

Appendix from R. E. Ricklefs and E. Bermingham, “The Causes of Evolutionary Radiations in Archipelagoes: Passerine Birds in the Lesser Antilles”

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Additional Supporting Materials

Species of Passerine Birds on the Archipelagoes

Hawaiian Islands (based on Pratt 1979; Berger 1981; James and Olson 1991): (1) *Corvus hawaiiensis* (Corvidae, one species), (2) *Myadestes* thrushes (Turdinae, five species [two sympatric]), (3) *Acrocephalus familiaris* (Acrocephalinae, one species), (4) *Chasiempis sandwichensis* (Monarchini, one species), (5) Hawaiian Oo and Kioea (Meliphagidae, five species [two sympatric]), and (6) Hawaiian honeycreepers (Drepanidini, 35 species, 22 extant, plus many fossil taxa).

Galápagos Islands (Harris 1973): (1) *Pyrocephalus rubinus* (Tyrannidae), (2) *Myiarchus magnirostris* (Tyrannidae), (3) *Progne modesta* (Hirundinidae), (4) *Nesomimus* mockingbirds (Mimidae, four allopatric species), (5) *Dendroica petechia* (Parulinae), and (6) Darwin’s finches (Thraupini, 13 species).

New Hebrides: Species numbered 33–56 in the systematic list of Diamond and Marshall (1976, app. 1), all of which represent independent colonizations: (1) *Hirundo tahitica*, (2) *Lalage maculosa*, (3) *Lalage leucopyga*, (4) *Coracina caledonica*, (5) *Turdus poliocephalus*, (6) *Cichlornis whitneyi*, (7) *Gerygone flavolateralis*, (8) *Rhipidura spilodera*, (9) *Rhipidura fuliginosa*, (10) *Myiagra caledonica*, (11) *Neolalage banksiana*, (12) *Clytorhynchus pachecephaloides*, (13) *Petroica multicolor*, (14) *Pachecephala pectoralis*, (15) *Artamus leucorhynchus*, (16) *Aplonis zelandicus*, (17) *Aplonis santvestris*, (18) *Phylidonyris notabilis*, (19) *Lichmera incana*, (20) *Myzomela cardinalis*, (21) *Zosterops flavifrons*, (22) *Zosterops lateralis*, (23) *Erythrura trichoa*, and (24) *Erythrura cyaneovirens*.

Lesser Antilles (Bond 1956, 1979; American Ornithologists’ Union 1998; Raffaele et al. 1998): (1) *Elaenia martinica*, (2) *Elaenia flavogaster*, (3) *Contopus latirostris*, (4) *Empidonax euleri*, (5) *Myiarchus nugator*, (6) *Myiarchus oberi*, (7) *Tyrannus dominicensis*, (8) *Progne dominicensis*, (9) *Troglodytes aedon*, (10) *Myadestes genibarbis*, (11) *Turdus fumigatus*, (12) *Turdus nudigenis*, (13) *Turdus plumbeus*, (14) *Cichlherminia lherminieri*, (15) *Mimus gilvus*, (16) endemic thrasher radiation (Miminae), (17) *Vireo altiloquus*, (18) *Dendroica adelaidae*, (19) *Dendroica petechia*, (20) *Dendroica plumbea*, (21) *Catheropeza bishopi*, (22) *Leucopeza semperi*, (23) *Coereba flaveola*, (24) *Tangara cucullata*, (25) *Euphonia musica*, (26) *Saltator albicollis*, (27) *Loxigilla noctis*, (28) *Melanospiza richardsoni*, (29) *Tiaris bicolor*, (30) *Volatinia jacarina*, (31) *Sporophila nigricollis*, (32) *Icterus dominicensis* species group, (33) *Quiscalus lugubris*, and (34) *Molothrus bonariensis*.

Because the species status of allopatric populations is difficult to ascertain, we define an autochthonous evolutionary radiation as the presence on a given island of more than one species derived from a single colonizing lineage to the archipelago. Thus, the three species of *Icterus* orioles in the Lesser Antilles do not qualify because each occurs on a different island even though they were apparently derived from a single invasion of an ancestral lineage of *Icterus* from the Greater Antilles (Lovette et al. 1999a; Omland et al. 1999). Although several endemic species of mockingbird (*Nesomimus*) have been described from the Galápagos Islands, none are sympatric (Harris 1973; Arbogast et al. 2006).

