Statistical distributions of West Indian land bird families

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ABSTRACT. Island distribution patterns of species in thirty-one families of West Indian land birds are analysed. Species—area regressions of individual families are ambiguous because the slopes of these regressions are a function of family size. Rarefaction gives the result of all islands supporting close to the expected number of families based on a random draw, although small islands tend to be family-poor and large islands family-rich. The expected number of species in each family was generated from a hypergeometric model, sampling without replacement from the total list of species. With this model no island has fewer species in any family than expected by chance, although some islands have more species than expected. Confamilial sympatry in the Columbidae and Mimidae is consistently greater than expected with this technique. Some assumptions of a random draw of species from an equivalent species pool for all islands are biologically unrealistic. However, the hypergeometric model avoids many biases inherent in species—area regressions of families and is preferable to regression analysis for preliminary identification of unusual family distributions.

Introduction

Competition is considered to be a major force organizing West Indian land bird communities. Lack (1976) emphasized its role in determining the distribution of confamilial species, and Johnston (1975) also believed that competition limited the coexistence of congeners. Studies of the taxon cycle (Ricklefs & Cox, 1978), habitat saturation (Terborgh & Faaborg, 1980), and interactions with anolis lizards (Wright, 1981) have all emphasized the role of competition in this system.

Terborgh (1973) also concluded that competition regulates the degree of sympatry within a family, based on his examination of species—area regressions of West Indian land bird families. The interpretation of species—area regressions is popular in ecology (Preston, 1962; MacArthur & Wilson, 1967), but is

problematic because the mechanisms that produce this relationship are not known (Connor & McCoy, 1979; Gilbert, 1980). Here, we demonstrate that this approach (Terborgh, 1973; Faaborg, 1979) is complicated by several statistical problems. Terborgh's (1973) conclusions are not supported by these regressions. Of course, many non-regression data have been taken as implicating competition among West Indian birds (Johnston, 1975; Ricklefs & Cox, 1978; Terborgh & Faaborg, 1980; Wright, 1981), but we are not addressing them in this paper. Instead, we have restricted our attention to the regression technique.

We have used two random models, rarefaction and a hypergeometric draw, to evaluate the distribution of West Indian land bird families. The models test two related, but distinct, null hypotheses. Rarefaction generates the expected number of families if species are drawn randomly. If competition limits the coexistence of confamilial species, we reason that islands should have more families than expected; competition will prevent many species in the same family from occurring together. This procedure is analogous to evaluating species/genus ratios to assess competitive effects (Simberloff, 1970, 1978). Observe that this model considers only the number of families on islands; it does not address the identity of those families.

In contrast, the hypergeometric draw generates an expected number of *species* within a single family, given no interactions. If competition within a family limits sympatry, our observations should fall below this expected value. By combining observations from many islands, we can assess whether any family tends to be over- or under-represented in island communities. If competition within a family is important, at least some families should be shown to be under-represented by this technique.

Naturally, the results of these two models depend heavily upon the designation of the source pool. For this study, we have simply used the combined species list for all the islands as the source pool. Information on

TABLE 1. Area and numbers of land bird species and families for nineteen West Indian islands

Island	Area (mi²)	No. of land bird species	No. of families
Cuba	44 164	79	27
Hispaniola	29 979	79	26
Jamaica	4411	69	25
Puerto Rico	3423	58	22
Guadeloupe	583	35	18
Martinique	385	41	19
Dominica	305	41	20
St Lucia	233	44	19
Barbados	160	16	10
St Vincent	133	39	19
Grenada	120	38	17
Antigua	108	24	15
St Croix	80	23	13
Grand Cayman	71	28	15
St Kitts	68	24	13
Barbuda	62	22	12
Montserrat	38	26	15
St Martin	33	16	11
St Thomas	32	23	13

habitat preference and mainland distributions could be used to modify this list considerably. However, we believe the combined list is valuable as an initial baseline for making comparisons (but see Terborgh, 1981, for a contrary opinion).

Although useful for studying distribution patterns, null models of this sort must not be considered a true 'test' of competition. The mere observation of a pattern in nature reveals nothing about the mechanisms that have produced it. Thus, even if the distributions turn out to be entirely consistent with the model, we cannot conclude that island colonization is random, and competition is unimportant. Instead, we can conclude only that, if competition is influencing the number of co-existing species, its effects are not manifested in these particular statistics. This is not a very strong inference, but it is the only one available for this type of data.

Materials and Methods

A list of breeding land birds, Falconiformes, Galliformes, and Columbiformes through Passeriformes, was constructed for nineteen islands in the Greater and Lesser Antilles (Appendix). The list was taken initially from Bond (1956, 1971) and modified with information from Schwartz and Klinikowski (1963), Kepler & Parkes (1972), Diamond (1973), Lack & Lack (1973), Lack et al. (1973), Lack (1976), Kepler & Kepler (1978) and Terborgh, Faaborg & Brockmann (1978). Species recently extinct and natural range extensions were included, but species introduced by man were excluded. The total numbers of species on all islands (Table 1) are consistent with the numbers published by Terborgh (1973). Island area measurements were taken from Terborgh (1973) so that the family regressions would be as similar as possible. Terborgh (1973) selected sixteen families for analysis; we have extended this list to include all thirty-one land bird families found on the nineteen islands. Species area regressions were computed on SPSS, version 8.0, and the rarefaction was calculated from the program given by Simberloff (1978).

