The Causes of Evolutionary Radiations in Archipelagoes: Passerine Birds in the Lesser Antilles

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abstract: To investigate why some lineages undergo evolutionary radiation, we compare the passerine avifaunas of the Hawaiian and Galápagos archipelagoes, which have supported well-known radiations of birds, with those of the Lesser Antilles, which have not. We focus on four steps required for the buildup of diversity through allopatric speciation and secondary sympatry: genetic divergence in isolation, persistence of island populations, recolonization of source islands, and ecological compatibility in secondary sympatry. Analysis of genetic divergence among island populations in the Lesser Antilles reveals evidence of both prolonged independent evolution and reexpansion of differentiated island populations through the archipelago but little evidence of secondary sympatry of divergent genetic lineages. Archipelagoes with high rates of colonization from continental or nearby large-island sources might fail to promote evolutionary radiations because colonists fill ecological space and constrain diversification through competition. However, morphological analysis demonstrated similar divergence between allopatric populations in species in Hawaii, Galápagos, and the Lesser Antilles, although the rate of divergence between secondarily sympatric species evidently is more rapid in Hawaii and the Galápagos. Alternatively, endemic buildup of diversity might be facilitated by the relative absence of pathogens in Hawaii and Galápagos that otherwise could prevent the secondary sympatry of populations owing to disease-mediated competition.

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Among birds, evolutionary radiations within archipelagoes include the Darwin's finches (Geospizinae) of the Galápagos (Lack 1947; Bowman 1961, 1963; Grant 1986; Burns et al. 2002) and the honeycreepers (Drepanidinae) of Hawaii (Amadon 1950; Pratt 1979; Fleischer and McIntosh 2001; James 2003). Birds are relatively mobile, and phylogenetic analysis of avian sister lineages provides no indication of speciation within islands as small as 1,000–10,000 km^2 (Fleischer and McIntosh 2001; Ricklefs and Bermingham 2001; Burns et al. 2002). Therefore, accumulation of species belonging to a single clade on individual islands within an archipelago is thought to involve genetic differentiation of island populations in isolation followed by reinvasion of one island by a sister population from another island (Lack 1947; Mayr 1963; Grant 1998; Coyne and Price 2000; Grant and Grant 2002). In the event that such secondarily sympatric populations do not interbreed, they are considered separate species (Mayr 1963; Templeton 1989; Coyne and Orr 2004).

Not all archipelagoes have supported evolutionary radiations. In the case of birds, neither the Lesser Antilles (Bond 1956, 1963, 1979) nor the New Hebrides (Vanuatu) (Medway and Marshall 1975; Diamond and Marshall 1976, 1977*a*), for example, are regarded as crucibles of species production. Instead, avian taxa inhabiting these archipelagoes represent primarily separate invasions from nearby continental or large-island sources of colonists (Bond 1963; Lack 1976; Ricklefs and Bermingham 2001). Although many of these taxa are old and have been described as endemic species and genera, they have generally not diversified in the sense of producing sympatric daughter species.

Although evolutionary radiation is understood in general outline (Givnish and Sytsma 1997; Grant 1998; Grant and Grant 1998; Schluter 2000), factors that promote or retard diversification are not. In this article, we use detailed phylogeographic analyses of Lesser Antillean birds (Ricklefs and Bermingham 1999, 2001, 2004) to explore factors that potentially could constrain the allopatric for-

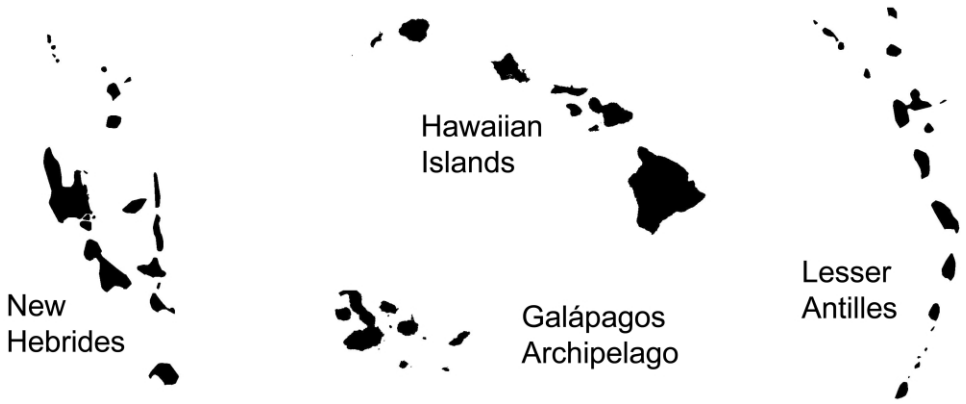

Figure 1: Maps of the New Hebrides, Lesser Antilles, Hawaii, and Galápagos archipelagoes to the same scale illustrate the general similarity of island size and distance.

mation of new species and their secondary sympatry within archipelagoes, which we define as an evolutionary radiation. We avoid the term "adaptive radiation" to forestall judgment concerning phenotypic or ecological diversification. Although evolutionary radiations characterize the diversification of life everywhere, islands provide suitable laboratories for studying this phenomenon owing to the discrete nature of populations and the clear distinction between allopatry and sympatry. Furthermore, evolutionary radiations within oceanic archipelagoes of volcanic origin have a clearly recognizable beginning, which is a colonization event from outside.

Evolutionary radiation leading to the co-occurrence of descendant species on the same island can occur only when four requirements for allopatric speciation are met (see, e.g., Allmon 1992; Mayr and Diamond 2001; Newton 2003): (1) dispersal between islands must be sufficiently low to permit genetic divergence, (2) island populations must persist long enough to diverge genetically to a point of incompatibility resulting from either premating or postmating isolating mechanisms, (3) isolated populations must occasionally recolonize other islands, and (4) newly sympatric sister taxa must be reproductively isolated and ecologically compatible.

