REVIEW AND SYNTHESIS

Niche conservatism as an emerging principle in ecology and conservation biology

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Abstract

The diversity of life is ultimately generated by evolution, and much attention has focused on the rapid evolution of ecological traits. Yet, the tendency for many ecological traits to instead remain similar over time [niche conservatism (NC)] has many consequences for the fundamental patterns and processes studied in ecology and conservation biology. Here, we describe the mounting evidence for the importance of NC to major topics in ecology (e.g. species richness, ecosystem function) and conservation (e.g. climate change, invasive species). We also review other areas where it may be important but has generally been overlooked, in both ecology (e.g. food webs, disease ecology, mutualistic interactions) and conservation (e.g. habitat modification). We summarize methods for testing for NC, and suggest that a commonly used and advocated method (involving a test for phylogenetic signal) is potentially problematic, and describe alternative approaches. We suggest that considering NC: (1) focuses attention on the within-species processes that cause traits to be conserved over time, (2) emphasizes connections between questions and research areas that are not obviously related (e.g. invasives, global warming, tropical richness), and (3) suggests new areas for research (e.g. why are some clades largely nocturnal? why do related species share diseases?).

INTRODUCTION

Evolution is the ultimate cause of the diversity of life, from the origin of species to the variety of ecological, physiological, morphological and behavioural traits that those species possess. Many biologists are enthralled by spectacular examples of the rapid evolution of species and ecological traits (e.g. Darwin's finches, Rift-lake cichlids) and concerned about evolutionary responses to human impacts (e.g. reduced body sizes in fisheries). Yet, there may also be many

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cases where observed evolutionary change is slow or absent, and species seem to retain similar traits over long periods of time. These instances of slow evolution may have many fundamental consequences for ecology. Furthermore, the current biodiversity crisis may reflect the consequences of slow evolution, particularly with regards to 'niches' of species.

The niche (*sensu* Hutchinson; see Holt 2009) describes the set of abiotic and biotic conditions where a species is able to persist. Outside the niche, individuals are not expected to leave descendants, nor populations to persist, nor clades to endure and proliferate. This abstract trait, the niche, is a function of many organismal traits (e.g. body size, tolerance to pH, feeding adaptations). Sometimes, these niche-related traits evolve rapidly (e.g. Schluter 2000). But quite often, these traits seem to change very slowly (e.g. Peterson *et al.* 1999; Wiens & Graham 2005).

The tendency of species and clades to retain their niches and related ecological traits over time is called niche conservatism (NC hereafter). This term was first coined by Harvey & Pagel (1991; although the concept has many antecedents) and was subsequently popularized by Holt & Gaines (1992), Peterson *et al.* (1999), Prinzing *et al.* (2001) and many others. NC is relevant to a variety of traits, from those determining the abiotic niche axes of a species (e.g. tolerance to cold and drought) to those determining resource utilization (e.g. microhabitat, diet) and other aspects of interspecific interactions. Furthermore, NC can occur at a variety of different spatial, temporal and phylogenetic scales. The fact that NC can occur at different scales is part of what makes it relevant to so many different topics, from intraspecific patterns and conservation biology over decades (e.g. responses of species to anthropogenic climate change and spread of invasive species), to speciation and community ecology, to large-scale patterns of biogeography and species richness generated over tens or hundreds of millions of years (e.g. Wiens & Graham 2005).

Here, we review the importance of NC to ecology and conservation. Ours is not the first review of NC. Wiens & Graham (2005) discussed the relevance of NC to many ecological and evolutionary questions, but focused on a single (general) trait, the tolerance of species to factors that limit their geographic ranges. Similarly, Pearman *et al.* (2008) reviewed some applications of phylogenies and environmental niche modelling to the study of NC. Here, we address NC more generally, and address several topics not previously considered in an NC framework. Losos (2008) reviewed tests for NC and whether NC is prevalent based on his preferred method [i.e. a test for phylogenetic signal using a Brownian motion (BM) model of trait evolution on a tree]. We argue that this method may sometimes be misleading and suggest a variety of alternative methods.

Below we provide our working definitions of the niche and NC. We then describe potential tests of NC, the increasing evidence for NC in many areas of ecology and conservation, new areas where NC has not been widely applied, and areas for future research.

What is the niche?

The niche has been defined in terms of the distribution of species, the functions they perform and the resources they consume (reviewed in Soberón 2007). These definitions can be separated into two classes (Soberón 2007). The Grinnellian niche or non-interactive niche, is important for understanding the large-scale geographic distribution of species. The Eltonian niche focuses on biotic interactions and resource–consumer dynamics, often at more local scales. NC is relevant to both facets of the Hutchinsonian niche.

Following Hutchinson (1957), we consider the niche as describing the set of biotic and abiotic conditions where a species can persist (Holt 2009). This includes both the distribution of a species and its interactions with other species. Much literature on NC has focused on climate and geographic distribution. However, the niche is also relevant to the fine-scale distribution of species (e.g. microhabitats), the resources they consume, and biotic interactions. For many parasitic or symbiotic organisms, their hosts may determine the 'abiotic' environment they experience (e.g. temperature, moisture, pH) and the Grinnellian and Eltonian concepts converge. Similarly, Grinnellian niche dimensions (e.g. temperature) may influence key aspects of the Eltonian niche (e.g. food availability, competition), which in turn influence large-scale distributions of species.
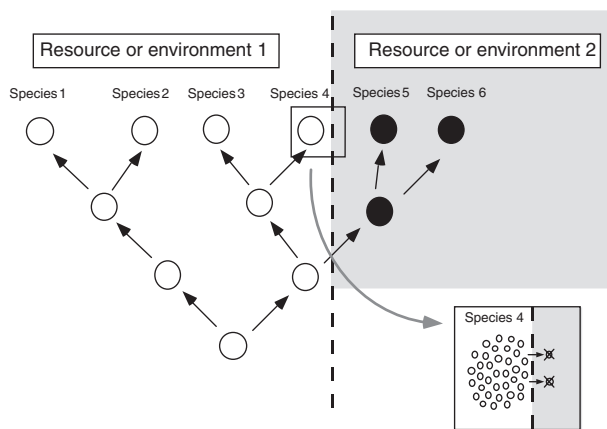
What is niche conservatism?

We define NC as the retention of niche-related ecological traits over time. This definition is intentionally broad, because NC can involve many traits and time scales, and can be detected using many tests (see below). NC is more inclusive than 'phylogenetic niche conservatism' (PNC), defined here as retention of ecological traits over time among related species. Importantly, NC can occur within species (e.g. constraining responses to global warming and spread of invasives), a level at which phylogeny may be irrelevant. Thus, defining NC based solely on a phylogenetic test may be inappropriate. Furthermore, there is a distinction between the definition of a concept and the specific test used to measure its effects empirically (e.g. competition is not defined based on a particular test).

Niche conservatism in a species or clade may be most apparent when contrasted with an alternative set of ecological conditions or resources that they fail to occupy

or utilize, and which are instead occupied by other species or clades (Fig. 1). Depending upon the organism and question, these alternative conditions may include temperate environments for tropical clades, different host or prey types, high vs. low pH soils, or the 'before and after' climate of a locality that has become 3 °C warmer.

Some authors (e.g. Losos 2008) have expressed concern over whether NC is a pattern or process. We argue that at one level, NC is a pattern of ecological similarity over time. However, NC can also be viewed as a process, if this pattern of ecological similarity helps create other patterns (e.g.