Faunal Similarities between Archipelagoes

One might argue that the difference between island groups in number of radiations is a fortuitous consequence of the particular taxa that colonized each. However, the passerines of the Lesser Antilles include species similar to those that underwent evolutionary radiations in Hawaii and the Galápagos. The ancestors of the Hawaiian drepanids were probably derived from a single colonization by an American cardueline finch (Fringillidae:

Carduelinae; Raikow 1977; Tarr and Fleischer 1995; Fleischer and McIntosh 2001; cf. Johnson et al. 1989). This subfamily is absent from the Lesser Antilles, but two species (*Loxia megalaga* and *Carduelis dominicensis*) occur on Hispaniola in the Greater Antilles (Raffaele et al. 1998). It has been suggested that the closest relative of the Galápagos geospizids is a clade of emberizid finches that includes *Melanospiza richardsoni* and is endemic to St. Lucia in the Lesser Antilles and *Tiaris*, one species of which is widespread in the Lesser Antilles (Baptista and Trail 1988; Sato et al. 2001; Burns et al. 2002). The Hawaiian thrushes *Myadestes obscura* and *Myadestes palmeri* are derived from a genus that is widely distributed in North and Central America (Lovette et al. 2002; Miller et al., forthcoming) and that occurs in the Lesser Antilles (*Myadestes genibarbis*).

Expansion by Single-Island Endemics

We calculated the probability that a population expanding from one island would encounter a sister population on another island for differentiated ($d > 0.02$) species of birds on the islands of St. Lucia, Martinique, Dominica, and Guadeloupe. These probabilities varied between 62% and 91% for each pair of islands considered. Thus, the potential for secondary sympatry appears to be high within the core islands of the Lesser Antilles.

Extinction of Island Populations

If prior extinction were a major factor in the absence of secondary sympatry in the more frequently colonized archipelagoes (i.e., the Lesser Antilles and New Hebrides), we would expect that old, differentiated taxa (i.e., endemics in the Lesser Antilles) would occupy a relatively smaller proportion of these islands compared with the distant archipelagoes. However, the distribution of number of islands per taxon does not differ between the Hawaiian and Galápagos archipelagoes, on one hand, and the Lesser Antilles and New Hebrides, on the other hand (table A1; Kruskal-Wallis $\chi^2 = 7.2$, $df = 3$, $P = .66$). If any difference emerges, it is that the Hawaiian archipelago has more single-island endemics, most of which are restricted to the youngest and largest island, Hawaii, a pattern that may have been reinforced by extinctions caused by pre-European humans. In any event, it appears unlikely that prior extinction or expansion by single-island endemics accounts sufficiently for the lack of secondary sympatry in the Lesser Antilles and New Hebrides.

Hybridization and Swamping

The only recently expanded species in which genetic divergence within any single island population exceeds 0.5% are the pearly eyed thrasher *Margarops fuscatus* (Hunt et al. 2001) and the yellow warbler *Dendroica petechia* (Klein and Brown 1994). In the case of *D. petechia*, Klein and Brown (1994) discovered mtDNA RFLP haplotypes differing by more than 1% (E. Bermingham and R. E. Ricklefs, unpublished data) in populations on Dominica and Guadeloupe. These haplotypes represent an older lineage derived from South America, now apparently restricted in distribution in the Lesser Antilles, and a more widespread younger lineage recently derived from the Greater Antilles. Populations of *Margarops fuscatus* in the northern Lesser Antilles contain three clades of mtDNA having average pairwise genetic distances of 0.7%, 1.0%, and 1.2% (Hunt et al. 2001). Although the clades are partly spatially segregated, they also present evidence of recent gene flow between formerly divergent island populations. Two endemic island populations of highly differentiated species, the house wren (*Troglodytes aedon*) on Dominica and the plumbeous warbler (*Dendroica plumbea*) on Guadeloupe, exhibit approximately 1% sequence divergence between a randomly selected pair of individuals. We have not pursued these cases in detail.

Coalescence Times for Mitochondrial Genes in Lesser Antillean Bird Populations

Coalescence times, measured in generations, for mitochondrial genes are on the order of the effective population size, measured in number of individuals, although confidence limits on coalescence times are large (Hudson and Turelli 2003). We use the following reasoning to provide a coarse estimate. Total population densities of passerine birds are 5–10 individuals per hectare in the Luquillo Forest, Puerto Rico (Recher 1970), and up to three times that level in the dry Guanica Forest of Puerto Rico (Kepler and Kepler 1970). Wunderle (1984) estimated densities of the bananaquit (*Coereba flaveola*) at 2–12 individuals per hectare in Grenada. An estimate of 10 passerine individuals per hectare comes to 1,000,000 individuals per 1,000 km², about the size of Guadeloupe. Assuming approximately 20 common species of passerine bird per island (Cox and Ricklefs 1977),

average population sizes on a large Lesser Antillean island are probably about 50,000 individuals. Effective population sizes would be smaller to the extent that populations have varied in size or gone through bottlenecks during unfavorable periods (e.g., drought, hurricanes, or volcanic eruptions).