We first determine whether differences in the occurrence of evolutionary radiations among four similar archipelagoes have statistical validity. We then use genetic divergence between island populations of passerine birds in the Lesser Antilles to evaluate requirements 1 (isolation), 2 (persistence), and 3 (recolonization). Specifically, we test hypotheses concerning factors that might prevent evolutionary radiations, namely, that (i) continuing dispersal of individuals prevents genetic divergence of island populations in archipelagoes, (ii) island populations do not persist long enough to diverge genetically to a speciation threshold, and (iii) secondary sympatry does not occur owing to too little movement between islands.

Evolutionary radiations of birds on the Galápagos and, especially, Hawaiian archipelagoes have at least partially filled the ecological space occupied by more phylogenetically diverse assemblages of species on less remote islands and continents (Schluter 1988; Burns et al. 2002; Lovette et al. 2002). This suggests that evolutionary radiations occur most readily where ecological space is available, conspicuously on new and/or remote islands (Schluter 1988). To address this issue, we use morphological diversity as a proxy for ecological diversity to determine whether sympatry is associated with a minimum level of ecological divergence.

We find that none of the requirements 1 through 3 for allopatric speciation appears to limit evolutionary radiation in the Lesser Antilles. Step 4, the achievement of ecological compatibility, might be hindered in the Lesser Antilles by the lack of ecological opportunity owing to the ecological diversity of colonizing lineages or by host-specific pathogens that prevent co-occurrence.

Material and Methods

The Archipelagoes

We initially compare four tropical archipelagoes that feature similar numbers of large islands and distances between islands, with the exception that the Galápagos Archipelago is more compact than the other three (fig. 1). The Galápagos Islands differ from the other island groups ecologically in the relative aridity of low-elevation habitats and the strong influence of El Niño–Southern Oscillation events on climate (Colinvaux 1984). Humans have had a profound effect on the avifaunas of each group of islands (Pregill and Olson 1981; Olson and Hilgartner 1982; Pre-

gill et al. 1988, 1994; James and Olson 1991; Steadman 1995, 2006; Steadman and Rolett 1996; Pregill and Crother 1999; Steadman et al. 2002; Steadman and Martin 2003), probably least in the Galápagos Islands, which currently supports a small human population distributed among four of the larger islands and which had no pre-European history of colonization (Perry 1984). Human-caused extinctions have reduced the diversity and distributions of some groups of island birds (Steadman 1995) but probably have caused the extinction of few passerines in the Lesser Antilles and New Hebrides. Indeed, the clearest example of evolutionary radiation in island passerine birds comes from the Hawaiian archipelago, which has suffered the greatest loss of island populations and species.

The island groups are all primarily volcanic in origin but differ in their relative ages, the Lesser Antilles (~20 Ma; Donnelly 1988, 1989; Perfit and Williams 1989; Iturralde-Vinent and MacPhee 1999) and New Hebrides (~20 Ma, but with extensive area only after 2 Ma; Mallick 1975) being older than the present-day Galápagos (at least 3.3 Ma; Cox 1983; Hall et al. 1983; Simpkin 1984; Sinton et al. 1996; Hoernle et al. 2000) and the main Hawaiian islands (~5.1 Ma; Clague and Dalrymple 1987; Carson and Clague 1995). Hawaii and the Galápagos, 3,800 and 850 km, respectively, from North and South America, are considerably farther from continental sources of colonization than the Lesser Antilles and New Hebrides. Grenada, in the southern Lesser Antilles, is approximately 150 km from the coast of Venezuela. Although Espiritu Santo in the New Hebrides is roughly 380 km from New Caledonia and 1,000 km from the coasts of Australia and New Guinea, a large number of colonists have reached the islands from the west by way of stepping-stone islands.

The Birds

We restrict this analysis to passerine birds (songbirds, or perching birds: order Passeriformes) because these comprise a well-characterized monophyletic group with reasonably uniform biological attributes and because most of the species from the Lesser Antilles for which we have estimated genetic distances are passerine birds. In addition, the conspicuous radiations of birds in the Galápagos Islands (the Darwin's finches: subfamily Geospizinae) and the Hawaiian Islands (the honeycreepers: subfamily Drepanidinae) are passerines; compared to other island birds, relatively few passerines have become extinct following human occupation.

Taxonomy and distributions of passerines were obtained from Bond (1956, 1979), the American Ornithologists' Union (1998), and Raffaele et al. (1998) for the Lesser Antilles; Diamond and Marshall (1976, 1977*a*) for the New Hebrides; Harris (1973) for the Galápagos Archipelago; and Pratt (1979), Berger (1981), and James and Olson (1991) for the Hawaiian Islands. A list of the colonizing lineages producing the contemporary avifauna of each of the island groups is provided in the appendix, available in the online edition of the *American Naturalist*.

Genetic and Morphological Analyses

Genetic divergence based on 842 base pairs of the partially overlapping mitochondrial ATPase 6 and ATPase 8 protein-coding genes has been reported in previous publications; materials, methods, and GenBank accessions can be accessed through the original articles (e.g., Lovette et al. 1998, 1999*a*, 1999*b*; Hunt et al. 2001). Details, including GenBank submission numbers, are provided in the electronic supplementary materials to an article by Ricklefs and Bermingham (2001; http://www.sciencemag.org/cgi/content/full/294/5546/1522/DC1).

