology, physiology, ecology and life history, as well as in their ecological niches (i.e. the biological and environmental conditions that allow persistence; Holt, 2009). The resultant pattern of similarity in ecological niches amongst related species has been termed phylogenetic niche conservatism (PNC).

PNC can be defined as the tendency of species to retain characteristics of their fundamental niche over time (Wiens & Graham, 2005). There has been a great deal of interest in PNC over recent years. Indeed, of the 356 papers published since 2000 with 'PNC' in their text (Google Scholar search 8th September 2010), more than half were published between 2008 and 2010. This surge of interest in PNC is probably because of its importance in

a number of different areas of biology. For example, it forms part of the explanation for a variety of biological patterns and processes, including the latitudinal species richness gradient and the maintenance of separated populations after speciation (Wiens & Donoghue, 2004; Wiens & Graham, 2005; Buckley *et al.*, 2010a; Wiens *et al.*, 2010). The idea that species niches are phylogenetically conserved is also a key assumption, whether stated explicitly or not, for methods such as environmental niche modelling, community phylogenetics and phylogenetic comparative analyses (Harvey & Pagel, 1991; Webb *et al.*, 2002; Pearman *et al.*, 2008). In addition, human-induced climate and land use changes have put new and urgent significance on our understanding of the ability of species and clades to adapt to novel environments and invasive species (Broennimann *et al.*, 2007; Tingley *et al.*, 2009; Sinervo *et al.*, 2010).

The microevolutionary mechanisms underlying PNC may include: (i) stabilizing selection, i.e. deviation from the ancestral niche reduces fitness so that selection favours individuals that live in the same habitats and have the same niches as their ancestors (e.g. Holt & Barfield, 2008); (ii) pleiotropy, i.e. if a gene allowing niche expansion is pleiotropically linked with another that reduces fitness, then niches may not change

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(e.g. Etterson & Shaw, 2001); (iii) gene flow, i.e. gene flow from one part of a species range to another may act to cancel adaptations in niche traits (e.g. Sexton *et al.*, 2009); (iv) limited genetic variation, i.e. if there is limited genetic variation in a trait, natural selection cannot act on it (e.g. Bradshaw, 1991); and (v) competition, predation and other biotic factors (e.g. Connell, 1961; for more detail on these mechanisms, see Wiens, 2004; Wiens & Graham, 2005; Wiens *et al.*, 2010).

Whereas population-level microevolutionary mechanisms cause PNC, their manifestation in the form of broad-scale ecological patterns (such as richness gradients; Wiens & Donoghue, 2004; Buckley *et al.*, 2010a) is at a different temporal and spatial scale. Assessment of PNC at broad scales requires inference across multiple species, so here we suggest that macroevolutionary models should be the tools of choice for this level of analysis. As we demonstrate later, phylogenetic comparative methods may provide the best methods for testing hypotheses about these macroevolutionary models and PNC.

PNC and the phylogenetic comparative method

The rationale underlying phylogenetic comparative methods is that species may be similar largely because they share evolutionary history, not because they represent independent evolutionary origins of traits and adaptations. As consequence of this, statistical methods that treat species as evolutionarily or statistically independent may be flawed and run the risk of generating invalid results. PNC is one of the prime mechanisms generating phylogenetic nonindependence of species (Harvey & Pagel, 1991).

Since it was first recognized that nonindependence of species was a major issue in comparative analysis, a suite of methods have been developed (e.g. Felsenstein, 1985; Hansen, 1997; Pagel, 1997, 1999). Initially, methods were developed with the main aim of correcting for nonindependence in the data. Subsequent developments involve more complex model-based approaches that allow one to make inferences about the underlying evolutionary process. These take several forms. For example, maximum likelihood methods allow variation in the rate of evolution to be modelled as a function of different processes (e.g. speed-up or slowdown; Pagel, 1997, 1999) or to incorporate assumptions about constraints on traits (Hansen, 1997; Hansen *et al.*, 2008). Diagnostic analyses also allow deviations from common models to be analysed (Blomberg *et al.*, 2003; Freckleton & Harvey, 2006).

Although individually, and in the absence of prior information, any given test is not diagnostic of a given process or model (Revell, 2008), when used within a hypothesis-driven framework, these approaches potentially allow inferences about the nature of evolution to

be made and for different models of evolution to be distinguished. For example, models have been used to demonstrate evidence of evolutionary constraints (Hansen *et al.*, 2008), niche filling evolution (Freckleton & Harvey, 2006) and trait evolution linked to diversification in adaptive radiation (Harmon *et al.*, 2003). Thus, such approaches provide a powerful tool with which to distinguish models of trait evolution.

