



Tansley review

Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes?

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Summary

Phylogenetic niche conservatism (PNC) is the tendency of lineages to retain their niche-related traits through speciation events. A recent surge in the availability of well-sampled molecular phylogenies has stimulated phylogenetic approaches to understanding ecological processes at large geographical scales and through macroevolutionary time. We stress that PNC is a pattern, not a process, and is found only in some traits and some lineages. At the simplest level, a pattern of PNC is an inevitable consequence of evolution – descent with modification and divergence of lineages – but several intrinsic causes, including physicochemical, developmental and genetic constraints, can lead directly to a marked pattern of PNC. A pattern of PNC can also be caused indirectly, as a by-product of other causes, such as extinction, dispersal limitation, competition and predation. Recognition of patterns of PNC can contribute to understanding macroevolutionary processes: for example, release from constraint in traits has been hypothesized to trigger adaptive radiations such as that of the angiosperms. Given the multiple causes of patterns of PNC, tests should address explicit questions about hypothesized processes. We conclude that PNC is a scientifically useful concept with applications to the practice of ecological research.

I. Introduction

A recent surge of interest in phylogenetic patterns of niche-related traits (Table 1) has emerged from the integration of community ecology, biogeography and phylogenetics. When closely related species are found to be ecologically similar, this is termed ‘niche conservatism’ (Harvey & Pagel, 1991; Ricklefs, 2010). *Phylogenetic niche conservatism* (PNC) is the tendency of lineages to retain their niche-related traits through speciation events and over macroevolutionary time (e.g. Ackerly, 2003; Cooper *et al.*, 2010; Wiens *et al.*, 2010).

It was pointed out in 2008 that nearly half of all articles found in Google Scholar referring to ‘phylogenetic niche conservatism’ had been published in the previous 3 yr (Losos, 2008a). By 2011, 55% of all the 664 articles indexed in Google Scholar using that term had been published in the previous 3 yr; hence, the literature on this topic has continued to grow rapidly (Fig. 1). Given the rapid recent growth in this literature, it is perhaps surprising that PNC was recognized more than a century ago by Tansley (1904), who stated (p. 193) that floristic diversity was geographically structured, *inter alia*, by ‘phylogenetic’ causes, and that in extreme instances some families ‘have become so highly specialised to particular

Table 1 Definitions

Term*	Definition
Niche	In use of this concept, we follow Cooper <i>et al.</i> (2010), Ricklefs (2008) and references therein. Broadly, the niche is the set of ecological conditions under which a species survives and individuals reproduce. It is usual to distinguish between the fundamental niche and realized niche. The fundamental niche is the set of conditions under which a species can exist, including physical conditions, vegetation and available resources. However, interactions with other organisms (competitors, pathogens and mutualists), and the capacity of the species to disperse and establish, limit opportunities to occupy the full potential range, resulting in a smaller actual or 'realized' niche (Hutchinson, 1957; Begon <i>et al.</i> , 2006; Losos, 2008a; Cooper <i>et al.</i> , 2010; Ricklefs, 2010). Although defined at the level of species, 'niche' is applied to clades in the PNC literature and, at this scale, is not well studied or formally defined (Losos, 2008a). Clearly, some processes that are important within species, such as sexual reproduction, do not apply at the level of clades. However, given that clades share ecological traits through heritability and descent, we assume that it is meaningful to discuss 'niche' at the level of clades.
Trait	We use 'trait' in the standard biological sense, that is, an observable heritable feature of an organism. Because the ecophysiological tolerances of few organisms have been investigated thoroughly, if at all, more readily observed 'traits' are used as surrogates for the assumed underlying functional traits of organisms. For example, traits related to climatic adaptations are often estimated using environmental niche modelling of their known distributional occurrences (Phillips <i>et al.</i> , 2006) and floral colour, scent and morphology are used as a proxy for pollination syndrome in plants (Fenster <i>et al.</i> , 2004). However, an erroneous assumption that a trait is niche-related, combined with a weak phylogenetic signal in the trait, could falsely lead to the conclusion that evolutionary constraint on niches is lacking in a lineage (Cooper <i>et al.</i> , 2010). Thus, PNC is always trait-specific and surrogacy assumptions should be tested (Sutherland & Bourne, 2009).
Constraint	Evolutionary constraint is an inherited bias or limitation on the genotypic or phenotypic variation within a lineage, such as developmental, genetic or architectural (e.g. allometric) constraints (Losos, 2011; Wagner, 2011b). Constraints can limit the range of adaptations and innovations that are exposed to drift and selection and thus result in PNC. Although used widely in the literature on PNC (e.g. Cooper <i>et al.</i> , 2010; Wiens <i>et al.</i> , 2010; Losos, 2011), this term is often misused ('phylogenetic constraint'; Losos, 2011). For an extended discussion on constraints, see Wagner (2011b, chapter 12). <i>Contra</i> Wagner, we exclude selection from constraints because they can act separately to limit variation, for example selection can act to eliminate or maintain a constraint.

*The terms 'niche', 'trait' and 'constraint' are widely used in ecology and comparative biology, and have been subjects of dispute. Here, we briefly clarify our usage of these terms. PNC, phylogenetic niche conservatism.

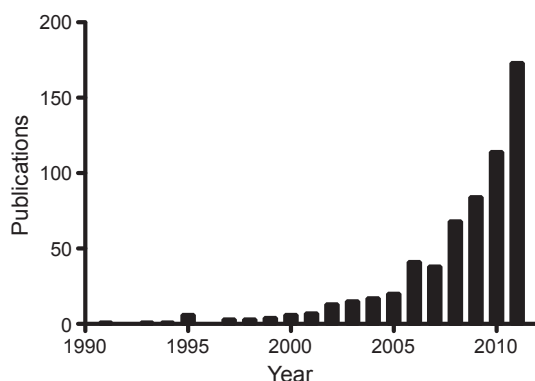


Fig. 1 Literature found in Google Scholar using the keywords 'phylogenetic niche conservatism', plotted against the date of publication. The search was conducted at the end of 2011.

circumstances of life as to preclude the possibility of their spreading beyond the area of prevalence of these particular environmental conditions'.

Increasingly, studies in biogeography and community assembly consider PNC and its underlying causes because they can help to explain (in combination with dispersal limitation and biotic interactions such as competition) why all groups of organisms do not appear in all geographic regions, biomes and communities. For example, the tropical conservatism hypothesis purports to explain the latitudinal diversity gradient by hypothesizing that many lineages of organisms originated in the tropics but, as a result of physiological constraints (or similar), have been unable to make the transition to temperate climates or, if they did so, were vulnerable to extinction in the climatically variable temperate latitudes

(Wiens & Donoghue, 2004; Löwenberg-Neto *et al.*, 2011; Condamine *et al.*, 2012). Recent multivariate investigations of community assembly have often found a significant pattern of PNC (Leibold *et al.*, 2010; Kooyman *et al.*, 2011; Sander & Wardell-Johnson, 2011; Schnitzler *et al.*, 2011; Hardy *et al.*, 2012; Ricklefs & Renner, 2012). For example, by comparing tropical forests along environmental gradients in India and Panama, Hardy *et al.* (2012) found that the realized climatic niches were strongly correlated between regions in shared clades, even though no species were shared.

'Phylogenetic biome conservatism' (Crisp *et al.*, 2009) is niche conservatism at the largest scale: at the geographical level of biomes and continents, and through long periods of macroevolutionary time. Here we concentrate on PNC, in which we include biome conservatism. We first discuss whether PNC is a pattern or a process and conclude that it is a pattern resulting from a diversity of processes, some of which act indirectly. Then we consider how we can test for patterns of PNC, focussing on its hypothesized drivers. Finally, we use examples to illustrate the scientific utility of considering patterns of PNC.

