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SPECIATION AND ECOLOGY REVISITED: PHYLOGENETIC NICHE CONSERVATISM AND THE ORIGIN OF SPECIES

JOHN J. WIENS

Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York 11794-5245
E-mail: wiensj@life.bio.sunysb.edu

Abstract.—Evolutionary biologists have often suggested that ecology is important in speciation, in that natural selection may drive adaptive divergence between lineages that inhabit different environments. I suggest that it is the tendency of lineages to maintain their ancestral ecological niche (phylogenetic niche conservatism) and their failure to adapt to new environments which frequently isolates incipient species and begins the process of speciation. Niche conservatism may be an important and widespread component of allopatric speciation but is largely unstudied. The perspective outlined here suggests roles for key microevolutionary processes (i.e., natural selection, adaptation) that are strikingly different from those proposed in previous literature on ecology and speciation. Yet, this perspective is complementary to the traditional view because it focuses on a different temporal stage of the speciation process.

Key words.—Adaptation, biogeography, ecology, natural selection, niche, speciation, vicariance.

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Ever since Darwin (1859), evolutionary biologists have suggested that ecology plays an important role in the origin of new species, and interest in the relationship between ecology and speciation has intensified in recent years (e.g., Funk 1998; Orr and Smith 1998; Schluter 1998, 2000, 2001; Schemske 2000; Via 2002). According to most authors, ecology is important in speciation because incipient species often occur in different environments or utilize different resources (e.g., microhabitats). Divergent natural selection on ecologically important traits in these incipient species then leads to different adaptations, evolutionary divergence, and reproductive isolation between them. Although there are many variations on this scenario (e.g., geographic mode, relative roles of natural vs. sexual selection), the recurring theme is that ecology is important in speciation because incipient species occur in different ecological settings and adaptation to these different ecological settings drives evolutionary divergence.

In this paper, I argue that ecology can play an additional role in the origin of species that is very different from the one described in most of the recent literature on ecology and speciation, but one that is in some ways quite obvious. I propose that the tendency of species to retain similar ecological niches over evolutionary time scales (phylogenetic niche conservatism; Ricklefs and Latham 1992; Peterson et al. 1999; Webb et al. 2002) and their failure to adapt to new environmental conditions is a key factor in initially isolating populations and creating new lineages. The importance of habitat specificity in geographic isolation was discussed extensively by Mayr (1963). However, Mayr did not discuss phylogenetic niche conservatism or its microevolutionary basis, and the general ecological and microevolutionary processes that underlie geographic isolation of lineages remain largely ignored and unstudied in recent literature in evolutionary biology and vicariance biogeography (e.g., Futuyma 1998; Brown and Lomolino 1998). Furthermore, the concept of niche conservatism is entirely absent from the burgeoning literature on ecology and speciation (e.g., Orr and Smith 1998; Schluter 1998; 2000, 2001; Via 2002).

Phylogenetic Niche Conservatism and Speciation

The geographic separation of an ancestral species into separate lineages is an important part of allopatric speciation under most widely held species concepts, even if different authors disagree about what characteristics these lineages must eventually attain for the speciation process to be considered complete (e.g., de Queiroz 1998; Futuyma 1998). I argue that phylogenetic niche conservatism, manifested by the failure of a species to adapt to novel ecological conditions, is an important component in this initial splitting of allopatric lineages. Allopatric speciation is generally considered to be the most common geographic mode (e.g., Futuyma 1998; Barraclough and Vogler 2000; Turelli et al. 2001), suggesting that niche conservatism may be of widespread importance. The role of niche conservatism in speciation is most apparent in the context of vicariance, but applies to other geographic modes of allopatric speciation (i.e., dispersal) as well.