Distinguishing among macroevolutionary models

A fundamental problem with interpreting patterns of PNC is that a given pattern could be explained by one of several different macroevolutionary models. The upshot of the past 20 years of research in comparative methods is that we are now able to distinguish between these various models. However, this also means that a variety of different methods for detecting PNC exist, each of which makes subtly different assumptions about the evolutionary mechanism that generates niche conservatism. We therefore need to link the different macroevolutionary models that can generate PNC with appropriate comparative methods for testing them. This is the main aim of this paper.

For example, both cats and dogs eat meat, not because of recent independent evolution, but largely because ancestral felids and canids ate meat and they inherited this dietary niche from their ancestors. This is *prima facie* PNC. On the other hand, recent analyses have suggested that environmental niche conservatism in carnivores is weak: there is little evidence for phylogenetic conservatism of environmental variables as represented by the ranges of species within this group (Freckleton & Jetz, 2009; Safi & Pettorelli, 2010). Conversely, in many adaptive radiations, e.g. Galapagos finches and African rift lake cichlids, trophic niches are not conserved but environmental niches are (Wiens *et al.*, 2010). Depending on the variable examined, the definition and measurement of niche and, to some extent, the phylogenetic level at which conservatism is assessed, our conclusions about conservatism can be greatly altered.

In this study, we begin by discussing the meaning of a 'niche' and, particularly with a view to comparative analysis, of measurable niche traits. We then highlight five macroevolutionary models (drift, niche retention, phylogenetic inertia, niche filling/shifting and evolutionary rates) that may generate niche conservatism and link these to published evolutionary models and comparative methods. We focus on phylogenetic comparative methods (rather than providing an exhaustive review of all possible methods for comparing niches among species) because we believe that comparative tests are the most appropriate way of testing for PNC at a macro-scale, and by definition, tests for PNC must include an explicit phylogenetic component. We emphasize that analysis of

evidence for PNC must be conducted within an explicit framework and with a clear underlying evolutionary model.

We also briefly point out how these methods can be practically applied, generally by referencing a function available in the R program (R Development Core Team, 2009) because this package is freely available, flexible and can perform all the analyses listed later in the text, so there is no need to use multiple programmes. For researchers uncomfortable with R, there are many other packages available that can perform many of the same analyses in a more user-friendly environment, for example Garland *et al.*'s PDAP (1993), a free program that runs on Microsoft DOS. Joe Felsenstein maintains a comprehensive list of these programs at <http://evolution.genetics.washington.edu/phylip/software.html#Comparative>.

Niches and traits

What do we mean by a niche?

A niche can be broadly defined as the set of conditions within which a species can survive. More precise definitions of niche have been previously reviewed in detail (for example, Chase & Leibold, 2003; Soberón, 2007; Soberón & Nakamura, 2009), so we will not attempt to do so here. At the simplest level, niches can be divided into two broad categories depending on the type of variables they include. The environmental or Grinnellian niche is defined by the set of environmental conditions a species requires to survive. The Eltonian niche, on the other hand, emphasizes resource needs and more fine-scale biotic interactions. In terms of the methods described later, most apply to both kinds of niche although there are some exceptions.

A further important niche definition is the distinction between the fundamental and realized niche (Connell, 1961; Pulliam, 2000). The fundamental niche is defined using the niche concepts mentioned previously. However, species are unlikely to fill their entire niche because of interactions with other species (e.g. competition; Connell, 1961) and limits on dispersal. The niche space a species actually occupies is its realized niche. Recent attempts notwithstanding (Kearney & Porter, 2004), without accurate information on species physiological limits and resource use requirements, it is almost impossible to exactly quantify the fundamental niche of a species. Thus, here, and in most studies of PNC, the niche used is the realized niche, although this is clearly not ideal (Soberón & Nakamura, 2009).

What do we mean by a trait?

