

The Geography of Speciation: Case Studies from Birds

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Abstract Our understanding of the origin of species, or speciation, is sometimes viewed as incomplete, a “mystery of mysteries.” We in fact know a lot about speciation, especially when we consider its two basic components, the geography of speciation and the biology of speciation (changes in phenotype and genotype that occur during the process). Our understanding of the geography of speciation is quite clear. The process involves the separation of a once-continuous range into two or more geographically isolated, or allopatric parts, which over time accrue genetic changes that result in new daughter species. Current distributions show that recently evolved species are currently allopatric, supporting the role of allopatry in speciation. However, many species originated in the early- to mid-Pleistocene, meaning that they persisted through the environmental perturbations of multiple glacial cycles. It has been assumed that species maintained allopatric distributions during these episodes of glacial advance and retreat. I used Grinnelian niche models to estimate species distributions at the Last Glacial Maximum and the Last Interglacial. For a pair of recently isolated warbler species, and a pair of relatively old sister species of gnatcatchers, allopatry was observed at all time periods. Thus, there is no mystery about the geography of speciation: at least in birds, allopatry predominates. The sentiment that speciation is mysterious comes, I argue, from the biological species concept, which requires populations to be reproductively isolated before recognizing them as species. Reproductive isolation is a complicated process that rarely occurs the same way twice, and I argue that this lack of generality has been misinterpreted as a mystery.

Keywords Species concepts · Speciation · Allopatry · Niche models

Speciation, or the origin of species, is often called Darwin’s “mystery of mysteries.” In fact, Via (2009:9939) remarked “The origin of species is only slightly less mysterious now than it was 150 years ago when Darwin published his famous book.” In part, this characterization is discouraging because in fact we know a great deal about how new species form. I believe that the perception that speciation is a mystery stems from the definition of species themselves. Various species concepts differ in their complexity and the types of biological changes considered necessary and sufficient to judge that speciation has occurred. The more complicated the species concept, the more mysterious speciation becomes. To dismantle the perception that speciation is mysterious, it is useful to divide the origin of species into two components, which we might for simplicity call the geography and the biology of speciation (Bush 1975). In this essay, I concentrate on our understanding of the geography of speciation in birds, arguably one of the best known vertebrate groups. I show that geography of speciation is straightforward under all species concepts, and that in fact speciation is only mysterious under certain definitions of species.

Species Concepts and Speciation

To illustrate the relationship between species concepts and speciation, I briefly review three common species concepts. This is important because one cannot discuss speciation without first specifying criteria for recognizing species (Wiens 2004). The Biological Species Concept (BSC) was largely formulated by the geneticist Theodosius Dobzhansky, and

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popularized by many subsequent evolutionary biologists, especially Ernst Mayr. One formulation of the BSC is “Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr 1942). Thus, speciation requires the evolution of characteristics that confer reproductive isolation to populations descended from a common ancestor. These characteristics can prevent individuals from choosing mates (pre-mating reproductive isolation) or result in sterile or inviable offspring should mating occur (post-mating reproductive isolation). There is little consistency among taxonomic groups in terms of which specific genetic, behavior, or ecological attributes contribute to reproductive isolation, which in effect is an epiphenomenon of character divergence.

A second species concept is the phylogenetic species concept (PSC), which was defined by Cracraft (1983): “A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent.” Here, speciation is simply the origin of diagnostic characteristics that reveal that a population or group of populations have had an independent evolutionary history. It might be a short or a long history, and the characteristics can be phenotypic, ecological, molecular, physiological or behavioral—in short, any heritable diagnostic feature. There is no requirement that species be reproductively isolated (Zink and McKittrick 1995).

For illustration, a third (among many other) species concept is the evolutionary species concept, a version of which is “An ‘evolutionary species’ is a single lineage of ancestor–descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate” (Wiley 1978). Here, no character evidence is needed, only the knowledge that a population or group of populations has “set off” on an independent evolutionary trajectory. For example, a population isolated on an island is in theory a species irrespective of whether it is distinguishable from its mainland progenitor.

The main distinguishing characteristics of these species concepts are summarized in Table 1. Each of the species concepts would define speciation as beginning with the allopatric separation of an ancestral species. Below, I focus on the geographic aspects of speciation, which is correctly

viewed as an extended process through time, rather than an instantaneous event.