Figure 1 Niche conservatism creates phylogenetic patterns in ecological data. For a given ecological variable, the clade originates as a single ancestral species that utilizes a given environment or resource (e.g. diet, host, habitat, climatic regime). Early in the history of the group, there is a niche shift to utilize an alternate resource or environment. At the present time, there are four species utilizing resource 1 and two species utilizing resource 2, and strong phylogenetic structure in resource use among these six species. We argue that a major driver of this pattern is the process (niche conservatism) illustrated in the inset for species 4 (where circles represent individuals); the species is currently utilizing resource 1 and individuals attempting to utilize resource 2 and expand the species niche have reduced fitness. Thus, the ancestral niche is conserved in species 4. This conservatism may be maintained through a variety of population-level processes in species 4, including lack of genetic variation for necessary traits, selection favouring consistent choice of resource 1, and competition with species already utilizing resource 2. Similar processes are assumed to occur in the other species utilizing both resource 1 and resource 2, in both the past and present. This figure also illustrates the combination of niche conservatism and the time-for-speciation effect in creating patterns of species richness. The clade originates in environment 1 and a shift to environment 2 occurs more recently. Given the greater time for speciation and accumulation of diversity in region 1 (time-for-speciation effect) and infrequent dispersal between environments (due to niche conservatism), there are now more species in environment 1 than environment 2.

climatic NC leading to local extinction as climate changes). Many other terms share this property of being a pattern at one level (and requiring a causal explanation) and a process at another (and providing a causal explanation for patterns at that level). For example, speciation is a pattern of one species splitting into two (a pattern explained by various evolutionary processes), and a process that creates more species (and thus part of a causal explanation for many species richness patterns). At the population-level, several different processes may give rise to NC, and distinguishing these processes is a major area for future research (see below). Importantly, the pattern of NC is created by these finer-scale processes, but NC can also be viewed as a process that helps create other patterns (e.g. diversity gradients).

HOW DO WE TEST FOR NICHE CONSERVATISM?

Overview

Niche conservatism is potentially relevant to many questions and scales. Thus, no single test will be appropriate in every case. Furthermore, a test of NC without a related question or application is somewhat meaningless. We expect niches to always be somewhat conserved (e.g. there are no sister species pairs with one in tropical rainforests and the other in deep sea vents) and yet rarely identical among species (Wiens & Graham 2005). Whether niches are 'conserved enough' will therefore depend on the details of the question and context; local extinction due to global warming may occur if climatic niches are conserved over decades whereas species richness patterns may require conservatism for tens of millions of years. We briefly review below some current approaches.

Tests for traits on trees

A common question related to NC is whether a given trait shows significant phylogenetic conservatism across a phylogeny, but this issue is surprisingly slippery. By phylogenetic conservatism, we mean that closely related species tend to share similar values for a given trait (typically more similar than distantly related species). Researchers have often used tests of 'phylogenetic signal', such as Pagel's (1999) lambda statistic or the *K*-statistic of Blomberg *et al.* (2003). Both tests address whether a trait meets the expectations of a BM model of change across a tree, in which trait divergence among species is expected to increase proportionally with the phylogenetic distance between them. Losos (2008) argued that the level of fit to this model should be the primary test of PNC (with only greater-than-expected fit being sufficient evidence). However, a relationship between time and change requires substantial change across the

phylogeny (Revell *et al.* 2008), whereas the pattern expected from NC is 'no change.' Therefore, a pattern of no signal or weak signal could either mean that the trait varies randomly across the phylogeny, or shows stasis. As this result could mean either no NC or strong NC, this test is potentially problematic.

One alternative approach is to compare the relative fit of different evolutionary models to the data, including a BM model, a model of stasis or stabilizing selection (as in an Ornstein-Uhlenbeck, OU, model, with one or more optima), and a model of white noise (e.g. Kozak & Wiens 2010). Finding that a character fits a model of stasis would potentially support NC, whereas a model of white noise would not. Importantly, significant fit to the BM model (phylogenetic signal) could also be consistent with NC (and previous studies claiming to find NC by this criterion have not necessarily been misled). We find no compelling argument for claiming that NC is present only when phylogenetic signal is stronger than expected under BM.

This type of model-fitting approach seems promising, but may also have limitations. Testing its efficacy under different simulated evolutionary scenarios should be a priority for future research.

Another approach is to use a time-calibrated phylogeny and estimate rates of trait evolution (e.g. Ackerly 2009b). This approach can then be used to compare rates of change in different traits and clades (e.g. O'Meara *et al.* 2006). However, two caveats should be made. First, estimates of trait 'disparity' (i.e. variance) within clades are not necessarily equivalent to rates of change, particularly if the phylogeny within clades is ignored (O'Meara *et al.* 2006). Second, comparisons of rates alone do not address whether niches are significantly conserved or not, only whether they are higher or lower than in another trait or clade. However, these rate comparisons could be combined with comparisons of alternative models (e.g. BM, OU) to provide a more complete assessment of NC than gained from either approach alone.

Similar tests can be applied to both continuous variables and those treated as categorical or discrete (e.g. arboreality, herbivory). For example, given a phylogeny and a categorical variable, one can measure the fit of the character to the tree, randomize states among taxa, and compare the observed fit to that in the randomizations (e.g. Crisp *et al.* 2009).

Tests based on species distribution modelling

Many tests of the relationship between NC, climate and geographic distribution involve species distribution models (SDMs, also called environmental niche models). For biogeographic hypotheses, a key idea is that climatically unsuitable conditions can limit geographic ranges when there is NC, and such conditions can potentially be

identified and tested using SDMs. For example, a hypothesis of climatic NC predicts that invasive species will spread primarily in regions that are climatically similar to their native range. SDMs can be used to test the spatial limits of this predicted range, and whether species diverge from these expectations (e.g. Peterson 2003), offering both an application and test of NC. SDMs and related approaches can also be used to help determine which climatic factors (if any) set the range limits of clades and species. Such analyses have been used to help explain patterns of species richness (e.g. climate prevents tropical clades from invading temperate regions; Wiens *et al.* 2006) and community structure (e.g. climate restricts clades with different microhabitat preferences to different regions; Stephens & Wiens 2009). Once potentially limiting climatic variables are identified with SDMs, their fit to the phylogeny (or rate of change) can then be tested as described above (e.g. Wiens *et al.* 2006; Stephens & Wiens 2009).

Peterson *et al.* (1999) proposed a test of NC based on whether the SDM for one species predicts the geographic range of its sister species, and Warren *et al.* (2008) proposed several variations on this test. Such tests are complementary to those based on entire phylogenies, but may be more relevant to smaller phylogenetic scales. An important direction for future work is to take NC tests based on SDMs and combine them with mechanistic modelling of species ranges, which incorporates physiological parameters and other factors in addition to climatic data (Kearney & Porter 2009).

Other tests

Again, a plethora of tests may be applied to a diversity of NC-related questions. Some tests are similar to those described above. For example, Cattin *et al.* (2004) found phylogenetic structure in food webs (a potential manifestation of NC) by showing a negative relationship between the phylogenetic distance between species and the similarity in the prey taxa consumed, using a Mantel test. This approach is related to a test of phylogenetic signal, but focuses on species in a given community, rather than a clade.

Rangel *et al.* (2007) used an innovative approach to test whether climatic NC drives large-scale patterns of species richness in South American birds. They simulated the evolution of species distributions under different rates of niche evolution among species, and evaluated which rate generated richness patterns most closely matching empirical patterns. They found that low rates of change (strong NC) offered the best fit. This general approach might be applied to many other NC-related questions (e.g. community assembly).

Other tests may apply to finer phylogenetic and temporal scales. For example, range shifts and local extinctions in

response to climate change offer strong evidence for NC over short time scales (e.g. Parmesan & Yohe 2003), as do analyses of climatic niches over time from modern and historical locality data (Tingley *et al.* 2009).

Paleontological studies offer additional evidence. For example, studies reviewed by Eldredge *et al.* (2005) showed that many fossil species did not go extinct or change morphologically in response to climate change, but instead shifted their geographic ranges to remain within their ancestral environment (i.e. 'habitat tracking'), a pattern we attribute to NC. In fact, NC is sufficiently prevalent in the fossil record that certain plant clades are used as indicators of past climates (e.g. palms = tropical). Stasis in morphological traits over time, a major topic in paleobiology (see Eldredge *et al.* 2005), may also offer evidence of NC, provided that the traits are niche-related.

Summary

All tests have limitations, and there is no universal test for NC. But the diversity of available tests allows one to confirm results with many approaches. Also, different tests may be relevant to NC in different contexts.

