History and the Species-Area Relationship in Lesser Antillean Birds

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abstract: We examined the species-area relationship for three historically distinct subsets of Lesser Antillean birds identified by molecular phylogenetic analysis of island and continental populations. The groups comprised recent colonists from continental or Greater Antillean source populations, old taxa having recently expanded distributions within the Lesser Antilles, and old endemic taxa lacking evidence of recent dispersal between islands. The number of young taxa was primarily related to distance from the source of colonists in South America. In a multiple regression, the logarithmic slope of the species-area relationship for this group was shallow (0.066 ± 0.016). Old endemic taxa were restricted to islands with high elevation, and within this subset, species richness was related primarily to island area, with a steep slope (0.719 ± 0.110). The number of recently spread endemic taxa was related primarily to island elevation, apparently reflecting the persistence of such populations on islands with large areas of forested and montane habitats. Historical analysis of the Lesser Antillean avifauna supports the dynamic concept of island biogeography of MacArthur and Wilson, rather than the more static view of David Lack, in that colonists exhibit dispersal limitation and extinction plays a role in shaping patterns of diversity. However, the avifauna of the Lesser Antilles is probably not in equilibrium at present, and the overall species-area relationship might reflect changing proportions of historically distinguishable subsets of species.

Keywords: colonization, equilibrium theory, extinction, island biogeography, Lesser Antilles, species-area relationship.

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MacArthur and Wilson's equilibrium theory of island biogeography explains the diversity of species on islands in terms of the balance between colonization and extinction (MacArthur and Wilson 1963, 1967; Schoener 1976; Durrett and Levin 1996). The theory states that diversity tends toward a steady state at which extinction equals colonization. This equilibrium number of species is less than the size of the mainland pool of potential colonists. At equilibrium, species continue to disappear from the islands, but new colonists from the mainland replace these, maintaining an approximately constant number of species. According to MacArthur and Wilson's theory, the number of species at equilibrium reflects the influence of such factors as island size and distance from sources of colonists on rates of extinction and immigration. In particular, because populations on small islands are believed to be more prone to extinction than those on large islands, the lower rate of extinction on larger islands was thought to underlie the familiar relationship between species and area observed among islands (Schoener 1976; Connor and McCoy 1979). Although MacArthur and Wilson (1967, pp. 19–20) recognized the contribution of habitat diversity to species diversity on islands, this relationship did not play a role in the development of their equilibrium model of the control of species diversity.

In contrast, David Lack (1976) argued that diversity on islands is limited by ecological opportunity, particularly habitat diversity, and that small islands are ecologically depauperate compared to large islands. Based on the frequent appearance of resident land birds outside their normal ranges in the West Indies, Lack also thought that diversity in that archipelago was not limited by colonization. Furthermore, established populations persisted on islands for long periods. Thus island biotas did not exhibit turnover of species in a steady state but rather became saturated with species according to the ecological opportunities that islands offered for the establishment of populations. In Lack's words (1976, p. 5), "On this latter theory [MacArthur and Wilson's] the critical factor is the rarity of dispersal, whereas I prefer to think it is ecological poverty, that chance is virtually excluded, and that com-

petition determines both the species which colonize and the species which fail, and also the total number of resident species."

The difference between the viewpoint of MacArthur and Wilson and that of Lack centers on the presence or absence of recurring extinction on islands and on the mechanism by which island area influences the number of species. MacArthur and Wilson's theory is neutral on the ecological diversity of islands compared to mainland source areas for colonists but more closely associates the species-area relationship with population processes as they are affected by area, hence the size and geographical extent of a population. As diversity on a particular island increased, "the more likely any given [species] will become extinct due to the smaller average population size acting through both ecological and genetical accident" (MacArthur and Wilson 1967, p. 22). MacArthur and Wilson seemed content to extend their argument concerning population size within a particular island as a function of species richness to differences in population size between islands as a function of island area.

Lack attributed the species-area relationship to changes in the ecological characteristics of the islands themselves as a function of island area. In both cases, over time the diversity of a newly formed island should exponentially approach either a steady state (MacArthur-Wilson) or an ecologically determined carrying capacity for species (Lack). The two views can be distinguished at equilibrium or saturation by the presence or absence of extinction (assuming no directional environmental change causing extinction through habitat shifts). Lack's view also predicts that species diversity is directly related to ecological diversity, which might be assessed by the variety of habitats on an island or a related variable such as elevation (Hamilton et al. 1964).

The number of extant land birds on 19 islands in the Lesser Antilles varies between 17 and 42 species (Ricklefs and Lovette 1999). Rapid postglacial climate change (Bonatti and Gartner 1973; Curtis et al. 2001) and human activities have caused the extinction of several island populations in the West Indies (Pregill et al. 1994), and present-day patterns might not reflect entirely "natural" conditions. However, most cases of extinction of birds from islands in the Lesser Antilles were of aquatic species, raptors, and parrots, and the fauna of small land birds remains largely intact. Forty-three island populations of doves, hummingbirds, and songbirds have been reported from fossil deposits on St. Eustatius, Antigua, Barbuda, and Montserrat, which are all small islands in the northern Lesser Antilles (Pregill et al. 1994). Of these, only six are missing from the contemporary avifaunas of those islands (Raffaele et al. 1998). Similar fossil deposits have not been found on larger core islands of the Lesser Antilles, from which extinctions are, in any event, less likely.

The arrival of Europeans in the islands brought about extensive clearing of native habitat for agriculture, especially at low elevations, and the introduction of potential predators of birds, including the mongoose (Horst et al. 2001). Habitat clearing may have had relatively little effect on native bird populations because few species appear to be restricted to lowland mesic forests, which were most frequently affected. Most of the narrow habitat endemics on the islands are restricted to high elevations or to other habitats such as dry scrub that are not suitable for agriculture. A few island populations in the Lesser Antilles have gone extinct since modern scientific collecting began in the late 1800s: the burrowing owl (*Athene cunicularia*) on St. Kitts, Nevis, Antigua, and Marie Galante; the Puerto Rican bullfinch (*Loxigilla portoricensis*) on St. Kitts; and the house wren (*Troglodytes aedon*) on Martinique. Several others are critically endangered and possibly extinct, including Semper's warbler (*Leucopeza semperi*) on St. Lucia, the house wren on Guadeloupe, and Euler's flycatcher (*Empidonax euleri*) on Grenada (Raffaele et al. 1998). These losses are few compared to the total of 455 island populations included in this analysis. Thus, the native avifauna of the Lesser Antilles appears to be largely intact, and analyses of species diversity probably are not biased by anthropogenic extinction.