II. What is phylogenetic niche conservatism?

A pattern of PNC could be an inexorable result of divergence between lineages through time (Cavender-Bares *et al.*, 2009). As closely related species share heritable traits through descent, then, as lineages diverge, traits will be more similar within clades than they are between clades. Simulation studies show that when a trait is evolved on a phylogeny under Brownian motion (BM) using a drift model, the trait exhibits a significant phylogenetic signal (PS), or

‘phylogenetic effect’ (Derrickson & Ricklefs, 1988; Losos, 2011), such that closely related species are more similar in trait values than are species selected at random from the tree (Blomberg *et al.*, 2003; Revell *et al.*, 2008). For a niche-related trait, this pattern fits the definition of PNC given above and, in this sense, PNC could be considered an inevitable consequence of evolutionary descent. Moreover, tests that are commonly used to detect PS, such as Blomberg’s *K* and randomization of the tip states in a phylogeny (Blomberg *et al.*, 2003; Revell *et al.*, 2008), are also used to detect a pattern of PNC in a phylogeny (Cooper *et al.*, 2010; Wiens *et al.*, 2010).

By contrast, Losos (2008a,b, 2011) argued that a pattern of PNC should be recognized only when there is ‘unusually great ecological similarity among closely related species’ (Losos, 2011), by which he means more similar than expected from phylogenetic relationships alone, under the null BM model. In a similar approach, Cooper *et al.* (2010) present tests using different macroevolutionary models for PNC, as measured by lower than expected trait variance through macroevolutionary time, relative to the BM null.

Here we accept that a base level of PNC is the inevitable consequence of trait drift as lineages diverge and, in the absence of confounding processes, is effectively no different from simple phylogenetic signal. Nevertheless, patterns of PNC vary among lineages, traits and models, and can vary independently of PS.

III. Pattern or process?

There is conflict in the literature about whether PNC is a process driving the structuring of communities (and biomes) or an emergent pattern resulting from one or several underlying causes (intrinsic or extrinsic processes) (Wiens & Graham, 2005; Losos, 2008a,b, 2011). Both views are put by Wiens *et al.* (2010, p. 1312). They argue that PNC is a process because it can lead to other patterns, such as diversity gradients. However, it is likely that the same processes leading to a pattern of PNC can also lead to other patterns (Cooper *et al.*, 2010; Losos, 2011). Like PNC, diversity gradients are patterns that result from multiple causes (Cardillo *et al.*, 2005; Goldie *et al.*, 2010) and some, but not necessarily all, could give rise to both kinds of pattern. For example, physiological constraints leading to cold intolerance have been implicated as a cause of both PNC and the latitudinal diversity gradient (Wiens, 2011). Alternatively, canalizing selection can lead to a lineage becoming confined to a narrow niche (Wagner, 2011a) but with respect to niche-related traits that are unlikely to cause a diversity gradient; for example, ratchet-like transitions in plant lineages from bee to bird pollination that are difficult to reverse (Thomson & Wilson, 2008; A. Toon *et al.*, unpublished). Additionally, a pattern of PNC can arise from disparate processes representing evolutionary extremes, such as drift on the one hand or strong stabilizing selection to a narrow optimum on the other (Hansen *et al.*, 2008; Cooper *et al.*, 2010; Losos, 2011).

PNC is a pattern arising from multiple processes and a strong pattern of PNC probably arises from interaction among processes, such as those illustrated in Fig. 2 and exemplified in section IV ‘What causes a pattern of PNC?’. More generally, a phylogeny is a pattern resulting from historical evolutionary processes, and terms

such as ‘phylogenetic constraint’, which imply that the phylogeny itself is exerting an effect, are illogical and misleading and should be avoided (Losos, 2011).

PNC becomes scientifically interesting when we attempt to explain why the pattern varies among lineages and traits, and in terms of hypothesized processes. For example, why has *Nothofagus* apparently been restricted to the rainforest biome for 70 Myr (Cook & Crisp, 2005b; Crisp *et al.*, 2009) whereas its sister group, the rest of the Fagales, has diversified into temperate deciduous forest, sclerophyll and even arid biomes? Is it constrained to its current adaptive peak by physiological trade-offs that severely limit its ability to move to a new peak? Has it lacked opportunities because of poor vagility or exclusion by antagonists in alternative biomes? Or is its current restriction to a narrow ecological range an artefact of extinction of past lineages that occurred in other biomes? We will argue that recognition of PNC should not be on the basis of trait mapping and simple phylogeny-based tests alone but is better addressed in the context of testing ecological and evolutionary hypotheses. In the following section, we consider the kinds of processes that are likely to lead to a pattern of PNC.

IV. What causes a pattern of PNC?

By definition, minimum conditions for PNC are that a trait should be niche-related and heritable (Fig. 2a). Likely causes of PNC are diverse and they can interact to produce complex outcomes (Revell *et al.*, 2008). They include neutral processes (e.g. drift), selection, constraints (e.g. lack of genetic variation, trait absence, canalization, linkage and co-adaptation of traits, trade-offs and the shape of the adaptive landscape), opportunity limitation (with respect to dispersal, competition, predation, pathogenesis and niche construction) and artefactual or indirect effects (e.g. extinction).

1. Drift

As discussed above, trait change in the absence of selection (i.e. drift) results in a base level of PNC that does not differ from PS, as measured by Blomberg’s *K* or tip randomization tests (Blomberg *et al.*, 2003; Losos, 2008a; Cooper *et al.*, 2010) (Fig. 2b). The degree of PNC resulting from drift could be considered a null expectation for some hypotheses relating to PNC. For instance, a nonadaptive radiation by strict allopatric speciation (Wiens, 2004), should result in a level of PNC that is indistinguishable from this null. Patterns of PNC become interesting where they diverge from simple PS (in either direction), and beg for an explanation in terms of specific testable hypotheses about the processes that have led to the pattern.

2. Stabilizing vs divergent selection

A strong pattern of PNC might result from sustained stabilizing selection (Fig. 2b). In particular, a pattern of PNC is expected to result from stabilizing selection on essential traits for survival in a given environment. Some functional traits, such as wings in birds and insects, and eyes in vertebrates, have been maintained through species-rich clades for tens to hundreds of millions of years, thus

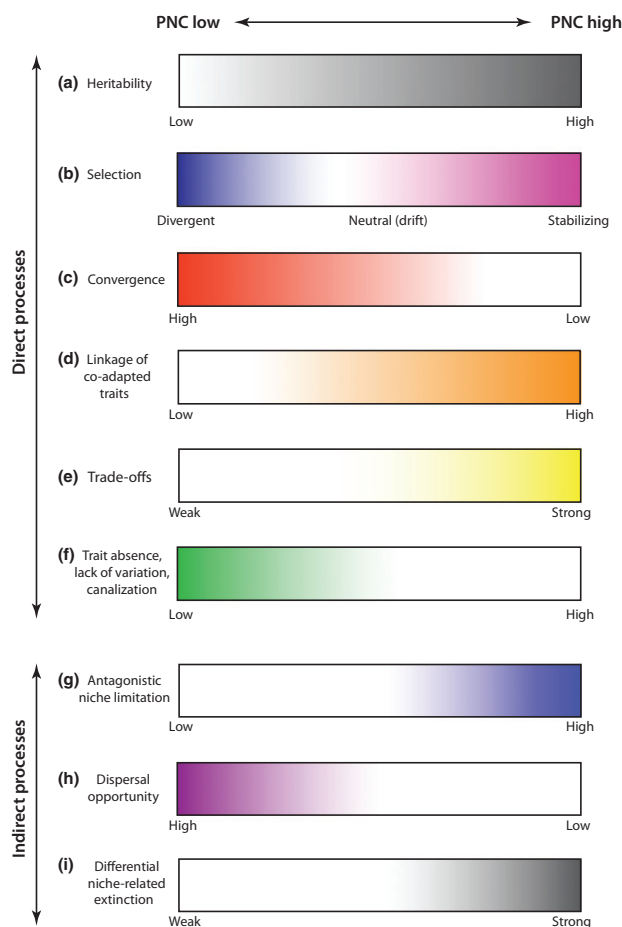


Fig. 2 Some evolutionary and ecological causes that can strengthen (or weaken) a pattern of phylogenetic niche conservatism.

