

**IDEA AND
PERSPECTIVE**

Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species

Jonathan B. Losos*
Museum of Comparative
Zoology and Department of
Organismic and Evolutionary
Biology, Harvard University,
26 Oxford Street, Cambridge,
MA 02138, USA
*Correspondence: E-mail:
jlosos@oeb.harvard.edu

Abstract

Ecologists are increasingly adopting an evolutionary perspective, and in recent years, the idea that closely related species are ecologically similar has become widespread. In this regard, phylogenetic signal must be distinguished from phylogenetic niche conservatism. Phylogenetic niche conservatism results when closely related species are more ecologically similar than would be expected based on their phylogenetic relationships; its occurrence suggests that some process is constraining divergence among closely related species. In contrast, phylogenetic signal refers to the situation in which ecological similarity between species is related to phylogenetic relatedness; this is the expected outcome of Brownian motion divergence and thus is necessary, but not sufficient, evidence for the existence of phylogenetic niche conservatism. Although many workers consider phylogenetic niche conservatism to be common, a review of case studies indicates that ecological and phylogenetic similarities often are not related. Consequently, ecologists should not assume that phylogenetic niche conservatism exists, but rather should empirically examine the extent to which it occurs.

Keywords

Phylogenetic effect, phylogenetic niche conservatism, phylogenetic signal.

Ecology Letters (2008) 11: 995–1007

INTRODUCTION

...species of the same genus have usually, though by no means invariably, some similarity in habits and constitution...

(Darwin 1859, p. 76)

In the last decade, ecologists increasingly have become interested in the extent to which Darwin was correct that closely related species tend to be ecologically similar. This focus stems from a number of related interests. At the broadest level, ecologists are interested in the evolutionary tapestry of life: how has ecological diversification produced the biological diversity we see today? In a similar vein, community ecologists now frequently compare the degree of phylogenetic relatedness of community members to that of species source pools to draw inferences about the processes structuring communities. In addition, the application of phylogenetic comparative methods to statistical analyses of ecological data is predicated on the

assumption that closely related species tend to be ecologically similar.

The relationship between phylogenetic relatedness and ecological similarity among species has been investigated using two approaches. The first is to quantify phylogenetic signal¹, which is the 'tendency for related species to resemble each other more than they resemble species drawn at random from the [phylogenetic] tree' (Blomberg & Garland 2002, p. 905). Phylogenetic signal would result if characters evolve in a Brownian motion-like manner, in which the amount of change in any given interval is generally small and random in direction; such a pattern of evolution could ensue either from genetic drift or from natural selection that randomly fluctuated through time in direction and magnitude. Consequently, in this scenario, a relationship would be expected

¹Also termed 'phylogenetic effect' (Derrickson & Ricklefs 1988). 'Phylogenetic inertia' is sometimes also used to mean the same thing, but this term has a long and twisted history in which it has taken a variety of different meanings to different workers (reviewed in Blomberg & Garland 2002).

between the degree of phylogenetic relatedness, quantified as the time since divergence between pairs of species, and the degree of phenotypic similarity between them; the less the amount of time since two species shared a common ancestor (i.e. the more closely related the two species), the less the expected phenotypic difference between them (Blomberg & Garland 2002).

The second approach to understanding the relationship between ecological and phylogenetic similarities revolves around the idea of 'phylogenetic niche conservatism' (PNC). In contrast to explanations for phylogenetic signal, the existence of PNC suggests that some factor is causing closely related species to be *more* similar ecologically than would be expected by simple Brownian motion descent with modification² (for discussion of methods to quantify phylogenetic signal and their relevance to PNC, see Freckleton *et al.* 2002; Blomberg *et al.* 2003; Revell *et al.* in press).

Phylogenetic signal and PNC have received increasing attention by ecologists³. In a 2002 *Annual Review of Ecology and Systematics*, Webb *et al.* (2002, p. 487) stated that 'phylogenetic analysis reveals that many (possibly the majority of) lineages studied show evidence for conservatism of dominant ecological character'. Three years later in another *Annual Review of Ecology and Systematics* article entitled, 'Niche conservatism: integrating evolution, ecology, and conservation biology', Wiens & Graham (2005, pp. 521–522) stated 'Species will always inhabit environments that bear some similarity to those of their close relatives... Thus, to some extent, niches will always be conserved. Yet few sister species may share identical niches; so niches may never be perfectly conserved either'.

Many recent studies, however, have taken the more extreme view that phylogenetic signal in ecological characters is widespread and pervasive, and thus constitute the *a priori* expectation when ecological variation within a clade is examined in a phylogenetic context (e.g. Duncan & Williams 2002; Anderson *et al.* 2004; Peres-Neto 2004; Mouillot *et al.* 2006; Swenson *et al.* 2006; Johnson & Stinchcombe 2007). Nonetheless, I believe that the universality of ecological phylogenetic signal and PNC has been overstated. The goal of this paper is to clarify the distinction between phylogenetic

signal and PNC and to examine evidence for the claims that they are ubiquitous. To do so, I must first explicitly define PNC and discuss how it can be quantified. I will then conclude by assessing the implications of this review for understanding the evolution of ecological patterns and processes.

WHAT IS PNC?