The slope of the regression between the common logarithms of species diversity and island area for the Lesser Antilles is 0.207 ± 0.046 ($n = 19$, $r^2 = 0.74$) (Ricklefs and Lovette 1999) This value is within the range of species-area relationships for island groups more generally (Schoener 1976; Connor and McCoy 1979). When a measure of habitat diversity, based on the proportion of island area in each of five habitat types, was included in the analysis, island area remained a significant effect (slope $= 0.126 \pm 0.052$), but habitat diversity also exerted a significant influence on species diversity, and most of the variation in species diversity was related to the correlated effects of island area and habitat diversity (Ricklefs and Lovette 1999). These results provide support for both the MacArthur-Wilson (area) and Lack (habitat diversity) viewpoints. Distance from South America and distance to the nearest island (Lack 1976, app. 10) also contribute significantly to variation in bird species richness in the Lesser Antilles (Ricklefs 1977). Thus contrary to Lack's hypothesis, distance to a major source of colonists appeared to influence the species richness of individual islands, provided that ecological diversity also did not decrease with distance from South America.

According to MacArthur and Wilson's hypothesis, the higher rate of extinction of populations on smaller islands would cause the slope of the species-area relationship

within an archipelago to increase in progressively older cohorts of colonists. Consistent with this prediction, Ricklefs and Cox (1972) showed that among birds of the West Indies, the slope of the species-area relationship was higher among endemic, highly differentiated (presumably old) species than it was for recent colonists. Ricklefs and Cox inferred relative age of island populations from geographic distribution and taxonomic differentiation; however, molecular phylogenetic studies have supported their conclusions (Ricklefs and Bermingham 1999). Thus, the species-area relationship exhibited by a regional biota depends on the distribution of colonization times of its members. Under constant conditions, colonization times assume an exponential distribution and the species-area relationship settles to an equilibrium value. When rates of extinction and colonization change over time, the slope of the species-area relationship reflects the colonization age structure of biota and therefore will reflect its history.

The colonization times of 39 lineages of birds within the Lesser Antilles, including most of the small land birds of shrub and forest habitats, suggest that colonization, extinction, or both may have varied dramatically over the history of the avifauna (Ricklefs and Bermingham 2001). The relative age of colonization of each of the lineages was estimated from the divergence of mitochondrial DNA (mtDNA) sequences between Lesser Antillean populations and their closest sister population in northern South America or the Greater Antilles. Heterogeneity also can be introduced to such data under constant conditions by a "speciation threshold" of genetic distance, below which divergence between mainland and island populations is retarded by migration (Cherry et al. 2002). Distinguishing among these causes will require additional data and analyses (see also Ricklefs and Bermingham 2002). Regardless of how this is resolved, however, the linear accumulation of species observed with respect to colonization age beyond a postulated speciation threshold further suggests that diversity within the archipelago as a whole is currently below steady state levels.

A number of species, particularly among the older taxa in the archipelago, exhibit secondary expansion through the island chain (Ricklefs and Bermingham 1999). The evidence for this consists of genetically undifferentiated or poorly differentiated (compared to the original colonization event) populations of an endemic species on many islands within the archipelago; some taxa show evidence of multiple secondary expansions. These examples confirm the conjecture of Ricklefs and Cox (1972) that geographically restricted populations can initiate new phases of colonization within the West Indies and begin a new "taxon cycle."

The heterogeneity of island biogeographic processes in the Lesser Antilles suggests that colonization-extinction equilibrium may not provide an adequate explanation for patterns of island diversity, even though the species-area relationship there appears to be typical of island archipelagoes elsewhere. The varied histories of birds within the Lesser Antilles suggests that different groups of species may have been influenced by different factors depending on when they colonized the archipelago and on their subsequent history of extinction and reexpansion within the island chain. Therefore, we have reanalyzed the relationship of species richness on islands with respect to area, elevation (as a measure of habitat diversity), and degree of isolation for each of three groups of species having different histories within the archipelago. By doing so, we hope to determine the status of the MacArthur-Wilson and Lack models for explaining patterns of species diversity on islands and for elucidating the ecological factors shaping species distributions.

Material and Methods

For each island, the area, maximum elevation, distance to northern South America, and distance to the nearest island were obtained from Lack (1976, app. 10). Maximum elevation was strongly correlated ($r^2 = 0.85$) with the diversity of habitat types obtained for many of these islands from vegetation maps in Stehle (1945; see Ricklefs and Lovette 1999). The weaker correlation between elevation and the logarithm of area ($r^2 = 0.40$, $n = 18$) allows us to assess the independent effects of area and habitat diversity on species richness. The number of species of land birds on each island was obtained from Raffaele et al. (1998).

Number of species and island area were $\log_{10}$ transformed for analysis. We did not include Barbados in the analysis because the island is young (Mesollela 1967; Bender et al. 1979) and lies well outside the main chain of Lesser Antillean islands. Most of the species constituting the depauperate avifauna of the island are recent colonists (Lovette et al. 1999). To simplify the species-area analysis, distance to Puerto Rico—the apparent northern source of colonists—was not considered. Distance from Puerto Rico is strongly negatively related to distance from South America. Moreover, bird species with Greater Antillean origins are relatively evenly distributed among the islands of the Lesser Antilles. In contrast, recent colonists from northern South America decrease in number steadily from south to north (Ricklefs and Cox 1972; Terborgh 1973).