It is also important to remember that the niche is multi-dimensional, and in any clade, some aspects may be conserved while others diversify. For example, Galapagos finches and Rift-lake cichlids are classic examples of adaptive radiation, particularly in trophic niches (Schluter 2000). Yet, within these radiations, all species occur under similar climatic conditions, and exhibit NC from that perspective. In addition, NC may be evident at some temporal and phylogenetic scales but not others. Any claim about conserved or labile niches may only apply to the trait(s) and time scale under study.

EMERGING EVIDENCE FOR NICHE CONSERVATISM IN ECOLOGY AND CONSERVATION BIOLOGY

Overview

In this section, we review the growing evidence for the importance of NC to many research areas in ecology and conservation. We also point out important areas in need of further research.

Species richness patterns

A major goal of ecology is to explain patterns of species richness, from global to local scales. Ultimately, explanations for diversity patterns must include the processes that directly change species numbers in a region or community: speciation, extinction (local or global) and dispersal (e.g.

Ricklefs 2004). These processes can be viewed as evolutionary or biogeographic. Yet, large-scale patterns of species diversity are often strongly associated with climate, and with other ecological factors at local scales (e.g. soil pH). These two perspectives are sometimes seen as being in conflict (i.e. evolution vs. ecology; Algar *et al.* 2009). The concept of NC offers a bridge between them (e.g. Wiens & Donoghue 2004). NC may explain why species fail to disperse between different climates and habitats (e.g. a tropical species cannot rapidly adapt to cold winter temperatures, and fails to colonize temperate regions). The tendency for a group to remain in its ancestral environment as it diversifies could lead to higher richness in some climates (e.g. tropical vs. temperate) or habitats (e.g. mesic vs. arid) than in others, even without differences in rates of speciation and extinction in different environments (Fig. 1). The idea that regions or habitats occupied longer will have more species is called the 'time-for-speciation' effect (TSE; review in Stephens & Wiens 2003). There is growing evidence that the combination of NC and TSE may help explain many richness patterns, including latitudinal, elevational, and local diversity.

Several studies have supported the role of NC and TSE in generating high tropical species richness. Wiens *et al.* (2006) showed that high tropical richness in treefrogs (Hylidae) is related to their origin and longer time in tropical regions (TSE), and that expansion of tropical clades into temperate North America is limited by a climatic variable (temperature seasonality), which shows significant phylogenetic signal (consistent with NC). Algar *et al.* (2009) claimed to refute this, but ignored both time and temperature seasonality, did not explicitly compare tropical and temperate regions, and offered no comparable alternative hypothesis. A similar pattern of ancient tropical origin and recent temperate dispersal occurs in ranid frogs (Wiens *et al.* 2009), which dominate the Old World tropics (unlike the predominately Neotropical hylids). Local diversity in New World bats also shows a strong latitudinal TSE (Stevens 2006). In birds, tropical regions globally are dominated by more basal clades, a pattern consistent with NC and TSE (Hawkins *et al.* 2007). A simulation study of South American birds showed that their richness patterns are best explained by strong climatic NC (Rangel *et al.* 2007). Recent analyses of global distribution patterns in plants showed evidence for NC constraining dispersal between major biomes (Crisp *et al.* 2009) and for TSE in explaining lowland tropical species richness (Jansson & Davies 2008). Analyses of climate and richness across mammal clades suggest that the mammalian latitudinal diversity gradient may be related to NC and the TSE (Buckley *et al.* 2010).

Other studies have suggested that tropical richness may be explained instead by higher rates of tropical speciation or temperate extinction (many reviewed in Mittelbach *et al.*

2007). However, most did not test for a biogeographic TSE at all, making it difficult to evaluate which hypothesis (rates vs. time) is more important in explaining diversity patterns. Furthermore, even if higher rates of tropical diversification (speciation extinction) prove to be more important than the TSE, NC might still be important in generating latitudinal diversity patterns, for example, by limiting dispersal of tropical species into temperate regions (e.g. Allen & Gillooly 2006). Reconciling the relative importance of diversification rates, TSE, and NC in generating the latitudinal diversity gradient is a major challenge for future research, and future studies should consider all of these processes, not just diversification rates.

Niche conservatism-based hypotheses can potentially explain many other diversity patterns beyond high tropical richness. For example, some groups actually have higher richness in temperate regions than in tropical regions. Analyses of predominately temperate clades of frogs and snakes (Smith *et al.* 2005; Pyron & Burbrink 2009) suggest that TSE and NC (i.e. temperate origins and climatic constraints on dispersal, respectively) explain their unusual diversity patterns. Richness varies elevationally as well as latitudinally, and in many clades and areas, regional richness is highest at mid-elevations (e.g. McCain 2005; Oömmen & Shanker 2005; Smith *et al.* 2007; Li *et al.* 2009; Kozak & Wiens 2010). This mid-elevation hump also appears to be caused by the TSE (based on studies in frogs, salamanders and fish; Smith *et al.* 2007; Wiens *et al.* 2007; Li *et al.* 2009; Kozak & Wiens 2010), with major clades seemingly originating in environments presently situated at mid-elevations, followed by dispersal to lower and higher elevations. NC is hypothesized to limit dispersal between elevational climatic zones, although rigorously demonstrating this remains a major challenge (but see Kozak & Wiens 2010). NC may help explain other elevational diversity patterns as well (e.g. decreasing richness at higher elevations).

Perhaps the least explored interface of NC and species richness relates to local-scale diversity. Local and regional species richness patterns are often strongly correlated (review in Harrison & Cornell 2008), and recent analyses demonstrate that effects of NC on regional diversity can trickle down to local communities. For example, Partel (2002) showed that local plant richness increased with increasing soil pH in regions of generally high pH but decreased in regions of low pH, and attributed this difference to the larger pool of species adapted to the prevailing pH level in each region. Harrison & Grace (2007) showed that the positive productivity-richness relationship in the California flora is driven by the large proportion of species regionally with evolutionary affinities to high-productivity conditions (moist, north-temperate environments) and that the consequences of this NC filtered down

to affect the richness and composition of local communities (see also Ackerly 2009a).

In addition to abiotic factors (e.g. climate, pH), biotic factors might also be involved in the interplay of NC and TSE in explaining patterns of local diversity. For example, Brown *et al.* (2000) argued that local species richness of *Enallagma* damselfly larvae in lakes with fish as top predators (fish lakes) is higher than in lakes where dragonfly larvae are top predators (fishless), because use of fish-lake habitat has been conserved in *Enallagma* for tens of millions of years. In contrast, fishless lakes (which require special adaptations to cope with predation by dragonflies) represent a habitat that has been colonized much more recently by *Enallagma*, leaving less time for speciation to build up diversity in these lakes.

In summary, there is now evidence that NC may be relevant to many richness patterns at many scales. Yet, most patterns to date have been addressed with only a handful of studies, and few have explicitly tested for both NC and the TSE.

Community assembly

Many recent studies have addressed the conservatism of niche-related traits among species in local communities (e.g. microhabitat preference), often with the goal of understanding community assembly (e.g. Prinzing *et al.* 2001; Cavender-Bares *et al.* 2004; Swenson & Enquist 2009). These studies offer many examples both for and against NC, depending on the clade and trait. Many studies involve 'community phylogenetics' (reviews in Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009), where NC is often key to interpreting patterns. Assuming strong NC, communities of closely related species may represent the effects of habitat filtering (close relatives with similar traits are 'filtered in' to a community from the regional species pool) and communities of distantly related species may represent the effects of competition (limiting coexistence of close relatives sharing similar traits and resource requirements). Tests of NC for each trait are essential for interpreting these patterns, as rapid trait evolution may lead to very different conclusions (e.g. Webb *et al.* 2002; Losos 2008). However, even given NC in the relevant traits, these expectations and interpretations (e.g. ecologically similar species competitively exclude each other) are surprisingly controversial (e.g. Mayfield & Levine 2010).