Although organisms occupy almost every conceivable habitat in the biosphere, most individual species inhabit only a limited set of ecological conditions. Vicariance begins when environmental change creates conditions within a species' geographic range that are outside of its ancestral ecological niche (i.e., the set of biotic and abiotic conditions in which that species is able to survive, reproduce, and maintain viable population numbers; Hutchinson 1957; Brown and Lomolino 1998). Individuals are unable (or unwilling) to persist in or disperse through these extreme ecological conditions, and the species' geographic range becomes fragmented. But given that organisms can collectively adapt to almost any ecological conditions, why do they not adapt to conditions at the geographic barrier, expand their niche, and maintain gene flow? A few barriers may be difficult for any species to colonize or cross—such as glaciers or lava flows—but many are clearly more subtle (Table 1). For example, many closely related species of organisms are confined to highland habitats. Many of these montane endemics were seemingly isolated when

TABLE 1. Examples of subtle habitat differences that appear to have geographically isolated closely related allopatric species. Note that in many cases the unsuitable habitat is occupied by species that are closely related to those occurring in suitable habitat. For example, montane forests in Mexico are occupied by hylid frog species that have close relatives in adjacent lowlands (Duellman 2001), and the saltwater and terrestrial habitats that isolate river-dwelling species of map turtle (*Graptemys*) are occupied by closely related genera in the same family (*Malaclemys*, *Terrapene*).

Suitable habitat	Unsuitable habitat	Organism	Location	References
Mesic montane forest	Lowlands	Birds, mammals, amphibians, insects	Southern Mexico	Peterson et al. (1999), Duellman (2001)
High gradient highland streams	Low gradient lowland streams	Fish	North America	Wiley and Mayden (1985), Mayden (1988)
Rivers	Saltwater, terrestrial	Map turtles (<i>Graptemys</i>), fish	North America	Wiley and Mayden (1985), Lamb et al. (1994)

climate change caused montane habitats to move upwards in elevation and become separated by intervening lowland habitats (Fig. 1). Yet, these lowland regions are often inhabited by close relatives of the montane species. Given that their close relatives thrive in lowlands, why do montane species fail to adapt to and occupy (or disperse through) lowland habitats during vicariance? Similarly, whereas some might be tempted to say that vicariance occurs because "fish can't fly," many aquatic habitats are physically connected by other aquatic habitats (i.e., most streams flow to rivers, rivers to oceans, and all oceans are connected). Therefore, many species of fish are isolated, at least in part, by habitats that differ in subtle characteristics (e.g., salinity, temperature) and that are inhabited by other species of fish (Table 1). What prevents a given fish species from adapting to and invading these adjacent habitats during vicariance?

Recent empirical and theoretical work on the evolution of geographic ranges and ecological niches suggests that four factors should maintain the ancestral niche and limit local adaptation during vicariance: lack of variability, natural selection, pleiotropy, and gene flow. The most obvious factor is a lack of variability in the traits that would allow dispersal across the barrier (e.g., Bradshaw 1991; Case and Taper 2000). This lack of variability may itself be the result of natural selection, weeding out variation in traits that would promote or allow dispersal out of the niche. Although lack of variability may explain some combinations of barriers and taxa, it seems less likely for many others (e.g., montane habitats), and most traits are thought to be genetically variable (e.g., Roff 1997).

Given that the intrinsic traits that limit the species range have the potential to vary and evolve within the species, natural selection should generally act to conserve the ancestral ecological niche (Holt and Gaines 1992; Holt 1996). When ecological factors (e.g., extreme temperatures, competition for food) reduce fitness outside of the ancestral niche, natural selection should favor traits that keep individuals within the niche, such as behavioral habitat selection. Habitat selection will also reduce opportunities for adaptation to conditions outside of the niche, because populations cannot adapt to conditions to which they are not exposed (e.g., Rosenzweig 1987; Holt 1996). Even if species lack active habitat choice (e.g., plants), demographic effects will tend to optimize traits for those parts of the species range where individual fitness is highest and where the largest number of individuals occur

(Holt and Gaines 1992). Thus, when species have the potential to evolve tolerance for a variety of ecological conditions (e.g., temperature), demography and natural selection should bias the evolution of tolerance towards the range of conditions encountered within the ancestral niche.