We divided the birds of the Lesser Antilles into three groups of species: (i) old endemic residents with highly differentiated island populations, (ii) old endemic residents that have expanded within the island chain subsequent to their initial colonization, in most cases recently, and (iii) recent colonists. The dividing line between old

and recent was an mtDNA sequence divergence (d) of 0.02 between island populations and continental sister populations or species, based on 842 base pairs of the mitochondrial ATP synthase 6 and 8 genes (Lovette et al. 1998; Ricklefs and Bermingham 2001). Few species with $d <$ 0.02 show geographic genetic structure within the Lesser Antilles, and using a cutoff value of 0.02 reduces ambiguity in assigning species to the "old" category (i). Only five species exhibited sequence divergences between 0.011 and 0.02 (*Columbina passerina*, *Vireo altiloquus*, *Quiscalus lugubris*, *Coereba flaveola*, and *Turdus fumigatus*); these are undifferentiated in the Lesser Antilles (except for *C. flaveola* on Grenada and St. Vincent) and none are endemic species, so they fit naturally into group iii. Furthermore, no colonization events fall between $0.020 < d < 0.034$.

We have analyzed sequence divergence for 11 old, unexpanded species (group i). Three of these, *Cyanophaia bicolor*, *Dendroica plumbea*, and *Tangara cucullata*, have closely related populations on two adjacent islands but were not counted as reexpanded taxa because of their restricted distributions. An additional 14 species for which we do not have sequence data were considered as old species based on the presence of gaps in their distributions, taxonomic distinction among island populations, or status as single-island endemics. Among taxa in the Lesser Antilles for which we have molecular evidence, gaps within the core of islands of Grenada to Guadeloupe occur only in old, endemic taxa.

Based on negligible sequence divergence between island populations, 10 species endemic to the Lesser Antilles were considered as old taxa with recent expansion through the archipelago. Two additional species not studied genetically, *Euphonia musica* and *Chaetura martinica*, were also placed in this category because they are endemic Lesser Antillean taxa (subspecies and species, respectively) with little phenotypic differentiation among island populations. Fifteen species were classified as recent colonists based on sequence divergence, and 13 additional species were placed in this category based on lack of taxonomic distinction both from mainland populations and among populations within the Lesser Antilles. Altogether, the Lesser Antillean land bird fauna includes 25 old taxa, 12 recently expanded old taxa, and 28 recent taxa for a total of 65 species (see app. A in the online edition of the *American Naturalist*).

Habitat distributions of most of the species in the Lesser Antilles were obtained previously from point counts in each of seven habitats ranging from (1) open grassland to (2) savanna, (3) scrub, (4) young secondary forest, (5) subclimax forest, (6) mature forest, and (7) cloud forest. The relative abundance of a species within any given habitat is the number of point-count stations (1–10) at which it was recorded. These data come from field studies in matched habitats on St. Kitts and St. Lucia (Cox and Ricklefs 1977), Grenada (Wunderle 1985), and Dominica (I. J. Lovette, unpublished data). The ordering of habitats from 1 through 7 paralleled a reciprocal averaging (Hill 1973) ordination of the habitats based on incidence matrices of birds (results not shown), indicating that birds discern differences between habitats based on criteria consistent with the vegetation structure variables that we used to classify habitat types. The four islands have 128 populations of birds, of which we observed all but 11 in our point counts. We quantified relative abundance within each habitat as the number out of 10 point-count stations at which at least one individual of a given species was recorded. For details, see Cox and Ricklefs (1977).

All statistical analyses were performed with the Statistical Analysis System version 8 (SAS Institute, Cary, N.C.). We used multiple regression (Proc GLM) and stepwise regression (Proc STEPWISE, MAXR, and FORWARD options) procedures in our analyses.

Results and Discussion

The habitat distribution of each of the three groups is shown in figure 1. Two aspects stand out. First, older taxa are currently distributed primarily in forested habitats, including montane forest, whereas more recent colonists occur predominately in lowland and more open habitats, including grassland and shrub land (ANOVA based on average habitat score per species [1–7], 3.3 vs. 5.0, $P <$ .0001). Furthermore, recently spread old taxa occur in more open habitats than endemic old taxa, but the significance of this difference is marginal (4.6 vs. 5.4, $P =$ .026). Second, old taxa that have spread recently through the Lesser Antilles are more abundant than old endemic taxa (ANOVA based on average abundance of each species over the habitats within which it was recorded: 3.7 out of a maximum of 10 vs. 1.5, $P <$ .0001). The average abundance of new colonists was intermediate (2.6, $P =$ .017 and .022); however, their different habitat distribution makes the comparison difficult to interpret. Nonetheless, the three groups of species that we distinguish in this analysis on the basis of genetic divergence and geographic distribution clearly differ ecologically in their habitat distribution and relative abundance.

The number of species in each of the three groups is shown by island in figure 2. The number of young species declines from south to north as distance increases from the coast of South America. Old endemic taxa are largely restricted to the core group of six high volcanic islands (Grenada to Guadeloupe, excluding the low-lying Marie Galante and Carriacou) and drop off rapidly to the north, especially on the low islands. Recently spread old taxa are more widely distributed.

The simple logarithmic regression of number of species

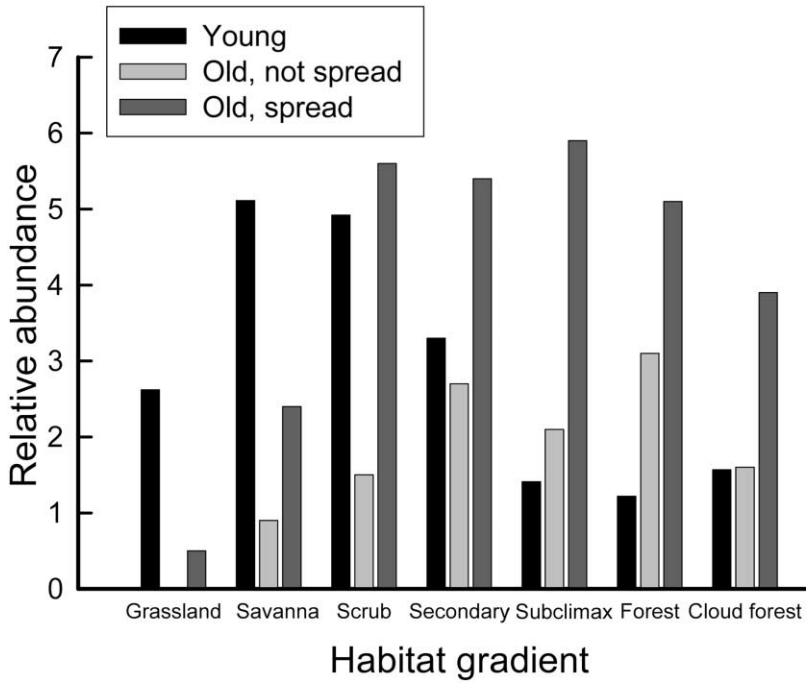

Figure 1: Average relative abundance per species of young, old, and reexpanded old taxa in habitats in which a species was recorded at one or more point-count stations out of 10. We calculated the average abundance of the species in each distribution group that we recorded in each habitat; zeros (species not seen) were not included in these averages.

on island area had a slope (z) of 0.175 ± 0.033 SE (n = 18, P = .001, r^2 = 0.64). When elevation, distance to mainland, and distance to nearest island were also included in a stepwise regression, the slope of the species-area relationship decreased to 0.098 ± 0.028 and both elevation and distance to mainland were significant effects in the model (table 1).