showing a strong pattern of PNC. Yet in all these lineages, when species have established in environments where the trait is no longer advantageous, the previously conserved trait is quickly lost. Such losses have occurred repeatedly in independent lineages, indicating that the pattern of PNC has probably been formed and maintained by selection. Examples include loss of flight in animals on islands, such as rails (Trewick, 1997) and possibly ratites (Phillips *et al.*, 2010), loss of flight in fireflies (South *et al.*, 2011) and loss of sight and pigmentation in cave-dwelling animals, such as salamanders (Wiens *et al.*, 2003) and subterranean diving beetles (Leys *et al.*, 2005). An example from plants is loss of photosynthesis: holoparasitic plants, which by definition lack chlorophyll and so cannot photosynthesize, appear to have originated five times independently within the Scrophulariaceae *sens. lat.* (dePamphilis *et al.*, 1997) and at least 12 times across angiosperms as a whole (Nickrent, 2008). At the other extreme, sustained divergent selection results in the antithesis of a pattern of PNC.

3. Convergence

Convergent selection results in similar traits appearing independently in different lineages, for example, among distantly related lineages experiencing similar selective pressures in different

biogeographic regions (Cavender-Bares *et al.*, 2009, box 1, fig. 2) (Fig. 2c). This will tend to reduce any pattern of PNC in a phylogeny.

4. Linkage of co-adapted traits

Some adaptive traits that are fundamental to life are conserved at the highest level, through very long periods and even across lineages that are otherwise highly diverged (Fig. 2d). Although stabilizing selection clearly plays a major role in conservation of such traits, many are complexes of co-adapted components, which commonly form networks, and linkage is a factor in their PNC (Wagner, 2011a,b). For example, the photosynthetic machinery is highly conserved throughout green plants: organisms that depend on photosynthesis cannot live in a continuously dark environment. Photosynthesis represents an example of a highly conserved core of co-adapted traits (Pigliucci & Preston, 2004; Young & Badyaev, 2006), and their underlying genetic, developmental and metabolic pathways (Sinervo & Svensson, 2002; Hoffmann & Rieseberg, 2008; Ortiz-Barrientos *et al.*, 2009; Wagner, 2009), which are so tightly linked that disruption of certain parts of the core function could make the whole complex unviable (Wagner, 2011a).

Wagner (2009) found that, in prokaryotes, the majority of enzymatic reaction combinations for a wide range of functions were highly constrained in a large sample (200 genera) of complete genome sequences. Components of these core functions were sometimes found to be highly labile, allowing rapid adaptive shifts at small evolutionary and ecological scales. Nevertheless, metabolic networks show great evolutionary plasticity and redundancy, enabling differently routed pathways even among close relatives (Wagner, 2011a,b), and a number of recent studies have found evidence for linked co-adapted traits that are selected together, for underlying genetic linkage between them, for their involvement in speciation, and for phylogenetic correlation of these complexes (Table 2).

Transitions between the most contrasting environments are likely to be limited (or simply prevented) by the inflexible core functions of tightly linked trait complexes, and these represent extremes of niche conservatism. For example, shifts by plants between aquatic and terrestrial environments have been rare. Such shifts require major life-history transitions, involving highly conserved and integrated co-adapted trait complexes responsible for essential functions such as gaseous exchange, internal water and nutrient transport, mechanical support and transfer of gametes (Niklas, 1997). Moreover, all life, at least to phylum level, originated and diversified for most of evolutionary history (c. 3.9 Gyr) in the sea: land was colonized late, only 400–500 Ma, and two-thirds of extant animal phyla have not made the transition (May, 1994).

5. Trade-offs

Narrowing of the habitable niche leading to a pattern of PNC can result from ecophysiological trade-offs required to protect vital functions against environmental extremes (Fig. 2e). For example,

reduction of xylem vessel diameter in woody plants that protects against freeze-thaw embolism compromises delivery of water to crowns at rates sufficient to maintain photosynthesis, and thus limits the crown height of plants in cold temperate climates (Choat *et al.*, 2011). A similar trade-off (but with respect to salt tolerance) limits the occurrence of mangroves in temperate climates (Stuart *et al.*, 2007).

6. Restricted genetic variation, trait absence and canalization

A species may be limited to a narrow niche and appear niche-conserved because of a lack of genetic variation in a limiting adaptive trait (Bradshaw, 1991; Hoffman *et al.*, 2003; Wiens & Graham, 2005); for example, as a result of interspecific competition restricting gene flow from the centre to the margin of a species' range, reducing the potential for adapting to a different niche at or beyond the margin (Case & Taper, 2000) (Fig. 2f).

Complete absence of a trait, possibly because underlying genetic, metabolic and developmental machinery is lacking, can result in extreme niche conservatism. It is not difficult to think of life history transitions that appear not to have occurred, for example no extant gymnosperm is herbaceous or annual, no plants maintain active flight and there are no deep sea-vent angiosperms. Further examples are cited by Wagner (2011a, p. 577; 2011b, p. 158). A fundamental physicochemical constraint on life is the requirement for liquid

water, which is readily lost as vapour or immobilized as ice. A number of lineages have independently evolved antifreeze proteins, allowing marine organisms to survive in the Arctic or Antarctic, or plants to overwinter in high latitudes (Carroll, 2009; Wagner, 2011b), but the vast majority of life on earth is constrained by intolerance of freezing temperatures. The necessary physiological tolerance traits either did not evolve in most lineages or did not survive.

Observed patterns of high biome-level conservatism (e.g. Crisp *et al.*, 2009; Kozak & Wiens, 2010a,b) could reflect basic tolerance limits restricting organisms to particular biomes, for example with respect to certain climatic parameters. One of the longest-recognized patterns of PNC is probably caused by the paucity of transitions from tropical to temperate zones, known as the tropical conservatism hypothesis (TCH: Wiens & Donoghue, 2004; Wiens & Graham, 2005; Donoghue, 2008; Hawkins *et al.*, 2011; Condamine *et al.*, 2012). Many plant families are well represented in the tropics but lack species occurring in the colder, more seasonal or drier biomes. The TCH posits that most families originated in warm wet regions but relatively few have evolved tolerance to freezing temperatures and highly seasonal environments, limiting their expansion into higher latitudes (Stuart *et al.*, 2007; Donoghue, 2008; Hawkins *et al.*, 2011).

