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NICHE CONSERVATISM: Integrating Evolution, Ecology, and Conservation Biology

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■ **Abstract** Niche conservatism is the tendency of species to retain ancestral ecological characteristics. In the recent literature, a debate has emerged as to whether niches are conserved. We suggest that simply testing whether niches are conserved is not by itself particularly helpful or interesting and that a more useful focus is on the patterns that niche conservatism may (or may not) create. We focus specifically on how niche conservatism in climatic tolerances may limit geographic range expansion and how this one type of niche conservatism may be important in (*a*) allopatric speciation, (*b*) historical biogeography, (*c*) patterns of species richness, (*d*) community structure, (*e*) the spread of invasive, human-introduced species, (*f*) responses of species to global climate change, and (*g*) human history, from 13,000 years ago to the present. We describe how these effects of niche conservatism can be examined with new tools for ecological niche modeling.

INTRODUCTION

The niche is a central concept in ecology and evolution that dates back at least to Grinnell (1917). Although many definitions of the niche have been proposed, the definition introduced by Hutchinson (1957) is particularly widespread and useful: The niche is the set of biotic and abiotic conditions in which a species is able to persist and maintain stable population sizes. Hutchinson (1957) also made the valuable distinction between the fundamental and realized niche. The fundamental niche describes the abiotic conditions in which a species is able to persist, whereas the realized niche describes the conditions in which a species persists given the presence of other species (e.g., competitors and predators).

Many aspects of the fundamental niche can be conserved over long evolutionary time scales. For example, tens of thousands of actinopterygian fish species are confined to aquatic habitats, and many fish clades are confined to either saltwater or freshwater. The tendency of species to retain aspects of their fundamental niche over time is called niche conservatism. We refer to niche conservatism as a process, although it may be caused by more than one factor at the population level (a feature it shares with other evolutionary processes, such as speciation and anagenesis).

In this review, we describe the importance of niche conservatism to evolution, ecology, and conservation biology. We outline how answers to some long-standing questions in these fields may lie (at least in part) in the inability of species to adapt to novel abiotic conditions over a given timescale. These questions include the following: How does a single species split to create two new species? Why are there more species in tropical regions than in temperate regions? Which introduced species are likely to invade a given region, and how far will they spread? How will species respond to global warming? The importance of niche conservatism does not depend on ecological traits being maintained indefinitely. Instead, these diverse patterns may be explained by niche conservatism at different timescales.

This review has three objectives: (*a*) to address the controversy over whether or not niches are conserved, (*b*) to highlight the diverse areas that niche conservatism might help explain, a topic that has not been reviewed previously, and (*c*) to describe methodological tools that can be used to test the effects of niche conservatism (i.e., GIS-based ecological niche modeling).

An important theme of our review is that both evolution and ecology are important in explaining biogeographic patterns. At the same time, we show how biogeography is important to diverse topics in evolution, ecology, conservation biology, and even human history, areas in which biogeography may not be widely appreciated.

ARE NICHES CONSERVED OR AREN'T THEY?

Considerable debate has emerged in the recent literature as to whether or not niches are conserved. Much of this debate was sparked by the landmark paper by Peterson et al. (1999). These authors combined museum locality data, climatic data, and niche modeling to show that climatic niches were conserved (similar) between many sister-species pairs of mammals, birds, and butterflies in Mexico. Their general assertion that niches are conserved was countered by other studies, which claimed that niches are evolutionarily labile, including studies of microhabitat preferences in *Anolis* lizards (Losos et al. 2003), morphometric variation in warblers (*Sylvia*) (Böhning-Gaese et al. 2003), and environmental niche models in dendrobatid frogs (Graham et al. 2004b). Other studies have supported niche conservatism. For example, Ricklefs & Latham (1992) showed that many congeneric plant species in Europe and North America had similar geographic ranges on each continent, a pattern interpreted as evidence for niche conservatism. Prinzig et al. (2001) argued for niche conservatism in six environmental variables in a sample of more than 1000 species of higher plants in Europe.

We believe that the question of whether niches are conserved or labile is not in itself particularly fruitful. Species will always inhabit environments that bear some similarity to those of their close relatives (i.e., few tropical rainforest species have a sister species in undersea vents). Thus, to some extent, niches will always be conserved. Yet, few sister species may share identical niches; so niches may never be perfectly conserved either. The answer to the question "Are niches conserved?" may simply depend on exactly how similar niches must be among species to be considered conserved.

Instead, a more constructive way to think about this issue may be to focus on specific outcomes of niche conservatism. For example, does niche conservatism drive allopatric speciation, high tropical species richness, or responses of species to climate change? In the next section, we describe the many effects of niche conservatism and their predicted empirical signatures.

In this review, we focus on niche conservatism in a very restricted sense in that we emphasize how conservatism in climatic tolerances limits geographic ranges of species and clades. We argue that even this one limited aspect of niche conservatism has a plethora of important consequences for ecology, evolution, and conservation biology. This aspect of niche conservatism is also the most readily studied through ecological niche modeling. Before we begin, however, we strongly emphasize that even though we believe niche conservatism may play some role in all of these areas in some cases, we do not think that it does so in every single case.

WHAT DOES NICHE CONSERVATISM DO?

Allopatric Speciation

The importance of niche conservatism to speciation may not be immediately obvious. After all, speciation is typically equated with divergence (e.g., Coyne & Orr 2004, Futuyma 1998) and not maintenance of ecological similarity over time. The importance of any process to speciation depends upon our concept of what species are and what speciation is.