Ecological and Phylogenetic Effects

Before discussing results from analyses based on the ages and distributions of taxa within the Lesser Antilles, we address the possibility that heterogeneous sampling with respect to ecological traits or taxonomic groups might confound these results. The primary concern would be that each of the distribution groups had a different mix of avian lineages or ecological types and that age distribution could not be analyzed independently of the effects of intrinsic organismal attributes or ecology on interisland movement and extinction probabilities of individual island populations. We used Faaborg's (1985) classification of species according to feeding guild (fruit, fly-catching insects, gleaning insects, nectarivorous, and miscellaneous) and primary habitat (dry forest, rain forest, widespread, and miscellaneous).

A contingency table of species classified with respect to feeding guild and distribution group did not reveal significant heterogeneity (G = 5.69, df = 8, P = .68). Thus species in different feeding guilds are equally likely to fall into each of the distribution groups, indicating that each ecological type passes through a similar history of distribution stages. A contingency table of species classified with respect to habitat and distribution group revealed significant heterogeneity (G = 24.1, df = 6, P = .0005), which is consistent with the distribution of species across habitats recorded by Cox, Wunderle, and Lovette (see figure 1).

The potential effects of phylogeny are more difficult to test. Feeding guild tends to be conservative within avian families, and so we would expect similar homogeneous distributions among distribution groups. However, different dispersal propensities of birds in different families, particularly the characteristic long-distance movements of doves (Columbidae), might also influence distribution. Most avian families are represented by few species in the Lesser Antilles (maximum eight in the Columbidae), and many of the cells in a contingency table of family and distribution group have zeros (six out of 30 among 10 families with four or more species). We circumvented this problem by adding 0.5 to each cell. The resulting contingency test (G = 20.2, df = 18, P = .32) was not signif-

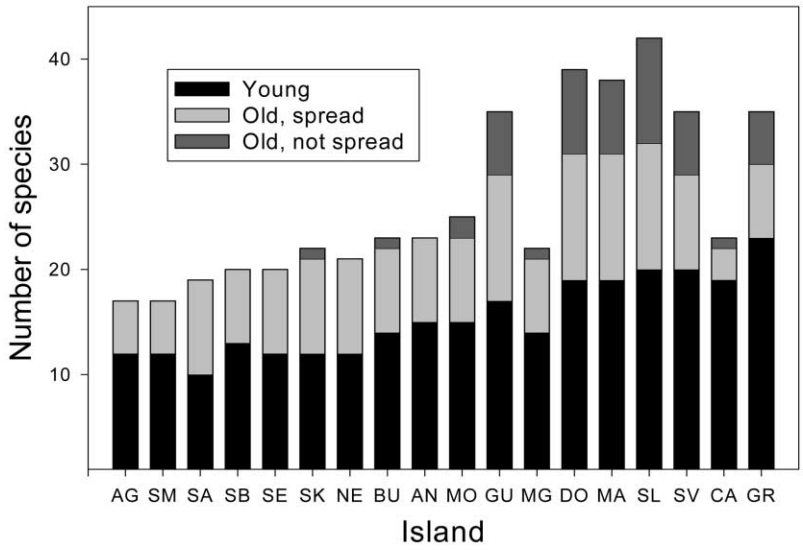

Figure 2: The number of species of young, old, and reexpanded old taxa of birds in the Lesser Antilles, arranged approximately from north (*left*) to south (*right*). The islands are Anguilla (*AG*), St. Martin (*SM*), Saba (*SA*), St. Bartholomew (*SB*), St. Eustatius (*SE*), St. Kitts (*SK*), Nevis (*NE*), Barbuda (*BU*), Antigua (*AN*), Montserrat (*MO*), Guadeloupe (*GU*), Marie Galante (*MG*), Dominica (*DO*), Martinique (*MA*), St. Lucia (*SL*), St. Vincent (*SV*), Carriacou (*CA*), and Grenada (*GR*).

icant. When we added only 0.1 to each cell, there was still no significant heterogeneity ($G = 25.4$, df $= 18$, $P = .11$).

Regardless of this overall result, some families appear to have skewed frequencies among the distribution groups. This is particularly noticeable for the Psittacidae, of which all four species are "old" and the Columbidae, of which seven out of eight are "young." This is consistent with the parrots currently being restricted to rain forest and most of the doves occurring in the dry lowland habitats. To determine whether these distributions might be statistically unlikely, we simulated random distributions of the species within each family across the three distribution groups with the probability of membership in a particular group equal to the frequency of all the Lesser Antillean birds in that group. The simulations were run with 1,000 trials, and we recorded the proportion of times that the number of species in the most frequent distribution group was as common as observed. For parrots, only 15 of 1,000 ($P = .015$) runs placed all four species in the old category, and for doves, only 14 of 1,000 ($P = .014$) runs placed seven or eight species in the young category. For the other eight families with four or more species in the Lesser Antilles, the probability values were .038, .038, .086, .101, .308, .312, .366, and .382.

Parrots and doves appear to have different histories in the islands, the younger ages of the doves reflecting either continuing migration through the islands (hence apparent young age) or recent colonization associated with drier habitats typical of recent glacial periods. Clearly, there is a phylogenetic effect in the assignment of species to different distribution groups, and it is possible that doves may not progress through these stages (as suggested by Ricklefs and Cox 1972). However, the rest of the avian families are more randomly spread among the distribution groups, and there is no significant heterogeneity in the contingency table overall.