For both the rarefaction and the hypergeometric model, the source fauna was defined as the total species list for all nineteen islands.

Results and Discussion

Problems with regression techniques

Regression may be useful for examining the relationship between species number and area, but biological conclusions drawn solely from these analyses are suspect. Regression does not reveal causal mechanisms (Connor & McCoy, 1979; Gilbert, 1980) and its statistical limitations may be easily overlooked. Terborgh (1973) regressed species number on log island area for sixteen families of West Indian land birds. He grouped the families according to the magnitude (high or low) of the slope and intercept, and loosely interpreted the groupings in terms of colonization potential and dispersibility. Following his approach, Faaborg (1979) regressed number of species in a family on log community size for land bridge islands and mainland areas in the Neotropics. Faaborg interpreted these regressions in terms of extinction probabilities for different families in biological reserves of small area. Neither author considered other regression models (e.g. log—log, linear—linear) but for a number of the families other regression models give a better fit. We will continue with the linear—log model for comparative purposes (Table 2).

The interpretation of regressions coefficients is popular in ecology (MacArthur & Wilson, 1967; other references in Connor & McCoy, 1979; Gilbert, 1980). However, we believe an unambiguous biological interpretation of the species—area regression slope is not possible. Consider the extreme case of a slope of zero. This situation could arise if all the species in a family were present on all islands.

TABLE 2. Species—log island area regression data. Slope and intercept values for species—log island area linear regressions of all families. Curvilinearity was detected by a run of signs test on the residual differences between observed and expected.

Family	No. of species	Slope	Intercept	Significance of regression	Residual analysis	r^2 adj.
Cathartidae	1	0.33	-0.66	F = 40.6, P = 0.00	*	0.69
Accipitridae	9	1.43	-2.33	F = 28.1, P = 0.00		0.60
Falconidae	2	0.19	0.48	F = 4.2, P = 0.06		0.15
Phasianidae	1	0.13	-0.28	F = 7.6, P = 0.01	*	0.27
Columbidae	17	2.30	0.15	F = 86.2, P = 0.00		0.83
Psittacidae	13	0.87	-1.42	F = 28.4, P = 0.00		0.60
Cuculidae	9	1.20	-0.75	F = 28.2, P = 0.00		0.60
Strigidae	8	1.07	-1.59	F = 37.6, P = 0.00	*	0.67
Nyctibiidae	1	0.20	-0.38	F = 9.2, P = 0.01	*	0.31
Caprim ulgidae	7	0.79	-1.21	F = 30.1, P = 0.00		0.62
Apodidae	6	0.92	-1.01	F = 19.2, P = 0.00		0.50
Trochilidae	14	0.25	2.23	F = 0.86, P = 0.36		0.05
Trogonidae	2	0.26	-0.54	F = 26.2, P = 0.00	*	0.58
Alcedinidae	1	0.03	0.09	F = 0.07, P = 0.79	*	0.00
Todiae	5	0.52	-1.03	F = 58.7, P = 0.00	*	0.76
Picidae	10	1.00	-1.85	F = 22.7, P = 0.00	*	0.55
Cotingidae	1	0.07	-0.13	F = 1.7, P = 0.21	*	0.04
Tyrannidae	14	1.09	1.11	F = 16.0, P = 0.00		0.45
Hirundinidae	3	0.63	-0.30	F = 34.4, P = 0.00	*	0.65
Corvidae	4	0.66	-1.31	F = 105.2, P = 0.00	*	0.85
Troglodytidae	2	0.27	-0.54	F = 26.2, P = 0.00	*	0.58
Mimidae	7	-0.24	3.07	F = 0.5, P = 0.49		0.03
Turdidae	10	0.74	-0.51	F = 7.7, P = 0.01		0.27
Sylviidae	1	0.13	-0.29	F = 7.6, P = 0.01	*	0.27
Dulidae	1	0.12	-0.25	F = 6.1, P = 0.02	*	0.22
Vireonidae	8	0.43	0.25	F = 16.6, P = 0.00		0.46
Parulidae	14	0.93	-0.57	F = 31.3, P = 0.00		0.63
Coerebidae	3	0.07	0.87	F = 1.6, P = 0.21	*	0.04
Thraupidae	8	0.87	-0.93	F = 13.7, P = 0.00		0.41
Icteridae	14	1.47	-1.75	F = 40.3, P = 0.00		0.69
Fringillidae	17	1.26	-0.17	F = 33.2, P = 0.00		0.64

^{*} Run of signs test, $P \le 0.05$.