Several authors (e.g., de Queiroz 1998, Mayden 1997, Wiens 2004b) have argued that species are lineages and that the characteristics used to define species under most concepts are simply traits that evolve in lineages, given enough time (e.g., postzygotic isolating mechanisms, diagnostic morphological traits, monophyletic gene genealogies). Given this view, speciation is the actual splitting of one lineage into two. For parapatric and sympatric speciation, lineage splitting is intimately related to divergence in traits associated with intrinsic reproductive isolation (Coyne & Orr 2004, Turelli et al. 2001). However, for allopatric speciation [often considered the most common geographic mode (Barraclough & Vogler 2000, Coyne & Orr 2004)] new lineages arise from the geographic separation of ancestral species into isolated sets of populations (Wiens 2004b). Even if one does not equate lineage splitting with speciation, the geographic separation of one lineage into two is considered an essential part of allopatric speciation under many concepts [e.g., biological species concept (Futuyma 1998)].

In many cases, this geographic separation may be associated with niche conservatism (Wiens 2004a). Allopatry is generally caused by a geographic barrier that consists of suboptimal environmental conditions for the species in question (e.g., deserts, mountains, or oceans). If a species can adapt to ecological conditions at this barrier, then gene flow will continue across it and allopatric speciation will not occur. Niche conservatism (in the broad sense) may be generally important in allopatric speciation because it will limit adaptation to ecological conditions at the geographic barrier. In some cases, this barrier may be associated with different microhabitat preferences (e.g., a river that separates terrestrial habitats), but in other cases, it may be associated with differences in climatic regimes (e.g., montane endemics separated by intervening lowlands or lowland endemics separated by intervening mountain ranges).

So far, no studies have adequately addressed the role of niche conservatism in allopatric speciation. Peterson et al. (1999) showed similarity in the climatic niche space of allopatric species pairs of birds, butterflies, and mammals on either side of the Isthmus of Tehuantepec in Mexico. However, they did not address whether the vicariance event that created these lineages was associated with conservatism in climatic tolerances. Graham et al. (2004b) showed differences in the climatic niches of allopatric species pairs of Andean frogs but did not address whether these niche differences were the cause of lineage splitting (e.g., as in parapatric speciation) or arose after speciation (e.g., species on different mesic mountaintops may have adapted to different climatic regimes, but their splitting into separate lineages may have been caused by a dry valley between them). Wiens (2004b) discussed how the role of niche conservatism in allopatric speciation might be tested.

Niche conservatism (and niche evolution) may also be important for species delimitation, the process of identifying and diagnosing species (Sites & Marshall 2003). When species are diagnosed, sample sizes are almost never large enough to infer with statistical confidence that a putative species is truly fixed for a trait or allele (Wiens & Servedio 2000) or that all alleles of a given locus in a given species form a monophyletic group. This situation makes species-level decisions based on traditional morphological and genetic data alone potentially problematic. However, if a set of populations of uncertain taxonomic status is geographically separated from closely related species by areas that are outside of the climatic niche envelope of all of these species (Figure 1), then gene flow with these species is unlikely because it would involve crossing unsuitable habitat. This pattern would support the hypothesis that the populations of uncertain status represent a distinct species. Differences in niche characteristics might also be important. If a set of populations occurs under climatic conditions that do not overlap those of closely related species (e.g., Graham et al. 2004b), then gene flow between these populations and other species may also be unlikely, and these populations may represent a distinct species. These similarities and differences in niche characteristics can be visualized and analyzed statistically with methods from ecological niche modeling (see below).

In a similar vein, Raxworthy et al. (2003) used niche modeling to infer areas in which species of chameleons (lizards) might be expected to occur given their known geographic distribution. They found that niche models for some species predicted their occurrence in disjunct areas of seemingly suitable habitat where

