

Notes and Comments

What Is Speciation and How Should We Study It?

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ABSTRACT: To understand speciation, we first need to know what species are. Yet debates over species concepts have seemed endless, with little obvious relevance to the study of speciation. Recently, there has been progress in resolving these debates, favoring a lineage-based, evolutionary species concept. This progress calls for reconsideration of the study of speciation. Traditional speciation research based on the biological species concept has led to great advances in understanding how nonallopatric speciation occurs and how species diverge and remain separate from each other. However, this research has neglected the question of how new species arise in the first place for the most common geographic mode (allopatric). A new and very different research program is needed to understand the ecological and evolutionary processes that split an ancestral species into new allopatric lineages. This research program will connect speciation to many other fundamental questions in evolutionary biology, ecology, biogeography, and conservation biology.

Keywords: biogeography, evolution, reproductive isolation, speciation, species concepts.

There is a crisis in evolutionary biology that is often recognized in theory but almost universally ignored in practice. This crisis can be summarized in two statements. First, our view of how speciation occurs depends on our concept of what species are (Cracraft 1983; Harrison 1998). Second, biologists disagree about what species are (e.g., Mayden 1997; Hey 2001; Pigliucci 2003). The origin of species is a fundamental issue in evolutionary biology, but without some agreement about what speciation is, it seems impossible to resolve.

Many biologists who study speciation have adopted the

theoretical framework of the biological species concept (BSC) and might claim that there is no such crisis. Under the paradigm of the BSC, speciation is viewed as the evolution of reproductive isolation between populations (Coyne 1994; Coyne and Orr 1998; Futuyma 1998; Noor 2002). Speciation research based on the BSC has led to exciting advances in our understanding of the evolution of intrinsic reproductive isolating mechanisms (Coyne and Orr 1998; Howard and Berlocher 1998; Turelli et al. 2001; Via 2001, 2002). However, various alternative species concepts have been proposed, both by systematists (i.e., the group of biologists dedicated to discovering and describing new species) and by other speciation biologists, including the evolutionary (Wiley 1978), phylogenetic (Cracraft 1983; Nixon and Wheeler 1990), cohesion (Templeton 1989), cluster (Mallet 1995), genealogical (Baum and Shaw 1995), and genic (Wu 2001) species concepts. These alternative concepts have been rejected by many speciation biologists (e.g., Coyne 1994; Coyne and Orr 1998; Schemske 2000; Barton 2001; Noor 2002).

The primary argument made by speciation biologists in favor of the BSC is that it best facilitates the study of "speciation" (Coyne 1992*a*, 1994; Coyne and Orr 1998; Noor 2002). However, our choice of species concept determines what we consider speciation to be (e.g., Cracraft 1983; Harrison 1998), making this a somewhat circular argument (i.e., using the research program to justify the species concept when the species concept determines the research program). A better approach may be to choose a species concept based on how well it captures what we mean by "species" and then develop a research program in speciation based on how species originate given our best understanding of what species are. In other words, the answer to the question "what is the best species concept for speciation research?" should be simply "the best species concept."

A related argument is that the field of evolutionary biology needs more data on how speciation works, not more discussion about what species are (Coyne 1992*b*; Noor 2002). But again, it is our choice of species concept that determines which data are relevant to how speciation

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works and which data are not. Within any branch of science, data should be collected within a solid conceptual or theoretical framework, and that framework must remain open for debate. If the conceptual foundation of a field is strong, then there should be only limited controversy and no fear of further discussion.

In this note, I will argue that there has been important progress in our understanding of the so-called species problem. This progress has come from identifying the actual source of disagreement about species concepts and recognizing the hidden potential for underlying agreement among seemingly disparate views (Mayden 1997; de Queiroz 1998). Remarkably, some resolution of the debates over species concepts now seems possible, even if there will never be universal agreement.

Recent progress on the issue of species concepts calls for reconsideration of what speciation is and how it might best be studied. Some evolutionary biologists have argued that considering any species concept besides the BSC will only lead to pointless philosophical debate with little relevance to the study of speciation (e.g., Coyne 1992*b*, 1994; Coyne and Orr 1998; Schemske 2000; Barton 2001; Noor 2002). My hope is that serious and open-minded consideration of a lineage-based species concept in speciation research can help focus investigation and suggest new areas for study. Rather than engaging in a lengthy defense of a particular species concept (which has been done elsewhere), my goal here is instead to explore the implications of a lineage-based species concept for the study of speciation (which has not).