Distribution Groups and Taxon Cycle Stages

Following E. O. Wilson (1961), Ricklefs and Cox (1972) proposed a temporal sequence of distribution from (1) colonizing to (2) differentiating, (3) fragmenting, and (4) endemic; taxa could return to stage 1 at any time. Unlike the taxon cycle stages of Ricklefs and Cox, the distribution groups in the present analysis have no reference to subspecific differentiation, nor do we use information on interisland divergence except to identify recently spread Antillean endemics. Thus, both young species and old spread species belong to stages 1 and 2 of the taxon cycle while old species belong to stages 3 and 4. These designations are consistent with habitat distributions within the islands, as seen in figure 1 and also in Ricklefs and Bermingham (1999). Here we distinguish young and old spread species owing to the continental and endemic sources of their expansion through the Lesser Antilles, which should affect their geographic distributions to some extent. In addition, there is a demonstrable difference,

Table 1: Stepwise multiple regressions of the logarithm of land bird species richness on several attributes of islands in the Lesser Antilles

Group	No. islands	No. species	Intercept	Area ($\log_{10}$ km^2)	Elevation (1,000 m)	Distance to mainland (100 km)	R^2
All	18	17–42	1.281 ± .073	.098 ± .028	.085 ± .037	−.027 ± .006	.875
Young	18	10–23	1.242 ± .050	.066 ± .016	NS	−.035 ± .004	.901
Old spread	18	5–12	.686 ± .052	NS	.268 ± .058	NS	.569
Old endemic	11	0–10	−.872 ± .298	.719 ± .110	NS	−.085 ± .025	.868

Note: Distance to nearest island was not significant in any of the analyses.

according to Faaborg's classification, in the habitat distributions of the young and spread groups ($G = 10.44$, df = 3, $P = .015$). This reflects a preponderance of wide habitat occupancy, including forests, among old spread species (six of 12) and a preponderance of dry (12 of 28) and miscellaneous (e.g., aerial or agricultural: nine of 28) habitats among the young species.

Grouping of species by taxonomic families and feeding guilds does not show strong biases with respect to the distribution groups used in this study. Heterogeneity with respect to primary habitat is consistent with the findings of this analysis and suggests a shift from dry, open lowland habitats to moist forest and montane habitats with increasing tenure in the Lesser Antilles (Wilson 1961; Greenslade 1968, 1969; Ricklefs and Cox 1972).

Young Species

The number of young species on an island is sensitive to the area of the island and its distance from the South American mainland source of colonists (table 1; Ricklefs and Cox 1972; Terborgh 1973). Mature forest and montane habitats evidently are not important because elevation is not a significant effect in this model. The effect of island area is relatively small ($z = 0.066$, a factor of 1.164 per 10-fold increase in area). It may be a fortuitous consequence of the mixture of northern and southern colonists and the fact that most of the small islands in the Lesser Antilles are in the north. However, the small island of Carriacou (19 young species, 34 km^2), which has about one-tenth the area of adjacent Grenada (23 young species, 320 km^2) and St. Vincent (20 species, 350 km^2) and had a land connection to Grenada during Pleistocene low sea levels, has close to the species richness predicted by the shallow species-area relationship ($0.5 \times [23 + 20] \times 10^{-0.066} = 18.5$). Thus, it appears that some young species may have failed to colonize some small islands within their contemporary distributions or disappeared from them subsequent to establishing populations.

The analysis of young species supports a MacArthur-Wilson concept of dispersal limitation in that their number decreases with distance from the mainland source of colonists in South America. The relative lack of dependence of the number of young species on island area suggests that all islands are colonized regardless of size and that too little time has passed for extinction of island populations or that continuing migration between islands has rescued declining populations from extinction (Brown and Kodric-Brown 1977). Thus the present distributions of young species probably represent the extent of their spread through the Lesser Antilles. Elevation is unimportant because most of the recent colonists to the Lesser Antilles are birds of open habitats characteristic of low elevations.

The distance effect is complex because colonists have entered the islands from both the north and the south and because their colonization of the Lesser Antilles takes place in stepping-stone fashion, one island at a time. Stepping-stone colonization is evident from the absence of gaps in the distributions of young colonists in the archipelago and also from the documented rapid expansion of the bare-eyed thrush (*Turdus nudigenis*) and glossy cowbird (*Molothrus bonariensis*) through the island chain (Bond 1956; Levesque 1997).

The distance effect in a stepping-stone model reflects the number of islands colonized and suggests that particular island populations become incapable of sustaining further colonization. If this happened more or less at random, owing to the particular circumstances for a newly established species on any particular island, then the number of young populations would fall off exponentially with the number of islands colonized. This effect can be seen in the decrease of young colonists originating from South America as one moves north through the Lesser Antilles, from 14 species on Grenada to two species on islands from St. Kitts northward (table 2).

In addition to distance from South America, we also tabulated the number of colonization steps to each island (see table 2), ranging from one (Grenada) to 10 (Saba). Steps from the north are more or less the same and in descending order. Steps and distance are highly correlated ($r = 0.967$). A stepwise regression of the logarithm of the number of young species that originated in the south revealed that number of steps was the first (and only) variable of significance, with a semilogarithmic regression

Table 2: Number of species of young colonists originating from the Greater Antilles and South America on islands in the Lesser Antilles

Location	VE	TR	TO	GR	SV	SL	MA	DO	GU	MO	AN	BU	SK	SE	SA	SB	SM	AG	VI	PR
North	3	4	4	9	10	12	12	13	11	11	10	10	10	9	8	11	10	10	11	12
South	14	14	13	14	10	8	7	6	6	5	6	5	4	2	2	2	2	2	2	4
Steps				1	2	3	4	5	6	7	7	7	8	9	10	9	9	9		

Note: Distributions from Raffaele et al. (1998). Steps are the number of colonization events going north from South America. Antigua (AN) and Barbuda (BU) were joined during Pleistocene sea level lows. St. Batholomew (SB), St. Martin (SM), and Anguilla (AG) also share a shallow bank, and the northern dispersal route is assumed to be from St. Kitts (SK). Puerto Rico (PR), Virgin Islands (VI), north; 14 species. Venezuela (VE), Trinidad (TR), Tobago (TO), south; 14 species. GR = Grenada, SV = St. Vincent, SL = St. Lucia, MA = Martinique, DO = Dominica, GU = Guadeloupe, SE = St. Eustatius, SA = Saba.

slope of -0.098 ± 0.006 ($F = 234$, df $= 1, 13$, $P < .0001$, $R^2 = 0.947$). Adding a quadratic term to the regression did not improve the fit significantly ($F = 4.2$, df $= 1, 12$, $P = .063$). Thus, the number of young colonists from the south falls off at a rate of about 20% per island. There are no gaps in the distributions of southern colonists.