Ecosystem function

Recent studies suggest that NC may have important consequences for ecosystem function. Maherali & Kliron-omos (2007) used experimental communities of mycorrhizal fungi to show that plant productivity (a common index of

ecosystem function) was lowest when communities contained only closely related fungal species. This seemingly occurs because two of the fungus families sampled have complementary effects on productivity (one protects plants against pathogens, the other enhances phosphorus uptake), but there is functional redundancy of species within families, such that NC in functional roles reduces the benefits of having confamilial species. Other authors have shown that ecosystem function (e.g. plant productivity) is associated with higher phylogenetic diversity, and that phylogenetic diversity may be a better predictor of ecosystem function than species richness or even functional diversity (e.g. Cadotte *et al.* 2008, 2009). However, the exact mechanisms by which phylogeny, traits and NC interact to drive higher productivity in these non-fungal systems remain an important area for future research. Presumably, phylogenetically diverse species capture important functional diversity not reflected in the functional traits measured, and NC leads to functional redundancy among close relatives (reducing the importance of species richness alone).

Invasive species

Invasive species are often considered a major threat to biodiversity, especially on islands (Dirzo & Raven 2003). Given climatic NC, the distribution of species in their native ranges may predict where they can successfully invade and subsequently spread (e.g. Peterson 2003). Recent studies have also shown that climatic niches of invasive populations may change significantly relative to the species' native range (e.g. Broennimann *et al.* 2007; Beaumont *et al.* 2009; Rodder & Lotters 2009). However, these counterexamples involved few species, as did the initial studies using SDMs to test for climatic similarity between native and introduced ranges (e.g. Peterson & Vieglais 2001). A study of 29 introduced reptile and amphibian species in North America (Wiens & Graham 2005) found a strong relationship between native and introduced range limits (poleward latitudinal extents). An earlier study of dozens of introduced bird and mammal species (Sax 2001) showed significant (but weaker) correlations between native and introduced latitudinal extents. In summary, there is some evidence for NC based on relationships between native and introduced latitudinal limits across dozens of species, whereas studies using SDMs of fewer species reveal more variable results. What are lacking are large-scale comparisons of climatic niches between native and introduced ranges, utilizing the available data from the hundreds of introduced animal species and thousands of introduced plants. Such studies are urgently needed to assess both short-term NC and the ability of SDMs to predict the spread of invasive species.

Responses to climate change

The threat of global climate change to biodiversity can be viewed from a NC perspective. If the climatic tolerance of a species is not wide enough to encompass the new conditions or acclimatize to them (physiologically or behaviourally), species with strong climatic NC must either migrate or go extinct, whereas more evolutionarily labile species can potentially adapt (Holt 1990). Persistence may depend on several other factors, including the speed of climatic change (e.g. Loarie *et al.* 2009), the location of suitable habitat to migrate to, dispersal rate, and changes in biotic niche dimensions (e.g. novel predators or competitors, loss of pollinators). Nevertheless, the strength and generality of climatic NC remains a critical issue in determining how species respond to climate change. For example, SDMs are frequently used to predict range shifts and extinction in response to climate change (e.g. Thomas *et al.* 2004), based on the assumption that climatic niches are conserved.

A review by Parmesan & Yohe (2003) found that hundreds of plant and animal species have modified their ranges latitudinally (poleward) and elevationally (upward) as climate has changed, suggesting widespread climatic NC. Subsequent studies have found similar patterns. For example, Tingley *et al.* (2009) documented the climatic niches of 53 California bird species from recent and historical distributional data and found that 48 tracked their climatic niche (exhibited NC) as climate warmed, leading to distributional shifts.

Responses to climate change can also be studied in a phylogenetic context. Willis *et al.* (2008) found that declines in abundance (and local extinctions) of plant species in Thoreau's woods (Concord, Massachusetts, USA) during the last 150 years are related to different responses to flowering times, which show strong phylogenetic signal. Specifically, species with temperature-insensitive flowering times had decreased abundances relative to temperature-sensitive species.

NEW FRONTIERS IN NICHE CONSERVATISM RESEARCH

Overview

In this section, we describe several areas where the concept of NC has been applied either rarely or not at all. Many of these topics share a common theme. In many different areas of ecology and conservation biology, researchers have found evidence for phylogenetic conservatism in an important ecological trait. The challenge for future NC research is not simply to document such phylogenetic trends, but to understand the ecological and evolutionary causes for the long-term stasis in these traits.

Temporal niche conservatism

In contrast to the spatial distribution of species and clades, the 'temporal niche' (e.g. Levin 2006) has received little attention in the NC literature. Yet, many organisms may show long-term evolutionary conservatism in the times at which they are active, reproductive, or present within a region (for migratory species), and this may have many ecological and evolutionary consequences. For example, in terrestrial vertebrates, diel (day–night) activity niches seem to be highly conserved across thousands of species and hundreds of millions of years. Nocturnality is conserved across most of the > 6000 species of amphibians, whereas diurnality is conserved across most of the thousands of species of reptiles, including squamates (especially lizards), turtles and birds (and many of the contradictory clades offer further examples of conservatism, like geckos and owls; Pough *et al.* 2009). These patterns are suggestive of strong temporal NC (i.e. conservatism in temporal niches), but require explicit testing.

Temporal NC may be related to the same physiological tolerances (e.g. to high or low temperatures) that limit the large-scale geographic distribution of species and clades; individuals may only be active during those times of the day or year with a certain set of environmental conditions. However, other mechanisms may also be involved. For example, daily activity patterns in animals may be constrained by their sensory systems (e.g. adaptations for night vision), and flowering times in plants by the temporal niche of their pollinators (Levin 2006). The temporal niche is an important area for new NC research, particularly as climate change leads to shifts in phenology (e.g. Parmesan & Yohe 2003), which may be strongly related to phylogeny (e.g. Willis *et al.* 2008).

Food webs

Explaining the structure of food webs is one of the great challenges in ecology. A groundbreaking study showed significant phylogenetic structure in food webs (Cattin *et al.* 2004), including terrestrial, marine and freshwater systems. Thus, there is a strong relationship between matrices of phylogenetic relatedness and trophic similarity of species (Fig. 2). These authors also showed that a model including both phylogeny and adaptation predicts empirical food-web structure better than traditional, strictly ecological models. Subsequent studies found phylogenetic signal in many other food webs (e.g. Ives & Godfray 2006; Rezende *et al.* 2009).

These studies also suggest the value of considering NC in food-web research, and not phylogenetic structure alone. Cattin *et al.* (2004) proposed that many aspects of food webs are explained by 'phylogenetic constraints.' But these constraints must have an underlying biological explanation.
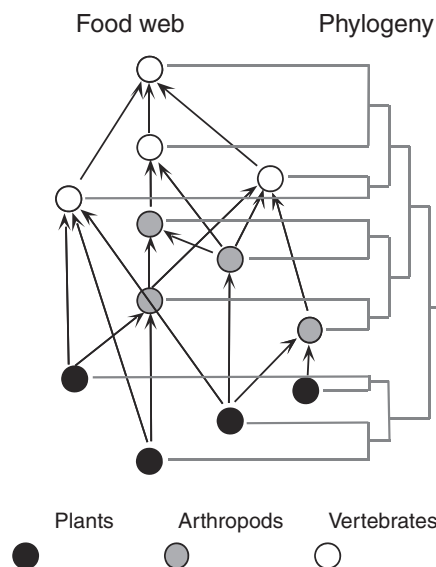
Figure 2 A hypothetical example illustrating phylogenetic structuring in food webs. Because many food webs span deep branches of the Tree of Life, from producers (e.g. plants), through consumers (Metazoa), to decomposers (fungi), broad-scale trophic structure seems likely to be highly conserved in most systems, with species within each of these ancient clades clustering within trophic levels. There is now evidence for significant phylogenetic structure in more complex, empirical food webs (including freshwater, marine, and terrestrial systems), such that more closely related species seem to share similar trophic levels and interactions (Cattin *et al.* 2004; Bersier & Kehrli 2008). A major challenge for future research on food webs is to understand the ecological and evolutionary processes that cause the conservatism in trophic niches that underlie these patterns of phylogenetic structure, especially patterns among more closely related species. Statistical analysis of this hypothetical example, using methods similar to those of Cattin *et al.* (2004), shows a significant relationship ($r = 0.42$; $P = 0.009$) between the phylogenetic distance between species (assuming equal branch lengths) and the Jaccard's distance ($1 −$ number of prey and consumers shared by each pair divided by the pair's total number of prey and consumers), based on a Mantel test with 1000 randomizations to evaluate significance.