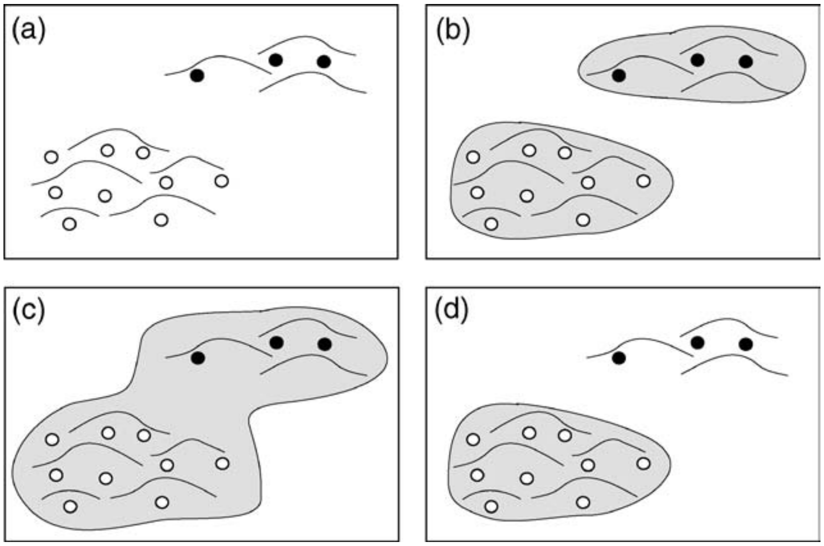

Figure 1 Hypothetical example illustrating niche conservatism, ecological niche modeling, and species delimitation. (*a*) Two sets of allopatric populations occur in two geographically separate montane regions. One set (*open circles*) is a previously described species, the other set (*closed circles*) is of unknown taxonomic status. (*b*) Ecological niche modeling shows that the two sets of populations share a similar climatic niche envelope (*shown in gray*). The intervening lowland areas between the montane regions is outside the envelope of acceptable environmental conditions, which suggests that niche conservatism may prevent gene flow between these two sets of populations and supports the hypothesis that they are distinct species. (*c*) The two sets of populations share a similar climatic niche envelope, but this niche envelope also includes the areas between them. This result suggests that niche conservatism is not important in isolating them and that there may be ongoing dispersal and gene flow between them (if no other barriers are present). This pattern would not add support to the hypothesis that they are distinct species. (*d*) The two sets of populations have dissimilar climatic niche envelopes (illustrated here by the restricted niche envelope of the known species). This result suggests that past niche evolution (and current niche conservatism) maintains the geographic separation of these populations and supports the hypothesis that they are distinct species.

these species were not presently recorded. These areas subsequently were found to contain several undescribed, closely related chameleon species.

Historical Biogeography

Historical biogeography uses phylogenies to help explain the geographic distribution of species and clades. In recent decades, historical biogeography has focused primarily on addressing specific hypotheses of geological connections among areas, rather than on the general ecological and evolutionary processes that explain the large-scale distribution of clades (reviewed by Wiens & Donoghue 2004).

Wiens & Donoghue (2004) argued that the interplay of niche conservatism and niche evolution may be critical in the biogeographic history of many groups. A major challenge in biogeography is to explain why clades have dispersed to some areas but not others. Climatic niche specialization seems to be important in many groups. For example, many clades, such as crocodiles, caecilians, and trogoniform birds (Wiens & Donoghue 2004), occur in tropical regions on two or more continents but are largely absent from geographically adjacent temperate regions. Some of these clades are extremely old [e.g., caecilians are more than 140 million years old (Zug et al. 2001)], which suggests that the general tropical niche can be conserved over very long time periods in some groups. Similarly, many clades (both old and young) are largely confined to temperate regions and occur on two or more continents; these clades include numerous groups of plants, insects, and fish (e.g., Donoghue & Smith 2004, Sanmartín et al. 2001). For example, with the exception of a derived clade of plethodontids (bolitoglossines), almost all salamanders occur in temperate climate regions of the Northern Hemisphere (Zug et al. 2001). This pattern suggests that the general temperate niche has been maintained in most salamander clades for more than 100 million years (Zug et al. 2001). Similarly, the boundaries between some of Earth's major biogeographic realms, recognized by both zoologists (Wallace 1876) and botanists (Good 1947), correspond to transitions between temperate and tropical climatic regimes within continents (i.e., Nearctic versus Neotropical; Palearctic versus Oriental) rather than the edges of continents.

Patterns of Species Richness

Species richness is a central topic in ecology and biogeography (Brown & Lomolino 1998, Rosenzweig 1995, Willig et al. 2003). In recent years, species richness has been studied primarily by ecologists seeking correlations between environmental variables and species numbers at specific locations throughout the globe. Although this research program has found strong correlations between climate and species richness (e.g., Francis & Currie 2003, Hawkins et al. 2003), it has generally not addressed how climate actually influences species numbers in a region or community (Wiens & Donoghue 2004). For example, there is no direct explanation for how high energy or productivity in a community or region can lead to a greater number of species (i.e., just because there are more individuals of a species at a given location does not mean that there will be more species). Instead, the processes that will actually change species numbers within a region involve evolution and biogeography, such as speciation, extinction, and dispersal of species into or out of a region (Wiens & Donoghue 2004).

Niche conservatism offers a mechanism that can help explain large-scale species-richness patterns in a way that reconciles both ecological and evolutionary perspectives. Several evolutionary ecologists have converged on a very similar

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explanation for the latitudinal gradient in species richness (i.e., Brown & Lomolino 1998, Farrell et al. 1992, Futuyma 1998, Ricklefs & Schluter 1993). This explanation, dubbed the "tropical conservatism hypothesis" by Wiens & Donoghue (2004), has three parts. First, many groups have more species in the tropics because they originated in the tropics and have had more time to speciate there. Second, species disperse from tropical regions to temperate regions rarely or not at all, because they lack adaptations to survive cold winter temperatures. Thus, niche conservatism helps to create and maintain a disparity in species richness between tropical and temperate regions. Third, tropical regions were much more extensive until relatively recently (roughly 30 to 40 mya), which explains why many extant groups originated in the tropics. Overall, the tropical conservatism hypothesis is consistent with the observation of ecological studies that show high species richness in tropical communities with high temperatures and rainfall (and energy and productivity) but links this pattern to processes that directly affect the number of species in each region (i.e., dispersal and speciation).

The tropical conservatism hypothesis has important implications for conservation. If most groups show the predicted pattern of many, older clades in tropical regions and fewer, younger clades in temperate regions, then there may be higher genetic and phylogenetic diversity for the same number of species in tropical regions than in temperate regions. If this pattern occurs, then loss of tropical habitats will have two important consequences (relative to temperate regions): the loss of more species per unit area and the loss of more genetic and phylogenetic diversity per species (for a similar argument for biodiversity hot spots, see Sechrest et al. 2002). Conversely, some authors have used the finding of higher genetic diversity in tropical faunas relative to temperate faunas as evidence to support the tropical conservatism hypothesis [in New World birds (Gaston & Blackburn 1996, Ricklefs & Schluter 1993)].