I will argue that the study of speciation under a lineage-based concept is the same as that for the BSC for non-allopatric speciation but that there is a critical difference for allopatric speciation, which is arguably the most common mode. BSC-based speciation research elucidates how species diverge and remain distinct from other species (species maintenance). However, it does not actually address how new allopatric species originate in the first place, in other words, the splitting of one species into two. Species maintenance is clearly important, but the origin of allopatric species must be a part of speciation research. For this to happen, we need a research program that addresses the ecological and microevolutionary processes that cause lineage splitting and geographic isolation. At the end of the note, I will outline how such a research program might proceed, borrowing heavily from theoretical and empirical studies of the evolutionary ecology of species range limits.

Distinguishing Species Concepts and Criteria: The Resolution of the Species Problem?

Several authors in systematic theory (e.g., Frost and Kluge 1994; Mayden 1997; de Queiroz 1998) have emphasized

a simple distinction with far-reaching implications for the species problem and speciation research. They argue that much of the disagreement over species concepts may result from confounding the evidence and methods used to recognize species as distinct (species delimitation) with our concept of what species actually are. These authors suggest that species are lineages and that previous disagreements have been about the best evidence to recognize these lineages as distinct. Characteristics used to define species in various species concepts are attributes that may develop in a lineage given enough time (Harrison 1998), such as diagnostic characters (phylogenetic species concept), exclusive or monophyletic gene genealogies (genealogical species concept), and intrinsic reproductive isolating mechanisms (BSC). These authors argued for a lineage-based concept equivalent to the evolutionary species concept (ESC; Simpson 1961; Wiley 1978; Frost and Kluge 1994). The ESC defines a sexual species as the largest single lineage in which there is integration through gene flow (for brevity, and following most other authors, I omit asexual species from this discussion). A lineage is a single line of direct ancestry and descent, such as a series of ancestor-to-descendant populations through time or a single branch of a phylogenetic tree (e.g., Simpson 1961; de Queiroz 1998).

Of course, recognizing that species are lineages does not make all the problematic aspects of species definition and delimitation simply disappear. For example, taxonomic decisions about lineages that are geographically isolated and weakly differentiated or lineages that exhibit limited gene flow with other lineages will always be difficult to resolve in a nonarbitrary fashion, regardless of the species concept one favors. Furthermore, there is considerable room for discussion about the exact definition of "lineage," the importance of gene flow in integrating populations over different timescales, and other issues. Some of these issues have been addressed elsewhere (e.g., Baum 1998; de Queiroz 1998), and revisiting and resolving them are not realistic goals for this note. Instead, I simply echo previous authors in saying that the ESC seems to best capture what we mean by species and species concept and move on to discuss the implications of this concept for the study of speciation.

What Speciation Is

Speciation as the Origin of New Lineages

If species are lineages, what then is speciation? Under the ESC, speciation is the origin of new lineages (Frost and Kluge 1994), specifically, the largest lineages that are connected by gene flow. Various processes may give rise to distinct lineages, and these can be classified based on tra-

ditional geographic modes of speciation (Brown and Lomolino 1998; Futuyma 1998).

Strictly allopatric speciation occurs when two sets of populations become geographically separated, such that there is little or no gene flow between them (fig. 1). These populations are considered separate lineages in that they are geographically isolated from gene flow with each other. In contrast to the traditional view of speciation under the BSC, there is no requirement that these lineages evolve additional reproductive isolating mechanisms. Under the BSC, allopatric lineages lacking these mechanisms are considered to still be “potentially interbreeding” (Mayr 1963) and are not considered to have speciated (e.g., Coyne and Orr 1998; Futuyma 1998; Turelli et al. 2001). These mech-

anisms are essential to maintain the distinctness of these lineages should they later become sympatric. However, these mechanisms did not create the allopatric lineages, and the importance of these mechanisms in maintaining the lineages as separate species may remain only hypothetical. Numerous studies have shown that seemingly distinct species can interbreed (including species that are not sister taxa), a finding that suggests that the evolution of intrinsic reproductive isolating mechanisms can lag behind the origin of distinct allopatric lineages (e.g., Coyne and Orr 1997) or be completely decoupled (e.g., Hillis 1988). Therefore, these mechanisms are not necessary for allopatric speciation under the ESC. Furthermore, lineages need not have exclusive gene genealogies or diagnostic