Some environments are marginal for most of life, for example, polar, deep underground, deep oceanic, high alpine and extreme

Table 2 Examples of conserved co-adapted trait complexes

Description	Evidence given for phylogenetic niche conservatism (PNC)	Reference
Plants		
Animal-dispersed fleshy fruits have phenotypic integration of display traits (morphology, colour and nutrition).	A high integration level found by phylogenetic contrasts was taken by the authors to indicate conservatism.	Valido <i>et al.</i> (2011)
In <i>Acer</i> , two disparate complexes of functionally integrated, co-evolving traits that were related to leaf size and sapling canopy allometry showed strong phylogenetic signal.	Randomization tests.	Ackerly & Donoghue (1998)
Floral trait integration patterns in <i>Schizanthus</i> were not related to phylogeny.	None: convergent selection for different pollinators appeared to have a stronger influence than phylogenetic inheritance.	Perez <i>et al.</i> (2007)
Antarctic fellfield plants tolerate severe environmental stresses using suites of co-adapted traits that are conserved in related species from temperate regions.	Authors suggest that selection has filtered pre-adapted temperate taxa for this extreme environment.	Block <i>et al.</i> (2009)
The α -crystallin-related, small heat shock proteins (smHSPs) are encoded by a family of genes expressed in different parts of the plant. Their functions appear critical for survival and recovery from heat stress.	Phylogenetic analysis suggests that the smHSP gene families arose by duplication and divergence of genes before the radiation of angiosperms.	Waters <i>et al.</i> (1996)
Other organisms		
In 12 food webs, latent trait complexes related to 'vulnerability' and 'foraging' were detected after body size (allometric) effects were factored out.	Significant correlation with phylogeny.	Rohr <i>et al.</i> (2010)
Phenotypic integration of conspicuousness, chemical defence, diet specialization, body mass, active metabolic rate and aerobic scope was found in aposematic frogs.	Phylogenetic correlations among traits but with multiple convergent origins.	Santos & Cannatella (2011)
Dormancy strategies (cryptobiosis) in tardigrades inhabiting hostile terrestrial environments involve a complex array of factors working at molecular (bioprotectants), physiological and structural levels.	Cryptobiosis is linked to multiple physiological and physical constraints and has been retained for long periods in two lineages.	Guidetti <i>et al.</i> (2011)
Distantly related lizards appear to exhibit a conservation of feeding kinematics and share the same three linked lingual types of food transport behaviour.	The shared traits appear to be ancestral in lizards.	Elias <i>et al.</i> (2000)

arid regions, and diversity of organisms in such regions is low. Shifts into (or out of) such environments are probably rare because of very strong ecological barriers and an absence of necessary adaptive traits. Nevertheless, some groups of organisms have shifted into such environments and probably persisted there for long periods of evolutionary time, for example, penguins in the Antarctic region (Baker *et al.*, 2006), ephemeral plants in very dry deserts and 'extremophile' prokaryotes in all of the above. An environment that is extreme or uninhabitable for one kind of organism can be optimal for another; for example, iron-sulphur metabolizing prokaryotes that thrive in deep oceanic hydrothermal vents and geothermal springs cannot inhabit the oxygen-rich terrestrial environment (Johnson & Hallberg, 2009). Presumably, most organisms lack the traits essential to survival in such extreme habitats. Shifts into such habitats might be severely limited for most species because of the steepness of the adaptive landscape, for example, by involving impossible trade-offs.

'Canalization' refers to apparently irreversible trait loss (Cronk, 2009), leading to permanent niche narrowing in a lineage and, possibly, a so-called 'evolutionary dead end'. When plants shift to holoparasitism, they lose the need to photosynthesize and the photosynthetic machinery is degraded or lost. Of the *c.* 12 shifts to parasitism of other seed plants, there do not appear to have been any reverse shifts (regaining photosynthetic capacity) in holoparasitic lineages (Nickrent *et al.*, 2005; Westwood *et al.*, 2010): holoparasites have become canalized. Another example of probable canalization is shifts of pollination syndrome in plants, which often show a directional bias towards specialized pollination by birds, long-tongued moths or flies (e.g. Fenster *et al.*, 2004; Tripp & Manos, 2008; Hodges & Derieg, 2009). It has been suggested that this bias results from structural-functional constraints on reverse transitions ('evolutionary ratchet'; Whittall & Hodges, 2007; Thomson & Wilson, 2008; Johnson, 2010; A. Toon *et al.*, unpublished). For example, in *Aquilegia*, a pollinating moth with a longer tongue than in other pollinating moths could have improved pollen transfer and thus selected for longer nectar-containing floral spurs, which elongated to the point where the other pollinators could no longer reach the nectar, making reversals unlikely (Whittall & Hodges, 2007).

7. Antagonistic interactions and niche overlap

Antagonistic interaction among closely related organisms appears to limit species to only part of their fundamental niche, even when they are not dispersal-limited, and can result in a pattern of PNC (Rabosky *et al.*, 2007; McPeck, 2008; Cavender-Bares *et al.*, 2009; Kozak & Wiens, 2010b; Mayfield & Levine, 2010; Wiens *et al.*, 2011) (Fig. 2g). Although competition is the most commonly cited antagonistic interaction, pathogens, herbivores and predators are expected to have a similar effect (Chesson & Kuang, 2008; Ricklefs, 2010).

A pattern of PNC can arise as an artefact from lack of opportunity caused by antagonism. (In this context, 'artefactual' denotes involving cryptic derivation from causes other than directly heritable niche preference). For example, Ricklefs (2010) suggests that antagonism from predators and pathogens can prevent closely

related species with similar fundamental niches from filling all their available niche space. Thus, realized niches can overlap by occupying different patches in a mosaic of co-located niche space, depending upon their differing vulnerabilities to the antagonists present in each patch. This spatial collocation of closely related species can result in phylogenetic clustering of traits that reflect the shared local or regional environment (i.e. the appearance of PNC), although these may not be the traits that actually distinguish the species' niches.

Alternatively, closely related species can co-exist in the same space through subtle interactions between their competitive ability and niche differences (Mayfield & Levine, 2010). For example, two plant species might differ in height, with the taller species a superior competitor when light is limiting; thus, competition eliminates all but the tallest plants. If plant height is constrained such that more closely related species have more similar heights, then competition will lead to co-existence of more closely related species, that is, spatial phylogenetic clustering and a pattern of PNC (Mayfield & Levine, 2010). Chesson & Kuang (2008) have shown that interaction between predation and competition can have similar effects.

8. Dispersal and opportunity

Life-history dispersal mechanisms, and rare long-distance dispersal and establishment, contribute to whether a species occupies all of its fundamental niche space or is restricted to only a part. Limitation of dispersal opportunities is commonly inferred to be a major factor in community assembly (e.g. Pennington *et al.*, 2009; Leibold *et al.*, 2010), especially at larger (continental and global) scales, even though surprisingly large gaps, such as oceans, have been crossed (Crisp *et al.*, 2009; Pennington *et al.*, 2009) (Fig. 2h). For example, rainforest trees from the same family occupy similar mesoclimatic niches in India and Panama, even though the sites are in different continents and share no species (Hardy *et al.*, 2012). That is, transoceanic dispersal occurs, but it is rare (Crisp *et al.*, 2009). Nonvagile groups are more likely to be spatially confined (e.g. to one land mass) than those with dispersal mechanisms or reproductive modes that are more likely to allow colonization of remote areas. Barriers to dispersal alone could result in a pattern of PNC by causing close location of related species and autocorrelation of environmental variables across the adjacent habitats. Testing ecophysiological tolerances of species in such a lineage might show that they are limited to the current habitat not by inherent constraints but by lack of opportunity to access other habitats.