Harvey & Pagel (1991) did not actually define PNC, but what they wrote suggested that it occurred for two reasons. First, in the course of species proliferation, unused ecological space may be filled by members of the most ecologically similar species, which then diverge to become a distinct species. As a result, a tendency would exist for ecologically similar species to be closely related. This scenario has been elaborated by Price (1997) and Harvey & Rambaut (2000).

Second, once the environment is fully occupied, the presence of sympatric species, better adapted to using other aspects of the environment, may prevent a species, or its descendants, from departing from its ancestral niche (see also Lord *et al.* 1995; Patterson & Givnish 2002). Habitat selection, in which members of a species prefer to remain in that part of the environment to which they are best adapted, reinforces this stabilizing selection (Ackerly 2003).

Wiens & Graham (2005, p. 519) took a broader view, defining PNC as 'the tendency of species to retain ancestral ecological characteristic', and citing four causes: stabilizing selection; gene flow that prevents populations from adapting to new niches; genetic constraints due to pleiotropy that prevent adaptation to new niches and lack of appropriate genetic variation. This definition of niche conservatism is more expansive in that it includes Harvey and Pagel's ideas, but adds three additional, non-adaptive explanations for niche similarity among related species.

As discussed above, evolutionary change in a Brownian motion-like manner, either under the guidance of genetic drift or randomly fluctuating natural selection, will produce phylogenetic signal (Revell *et al.* in press). Neither Harvey & Pagel (1991) nor Wiens & Graham (2005) considered this similarity to qualify as PNC. Rather, and as the term 'conservatism' implies, PNC refers to the phenomenon that closely related species are *more* ecologically similar than might be expected solely as a Brownian motion evolution. In other words, one would expect related species to diverge ecologically through time. PNC is the observation that related species differ less ecologically than might be expected if ecological diversification had occurred in an unconstrained manner⁴.

²Some workers use 'niche conservatism' and 'phylogenetic signal' interchangeably (e.g. Swenson *et al.* 2007). Because of this ambiguity, Pearman *et al.* (2008) recommended that the term 'niche conservatism' not be used at all. However, Harvey & Pagel's (1991) original use of the term 'phylogenetic niche conservatism', and its treatment in an authoritative recent review (Wiens & Graham 2005), make clear the important distinction between them: phylogenetic signal is a relationship between ecological and phylogenetic similarities, whereas PNC is the phenomenon that closely related species are more similar ecologically than expected based on phylogenetic relationships.

³A search for 'phylogenetic niche conservatism' on Google Scholar will reveal that nearly half of all scientific articles using this term were published after 2005.

⁴In Wiens and Graham's definition of PNC quoted above, 'retain' should probably be interpreted to mean that descendants diverge ecologically from their ancestors less than would be expected if no deterministic processes were affecting ecological evolution.

HOW PREVALENT ARE PNC AND ECOLOGICAL PHYLOGENETIC SIGNAL?

Several recent papers have mentioned that published studies on environmental niche modelling do not consistently detect phylogenetic signal, but these conclusions have been based on relatively few studies (Knouft *et al.* 2006; Webb *et al.* 2006b; Pearman *et al.* 2008). Here I review the studies of which I am aware that have quantified a relationship between phylogenetic relatedness and all kinds of ecological similarity. Given that these studies encompass a huge range of taxa, traits, and phylogenetic and analytical methods, I agree with Pearman *et al.* (2008) that a formal meta-analysis would be premature. I also mention a number of studies that have presented qualitative evidence concerning the existence of phylogenetic signal and PNC.

Although 'niche' is the middle word in PNC, most studies have been more narrowly focused on particular ecological variables. Wiens and Graham (2005, p. 521) 'focus on niche conservatism in a very restricted sense in that we emphasize how conservatism in climatic tolerances limits geographic ranges of species and clades', whereas Webb *et al.* (2002, p. 487) '...show evidence for conservatism of dominant ecological character'.

In this spirit, my discussion below will include studies that measure any aspect of ecology (e.g. habitat type, diet)⁵. However, I do not consider studies that use morphological surrogates for ecology (e.g. Böhning-Gaese *et al.* 2003; Ackerly *et al.* 2006; Kerkhoff *et al.* 2006; Slingsby & Verboom 2006; Swenson *et al.* 2007) because morphology does not necessarily predict ecology, and most studies do not investigate the relationship between the two [admittedly, in some cases, the rationale for expecting a strong ecomorphological relationship is strong (e.g. Swenson *et al.* 2007), but I felt that deciding whether to include such studies on a case-by-case basis would introduce too much subjectivity]. I also do not include studies that are not explicitly phylogenetic (e.g. nested analysis of variance approaches, usually based on taxonomic ranks); such studies show the same general pattern of mixed results as discussed below.

Case studies

Two approaches have been taken to documenting PNC. The first is the detection of old clades that show little ecological variation among species. For example, all

actinopterygian fish are aquatic (Wiens & Graham 2005) and many families of flowering plants are limited to the tropics, without a single member that has been able to cross into temperate areas (Ricklefs & Renner 1994); a variety of other groups show similar tropical patterns (Wiens & Donoghue 2004). Many other large and old clades exhibit little variation in various ecological parameters [e.g. desmognathine salamanders (Kozak *et al.* 2005); many chaparral plants (Ackerly 2004)]. Similarly, data on fossils indicate that clade members have sometimes occupied similar environments throughout the clades' history, also suggesting PNC. Examination of fossil *Ginkgo*, for example, indicates that trees in this genus have utilized disturbed streamside and levee environments since the late Cretaceous (Royer *et al.* 2003). Certainly, such examples suggest that some non-random process is at work to prevent niche expansion in these groups; given their age, if evolutionary diversification had been unconstrained, we would expect to see greater ecological diversity.