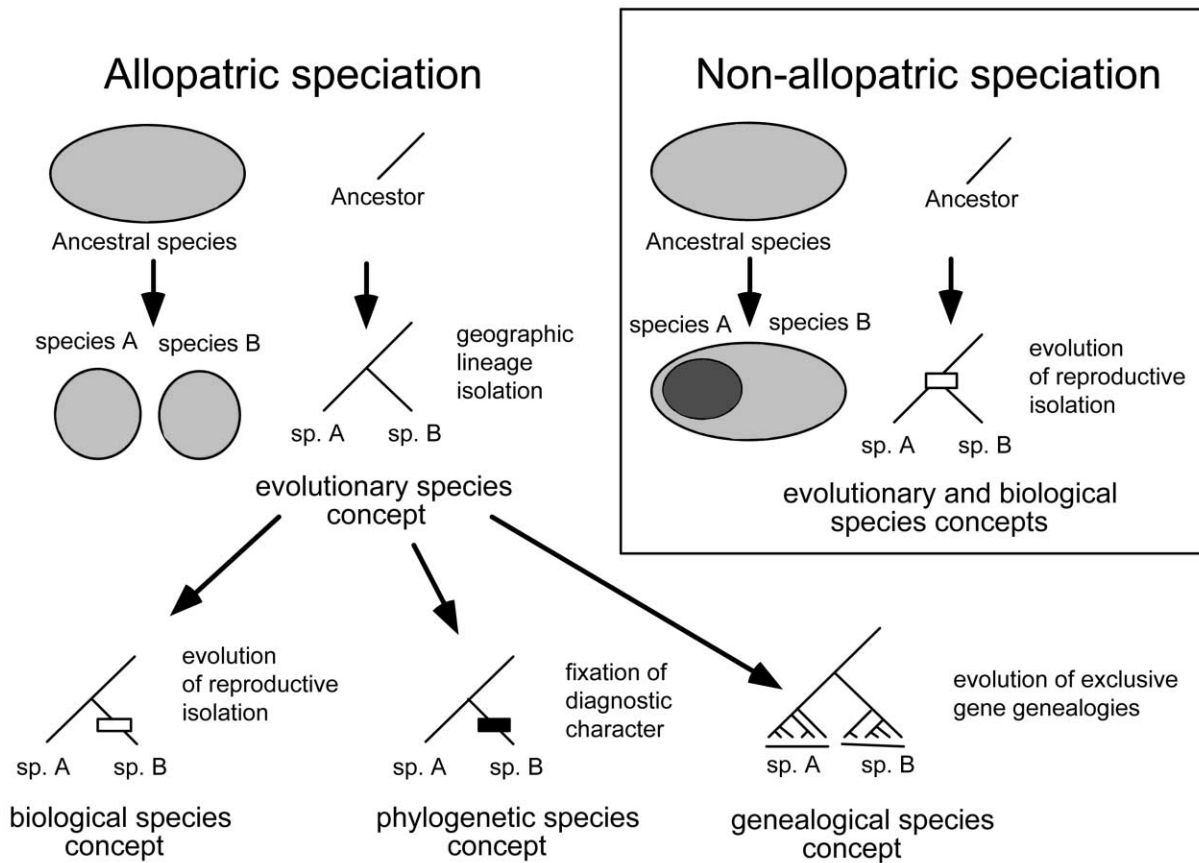


Figure 1: Implications of different species concepts for the study of speciation. For allopatric speciation, speciation is equivalent to the origin of new lineages under the evolutionary species concept (ESC). For other species concepts, speciation is considered to occur when these new lineages acquire certain characteristics that are important for keeping these lineages separate (reproductive isolation for the biological species concept [BSC]; isolation and ecological divergence for the cohesion species concept) or for recognizing these lineages as distinct (i.e., diagnostic characters for the phylogenetic species concept; monophyletic gene genealogies for the genealogical species concept). Studies of allopatric speciation based on the BSC typically focus on the evolution of reproductive isolating mechanisms between geographically isolated lineages and do not necessarily address how new allopatric lineages arise. For nonallopatric modes, the origin of new lineages is tightly associated with the evolution of reproductive isolating mechanisms, and speciation may be equivalent under the ESC and BSC. For both allopatric and nonallopatric modes, speciation is thought to occur under the phylogenetic and genealogical species concepts when a diagnostic character becomes fixed or when gene genealogies become exclusive.

morphological, behavioral, or genetic differences. Those attributes are critical for recognizing a species as distinct, but if those attributes do not help create the new lineages, the evolution of those attributes is not a part of speciation under the ESC.

Given this view, should every allopatric population be recognized as an evolutionary species? No. The ESC defines species as the largest lineage integrated by gene flow (Frost and Kluge 1994), given that a species may contain sublineages that are only briefly isolated from gene flow with each other (e.g., several generations). Even though new allopatric species may be indistinguishable from each other when they first split, no one is likely to treat populations that are effectively identical as distinct species, especially without evidence that gene flow has ceased. In practical terms, only populations that are isolated long enough to diverge are recognized as evolutionary species. The fact that some lineages may be only temporarily isolated reinforces the need to study the mechanisms of intrinsic reproductive isolation, the focus of traditional BSC-based speciation research. But given that the duration of geographic isolation is a critical issue, then we should also study the ecological and evolutionary factors that cause allopatry and that determine how long geographic isolation will last. This topic has been largely ignored in recent speciation research, but it is central to the research program proposed below.