Thus, a low slope could indicate good dispersibility and a tendency for all species in the family to reach all islands. Terborgh (1973) has interpreted the low slopes for the Trochilidae and Mimidae in this way. On the other hand, a slope of zero will also be generated if each island supports only a single species in a family. In this case, a low slope would indicate poor dispersal ability or a strong tendency to endemize. The Todidae approach this distribution. We stress that the species—area regression slope is nothing more than an estimate of the difference in faunal size of two islands of different area. Colonization potential or dispersibility cannot be properly inferred from this measure alone, since very different distributions can produce identical estimates.

Species-area regressions and competition. An important consideration in linear regression is the distribution of the residuals, which may reveal information about the fit of the model. Curvilinearity in the residuals suggests that the model has been fitted incorrectly, and a different transformation is required to linearize the relationship between y and x. Faaborg (1979) noted such a trend in his regressions of Neotropical Tyrannidae and Fringillidae. For West Indian land bird families, curvilinearity is evident in fifteen of the thirty-one regressions (Table 2). Although most of the small families (which Terborgh did not consider) are poorly linearized by a log-area transformation, many of the regressions for larger families also suggest curvilinearity or heteroscedasticity. These problems arise, in part, because the data have all been forced into a single functional form. One would not necessarily expect all thirty-one families to show a linear relationship with log area, even though the aggregate – total number of species ν . log area – fits this form well. Terborgh's (1973) and Faaborg's (1979) use of a single transformation certainly facilitates comparisons, but is not a valid procedure unless the transformation provides a good fit for all of the families being compared.

Terborgh has argued that regression data support the idea that competition limits sympatry among West Indian land bird families. We do not believe the data presented in Table 2 can support such an interpretation. The r^2 values vary widely among different

families. Species number in families such as Columbidae is well correlated with area $(r^2 =$ 0.83). In many families, however, little of the variation in species number is explained by variation in island area. Furthermore, the regressions of the Mimidae and the Trochilidae (Terborgh, 1973: Fig. 6) are not even significant, suggesting that area has no direct influence on species number in these families. Of course, these regressions can always be interpreted within a competitive framework, as Terborgh (1973) and others (e.g. Wright, 1981) have done. However, species—area regressions, by themselves, provide no information on species interactions. Our contention is that competition cannot be inferred validly from these data.

The effect of family size on slope. Comparisons of family regressions are further complicated because the dependent variable is restricted to quite small values in some families: the number of species on any island cannot exceed the number of species in a family. For example, because there are seventeen species of Columbidae in the West Indies, the Y observation for this regression can vary between 0 and 17. But a family with only a single representative species, such as Cotingidae, will generate only zeros or ones for the fitted regression line. Regardless of the influence of area, families with few species will generate regression lines with restricted slope and

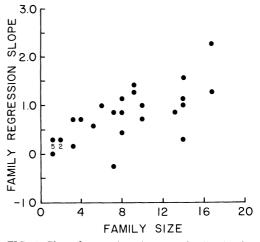


FIG. 1. Plot of regression slopes on family size for West Indian land bird families. r = 0.76, P < 0.001. As family size decreases, the slope of the species area regression is restricted to small values. Data from Table 2.

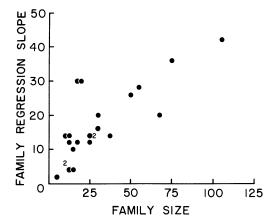


FIG. 2. Plot of regression slopes on family size for Neotropical land bird families. r = 0.80, P < 0.001. Family species number was not regressed directly on log area, but on log community size (total species number), which is highly correlated with log area (r = 0.92, P < 0.001). Data taken directly from published regression slopes and family sizes in Faaborg (1979).

intercept values. As family size increases, the range of potential slope and intercept estimates also increases.

Before biological significance is attributed to differences in slope or intercept, the effect of family size should be evaluated. For West Indian land birds, slope and family size are significantly correlated (r = 0.76, P < 0.001; Fig. 1), but intercept and family size are not significantly correlated (r = 0.0002, P > 0.05). For Faaborg's data on Neotropical birds, family size is significantly correlated with both slope (r = 0.78, P < 0.001; Fig. 2) and intercept (r = -0.64, P < 0.01). It is important to note that slope and intercept are often mathematically related (White & Gould, 1965).

Because much of the variation in slope appears to be an artefact of family size, we caution against attributing biological significance to species—area regression parameters, which should be viewed only as fitted constants.

Competition and the distribution of families on islands

The number of families on islands. Despite the problems inherent in species—area regressions, the biological question is still interesting:

Are there unusual distribution patterns within different families? Many authors (Terborgh, 1971, 1973; Terborgh & Diamond, 1970; Lack, 1976) have suggested that species in the same family compete more intensely than species in different families. If this hypothesis is correct, islands should support more families than expected, because competition prevents many species in any one family from cooccurring. Rarefaction (Simberloff, 1970, 1978) can be used to find the expected number of families on islands if species are drawn at random (without replacement) from the source fauna. Terborgh (1973, 1981) argues that species are probably not drawn randomly in this fashion. Although he is probably correct, we believe that random colonization is the simplest hypothesis for a preliminary evaluation of confamilial competition.