Morphological analyses are based on the means of $\log_{10}$-transformed measurements for each species, including total length, wing, tarsus, middle toe, tail, and the length, width, and depth of the bill (Ricklefs and Travis 1980). The morphological variables were subjected to a principal components analysis (PCA) of the variance-covariance matrix of the log-transformed values (Ricklefs and Travis 1980; Legendre and Legendre 1998). Morphology provides a reasonable assessment of foraging substrate, feeding movements, and prey size (e.g., Miles and Ricklefs 1984; Miles et al. 1987). Pairwise distance (D_{ij}) between two species (i and j) in morphological space was calculated as the Euclidean distance based on n measurements, that is,

$$D_{ij} = \sqrt{\sum_{k=1}^{n} (x_{ik} - x_{jk})^2},$$

where x_{ik} and x_{jk} are the values for measurement k for species i and j, respectively. For each species, the smallest distance to another species was designated as the nearest neighbor distance (NND; Ricklefs and Travis 1980). When the nearest neighbor distance was based on all eight measurements, it was designated NND_8. In other comparisons based on fewer measurements, generally taken from literature sources (see "Results"), pairwise distances and nearest neighbor distances were designated D_n and NND_n. Because each measurement contributes approximately equally to the total Euclidean distance, the ratio of the expected distances with y and z measurements, which is $(y/z)^{1/2}$, provides a basis for comparison. All statistical analyses were performed with SAS software (SAS, Cary, NC) or with the PopTools add-in to Excel (http://www.cse.csiro.au/poptools/) and are described in "Results."

Results

The Frequency of Evolutionary Radiations

The number of independent colonizations to an archipelago is associated with the frequency of evolutionary radiations and levels of endemism within the island group (table 1). In the Hawaiian Islands, one ancestral stock of cardueline finch gave rise to at least 35 historical species, including 15 species of honeycreepers on the island of Hawaii alone (Amadon 1950; Pratt 1979), and many additional forms that are now extinct (James and Olson 1991; James 2003). In the Galápagos Islands, a single ancestral stock produced a monophyletic clade of 13 species of Darwin's finches, with up to 11 species on a single island (Lack 1947; Harris 1973; Grant 1986; Petren et al. 1999; Sato et al. 1999), although the definition of species within this group is somewhat uncertain (Zink 2002) and hybridization between named species is not uncommon (Grant and Grant 1998). In the Lesser Antilles, the only evolutionary radiation among passerine birds comprises four endemic species of thrashers (Mimidae; Hunt et al. 2001), all four of which coexist on the islands of St. Lucia and Martinique. No evolutionary radiations are apparent in the New Hebrides (Diamond and Marshall 1976).

The current passerine avifaunas of the Hawaiian and Galápagos archipelagoes have each been derived from six colonization events and together have produced at least 62 historical species, of which 97% are endemic (table 1; also see appendix). In the New Hebrides and Lesser Antilles, 24 and 34 colonization events have together produced 61 species, of which only 33% are endemic. Differences in the proportions of endemic genera and species between these two sets of archipelagoes are highly significant ($G = 22.4$, $P < 10^{-5}$ and $G = 63.5$, $P < 10^{-14}$, respectively).

In the New Hebrides and Lesser Antilles, one of 58 colonization events represented among extant taxa resulted in a modest evolutionary radiation. In the Hawaiian and Galápagos archipelagoes, three of 12 colonization events produced radiations that built overall diversity to approximately the levels of the less remote archipelagoes. If we assume that the colonizing lineages are independent, then, from a statistical standpoint, one of 58 and three of 12 differ significantly ($G = 5.6$, $P = .018$).

Because of avifaunal similarities between the Lesser Antilles, Galápagos, and Hawaii (see appendix), the presence or absence of evolutionary radiations is unlikely to be related to particular characteristics of passerine colonists of archipelagoes. Specifically, near relatives of the finches and thrushes that gave rise to the evolutionary radiations in the Galápagos and Hawaiian archipelagoes are present in the Lesser Antilles (Tarr and Fleischer 1995; Burns et al. 2002; Lovette et al. 2002; Miller et al., forthcoming). Accordingly, we examine the birds of the Lesser Antilles, the only regional assemblage of passerines studied from a DNA-based phylogeographic perspective (Seutin et al. 1993, 1994; Lovette et al. 1998, 1999*a*, 1999*b*; Ricklefs and Bermingham 1999, 2001; Hunt et al. 2001; Miller et al., forthcoming), in terms of the four requirements for evolutionary radiation: genetic divergence in allopatry, persistence of diverging populations, opportunity for secondary sympatry, and ecological compatibility of secondarily sympatric populations.

Step 1: Opportunity for Genetic Divergence

Differentiation of island populations of birds in the Lesser Antilles is suggested by subspecific names assigned to many of these (Bond 1956). Gaps in the distributions of several species (Bond 1956; Ricklefs and Cox 1972) further suggest that individuals of some species move between islands too infrequently to recolonize islands left unoccupied following extinction, let alone to prevent genetic differentiation. Recent molecular phylogenetic studies of birds in the Lesser Antilles (Seutin et al. 1993, 1994; Lovette et al. 1998, 1999*a*, 1999*b*; Ricklefs and Bermingham 1999, 2001; Hunt et al. 2001) show that genetic divergence between allopatric populations is common, especially for endemic Antillean taxa. We have surveyed 25 monophyletic lineages of passerine birds within the Lesser Antilles, 22 of which were represented by two or more island populations. Of these, eight exhibit mitochondrial (ATPase 6, 8) nucleotide divergences between at least one pair of islands greater than 0.5%, which exceeds most (>97%) within-population genetic distances. Based on estimated coalescence times (see "Step 3: Recolonization Ability"), the expected level of genetic diversity in mtDNA within island populations is about 0.1% nucleotide divergence, which is close to the median observed in 104 island populations of 32 species (Ricklefs and Bermingham 2001; R. E. Ricklefs and E. Bermingham, unpublished data). Seven species had interisland divergences exceeding 1%, and five exceeded 2%.