Speciation may also occur through parapatric or sympatric modes (or through some combination of allopatric and nonallopatric models). Many mechanisms may drive the origin of new lineages under these modes, including hybridization, polyploidy, differences in microhabitat choice, and mating asynchrony (Futuyma 1998; Howard and Berlocher 1998). Without allopatry, new lineages may be unlikely to arise without the evolution of intrinsic reproductive isolating mechanisms (Turelli et al. 2001). Thus, nonallopatric speciation may be equivalent under the BSC and ESC (fig. 1).

Geographic Reproductive Isolation versus Evolution of Isolating Mechanisms

The fundamental difference between the BSC and ESC for speciation research comes down to how species arise in allopatry. This is not a trivial distinction, however, because the allopatric mode is widely thought to be the most common geographic form of speciation (e.g., Mayr 1942, 1963; Futuyma 1998; Barraclough and Vogler 2000; Turelli et al. 2001; but see Losos and Glor 2003).

I would argue that “reproductive isolation” is critical to allopatric speciation under both the ESC and BSC. The different implications of these concepts for studies of allopatric speciation hinge on the difference between line-

ages being reproductively isolated (ESC) and the evolution of reproductive isolating mechanisms as part of the speciation process (BSC). Although not widely acknowledged, allopatry can be considered a type of premating reproductive isolation (e.g., Kirkpatrick and Ravigné 2002). Thus, populations that are truly and permanently allopatric are reproductively isolated from each other (i.e., they are no longer actually interbreeding), even if they are still “potentially interbreeding” under the BSC. As I will explain below, each case of allopatry has a biological basis. The biological basis of allopatry can be considered a reproductive isolating mechanism. A useful insight gained from these unorthodox definitions is that allopatric populations can be “reproductively isolated” without having evolved reproductive isolating mechanisms during the time frame of speciation.

A simple example illustrates this distinction (fig. 2). Many species of forest-dwelling organisms are allopatric with respect to their sister taxa because of geographic barriers involving unsuitable, nonforest habitat. These lineages are “reproductively isolated” because they cannot disperse through these unsuitable habitats, and the “reproductive isolating mechanism” is specificity to forest habitat. This trait evolved long before these lineages became geographically isolated. Therefore, these lineages are “reproductively isolated” by habitat specificity, even if there was no evolution of isolating mechanisms during the time frame in which these lineages became isolated. In fact, most cases of allopatry may result from habitat specificity (Mayr 1963; see below), and habitat specificity may evolve long before the separation of a given species pair.