Nonetheless, generalizing from a series of case studies can be difficult, and many counterexamples exist. For example, an aquatic lifestyle has repeatedly evolved within tetrapods (Vermeij & Dudley 2000). Similarly, Silvertown *et al.* (2006a) discussed many instances in which congeneric plants differ substantially in aspects of habitat use. Among angiosperms, temperate area trees have evolved repeatedly from tropical ancestors (Ricklefs 2005), and among felids, close relatives often differ greatly in climatic niche (based on phylogeny in Johnson *et al.* 2006).

Statistical approaches

The second approach is statistical. Ecological data for species are compared in a phylogenetic framework to investigate whether a relationship exists between ecological and phylogenetic similarities. In this regard, the distinction between PNC and phylogenetic signal is important. Phylogenetic signal indicates that a relationship exists between the degree of phylogenetic relatedness and phenotypic similarity; by contrast, documentation of PNC requires demonstrating that phenotypic similarity of closely related species is significantly *greater* than would be expected based on phylogenetic relatedness (i.e. phylogenetic signal would have to be even greater than expected to result from Brownian motion). Only a few studies have investigated PNC in this way (e.g. Desdevices *et al.* 2002, 2003; Losos *et al.* 2003), although new statistical methods will facilitate additional investigation (Freckleton *et al.* 2002; Blomberg *et al.* 2003; see also Revell *et al.* in press). Thus, documentation of phylogenetic signal is necessary, but not sufficient, to demonstrate PNC; conversely, lack of phylogenetic signal is sufficient to indicate that PNC does not occur.

⁵I recognize that such characters may not necessarily reflect the 'niche' of a species. No study to date has conducted a formal, comparative study of the niche of a clade (Chase and Leibold, 2003), and hence discussion of PNC in this sense of 'niche' is not possible. However, most of the studies I discuss have measured ecological factors that are probably important components of species' niches.

Phylogenetic signal has been detected in a number of studies, including ecophysiological traits among European plants (Prinzing *et al.* 2001), growth form and habitat use among plant species in Costa Rican rainforests (Chazdon *et al.* 2003), host use in fish parasites (Desdevises *et al.* 2002), diet in non-snake squamates (Vitt & Pianka 2005), herbivore identity among host plants (Weiblen *et al.* 2006), susceptibility to fungal pathogens in Panamanian trees (Gilbert & Webb 2007), ecological determinants of lake occupancy in sunfish (Helmus *et al.* 2007) and climatic niche among neotropical hyliid frogs (Wiens *et al.* 2006). In a particularly novel and intriguing study, Webb *et al.* (2006a) showed that seedling survival was negatively related to the degree of phylogenetic similarity among nearby heterospecific plants, presumably because of a relationship between phylogenetic and ecological similarities (see also Swenson *et al.* 2007, who show that the phylogenetic similarity of neighbouring trees decreases with increasing plant size class).

Phylogenetic information can be used to assess niche conservatism in another way. Peterson *et al.* (1999) compared sister taxa separated by the Isthmus of Tehuantepec and showed that the environmental niche for one species usually was a statistically significant predictor of the environmental niche of its sister taxon [see also Warner *et al.* (in press) for a new approach to analysing these data]. Kozak & Wiens (2006) found a similar pattern among montane salamanders in eastern North America (see also Qian & Ricklefs 2004 on trees of eastern North America and Asia).

On the other hand, lack of a relationship, or even a negative relationship, between phylogenetic and ecological similarity has been reported in a number of studies including niche overlap and habitat use in Florida oaks (Cavender-Bares *et al.* 2004) and English meadow plants (Silvertown *et al.* 2006a,b); habitat use, activity time and prey size (using body size as a proxy for the latter) in a community of Cuban *Anolis* lizards (Losos *et al.* 2003); and environmental niche as determined using Geographic Information System (GIS) methods among dendrobatid frogs (Graham *et al.* 2004), *Aphelocoma* jays (Rice *et al.* 2003) and members of the *Anolis sagrei* species group (Knouft *et al.* 2006).

In still other cases, results are mixed. For example,

- Lindeman (2000) found patterns suggesting phylogenetic signal among five species of sympatric turtles, although only one of four ecological variables, diet, was actually significantly related to phylogenetic similarity at the $P = 0.05$ level, and then for only one of two phylogenetic hypotheses;
- Similarity in diet is related to phylogenetic similarity in Amazonian lizards, but the relationship between similarity in habitat use and phylogeny is not significant (Vitt *et al.* 1999);
- In an examination of 151 European birds, Böhning-Gaese & Oberrath (1999) found a significant relationship between phylogenetic similarity and similarity in diet, but no relationship for 11 other behavioural and ecological variables;
- Mouillot *et al.* (2006) found that the number of hosts, but not their taxonomic identity, was conserved in fleas, but the opposite pattern was detected for helminth parasites;
- Freckleton *et al.* (2002) reviewed phylogenetic signal in 26 studies. Most of the characters were potential surrogates for ecological variation (e.g. morphological and physiological characters, latitude); among variables that directly measured aspects of ecology, many, but not all, exhibited a relationship between ecological similarity and phylogenetic relatedness. Some studies showed variation among characters (e.g. a study of lepidopterans found that 'niche axis 1' was unrelated to phylogeny, but 'niche axis 2' was strongly phylogenetically related).