Studies of NC can address the processes that cause species in a clade to share similar values for an ecological trait. From this perspective, finding phylogenetic conservatism is not an endpoint, but a starting point that opens up an array of new questions. For example, to what extent is conservatism in food-web structure explained by conservatism in body size vs. other traits? Rezende *et al.* (2009) have begun to study these patterns in more detail (see also Bersier & Kehrli 2008), and have suggested that phylogenetic signal in food webs is associated with the tendency of related species to share similar habitat and body size. Recent studies have also begun to model the assembly of food webs in terms of the evolution of species and their trophic interactions (e.g.

Loeuille & Loreau 2005; Rossberg *et al.* 2006; Ingram *et al.* 2009). The importance of trait conservatism in food webs suggests that NC could be important for related topics as well, such as energy flow and nutrient cycling.

## Disease ecology and host–parasite relationships

Host–pathogen relationships can also be interpreted in a NC framework (Fig. 3). There is a rich literature documenting close relationships between phylogenies of parasites and hosts over millions of years and through multiple speciation events (e.g. endoparasitic worms and their vertebrate hosts; Brooks & McLennan 1991; malaria and their insect vectors and vertebrate hosts; Martinsen *et al.* 2008; lice on birds and mammals; Clayton *et al.* 2004). Moreover, recent studies have demonstrated that closely related host species are vulnerable to similar communities of pathogens, in both plants (Gilbert & Webb 2007) and animals (Davies & Pedersen 2008).

Phylogenetic structure in pathogen host range can be interpreted as NC within the pathogens. From this perspective, the critical issue is to understand the specific ecological mechanisms that underlie patterns of phylogenetic conservatism (e.g. Clayton *et al.* 2004). For example, the phylogenetically restricted host range of a pathogen clade may reflect NC in tolerances to internal host–environments (e.g. warm vs. cold-blooded), conserved responses to aspects of the host clade's immune defenses, or conservatism in the utilization of intermediate hosts and vectors. Intriguingly, studies of some RNA viruses show little evolutionary conservatism in their host usage (Kuiken *et al.* 2006). Instead, very fast mutation rates and short generation times seem to provide the evolutionary potential for crossing barriers between phylogenetically distant hosts, for example, by allowing rapid adaptation to novel cell surface types (Kuiken *et al.* 2006).

Patterns of NC in pathogens have consequences for conservation and human health. Understanding what factors determine the host range of a disease or parasite species is key to predict the likelihood of future emergent infectious disease events (Davies & Pedersen 2008). NC may also be important for understanding which disease treatments will be most effective in the long term. The ability to adapt to environments created by treatment regimes can be viewed as niche evolution, and treatments that target more highly conserved traits of infectious species may be more successful (Ewald 1994).

Positive interspecific interactions

Niche conservatism is relevant to many other types of interspecific interactions, including mutualisms and facilitation. Many of these interactions are conserved across tens of
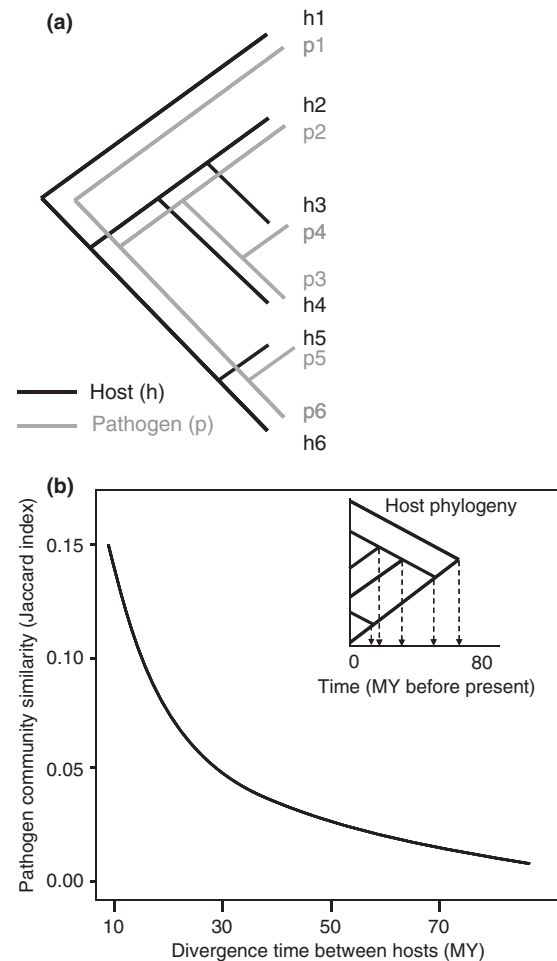
Figure 3 Examples of niche conservatism in disease ecology. (a) Niche conservatism in pathogens is expected to limit switching to new hosts, which should lead to congruent phylogenies between the pathogens and their hosts over time. This hypothetical example shows trees for a pathogen clade (p1–p6) and their host (h1–h6) clade: as host lineages diverge, so do their pathogens. Tight niche conservatism in pathogen host range may inhibit host-switching, effectively isolating pathogens within host lineages. If there are occasional host jumps, these are expected to be between closely related pathogen and host lineages, as depicted in the h2–h4 and p2–p4 clades. Although congruent phylogenies such as these are frequently observed in empirical studies (e.g., Clayton *et al.* 2004), the ecological mechanisms underlying this niche conservatism remain poorly understood in many systems. (b) These patterns of niche conservatism in host range, when summed across multiple pathogen clades, should lead to closely related host species sharing similar pathogen communities, a pattern demonstrated recently in plant and primate pathogens (Gilbert & Webb 2007; Davies & Pedersen 2008). This graph illustrates the relationship between similarity in pathogen community composition and the evolutionary distance separating their primate host taxa, with the latter calculated (see inset) based on a time-calibrated primate phylogeny (figure modified from Davies & Pedersen 2008).

millions of years. For figs and their pollinating fig-wasps, a tight mutualism has been maintained for > 60 million years, and is conserved among *c.* 800 fig species distributed around the world (Rønsted *et al.* 2005). More generally, phylogenetic studies of interaction networks between plants and animals (i.e. pollinators, seed dispersers) show that related animal species tend to interact with sets of related plant species, and *vice versa* (Rezende *et al.* 2007), suggesting NC. Other mutualistic interactions may also be conserved and ancient. For example, fungal lineages associated with lichen symbioses appear to be very old, suggesting an ancient symbiosis (Lutzoni *et al.* 2001). Bacterial endosymbionts are important to many organismal functions, such as herbivory. A recent summary (Moran *et al.* 2008; their Table 1) of the estimated ages of mutualistic interactions between insects and their bacterial endosymbionts reveals seven systems each conserved for > 100 million years. NC in endosymbionts may also drive NC in their hosts, as aphid thermal tolerances are determined (at least in part) by their endosymbiotic bacteria (Dunbar *et al.* 2007). Conversely, analyses of facilitation in plants (Valiente-Banuet *et al.* 2006) show that mesic-adapted clades can expand their niches into arid regions if they grow under the canopy of xeric-adapted lineages (i.e. 'nurse plants'). These are just a few examples of how NC and positive interspecific interactions may be intertwined. However, as with food webs and disease ecology, the ecological mechanisms that underlie NC in these cases remain understudied.

Finally, a recent study (Gómez *et al.* 2010) found evidence for phylogenetic conservatism in all types of interspecific interactions (host–parasite, predator–prey, mutualism) in 116 clades (genera) across the Tree of Life. These authors including generalists and specialists and viruses, bacteria, fungi, plants and animals.