The number of young colonists from the north was not related to distance and was only weakly related to the area of the island ($b = 0.071 \pm 0.022$, $F = 10.2$, df $= 1, 13$, $P = .029$, $R^2 = 0.42$). Therefore, as seen in table 2, northern colonists are not dispersal limited but are slightly sensitive to island area, with a few species being absent from the smaller northern islands in the chain. This could result from extinction of intermediate island populations or from colonists bypassing islands. Gaps in the distributions of northern colonists include *Columba leucocephala* (St. Kitts, St. Eustatius, Saba), *Geotrygon mystacea* (St. Martin, Anguilla), *Coccyzus minor* (Antigua, Barbuda, St. Eustatius, Saba), and *Dendroica petechia* (Saba). *Cypseloides niger*, which is found from Grenada through Montserrat but not in the northern islands, migrates to South America during the nonbreeding season. *Turdus plumbeus*, which is found only on Dominica in the Lesser Antilles, is enigmatic. Its population on Dominica possibly is the result of a human introduction. *Myadestes genibarbis*, occurring in forest habitats from St. Vincent to Dominica but not further north, is unexplainable.

The lack of a distance effect among northern colonists might result from the dispersal barrier posed by the Anegada Strait between the Virgin Islands (Greater Antilles) and the small islands of Anguilla and Saba in the northern Lesser Antilles, which may be sufficient that only good colonists can invade. Accordingly, distances between islands in the Lesser Antilles would be weaker barriers to dispersal than the barrier that colonists of the archipelago from the north first crossed. Alternatively, island life in the Greater Antilles may predispose populations for success in the Lesser Antilles. The possibility that northern species arrived first in the islands and their presence slowed the colonization of later arriving southern species can be rejected by comparing the inferred colonization times of the two groups. Genetic distances do not differ significantly between the two groups either by parametric analysis of variance or nonparametric tests (Kruskal-Wallis $\chi^2 = 1.16$, df $= 1$, $P = .28$). Nor do the proportions of young ($d < 0.02$) and old colonists differ between birds of northern and southern origin ($G = 1.24$, df $= 1$, $P = .27$). We also determined that the feeding guilds and habitats (Faaborg 1985) of northern colonists ($n = 14$) and southern colonists ($n = 14$) do not differ significantly (guilds: $G = 0.83$, df $= 4$, $P = .94$; habitats, 0.5 added per cell: $G = 4.96$, df $= 3$, $P = .17$).

Widespread Endemics

The number of recently expanded old colonists on an island is statistically related only to the maximum elevation of the island, which implies that forested and montane habitats are important for the colonization of some older elements of the avifauna. However, some of the species also extend to more open habitats and many have colonized low-lying islands in the Lesser Antilles. The slope of the regression in table 1 (0.268 per 1,000 m of elevation) indicates that the number of recently expanded old colonists increases by a factor of 1.85 for each 1,000-m increase in elevation, which encompasses most of the variation in elevation within the Lesser Antilles.

All 12 widespread endemics occur on the four large core islands of the central Lesser Antilles, from Guadeloupe in the north to St. Lucia in the south. Numbers decrease both to the south and to the north, suggesting some dispersal limitation but also explaining why distance from South America was not a significant effect. The pattern of island occupancy to the north also indicates possible cases of extinction of populations judging from gaps in distribution. For example, the Lesser Antillean flycatcher (*Myiarchus oberi*) does not occur on Montserrat and Antigua but is present on the more distant islands of Barbuda and St. Kitts. Moreover, Barbuda and Antigua formed a single island during Pleistocene sea-level lows, and therefore the two islands would almost certainly have shared all of their

avifaunas as recently as 12,000 yr ago. The brown trembler (*Cinclocerthia ruficauda*) does not occur on Antigua and Barbuda but is present on St. Kitts, St. Eustatius, and Saba. This might be due to the higher elevations and presence of moist forest on the latter islands, but the Antillean euphonia (*Euphonia musica*) also is a forest bird and occurs on Antigua, Barbuda, and Saba, but not on Montserrat, St. Kitts, or St. Eustatius.

The gaps shown by secondarily expanded species in their distributions in the northern Lesser Antilles suggest that populations of reexpanded endemic taxa may be vulnerable to extinction even though they appear to spread easily between the islands. The predominant use of forest and montane habitats by these birds (figure 1) may underlie this difference, particularly if extinction has resulted from clearing of forest habitats, hunting, and introduction of predators by humans. However, Terborgh (1973) and Terborgh et al. (1978) emphasized the broad habitat distributions of birds in the northern Lesser Antilles and the independence of the avifaunas of these islands from wet, forested habitats. It is also possible that the heterogeneous island occupancy of some recently spread endemics may have been caused by haphazard colonization not seen in recent colonists from South America.

Restricted Endemics

Old endemic species are extremely sensitive to island area ($z = 0.719$) and somewhat sensitive to distance to the South American mainland (-18% per 100 km). The intercepts of the regressions in table 1 indicate the number of species on islands having an area of 1 km^2. These intercepts are 17.3, 5.4, and 0.3 species for young, reexpanded old, and old endemic taxa, respectively (antilogs of the intercepts in table 1), emphasizing the influence of island area on the persistence of old endemics. Judging from mtDNA genetic divergences of 3%–8% between some old endemic populations and their closest sister populations, we can estimate persistence times of surviving populations to be a minimum of 1.5–4 million years on individual islands.