Thus, an ESC-based approach to speciation focuses directly on how lineages become isolated from gene flow with each other, whether by geographic barriers (in strict allopatry) or intrinsic isolating mechanisms (in parapatry or sympatry). In contrast, BSC-based studies typically treat allopatric speciation as the loss of “potential interbreeding” between lineages that might one day become sympatric (or have already) rather than as the loss of actual interbreeding.

Intrinsic reproductive isolating mechanisms are critically important, even for allopatric species, and the traditional emphasis on them in speciation research clearly is not misplaced. Without these mechanisms, species that are separated by geographic barriers may fuse if they become sympatric. However, it is important to note that these mechanisms maintain the integrity of allopatric lineages that actually originated through their geographic isolation. Even researchers that use the BSC-based definition of speciation rarely attempt to distinguish between “speciation” (i.e., the point when intrinsic reproductive isolation is first attained) and the evolution of isolating mechanisms that arise after “speciation” is completed (species

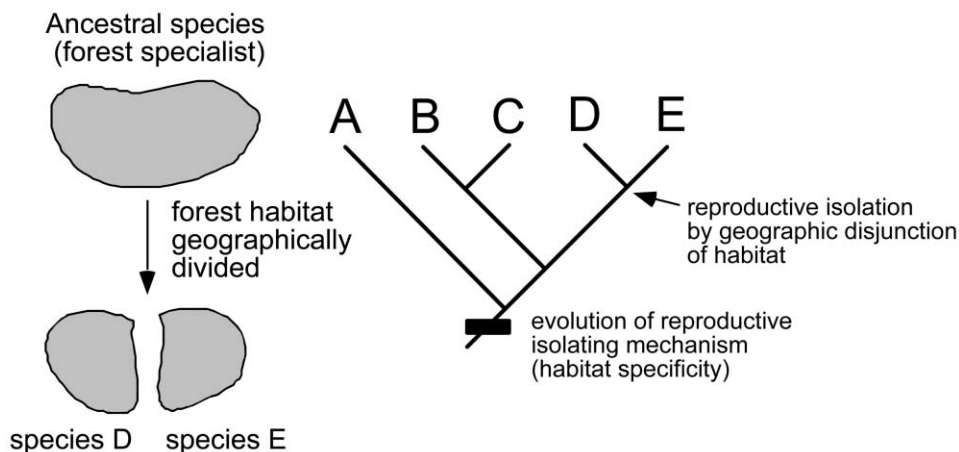


Figure 2: Hypothetical example showing a case where the “reproductive isolation” that creates a pair of new lineages (species D and E) occurs long after the evolution of the “reproductive isolating mechanism.” Members of this clade are primitively confined to moist forests. A geographic barrier divided the range of the ancestor of species D and E (e.g., climate change caused the forests to shrink and divide). These two lineages became “reproductively isolated” (i.e., isolated from gene flow) by their specificity to forest habitat. The reproductive isolating mechanism is specificity to forest habitat, which evolved before these lineages became isolated by allopatry. Under the biological species concept, speciation is typically equated with the evolution of reproductive isolating mechanisms (loss of potential interbreeding) rather than with reproductive isolation (loss of actual interbreeding) itself. Under a lineage-based species concept, speciation is equivalent to the process or processes by which new lineages become reproductively isolated from each other (e.g., allopatry through habitat specificity). The other species in this clade may have evolved by the same mechanism or different mechanisms, but they are not the focus of this example.

differences; Templeton 1981). Thus, much of speciation research based on the BSC may fail to address speciation, even under the BSC-based definition of speciation.

Other Species Concepts

Not all researchers in speciation biology focus exclusively on the evolution of reproductive isolating mechanisms. For example, some consider speciation to include the evolution of morphological differences among closely related species (e.g., Hollocher et al. 2000). Although phenotypic and genotypic differences are important for recognizing lineages as distinct, the evolution of these characters may not be responsible for the origin of these lineages, particularly in allopatry. Thus, the evolution of these characters is not necessarily part of the process of speciation under a lineage-based concept. Similarly, researchers advocating the genealogical species concept consider speciation to occur when the haplotype lineages of an incipient species from one or more genes become exclusive (e.g., Shaw 1998). Exclusivity is a consequence of lineages being isolated from gene flow with each other for a sufficiently long period of time (Neigel and Avise 1986) and can be important evidence in recognizing species as distinct. However, haplotype exclusivity is a consequence, not a cause, of lineage separation.