For the West Indian land birds, the number of families on all islands is within the expected range produced by rarefaction (Fig. 3). However, there is a significant positive correlation

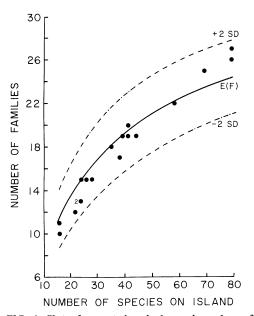


FIG. 3. Plot of expected and observed numbers of land bird families on nineteen West Indian islands. Expected numbers of families and approximate 95% confidence intervals were calculated by rarefaction, drawing species randomly from the total list in the Appendix. All observations are within two standard deviations of the expected values, but the residuals are positively correlated (r = 0.83, P < 0.001) with the total number of species on the island (see text).

(r = 0.83, P < 0.001) between the number of species on the island and the residual difference between the observed and the expected number of families. This correlation suggests that large islands tend to be relatively family-rich and small islands relatively family-poor. Thus, on small islands, species tend to be concentrated in relatively few families. These results may reflect the habitat diversity of the islands. Small islands have few habitats and may be able to support only a few families. Large islands may be family-rich because of greater habitat diversity. Thus, of the seven single-

species families, six are found only in the Greater Antilles. The exception is the king-fisher *Ceryle torquata*, which is present on Guadeloupe, Martinique and Dominica. Overall, the rarefaction results do not suggest that competition has influenced the species/family ratio, although taxonomic ratios may be weak indicators of species interactions (Simberloff, 1978).

A random-sampling model of family distributions. Rarefaction is useful for examining the number of families found on islands, but does not reveal patterns within families. If

TABLE 3. Cumulative probabilities for observed number of species in different families. Equation (4) was used to estimate the probability of finding the observed number of species or fewer, in each family on each island. No observation had a probability < 0.05. To determine the upper tail, the continuity correction $1 - P(x \le \text{observed} - 1)$) was used. A + indicates that the probability of drawing the observed number or more species in a family is < 0.05, and * indicates P < 0.025. All other entries in the table are > 0.05, for both tails.

Family (total no. of species)	Isla	and (total	no. c	of spe	ecies)													
	Cuba (79)	Hispaniola (79)	Jamaica (69)	Puerto Rico (58)	St Lucia (44)	Dominica (41)	Martinique (41)	St Vincent (39)	Grenada (38)	Guadeloupe (35)	Grand Cayman (28)	Monserrat (26)	St Kitts (24)	Antigua (24)	St Thomas (23)	St Croix (23)	Barbuda (22)	Barbados (16)	St Martin (16)
Columbidae (17) Fringillidae (17) Icteridae (14) Parulidae (14) Tyrannidae (14) Tyrannidae (14) Trochilidae (13) Turdidae (10) Picidae (10) Accipitridae (9) Cuculidae (9) Vireonidae (8) Thraupidae (8) Caprimulgidae (7) Mimidae (7) Apodidae (6) Todidae (5) Corvidae (4) Hirundinidae (3) Coerebidae (3) Falconidae (2) Troglodytidae (2) Cathartidae (1) Nyctibiidae (1) Alcedinidae (1) Cotingidae (1) Sylviidae (1) Dulidae (1) Phasianidae (1)	*	+	+	+	*	+	*	*		*		+	+	+	*	*	*		

each island community is considered to be a random sample of the entire species pool, a hypergeometric distribution, sampling without replacement, gives the expected number of species in each family and the variance:

$$E = \frac{nF}{N} \tag{1}$$

$$\sigma^2 = \left(\frac{nF}{N}\right) \left(1 - \frac{F}{N}\right) \left(\frac{N-n}{N-1}\right) \tag{2}$$

where N = the total number of potential colonizing species for an island, F = the total number of potential colonizing species in a family, and n = the number of species on the island. The probability of drawing x species in a family is:

$$P(X=x) = \frac{\binom{F}{x} \binom{N-F}{n-x}}{\binom{N}{n}}$$
(3)

and the cumulative probability of drawing x or fewer species is:

$$P(X \le c) = \frac{\sum_{x=0}^{c} {F \choose x} {N-F \choose n-x}}{{N \choose n}}$$
(4)

Equation (4) was used to calculate the exact probabilities for randomly drawing the observed number of species or fewer in each family. A one-tailed test for observed less than expected shows that no island has fewer species in any family than expected by chance (P < 0.05). Because the hypergeometric distribution is discrete, the following continuity correction is used to calculate the upper tail:

$$P(X \ge x) = 1 - P(X \le (x - 1))$$
 (5)