Overall, these results do not support the idea that phylogenetic signal, much less PNC, is ubiquitous. Rather, it occurs in some clades for some traits, but not in others. This conclusion is in accord with Pearman *et al.*'s (2008) review of niche stability and evolution, in which they argue that there are many reasons to expect that niches may sometimes exhibit great evolutionary lability. Consequently, researchers should remain agnostic *a priori* and allow the data to inform about patterns of ecological evolution within a clade.

IMPLICATIONS

The conclusion that phylogenetic signal cannot be assumed for ecological characters has important implications in a number of different respects. In all cases, the solution is straightforward: researchers should collect the requisite ecological data and investigate whether ecological similarity among species is statistically associated with phylogenetic relatedness.

Phylogenetic structure of communities

Ecologists are increasingly investigating the phylogenetic structure of communities to examine whether co-occurring species are more or less closely related to each other relative to species in a regional source pool (Webb *et al.* in press). Interpretation of observed patterns is often predicated, implicitly or explicitly, on the assumption of phylogenetic signal (e.g. Swenson *et al.* 2006; Johnson & Stinchcombe 2007). For example, many studies have detected phylogenetic overdispersion of co-occurring species (i.e. co-occurring species being less phylogenetically related than expected by

chance) and have attributed this phenomenon to competitive exclusion of closely related sympatric species, with the assumption that closely related species are ecologically similar. This conclusion is usually suggested without any data on the actual phylogenetic distribution of ecological traits. As the discussion above indicates, an alternative possibility is that closely related species are ecologically divergent, and that environmental filtering [in which only ecologically similar species can exist at a site (Webb *et al.* 2002)] is responsible for the presence of distantly related, but ecologically similar, species within a community (Kraft *et al.* 2007). By the same token, phylogenetic clustering (i.e. sympatric species being more closely related than expected by chance) could result from environmental filtering and the existence of phylogenetic signal, but also could result from ecological divergence of closely related species facilitating coexistence (Webb *et al.* 2002; but see Kraft *et al.* 2007). In other words, interpretation of patterns of phylogenetic composition of communities is not possible without actual ecological data for the constituent species.

Phylogenetic comparative methods

Now *de rigueur* in any cross-species statistical analysis, phylogenetic comparative methods are predicated on the assumption that species do not represent statistically independent points due to similarity resulting from shared ancestry (Felsenstein 1985). If, however, this assumption does not hold, one may question whether phylogenetic comparative methods should still be used, given the possible errors that could be introduced by mistaken inferences concerning the phylogenetic topology or rates of character evolution. In such cases, non-phylogenetic analyses, which do not require assumptions about tree topology or rates of change, might be preferable (Gittleman & Luh 1994; Bjorklund 1997; Losos 1999; but see Garland *et al.* 2005).

Of course, even if phylogenetic information were not used in such analyses, it would not mean that phylogenetic information is not important. Quite the contrary, only by examining the ecological variation in a phylogenetic context could one determine that no phylogenetic signal exists and thus that phylogenetic comparative methods are unnecessary. Thus, regardless of the existence of phylogenetic signal, phylogenetic information is critical for comparative statistical analyses.

Environmental niche modelling of past and future species

The advent of environmental niche modelling has led increasing numbers of workers to predict the distribution of species either in the past or future. A critical assumption in this enterprise is that environmental niches are stable through time so that the distribution of a species retro- or

prospectively can be predicted based on its niche requirements today. One line of evidence often put forward to support this assumption is the existence of PNC (reviewed in Pearman *et al.* 2008); however, as I have reviewed, PNC is not ubiquitous, and thus its existence cannot be taken as justification for this assumption.

Evolutionary history of a clade

The evolutionary scenarios that would produce PNC are very different from those that would produce an absence of phylogenetic signal. A number of different processes discussed earlier could lead to closely related species being more ecologically similar than expected based on phylogenetic similarity. For example, a scenario in which niche space is progressively filled, providing little opportunity for newly arisen species to diverge greatly would produce such an outcome (Price 1997). More generally, any time the rate of evolutionary divergence was greater early in a clade's history than later on would lead to a phylogeny in which closely related species are more ecologically similar than would be predicted based on their phylogenetic relationships (Revell *et al.* in press). Conversely, convergent evolution is the antithesis of phylogenetic signal. Any situation that promotes convergent evolution among extant species is likely to lead to little or no phylogenetic signal.

DO ECOLOGICAL CHARACTERS DISPLAY LESS PHYLOGENETIC SIGNAL THAN OTHER TYPES OF CHARACTERS?

A number of factors could account for the low phylogenetic signal in ecological characters compared to morphological or physiological characters (Freckleton *et al.* 2002; Blomberg *et al.* 2003). First, many ecological characters exhibit considerable temporal and geographical variation; estimates based on measurements taken from a single population at a single point in time may introduce considerable error into cross-species comparative studies [a similar explanation has been put forth to explain low phylogenetic signal in behavioural characters (Gittleman *et al.* 1996; Blomberg *et al.* 2003)].