The Trembler on St. Vincent

Several highly divergent populations of tremblers (*Cinclocerthia*) occupy islands of the Lesser Antilles from Saba and Barbuda in the north to St. Vincent in the south. The St. Vincent population (*C. ruficauda tenebrosa*) is genetically undifferentiated from that on Dominica (*C. ruficauda ruficauda*), although the intervening populations on Martinique and St. Lucia are genetically distant and are placed in another species (*C. gutturalis*). Measurements of individuals on the two islands provided by Ridgway (1907) do not differ, and although Ridgway notes differences in coloration, one of us (R.E.R.) could not distinguish specimens from the two islands in the collection of the Louisiana State University Museum of Natural History. We speculate that *C. ruficauda* might not have arrived on St. Vincent until the late 1800s, based on the dates of description of the named populations of tremblers in the Lesser Antilles: Dominica (1835), Guadeloupe (1843), Martinique (1843), Nevis (1855), St. Lucia (1866), St. Vincent (1880) (Ridgway 1907). The type specimen of the St. Vincent subspecies (*C. ruficauda tenebrosa*) was collected in 1878 (USNM 074060 [United States National Museum]). European colonists are well known for introducing exotic birds to islands (e.g., Duncan [1997]), and we suspect that this has also been the case with the red-legged thrush (*Turdus plumbeus*) population on Dominica, which does not differ genetically from the population on Puerto Rico, 600 km to the west (R. E. Ricklefs and E. Bermingham, unpublished data).

Morphological Diversification in Archipelagoes

We assess the degree of ecological diversification by estimating the dimensions of morphological spaces occupied by passerine birds on the Hawaiian and Galápagos islands and St. Lucia in the Lesser Antilles. These spaces are compared to that occupied by a larger sample of continental Neotropical passerines.

Six principal components analyses of passerine birds are summarized here, based primarily on unpublished measurements: Neotropics (195 species), St. Lucia (27 species; Travis and Ricklefs 1983), Hawaiian native passerines (32 species and well-differentiated island populations), Hawaiian drepanids (22 species), Galápagos native passerines (21 species and well-differentiated island populations), and Galápagos geospizids (13 species). Measurements are the \log_{10} -transformed values for total length, lengths of the wing, tail, tarsus, and middle toe, and the length, width, and depth of the beak. Square roots of the first three eigenvalues shown in figure A1 represent the standard deviations of the species' positions projected onto the first three axes of the morphological space. The first axis represents variation in size, and the second and third axes represent variation in shape but do not necessarily feature the same measurements in different samples of species.

The results indicate, first, that the small sample of continental passerine taxa that have colonized St. Lucia in the Lesser Antilles has retained most of the morphological diversity of mainland assemblages, based on measurements used in this analysis. Second, evolutionary radiations in the Galápagos and, especially, Hawaiian archipelagos have filled a substantial portion of the morphological space occupied by continental bird assemblages (Schluter 1988; Burns et al. 2002). Third, whereas bird assemblages on remote archipelagoes show less size variation than continental assemblages, they exhibit greater diversity on the second (shape) axis. At least in Hawaii, this shape axis has been generated by diversification within the archipelago (Lovette et al. 2002). In Galápagos, shapes exhibited by geospizids are more conservative, but other passerine colonists have extended this axis of variation.

Morphological Diversification in Hawaiian and Galápagos Passerines

The Hawaiian honeycreepers have proliferated and diversified morphologically (Amadon 1950; Raikow 1977; Lovette et al. 2002), to a greater extent than the Lesser Antillean endemic thrashers. If morphological (ecological) divergence in allopatry were an important component of evolutionary diversification, one might expect to find greater morphological distances between allopatric populations within species of Hawaiian honeycreepers. We used measurements of wing, tail, tarsus, and culmen provided by Amadon (1950, table 2) to calculate morphological distance between allopatric and sympatric populations. The average allopatric distance (D_4) was 0.048 (± 0.031 SD, $n = 22$), and the average sympatric distance among congeneric populations (using

Sibley and Munroe 1990 to update taxonomy) was 0.215 (± 0.084 SD, $n = 5$). Because only four measurements were used, these distances have to be multiplied by $(5/4)^{1/2} = 1.12$ to make them comparable to D_s values calculated for the Lesser Antilles from data of Ridgway (1901–1907). Accordingly, the allopatric and sympatric distances become 0.054 and 0.241, respectively, which do not differ significantly from comparable values for Lesser Antillean mimids. The average genetic distance among a small sample of honeycreeper species is 4.2% (Tarr and Fleischer 1995), which is considerably less than that among species of endemic Lesser Antillean mimids, suggesting that morphological diversification has proceeded more rapidly in the drepanid radiation.