Eleven of 14 species with maximum interisland divergences less than 0.5% have conspecific populations in northern South America or the Greater Antilles. Evidently, these are either recent colonists to the Lesser Antilles (Ricklefs and Bermingham 2001) or species with continuing high levels of movement between source areas and the Lesser Antilles and among islands within the archipelago (Johnson et al. 2000; Cherry et al. 2002). The other three species are endemic Lesser Antillean taxa with either recent secondary phases of colonization within the archipelago or recent high levels of gene flow.

Five of 13 of the endemic Lesser Antillean taxa (>2.0% divergence from source) that we have surveyed exhibit interisland divergences within the range of 2%–8%. Such

Table 1: Characteristics of the described passerine faunas of four archipelagoes[a]

Characteristic	Lesser Antilles	New Hebrides	Galápagos	Hawaii
Total area (km^2) (Stattersfield et al. 1998)	6,300	13,000	8,000	16,300
Maximum elevation (m)	1,500	1,800	1,700	4,200
Nearest continent (distance, km)	South America (150)	Australia (1,000)	South America (850)	North America (3,800)
Number of colonizations	34	24	6	6
Number of genera (endemic)	30 (8)	18 (1)	8 (4)	16 (14)
Number of species (endemic)	37 (16)	24 (4)	21 (19)	41 (41)
Maximum number of species on one island	28	22	16	21
Radiations	1[b]	0	1[c]	2[d]
Number of taxa produced	4	0	13	35[e]

[a] Sources of data: Lesser Antilles (Bond 1956, 1979; American Ornithologists' Union 1998; Raffaele et al. 1998); New Hebrides (Diamond and Marshall 1976, 1977*b*); Galápagos (Harris 1973); Hawaii (Pratt 1979; Berger 1981; James and Olson 1991).

[b] The endemic thrashers (Sturnidae: Mimini; Hunt et al. 2001); a second radiation resulted in two sympatric species of the nonpasserine, hummingbird (Trochiliformes) genus *Eulampis* (E. Bermingham and R. E. Ricklefs, unpublished data).

[c] The Galápagos finches (Geospizinae) derived from a continental or West Indian emberizid colonist (Fringillidae: Emberizinae; Burns et al. 2002).

[d] The Hawaiian honeycreepers (Drepanidinae) derived from a cardueline finch (Fringillidae: Carduelinae) plus the Hawaiian thrush (Omao, belonging to the American genus *Myadestes*) represented by two species on the island of Kauai (Fleischer and McIntosh 2001; Lovette et al. 2002).

[e] The number of species described from living material, 13 of which are extinct; at least 24 additional fossil taxa have been described (James 2003).

levels are characteristic of congeneric and, in many cases, sympatric North American species of passerine birds (4.4% ± 1.9% SD, $n = 11$; Seutin et al. 1993; 5.1% ± 3.0% SD, range = 0.4%–10.9%, $n = 35$; Klicka and Zink 1997; also see Avise 1994; Tarr and Fleischer 1995; Zink 1996; Lovette et al. 2002; Weir and Schluter 2004). These levels are also consistent with the average divergence in mtDNA sequences of 3%–4% observed between species of Hawaiian honeycreepers (Tarr and Fleischer 1993, 1995; Fleischer and McIntosh 2001; Lovette et al. 2002) and the maximum divergence in mtDNA sequences between species of Darwin's finches in Galápagos (about 4%; Sato et al. 1999). Thus, although many taxa are widespread throughout the Lesser Antilles, genetic divergence among a number of conspecific populations is similar to levels exhibited by sympatric species found on islands in the Galápagos and Hawaiian archipelagoes.

Step 2: Persistence of Island Populations

The presence of highly differentiated island populations suggests that some species persist long enough for phases of secondary colonization within the archipelago to result in more than one taxon of an autochthonous clade on a single island (i.e., an evolutionary radiation). Nonetheless, gaps in the distribution of older taxa indicate that extinction may be a significant process in the Lesser Antilles (Ricklefs and Cox 1972; Ricklefs and Bermingham 1999). Gaps occur mostly in species with interisland genetic divergences exceeding 2%. Extinction of individual island populations reduces the probability that colonization will result in secondary sympatry.

Based on comparisons of the distributions of recently expanded and older endemic Lesser Antillean taxa, Ricklefs and Bermingham (1999) estimated that individual island populations disappear at an average rate of about 0.5 Ma^{-1} on the larger islands of the Lesser Antilles. No island gaps have appeared among species that have spread through the archipelago more recently than 1 Ma. Accordingly, the average life span of a population on the larger islands in the Lesser Antilles appears to be at least 2 Ma. Thus, population persistence appears not to limit the potential for secondary sympatry, at least not in the Lesser Antilles.

Step 3: Recolonization Ability and the Paucity of Secondary Sympatry in the Lesser Antilles

Secondary sympatry depends on the recolonization of islands following periods of genetic divergence. Of 13 species of old (>2% sequence divergence) Lesser Antillean lineages for which we have estimated colonization times based on molecular phylogenies (Ricklefs and Bermingham 2001), seven (54%) show secondary expansion with genetic divergences of less than 1% between at least some pairs of island populations. If one assumes that 1% sequence divergence is equivalent to 0.5 Ma (Lovette 2004), this represents an exponential rate of secondary expansion of 1.23 per taxon per Ma (i.e., $-\ln[0.54]/0.5$ Ma). If periods of secondary expansion occurred at random (i.e., exponentially) over time, this rate would correspond to an average waiting time of 1.6% mtDNA genetic differentiation between colonization phases, with 10% of waiting times exceeding 3.7% mtDNA differentiation. Thus, opportunities for secondary sympatry of genetically divergent sister populations appear to be reasonably high. Yet, only among

the endemic Mimidae have expansions resulted in sympatric sister taxa.

Secondary sympatry might be absent from the Lesser Antilles because secondary expansions (i) originate from single-island endemics, (ii) swamp sister populations on other islands through hybridization, or (iii) exclude, or succumb to exclusion by, sister taxa remaining on invaded islands.