Second, environmental factors do not necessarily covary; phylogenetic signal for one ecological feature does not imply signal for other features. Thus, lack of phylogenetic signal for one character does not mean that a clade does not exhibit phylogenetic signal for some other environmental feature, as several of the studies cited above illustrate (e.g. Vitt *et al.* 1999).

SAMPLING, SCALE AND PHYLOGENETIC SIGNAL

The phylogenetic signal of a subset of species may differ from the signal for the more inclusive group. In some cases,

such as the species that occur within a community when compared to all of the species within a region or a clade, the difference in signal may tell us something about the ecological and evolutionary processes that regulate community composition. In other cases, however, sampling may reflect the constraints and methods of a particular study; as a result, differences in signal between the sample and the more inclusive group may be misleading. Sampling may be an issue in a variety of ways: community vs. clade perspectives, degree of phylogenetic inclusiveness and bias due to incomplete sampling of species. I discuss each in turn.

Community vs. clade perspective

Some ecological studies are limited to species from a single community (e.g. Lindeman 2000; Losos *et al.* 2003; Silvertown *et al.* 2006a,b). These studies often show little or no phylogenetic signal. For example, in English meadows 'coexisting [plant] congeners are often as ecologically different from each other as they are from unrelated members of the same communities' (Silvertown *et al.* 2006a, p. S45). By contrast, studies that include a regional pool of species or that sample a clade without regard to area of occurrence detect phylogenetic signal more frequently (e.g. Cavender-Bares *et al.* 2006).

Several different scenarios could produce a situation in which species in local communities do not exhibit phylogenetic signal. First, if closely related species within a regional species pool are ecologically similar, and if a limit to ecological similarity exists, then competitive exclusion would lead to only distantly related species being able to coexist. This 'phylogenetic overdispersion' (Webb *et al.* 2002) would diminish or eliminate PNC within the community, even if it characterizes the clade as a whole (Ackerly *et al.* 2006; Kraft *et al.* 2007).

Second, closely related species may diverge ecologically in sympatry to minimize resource overlap. This divergence would decrease the ecological similarity of closely related species, thus diminishing or eliminating phylogenetic signal within a community (Silvertown *et al.* 2006b), even if it still exists among the species in the broader and more diverse regional pool.

Finally, third, throughout a region, closely related species may diverge in some ecological aspect (e.g. temperature tolerance) to adapt to different parts of the environment, and this divergence may be repeated across many clades, producing suites of distantly related species convergently adapted to the same ecological conditions. If only species with certain ecological attributes (e.g. heat tolerance) can occur in a given community, then communities may be phylogenetically overdispersed and exhibit no phylogenetic signal (Kraft *et al.* 2007). Note that in the first two

processes, phylogenetic signal might exist for the clade as a whole, even if it does not occur among the species within a community. By contrast, in the third scenario, phylogenetic signal likely would not exist either for species within a community, nor for the entire clade.

The only study to explicitly examine these ideas focused on Floridian oaks (Cavender-Bares *et al.* 2004). Closely related oaks species are dissimilar ecologically and tend not to co-occur. Distantly related species that do co-occur are those that have convergently evolved physiological adaptations to the same environmental conditions. This example thus illustrates the third scenario above.

Phylogenetic scale

Cavender-Bares *et al.* (2006) suggested that the degree of phylogenetic signal within a community is a function of phylogenetic scale (i.e. how phylogenetically inclusive a study is); although it may not be evident in particular clades (e.g. oaks), signal may be revealed if the phylogenetic scale of a study is greatly expanded (e.g. to all angiosperms). The data support this claim for Floridian communities (although physiological and morphological characters were used as indirect measures of ecology). However, the lack of phylogenetic signal in English meadows, calculated using all angiosperms (Silvertown *et al.* 2006b), indicates that the universality of this suggestion remains to be tested.

Similarly, when considering entire clades, rather than just communities, phylogenetic scale may be an issue. In many cases, the greater the phylogenetic scale of a study, the stronger the phylogenetic signal may be (Cavender-Bares *et al.* 2006), although few quantitative data are available. On the other hand, on some occasions, a greater phylogenetic scale may decrease evidence of PNC if between-clade convergence has occurred. For example, to the extent that the classic story of marsupial-placental convergence is correct (e.g. Springer *et al.* 1997), the relationship between ecological and phylogenetic similarity may be greater within the placental and marsupial clades than in the more inclusive clade that contains both.

A related issue concerns the recent trend towards dividing what was formerly a single widespread series into many, usually geographically non-overlapping, species on the basis of molecular data. The resulting increase in species-level diversity is a two-edged sword with regard to the estimation of phylogenetic signal. On the one hand, if many currently recognized species actually constitute complexes of closely related but distinct species, then failure to recognize this species level diversity may underestimate the true phylogenetic signal of a clade. Conversely, to the extent that overzealous splitting may lead to a profusion of ecologically similar species-level taxa, then estimates of phylogenetic signal may be increased and may come to primarily reflect

patterns of geographic variation. Of course, this issue boils down to the perennial dispute about what constitutes a species.

Biases due to the particular species included in a study

In cases in which ecological phylogenetic signal exists, a plot of phylogenetic relatedness vs. ecological similarity among all pairs of species often is triangular in shape: closely related species are ecologically similar, but distantly related species exhibit great variation in the degree of ecological resemblance (e.g. Böhning-Gaese *et al.* 2003; Davis 2005). As a result, studies that non-randomly sample to avoid including closely related species – a sampling strategy that would make sense to avoid the problems of phylogenetic signal on statistical analysis – will underestimate the phylogenetic signal in the group as a whole.