Each of the definitions above requires traits with which to characterize the species niche. However, we need to be clear about what we mean by a trait. This question,

already considered a 'vital issue' in the 1970s (Gould & Lewontin, 1979), has been debated extensively (e.g. Björklund, 1997; Blows, 2007). Geneticists think of traits in terms of features that are coded for by genes; however, in comparative studies, the definition of a trait is often much broader including attributes such as the behaviour, ecology or environmental preferences of a species (e.g. see ecological 'traits' in Freckleton *et al.*, 2002). Opinions differ as to whether all these factors are traits *per se*, and also whether the term trait applies at the individual-, population- or species-level (Björklund, 1997; Blows, 2007). Here, for the sake of simplicity, we very broadly define traits as any features of a species that can change over time, either by direct genetic control (e.g. morphological features) or indirectly in response to changes in other traits (e.g. the temperature at which a species lives does not evolve directly but changes in response to changes in species thermal tolerances, diet and body size).

Traits and niches

To study PNC, we need to define the traits that might be shaped by niche conservatism. Trait choice is of course shaped by the hypothesis being tested, e.g. for species richness gradients along environmental gradients, the traits used may be species' environmental preferences (e.g. Buckley *et al.*, 2010a). For the methods described later in the text, we outline the kinds of traits which should, and should not, be used for each method (Table 1).

For Grinnellian niches, key traits include species' physiological constraints. However, there are few data on species upper or lower critical limits e.g. lethal temperatures (see Huey *et al.*, 2009; Sinervo *et al.*, 2010 for exceptions). Instead, ecological niche traits must often be derived from environmental variable values across the species geographical range (e.g. Dormann *et al.*, 2010). Sometimes correlative niche modelling is used to detect which environmental variables, or combinations of environmental variables, appear to set the limits of species ranges. These variables are then used as traits (e.g. Stephens & Wiens, 2009; Kozak & Wiens, 2010). However, methodological limitations for the appropriate assessment of variable importance remain, especially as pertaining to the fundamental niche (McPherson & Jetz, 2007; Buckley *et al.*, 2010b).

To precisely define Eltonian niches, information on resource use and species interactions is also needed. Such data are rare, so morphological traits that have a link to resource use are often used instead, e.g. bill shape in Darwin's finches as proxy for dietary information (Lack, 1947). Care must be taken when including morphological traits as not all will be subject to the mechanisms driving niche conservatism: sexually selected traits are a conspicuous example.

Table 1 Summary of macroevolutionary models generating niche conservatism and the types of traits they involve, together with suggested tests and examples.

Type	Outline	Types of traits	Tests	References	Examples
Drift Fig. 1a	Species inherit their niches from ancestors and slowly diverge. Arguably, this is the Brownian model, whereby differences between species accumulate over time	Any trait	Pagel's λ . Blomberg's K . $\lambda = 1$ (or $K = 1$) indicates Brownian evolution	Pagel (1999), Blomberg <i>et al.</i> (2003)	Examples in Freckleton <i>et al.</i> (2002)
Niche retention Fig. 1b	Species have niches which are more similar to their ancestors than expected under Brownian motion. This may result from constraints or stabilizing selection	Most relevant to resource use traits; less to environmental traits, which may change too quickly	Blomberg's K : $K > 1$. Phylogenetic simulations Pagel's δ : $\delta > 1$	Blomberg <i>et al.</i> (2003), Losos <i>et al.</i> (2003), Pagel (1999)	<i>Anolis</i> lizards: Losos <i>et al.</i> (2003)
Phylogenetic inertia Fig. 1c	Rate of niche evolution does not keep pace with change in the environment, and species take a long time to achieve new optimum. Thus, ancestral niches' characters are retained	Any trait provided that the trait evolves more slowly than the changing environmental conditions	SLOUCH: test for constraint on trait and evidence for inertia. Compare fit of Ornstein-Uhlenbeck versus other models	Hansen <i>et al.</i> (2008), Kozak & Wiens (2010)	<i>Lioiaemus</i> lizards: Labra <i>et al.</i> (2009); plethodontid salamanders: Kozak & Wiens (2010)
Niche filling/Shifting Fig. 1d	As evolution proceeds, niches are filled and the differences among the niches of ancestors and descendants become progressively smaller. Particularly applies to adaptive radiations of species within the same guild	Ecological or morphological traits (or select environmental traits) which partition niche space among species within a guild	Freckleton and Harvey's randomization test. Pagel's δ : $\delta > 1$	Freckleton & Harvey (2006), Pagel (1999)	<i>Phylloscopus</i> warblers: Freckleton & Harvey (2006)
Evolutionary rate Fig. 1e	For the same trait in two groups, a higher rate of change in one group compared with another is evidence of less-constrained evolution	Any trait, but more appropriate for environmental or ecological traits	Compare θ , Brownian rate parameter (σ^2), or <i>felsen</i> values	Thomas <i>et al.</i> (2006), Ackerly (2009)	Shorebirds: Thomas <i>et al.</i> (2006)