Niche conservatism may explain many other patterns of species richness as well, such as the low species richness of many clades in arid regions and the reverse latitudinal gradient (higher richness in temperate regions) seen in some groups (e.g., Brown & Lomolino 1998, Ricklefs & Schluter 1993). Any novel set of environmental conditions is potentially a long-term barrier to dispersal for some clades, and niche conservatism should tend to create a disparity in species richness between habitats or regions over time for many different groups of organisms.

We do not claim that the tropical conservatism hypothesis is the sole explanation for the latitudinal diversity gradient in all groups. For example, some groups appear to have higher rates of diversification in the tropics [birds and butterflies (Cardillo 1999)], a pattern which suggests that the tropical conservatism hypothesis is unnecessary to explain high tropical species richness in these groups. The causes of this higher diversification rate are unclear. One potential cause is a greater tendency for montane endemism in tropical regions (as opposed to more elevational generalists in temperate regions), which may be related to a greater zonation of climatic regimes at different elevations in tropical regions [associated with reduced seasonal temperature variation (Janzen 1967)]. In support of this hypothesis, the Andes

Mountains of South America contain higher species richness of birds than do the adjacent Amazonian rainforests (Rahbek & Graves 2001). Interestingly, if Janzen's hypothesis is correct, the extensive speciation in tropical montane regions may also involve the limited ability of climatic specialists to disperse between climatic regimes at different elevations (i.e., niche conservatism at a smaller spatial scale).

Community Structure

Community structure is used here as the guild composition of an assemblage (e.g., the number of sympatric microhabitat and diet specialists). In some cases, differences in community structure between regions may result from niche conservatism, which limits dispersal of lineages with different ecological traits between regions (e.g., Ackerly 2003, Webb et al. 2002). In these cases, the ecological structure of a given community cannot be understood simply by examination of ecological characteristics of the species present in that community or even the phylogeny of those species. Instead, community structure may result from constraints on the dispersal of lineages that are not presently represented in those communities (Wiens & Donoghue 2004).

For example, in emydid turtles in eastern North America, communities in the northeast are dominated by semiaquatic emydine lineages, whereas communities in the southeast are dominated by aquatic deirochelyine species (Stephens & Wiens 2004). Although some aquatic deirochelyines have invaded northeastern communities, most semiaquatic emydines have failed to invade southern communities.

Why have these lineages remained in the northeast? Two obvious explanations are competition and niche conservatism. Competition with other emydids seems unlikely, given that southeastern deirochelyines either occur far south of these emydine species or overlap their geographic ranges extensively. Ecological niche modeling (P.R. Stephens & J.J. Wiens, unpublished data) suggests that high summer temperatures may limit the spread of these emydine lineages into southeastern communities. Thus, the tendency of the northern semiaquatic lineages to retain their ancestral niche seemingly has created significant differences in emydid community structure across eastern North America.

In this example, competition seemingly is unimportant in creating these geographic patterns of community structure. In other cases, competition may determine which guilds and lineages can invade a community and which cannot. Furthermore, in many cases, differences in community structure between regions seem to result from biogeographic constraints unrelated to climatic niche conservatism [e.g., islands and different continents (Cadle & Green 1993)] or absent guilds simply evolve from within the local species pool [some Caribbean *Anolis* (Losos et al. 1998)].

Invasive Species

Invasive species are thought to be one of the major threats to biodiversity (e.g., Wilcove et al. 1998, Wilson 1992). Niche conservatism may determine which species can invade which regions and where they will spread within those regions (reviewed by Peterson 2003, Peterson & Vieglais 2001). If their fundamental niches are conserved, species will only be able to invade regions that have a climate similar to that of their native range. Peterson and collaborators have shown several examples in which ecological niche modeling of the climatic characteristics of the native range of a species can predict its introduced range.

The introduced reptile and amphibian fauna of North America exemplifies the idea that niche conservatism determines which exotic species can become established and where (Conant & Collins 1991, Stebbins 2003). Southern Florida, a region whose native vegetation includes moist subtropical forests, now contains numerous introduced species of reptiles and amphibians from tropical regions around the world, including species from the West Indies (e.g., the frogs *Osteopilus septentrionalis*, *Eleutherodactylus coqui*, and *E. planirostris*; many lizards, including species of *Anolis*, *Leiocephalus*, and *Sphaerodactylus*), Central and South America (the toad *Bufo marinus* and lizards *Cnemidophorus lemniscatus*, *Ameiva ameiva*, *Ctenosaura pectinata*, *Iguana iguana*, and *Basiliscus vittatus*), and Southeast Asia (the lizard *Gekko gecko* and the snake *Rhamphotyphlops braminus*). None of these species have successfully invaded more temperate regions north of Florida, even though many have been present and widespread in Florida for decades. The only exotic species that are well established in temperate eastern North America are two lizards from temperate Europe, which have populations in Kansas and New York (*Podarcis muralis*) and Ohio (*Podarcis sicula*). A species of gecko from Mediterranean Europe (*Hemidactylus turcicus*) is widespread in the southern United States, and one from the Middle East and Central and South Asia (*Cyrtopodion scabrum*) is established in coastal Texas. In the western United States, successful introductions have consisted mostly of eastern species from similar latitudes (the amphibians *Rana berlandieri*, *R. catesbiana*, and *Ambystoma tigrinum* and the turtles *Apalone spinifera*, *Chelydra serpentina*, and *Trachemys scripta*). The African clawed frog (*Xenopus laevis*) has also been introduced into Mediterranean climate regions of southern California, and the natural range of this species includes Mediterranean climate regions of southern Africa. Although two species common in eastern North America have been widely introduced into tropical regions throughout the world (the frog *R. catesbiana* and the turtle *Trachemys scripta*), the native ranges of these species extend into tropical Mexico.