Equation (5) was used to test whether any island has more species in a family than expected by chance (P < 0.05). Surprisingly, the positive deviations fall mostly in two families: the Columbidae and the Mimidae (Table 3). The Columbidae are over-represented to the north, on Cuba, Hispaniola, Jamaica, Puerto Rico, Antigua, St Croix, St Thomas, and Barbuda. The Mimidae are over-represented to the south, in the Lesser Antilles (St Lucia,

TABLE 4. Fisher's combined probabilities for overall family distributions. Fisher's test for combining probabilities was used to evaluate the individual probabilities generated in Table 3 for each family. The sum $-2\Sigma \ln{(p_i)}$ of the individual probabilities p_i has a chi-square distribution with 2n degrees of freedom.

Family	Observed <	Observed >
	expected	expected
	$(\chi^2, df = 38)$	$(\chi^2, df = 38)$
Cathartidae	5.11	6.22
Accipitridae	29.89	16.00
Falconidae	2.11	43.33
Phasianidae	1.98	6.82
Columbidae	1.18	102.80 * * *
Psittacidae	66.48(**)	1.67
Cuculidae	11.12	35.93
Strigidae	25.77	11.48
Nyctibiidae	6.04	4.24
Caprim ulgidae	27.46	35.30
Apodidae	13.46	24.09
Trochilidae	20.21	36.14
Trogonidae	12.17	2.01
Alcedinidae	6.54	10.22
Todidae	27.70	4.94
Picidae	52.10	4.94
Cotingidae	6.97	2.25
Tyrannidae	5.40	55.27(*)
Hirundinidae	2.59	34.79
Corvidae	20.41	4.10
Troglodytidae	9.44	14.03
Mimidae	9.89	81.09***
Turdidae	29.29	12.30
Sylviidae	6.82	1.98
Dulidae	6.82	1.98
Vireonidae	16.35	16.53
Parulidae	34.23	10.00
Coerebidae	3.65	37.06
Thraupidae	8.12	15.11
Icteridae	33.71	12.49
Fringillidae	20.02	20.50

(*) P < 0.05; (**) P < 0.01; *** P < 0.0004 for overall error rate of P < 0.05.

Dominica, St Vincent, Guadeloupe, Martinique, St Kitts and Montserrat).

Fisher's test of combined probabilities (Sokal & Rohlf, 1969), which has a chi-squared distribution, was used to evaluate the distribution of each family throughout the archipelago (Table 4). The Columbidae, Mimidae and Tyrannidae are found more often than expected by chance, and the Psittacidae are found less often than expected. All other families are within the expected range of the null model (P > 0.05).

We agree with Terborgh (1973) that the

Columbidae are exceptionally well represented; all islands have more pigeon and dove species than expected by chance alone, and eight of the observations are statistically significant (P < 0.05). Terborgh also considered the Fringillidae to be good dispersers because the regression equation for this group, like that of the Columbidae, has a relatively large slope and intercept. However, the Fringillidae distribution is very similar to the expected distribution, and has a small chi-square value (Table 4). Thus, two families with equal numbers of species may generate similar regression lines, but show very different distribution patterns (Fig. 4).

Although both the Trochilidae and the Mimidae have regression slopes that do not differ significantly from 0, only the Mimidae have a significant overall distribution. The family is especially well represented in the Lesser Antilles, though none of the four Greater Antilles contains significantly fewer Mimidae than expected. The West Indian

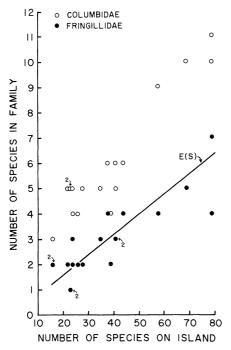


FIG. 4. Plot of expected and observed numbers of West Indian Columbidae and Fringillidae species. The expected values were generated from Equation (1). Each family has seventeen West Indian species (Table 2), so the expected line is the same for both families.

Mimidae are probably of North American origin, although the endemic genus *Margarops* shows no affinity with any continental genera (Bond, 1963). Terborgh (1973) has suggested that the West Indies have served as both a refugium and a centre of radiation for several species in this family.

Because we have conducted thirty-one two-tailed tests for all of the families, it is unsafe to reject at the 0.05 level the null hypothesis that species in each family are a random sample of the source pool. Probabilities this low would be expected for at least some observations, even if all the species were randomly distributed. If Bonferonni's approximation (Myers, 1979) is used to set the overall error rate at 0.05, the critical level for any individual test is 0.0008 (0.0004 for a two-tailed test). At this level, only the Columbidae and Mimidae distributions are significant for a one- or two-tailed test.

As with the linear regressions, the restriction of the dependent variable causes some statistical problems. In small families the probabilities for the observed number of species do not vary continuously between 0 and 1, but are restricted to only a few possible values. As family size increases, the probabilities can vary more continuously and the statistic approaches a true chi-square distribution. Therefore the results for small families may not be informative.