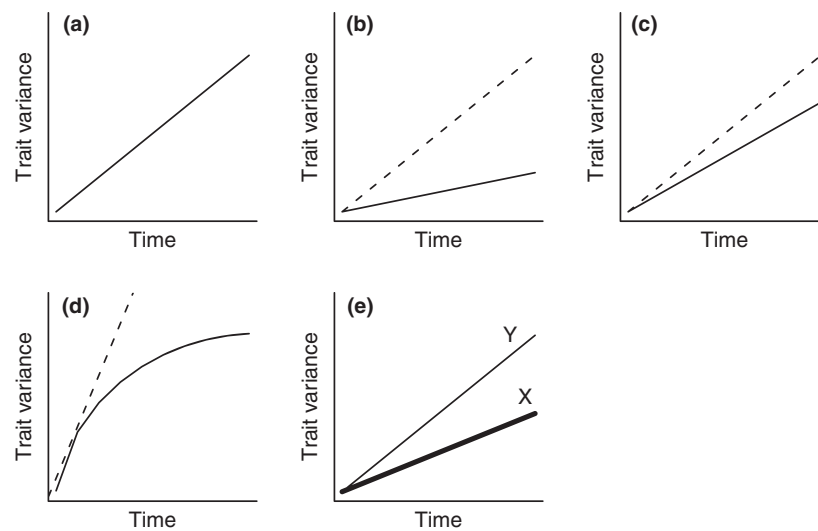


Fig. 1 Conceptual figure showing how the variance of a niche trait should change through time under five different macroevolutionary models of phylogenetic niche conservatism. (a) drift; (b) niche retention; (c) phylogenetic inertia; (d) niche filling; (e) evolutionary rates. In (b), (c) and (d), the dashed line represents the prediction under Brownian motion, which would not be considered niche conservatism under these three models. In (e), two clades are being compared: clade X is evolving more slowly than clade Y, i.e. clade X shows more niche conservatism under the evolutionary rates model. Note that some of these models result in very similar patterns making it impossible to discriminate between them. Therefore, clearly defining the hypothesized underlying model *a priori* is crucial. See text and Table 1 for more details.

Macroevolutionary models of niche conservatism

Table 1 contains a summary of five macroevolutionary models thought to generate PNC. Figure 1 shows how the variance of niche traits is expected to change through time for each of the five different models. We discuss these in more detail later in the text with recent examples from the literature. We focus on these five macroevolutionary models because our aim was to associate each model with a comparative method. For this reason, we include only phylogeny-based methods (for details on a variety of additional, not necessarily comparative phylogenetic research approaches, see Wiens *et al.*, 2010). We recommend that researchers consider which macroevolutionary model best fits their hypotheses and data, and then test for PNC using this model. Some of these models result in the same patterns (Fig. 1) making it impossible to discriminate between them. Therefore, using all five models on one data set would be counterproductive because these models could give conflicting results, so clearly defining the hypothesized underlying model *a priori* is crucial.

Drift

The simplest macroevolutionary model for PNC is that species inherit their niches from their ancestors and then slowly diverge over time. This is essentially the Brownian

motion model of trait evolution whereby traits evolve up the phylogeny via random walk, and trait differences accumulate over time (Fig. 1a; Felsenstein, 1973, 1985). Predictions of ‘niche similarity’ are essentially based on this model (e.g. Peterson *et al.*, 1999). The easiest way of testing whether or not niche traits evolve according to Brownian motion is to estimate Pagel’s λ (Pagel, 1999). λ is a multiplier of the off-diagonal elements of a variance-covariance matrix, which best fits the distribution of data at the tips of a phylogeny (Freckleton *et al.*, 2002). It is estimated using maximum likelihood and varies from 0, where traits have no phylogenetic structure, to 1, where traits evolve according to a Brownian process. To test the drift model of PNC, λ should be estimated and then likelihood ratio tests can be used to test whether λ is significantly different from 1. If λ is not significantly different from 1, this indicates that the niche trait is evolving by Brownian motion. As an alternative measure of phylogenetic signal, Blomberg’s K can also be estimated (Blomberg *et al.*, 2003). Between 0 and 1, K has the same interpretation as λ . Values of K higher than 1 indicate that species traits are more similar than expected under Brownian motion (see niche retention).