The correspondence between the native climate of these exotic species and their introduced range seems striking. As a crude quantitative index of this association, regression (Figure 2) of the estimated northernmost latitudinal range limits of 35 of these species (those for which information on introduced ranges were available) in their native and introduced ranges shows a highly significant relationship ($r^2 = 0.792$, $P < 0.0001$). This pattern seems to reflect the effects of niche conservatism.

Not all groups of invaders may show this level of climate matching. For example, some introduced mammalian species seem to tolerate both temperate and tropical regions (e.g., rats). Unlike most other plants and animals, mammals are endotherms, which physiologically maintain similar body temperatures across

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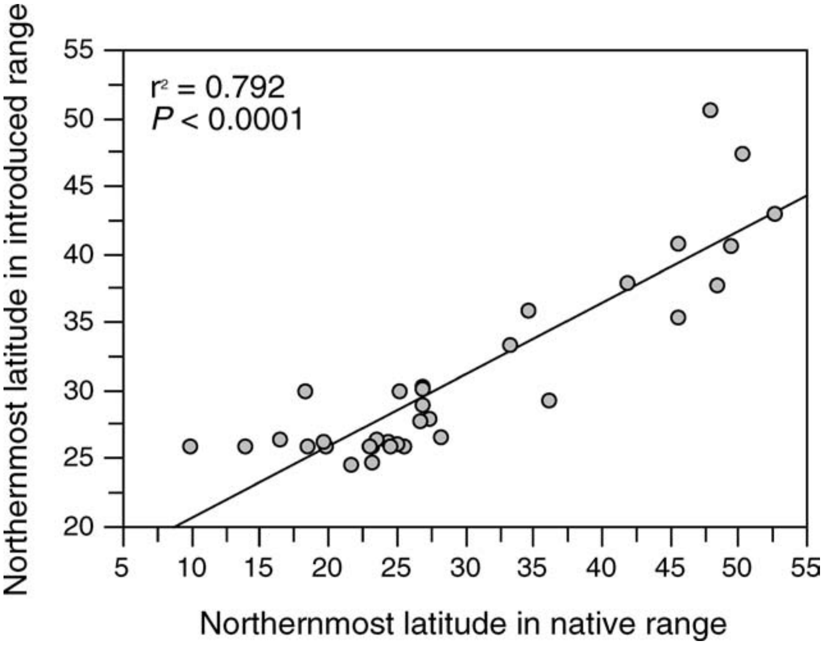

Figure 2 Relationship between northern range limits for 35 species of reptile and amphibian in their native and introduced ranges (in North America). The significant relationship implies that niche conservatism in climatic tolerances determines which exotic species become established in a region.

a range of environmental temperatures, and this characteristic may allow some species to tolerate a broad range of climatic conditions.

Invasive species are important as a threat to biodiversity, but they also offer an intriguing system by which to study the ecological and evolutionary causes of biogeographic patterns. Invasive species represent replicated biogeographic experiments that can be used to test for the impact of niche conservatism on range limits. If niche conservatism in climatic tolerance determines the range limits of species, then we should expect to see consistent parallels between their climatic distribution in their native and introduced ranges. Conversely, if introduced tropical species routinely spread into temperate regions or vice versa, then competition (or other biotic factors) may be more important in setting geographic range limits in their native ranges. Overall, we think that the application of data on invasive species to historical biogeography could be an exciting area for future research.

Responses to Global Climate Change

In many ways, niche conservatism is the underlying process that makes global climate change a danger to the world's biota. If species could simply adapt to changing climatic conditions, then we would have little cause for concern. On the other hand, given niche conservatism in climatic tolerances, species should shift their geographic ranges in the face of global warming to track their ancestral climatic regime, moving poleward in latitude and downward in elevation; species that cannot adapt and cannot shift their geographic ranges (e.g., due to habitat destruction or geographic constraints) may be at risk of extinction. Many studies have now addressed the effects of global warming on plant and animal distributions, and Parmesan & Yohe (2003) recently analyzed an extensive database that incorporates the results of hundreds of previous studies. Their analysis included more than 1700 species of plants, animals, and lichens from terrestrial, freshwater, and marine environments. For 99 species with quantitative data, they found that species (overall) moved an average of 6.1 km per decade poleward and 6.1 m per decade upward in elevation. For more than 1045 species with qualitative data, only 27% showed stable geographic ranges, and for the other 73%, most changes (75% to 81%) were in the direction predicted (poleward) for both northern and southern range limits. These results not only show a significant impact of global warming but also suggest that many species respond to climate change as predicted by niche conservatism, rather than with rapid evolution of climatic tolerances.

Recently, several authors have assumed niche conservatism to evaluate the potential large-scale impact of global warming on regional biotas. Peterson et al. (2002) used niche modeling to address how Mexican birds, butterflies, and mammals may be effected by global warming. Thomas et al. (2004) modeled the effects of climate change on many taxa and regions and concluded that climatic warming may be an important threat to global biodiversity. Although the effects of global warming may be very difficult to mitigate, some authors have suggested the intriguing possibility that species can be managed to minimize the effects of niche conservatism and maximize the potential for rapid adaptive evolution, including their response to changing climate (Rice & Emery 2003, Stockwell et al. 2003).