The Bottom Line

There are two general evolutionary processes that are responsible for the diversity of life: the origin (splitting) of new lineages and evolutionary change (divergence) within those lineages. Divergence is undeniably important, but the unique intellectual contribution of speciation research to the field of evolutionary biology is to explain how splitting occurs. In general, most speciation research has focused on divergence, emphasizing divergence in characters that are important in either nonallopatric splitting, species maintenance (i.e., traits that prevent lineages from interbreeding with other lineages), or species delimitation (i.e., traits that allow us to recognize lineages as distinct). This research is all critically important but still leaves open the question of how new allopatric lineages arise (i.e., how splitting occurs). In the next section, I will outline how we might rectify this situation.

How Do New Lineages Arise?

The Ecology and Evolution of Allopatry

If speciation is the origin of new lineages, how do new lineages arise? For parapatric and sympatric speciation, lineage separation should be intimately tied to the evolution of intrinsic reproductive isolating mechanisms. There is a growing body of work that addresses nonallo-

patric speciation via these mechanisms (e.g., Howard and Berlocher 1998; Turelli et al. 2001; Via 2001, 2002). This research is generally based on the BSC rather than on a lineage concept but should nevertheless be directly relevant to the origin of these nonallopatric lineages. However, allopatric speciation is generally thought to be the most common geographic mode.

In most descriptions of allopatric speciation, the splitting of an ancestral species is simply described as occurring through “geographic barriers.” Yet allopatry is not simply a geographic phenomenon but rather the outcome of ecological and microevolutionary processes. The ecological and evolutionary basis for allopatry has largely been ignored in recent speciation research (particularly for non-marine systems), but it is critical to understanding the origin of new lineages. I have argued that many of the same microevolutionary processes that are involved in lineage divergence are also involved in lineage splitting but that these processes play radically different roles in each (table 1; Wiens 2004). In general, adaptation is thought to play a key role in lineage divergence and speciation (e.g., Schluter 2001; Turelli et al. 2001). In contrast, the failure of populations to adapt to ecological conditions at the edge of the species range may often be responsible for their geographic isolation (and thus, lineage splitting).

It is obviously true that geographic isolation typically requires the separation of suitable habitats by unsuitable habitats (e.g., Mayr 1963). It is therefore also true (but less obvious) that a key factor in allopatric speciation is the failure of species to adapt to and cross these physically adjacent habitats. Given this view, vicariance can be seen as a race between environmental change and adaptation to that change; speciation occurs if adaptation loses (i.e., populations can no longer persist in the area that becomes the geographic barrier). Similarly, allopatric speciation via dispersal only occurs when individuals of a species some-

how circumvent the ecological conditions that normally restrict their distribution and found a new population.

Superficially, it might seem that most geographic barriers involve habitat differences that are so extreme that there is little chance for adaptation to permit crossing these barriers. Yet, many species appear to be geographically isolated by relatively subtle differences in habitat, where the barrier of unsuitable habitat is inhabited by close relatives of the species occurring in suitable habitats (e.g., montane endemics separated by lowland habitat). In such cases, it seems that adaptation that would allow crossing the geographic barrier is theoretically possible but is somehow prevented. Empirical and theoretical work on the evolution of species range limits (e.g., Hoffman and Blows 1994; Kirkpatrick and Barton 1997; Jenkins and Hoffman 1999) suggests that adaptation that would allow expansion of the geographic range and ecological niche may be limited by natural selection, pleiotropy, gene flow, and lack of variability (Wiens 2004).