Comparisons among Darwin’s finches (Geospizinae) within the Galápagos Archipelago presented in table A2 are all between species that are sympatric on many islands. Morphological divergence appears to increase with genetic distance. When corrected to the equivalent of five measurements ($\times [5/8]^{1/2} = 0.79$), morphological divergence is much greater in the finches for a given genetic distance than it is among the mimids of the Lesser Antilles. It would appear that secondary sympatry has driven morphological divergence much more rapidly in the Galápagos Archipelago (Burns et al. 2002) and probably in Hawaii (Schluter 1988) than it has in the Lesser Antilles. From principal component axes portrayed in figure A1, it is evident, however, that most of the divergence among Darwin’s finches has involved changes in overall size, whereas shape diversification has been relatively more prominent among the Hawaiian honeycreepers.

Comparisons among the four species of Galápagos mockingbirds (*Nesomimus*) presented in table A2 are from allopatric populations. There is no sympatry in these birds. The relative ages judged by genetic distances between the mockingbird species exceed the most basal divergences between extant Geospizinae, but morphological divergence has proceeded slowly compared with Darwin’s finches.

Table A1
Numbers of islands occupied by species of passerine bird in four archipelagoes

Archipelago	No. of islands occupied						Mean	SD
	1	2	3	4	5	6+		
Hawaiian drepanids ($n = 23$)	10	4		4		5	2.8	2.0
Galápagos geospizids ($n = 13$)	2	2		1	1	7	4.4	1.9
Lesser Antillean endemic passerines ($n = 16$)	3	2	1	5	2	3	3.6	1.8
New Hebrides passerines ($n = 24$)	2	2	6	4	4	6	4.0	1.6

Note: We tabulated the number of core islands in the Hawaiian chain (Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii) inhabited by each species of honeycreeper, including extinct populations. In the Galápagos Archipelago, we considered Darwin’s finches on the islands of Isabella, Fernandina, Santiago, Santa Cruz, Floreana, San Cristobal, Española, and Santa Fe. These were compared with the number of core islands in the Lesser Antilles (Grenada, St. Vincent, St. Lucia, Martinique, Dominica, and Guadeloupe) inhabited by each species of endemic passerine and the number out of six major islands in the New Hebrides (Espiritu Santo, Malekula, Efate, Erromanga, Tanna, and Aneityum; Medway and Marshall 1975, app. B) inhabited by each species of passerine.

Table A2
Morphological divergence and genetic distance in comparisons among species of Darwin’s finches and mockingbirds (*Nesomimus*) in the Galápagos Archipelago

Comparison	Sample	Genetic distance (%)	Morphological distance			
			D_s	SD	$0.79 \times D_s$	SD
Within <i>Geospiza</i>	5	<.7	.143	.030	.113	.024
Within <i>Chamarhynchus</i>	4	<1.0	.099	.049	.078	.039
<i>Platyspiza-Certhidia</i>	1	3.9	.393310	...
<i>Camarhynchus-Platyspiza</i>	1	2.6	.330261	...
Within <i>Nesomimus</i>	6	5.4	.131	.068	.104	.054

Note: Morphological distance based on unpublished measurements of R. E. Ricklefs. Genetic distances for Darwin’s finches are from Sato et al. (1999); genetic distances for Galápagos mockingbirds (*Nesomimus trifasciatus*, *Nesomimus parvulus*, *Nesomimus macdonaldi*, *Nesomimus melanotis*) are from figure 2 (ND2 ML distances based on the GTR + Γ model of nucleotide substitution) of Arbogast et al. (2006).

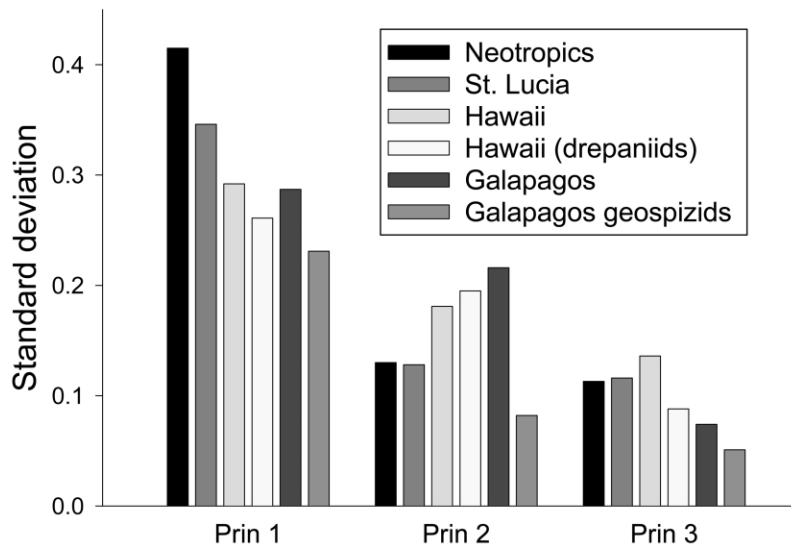


Figure A1: Relative sizes of the first through third axes of morphological variation in three island settings and among continental tropical passerines.

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