The significance of this bias depends on the goal of a study. If the intent is to investigate phylogenetic signal, then sampling should be random and ideally as complete as possible to produce an accurate and unbiased estimate. Alternatively, for many purposes, the phylogenetic signal of the sample may be more relevant than the signal of the group from which it is drawn. For example, with reference to the effect of phylogenetic signal on statistical analyses (discussed above), the relevant concern is the sample under study.

ISLAND VS. MAINLAND

A number of workers (e.g. Webb *et al.* 2002; Edwards & Donoghue 2006) have suggested that lack of phylogenetic signal may be primarily an island phenomenon because insular settings are renowned for their adaptive radiations (e.g. Carlquist 1974), which, because of their high rates of evolutionary diversification early in their history and near simultaneous cladogenesis (Simpson 1953; Schluter 2000), may exhibit low phylogenetic signal (Harvey & Pagel 1991). Certainly, some examples, such as Caribbean *Anolis* lizards (Losos *et al.* 2003; Knouft *et al.* 2006), support this contention. However, a number of the cases of lack of PNC cited above are not obviously from adaptively radiating clades, and most are not from island taxa.

PNC: PATTERN OR PROCESS

Wiens & Graham (2005, p. 519) ‘refer to niche conservatism as a process, although it may be caused by more than one factor at the population level (a feature it shares with other evolutionary processes, such as speciation and anagenesis)’. I do not agree. PNC is a historical pattern of evolution; it is a description of what happened, but it is not a statement about how it happened. The possible underlying causes of

PNC discussed by Wiens & Graham (2005) and Harvey & Pagel (1991) – e.g. lack of genetic variation, stabilizing selection, patterns of niche-filling, gene flow – are fundamentally different. Thus, to state that members of a clade failed to adapt to some aspect of the environment because of PNC is not a mechanistically informative statement and risks fostering the impression that we actually know why this failure to evolve occurred⁶. Rather, PNC is a statement of historical pattern manifest on a phylogeny; its detection invites investigation as to its causes, and the works cited above suggest the possible causes requiring study. A nice example of this sort of approach is Wiens’ (2004a,b) discussion of the role of PNC in allopatric speciation.

CONCLUSIONS

Wiens & Graham (2005) argued that it is no longer fruitful to argue about whether PNC occurs; rather, the field needs to move on to discuss the outcomes of PNC when it does occur. I certainly agree that this is an important issue well worth further investigation. Nonetheless, I also believe that further research into the extent and occurrence of PNC, and phylogenetic signal more generally, is still needed. Many authors take the viewpoint that phylogenetic signal is the expected situation, and thus the null expectation for a given study.

Knouft *et al.* (2006) concluded a review of studies examining the evolution of environmental niches, as determined by GIS approaches, by stating: ‘the balance of evidence to date provides little consistent evidence that environmental niches are phylogenetically conservative’. My examination of the studies above leads me to broaden this conclusion: the evidence at hand does not support the idea that phylogenetic signal should be the expected outcome of evolutionary diversification, particularly at the relatively low phylogenetic levels and with the characters and sampling regimes used by most studies in the field of evolutionary ecology. Only direct examination of the distribution of ecological characters on a phylogeny can provide evidence one way or another for any particular clade.

ACKNOWLEDGEMENTS

This manuscript benefited from critical reading by D. Ackerly, J. Chase, K. Dexter, R. Ricklefs, C. Webb and an anonymous referee, and from assistance with references from R. Glor and L. Harmon.

⁶The same criticism can be levied against the term ‘phylogenetic constraint’, which is often used in the literature as if it were an evolutionary phenomenon on par with developmental, genetic or architectural constraints (Losos and Miles, 1994).