We note, however, that phylogenetic signal is not a symptom unique to PNC. High phylogenetic signal does not always mean that traits are ecologically conserved and, conversely, low phylogenetic signal does not necessarily mean that traits are labile (Revell *et al.*, 2008). It could even indicate evolutionary stasis i.e. trait

conservatism (Wiens *et al.*, 2010). Instead, phylogenetic signal is context (i.e. data and phylogeny) dependent and can be influenced by scale, convergent evolution, taxonomic inflation and cryptic species (Losos, 2008). For example, a trait that has not been subject to any selection and is evolving according to drift will show a Brownian pattern of trait evolution. Hansen *et al.* (2008) noted that this process is identical to one in which traits were evolving to an optimum which itself evolved according to a Brownian process (i.e. the Ornstein–Uhlenbeck (OU) model of evolution, see phylogenetic inertia). Because of this, using λ or K (or any other measure of phylogenetic signal e.g. Mantel tests) to infer PNC must be performed with consideration of the traits involved and hypotheses to be tested. Phylogenetic dependence in traits that are assumed to be key niche traits can be taken as evidence of PNC. However, phylogenetic dependence in general cannot.

Not all researchers agree that finding phylogenetic signal in a niche variable indicates niche conservatism. Losos (2008) argued that although evidence of phylogenetic signal is necessary to demonstrate PNC, niches need to be more similar than expected under Brownian motion to truly be conserved (see niche retention). Wiens *et al.* (2010), on the other hand, believe that phylogenetic signal alone can constitute evidence of PNC, even if the signal is weak (i.e. λ or $K > 0$). Such differences in opinion certainly contribute to the confusion about PNC. We believe that phylogenetic signal alone can provide evidence of PNC under the drift model, but only if λ or K is not significantly different from 1, i.e. if niche evolution is Brownian. λ or K values significantly lower than 1 may be the result of processes described previously (see Revell *et al.*, 2008).

Example

Freckleton *et al.* (2002) took data from 26 sources and 106 ecological traits and estimated Pagel's λ for each. They discovered that for a number of these traits (e.g. actual evapotranspiration in termites), λ estimates were not significantly different from 1. Therefore, provided these traits are considered to be key niche traits, we can conclude that they are phylogenetically conserved.

Practicalities

R functions for estimating λ : *pglmEstLambda* in CAIC (available from <http://R-Forge.R-project.org/projects/caic>), or *fitContinuous* in GEIGER (Harmon *et al.*, 2008). R functions for estimating K : *Kcalc* in picante (Kembel *et al.*, 2010).

Niche retention (or niche equivalency)

Here, the niches of ancestors and their descendents are more similar than expected under the Brownian motion model (PNC *sensu* Losos, 2008). In some cases, ancestors and descendents may even have virtually identical niches

in reality there is likely to be some change over time but this will always be slower than expected under Brownian motion). This is probably the most common type of PNC discussed in both the evolutionary and palaeontological literature (e.g. Graham *et al.*, 2004; Eldredge *et al.*, 2005; Knouft *et al.*, 2006; Pfenninger *et al.*, 2007; Losos, 2008; Warren *et al.*, 2008), and anecdotal evidence of niche retention abounds (e.g. half of all angiosperm families are restricted to the tropics; Ricklefs & Renner, 1994). Niche retention may be the result of stabilizing selection or evolutionary constraints such as those imposed by developmental, physiological or population-level genetic factors (Wiens *et al.*, 2010; Wiens, 2004; Wiens & Graham, 2005).

Tests of niche retention are not always in the context of the Brownian model and range from comparisons of fossil taxa to their modern counterparts (e.g. *Ginkgo*; Royer *et al.*, 2003) to quantitative approaches involving niche models (Graham *et al.*, 2004; Warren *et al.*, 2008). A simple method may be to estimate Blomberg's K (see 'Drift'; Blomberg *et al.*, 2003) as values of K higher than 1 indicate that species traits are more similar than expected under Brownian motion. Pagel's δ (Pagel, 1999) could be used in a similar way. For this method, node depths are raised to the power δ and maximum likelihood is used to find the value of δ , which best fits the data. $\delta > 1$ indicates that traits change proportionally more in later branches, i.e. recent evolution influences traits more than changes deeper in the phylogeny. $\delta < 1$, on the other hand, implies that traits change rapidly early in the phylogeny but remain stable closer to the present. Therefore, low values of δ for key niche traits can be interpreted as evidence of niche conservatism.