Conservation and habitat modification

Habitat destruction is often considered the most important current threat to biodiversity (e.g. Dirzo & Raven 2003), and can also be seen from the framework of NC: habitat is modified faster than a species can adapt to these changes (Holt & Gomulkiewicz 2004). To some, this may seem trivial; little evolutionary perspective seems necessary to understand why cutting down a forest leads to extinction of endemic, forest-dwelling species. But threats from habitat modification will depend on the interaction between the type of modification (e.g. clearcutting, selective logging, agriculture, pollution), tolerances of species to that modification (e.g. ability to withstand heat, low pH), and whether those tolerances will evolve rapidly or be conserved.

Recent studies have shown that habitat modification can have non-random phylogenetic effects on impacted communities (e.g. Knapp *et al.* 2008; Dinnage 2009; Helmus

et al. 2010; for an older example, see Warwick & Clarke 1995). Specifically, anthropogenic disturbances tend to decrease phylogenetic diversity, suggesting that only some clades can tolerate a given modification, leaving a pool of more closely related species afterwards (Fig. 4). For example, a detailed study of zooplankton in north-temperate lakes (Helmus *et al.* 2010) demonstrated this pattern, and also suggested that sensitivity to each disturbance regime (e.g. decreased pH, increased nitrogen) was phylogenetically conserved and differed between clades. These latter analyses pave the way for understanding how these sensitivities evolved across the phylogeny.

Given information on the ecological requirements necessary for persistence of a species in intact vs. modified habitats (e.g. microclimates, food resources), studying habitat modification from a NC perspective can help elucidate the potential for those requirements to evolve,
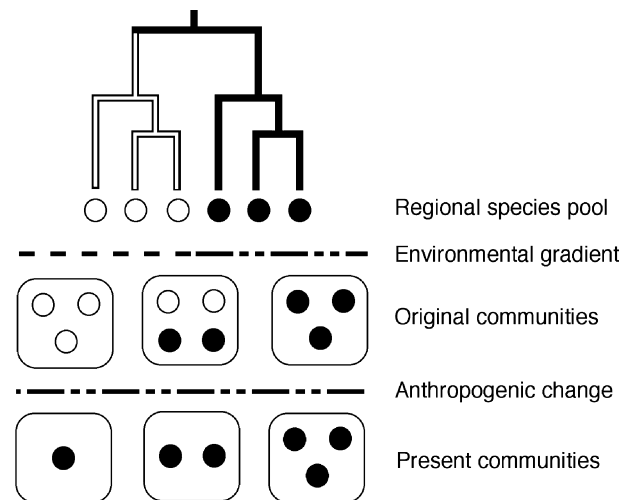
Figure 4 Niche conservatism, phylogeny and anthropogenic change. Six species belong to two clades (black vs. white circles) and occur in three communities (squares; where circles represent species from each clade). In the top row of communities, the distribution of species is associated with phylogenetically conserved tolerances to a range of conditions along a natural environmental gradient. In the bottom set of communities, species composition has now changed due to conserved tolerances to anthropogenic changes, with the loss of one of the clades from these communities and a reduction in phylogenetic diversity. Empirical studies have now demonstrated changes in the phylogenetic composition of communities in response to climate change, pollution, invasive species, agriculture, urbanization, and other human modifications (Knapp *et al.* 2008; Willis *et al.* 2008; Dinnage 2009; Helmus *et al.* 2010), and in some cases have shown the specific biological traits that are conserved and seemingly underlie these responses (e.g. flowering time and climate change; Willis *et al.* 2008). Anthropogenic changes have also been shown to lead to a loss of phylogenetic diversity (e.g. Helmus *et al.* 2010), seemingly through conservatism of niche-related traits.

based on their ability (or inability) to evolve in the past. At this point, we know little about whether the relevant traits might evolve rapidly or be conserved, and if processes that maintain NC might be circumvented (excepting the obvious interest in maintaining diversity within species). A deeper understanding of what habitat modifications a species or clade can (or cannot) tolerate and adapt to may also suggest how to modify human-altered landscapes to allow their persistence.

THE FINAL FRONTIER: CAUSES OF NICHE CONSERVATISM

We argue that the major area for future research in NC is to obtain a better mechanistic understanding of why it occurs. In many cases, researchers have shown phylogenetic patterns (e.g. association between host and parasite phylogenies), but the specific ecological traits that underlie these patterns remain unclear. In some cases, correlative studies may identify the specific traits that underlie these ecological patterns. In other cases, extensive experimental work may be needed. Such studies may be trait and taxon specific. But once the specific trait is identified, the next question is: what limits changes in this trait over time?

The role of competition and other biotic interactions in constraining niche evolution remains poorly studied and is a major question for future research in NC. For example, have most species in clade A remained in habitat X because clade B already occupies habitat Y? This could potentially be supported if, within clade A, there are repeated shifts to habitat Y in regions where clade B is absent. Other interspecific interactions could also limit or enhance niche evolution in a species or clade. As mentioned above, the abiotic tolerance of an endosymbiont may limit the environmental niche of its host (in aphids), and positive interspecific interactions may expand the environmental niche (nurse plants provide shade for mesic lineages in deserts).

Several population-level processes may underlie NC. First, the evolution of niche-related traits may be constrained by limited genetic variation in those traits (e.g. Bradshaw 1991).

Second, even if there is genetic variation, natural selection may still lead to NC. For example, behavioural habitat choice should cause animals to consistently avoid habitats in which their fitness will be lower (e.g. deserts for forest dwellers), leading to NC (e.g. Holt & Barfield 2008). Similarly, selection should favour individuals that choose the dietary or microhabitat resources they are best adapted to utilize (e.g. small seeds for small finches), and these choices may increase specialization and reduce opportunities to adapt to alternate resources. In sessile organisms, traits are expected to evolve towards those conditions where most individuals of the species occur (e.g. Holt & Gaines 1992).

Pleiotropy and trade-offs between traits may also lead to selection against niche evolution (e.g. Jenkins & Hoffman 1999; Etterson & Shaw 2001). NC may also be enhanced by very sharp contrasts in conditions in space and time (e.g. the edge between marine and terrestrial environments, serpentine and non-serpentine soils), whereas niche evolution may be facilitated when environmental gradients are more gradual (Holt & Gomulkiewicz 2004).

Third, niche evolution may be impeded by gene flow. For example, where species ranges are limited by unfavourable environmental conditions, adaptation to those extralimital conditions may be reduced by gene flow from the centre of the range (e.g. Kirkpatrick & Barton 1997). Analogous processes should limit evolution of novel niche-related traits within populations, leading to conservatism (assuming no trait-related assortative mating).

The processes described above have generally been demonstrated in both theoretical and empirical studies. However, the empirical studies have not done so with the intention of addressing NC *per se*, and the relative importance of these processes remains largely unknown. It is also possible that the causes of NC in a trait might change across the history of a clade or range of a species, even as the trait itself remains constant.

In summary, we argue that the major area for future research in NC is to understand its ecological and evolutionary underpinnings, rather than simply documenting it. Some important questions include: what is the relative importance of competition relative to tolerance to abiotic factors in NC? What microevolutionary processes underlie NC? For example, is lack of genetic variation typically a limiting factor, or is selection more important? How do the answers to these questions vary with the topic (large-scale species richness vs. host–parasite relationships), environment, traits and organisms involved?

CONCLUSIONS

In this article, we have argued that NC may be relevant to many different patterns and questions in ecology and conservation biology, and have suggested many areas for future research. But why think about these questions in terms of NC?

For many questions, the importance of NC is related to the importance of phylogeny. Our review highlights the need for ecologists and conservation biologists to be aware that many of the traits and patterns they study may have ancient roots that go far deeper than the species and ecological conditions seen today (and may not be fully understood by examining those species and conditions alone). Thinking about NC encourages thinking about phylogeny. However, this is hardly new (e.g. Brooks & McLennan 1991).

More importantly, the concept of NC speaks to why phylogeny matters. NC and phylogeny are not the same thing. Similarity in a trait among species cannot be explained by phylogeny alone, but instead must be explained by population-level processes, including some that may be quite ecological (e.g. behavioural habitat selection, competition) or more evolutionary (e.g. limited genetic variation). Thinking about NC reminds us that even though phylogeny is important for understanding the evolution and distribution of traits among taxa, those phylogenetic patterns may themselves have strong ecological underpinnings. Nevertheless, simply attributing a pattern to NC does not identify which specific process generates NC in a given case.