REFERENCES

- Ackerly, D.D. (2003). Community assembly, niche conservatism and adaptive evolution in changing environments. *Int. J. Plant Sci.*, 164, S165–S184.
- Ackerly, D.D. (2004). Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. *Am. Nat.*, 163, 654–671.
- Ackerly, D.D., Schilck, D.W. & Webb, C.O. (2006). Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology*, 87, S50–S61.
- Anderson, M.T., Lachance, M.-A. & Starmer, W.T. (2004). The relationship of phylogeny to community structure: the cactus yeast community. *Am. Nat.*, 164, 709–721.
- Bjorklund, M. (1997). Are 'comparative methods' always necessary? *Oikos*, 80, 607–613.
- Blomberg, S.P. & Garland, T. Jr (2002). Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J. Evol. Biol.*, 15, 899–910.
- Blomberg, S.P., Garland, T. Jr & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745.
- Böhning-Gaese, K. & Oberrath, R. (1999). Phylogenetic effects on morphological, life-history, behavioural and ecological traits of birds. *Evol. Ecol. Res.*, 1, 347–364.
- Böhning-Gaese, K., Schuda, M.D. & Helbig, A.J. (2003). Weak phylogenetic effects on ecological niches of *Sylvia* warblers. *J. Evol. Biol.*, 16, 956–965.
- Carlquist, S. (1974). *Island Biology*. Columbia University Press, New York.
- Cavender-Bares, J., Ackerly, D.D., Baum, D. & Bazzaz, F.A. (2004). Phylogenetic overdispersion in Floridian oak communities. *Am. Nat.*, 163, 823–843.
- Cavender-Bares, J., Keen, A. & Miles, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology*, 87, S109–S122.
- Chase, J.M. & Leibold, M.A. (2003). *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago.
- Chazdon, R.L., Careaga, S., Webb, C. & Vargas, O. (2003). Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecol. Monogr.*, 73, 331–348.
- Darwin, C. (1859). *On the Origin of Species*. J. Murray, London.
- Davis, E.B. (2005). Comparison of climate space and phylogeny of *Marmota* (Mammalia: Rodentia) indicates a connection between evolutionary history and climate preference. *Proc. R. Soc. Lond. B*, 272, 519–526.
- Derrickson, E.R. & Ricklefs, R.E. (1988). Taxon-dependent diversification of life-history traits and the perception of phylogenetic constraints. *Func. Ecol.*, 2, 417–423.
- Desdés, Y., Morand, S. & Legendre, P. (2002). Evolution and determinants of host specificity in the genus *Lamellodiscus* (Monogenea). *Biol. J. Linn. Soc.*, 77, 431–443.
- Desdés, Y., Legendre, P., Azouzi, L. & Morand, S. (2003). Quantifying phylogenetically structured environmental variation. *Evolution*, 57, 2647–2652.
- Duncan, R.P. & Williams, P.A. (2002). Darwin's naturalization hypothesis challenged. *Nature*, 417, 608–609.
- Edwards, E.J. & Donoghue, M.J. (2006). *Pereskia* and the origin of the cactus life form. *Am. Nat.*, 167, 777–793.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.*, 125, 1–15.
- Freckleton, R.P., Harvey, P.H. & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.*, 160, 712–726.
- Garland, T. Jr, Bennett, A.F. & Rezende, E.L. (2005). Phylogenetic approaches in comparative physiology. *J. Exp. Biol.*, 208, 3015–3035.
- Gilbert, G.S. & Webb, C.O. (2007). Phylogenetic signal in plant pathogen-host range. *Proc. Natl Acad. Sci. U.S.A.*, 104, 4979–4983.
- Gittleman, J.L. & Luh, H.-K. (1994). Phylogeny, evolutionary models and comparative methods: a simulation study. In: *Phylogenetics and Ecology* (eds Eggleton, P. & Vane-Wright, R.). Academic Press, London, pp. 103–122.
- Gittleman, J.L., Anderson, C.G., Kot, M. & Luh, H.-K. (1996). Phylogenetic lability and rates of evolution: a comparison of behavioral, morphological, and life history traits. In: *Phylogenies and the Comparative Method in Animal Behavior* (ed. Martins, E.P.). Oxford University Press, Oxford, pp. 166–205.
- 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.
- Harvey, P.H. & Pagel, M.D. (1991). *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Harvey, P.H. & Rambaut, A. (2000). Comparative analyses for adaptive radiations. *Philos. Trans. R. Soc. Lond. B*, 355, 1599–1605.
- Helmus, M.R., Savage, K., Diebel, M.W., Maxted, J.T. & Ives, A.R. (2007). Separating the determinants of phylogenetic community structure. *Ecol. Lett.*, 10, 917–925.
- Johnson, M.T.J. & Stinchcombe, J.R. (2007). An emerging synthesis between community ecology and evolutionary biology. *Trends Ecol. Evol.*, 22, 250–257.
- Johnson, W.E., Eizirik, E., Pecon-Slattery, J., Murphy, W.J., Antunes, A., Teeling, E. *et al.* (2006). The late Miocene radiation of modern Felidae: a genetic assessment. *Science*, 311, 73–77.
- Kerkhoff, A.J., Fagan, W.F., Elser, J.J. & Enquist, B.J. (2006). Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *Am. Nat.*, 169, E103–E122.
- Knauft, J.H., Losos, J.B., Glor, R.E. & Kolbe, J.J. (2006). Phylogenetic analysis of the evolution of the niche in lizards of the *Anolis sagrei* group. *Ecology*, 87, S29–S38.
- 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., Larson, A., Bonett, R.M. & Harmon, L.J. (2005). Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: Desmognathus). *Evolution*, 59, 2000–2016.
- Kraft, N.J.B., Cornwell, W.K., Webb, C.O. & Ackerly, D.D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *Am. Nat.*, 170, 271–283.
- Lindeman, P.V. (2000). Resource use of five sympatric turtle species: effects of competition, phylogeny, and morphology. *Can. J. Zool.*, 78, 992–1008.
- Lord, J., Westoby, M. & Leishman, M. (1995). Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. *Am. Nat.*, 146, 349–364.