The Geography of Speciation

Earth history over the past two million years, roughly the Pleistocene, was typified by regular and massive habitat alterations. Of course, the ultimate cause was global climate change, which resulted in multiple episodes of glacial advance and retreat at more or less regular intervals. The effects of these glacial cycles are clear. Species ranges were regularly shifted, compressed, subdivided, eliminated or greatly expanded. In other words, a wide-ranging species, perhaps a habitat generalist, would be pushed southwards as climate deteriorated (cooled). As the glacial cycle advanced and ice sheets pushed south, changing the distribution of plant communities on which the species depended, the species’ range might not only be displaced southward but it could be fragmented into geographically isolated components.

When once-continuous populations are isolated geographically from each other, a situation termed allopatry (living in different places), they begin to accumulate mutations unique to their geographic group, and the process of genetic divergence begins. The process can be driven by natural selection, sexual selection or even genetic drift. If the newly isolated populations are incompletely isolated, i.e., some individuals can move from one newly isolated area to the other, the process will be slowed, or perhaps prevented. An axiom of population genetics is that a little gene flow goes a long way—gene flow via dispersing individuals is a “genetic glue” that keeps populations from emerging on their own separate evolutionary trajectory. But if the populations remain isolated they will accumulate enough divergence in their genetics, ecology or morphology that they will become different species (Mayr 1942). The nature of divergence will determine whether speciation has occurred under different species concepts. If allopatric taxa exhibit diagnostic character differences, they are species under the PSC. Only if these diagnostic differences also function as reproductive isolating mechanisms will the taxa be considered biological species. In any event, it appears that species evolved regularly throughout the Pleistocene in northern temperate areas as a result of glacial cycles and the habitat changes they caused (Klicka and Zink 1997, 1999).

Study of the distribution of bird species played a prominent role in identifying the importance of geographic isolation in the speciation process. In particular, analysis of the ranges of newly separated species, or sister species, was instrumental. The bulk of extant sister species of birds are allopatric or nearly so; those with some overlap are evolutionarily “older,” implying that they evolved sufficient ecological differences to allow coexistence in some areas, usually where the ranges

Table 1 Some characteristics required of populations to be considered distinct species under three different species concepts

Species concept	Geographic isolation (allopatry)	Diagnostic characters	Reproductive isolation
Biological	Yes	Yes	Yes
Phylogenetic	Yes	Yes	No
Evolutionary	Yes	No	No

meet (Chesser and Zink 1994). Thus, the spatial isolation of sister species is a signature of allopatric speciation.

There are always potential exceptions to allopatric speciation, such as speciation occurring without geographic isolation, which is termed sympatric speciation. However, there is little if any evidence for this mode of speciation in birds.

Two Case Studies of the Role of Allopatry in Bird Speciation as Revealed by Niche Modeling

The fact that sister species have allopatric distributions today is quite compelling evidence of the importance of geographic isolation in the speciation process. However, to date we have only assumed that allopatry was maintained from the point of initial divergence. For example, although sister species are today allopatric (or “parapatric,” meaning the ranges abut), we could only speculate that at earlier times, in different glacial regimes, the taxa were also allopatric. Recent developments in the field of niche modeling (Peterson et al. 2012) permit us to examine the distributions of modern species at earlier points in time, to assess the consistency of allopatry during species’ histories. I present two case studies that involve two pairs of currently allopatric species, a pair of North American warbler species and a pair of North American gnatcatcher species. I reconstruct

their historical distributions to test whether they have been allopatric throughout their evolutionary divergence.

The two warblers have been variously treated as species and subspecies, the Myrtle Warbler (*Dendroica coronata*) and the Audubon’s Warbler (*Dendroica auduboni*). They are extremely similar in size and shape, with the primary difference being that the former has a white throat and the latter a yellow throat. They are also very similar in their DNA sequences, meaning that their plumage differences evolved recently (Milá et al. 2007, Brelsford and Irwin 2009). They are mostly allopatric, but their ranges overlap in a small area in British Columbia, where some hybridization occurs. This is why some researchers consider them the same species (under the BSC), whereas others such as the current author finds this irrelevant and consider them two species under the PSC.