In addition to the present crisis, niche conservatism may also be associated with major historical mass extinctions. The history of life on earth has been marked by five major extinction events (Benton 1995). The ultimate cause of these events remains controversial, but relatively rapid climate change is considered to be among the most important proximate factors in many of them (Hallam & Wignall 1997). Mass extinctions associated with rapid climate change may be another manifestation of niche conservatism.

Human History and Agriculture

Niche conservatism also seems to have had a profound impact on human history. Diamond (1997) has proposed that the ultimate cause of the different histories and fates of human societies lies in the shape of the continents on which these societies developed. Although not discussed explicitly by Diamond, the reason that continental axis matters clearly is niche conservatism.

A major feature of recent human history was the conquest of much of Africa and the New World by Europeans, and its many consequences. But why were the peoples of Africa and the New World conquered by Europeans and not vice versa? Diamond argues for a chain of causality that explains the major features of human history from the end of the Ice Ages to the present. For continents that have their greatest length on their longitudinal axis (i.e., Eurasia), domesticated plant and animal species can be readily spread between between regions, and a large "package" of domesticated species can accumulate in one place. More domesticated species lead to greater food production, food surpluses, and food storage. Greater food availability allows for high population densities in fixed locations, which permits many individuals to pursue other activities besides food production. These activities include development of technology (e.g., ocean-going ships, guns, and steel), writing, and government. Furthermore, a large number of domesticated mammal species may have lead to a large pool of diseases ("germs") in European populations that eventually decimated the native peoples of Africa, Australia, and the New World. (Although Australia is shaped like Eurasia, it has a restricted pool of candidate species for domestication, seemingly because of biogeographic isolation and prehistoric extinction of the megafauna).

Niche conservatism may explain the difficulty in spreading domesticated species (or any species) bewteen different climatic regimes and the ease of spreading them across the same climatic regime. For example, food production is thought to have originated in southwest Asia (the Fertile Crescent) around 8000 B.C., and the same suite of domesticated species (e.g., pea, chickpea, wheat, barley, sheep, and goat) was then transported to Europe, North Africa, Central Asia, and the Indus Valley region (Pakistan). These species showed limited diffusion into adjacent tropical regions of Africa and Asia. In the New World, different sets of species were domesticated independently in North America, the Middle American highlands, and South America, or the same species (or close relatives) were domesticated independently in different regions (e.g., lima beans, cotton, chili peppers, and squashes). Relatively few species spread between regions, or diffusion was very slow. Diamond postulates that diffusion was limited because of differences in climate between regions (e.g., North America versus Mexico) or because areas of similar climate (e.g., montane Middle America and montane South America) were separated by areas of dissimilar climate, and these species could not tolerate radically different climatic regimes. Thus, the domesticated llamas, guinea pigs, and potatoes of the South American highlands never spread to montane Middle America, and the domestic turkeys of Mexico never spread to montane South America, presumably because of the intervening hot tropical lowlands that separate these cooler montane regions.

Diamond's analysis also has interesting implications for the study of niche conservatism. Domesticated species are raised under conditions in which competition with native biota presumably is limited. This observation supports the idea that physiological tolerances to climate may be sufficient to determine large-scale biogeographic patterns in the diverse plant and animal lineages that have

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been domesticated (although other biotic factors, such as disease, could be important in some cases). Furthermore, the spread of some domesticated species between climatic regions (e.g., corn from Mexico to temperate North America) suggests that the physiological tolerances that underlie climatic barriers can be overcome with artificial selection. In parallel to invasive species, the relationships between domesticated species and climate suggests that the agricultural sciences may offer a useful database for studies of niche conservatism, niche evolution, and biogeography.

TESTING FOR THE EFFECTS OF NICHE CONSERVATISM

We have discussed how niche conservatism can have a variety of consequences at different spatial and temporal scales. However, these diverse effects can all be reduced to a common cause: the evolutionary specialization of a species or clade to a particular climatic regime limits their dispersal. Ecological niche modeling can be used to help test whether climatic factors do limit the distribution of species and can set the stage for additional phylogenetic, ecological, and physiological studies.

Niche modeling applies powerful new computational tools to museum locality data assembled through decades of fieldwork (reviewed by Graham et al. 2004a). The general approach combines three elements: (*a*) georeferenced localities for the species in question (i.e., localities where a species has been collected and for which latitude and longitude coordinates are available), (*b*) data on climatic variables (e.g., yearly mean, variance, minimum, and maximum for temperature and precipitation at each site) at those sites and in surrounding areas, and (*c*) algorithms that estimate the climatic niche envelope of these species on the basis of the distribution of climatic variables where they occur and do not occur within a region.

Locality data for individual species are available from natural history museums. Many localities are georeferenced, and many databases of georeferenced localities are becoming available on the Internet, depending upon the organism and region (Graham et al. 2004a). Even if localities are not georeferenced, georeferencing can be quite straightforward (if time consuming) with Internet resources (e.g., Alexandria digital library gazetteer server, global directory of cities and towns, and Topozone).