- Losos, J.B. (1999). Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods. *Anim. Behav.*, 58, 1319–1324.
- Losos, J.B., Leal, M., Glor, R.E., de Queiroz, K., Hertz, P.E., Rodríguez Schettino, L. *et al.* (2003). Niche lability in the evolution of a Caribbean lizard community. *Nature*, 423, 542–545.
- Losos, J.B. & Miles, D.B. (1994). Adaptation, constraint, and the comparative method: phylogenetic issues and methods. In: *Ecological Morphology: Integrative organismal Biology* (eds Wainwright, P.C. & Reilly, S.M.). University of Chicago Press, Chicago, pp. 60–98.
- Mouillot, D., Krasnov, B.R., Shenbrot, G.I., Gaston, K.J. & Poulin, R. (2006). Conservatism of host specificity in parasites. *Ecography*, 29, 596–602.
- Patterson, T.B. & Givnish, T.J. (2002). Phylogeny, concerted convergence, and phylogenetic niche conservatism in the core Liliales: insights from *rbcL* and *ndbF* sequence data. *Evolution*, 56, 233–252.
- Pearman, P.B., Guisan, A., Broennimann, O. & Randin, C.F. (2008). Niche dynamics in space and time. *Trends Ecol. Evol.*, 23, 149–158.
- Peres-Neto, P.R. (2004). Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. *Oecologia*, 140, 352–360.
- Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, 285, 1265–1267.
- Price, T. (1997). Correlated evolution and independent contrasts. *Philos. Trans. R. Soc. Lond. B*, 352, 519–529.
- Prinzing, A., Durka, W., Klotz, S. & Brandl, R. (2001). The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. Lond. B*, 268, 2383–2389.
- Qian, H. & Ricklefs, R.E. (2004). Geographical distribution and ecological conservatism of disjunct genera of vascular plants in eastern Asia and eastern North America. *J. Ecol.*, 92, 253–265.
- Revell, L.J., Collar, D.C. & Harmon, L.J. (in press). Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.*
- Rice, N.H., Martínez-Meyer, E. & Peterson, A.T. (2003). Ecological niche differentiation in the *Apbelocoma* jays: a phylogenetic perspective. *Biol. J. Linn. Soc.*, 80, 369–383.
- Ricklefs, R.E. (2005). Historical and ecological dimensions of global patterns in plant diversity. *Biol. Scr.*, 55, 583–603.
- Ricklefs, R.E. & Renner, S.S. (1994). Species richness within families of flowering plants. *Evolution*, 48, 1619–1636.
- Royer, D.L., Hickey, L.J. & Wing, S.L. (2003). Ecological conservatism in the 'living fossil' *Ginkgo*. *Paleobiology*, 29, 84–104.
- Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- Silvertown, J., Dodd, M., Gowing, D., Lawson, C. & McConway, K. (2006a). Phylogeny and the hierarchical organization of plant diversity. *Ecology*, 87, S39–S49.
- Silvertown, J., McConway, K.J., Gowing, D.J., Dodd, M.E., Fay, M.F., Joseph, J.A. *et al.* (2006b). Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proc. R. Soc. Lond. B*, 273, 39–44.
- Simpson, G.G. (1953). *The Major Features of Evolution*. Columbia University Press, New York.
- Slingsby, J.A. & Verboom, G.A. (2006). Phylogenetic related limits co-occurrence at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *Amer. Nat.*, 168, 14–27.
- Springer, M.S., Kirsch, J.A.W. & Case, J.A. (1997). The chronicle of marsupial evolution. In: *Molecular Evolution and Adaptive Radiation* (eds Givnish, T.J. & Sytsma, K.J.). Cambridge University Press, Cambridge, pp. 129–162.
- Swenson, N.G., Enquist, B.J., Pither, J., Thompson, J. & Zimmerman, J.K. (2006). The problem and promise of scale dependency in community phylogenetics. *Ecology*, 87, 2418–2424.
- Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007). The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology*, 88, 1770–1780.
- Vermeij, G.J. & Dudley, R. (2000). Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? *Biol. J. Linn. Soc.*, 20, 541–554.
- Vitt, L.J. & Pianka, E.R. (2005). Deep history impacts present-day ecology and biodiversity. *Proc. Natl Acad. Sci. U.S.A.*, 102, 7877–7881.
- Vitt, L.J., Zani, P.A. & Espósito, M.C. (1999). Historical ecology of Amazonian lizards: implications for community ecology. *Oikos*, 87, 286–294.
- Warner, D., Glor, R. & Turelli, M. (in press). Climate niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*.
- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Ann. Rev. Ecol. Syst.*, 33, 475–505.
- Webb, C.O., Gilbert, G.S. & Donoghue, M.J. (2006a). Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology*, 87, S123–S131.
- Webb, C.O., Losos, J.B. & Agrawal, A.A. (2006b). Integrating phylogenies into community ecology. *Ecology*, 87, S1–S2.
- Webb, C.O., Cannon, C.H. & Davies, S.J. (in press). Ecological organization, biogeography, and the phylogenetic structure of tropical forest tree communities. In: *Tropical Forest Community Ecology* (eds Carson, W. & Schnitzer, S.).
- Weiblen, G.D., Webb, C.O., Novotny, V., Basset, Y. & Miller, S.E. (2006). Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology*, 87, S62–S75.
- Wiens, J.J. (2004a). Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, 58, 193–197.
- Wiens, J.J. (2004b). What is speciation and how should we study it? *Am. Nat.*, 163, 914–923.
- Wiens, J.J. & Donoghue, M.J. (2004). Historical biogeography, ecology, and species richness. *Trends Ecol. Evol.*, 19, 639–644.
- Wiens, J.J. & Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Ann. Rev. Ecol. Syst.*, 36, 519–539.
- Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006). Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *Am. Nat.*, 168, 579–596.

Editor, Nicholas Gotelli

Manuscript received 21 March 2008

First decision made 18 April 2008

Manuscript accepted 22 May 2008