Have these warbler species historically been allopatric, or mostly so? To answer this, one can use niche models. These involve taking a set of modern occurrence records, and a set of various climate variables such as temperature and rainfall, and building a model that predicts their current distributions. This is called a species distribution model or niche model and basically describes the environmental conditions favorable to the species; it is sometimes called the “Grinnellian” niche, after the famous Berkeley ornithologist Joseph Grinnell. A species might have a smaller distribution than predicted owing

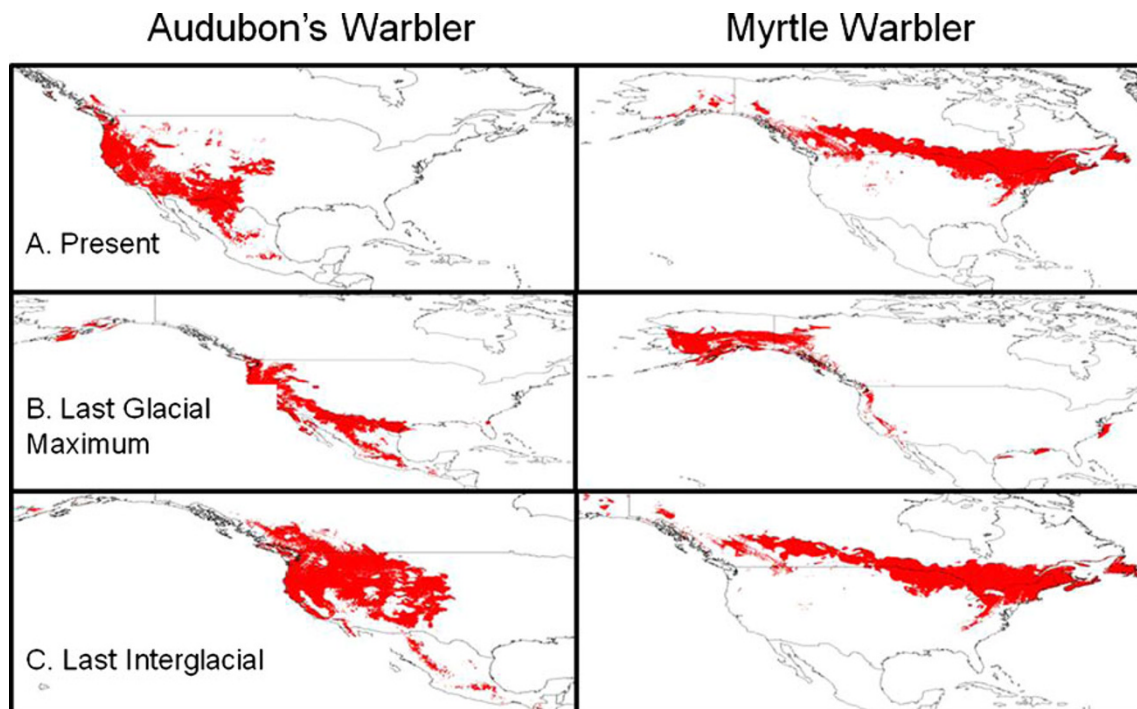


Fig. 1 Predicted distributions of Audubon’s Warbler and Myrtle Warbler at the present time (a), Last Glacial Maximum (b), and Last Interglacial (c). The niche models were constructed by entering breeding records from the breeding bird survey (accessed at www.pwrc.usgs.gov/bbs) into MAXENT ver 3.2.2. (Phillips et al. 2006). Climatic data (19 layers) were