Similarly, organismal traits that would allow range expansion during vicariance may be pleiotropically linked to traits that reduce fitness. For example, evolution of increased cold resistance at the southern border of the geographic range of *Drosophila serrata* is associated with decreased fecundity, representing a pleiotropic trade-off in fitness that prevents range expansion (Jenkins and Hoffman 1999).

Gene flow between the center and periphery of the range of a species can also impede local adaptation to conditions at the edge of the species range (e.g., Haldane 1956; Stearns and Sage 1980; Holt and Gaines 1992; Holt and Gomulkiwicz 1997; Kirkpatrick and Barton 1997; Case and Taper 2000). Similarly, during vicariance, asymmetric gene flow from larger populations closer to the center of the range of each incipient species may flood small populations adjacent to the geographic barrier with maladapted individuals, preventing local adaptation.

In summary, these four factors (either alone or together) will prevent local adaptation to conditions at the geographic barrier and form the microevolutionary basis for phylogenetic niche conservatism and vicariance. Very similar processes may drive allopatric lineage splitting via dispersal. Prior to the dispersal event, the geographic range of an ancestral species is confined to a certain set of ecological conditions. During dispersal, some individuals found a new population in a separate and isolated geographic area with similar ecological conditions. Niche conservatism is important in limiting gene flow between colonists and individuals in the ancestral geographic range, and in determining which locations are acceptable for colonization in the first place. Although vicariance and dispersal are the two classic models of allopatric speciation, it should be noted that some allopatric models do not involve niche conservatism, such as isolation-by-distance in marine systems (Palumbi 1994).

Comparison with Previous Views on Ecology and Speciation

The view of ecology and speciation outlined here suggests roles for key evolutionary processes that are very different