Expansion by single-island endemics. Evidence for mechanism (i) would be obliterated by the expansion itself. However, single-island endemics are rare in the passerine fauna of the Lesser Antilles. Only three of 16 endemic Lesser Antillean passerine lineages are currently restricted to a single island: *Melanospiza richardsoni* and *Leucopeza semperi* on St. Lucia and *Catheropeza bishopi* on St. Vincent (fig. 2, case *I*). We calculated that 62%–91% of secondarily expanding populations within the core Lesser Antillean islands would encounter sister populations on at least one other of these islands (see appendix).

Hybridization and swamping. Mechanism (ii) would pertain if a colonizing population and its resident sister population on an island were behaviorally and genetically compatible. If the secondary expansion were relatively recent, that is, within the coalescence time of the resulting population, secondary colonization could be recognized in principle by the coexistence of divergent lineages from more than one island. Few mtDNA genetic distances within island populations exceed 0.005, or 0.5%. Among well-sampled, widespread Lesser Antillean passerines, only two species (the pearly eyed thrasher *Margarops fuscatus*, and the yellow warbler *Dendroica petechia*) exhibit relatively divergent haplotypes on single islands, suggestive of the mixing of previously isolated populations (fig. 2, case *VI*; see appendix for details).

If secondary sympatry occurred at a time in the past longer than the coalescence time of the population, coexisting differentiated lineages would probably have been lost by drift, leaving a single one of the lineages in the contemporary population. Because lineages are lost at random, however, evidence of secondary sympatry might appear as geographically unordered distributions of divergent lineages among islands (fig. 2, case V). The only plausible case for geographically unordered divergent lineages within a species among passerine birds of the Lesser Antilles is the trembler (*Cinclocerthia ruficauda*). In this species, a single St. Vincent individual was closely related to individuals on Dominica ($d = 0.00\%$); the intervening island population (*Cinclocerthia gutturalis* on St. Lucia) was 4.3% divergent from both of these. We believe it is possible that *C. ruficauda* was introduced to St. Vincent from Dominica during the nineteenth century (see appendix).

Exclusion of resident by colonist. Mechanism (iii), namely competitive exclusion of resident populations by a colonizing, reproductively incompatible sister lineage, would obliterate the evidence of its having occurred, as in the case of mechanism (i), leading at the extreme to the widespread distribution of a single endemic lineage (fig. 2, case III). Only the endemic Lesser Antillean bullfinch (*Loxigilla noctis*) exhibits such a distribution, which also could have

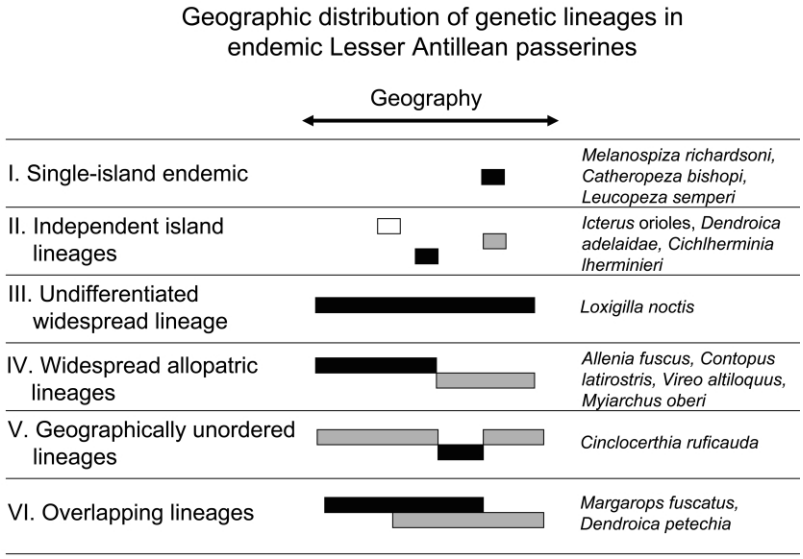

Figure 2: Schematic diagram of the distribution of divergent lineages across islands (geography) according to several scenarios. Shaded bars within each scenario represent different haplotypes. The horizontal extent of each bar represents the geographic distribution of the haplotype.

resulted if *L. noctis* had been restricted to a single island before its recent expansion.

The more common outcome of secondary expansion within the Lesser Antilles is an abrupt genetic boundary between adjacent sets of island populations, within each of which there is little genetic differentiation (fig. 2, case IV; see below). Eight species show allopatric distribution of divergent lineages with breaks between adjacent islands. These are *Saltator albicollis* (Martinique-Dominica [MA-DO], 0.6%), *Myiarchus oberi* (MA-DO, 0.9%), *Myadestes genibarbis* (MA-DO, 1.0%), *Coereba flaveola* (St. Vincent–St. Lucia [SV-SL], 1.2%), *Allenia fuscus* (MA-DO, 2.4%), *Contopus latirostris/Contopus oberi* (SL-MA, 3.5%), *Vireo altiloquus* (SV-SL, 5.2%), and *Cichlherminia lherminieri* (DO-Guadeloupe, 6.8%). In the case of *V. altiloquus* and *C. flaveola*, these breaks have been verified by restriction fragment length polymorphism analysis of 33 and 19 individuals, respectively, from St. Vincent and St. Lucia (Lovette et al. 1999*b*). Overall, the few cases of secondary sympatry among endemic Lesser Antillean birds stand in stark contrast to the ample evidence for re-expansion of ranges within the Lesser Antilles leading to adjacent differentiated island populations.