9. Extinction

Some patterns of PNC might be an artefact of differential extinction rather than the trait of interest itself being highly conserved. For example, in eucalypts, Crisp *et al.* (2011) inferred a single shift from rainforest into the sclerophyll biome *c.* 62 Ma (Palaeocene), coincident with the origin of a specialized anatomical adaptation to epicormic resprouting after wildfires, which characterize the sclerophyll biome (Fig. 2i). Tests using tip randomization (Table 3) indicated that both biome occupancy

and epicormic anatomy were significantly conserved across Myrtaceae, including eucalypts. Consider instead that there might have been multiple independent shifts to epicormic resprouting and into the sclerophyll biome rather than long-term conservation of the trait and occupancy of the biome (Fig. 3). Consider also that these shifts could have occurred later than the Paleocene and perhaps following the post-Eocene global change to a drier, more seasonal climate (Zachos *et al.*, 2001). At the same time, this change in climate might have caused extinction of the niche-conserved eucalypt lineages that did not shift and were trapped in a shrinking rainforest biome that today is restricted to fragmented patches along the east coast of Australia. Without such extinctions, and using a phylogeny that included these conserved rainforest lineages, the shifts would probably reconstruct as both homoplastic and more recent, whereas with the conserved lineages excised from the phylogeny by extinction, the adaptive shifts would probably coalesce deeper in the tree, possibly to a single origin, as reconstructed by Crisp *et al.* (Fig. 3). To choose between these alternative hypotheses would require independent evidence, for instance an Eocene or more recent fossil record of wet-forest eucalypts that lack the specialized fire-adapted epicormic anatomy. However, the only known Eocene eucalypt fossils (Gandolfo *et al.*, 2011) do not represent stem anatomy and no other suitably preserved wood fossils are known either (Rozefelds, 1996).

The above scenario is extreme, requiring extinction of all hypothetical rainforest-dwelling eucalypts. However, note that the sister group of the 800 species of eucalypts is the small, and perhaps nearly extinct, *Stockwellia* clade of four rainforest species that lack the epicormic resprouting structures (Crisp *et al.*, 2011). It also demonstrates the difficulty (or ambiguity) in reconstructing traits using phylogenies, without the benefit of a good fossil record.

In a similar example, origins of fire-adaptive traits in *Pinus* have been traced to the early Cretaceous (He *et al.*, 2012) but, noting that many pinaceous fossils cannot be assigned to extant clades, the authors suggest that these fossils represent taxa that were unable to adapt to new fire regimes and went extinct. If most such taxa went extinct, this could have created an appearance of PNC in the fire-adaptive traits.

V. Tests for PNC

Because some degree of PNC is inevitable, questions relating to patterns of PNC in ecology need to be specific, context-based and framed in terms of the hypothesized process(es). Tests for *phylogenetic* NC are necessarily tree-based. Table 3 summarizes several commonly used tests but is not exhaustive; see recent reviews (Losos, 2008b; Ackerly, 2009; Cooper *et al.*, 2010; Pavoine *et al.*, 2010; Wiens *et al.*, 2010; Peterson, 2011; Münkemüller *et al.*, 2012) for additional tests and examples.

1. Generalized tests: tip randomization and tests of models of character change

The frequently used tip randomization test for a pattern of PNC measures the fit of the character of interest to the phylogeny. It

randomizes states of the character among tips of the phylogeny and compares the observed fit to that in the randomizations (Crisp *et al.*, 2009; Wiens *et al.*, 2010). A significant result indicates that phylogenetic clustering of the trait is greater than expected by chance. Blomberg's K (2003) tests the fit of estimated character evolution against a Brownian motion model of character change (drift). A value close to 1.0 indicates that character evolution fits a BM model, a value > 1.0 indicates closely related lineages are more similar than expected under a BM model, whereas a value < 1.0 indicates overdispersion: closely related lineages are more different from one another than expected under a BM model. A variant of this approach uses the original tree and data to calculate and then randomize standardized contrasts, relative to a BM null model (Freckleton & Harvey, 2006). Pagel's λ is similar to K , with values < 1.0 indicating that traits are less similar among species than expected from their phylogenetic relationships and values > 1.0 showing the reverse (Pagel, 1999). A recent simulation study compares these and other measures of PS, finding that λ generally outperforms K , although the latter is suitable for models with changing evolutionary rates (Münkemüller *et al.*, 2012).

Tip randomizations and tests of models of character change are used to detect phylogenetic signal in general but, when applied to niche-related traits, can be used to test patterns of PNC. However, the relationship between tests of PS and PNC is complex: high PS does not necessarily indicate that traits are conserved and, conversely, low PS does not necessarily mean that traits are labile (Revell *et al.*, 2008; Cooper *et al.*, 2010; Kozak & Wiens, 2010b; Wiens *et al.*, 2010). For instance, Revell *et al.* (2008, fig. 4a) present a niche conservatism model in which stable selection (resulting in PNC) is occasionally disrupted by stochastic shifts in fitness peaks. Depending upon the variance of peak shifts, PS varies from nearly $K \sim 0$ (significantly low PS) to $K \geq 1.0$ (high PS, marginally above the BM null). An extreme case of PNC might be a clade that exhibits stasis in a niche-related trait, thus combining zero PS with high PNC, such that closely related species would be as similar as any pair chosen at random from the tree (e.g. strong and constant stabilizing selection, scenario 3C, Revell *et al.*, 2008; 'niche retention' example, Cooper *et al.*, 2010). A real example of this is *Nothofagus*, which shows relative stasis in biome occupancy throughout the clade and is cited as an example of strong PNC (Crisp *et al.*, 2009).

These tests can be used for different interpretations of PNC. If a pattern of PNC is simply considered an inevitable consequence of heritability (Fig. 2 and section II above), many traits will yield a significant result from tip randomization tests. An hypothesis of a pattern of PNC can be rejected if the distribution of the trait on the phylogeny is no different from random, or if Blomberg's $K < 1.0$ (given the caveats above). If PNC is defined more restrictively, such as under Losos' (2008a) view that the trait needs to be 'constrained' and show stronger phylogenetic clustering of the trait than expected under a BM random walk, then only Blomberg's K is applicable. An hypothesis of PNC would be rejected for cases where $K \leq 1$. The following example illustrates this more restrictive definition of PNC.

In a study of community phylogenetic structure in tropical forests, Baraloto *et al.* (2012) measured a number of plant

Table 3 Tests for phylogenetic niche conservatism (PNC)