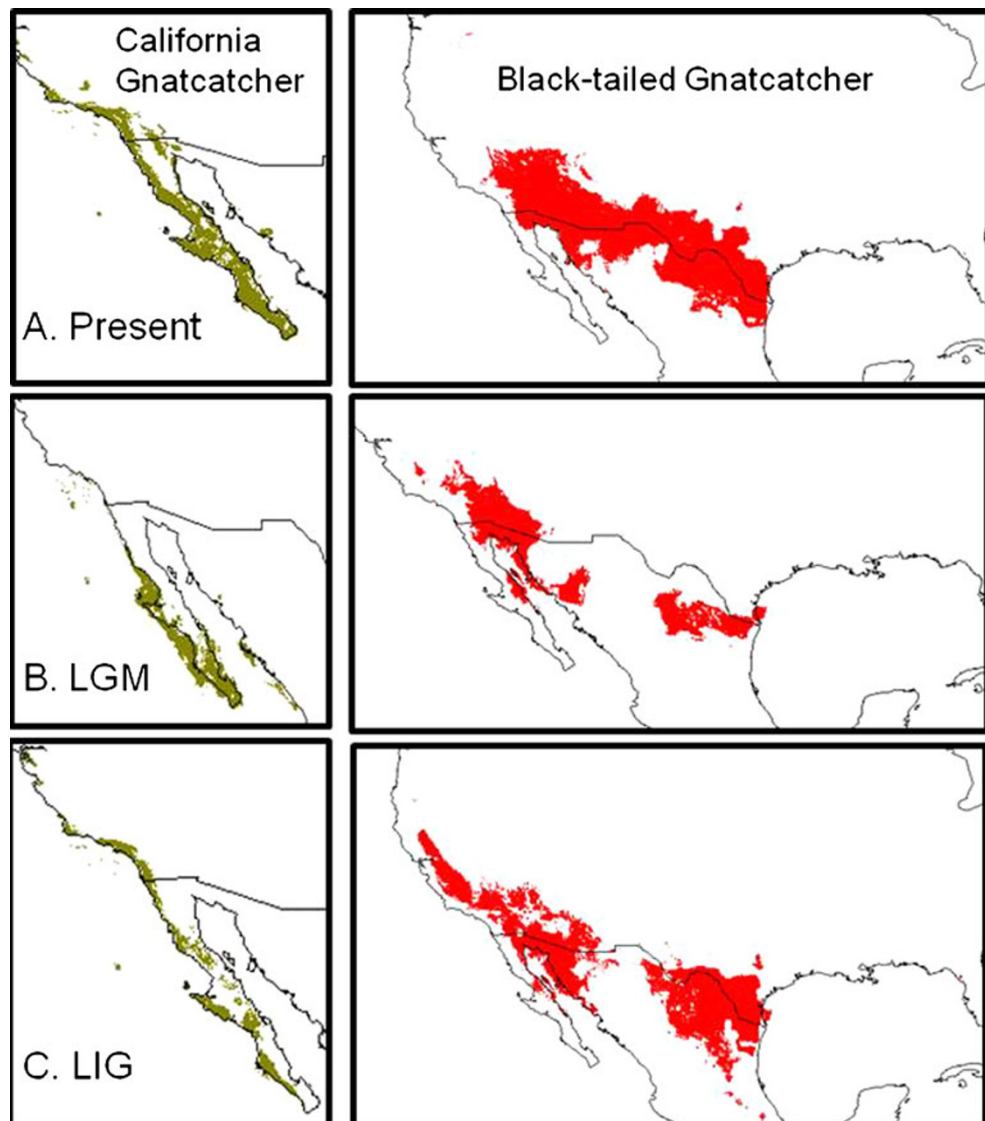
obtained from the Worldclim bioclimatic database (Hijmans et al. 2005), and Maxent was set to use 30% of values for training. Distribution maps were coded to show either presence or absence based on a minimum threshold of predicted occurrence

to the presence of competitors (sometimes called the Eltonian or realized niche).

If a niche model can predict where a species occurs at present, we then take a set of climate variables from the past and use the model to predict where the species could have occurred at that time (Peterson 2001, Peterson et al. 2012, Waltari et al. 2007). This procedure assumes that the niche of the species has not changed over time. Also, the models only predict where the conditions under which the species lives today occurred at some previous time, not whether the species in fact occurred there (i.e., a competitor might have excluded the species from some area). However, this is a common procedure and many scientists have concluded that the methods are robust. I used niche modeling to determine whether the two species pairs of warblers were allopatric at the Last Glacial Maximum (LGM) about 21,000 years before present (ybp) and at the Last Interglacial (LIG), ca. 120,000 ybp, times for which climate data are available.