Step 4: Morphological Divergence in Allopatry and Compatibility in Secondary Sympatry

It is a well-established principle in ecology that species with similar ecological requirements do not coexist readily. However, the degree of ecological divergence required for coexistence is a matter of debate. Moreover, the threshold for coexistence might be smaller than the divergence observed between species in natural assemblages because strong competition, while not necessarily precluding coexistence, might select for further divergence subsequent to achieving secondary sympatry (Grant 1972, 1986; Arthur 1982; Schluter 1996). We approach the issue of ecological compatibility through an analysis of morphological divergence of island populations in allopatry and sympatry. Presumably, evolutionary radiation requires the accumulation of sufficient differences between populations in allopatry that, on secondary sympatry, individuals from the different populations are unlikely to reproduce but can coexist ecologically.

Morphological diversification in archipelagoes. Comparisons of morphological spaces occupied by birds in the Galápagos, Hawaiian, and Lesser Antillean archipelagoes (see appendix) show that whether the source of diversity comes from evolutionary radiations (Galápagos and especially Hawaii) or colonization (St. Lucia in the Lesser Antilles; Travis and Ricklefs 1983), birds on archipelagoes have filled a substantial portion of the morphological space occupied by continental bird assemblages (Schluter 1988; Burns et al. 2002).

Divergence among allopatric populations. The average distance of a species to its nearest neighbor in morphological space is a measure of the density of species packing and provides an indication of the minimum morphological distance consistent with coexistence. Within local assemblages of passerine birds in continental areas, NND is very close to 0.20 $\log_{10}$ units, based on eight measurements (Ricklefs and Travis 1980; Travis and Ricklefs 1983). The NND_8 within habitats on St. Lucia and St. Kitts in the Lesser Antilles averaged somewhat higher (0.26 and 0.29, respectively), reflecting the relative impoverishment of the avifauna on these islands (Travis and Ricklefs 1983). Nonetheless, the value of 0.20 provides an approximate yardstick for ecological compatibility within an assemblage of passerine birds.

We calculated the divergence between allopatric populations of the same species on different islands in the Lesser Antilles based on measurements provided by Ridgway (1901, 1902, 1904, 1907) for the lengths of the wing, tail, tarsus, middle toe, and culmen (bill). For five measurements, the corresponding yardstick for ecological compatibility is $NND_5 = 0.16$. Comparisons were restricted to adjacent islands. Thus, a species that occurs on n islands is represented by a maximum of $n - 1$ comparisons, which have been averaged. Data for males and females were compared separately. In most cases, the sexes differed little. The endemic thrashers (mimids, not including *Mimus*), which represent the only evolutionary radiation within the Lesser Antilles, were also compared separately.

The average of the species means for morphological divergences (D_5) between allopatric populations (males only) for nonmimids (0.047 ± 0.044 SD, range 0.021–0.074, $n = 17$) and mimids (0.056 ± 0.029 SD, range 0.021–0.087, $n = 4$) was less than the average NND in passerine communities ($NND_5 \approx 0.16$). Divergence between sympatric populations of the endemic Lesser Antillean mimids averaged 0.188 (±0.049 SD, range 0.133–0.242, $n = 4$).

To investigate the rate at which morphological divergence in allopatry might reach the average NND within passerine communities with time, we compared morphological distances between island populations of species in the Lesser Antilles to genetic distance. Morphological divergence (D_5) in allopatry was weakly related to genetic distance in nonmimids and more strongly related to genetic distance among the few mimid comparisons (fig. 3). In an analysis of covariance, the slopes of these relationships did not differ (interaction term; $F = 3.7$, df = 1, 17, $P = .070$). With the interaction removed, mimids and nonmimids also did not differ ($F = 1.1$, df = 1, 18,

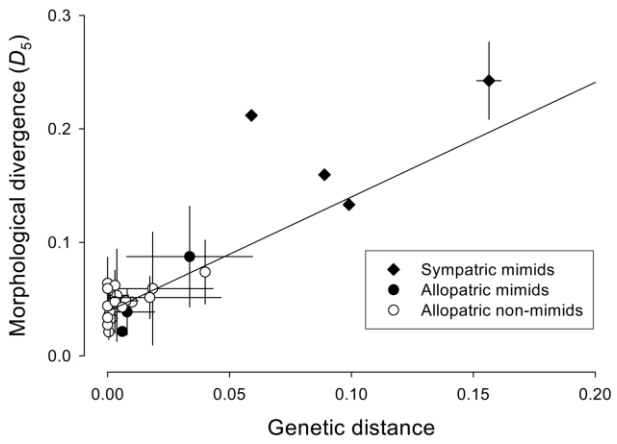

Figure 3: The relationship between morphological and mtDNA genetic divergence in Lessser Antillean passerine birds. Open circles represent divergence between adjacent island populations of the same species, excluding members of the family Mimidae, which are shown as solid circles. Solid diamonds represent divergence between different species of the endemic Lesser Antillean mimids on the same island. Morphological divergence is based on five external measurements from Ridgway (1901, 1902, 1904, 1907). Plotted values are averages within species or sympatric comparison. Error bars represent standard deviations. For allopatric non-mimids, $F = 7.4$, df $= 1, 15$, $P = .016$, $r^2 = 0.33$, slope $b = 0.77 \pm 0.28$ SE, intercept $= 0.042 \pm 0.003$ SE. For allopatric mimids, $F = 14.2$, df $= 1, 2$, $P = .064$, $r^2 = 0.88$, slope $b = 1.82 \pm 0.48$ SE, intercept $= 0.024 \pm 0.008$ SE, $t = 2.8$, $P = .11$. For the common relationship among allopatric comparisons, $F = 15.5$, df $= 1, 19$, $P = .0009$, $R^2 = 0.45$, intercept $= 0.039 \pm 0.003$ SE, slope $= 1.01 \pm 0.26$ SE. Absence of error bars for sympatric mimid comparisons indicates $n = 1$.