Alternatively, phylogenetic simulations could be used, i.e. niche trait data for a phylogeny could be simulated using a chosen model of evolution. Differences among these simulated niche traits can be compared to real differences among species or clades to determine whether observed niche differences are less than expected under Brownian motion (Losos *et al.*, 2003; Losos, 2008).

Example

Losos *et al.* (2003) investigated niche conservatism in 11 species of Caribbean *Anolis* lizards. They calculated the ratio of the mean ecological distance among species within the clade and the mean ecological distance of species within the clade to other species. If there is significant niche conservatism, the expectation is that this ratio will be small, i.e. little difference within clades but large differences among clades. They compared these observed ratios to those calculated using phylogenetic simulations (using gradual or speciation modes of evolution). The ecological differences among clades were not significantly smaller than expected by random divergence (drift) and therefore their results suggested that these species of *Anolis* have fairly labile niches

according to the niche retention model. Note that the opposite conclusion would apply if using the drift model.

Practicalities

R functions for estimating K : *Kcalc* in *picante* (Kembel *et al.*, 2010). R functions for estimating δ : *fitContinuous* function in *GEIGER* (Harmon *et al.*, 2008).

Performing phylogenetic simulations requires the following R functions: (i) for calculating phylogenetic distances: *cophenetic* in *ape* (Paradis *et al.*, 2004), (ii) for calculating distance matrices: *dist* in *stats* (R Development Core Team, 2009), (iii) for simulating data on a phylogenetic tree: *sim.char* function in *GEIGER* (Harmon *et al.*, 2008).

Phylogenetic inertia

Phylogenetic inertia occurs where the rate of evolution of a trait is too slow to match the rate of change of an external driver such as environmental change (Hansen, 1997; Labra *et al.*, 2009). Because of this, species take a long time to reach a new trait optimum in a changed environment, thus retaining ancestral niche characteristics. This model could be applied to any kind of trait; however, there must be some mechanism whereby the trait examined is constrained such that it evolves more slowly than the environment.

Phylogenetic inertia can be detected using a modified form of the OU model of evolution. The OU model is an adaptation of the Brownian model where trait values evolve towards an optimal phenotype which itself evolves by Brownian motion (Lande, 1976; Felsenstein, 1988; Hansen, 1997). This model incorporates a parameter that explicitly measures phylogenetic inertia, according to which the rate of evolution of the focal trait to the optimum is lagged relative to the change in trait optimum (Hansen *et al.*, 2008). This model may be parameterized and tested using maximum likelihood methods.

Wiens *et al.* (2010) recommend fitting OU, Brownian and white noise models to niche traits and then comparing the fit of the models. For phylogenetic inertia, the OU model is predicted to fit significantly better than either the Brownian or white noise model and provide evidence of niche conservatism (e.g. Kozak & Wiens, 2010, provided that the niche variables of all species are tightly constrained to the optimum or optima). A strong fit of the Brownian model would also indicate PNC by the drift model (Wiens *et al.*, 2010). This approach is very dependent on interpretation, however. Notably, a significant fit of the OU model is usually almost identical to finding a value of λ or $K < 1$ for the same data set, which under the drift model is evidence against PNC. Thus, the interpretation of conservatism in the context of the OU model and phylogenetic inertia is that traits fail to track phylogeny because they evolve too slowly; in the context

of the drift model, traits fail to track phylogeny because they evolve too quickly.

Example

Kozak & Wiens (2010) fitted white noise, Brownian and various OU models to the climatic niches of North American plethodontid salamanders (Plethodontidae). They found that the best fitting models were OU models that assumed separate adaptive optima for climatic regimes located at low, mid, and high elevations. They conclude that the broad-scale climate niches of salamanders showed PNC.

Practicalities

R functions for fitting OU models of evolution: *fitContinuous* function in *GEIGER* (also Brownian models; Harmon *et al.*, 2008), or *oubm.fit* in *SLOUCH* (Hansen *et al.*, 2008).