We see at least two other major advantages to thinking about questions in ecology and conservation in a NC framework. The first is in making connections between topics and questions whose relationships might not otherwise be obvious. For example, thinking about climatic NC over time can connect research on responses to global warming, distributions of invasive species, and patterns of species richness and community structure. Thus, when placed in the framework of NC, the observation that tropical species of *Drosophila* lack genetic variation for the traits underlying cold tolerance (Kellermann *et al.* 2009) becomes relevant to explaining many different patterns.

The other advantage is to stimulate new research. Many of us study ecology and conservation because we are interested in the diversity of living things and how that diversity originated and can be preserved. Given this, one might (for example) study a group of organisms that shows interesting ecological variation and try to understand the causes of this variation (e.g. crossbills, silverswords). From this perspective, studying a group of species to understand why they all share the same trait might seem unthinkable. But from the perspective of NC, this is a potentially interesting and important research program.

To give another example, landmark papers have now documented phylogenetic structure (and conservatism) in food webs and mutualistic interaction networks (e.g. Cattin *et al.* 2004; Rezende *et al.* 2007). A critical next step in such research is to understand by what ecological and evolutionary processes this phylogenetic structure comes about. This is the province of NC.

In this review, we have described the relevance of NC to many topics, from the oldest questions in ecology to the most pressing issues in conservation, emphasizing topics not previously considered in this framework. We believe that NC is emerging as a potentially important and widespread principle in ecology, but one that has only begun being studied. Major questions for future research will be to understand what processes underlie NC in these diverse contexts, and how this knowledge might be used to help preserve biodiversity.

REFERENCES

Ackerly, D.D. (2009a). Evolution, origin and age of lineages in the Californian and Mediterranean floras. *J. Biogeography*, 36, 1221–1233.

Ackerly, D.D. (2009b). Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. *Proc. Natl. Acad. Sci. USA*, 106, 1699–1706.

Algar, A.C., Kerr, J.T. & Currie, D.J. (2009). Evolutionary constraints on regional faunas: whom, but not how many. *Ecol. Lett.*, 12, 57–65.

Allen, A.P. & Gillooly, J.F. (2006). Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol. Lett.*, 9, 947–954.

Beaumont, L.J., Gallagher, R.V., Thuiller, W., Downey, P.O., Leishman, M.R. & Hughes, L. (2009). Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Divers. Distrib.*, 15, 409–420.

Bersier, L.F. & Kehrli, P. (2008). The signature of phylogenetic constraints on food-web structure. *Ecol. Complex.*, 5, 132–139.

Blomberg, S.P., Garland, T. & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, 57, 717–745.

Bradshaw, A.D. (1991). Genostasis and the limits to evolution. *Philos. Trans. R. Soc. Lond. B*, 333, 289–305.

Broennimann, O., Treier, U.A., Muller-Scharer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecol. Lett.*, 10, 701–709.

Brooks, D.R. & McLennan, D.A. (1991). *Phylogeny, Ecology, and Behavior*. University of Chicago Press, Chicago.

Brown, J.M., McPeek, M.A. & May, M.L. (2000). A phylogenetic perspective on habitat shifts and diversity in the North American *Enallagma* damselflies. *Syst. Biol.*, 49, 697–712.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L. *et al.* (2010). Phylogeny, niche conservatism, and the latitudinal diversity gradient in mammals. *Proc. R. Soc. Lond. B*, 277, 2131–2138.

Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl. Acad. Sci. USA*, 105, 17012–17017.

Cadotte, M.W., Cavender-Bares, J., Tilman, D. & Oakley, T.H. (2009). Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS ONE*, 4, e5695.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R. & Gabriel, J.P. (2004). Phylogenetic constraints and adaptation explain food-web structure. *Nature*, 427, 835–839.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A. & Bazzaz, F.A. (2004). Phylogenetic overdispersion in Floridian oak communities. *Am. Nat.*, 163, 823–843.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009). The merging of community ecology and phylogenetic biology. *Ecol. Lett.*, 12, 693–715.

Clayton, D.H., Bush, S.E. & Johnson, K.P. (2004). Ecology of congruence: past meets present. *Syst. Biol.*, 53, 165–173.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S. *et al.* (2009). Phylogenetic biome conservatism on a global scale. *Nature*, 458, 754–756.

Davies, T.J. & Pedersen, A.B. (2008). Phylogeny and geography predict pathogen community similarity in wild primates and humans. *Proc. R. Soc. Lond. B*, 275, 1695–1701.

Dinnage, R. (2009). Disturbance alters the phylogenetic composition and structure of plant communities in an old field system. *PLoS ONE*, 4, e7071.

Dirzo, R. & Raven, P.H. (2003). Global state of biodiversity and loss. *Annu. Rev. Environ. Resour.*, 28, 137–167.

Dunbar, H.E., Wilson, A.C., Ferguson, N.R. & Moran, N.A. (2007). Aphid thermal tolerance is governed by a point mutation in bacterial symbionts. *PLoS Biol.*, 5, e96.

Eldredge, N., Thompson, J.N., Brakefield, P.M., Gavrilets, S., Jablonski, D., Jackson, J.B.C. *et al.* (2005). The dynamics of evolutionary stasis. *Paleobiology*, 31, 133–145.

Etterson, J.R. & Shaw, R.G. (2001). Constraint to adaptive evolution in response to global warming. *Science*, 294, 151–154.

Ewald, P. (1994). *Evolution of Infectious Disease*. Oxford University Press, New York.

Gilbert, G.S. & Webb, C.O. (2007). Phylogenetic signal in plant pathogen-host range. *Proc. Natl. Acad. Sci. USA*, 104, 4979–4983.

Gómez, J.M., Verdú, M. & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the entire tree of life. *Nature*, 465, 918–921.

Harrison, S. & Cornell, H.V. (2008). Toward a better understanding of regional causes of local species richness. *Ecol. Lett.*, 11, 969–979.

Harrison, S. & Grace, J.B. (2007). Biogeographic affinity helps explain productivity-richness relationships at regional and local scales. *Am. Nat.*, 170, S5–S15.

Harvey, P.H. & Pagel, M.R. (1991). *The comparative method in evolutionary biology*. Oxford University Press.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2007). Climate, niche conservatism, and the global bird diversity gradient. *Am. Nat.*, 170, S16–S27.

Helmus, M.R., Keller, W., Paterson, M.J., Cannon, C.H., Yan, N.D. & Rusak, J.A. (2010). Communities contain closely related species during ecosystem disturbance. *Ecol. Lett.*, 13, 162–174.

Holt, R.D. (1990). The microevolutionary consequences of climate change. *Trends Ecol. Evol.*, 5, 311–315.

Holt, R.D. (2009). Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc. Natl. Acad. Sci. USA*, 106, 19659–19665.

Holt, R.D. & Barfield, M. (2008). Habitat selection and niche conservatism. *Isr. J. Ecol. Evol.*, 54, 295–309.

Holt, R.D. & Gaines, M.S. (1992). Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evol. Ecol.*, 6, 433–447.

Holt, R.D. & Gomulkiewicz, R. (2004). Conservation implication of niche conservatism and evolution in heterogeneous environments. In: *Evolutionary Conservation Biology* (eds Ferriere, R., Dieckmann, U. & Couvet, D.D.). Cambridge University Press, Cambridge, UK, pp. 244–264.

Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symp.*, 22, 415–427.

Ingram, T., Harmon, L.J. & Shurin, J.B. (2009). Niche evolution, trophic structure, and species turnover in model food webs. *Am. Nat.*, 174, 56–67.

Ives, A.R. & Godfray, H.C.J. (2006). Phylogenetic analysis of trophic associations. *Am. Nat.*, 168, E1–E14.

Jansson, R. & Davies, T.J. (2008). Global variation in diversification rates of flowering plants: energy versus climate change. *Ecol. Lett.*, 11, 173–183.