Test	Procedure	Null hypothesis	Strengths	Limitations	Examples
Tip randomization	Monte Carlo shuffling of terminal trait states in a phylogeny (Blomberg <i>et al.</i> , 2003; Wiens <i>et al.</i> , 2010).	Phylogenetic clustering of trait is random across the tree.	Simplicity.	Tests only for phylogenetic signal in the trait. Null hypothesis is probably too lenient. Depends on variation in the trait: evolutionary stasis yields a null result. An absolute criterion for PNC with limited use for comparative questions.	Biome (as a surrogate for macro-climatic niche) was conserved across phylogenies of all 13 plant taxa tested (Crisp <i>et al.</i> , 2009).
Models of trait evolution	Models the correlation between the species' trait values and the total phylogenetic distance from a specified node of the tree. For example, <i>K</i> (Blomberg <i>et al.</i> , 2003) and generalized least squares (λ) test for directional evolution (Pagel, 1999).	Trait divergence with time on phylogeny fits a Brownian motion (BM) model of continuous divergence (Losos, 2008a).	Either stasis (PNC) or directional change in the trait could lead to rejection of the null (Wiens <i>et al.</i> , 2010).	An absolute criterion for PNC with limited use for comparative questions.	Ecological traits in plants promoting successful invasion appear to be shared among close relatives (as measured by <i>K</i>), indicating that phylogenetic relationships can be useful predictors of invasion success at large spatial scales (Cadotte <i>et al.</i> , 2009).
Comparative tests	Compare rates of change in time-calibrated trees (O'Meara <i>et al.</i> , 2006; Thomas <i>et al.</i> , 2006; Ackerly, 2009). Implemented in R package <small>GEIGER</small> (Harmon <i>et al.</i> , 2008).	BM model.	These tests treat PNC as a relative (not absolute) concept and are more applicable to specific evolutionary questions.	An absolute criterion for PNC with limited use for comparative questions.	Large genome sizes are known in Santalales and some monocot clades. A comparative rate change test indicated that these groups (especially Santalales) have a significantly higher rate of genome size evolution than in other angiosperms, which do not differ greatly in rate (O'Meara <i>et al.</i> , 2006).
Multiple model fitting	Test relative fit of various nonstasis models, for example, those described above plus Ornstein–Uhlenbeck (OU) and white noise models (Kozak & Wiens, 2010b). Bayesian model fitting using <small>AUTEUR</small> (Eastman <i>et al.</i> , 2011).	Either BM or no change (stasis) in relevant trait.	Finds best-fitting model of change, rather than simply testing for absolute PNC.	Vulnerable to a 'black-box' approach: requires a clearly stated null with respect to a relevant question, rather than just seeking the best-fit model.	In a multivariate analysis of diversification in plethodontid salamanders, the fit of BM (null) and OU (stasis) models was compared and BM found to fit better for most clades (Kozak & Wiens, 2010b). The four clades fitting OU were excluded from further analyses.
Community assembly models	Multivariate modelling of floristic data across hierarchically structured sites (plots, gradients and regions), adaptive traits, dispersal opportunity, abiotic factors such as climate and soil, biotic factors such as competition and pathogens, and phylogeny.	Multiple hypotheses tested simultaneously, with multiple nulls.	Teases apart the relative significance of different factors.		Speciation in four major lineages in the Cape diversity hotspot was correlated with soil shifts in some taxa, fire-survival strategy in others, and pollinator shifts in others. PNC was found in different traits in different lineages (Schnitzler <i>et al.</i> , 2011).

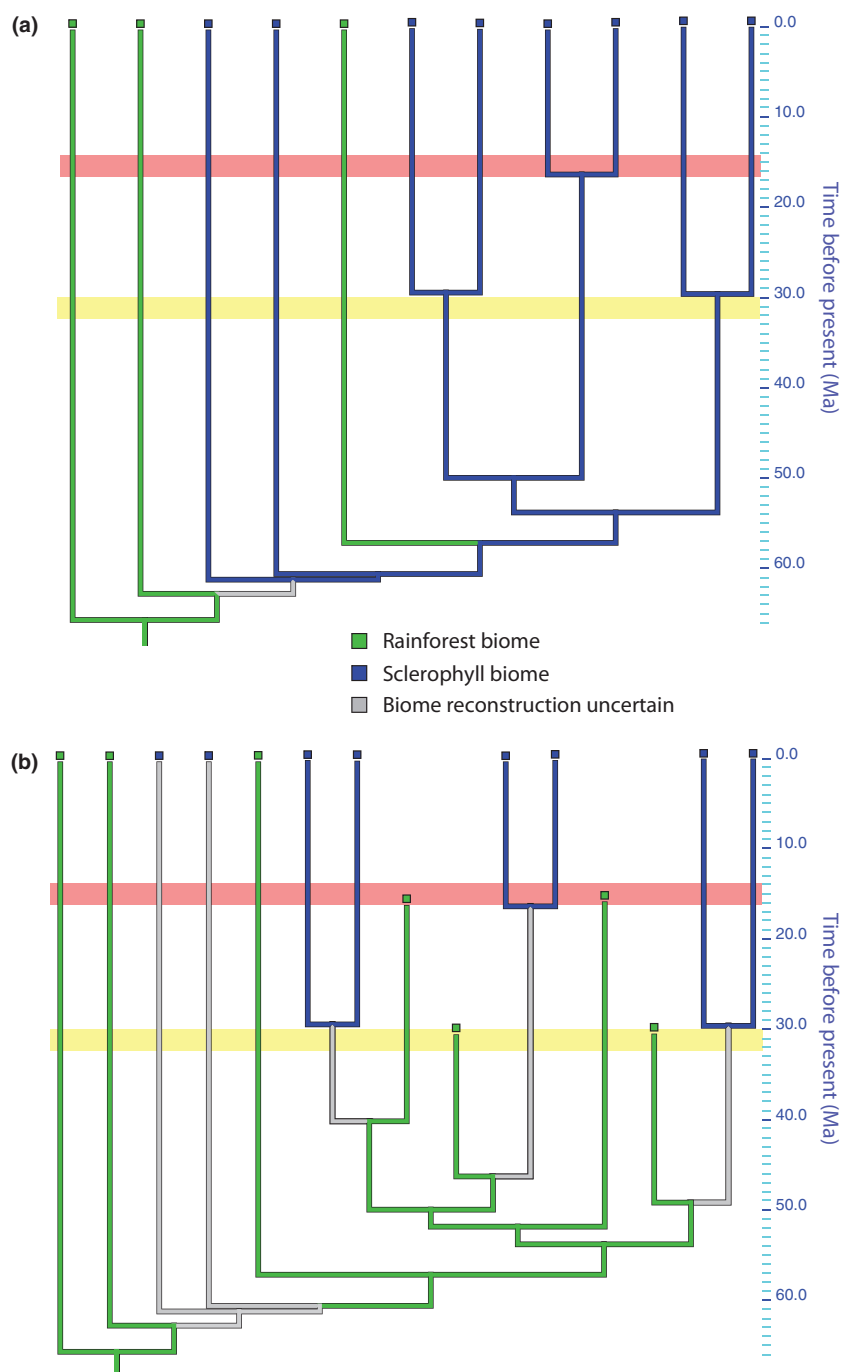


Fig. 3 Hypothetical illustration of a phylogenetic artefact created by differential extinction of lineages with a conserved intolerance of fire, limiting them to the rainforest biome. (a) Dated phylogeny of extant taxa mapped with biome of occurrence. A single transition from the ancestral, nonflammable rainforest biome to the derived, flammable sclerophyll biome is inferred to have occurred *c.* 62 Ma. (b) The same phylogeny with the addition of several rainforest-occurring lineages that went extinct after the climate became drier and more seasonal, favouring spread of the sclerophyll biome while the rainforest biome contracted. In this reconstruction, there were three separate shifts from rainforest to sclerophyll that occurred much more recently, probably in response to the climate change events, indicated by yellow and red bars, that also caused extinction of the rainforest lineages. Rainforest biome, green; sclerophyll biome, blue; biome reconstruction uncertain, grey.

functional traits across nearly 700 tree species and derived two composite traits (representing leaf and stem 'economics') using principal components analysis (PCA). Using a time-calibrated phylogeny of the species, both composite traits were tested for phylogenetic signal against both the null models described above. For the first model, BM evolution of the traits was simulated on the tree and, for the second, zero-PS was simulated by randomizing the tips. The study found that trait similarity was higher among more closely related species and decreased towards the root of the phylogeny (Fig. 4). Among recently diverged species, phylogenetic signal (measured by autocorrelation of trait similarity with depth in the phylogeny) was significantly greater than expected under the

zero-PS null model but less than expected under the BM model, although mostly nonsignificantly. The authors interpreted these results as showing significant PS in the traits but absence of PNC, under Losos' criterion that PNC should give a stronger signal than expected under a BM model.

2. Question-specific tests

Disagreement between authors on basic questions, such as whether the BM model represents PNC or a null against which PNC is tested, shows that PNC is a controversial concept (Derrickson & Ricklefs, 1988; Losos, 2008b; Wiens, 2008; Cooper *et al.*, 2010).