Equilibrium and predicted levels of sympatry

Terborgh discusses several instances in which (1973: 347) 'the level of local sympatry deviates conspicuously from the regular pattern displayed by most families'. He concludes that these deviations (1973: 348) 'suggest the range of uncertainty within which the processes regulating sympatry appear to operate'.

We stress that species—area regressions in no way imply a process regulating sympatry, and that many of the cases described may not require a special explanation. Terborgh writes (1973: 347) that 'An especially clear case is that of hummingbirds in Puerto Rico, where there are 5 species instead of the predicted 2 or 3. This condition results fortuitously from the fact that Puerto Rico is situated at the confluence of two currents of dispersal, one

derived from the west via the Greater Antilles and the other from the east via the Lesser Antilles (Bond, 1963).' However, the probability of randomly drawing five or more hummingbirds from this list is 0.323, so this observation may not warrant any special explanation.

Terborgh also claims unexpected sympatry in finding three Jamaican vireos, while all other islands support two or fewer. Yet, the probability of randomly drawing three or more vireos from this list is 0.510, so this may not be an unusual finding. We agree with Terborgh that Jamaica harbours unexpected sympatry in flycatchers (eight species, P = 0.043), but reject his suggestion (1973: 348) that this 'represents an unstable excess over the equilibrium state'. Terborgh did not mention an unusual level of sympatry in the Cuban hawks; of the nine West Indian Accipitridae, seven are found on Cuba (P = 0.014).

Overall, the number of species in most families is within the limits of chance if species were drawn randomly from the available list, although pigeons and mockingbirds are consistently over-represented.

Thus, with the framework of this null model, we find no evidence for Terborgh's conclusions (1973: 348) that 'insular faunas oscillate about an equilibrium state', or that 'the level of sympatry within competing groups are held within close bounds by the opposition of contrary tendencies'.

Conclusions

Despite their popularity, species—area regressions are not very useful in examining the distribution of families. The slope and intercept of the regressions are primarily functions of family size, and the distributions of different families cannot all be linearized by the same transformation. Consequently, comparisons of regression lines for different families are not useful. Random sampling models avoid these biases, and allow one to compare families on an equal basis, although some of the assumptions of the model may be biologically unrealistic. Habitat requirements will undoubtedly restrict the distribution of some species, and the source pool may not be

equivalent for all islands. The increasing proportion of South American species in the southern Lesser Antilles (Terborgh, 1973; Bond, 1979) is good evidence of a changing source pool.

Thus any statistical analysis of the West Indian avifauna must be interpreted cautiously. Our particular null model reveals strong patterns in the distribution of the Columbidae and the Mimidae. It is noteworthy that these distributions follow a geographic pattern: the Columbidae are over-represented in the north, and the Mimidae in the south. These patterns may reflect long-term historical processes of speciation or climatic change (Olson, 1978) rather than short-term ecological processes such as dispersal or competition.

The analysis of species lists is only a preliminary approach to the study of insular distributions. It is not a substitute for autecological and experimental studies. However, species lists may reveal interesting distribution patterns, provided the source pool for an island has been realistically estimated. Further analyses of this sort should incorporate more biological information into the assessment of a realistic source fauna.

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Appendix. A list of breeding land birds on nineteen West Indian islands.

+ = resident, breeding species; x = extinct species; I = introduced species; E = species endemic to single island; ? = status uncertain

	Cuba	Hispaniola	Jamaica	Puerto Rico	Guadeloupe	Martinique	Dominica	St Lucia	Barbados	St Vincent	Grenada	Antigua	St Croix	Grand Cayman	St Kitts	Barbuda	Montserrat	St Martin	St Thomas
CATHARTIDAE (vultures) Cathartes aura	+	+	+	I															
ACCIPITRIDAE (hawks) Chondrohierax uncinatus C. wilsonii Rostrhamus sociabilis Accipiter striatus A. gundlachi Buteo jamaicensis	E + + E +	+	+	+							+				+				
B. platypterus B. ridgewayi Buteogallus anthracinus	+	E		+		+	+	+		+	+	+							
FALCONIDAE (falcons) Caracara plancus Falco sparverius	++	+	+	+	+	+	+	+		+	+	+	+		+	+	+	+	+
PHASIANIDAE (pheasants, quails) Colinus virginianus	+																		
COLUMBIDAE (pigeons, doves) Columba leucocephala C. squamosa C. caribaea C. inornata Zenaida macroura	+ + +	+ + + + +	+ ? E +	+ + + + +	+	+	+	+	+	+	+	++	+	+	+	+	+	?	+
Z. auriculata Z. aurita Z. asiatica Columbina passerina	+ + +	++++	++++	++++	+	+++++++	+	+ + +	+	+ ? +	+ + + +	+	+	+++++	+	+	+	+	+
Leptotila jamaicensis L. wellsi Geotrygon versicolor G. caniceps	+	+	+ E								E			+					
G. montana G. chrysia G. mystacea Starnoenas cyanocephala	+ + E	+	+	+	+	+	+	+		+	+	+	+		+	+	+		+
PSITTACIDAE (parrots) Amazona imperialis	D						E			_									
A. guildingii A. versicolor A. arausiaca A. leucocephala	+						E	E		Е				+					
A. ventralis A. collaria A. vittata A. agilis		Е	E E	E															
Aratinga chloroptera A. euops A. nana Ara tricolor	E Ex	Е	+	?x															