$P = .32$), and the common relationship indicated divergence in morphology in allopatry at an average rate of about 0.10 distance units per 10% (~5 Ma) sequence divergence. Assuming an intercept of $D = 0.04$, the average NND within passerine communities would be reached at $D = 0.12$ (~6 Ma), which exceeds the largest within-species differences between island populations in the Lesser Antilles.

We also used ANCOVA to determine whether the relationship between morphological and genetic divergence differed between allopatric and sympatric populations of mimids. Neither the interaction term ($F = 0.6$, df $= 1, 4$, $P = .47$) nor the difference between allopatry and sympatry ($F = 2.5$, df $= 1, 5$, $P = .18$) was significant. When allopatric and sympatric populations were considered together, the regression of morphological divergence and genetic distance had an intercept of 0.041 (± 0.023 SE) and a slope of 0.134 (± 0.029) distance units per 10% sequence divergence ($F = 20.8$, df $= 1, 6$, $P < .0039$, $r^2 = 0.78$). In the Galápagos Islands, the average genetic distance between allopatric "species" of the mockingbird *Nesomimus* was 5.4%, and the average morphological distance (D_5) was 0.104 (see appendix). Thus, these mockingbirds lie close to the morphological-genotypic distance relationship observed among Lesser Antillean mimids (predicted $D_5 = 0.113$).

In the Hawaiian honeycreepers, morphological divergence among allopatric populations (average $D_5 = 0.054$) and sympatric species (0.241) was similar to that in the Lesser Antillean mimids (see above and appendix). However, considering that the stem age of the honeycreeper clades is only about 6 Ma (Fleischer and McIntosh 2001; Lovette et al. 2002) and that the average genetic distance established between a small number of sympatric species is 4.2% mtDNA sequence divergence, the rate of morphological diversification, at least in sympatry, has been very rapid (e.g., 0.57 units of morphological distance per 10% sequence divergence). In the Galápagos Geospizinae, divergence among sympatric species of *Geospiza* ($D_5 = 0.113$) and *Camarhynchus* (0.078) is substantially less than the suggested yardstick for ecological compatibility (0.160), but genetic distances are also small (<1.0%), indicating a higher rate of morphological diversification than in Hawaii, although morphological differences occur primarily on size, rather than shape, axes (see appendix).

Discussion

Our analysis of island populations in the Lesser Antilles casts doubt on the importance of evolutionary divergence (step 1), population persistence (step 2), and secondary colonization within the archipelago (step 3) in limiting evolutionary radiation. Instead, it appears that island populations are able to achieve reproductive isolation in allopatry and ecological compatibility in sympatry (step 4).

The origins of reproductive isolation. Genetic divergence between some allopatric island populations of Lesser Antillean birds is consistent with differences observed between congeneric species and, in some cases, related genera in both continental faunas and in the Hawaiian and Galápagos archipelagoes. We do not know whether these levels of genetic distance represent sufficient genetic divergence to produce postmating reproductive isolation among sympatric sister taxa or are merely associated with the divergence of species recognition signals involved in premating isolation. Even the most extreme mitochondrial genetic divergence observed between allopatric island populations in the Lesser Antilles (~7%) does not preclude complete mixing of gene pools between many hybridizing species (Price and Bouvier 2002). Thus, behavioral/morphological change leading to premating isolation might be important, or even required, for reproductive incompatibility (Alatalo et al. 1994; Grant and Grant 1996, 1998; Saetre et al. 1997, 2001; Veen et al. 2001). Song plasticity,

including cultural learning, often from male parents, is prominent in songbirds (Nowicki et al. 1998; Searcy et al. 2002), including mimids (Brenowitz and Beecher 2005), and might form the basis of population differentiation sufficient for premating incompatibility (Grant and Grant 1997*a*; Price 1998; Rundle and Schluter 1998; Simoes et al. 2000).

The origins of ecological compatibility. Morphological distances between allopatric populations of Darwin's finch and honeycreeper species do not exceed those between Lesser Antillean passerines. Thus, competition between sister populations initially following secondary sympatry might not differ among these archipelagoes. However, sparse occupation of ecological space in the early stages of colonization might have allowed rapid divergence in allopatry in response to intraspecific selection pressure to adapt to local conditions (Schluter 1988) and thus permitted long-term coexistence. Ecological differences between the Lesser Antilles, Hawaii, and the New Hebrides probably are not important, as the archipelagoes have similar ranges of altitude and wet-dry gradients. The drier climate of the Galápagos Archipelago does not appear to have inhibited evolutionary diversification.

If limited ecological space were filled by colonization in the Lesser Antilles and New Hebrides and to a similar level by evolutionary diversification in the Galápagos and Hawaiian archipelagoes, this would imply that the radiations of Galápagos and Hawaiian birds slowed over time. Insufficient phylogenetic evidence is available to test this idea. It might be significant that the oldest extant lineage in the Lesser Antilles (14.3%; Hunt et al. 2001; Ricklefs and Bermingham 2001), which is comparable in age to the colonization of Hawaii by ancestors of the drepanids and the Hawaiian thrush (13%–18%; Lovette et al. 2002), was the ancestor of the present-day endemic thrashers. The subsequent filling of ecological space might also have reduced the rate of establishment of new colonists from the continent; however, estimated colonization times for passerines in the Lesser Antilles provide no indication of slowing (Ricklefs and Bermingham 2001). Unfortunately, we have no information on the relative ages of New Hebridean birds. The low level of endemism, even compared with levels in the Lesser Antilles, suggests recent derivation of the avifauna.

Although competitive exclusion owing to lack of differentiation might explain ecological incompatibility of sister populations on islands, several considerations weigh against this. First, most islands harbor relatively few species of birds compared to continental areas with similar environments. Thus, at present, habitats in the Lesser Antilles are relatively less "saturated" ecologically (Ricklefs and Cox 1978; Cox and Ricklefs 1977; Terborgh et al. 1978; Terborgh and Faaborg 1980; Travis and Ricklefs 1983) and morphologically (Travis and Ricklefs 1983) than in continental regions, possibly leaving room for increased diversity. Historical analysis of colonization times suggests that the avifauna of the Lesser Antilles is well below an archipelago-wide equilibrium number of species (Ricklefs and Bermingham 2001).