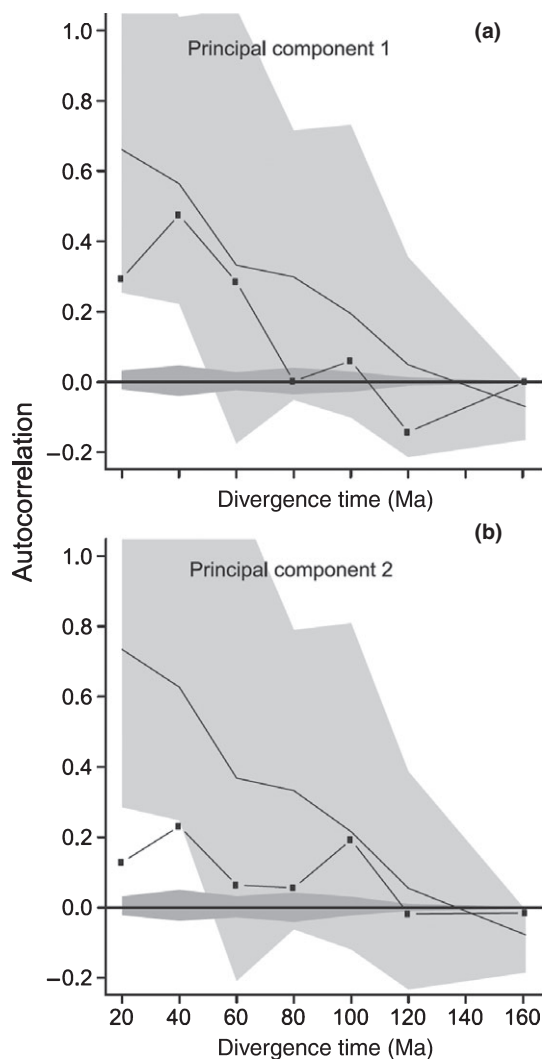


Fig. 4 An example showing contrasting inferences of phylogenetic signal (PS) and phylogenetic niche conservatism (PNC) using different null models, from Baraloto *et al.* (2012). Plant functional trait similarity in tropical forest trees, estimated by loadings on the first two principal components analysis (PCA) vectors (broken line with dots), is plotted against phylogenetic distance. The sloping line represents a simulated Brownian motion (BM; drift) null model and the horizontal line a zero-PS null model. Grey envelopes represent 95% confidence intervals for the null models. (a) PCA vector 1 representing composite leaf traits; (b) PCA vector 2 representing composite stem traits. Under the zero-PS null, both vectors show significant phylogenetic signal in the traits among closely related species, decreasing with phylogenetic depth. Under the BM null model, there is generally less phylogenetic signal than expected (although not significantly so), which the authors interpret using Losos' (2008a) criterion as absence of PNC in these traits.

Recognizing PNC as a pattern with multiple causes leads to more targeted tests for PNC, addressing the hypothesized causal factors. Increasingly, research is directed towards identifying the role of hypothesized causal factors of PNC, rather than towards discovering evidence of PNC *per se*.

Comparative tests and multiple model fitting Comparative hypotheses should lead to specific questions about PNC, such as

'Is this trait more conserved than another?' or 'Is this trait correlated with niche occupancy?' (e.g. He *et al.*, 2012). Suppose that a conserved complex of co-adapted traits is hypothesized to maintain an essential metabolic function (Wagner, 2011a). Suspected core traits in the complex could be tested for patterns of PNC individually using a generalized test, and their hypothesized functional links could be assessed using tests of correlated evolution (Pagel, 1994). In contrast, an artefactual pattern of PNC might be suspected in environmental traits as a result of closely related taxa co-occurring as a result of dispersal limitation or overlapping realized niches. If this effect is suspected, the ecophysiological tolerances of the species to the shared environmental traits should be tested to determine whether the traits are actually niche-limiting.

In the *Nothofagus* example mentioned above (in the section on generalized tests), both the Blomberg's *K* and tip randomization tests lack the power to detect a signal of PNC in a trait showing stasis (or nearly so) throughout a clade because randomization would have no effect on the phylogenetic distribution of an invariant trait (Crisp *et al.*, 2009). This problem disappears if a comparative question is asked, for example, 'Is this trait more conserved in this lineage than in its sister group?' Addition of the sister group (*Fagales* in this example), which is less conserved and has undergone multiple biome shifts, would allow a comparison between the two lineages, for example, using tests for different rates of trait evolution in two parts of a phylogeny (Table 3; O'Meara *et al.*, 2006; Thomas *et al.*, 2006; Ackerly, 2009). If the sister group lacked sufficient species (e.g. were monotypic), then further sister groups could be added to balance diversity in the clades being compared.

Shifts in strength of PNC are potentially detectable, for example, using Pagel's δ , which detects acceleration or deceleration of evolutionary rate in a trait across a whole tree, and a rate change occurs nearer the root or tips (Pagel, 1999; Cooper *et al.*, 2010). A useful extension of these tests would be to pinpoint where, in a phylogeny, shifts in the strength of PNC signal occur, for instance to evolutionary stasis, as in *Nothofagus*. A new Bayesian reversible-jump Markov chain Monte Carlo (MCMC) method (AUTEUR; Eastman *et al.*, 2011) can detect trait rate shifts in particular branches of a phylogeny by comparing models with different levels of rate complexity. This study introducing the test found exceptionally high rates of body-size evolution in a group of turtles compared with those in related lineages. In a recent significant extension of the Ornstein–Uhlenbeck model (OU_{WIE}; Beaulieu *et al.*, 2012), different selective regimes can be modelled in different branches of a phylogeny and each selective regime can be assigned a separate trait optimum, a rate of stochastic motion parameter, and a parameter for the strength of selection. The authors illustrate their method by investigating asymmetry in the strength of selection and stochastic motion acting on genome size due to growth form (woody vs herbaceous) in monocots.

3. Community assembly models

The current multivariate modelling approach to community assembly can help tease apart the roles of hypothesized adaptive traits, dispersal opportunity or limitation, abiotic factors such as

climate and soil, biotic factors such as competition and pathogens, and phylogenetic relatedness of the taxa (Leibold *et al.*, 2010; Kooyman *et al.*, 2011; Schnitzler *et al.*, 2011; Baraloto *et al.*, 2012; Hardy *et al.*, 2012). In these studies, it is important to test for PNC and enquire into the cause(s) of any pattern that is found (Wiens *et al.*, 2010). For example, upon finding a pattern of climatic niche conservatism in the same plant lineages occurring in different continents, but without sharing any species, Hardy *et al.* (2012) hypothesized that transoceanic dispersal had occurred but was rare.

4. Challenges

Tests for patterns of PNC might need revision considering that likelihood of trait shifts need not be symmetrical and trait states might affect diversification rate (Maddison, 2006; Maddison *et al.*, 2007; Goldberg *et al.*, 2011). For example, the tip randomization test might falsely reject a pattern of PNC in a clade with a conserved trait that is associated with a slow diversification rate because lineages having this trait would have low species diversity relative to their more rapidly diversifying sister lineages. Because the tip randomization test works by detecting clusters of species having the conserved trait, species-poor clusters might not be distinguishable from random clusters.

A problem for modelling trait evolution on phylogenies, particularly the BM-based null, is that model parameters are derived from the tip states and therefore will suffer the problems described in the previous paragraph. To be accurate, such modelling requires independent measures of ancestral trait states and evolutionary rates (Oakley & Cunningham, 2000; Cook & Crisp, 2005a). A more suitable option in the absence of such information may be comparative tests, asking whether a 'niche-related' trait is more limited in rate variation than a 'neutral' trait that is not niche-related (e.g. Table 3: Ackerly, 2009; Cooper *et al.*, 2010, model 1e).