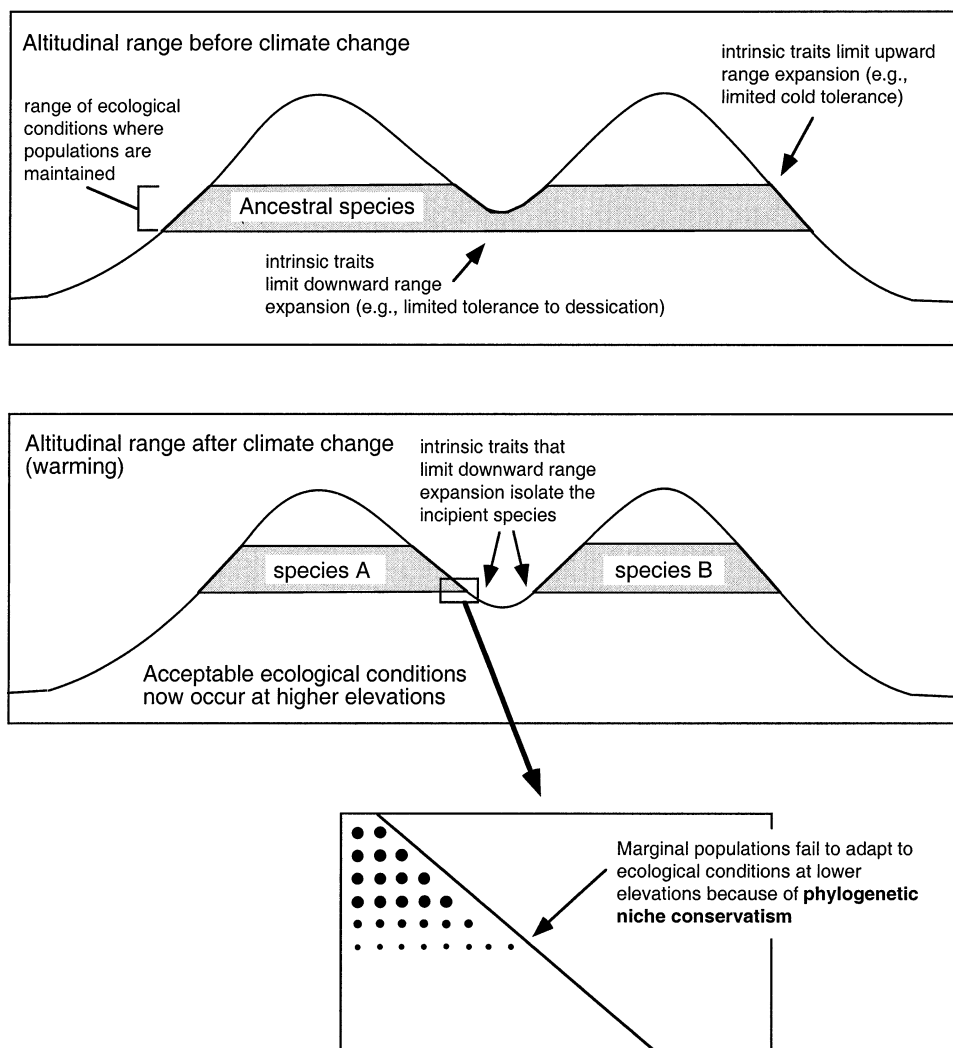


FIG. 1. Hypothetical example illustrating how phylogenetic niche conservatism initiates vicariant allopatric speciation. A montane species initially occupies a certain elevational range. The upper and lower limits of this range are set by the combination of extrinsic ecological factors (e.g., low temperatures at high elevations, low humidity at lower elevations), and intrinsic organismal traits, such as limited tolerance to cold (upper) and to desiccation (lower) and behavioral selection of habitats that are within the elevational range. Prior to climate change, the range of ecological conditions in which the species can maintain viable populations (the niche) occurs at relatively low elevations, and there is continuous habitat and gene flow connecting the populations inhabiting the two mountain peaks. Because of niche conservatism, the set of acceptable ecological conditions (e.g., range of temperature and humidity) remains similar over time. When the climate becomes warmer and drier, this set of acceptable ecological conditions occurs at a higher elevational range. Populations therefore move to higher elevations rather than adapting to the warmer and drier conditions that now occur at the lower end of their previous elevational range. As a consequence, the valley between the two peaks is outside of the niche of the ancestral species, and there is no gene flow between populations on the two peaks. These populations therefore become geographically isolated, and eventually become the distinct species A and B (exactly how and when the latter happens depends upon the species concept that one favors). In theory, the populations adjacent to the valley could adapt to the low elevation conditions and maintain gene flow, but adaptation is impeded by the microevolutionary factors that maintain niche conservatism (e.g., natural selection, gene flow). This example illustrates that vicariance is not simply a geographic event, but rather the outcome of ecological and microevolutionary processes that have been largely ignored in the study of speciation.

from those described in the previous literature (e.g., Orr and Smith 1998; Schluter 1998; 2001). In the traditional view, the processes of natural selection, adaptation, and ecological specialization all act to drive divergence between lineages inhabiting different environments. In the view outlined here, natural selection acts to maintain the ecological niches of lineages over time and thereby limits dispersal across geographic barriers during vicariance. In other words, natural selection promotes speciation by limiting ecological diver-

gence. Similarly, in contrast to the traditional view, adaptation may actually prevent this initial stage of speciation, by allowing species to persist in or invade the novel ecological setting of a potential geographic barrier and thereby maintain gene flow between otherwise isolated populations. Finally, under the perspective discussed here, ecological specialization is a critical factor in promoting speciation, but not during the time frame of lineage splitting. Ecological specialization can limit the habitat breadth of a species and

thereby increase the number and effectiveness of potential geographic barriers (e.g., Futuyma 1998). Thus, vicariance and geographic isolation may represent the legacy of ecological specialization in the distant past.