	Cuba	Hispaniola	Jamaica	Puerto Rico	Guadeloupe	Martinique	Dominica	St Lucia	Barbados	St Vincent	Grenada	Antigua	St Croix	Grand Cayman	St Kitts	Barbuda	Montserrat	St Martin	St Thomas
CUCULIDAE (cuckoos, anis)																			
Coccyzus minor	+	+	+	+	+	, +	+	+		+	+	+ 3		+		+ x	+	+	+
C. americanus Hyetornis pluvialis	+	+	+ E	+									+						
H. rufigularis		Е	E																
Saurothera merlini	+	ь																	
S. longirostris	•	Е																	
S. vetula		_	E																
S. vieillot				E															
Crotophaga ani	+	+	+	+	+	+	+	+		+	+		+	+			+		+
STRIGIDAE (owls)																			
Tyto alba	+	+	+				+			+	+			+					
Otus nudipes				+									+						+
Gymnoglaux lawrencii	E																		
Speotyto cunicularia	_	+										+x			+x				
Glaucidium siju	E																		
Asio flammeus		+		+															
A. stygius Pseudoscops grammicus	+	+	E																
NVCTIBILD AE (moto on)																			
NYCTIBIIDAE (potoos) Nyctibius griseus		+	+																
CAPRIMULGIDAE (nightjars) Caprimulgus rufus C. vociferus C. cubanensis C. cayennensis Siphonorhis brewsteri	+	+ E		+		+		+											
S. americanus Chordeiles minor	+	+	Ex +	+									+	+					+
		•		•									•	•					,
APODIDAE (swifts) Chaetura brachyura										+									
C. cinereiventris											+								
C. martinica					+	+	+	+		+	•								
Streptoprocne zonaris	+	+	+					•		•									
Cypseloides niger	+	+	+	+	+	+	+	+		+					+		+		
Tachornis phoenicobia	+	+	+																
TROCHILIDAE (hummingbirds)																			
Glaucis hirsuta											+								
Chlorostilbon maugaeus				E															
C. swainsonii		Е																	
C. ricordii	+																		
Cyanophaia bicolor Anthracothorax mango			E			+	+												
A. dominicus		+		+															
A. viridis		т		+ E															+
Eulampis jugularis					+	+	+	+		4	_				1.				
Sericotes holosericeus				+	+	+	+	+	+	+	+	+ +	+		+ + ·	L	+	L	_
Orthorhyncus cristatus				+	+	+	+	+					+		+ .	, .	+ .	r .	T _
Trochilus polytmus			E	•		•	•		•		•		•		'				r
Mellisuga helenae	E		_																
M. minima		+	+																

	Cuba	Hispaniola	Jamaica	Puerto Rico	Guadeloupe	Martinique	Dominica	St Lucia	Barbados	St Vincent	Grenada	Antigna	St Croix	Grand Cayman	St Kitts	Barbuda	Montserrat	St Martin	St Thomas
TROGONIDAE (trogons) Temnotrogon roseigaster Priotelus temnurus	E	E																	
ALCEDINIDAE (kingfishers) Ceryle torquata					+	+	+												
TODIDAE (todies) Todus multicolor T. angustirostris T. mexicanus T. todus T. subulatus	E	E E	E	E															
PICIDAE (woodpeckers) Nesoctites micromegas Colaptes auratus C. fernandinae Melanerpes portoricensis M. herminieri M. superciliaris M. radiolatus M. striatus Xiphidiopicus percussus Campephilus principalis	+ E + E +	E E	Е	Е	E									+					
COTINGIDAE (cotingas) Platypsaris niger			Е																
TYRANNIDAE (flycatchers) Tyrannus melancholicus T. dominicensis T. cubensis T. caudifasciatus Myiarchus tyrannulus M. stolidus M. barbirostris M. validus Contopus latirostris C. caribaeus Empidonax euleri Elaenia flavogaster E. martinica E. fallax Myionagis cotta	+ + + + +	+ + + + +	+ + + + E + E	+ + + + +	+ + +	+ + + +	+ + +	+ + +	+	+ + + + + + + + + + + + + + + + + + + +	? + + + +	+	+ +	+ + + +	+ +	++++	+	+	+ +
Myiopagis cotta HIRUNDINIDAE (swallows) Kalochelidon euchrysia Petrochelidon fulva Progne subis	++	+++++	++++	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+
CORVIDAE (crows) Corvus nasicus C. leucognaphalus C. jamaicensis C. palmarum	+	+	E	+															