VI. Conclusion: is a concept of PNC scientifically useful?

Whether we need an absolute criterion of PNC is a moot point. PNC is not universal in traits or lineages but a pattern conditional upon an interaction between intrinsic constraints and the biotic and abiotic environments. We have shown that the processes contributing to a pattern of PNC are diverse and many are well understood, but under different names. Some indirect processes, such as extinction, antagonism and dispersal limitation, can be positively misleading with respect to whether evolution of niche-related traits has been constrained.

If, as we suggest, PNC is a pattern that can have different causes, then is it an important concept? We believe that the answer is 'yes' because it can contribute to understanding macroevolutionary processes. By way of illustration, perhaps the most famous example of a major radiation in plants is that of the angiosperms (Friis *et al.*, 2011): part of Darwin's 'abominable mystery' was why they appeared so suddenly in the fossil record in such diversity (Crepet & Niklas, 2009). This appears to be a clear example of adaptive diversification following release from a strong intrinsic constraint

on leaf traits. This constraint was reflected in a PNC pattern that had been maintained through hundreds of million years of evolution. By comparison with their sister group, the gymnosperms, the rise in angiosperm diversity was dramatic, even after differential Cenozoic extinctions are taken into account (Crisp & Cook, 2011). Many competing hypotheses have been proposed to solve the 'abominable mystery', for example through interactions with simultaneously diversifying insects (reviewed by Crepet & Niklas, 2009; see also Bond & Scott, 2010). Now it appears that release from constraint on a co-adapted complex of conserved leaf ecophysiological traits, which determine the efficiency of photosynthesis and growth rates, might have been partly responsible (Brodribb & Feild, 2010; Feild *et al.*, 2011a,b) (Fig. 5). A mid-Cretaceous increase in angiosperm leaf vein density also increased leaf hydraulic efficiency and dramatically increased the capacity of leaves to photosynthesize and assimilate CO₂ (Brodribb & Feild, 2010). Vein density and photosynthetic capacity are highly correlated and, as vein density can be measured in leaf fossils, these authors showed that early angiosperms produced leaves with low photosynthetic rates, comparable with those of other vascular

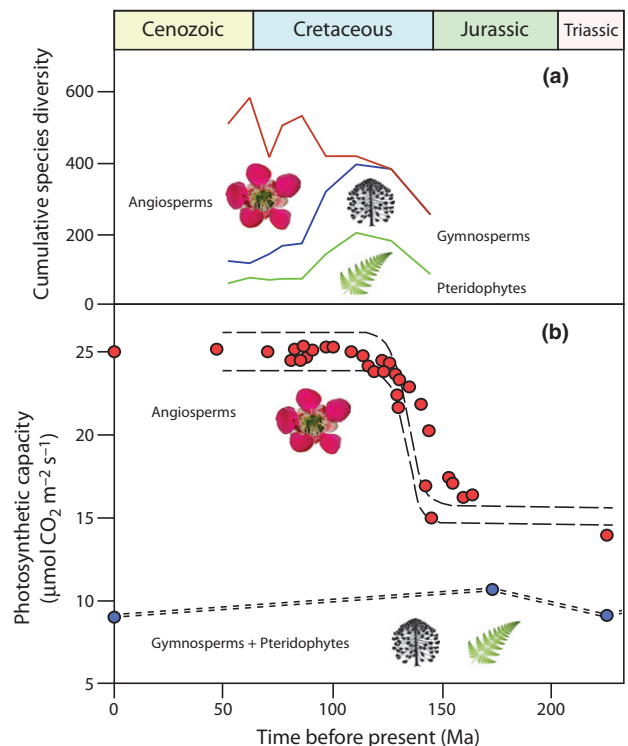


Fig. 5 The dramatic mid-Cretaceous radiation of angiosperms followed release from conserved slow photosynthesis rates, which remained conserved in other vascular plants until the present. (a) Trend through the Cretaceous in species diversity of angiosperms, gymnosperms and pteridophytes (free-sporing plants) using data from Friis *et al.* (2011). (b) An abrupt surge in maximum angiosperm photosynthesis capacity (P_c) is evident in the mid Cretaceous, rising from levels close to the non-angiosperm maximum, to levels far beyond those of other clades. Relatively high P_c in angiosperms is thought to have contributed significantly to their success over competing clades. Plots of reconstructed leaf P_c in C₃ angiosperms (red dots, long-dash lines) and non-angiosperm vascular plants (blue dots, short-dash line) are redrawn from Brodribb and Feild (2010, fig. 3). Photosynthetic capacities are reconstructed values from leaf vein density and a coupled hydraulic photosynthetic model (for details, see Brodribb & Feild, 2010).

plants (ferns and gymnosperms) and of a few extant low-diversity angiosperm lineages. Low vein densities have been conserved through 350 Myr of evolution in ferns, gymnosperms and early angiosperms (Fig. 5). The reason for this constraint remains unclear (Brodribb & Feild, 2010) and merits further investigation. During the mid-Cretaceous, angiosperms rapidly diversified into a much greater range of life forms and occupied a greater range of habitats, and into greater species diversity, than had been seen in other lineages of seed plants (Crepet & Niklas, 2009; Friis *et al.*, 2011), consistent with the hypothesis that an initial release from constraint drove the adaptive radiation. The surge in angiosperm diversity was unlikely to have resulted from extinctions in other vascular plants reducing competition because it occurred in the mid-Cretaceous period, when diversity in those taxa was relatively stable (Lidgard & Crane, 1988; Niklas & Tiffney, 1994; Lupia *et al.*, 1999; Crepet & Niklas, 2009) (Fig. 5). The key insight here was the recognition that, after a core metabolic function had been conserved through hundreds of million years, an evolutionary novelty in the lineage released the constraint and apparently led to a rapid diversification of the angiosperms. The extent to which release from evolutionary constraints has led to adaptive radiations in general merits further research.

Rapidly developing research on genotypic, metabolic and developmental networks is helping us understand the complex interplay between constraint and evolutionary change. Genotypic networks harbour multiple pathways to the same (or similar) phenotypes and it is paradoxical that this redundancy facilitates both conservatism and the capacity for rapid adaptive shifts (Wagner, 2011a,b). Redundancy allows vital functions to be conserved because if a critical pathway is blocked, for example, by a new toxin in the environment, the blockage can sometimes be easily bypassed by shifts to alternative pathways. This is in large part why resistance to pesticides in insects or to antibiotics in microbes can evolve so quickly. Thus, organisms and populations have the flexibility to respond readily to threats to essential functions (conservatism) while retaining the capacity to shift adaptively in a new environment, for example by losing the previously conserved ability to fly after colonizing islands.

Other applications using a concept of PNC include adapting conservation biology and agriculture to rapid environmental change. For example, ecological traits that promote invasiveness show a pattern of PNC in some lineages (e.g. Asteraceae, Caryophyllaceae, Poaceae and Solanaceae), hence potential environmental weeds might be predictable from their phylogenetic relatedness to known invaders (Cadotte *et al.*, 2009). In a clade including crop plants, identification of conserved climatic tolerances could assist biotechnological research in adapting the crop to a changing climate.

More generally, it is essential to take phylogeny into account in comparative ecological research by asking whether (and the degree to which) a pattern is driven by ecological factors or reflects phylogenetic history. If an ecological pattern is found to be significantly related to phylogeny, then it should be determined whether the pattern results from evolutionary limits on traits or from misleading effects such as differential extinction. Therefore, questions (and tests) should be framed in terms of the specific

research problem, such as in the examples given above. Merely establishing that there is a pattern of PNC does not address the underlying processes, but the initial general test can lead to specific tests addressing the hypothesized drivers.

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