Although the view of ecology and speciation outlined here is very different from that discussed in the recent literature, these views are complementary because they emphasize different temporal stages of the speciation process. The model outlined here focuses on the first part of allopatric speciation, the initial origin of lineages, whereas the traditional view focuses on the subsequent divergence of these lineages (which is obviously important in reducing or preventing future gene flow between lineages). This model of geographic isolation through niche conservatism does not assume that species remain ecologically identical over long periods of time, only that they maintain the ecological traits that prevent dispersal across the barrier during the time frame of lineage splitting. Furthermore, lineage splitting may be important for later divergence, because it prevents gene flow from impeding the adaptation of populations to different local environments (Futuyma 1987)

Areas for Future Research

A fundamental question in ecology, ecological biogeography, and conservation biology is “what limits the distribution of species?” Focusing on the mechanisms of allopatric lineage splitting suggests that this should be a critical question in speciation research as well. The inability of species to adapt to certain abiotic conditions over short evolutionary time scales may often drive vicariance, but biotic factors (e.g., competition with closely related species) may also be important (e.g., Darwin 1859), and there may be interactions between biotic and abiotic factors. For example, some recently diverged montane salamander species (*Plethodon shenandoah*, *P. hubrichti*, *P. nettingi*) may be geographically isolated from each other because of a closely related lowland species (*P. cinereus*) that is a superior competitor in lowlands but inferior in certain physiologically stressful highland habitats (Jaeger 1971; Dunson and Travis 1991; Petranka 1998). Many studies have sought the geographic barriers involved in specific speciation events (e.g., Patton and da Silva 1998), but few have taken the next step by identifying the extrinsic ecological factors and intrinsic organismal traits that underlie these barriers. No studies have identified the microevolutionary forces that constrain adaptation during vicariance (e.g., selection, gene flow, pleiotropy), although some have addressed how these processes may determine species range limits outside the context of speciation (e.g., Hoffman and Blows 1994; Jenkins and Hoffman 1999; Hoffman et al. 2003). Questions of how allopatric lineages subsequently become sympatric (i.e., changes in the geographic barrier, adaptation, or both) and what factors determine the duration of their geographic isolation have also been surprisingly neglected. Studies of niche conservatism and the causes of allopatric range splitting may have important implications for major issues in conservation biology (e.g., how organisms respond to human-induced habitat modification and climate change, how exotic species are able to invade biogeographically distant communities; Peterson and Vieglais 2001; Pe-

terson et al. 2002), and vice versa, with each discipline providing insights at different temporal scales. In summary, we presently can only speculate about how the first part of allopatric speciation occurs because the relevant processes have generally not been studied in the context of speciation.

A variety of new and old tools might be used to help address these questions. Geographic, phylogenetic, and geological data for co-occurring species with similar habitat preferences can be used to infer the vicariant splitting of habitats and species (e.g., Wiley and Mayden 1985). New methods for ecological niche modeling software can be applied to distributional databases to help infer the ecological factors that isolate sister species (e.g., Peterson et al. 1999; Peterson 2001). These factors can then be tested further with field and laboratory experiments. Selection experiments and analyses of quantitative trait loci can be used to infer the genetic variability and basis for these limiting traits (e.g., Hoffman et al. 2003). Molecular markers can be used to infer patterns of gene flow between central and peripheral populations. Clearly, however, inferring microevolutionary and ecological processes that occurred thousands or millions of years ago based on present day patterns and processes must be done with appropriate caution. New theoretical work is also needed. Minimally, the rich body of theory on the ecology and evolution of geographic range limits (e.g., Kirkpatrick and Barton 1997; Case and Taper 2000; Holt and Keitt 2000) should be extended to incorporate vicariance and lineage-splitting via dispersal.

Conclusions

In this paper, I have described a view of ecology and speciation that is very different from those discussed in the recent literature. I have outlined how phylogenetic niche conservatism, rather than ecological divergence, contributes to the formation of geographically isolated lineages, the necessary first stage of the most common (allopatric) mode of speciation. Yet, this model is complementary to traditional studies of ecology and speciation, which focus on the divergence of lineages rather than their origin per se. Taken together, these two views suggest a much broader role for ecology in speciation than has been suggested previously.

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Corresponding Editor: R. Harrison