The significant effect of distance to mainland for old endemics might be the remnant of such an effect in the original colonists from the south. The smaller islands in the main part of the island chain, such as Marie Galante and Carriacou, also lack old endemics, emphasizing the importance of area and, potentially, elevation in determining the number of old endemics. Only one old endemic population, that of the Adelaide warbler (*Dendroica adelaidae*) on Barbuda, occurs on a low-lying island. Accordingly, the lack of an elevation effect in the multiple regression is somewhat surprising. This may reflect the fact that only islands with endemic species ($n = 11$) were included in the regression and all but one of these islands had high elevation. However, when all the islands are included in the regression by using log (species + 0.5) as the dependent variable, the logarithm of area (slope = 0.393 ± 0.123, $t = 3.2$, $P = .0064$) and distance (slope = -0.106 ± 0.027, $t = -3.9$, $P = .0016$) remained significant effects, and elevation (slope = 0.294 ± 0.162, $t = 1.8$, $P = .091$) remained insignificant or became only marginally significant. This implies that populations can persist for long periods on large low-lying islands in spite of the absence of forested habitats from such islands. The complementary side of this argument is that high elevation does not guarantee persistence on small islands.

Species-Area Relationship

The relationship between species and area for birds of the Lesser Antilles varies depending on the history of the taxa in the island chain. Species that have colonized recently from South America or the Greater Antilles or that have undergone recent phases of expansion within the Lesser Antilles are relatively insensitive to island area (figure 3). The number of old endemics decreases rapidly with decreasing area; none presently occur on islands less than about 100 km^2 in area.

According to the MacArthur-Wilson theory of island biogeography, the number of species on an island represents a balance between colonization and extinction. MacArthur and Wilson suggested that rate of colonization should depend on the distance to the source of colonists

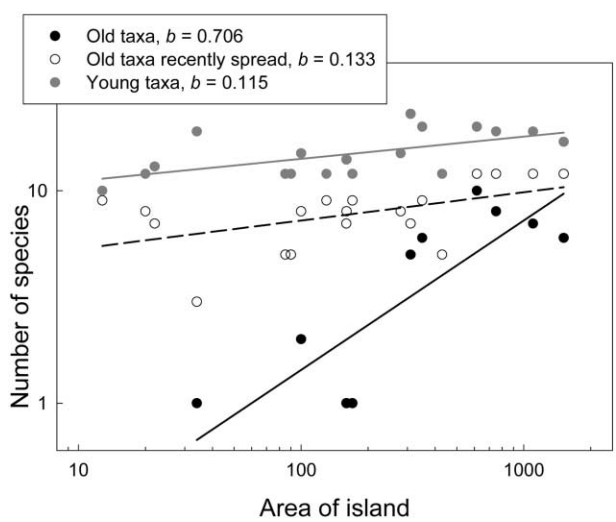

Figure 3: Species-area relationships for three historically distinguished groups of birds in the Lesser Antilles. The slopes are calculated for simple logarithmic regressions of species on area.

and that rate of extinction should increase with decreasing island size. Lack believed that dispersal did not limit species richness on islands in the West Indies but that species diversity varied in accordance with ecological diversity, which controlled the ability of species to become established. Extinction and turnover of species was not an important element in Lack's concept.

Evidence from colonization times and present-day distributions of birds in the Lesser Antilles support dispersal limitation and island population extinction and hence the more dynamic geographic concept of MacArthur and Wilson in contrast to the more static ecological concept of Lack. Nevertheless, one must ascertain whether diversity is currently in a steady state within the archipelago before interpreting patterns of diversity in the context of the MacArthur-Wilson model. Colonization rates, extinction rates, or both may have been heterogeneous over the history of the contemporary Lesser Antillean avifauna. More importantly, the observed linear accumulation of lineages with respect to age of the old taxa (Ricklefs and Bermingham 2001) contradicts the expected exponential approach to equilibrium predicted from persistent background extinction of birds from the archipelago as a whole or exhaustion of the continental pool of colonists. With current rates of colonization, the diversity of the archipelago could increase substantially, potentially increasing diversity on individual islands.

The number of species on a particular island reflects colonization from outside the archipelago, expansion of endemic taxa from within the archipelago, and extinction of individual island populations. Time to extinction evidently depends on island area and the size of a population, and extinction establishes a clear relationship between number of species and island area. However, the slope of the species area curve reflects the age structure of taxa within the archipelago. At the present time, the Lesser Antilles appear to have a large proportion of relatively young taxa or taxa experiencing continuing migration from the source and among islands, which exhibit little extinction of island populations. The species-area relationship of recent colonists has an allometric slope of 0.115 ± 0.033 ($n = 18$, $r^2 = 0.44$).

If the age-structure of the avifauna reflects heterogeneity in either colonization or extinction and if conditions remain constant, the age structure of the avifauna will progressively favor older taxa, and the slope of the species-area relationship will increase with time. Under these conditions it would not approach the upper bound indicated by the species-area slope for endemic island populations (0.706 ± 0.163, $n = 11$, $r^2 = 0.68$) as long as young taxa colonized small islands from both outside and inside the archipelago. Nonetheless, the species-area slope for the present-day avifauna (0.175) reflects the young age structure of the avifauna. It is important to develop genetic and other analyses to determine whether the current age structure of taxa in the Lesser Antilles has reached its steady state and, if not, to estimate the direction and rate of change. In a more broadly comparative context, it would be instructive to determine how much of the variation in species-area slopes of different archipelagoes is due to variation in the age distribution of colonists and the amount of secondary expansion among endemic taxa.

Our historical analysis provides some insights into an enigmatic empirical pattern in the slope of the species-area relationship. Schoener (1976) and Connor and McCoy (1979) found that the value of z decreases with increasing isolation of an archipelago. MacArthur and Wilson (1967) had predicted, in contrast, that reduced colonization of more distant archipelagoes would result in steeper species-area slopes, reflecting the greater role of extinction within the island group. This idea would receive support from our finding that old endemic populations have higher species-area slopes than recent colonists, reflecting the history of extinction of individual island populations. However, birds that can colonize islands across long distances also appear to resist extinction, possibly through frequent recolonization of smaller islands within an archipelago. Thus, distance would appear to select for high dispersal capacity (e.g., Diamond 1975), which would reduce the slope of the species area relationship through recolonization of empty islands (Hanski 1997) or rescue of island populations in decline (Brown and Kodric-Brown 1977) by neighboring island populations. As we suggested, selection for dispersal ability might explain the different penetration of the Lesser Antilles by colonists from the south and from the north.