Niche filling/shifting

During clade radiations, there are two opposing predictions about how niches will evolve. In a niche filling model, as evolution proceeds, niches are filled and as a consequence, the phenotypic distance from old niches to new niches becomes smaller and smaller, and the niches of new species look more and more like those of their ancestors (Fig. 1d; Price, 1997; Harvey & Rambaut, 2000; Freckleton & Harvey, 2006). In the alternative case, as a consequence of selection to exploit new resources, the niches of new species shift into a different portion of niche space and are thus more different than expected under random drift. This model only applies to ecological or morphological traits that partition Eltonian niche space among species within a guild. It is therefore not necessarily directly applicable to broad-scale environmental niches unless the clade partitions environmental niche space among its members as, for example, in groups where different species live at different elevations (e.g. some New Guinean possums; Flannery, 1995).

Testing the niche filling model can be performed using the randomization test described in Freckleton & Harvey (2006). First, the trait variance of the original data is calculated and standardized contrasts (independent contrasts divided by the square root of the sum of the branch lengths between the node and its descendents) are estimated. These standardized contrasts are then randomized on the tree a number of times, with the trait variance estimated for each pseudoreplicate. Finally, the distribution of the trait variances calculated using the previously generated pseudoreplicates is compared to the observed trait variance (see Freckleton & Harvey, 2006 for more details). Under the null model of random drift, the observed variance is expected to lie within the distribution of random trait variances. If the variance is lower than expected, then differences among the niches of close relatives are also less than expected, indicating

niche conservatism by the niche filling model. If the variance is larger than expected, this may indicate a niche shift.

An alternative test is to estimate Pagel's δ (1999) (see niche retention). Niche filling fits the pattern of trait changes diminishing towards the present i.e. $\delta < 1$; therefore, low values of δ in niche traits can provide evidence for the niche filling model.

Example

Freckleton & Harvey (2006) used their randomization test to determine whether two radiations of warblers occurred via a niche filling model. As traits, they used two components of feeding ecology: body size and prey size. They found that Old World leaf warblers (*Phylloscopus*; 12 species) showed significant evidence of PNC by niche filling, whereas the evolution of the *Dendroica* warblers (14 species) was better fitted by a Brownian motion model (leading to the conclusion that there is not niche conservatism under the niche filling model, although this would be PNC under drift).

Practicalities

R functions for randomization test: *pic* in ape to calculate standardized contrasts. Alternatively, a program (Mac OS X format) and C++ Code to perform the randomization tests are available from the supplementary information of Freckleton & Harvey, 2006 (Data set S1). R functions for estimating δ : *fitContinuous* function in GEIGER (Harmon *et al.*, 2008).

Evolutionary rate

Clades with low rates of niche evolution have similar ancestors and descendants and should therefore have conserved niches. Unlike the four macroevolutionary models described previously, calculating the rate of evolution across all species in a group will not be very useful. Instead, comparing rates of evolution in niche traits among clades can be used to infer differences in the degree of PNC among groups (Ackerly, 2009), i.e. clades with lower rates of evolution will have more conserved niches than clades with higher rates of evolution. This method applies only to comparisons of the degree of niche conservatism amongst groups (e.g. in Fig. 1e, clade X shows more PNC than clade Y) and can be used with any trait though it is probably most appropriate for ecological or environmental traits. Such traits are likely to evolve quickly enough for differences to be detected, and will be less influenced by other selection pressures and constraints, compared to morphological traits. Note that this method alone does not test whether niches are conserved or not, but instead provides information on differences in the degree of PNC among traits or groups.

Evolutionary rate can be measured in a number of ways. For example, if traits are distributed paraphyletically (i.e. distributed across different clades so that the

trait does not just appear in all the descendants from one ancestor) one can estimate θ (Thomas *et al.*, 2006). This is a parameter that measures the ratio of the rate of evolution of a trait on branches with one state, relative to branches in another state, accounting at the same time for differences in the mean state of traits on these two sets of branches. Alternatively, one can estimate the Brownian rate parameter, σ^2 , which describes the rate at which the trait values of related species diverge from one another and is equal to the rate of change in traits per unit time (Felsenstein, 1985). Other measures of rate such as the 'felsen', the rate of phenotypic diversification defined as an increase of one unit per million years in the variance among sister taxa of natural log-transformed trait values (Ackerly, 2009), could also be used.

Example

Thomas *et al.* (2006) estimated θ values for shorebird species (Charadrii) with different developmental strategies, specifically those with young that feed themselves (precocial) versus those with young that are fed by their parents (semi-precocial). As niche traits, they used parental care, mating behaviour and secondary sexual characters. They found that rates of evolution of these traits were generally higher in species with precocial young, i.e. species with semi-precocial young showed more niche conservatism than species with precocial young.