Fine-scale climatic data sets are freely available that cover the entire planet (e.g., R. Hijman's WORLDCLIM at http://biogeo.berkeley.edu/worldclim/worldclim.htm). These data sets are based on information from a large number of weather stations, augmented by statistical extrapolations to locations without weather stations by use of digital elevation models. Many climatic variables are available, although many may be tightly correlated and largely redundant. Rather than analyze all of them, a better approach may be to choose a limited number that are not strongly correlated and that are considered (a priori) to be potentially important in limiting distributions within the group, such as coldest yearly temperatures or precipitation during the driest quarter.

A variety of methods are available to construct ecological niche models (reviewed by Guisan & Zimmerman 2000). These methods can be grouped into several categories, such as environmental envelopes (e.g., BIOCLIM (Nix 1986) and DOMAIN (Carpenter et al. 1993)], generalized regression methods (e.g., Lehman et al. 2002, Pearce & Ferrier 2000), ordination approaches (Austin 1985, Guisan et al. 1999, Hirzel et al. 2002), Bayesian methods (e.g., Gelfand et al. 2003), and genetic algorithms [e.g., GARP (Stockwell & Peters 1999)]. In general, a statistical model is used to establish a relationship between point-locality data (either sites where a species is recorded or localities for both presence and absence) and environmental layers (describing variation in a climatic variable over space). The model is then used to create a predicted map of a species' distribution, given these environmental variables.

When the niche envelope is projected onto a species' range map, one can visualize whether climatic variables predict (match) or overpredict the species range limits. Matching supports the hypothesis that the specialized climatic tolerances of a species may limit its geographic spread (but does not necessarily rule out other hypotheses, see below). In contrast, when the range is overpredicted, the climatic variables indicate that the species should have a more extensive geographic range than it actually does. This pattern of overprediction suggests that climate is not the primary factor that limits the geographic range of the species in that region, and that other factors may be responsible instead of niche conservatism (e.g., oceanic or riverine barriers to dispersal or competitors). In Table 1, we outline how the results of ecological niche modeling (and other types of evidence) might be used to determine the role of niche conservatism in each of the areas outlined in this paper.

The next challenge is to determine which climatic variables are most important in limiting the distribution of a species. Relatively few methods have been developed specifically for this purpose. However, most methods can be run with single variables to evaluate which variable most closely matches the geographic range of a species. Peterson & Cohoon (1999) have used bootstrapping to evaluate the performance of each variable. The DOMAIN and BIOCLIM methods in DIVA-GIS [http://www.diva-gis.org/ (Hijmans et al. 2002)] can identify the most-limiting variable for a given species for any point (pixel) on a map. Finally, logistic regression analyses of presence and (carefully selected) absence localities can also be used to identify the most important limiting variables.

Once the most-limiting variable (or combination of variables) is identified, its distribution among species can be mapped onto a phylogeny to determine how long this aspect of the niche has been conserved over the evolutionary history of the group (for a similar example, see Rice et al. 2003). Results from niche modeling can also set the stage for future observational and experimental studies to test how exactly this climatic variable interacts with the biology of the organism to set geographic range limits [e.g., physiological tolerances and interactions with other species (Gross & Price 2000, Kearney & Porter 2004)].

TABLE 1 Expected patterns resulting from niche conservatism

Topic	Pattern predicted from niche conservatism	Pattern that rejects niche conservatism
Allopatric speciation	Allopatric sister species have similar niche characteristics; geographic area that separates them is outside of their climatic niche envelope (see also Wiens 2004b)	Area that separates allopatric sister species is within their climatic niche envelope; nonclimatic barriers separate them (e.g., river or ocean)
Historical biogeography	Limited dispersal between different climatic regimes (e.g., temperate, tropical, mesic, or arid) relative to within-climatic regimes; species and clades fail to disperse into geographically adjacent regions with different climatic regimes	Dispersal between different climatic regimes equal to or greater than dispersal within-climatic regimes; dispersal within group is limited only by nonclimatic barriers (e.g., rivers or oceans for terrestrial organisms)
Species richness	(*a*) Group with high tropical species richness will originate in tropical regions (as shown by ancestral area reconstruction on a phylogeny), (*b*) significant relationship between amount of time the group has been present in each region and number of species in each region (e.g., Stephens & Wiens 2003), and (*c*) distribution of cool winter temperatures predicts poleward range limits of many or most tropical lineages in the group (Wiens & Donoghue 2004); expect similar patterns for ancestrally temperate groups or for groups in arid versus mesic environments	(*a*) Despite higher species richness in tropical region, group originated in temperate regions, (*b*) group dispersed to tropical regions relatively recently, despite higher species richness there, which suggests that latitudinal differences in species richness arose primarily from latitudinal differences in rates of diversification (rate of speciation—rate of extinction), and (*c*) even if group arose in tropical regions and dispersed to temperate regions recently, cool winter temperatures do not predict poleward range limts of tropical lineages, and poleward disperse is limited instead by traditional biogeographic barriers (e.g., water) or other climatic variables (e.g., limited precipitation)
Community structure	In a given region, the absence of a given guild is explained by specialized climatic tolerances that limit the large-scale dispersal of the clade representing that guild; climatic variables predict range limits of clade and do not overpredict into the region or community in question; geographic distribution of potential competitors do not abut the range of the clade but instead are either broadly disjunct or broadly overlapping	Environmental niche envelope for the guild/clade includes the community or region in which it is absent, which suggests that competition or other factors prevent clade from entering the region or community; if competition is important in setting range limits, then potential competitors are expected to geographically abut range of absent clade
Invasive species	Climatic conditions in invaded region similar to those of native range; niche modeling of native range predicts some or all of introduced range (Peterson 2003)	Significant differences between climatic conditions in native and introduced ranges; niche modeling of native range fails to predict introduced range
Climate change (global warming)	Species ranges will shift to track their ancestral (prewarming) climatic regime; ecological niche remains the same over time but geographic distributions do not (poleward shift)	Species adapt and shift environmental tolerances to cope with changing climate rather than changing geographic range as predicted; ecological niche changes and geographic distribution remains the same or changes in opposite direction than expected (i.e., toward equator)
Human history and agriculture	Similar to invasive species; for domesticated species, expect that ecological niche model of their native (nondomesticated) geographic distribution will predict into different regions with similar climates where these species are utilized today.	Domesticated species thrive under climatic conditions that are outside the environmental niche envelope of the native (nondomesticated) populations