Jenkins, N.L. & Hoffman, A.A. (1999). Limits to the southern border of *Drosophila serrata:* cold resistance, heritability, and trade-offs. *Evolution*, 53, 1823–1834.

Kearney, M. & Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.*, 12, 334–350.

Kellermann, V., van Heerwaarden, B., Sgro, C.M. & Hoffmann, A.A. (2009). Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science*, 325, 1244–1246.

Kirkpatrick, M. & Barton, N.H. (1997). Evolution of a species' range. *Am. Nat.*, 150, 1–23.

Knapp, S., Kuhn, I., Schweiger, O. & Klotz, S. (2008). Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecol. Lett.*, 11, 1054–1064.

Kozak, K.H. & Wiens, J.J. (2010). Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *Am. Nat.*, 176, 40–54.

Kuiken, T., Holmes, E.C., McCauley, J., Rimmelzwaan, G.F., Williams, C.S. & Grenfell, B.T. (2006). Host species barriers to influenza virus infections. *Science*, 21, 394–397.

Levin, D. (2006). Flowering phenology in relation to adaptive radiation. *Syst. Bot.*, 31, 239–246.

Li, J., He, Q., Hua, X., Zho, J., Xu, H., Chen, J. *et al.* (2009). Climate and history explain the species richness peak at mid-elevation for *Schizothorax* fishes (Cypriniformes: Cyprinidae) distributed in the Tibetan Plateau and its adjacent regions. *Glob. Ecol. Biogeogr.*, 18, 264–272.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009). The velocity of climate change. *Nature*, 462, 1052–1055.

Loeuille, N. & Loreau, M. (2005). Evolutionary emergence of size structured food webs. *Proc. Natl. Acad. Sci. USA*, 102, 5761–5766.

Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal, and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.*, 11, 995–1007.

Lutzoni, F., Pagel, M. & Reeb, V. (2001). Major fungal lineages are derived from lichen symbiotic ancestors. *Nature*, 411, 937–940.

Maherali, H. & Klironomos, J.N. (2007). Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science*, 316, 1746–1748.

Martinsen, E.S., Perkins, S.L. & Schall, J.J. (2008). A three-genome phylogeny of malaria parasites (*Plasmodium* and closely related genera): evolution of life-history traits and host switches. *Mol. Phylogenet. Evol.*, 47, 261–273.

Mayfield, M.M. & Levine, J.M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* DOI: 10.1111/j.1461-0248.2010.01509.x.

McCain, C.M. (2005). Elevational gradients in diversity of small mammals. *Ecology*, 86, 366–372.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B. *et al.* (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.*, 10, 315–331.

Moran, N.A., McCutcheon, J.P. & Nakabachi, A. (2008). Genomics and evolution of heritable bacterial symbionts. *Ann. Rev. Genetics*, 42, 165–190.

O'Meara, B.C., Ané, C., Sanderson, M.J. & Wainwright, P.C. (2006). Testing for different rates of continuous trait evolution using likelihood. *Evolution*, 60, 922–933.

Oömmen, M.A. & Shanker, K. (2005). Elevational species richness patterns emerge from multiple local scale mechanisms in Himalayan plants. *Ecology*, 86, 3039–3047.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

Partel, M. (2002). Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, 83, 2361–2366.

Pearman, P.B., Guisan, A., Broennimann, O. & Rand, C.F. (2008). Niche dynamics in space and time. *Trends Ecol. Evol.*, 23, 149–158.

Peterson, A.T. (2003). Predicting the geography of species' invasions via ecological niche modeling. *Q. Rev. Biol.*, 78, 419–433.

Peterson, A.T. & Vieglais, D.A. (2001). Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *Bioscience*, 51, 363–371.

Peterson, A.T., J. Soberón, J. & Sánchez-Cordero, V. (1999). Conservatism of ecological niches in evolutionary time. *Science*, 285, 1265–1267.

Pough, F.H., Heiser, J.B. & Janis, C.M. (2009). *Vertebrate Life*. Benjamin-Cummings, San Francisco, CA.

Prinzing, A., Durka, W. & Klotz, S. (2001). The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. Lond. B*, 268, 2383–2389.

Pyron, R.A. & Burbrink, F.T. (2009). Can the tropical conservatism hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lampropeltini. *Glob. Ecol. Biogeogr.*, 18, 406–415.

Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Colwell, R.K. (2007). Species richness and evolutionary niche dynamics: a spatial pattern-oriented simulation experiment. *Am. Nat.*, 170, 602–616.

Revell, L.J., Harmon, L.J. & Collar, D.C. (2008). Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.*, 57, 591–601.

Rezende, E., Lavabre, J., Guimaraes, P., Jordano, P. & Bascompte, J. (2007). Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*, 448, 925–928.

Rezende, E., Albert, E.M., Fortuna, M.A. & Bascompte, J. (2009). Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecol. Lett.*, 12, 779–788.

Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.*, 7, 1–15.

Rodder, D. & Lotters, S. (2009). Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Glob. Ecol. Biogeogr.*, 18, 674–687.

Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A. & Savolainen, V. (2005). 60 Million years of co-divergence in the fig-wasp symbiosis. *Proc. R. Soc. Lond. B*, 272, 2593–2599.

Rossberg, A.G., Matsuda, H., Amemiya, T. & Itoh, K. (2006). Food webs: experts consuming families of experts. *J. Theor. Biol.*, 241, 552–563.

Sax, D.F. (2001). Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *J. Biogeogr.*, 28, 139–150.

Schluter, D. (2000). *The Ecology of Adaptive Radiations*. Oxford University Press, Oxford.

Smith, S.A., Stephens, P.R. & Wiens, J.J. (2005). Replicate patterns of species richness, historical biogeography, and phylogeny in Holarctic treefrogs. *Evolution*, 59, 2433–2450.

Smith, S.A., Nieto Montes de Oca, A., Reeder, T.W. & Wiens, J.J. (2007). A phylogenetic perspective on elevational species richness patterns in Middle American treefrogs: why so few species in lowland tropical rainforests? *Evolution*, 61, 1188–1207.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.*, 10, 1115–1123.

Stephens, P.R. & Wiens, J.J. (2003). Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *Am. Nat.*, 161, 112–128.

Stephens, P.R. & Wiens, J.J. (2009). Bridging the gap between historical biogeography and community ecology: niche conservatism and community structure in emydid turtles. *Mol. Ecol.*, 18, 4664–4679.

Stevens, R.D. (2006). Historical processes enhance patterns of diversity along latitudinal gradients. *Proc. R. Soc. Lond. B*, 273, 2283–2289.

Swenson, N.J. & Enquist, B.J. (2009). Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, 90, 2161–2170.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Moritz, C. (2009). Birds track their Grinnellian niche through a century of climate change. *Proc. Natl. Acad. Sci. USA*, 106, 19637–19643.

Valiente-Banuet, A., Rumebe, A.V., Verdú, M. & Callaway, R.M. (2006). Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. *Proc. Natl. Acad. Sci. USA*, 103, 16812–16817.

Vamosi, S.M., Heard, S.B., Vamosi, J.C. & Webb, C.O. (2009). Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol. Ecol.*, 18, 572–592.

Warren, D.L., Glor, R.E. & Turelli, M. (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*, 62, 2868–2883.

Warwick, R.M. & Clarke, K.R. (1995). New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol. Prog. Ser.*, 129, 301–305.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Ann. Rev. Ecol. Evol. Syst.*, 33, 475–505.

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. Evol. 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.

Wiens, J.J., Parra-Olea, G., Garcia-Paris, M. & Wake, D.B. (2007). Phylogenetic history underlies elevational patterns of biodiversity in tropical salamanders. *Proc. R. Soc. Lond. B*, 274, 919–928.

Wiens, J.J., Sukumaran, J., Pyron, R.A. & Brown, R.M. (2009). Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). *Evolution*, 63, 1217–1231.

Willis, C.G., Ruhfel, B., Primack, R.B., Miller-Rushing, A.J. & Davis, C.C. (2008). Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proc. Natl. Acad. Sci. USA*, 105, 17029–17033.