Practicalities

R functions for estimating σ^2 : standardized independent contrasts can be calculated using the *pic* function of ape (Paradis *et al.*, 2004), then entered into the following equation to estimate σ^2 :

$$\sigma^2 = \frac{\sum (\text{standardized independent contrasts})^2}{\text{number of species}} \quad (1)$$

or the *fitContinuous* function in GEIGER (Harmon *et al.*, 2008) can be used although this is slower.

Key assumptions

First, on a methodological note, most methods discussed previously require a phylogeny with reasonably well-estimated topology and branch lengths, a requirement that would have been strongly limiting only 10 years ago, but that can now be met, thanks to recent progress in both molecular (Sanderson, 2002, 2003; Thorne & Kishino, 2002; Drummond *et al.*, 2006; Drummond & Rambaut, 2007) and paleontological dating (Marshall, 1997, 2008; Marjanović & Laurin, 2007, 2008). Extensive compilations of time-calibrated trees are now becoming available (Hedges & Kumar, 2009), so this should not be a major limitation. Note that phylogenies with arbitrary branch lengths (e.g. all branch lengths of equal length) are not appropriate for these kinds of analyses.

One of the key issues we highlight is that tests for niche conservatism are usually made on the strong assumption that the traits examined are indeed niche traits, which influence the survival of the species involved. If this assumption is not correct, then tests of conservatism may go astray. For example, as highlighted previously, strong phylogenetic dependence is compatible both with random neutral drift and with strong selection to an optimum (Hansen *et al.*, 2008), which are two opposing models for trait evolution. In the former case, niches are conserved (according to the drift model), in the latter they are not, inasmuch as traits are evolving rapidly in response to changes in the environment. In one model, a phylogenetic signal arising from random neutral drift would not qualify as PNC, but in another, it would (but see Wiens *et al.*, 2010 for different viewpoint). Further, as illustrated by Freckleton & Jetz (2009), potentially spurious phylogenetic dependence may arise from the spatial proximity of closely related species (e.g. because of dispersal limitation) combined with the strong spatial autocorrelation inherent in environmental variables. Both issues may inflate the apparent strength and shape of environmental constraints on species distributions and may strongly limit the degree to which 'environmental traits' represent actual physiological limits or some approximation of the fundamental niche. In turn, lack of phylogenetic signal cannot be taken as evidence of lack of evolutionary constraints on niches. It may simply be that traits that show weak signal do not have any fitness consequences for individuals. This possibility should not be ignored, particularly when examining the lability of environmental niches. Environmental variables, e.g. as averaged across species' geographical ranges or derived from correlative niche models, may show very weak phylogenetic signal. This may arise from samples being collected at the wrong scale (grain) or with a geographical/environmental bias (Menke *et al.*, 2009). One explanation for this is that certain environmental variables may not represent part of species niches at all, and that ranges are distributed with no direct influence of environmental variables on the evolution of niches. Tests of niche conservatism are made on a strong assumption that this is not the case, as tests for niche conservatism do not test whether niches are influenced by environment: rather they test different mechanisms by which this influence evolves.

Conclusions

There is a lot of disagreement in the literature about niche conservatism, with confusion over its precise definition and the best method with which to test for its presence. This is particularly problematic since PNC varies along a continuum and is affected by scale or point of reference – to some extent, all niches are labile because species niches are not identical, but equally all species share some similarities (e.g. they all inhabit Earth) so are also somewhat conserved (Wiens &

Graham, 2005; Warren *et al.*, 2008). We believe that a lot of this confusion can be alleviated if researchers think carefully about their hypotheses and then choose an appropriate test depending on the macroevolutionary model, which they believe underlies the pattern in their group. Wiens (2008), Wiens *et al.* (2010) suggest that stating whether PNC occurs or not in a given trait is not very 'fruitful'. Instead, one should be testing a specific hypothesis about the effects PNC may have in a particular case. The macroevolutionary model framework proposed here offers a robust way with which to test many of these hypotheses. For example, the effects of global change on species distributions may be best modelled by testing for phylogenetic inertia as the concern is that the environment will change more quickly than species niches are able to evolve. Adaptive radiations could be investigated using niche filling models. Latitudinal gradients in species richness could be modelled using drift or niche retention methods. Testing for the presence of PNC with a clear underlying model should therefore help to clarify the niche conservatism literature.

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