The observation that climatic variables predict the range limits of a species does not rule out a role for nonclimatic factors in limiting range expansion. For example, range limits might be set by the interactions of climate, resource availability, and competition (e.g., Case & Taper 2000, Darwin 1859, MacArthur 1972). There is an extensive literature that emphasizes the importance of competition in setting species geographic range limits (e.g., Connell 1961, Darwin 1859, MacArthur 1972). Although biotic interactions may be difficult to rule out, some patterns of distribution may favor climate as an explanation over competition (e.g., Anderson et al. 2002). For example, if the geographic range of a given species is predicted by climate and it shows only extensive geographic overlap or distant allopatry with those species that are most likely to be competitors, competition may be a less likely explanation than is climate alone. Again, local-scale studies that test the roles of biotic factors and physiological tolerances to abiotic conditions in setting geographic range limits are an important complement to ecological niche modeling at a biogeographic scale.

WHAT CAUSES NICHE CONSERVATISM?

At the population level, we see niche conservatism as the failure of adaptive evolution to allow range expansion into new climatic regimes. Empirical and theoretical work on species ranges suggests that four general factors may be important causes of niche conservatism: natural selection, gene flow, pleiotropy, and lack of variability (Wiens 2004a,b).

Natural (stabilizing) selection should be an important factor in the conservation of niches over time. If ecological conditions reduce fitness or population growth outside the niche, then natural selection should favor traits that keep individuals inside the niche (Holt 1996, Holt & Gaines 1992). An obvious example is behavioral habitat selection. For species that lack behavioral habitat selection (e.g., plants), natural selection will be biased toward those environmental conditions in which the largest number of individuals occurs (Holt & Gaines 1992).

Gene flow may also be an important force preventing niche expansion. Small populations at the edge of the geographic range may be flooded by individuals from the center, which may prevent these populations from adapting to environmental conditions outside the range (e.g., Haldane 1956, Holt 1996, Holt & Gaines 1992, Holt & Gomulkiewicz 1997, Kirkpatrick & Barton 1997, Stearns & Sage 1980).

Traits that would allow range expansion may be pleiotropically linked to traits that reduce fitness. In *Drosophila serrata* in Australia, range expansion into cooler temperate regions may be limited because evolution of increased cold resistance is associated with decreased fecundity (Jenkins & Hoffman 1999). Similarly, Etterson & Shaw (2001) have presented evidence that adaptation to warmer climatic regimes is slowed by genetic correlations among traits that are antagonistic to the direction of selection.

Finally, species may not evolve to expand their geographic range and niche because they lack genetic variation in the appropriate traits (e.g., Bradshaw 1991, Case & Taper 2000). Lack of variation may be very important in some cases (e.g., Hoffman et al. 2003), but several lines of evidence suggest that it may not be a universal explanation (Ackerly 2003). This evidence includes differences in climatic regimes among some closely related species (e.g., closely related montane and lowland endemics) and the evidence for genetic variation in most quantitative traits (e.g., Roff 1997), particularly those of ecological significance (e.g., Geber & Griffen 2003). Although the general causes niche conservatism at the population-genetic level have been discussed, the actual physiological traits that underlie niche conservatism (e.g., limited tolerance to heat, cold, or dessication) are poorly studied and may be relatively taxon specific.

CONCLUSIONS

In recent years, a controversy has developed over whether niches are evolutionarily conserved. Rather than debating whether niche conservatism exists, we suggest that a more useful focus for research would be to test the specifics of what niche conservatism may (or may not) do. In this review, we described the potential implications of one aspect of niche conservatism (the effects of climatic tolerances on dispersal) for many different areas of evolution, ecology, and conservation biology. Our review is not exhaustive, and this aspect of niche conservatism may be important in many other areas as well (e.g., intraspecific phylogeography). These diverse effects of niche conservatism may simply reflect the same process playing out over different temporal scales—whether for decades, or hundreds to thousands of years (i.e., invasive species, response to climate change, human history), thousands to millions of years (i.e., allopatric speciation), or tens or even hundreds of millions of years (i.e., historical biogeography, community structure, species richness). If this idea is true, then studies in diverse areas of ecology, evolution, and conservation biology may have unexpected relevance for each other. For example, invasive species offer many replicated "experiments" in large-scale biogeography, and studies of the role of niche conservatism in speciation and historical biogeography may offer insights both into how organisms have responded to climate change in the past and how future climate change may affect them. New tools from environmental bioinformatics should facilitate empirical tests of the role of niche conservatism across many different systems and questions, especially when coupled with phylogenetic analyses and with ecological and physiological studies at the local scale.

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