Ecological Saturation and Equilibrium in the Avifauna of the Lesser Antilles

Our analyses show that the species-area relationship varies with the age of a taxon and its propensity to initiate new phases of colonization within an archipelago. Earlier analyses of the distribution of colonization times of birds in the Lesser Antilles (Ricklefs and Bermingham 2001) also raised the possibility that the regional avifauna was not in equilibrium and that its age structure varied over time. Thus, differences in slope of this relationship between different archipelagoes might reflect differences in the history of their biotas as well as their geographic and ecological settings. Moreover, when the number of species within a regional avifauna changes, the intercept of the species-area relationship also will likely change. Thus, the issue of equilibrium is important to understanding the species-area relationship in general and the applicability of the

MacArthur-Wilson colonization-extinction model in particular.

Several studies published by John Terborgh, John Faaborg, and their colleagues during the 1970s and 1980s addressed the issue of equilibrium and the role of species interactions in maintaining that equilibrium. Evidence was drawn from species-area relationships for members of different feeding guilds on islands (Terborgh 1973; Faaborg 1982), saturation curves relating local habitat diversity to island diversity (Terborgh and Faaborg 1980), size distributions within feeding guilds on islands compared to null distributions (Faaborg 1982; Case et al. 1983), and distributions of species among feeding guilds on oceanic and land-bridge islands (Faaborg 1985). The results of these studies were interpreted as strong evidence for ecological sorting and species interactions on islands, suggesting that island avifaunas are saturated and that the diversity of the system is in colonization-extinction equilibrium.

We make two comments about these studies. First, evidence of species interactions structuring ecological communities is not sufficient to conclude that such interactions limit membership in communities and determine either local or regional diversity. Competition and other interactions are strong forces, but communities are shaped by extrinsic factors as well (Ricklefs and Schluter 1993), including the pressure of colonization on island diversity in the MacArthur-Wilson model. Even if the species present on an island were organized ecologically by their interactions, this would not preclude the invasion of additional species, forcing a new organization on the assemblage. Local diversity within habitats is strongly correlated with island species richness in the West Indies (Cox and Ricklefs 1977; Ricklefs and Cox 1978; Ricklefs 2000), showing that species packing within communities in similar habitats is flexible. Terborgh and Faaborg (1980) found evidence for saturating species richness in island habitats but only in the largest islands in the Greater Antilles, beyond the size range of islands considered in this analysis.

Second, tests of community organization based on consistency in the distribution of species among feeding guilds within islands and nonrandomness of size distributions are confounded within regional faunas by nonindependence of the island biotas. Avifaunas within the West Indies, particularly the Lesser Antilles, are mostly derived from the same set of colonizing lineages, even though representatives on different islands may be divergent within the archipelago and have different species names. Consistency of guild membership in the Lesser Antilles also obscures the fact that some groups of birds (suboscine passerines and woodpeckers are good examples; Ricklefs and Cox 1972) are poor colonists and the West Indies are depauperate in these functional types. Some organization of the species associations on each island are evident, especially on the smaller islands (Faaborg 1982; Travis and Ricklefs 1983), but this does not address the regulation of diversity within habitats or islands by species interactions. That task requires a direct test of the temporal homogeneity of processes that influence species richness, in this case colonization and extinction, which is possible for birds only through historical phylogenetic analyses of the age distribution of island populations. Our studies of Lesser Antillean birds are by no means conclusive, but they strongly point to the possibility of substantial change in the overall diversity of the regional avifauna over time and its presently being below its colonization-extinction equilibrium.

Conclusions

David Lack was wrong to the extent that the avifaunas of Lesser Antillean islands are not close to ecological saturation—this is certainly true of the smaller islands—and that colonization leading to population establishment is infrequent in spite of movement of vagrants through the islands. Moreover, the steep species-area relationship in the number of endemic species suggests a strong role for extinction, contrary to Lack's idea of faunal stability. Stepwise regressions indicated that ecological diversity, for which we used elevation as a proxy, influenced only the number of recently spread Lesser Antillean endemics. Indeed, this effect is probably due to extinction rather than failure to establish new populations; old endemic populations are restricted to islands with high elevations where they tend to occur in forest and montane habitats. Thus, although these species might reach lower islands, their persistence appears to depend on the presence of higher elevation habitats that might provide a refuge from competitive pressures from most new colonists. Alternatively, this apparent dependence of diversity on habitat heterogeneity might also reflect the historical development of the avifauna of the archipelago, particularly the predominance of wet forest habitats before the middle Pleistocene, when most of the older taxa colonized the Lesser Antilles, and the onset of cooler and drier Caribbean climates associated with glaciation to the north, during which most new colonization events presumably have occurred.

Although Lack's ideas about the assembly of island avifaunas are not supportable, one must also exercise caution in applying MacArthur and Wilson's equilibrium ideas. The MacArthur-Wilson model describes the dynamics of colonization and extinction with respect to diversity, and thus it applies to any system whether it is in equilibrium or not. Furthermore, the species-area relationship that pertains at equilibrium may develop its basic pattern before a system has reached equilibrium. Simple simulations of a MacArthur-Wilson process with area-independent col-

onization and area-dependent extinction (results not shown) exhibit increasing slope of the species-area relationship with time because smaller islands with lower diversity reach equilibrium faster (MacArthur and Wilson 1967).

Dispersal limitation and extinction are intrinsic features of the Lesser Antillean avifauna; however, the system does not appear to be in equilibrium, and the processes responsible for establishing patterns of diversity possibly are not homogeneous over time. History clearly influences contemporary patterns of diversity (Ricklefs and Schluter 1993). We have shown here that phylogenetic data analyzed across taxa can provide insights into the history of a fauna and that faunas may consist of historically distinguishable elements with unique ecological and biogeographic characteristics. Habitat relationships and probably extinction rates of species change over time (Ricklefs and Cox 1972; Ricklefs and Bermingham 1999), and so species cannot be considered independently of their history. The species-area relationship can be interpreted in terms of the historical development of a biota, and variation in its slope may reflect differences in the histories of biotas, but it does not in and of itself provide insight into the processes responsible for this development. Whether island biotas are dispersal or persistence limited, whether extinction and colonization have been homogeneous over time, and whether island systems have achieved equilibrium patterns of diversity, can only be answered by historical analysis.

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