Second, as we have pointed out, contemporary divergence in allopatry appears to be no greater in the Hawaiian and Galápagos passerine faunas than in the Lesser Antillean passerine fauna. Third, new colonists seem to enter the archipelago without hindrance, judging by the fact that many recent colonists have expanded through the archipelago by means of multiple stepping-stone colonization events. Although colonists from outside the archipelago are likely to be more divergent from island residents than secondarily sympatric sister populations from elsewhere within the archipelago, recent colonists and endemic residents cannot be distinguished on the basis of the eight morphological measurements used in this study (canonical discriminant analysis: $F = 0.74$, $\mathrm{df} = 8, 25$, $P = .66$). Thus, the filling of ecomorphological space by residents does not appear to preclude colonization within the same portion of space.

The potential role of disease organisms. An additional possibility that has not been considered is incompatibility between native and colonizing sister populations caused by shared pathogens—apparent competition (Holt 1977; Holt and Lawton 1994; Bonsall and Hassell 1997; Chaneton and Bonsall 2000; Tompkins et al. 2000, 2002; Morris et al. 2004). Colonists bring with them pathogens to which they have evolved effective resistance, and these pathogens might depress potential local host populations. The extinction and near extinction of many native Hawaiian birds by introduced malaria and poxvirus provides a model for this mechanism (Van Riper et al. 1986; Jarvi et al. 2001). The apicomplexan blood parasites *Plasmodium* and *Haemoproteus* exhibit significant host species × island interactions in prevalence in the Lesser Antilles (Apanius et al. 2000; Fallon et al. 2003), indicating island-specific host-pathogen relationships that could result from coevolutionary interactions in genetically isolated island populations. If parasites evolved locally to host populations on one island, host sister populations on other islands would not be selected to acquire resistance. In this way, secondary sympatry could be prevented by dangerous pathogens either carried to or encountered in a novel island setting. This mechanism of incompatibility between secondarily sympatric sister populations might be absent from infrequently colonized archipelagoes, such as Hawaii and Galápagos. Disease organisms might be poorly represented in such remote locations owing to the small number of colonizing hosts (species and individuals), lack of suitable vectors, and stochastic loss of pathogens from host pop-

ulations on isolated islands (e.g., Van Riper et al. 1986; Font and Tate 1994; Krebs et al. 1998).

Conclusions

What do comparisons between archipelagoes tell us about evolutionary diversification? First, in many species, movement of individuals between islands is too infrequent to prevent diversification in allopatry. Even in the Lesser Antilles, where new colonists rapidly island hop through the archipelago, most of the widespread taxa and all of the older restricted taxa exhibit fixed genetic differences between some island populations. Thus, gene flow between islands is often too low to prevent differentiation, even with respect to apparently "neutral" genetic variation. Second, some individual island populations in the Lesser Antilles are as old as many secondarily sympatric species of honeycreepers in the Hawaiian archipelago or the entire radiation of Darwin's finches in the Galápagos Archipelago. Thus, the persistence of island populations long enough to establish reproductive isolation—primarily by prezygotic mechanisms—in an allopatric model of species formation should not hinder secondary sympatry, at least not in the Lesser Antilles. Third, secondary colonization of islands occurs relatively frequently, as shown by recently expanded distributions of endemic Lesser Antillean passerine birds (Ricklefs and Bermingham 1999, 2001). Thus, none of these steps in species formation through allopatric divergence followed by secondary colonization appears to limit evolutionary diversification.

Although similar data are lacking for other archipelagoes, the general absence in the Lesser Antilles of populations with mixed divergent lineages indicates contemporary as well as historical impediments to secondary sympatry. It may be significant that two of the three cases indicating coexisting divergent mtDNA lineages occurred among the endemic Lesser Antillean thrashers (*Margarops fuscatus*, *Cinclocerthia ruficauda*), which belong to the only radiation of passerine birds in the archipelago. The paucity of mixing and introgression further suggests that the problem with compatibility is not primarily ecological, because this presumably would not prevent mixing of reproductively compatible native and colonizing populations. If coexistence were made more difficult through apparent competition mediated by pathogens, then ecological compatibility might be less of a problem in remote islands, which have fewer suitable disease vectors and fewer lineages of disease organisms.

Why do some lineages diversify and others do not? Particular attributes of some lineages might promote diversification (Heard and Hauser 1995; Barraclough et al. 1998; Ricklefs and Renner 2000). Lovette et al. (2002) and Burns et al. (2002) suggested that the Hawaiian honeycreepers and Darwin's finches originated from groups exhibiting high morphological diversity in beak dimensions among continental and West Indian species, indicating a propensity for evolutionary radiation. Evolutionary radiation also might be a matter of chance (Ricklefs 2003). In either case, the small number of lineages that have diversified provides little statistical power to assess causative factors through comparative analysis. Nonetheless, many avenues for investigating evolutionary radiation remain. These include phylogenetic and ecomorphological characterization of radiations, particularly in comparison to lineages that have not diversified (Schluter 1988; Losos 1995; Losos et al. 1998; Kornfeld and Smith 2000; Burns et al. 2002; Lovette et al. 2002), studies of the abundance and host distributions of pathogens in remote and near groups of islands (Ricklefs and Fallon 2002; Fallon et al. 2003), and experimental studies of premating isolating mechanisms between allopatric populations (Grant and Grant 1997*b*; Coyne and Orr 2004). Certainly, evolutionary radiations on islands remain one of the most important systems for understanding the process of speciation.

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