The reconstructed distribution of the warblers at the present time (Fig. 1A) corresponds well with their known distribution, permitting confidence in ancestral range reconstructions. The predicted distributions of the warblers at the LGM (Fig. 1B) and LIG (Fig. 1C) suggest a long history of allopatry. In addition, predicted distributions at the LIG (Fig. 1C) are very similar to the current ones, suggesting continuity in distributions during the last two interglacial periods (LIG and present). Thus, the warblers have been allopatric for at least 120,000 years, reinforcing the role of allopatry in maintaining (and initiating) their evolutionary divergence. Incidentally, this result also gives a minimum estimate of the time since they became separate species. The niche model suggests they have been isolated since at least the LIG, but likely not much longer, owing to the small number of genetic differences between them (Milá et al. 2007; but see Brelsford and Irwin 2009).

Fig. 2 Predicted distributions of California Gnatcatcher and Black-tailed Gnatcatcher at the present time (a), Last Glacial Maximum (b), and Last Interglacial (c). See legend to Fig. 1 for methods



Two other sister species, the California Gnatcatcher (*Poliophtila californica*) and the Black-tailed Gnatcatcher (*Poliophtila melanura*) today have allopatric ranges. The gnatcatchers differ from the warblers in at least two important ways, namely they are sedentary (the warblers are migratory), and they are very different genetically. In particular, the nucleotide divergence between the species is almost 5% at a mitochondrial DNA gene (Zink and Blackwell 1998). Molecular evolutionists believe that DNA substitutions occur in a roughly clock-like manner, and given some standard calibrations of the rate of mtDNA evolution in birds, it is likely that the two gnatcatcher species last shared a common ancestor over a million years ago. This means that they have been separate species and remained distinct throughout the many glacial advances and retreats that have occurred during the past million years. Given their distinctiveness, we can therefore predict that we should, as we did in the case of the warblers, observe allopatry at the LGM and LIG.

The predicted current distributions (Fig. 2A) are very close to the known distributions of the two gnatcatchers, suggesting that the model captures the main climate features that determine gnatcatcher distributions. LGM (Fig. 2B) and LIG (Fig. 2C) reconstructed distributions for the two gnatcatcher species show clearly that allopatry has been a dominant feature of their historical ranges.

It is natural to wonder why the two gnatcatchers have separate ranges at present. That is, one might expect that a sufficient amount of time had passed since they speciated for them to evolve ecological differences that would allow them to “invade” the ranges of each other and coexist over the same area. The fact that they are allopatric suggests they are too similar ecologically to coexist (termed niche conservatism; see McCormick et al. 2010), and hence, they remain allopatrically distributed. However, more sophisticated niche tests are required to confirm this hypothesis. Alternatively, the two species might be behaviorally antagonistic towards each other, preventing coexistence.

The Geography of Speciation is Not a Mystery: Allopatry Prevails

For decades, we have looked to the modern distributions of species and observed the signatures of allopatric divergence. Studies of birds were important in providing numerous examples. However, we have only recently begun to use niche modeling to examine the role of allopatry in species' histories. I have shown here with two examples that indeed allopatry is a hallmark of the speciation process. That is, the geography of speciation is almost certainly a process involving allopatry. There is, then, nothing mysterious about this part of the speciation process.

Where is the Mystery in Speciation?

The answer to this question is a topic for a different essay. However, it involves the second part of the speciation process, namely how characters evolve during the speciation process, or as I termed it above, the “biology” of speciation. Some species concepts, such as the BSC, require a complicated set of events to occur before two diagnostically different populations are recognized as two species, and therefore inferring that speciation has occurred (Table 1). There is a myriad of ways in which two allopatric populations can acquire the character differences they need to be reproductively isolated. There are few if any generalities in this process across animals and plants, and what generalities exist are limited to specific groups. It is my opinion that because there are so few generalities, speciation has been considered mysterious. In short, if you realize that two species can become reproductively isolated by unique means, there is no mystery, only a lack of generality. The biology of speciation, then, is not a mystery either. It is just that the biology of speciation is more complex than the geography of speciation. This in my opinion does not qualify as a biological mystery, it just reveals once more the complex nature of biological variation that so intrigues us with understanding life in the first place.

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