Natural selection should favor individuals that choose habitats where their fitness is highest (Holt and Gaines 1992; Holt 1996). This process will promote behavioral habitat selection and niche conservatism and will tend to slow adaptation to novel ecological conditions at the geographic barrier. Behavioral habitat selection will then make it difficult for organisms to adapt to conditions that they actively avoid (Holt 1987, 1996; Rosenzweig 1987). Even if organisms lack behavioral habitat selection, demography and selection should tend to optimize limiting traits (e.g., heat tolerance) for those conditions where fitness is highest and the largest number of individuals occurs (Holt and Gaines 1992). Pleiotropy may genetically link traits that would allow range expansion across the geographic barrier to traits that reduce fitness (e.g., cold resistance and decreased fecundity in *Drosophila*; Jenkins and Hoffman 1999). Gene flow should slow adaptation to conditions at

Table 1: Simplified comparison of contrasting roles of evolutionary processes involved in allopatric lineage splitting (allopatric speciation under a lineage-based concept) versus lineage divergence

Evolutionary process	Role in lineage splitting	Role in lineage divergence
Adaptation	Limits speciation by facilitating dispersal across a geographic barrier	Promotes divergence of populations in different ecological settings
Natural selection	Promotes speciation by selecting against individuals that leave the ancestral habitat or niche (inhibits ecological divergence)	Promotes divergent adaptation of populations to different ecological settings
Gene flow	Promotes speciation by limiting local adaptation to geographic barrier (but gene flow across barrier inhibits speciation)	Inhibits lineage divergence by limiting local adaptation
Mutation (genetic variability)	Inhibits speciation by facilitating adaptation to geographic barrier	Provides raw material for local adaptation and divergence
Ecological specialization	Promotes speciation prior to lineage splitting; creates habitat specificity underlying geographic barriers	Promotes divergence after lineage splitting

the geographic barrier by flooding small, peripheral populations adjacent to the barrier with maladapted individuals from larger populations at the center of the range (e.g., Haldane 1956; Holt and Gaines 1992; Kawecki 1995; Holt and Gomulkiewicz 1997; Kirkpatrick and Barton 1997; Case and Taper 2000). Lack of variability in the traits that would allow crossing or colonization of the geographic barrier may also be important (e.g., Case and Taper 2000). However, it would be premature to assume that most cases of allopatric splitting result from insufficient genetic variation, given that the traits that limit species ranges often seem to vary among closely related species and that most traits are thought to be genetically variable (Roff 1997). Clearly, the ability and willingness of individuals to disperse also play an important role in geographic isolation (Brown and Lomolino 1998), and the evolution of dispersal may interact with adaptation to unsuitable habitats.

A New Research Program in Allopatric Speciation

Future empirical work on allopatric speciation should minimally address three general questions. First, what are the extrinsic ecological factors that cause geographic range splitting? Are they typically abiotic (e.g., temperature, moisture, salinity), biotic (e.g., competition), or a combination of the two? Second, what intrinsic organismal traits underlie these ecological factors? For example, is physiological stress usually the limiting factor (e.g., heat tolerance, desiccation resistance)? Third, what microevolutionary factors impede adaptive evolution in these limiting organismal traits during the time frame of speciation?

The following general research program might be used to study the biological basis of allopatric speciation. First, identify a single vicariance event based on the co-occurrence of multiple sister species in the same area sharing similar habitat preferences and a similar geographic disjunction (e.g., Wiley and Mayden 1985; Peterson et al. 1999). Focusing on vicariance is not required, but it may avoid idiosyncratic aspects of dispersal. Next, identify the nature and timing of the environmental change that created this disjunction of habitats based on concordance between geological evidence and levels of molecular divergence between sister species (e.g., Near et al. 2003). Then focus on a particular pair of sister species and identify the specific ecological factors that underlie their inability to cross the geographic barrier. This task may be facilitated using ecological niche modeling (e.g., Peterson et al. 1999; Peterson 2001) to identify the environmental variables that predict the current distribution and range limits of these species. Ecological niche modeling might also be used to predict the spatial distribution of these environmental variables at the time of lineage splitting (e.g., Huggall et al. 2002) and to infer whether the ecological vari-