	Cuba	Hispaniola	Jamaica	Puerto Rico	Guadeloupe	Martinique	Dominica	St Lucia	Barbados	St Vincent	Grenada	Antigua	St Croix	Grand Cayman	St Kitts	Barbuda	Montserrat	St Martin	St Thomas
TROGLODYTIDAE (wrens)												***************************************	Barrio.					_	
Troglodytes aedon Ferminia cerverai	E				+	+	+	+		+	+								
MIMIDAE (mockingbirds)																			
Mimus polyglottos	+	+	+	+									+	+					+
M. gilvus					+	+	+	+		+	+								
M. gundlachii			+																
Margarops fuscus				+	+	+	+	+	+	+	+	+			+	+	+		+
M. fuscatus Cinclocerthia ruficauda				+	+	+	+	+		+		+	+			+	+	+	+
Ramphocinclus brachyurus					Т.	+	т	+							•				
TURDIDAE (thrushes)																			
Turdus nudigenis						+		+		+	+								
T. fumigatus										+	+								
T. jamaicensis			E																
T. swalesi		E	_																
T. aurantius			E											_					
Mimocichla ravida														E					
M. plumbea	+	+		+	+		+	+											
Cichlherminia Iherminieri	E				+		+	+									+		
Myadestes elisabeth M. genibarbis	E	+	+			+	+	+		+									
SYLVIIDAE (old world warblers)																			
Polyoptila lembeyei	E																		
DULIDAE (palm chats)																			
Dulus dominicus		E																	
VIREONIDAE (vireos)																			
Vireo nanus		E	_																
V. modestus			E																
V. crassirostris	Е													+					
V. gundlachii	E			Е															
V. latimeri V. osburni			Е	Е															
V. altiloquus	+	+	+	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+
V. magister														+					
PARULIDAE (wood warblers)																			
Dendroica angelae				\mathbf{E}															
D. petechia	+	+	+	+	+	+	+	+	+			+	+	+	+	+	+	+	+
D. adelaidae				+				+								+			
D. pityophila	+																		
D. pinus		+																	
D. vitellina			г											+					
D. pharetra			E		4														
D. plumbea					+		+			E									
Catharopeza bishopi Leucopeza semperi								E		ட									
Leucopeza semperi Microligea palustris		E						ن											
Xenoligia montana		E																	
Teretistris fernandinae	Е																		
T. fornsi	E																		

	Cuba	Hispaniola	Jamaica	Puerto Rico	Guadeloupe	Martinique	Dominica	St Lucia	Barbados	St Vincent	Grenada	Antigua	St Croix	Grand Cayman	St Kitts	Barbuda	,Montserrat	St Martin	St Thomas
COEREBIDAE (honeycreepers)																			
Coereba flaveola		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Cyanerpes cyaneus	+		_																
Euneornis campestris			E																
THRAUPIDAE (tanagers)																			
Euphonia musica		+		+	+	+	+	+		+	+	+				+	+		
Pyrrhuphonia jamaica			\mathbf{E}																
Tangara cucullata										+	+								
Spindalis zena	+	+	+	+										+					
Phaenicophilus palmarum		E																	
P. poliocephalus		E		_															
Neospingus speculiferus		Е		E															
Calyptophilus frugivorus		E																	
ICTERIDAE (troupials)																			
Molothrus bonariensis		+		+		+		+	+	+	+	+	I						
Quiscalus niger	+	+	+	+										+					
Q. lugubris					+	+	+	+	+	+	+	I			I	I	+		
Dives atroviolaceus	\mathbf{E}																		
Icterus dominicensis	+	+		+													_		
I. oberi I. laudabilis								Е									E		
I. tauaabuis I. bonana						Е		Е											
I. leucopteryx			+			Ľ								+					
Agelaius phoeniceus	+		•											•					
A. humeralis	+	+																	
A. xanthomus				E															
Nesopsar nigerrimus			E																
Sturnella magna	+																		
FRINGILLIDAE (finches)																			
Carduelis dominicensis		E																	
Loxia leucoptera		+																	
Volatinia jacarina											+								
Sporophila nigricollis											+								
Melopyrrha nigra	+													+					
Loxigilla portoricensis				+											+ x				
L. violacea		+	+																_
L. noctis					+	+	+	+	+	+	+	+			+	+	+	+	?
Melanospiza richardsoni								E											
Tiaris olivacea T. bicolor	+	+	+	+	_	_	_	_	_	_	_	_	_	+	_	_	_	_	_
T. canora	Е	т	т	т	т	т	т	т	т	т	т	т	т		т	т	т	т	т
Loxipasser anoxanthus	ட		Е																
Saltator albicollis			_		+	+	+	+											
Torreornis inexpectata	\mathbf{E}																		
Ammodramus savannarum		+	+	+															
Zonotrichia capensis		+																	