ables that limited dispersal during lineage splitting are likely to be the same as those limiting dispersal today. If so, the next step is to identify the specific organismal traits that prevent individuals from colonizing or crossing the geographic barrier (e.g., tolerance to cold or desiccation), using detailed ecological observations, comparisons, and experiments with populations adjacent to (and not adjacent to) the geographic barrier (e.g., Hoffman and Blows 1994; Jenkins and Hoffman 1999). The final step is to determine what population genetic factors may limit adaptation in these traits to ecological conditions at the geographic barrier. This step might include testing for variability and heritability in the limiting organismal trait within and between populations of each species (e.g., Hoffman et al. 2003), examining patterns of trait variation and migration (i.e., using molecular markers) across the range of each species to determine whether gene flow has stymied local adaptation adjacent to the geographic barrier (e.g., Stearns and Sage 1980), and seeking evidence of behavioral habitat selection driven by natural selection (in animals) or by decreases in population sizes or fecundity in populations adjacent to the geographic barrier (e.g., Gross and Price 2000).

This research program will doubtless be challenging. Nevertheless, various studies cited above (many outside the context of speciation research) have documented the feasibility of nearly every step. Theoretical studies should also provide an important complement to empirical studies, particularly for questions that prove empirically intractable. Many theoretical studies have already addressed similar issues in the context of range limits (e.g., Kirkpatrick and Barton 1997; Case and Taper 2000).

There are many other questions regarding allopatric lineage formation that also have been neglected. For example, in the preceding discussion, I have implicitly assumed that the development of allopatry is relatively short, discrete, and independent of evolutionary divergence. Does allopatric speciation typically result from simple splitting of populations in similar habitats or does ecological divergence also play a role in geographic isolation (e.g., Schemske 2000)? How might the processes involved in lineage splitting and lineage divergence interact? Does gene flow between new allopatric species typically cease after a few hundred or a few million years? When did the intrinsic traits that geographically isolated the species (i.e., habitat specificity) evolve during the phylogenetic history of the clade? Are most sister species within a clade prevented from interbreeding by their allopatry alone or by intrinsic reproductive isolating mechanisms?

I acknowledge that some evolutionary biologists may consider allopatric lineage splitting to be less interesting than traditional speciation research (although this is more a matter of personal taste than a scientific argument). Nev-

ertheless, the issue of how lineages arise in allopatry is intimately related to fundamental questions in evolutionary biology (e.g., what limits adaptation?), ecology (e.g., how does the niche evolve over time? how does competition influence species distributions?), biogeography (e.g., what causes vicariance? what determines a species' geographic range?), and conservation biology (e.g., how quickly can species adapt to habitat modification and climate change?). Even within the context of traditional BSC-based research, allopatric lineage splitting has long been recognized as a necessary first stage in allopatric speciation (e.g., Mayr 1963; Futuyma 1998), although the topic has been largely eclipsed by other questions in recent speciation studies.

Conclusions

Understanding the origin of species requires understanding what species are. Yet there has been little consensus as to the most appropriate species concept, despite active research based on the biological species concept. Recent reviews have suggested that much of this disagreement may result from confusing concepts of what species are with criteria for recognizing species as distinct. The evolutionary species concept, which emphasizes the idea that species are lineages, seems free from this confusion and may offer a more sound conceptual foundation for the study of speciation. In this note, I have explored the implications of a lineage-based concept for the study of speciation.

Most modern speciation research has addressed how lineages evolve to remain separate (i.e., the BSC) or how lineages diverge to become phenotypically or genetically distinguishable. Although this research clearly is important and interesting, it does not necessarily address the question of how new lineages arise in the first place. This is particularly true for allopatric speciation, which is often considered to be the most common geographic mode. Instead, a different research program is needed, focusing on the ecological and microevolutionary factors that cause geographic isolation. Such a research program will connect speciation to many other fundamental questions in evolutionary biology, ecology, biogeography, and conservation biology.

The point of this note is not to suggest that researchers interested in speciation should stop studying the evolution of intrinsic reproductive isolating mechanisms. These mechanisms are essential in nonallopatric speciation and in maintaining the distinctness of formerly allopatric lineages that come into sympatry. However, their direct relevance to a particular speciation event should depend on the geographic context. For example, postzygotic isolating mechanisms are probably not responsible for the origin of lineages that have been completely allopatric since their

initial splitting. In these cases, the mechanisms that underlie geographic isolation may be more directly relevant to the origin of reproductive isolation and lineage splitting.

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