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# Neotropical land-bridge avifaunas: new approaches to null hypotheses in biogeography

Gary R. Graves and Nicholas J. Gotelli

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The construction of null hypotheses and statistical tests for non-random avian distributions has been vigorously debated by island biogeographers. Less attention has been given to the underlying quality of the data, which often consist of species lists from islands and adjacent mainland areas. We believe three major problems with past analyses make it difficult to interpret the results.

1. Source pools for statistical tests are constructed unrealistically. Arbitrary geopolitical units are used to define source pools. Archipelagos are analyzed as "closed" systems with equivalent source pools for all islands.
2. Habitat preferences and availability are not explicitly incorporated in null models.
3. Estimates of colonization potential based on species incidence functions may not be satisfactory. Incidence functions do not incorporate available habitat and distance effects.

We propose new organism-based methods for the analysis of birds on islands that incorporate geometrically standardized source pools, habitat availability, and geographic ranges of source pool species. We apply these methods in an analysis of seven Neotropical land-bridge island avifaunas. With few exceptions, land-bridge island communities appear to be a random subset of the mainland "habitat" pool, at the family level. A comparison of "total" and "habitat" pool shows that the habitat pool is a superior predictor of species richness in each family. Finally, species with widespread mainland ranges are disproportionately common on islands. Our results suggest that habitat availability and area of a species range are responsible for some of the differences between island and mainland communities.

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Построение 0-гипотезы и статистическая проверка нерандомических типов распределения птиц активно дебатировалась островными биогеографами. Меньшее внимание уделяется качественному содержанию полученных материалов, часто представляющих списки видов птиц с островов и прилегающих материковых территорий. Мы полагаем, что интерпретацию результатов затрудняют три, ранее проанализированные проблемы:

1. Пулы источников расселения для статистических анализов составляются нереалистично. Произвольные географические единицы используются для идентификации пулов. Архипелаги рассматриваются как "замкнутые" системы с эквивалентными пулами источников для всех островов.
2. Биотические предпочтения и доступность не включаются безоговорочно в 0-модели.
3. Определения потенциала колонизации на основании сферы функционирования видов не могут быть удовлетворительными. Сферы функционирования не включают доступность местообитаний и эффекты удаления.

Мы предлагаем новые методы, основанные на уровне организма, для анализа населения птиц на островах, которые включают геометрически стандартизированные пулы источников, доступность местообитания и географическое районирование пула местообитаний вида. Мы применяем эти методы для анализа 7-ми неотропических авиофаун сухопутного моста. За немногими исключениями, сообщества островов сухопутного моста представляют рандомический вариант материкового пула источников расселения на уровне семейств. Сравнение "общего" и "биотического" пула показывает, что пул источников расселения – основной фактор, определяющий богатство видов каждого семейства. Наконец, виды с широкими материковыми ареалами диспропорционально сходны на островах. Наши результаты показали, что доступность местообитаний и территория ареала вида определяет некоторые различия между сообществами островов и материка.

## 1. Introduction

For more than a century, the distribution of birds on islands has been a focal point in biogeography (Darwin 1859, MacArthur and Wilson 1967). Avian distributions are often claimed to manifest the effects of interspecific competition (Diamond 1975, Lack 1976), although the evidence has been hotly debated (Simberloff 1978a, Connor and Simberloff 1979, Strong et al. 1979, Grant and Abbott 1980, Wright and Biehl 1982, Diamond and Gilpin 1982). Island archipelagos, especially the Galapagos, West Indies, and New Hebrides, have been analyzed in many papers. Different authors have examined the same data and arrived at opposite conclusions about the effects of competition (e.g., Connor and Simberloff 1978 vis-a-vis Alatalo 1982). Much of this debate has been centered on the construction of null hypotheses and statistical tests for non-randomness. Less attention has been given to the underlying quality of the data. Consequently, we believe that three major problems with past analyses make it difficult to interpret the results:

- 1) Source pools for statistical tests are constructed unrealistically.
- 2) Habitat preferences are not explicitly incorporated into null models.
- 3) Estimates of colonization potential based on "incidence functions" are inadequate.

We discuss these three points in greater detail below and outline a new approach to the construction of source pools for null models in biogeography. We use this method to analyze avian distributions on seven Neotropical land-bridge islands.

### 1.1. Construction of appropriate source pools

Species pools have been constructed from the avifaunas of the mainland adjacent to an island or archipelago (Grant 1966, Simberloff 1970, Terborgh and Winter 1978, Faaborg 1979) or from the archipelago itself (Connor and Simberloff 1978, Gotelli and Abele 1982, Diamond 1982). With the exception of highly isolated archipelagos (e.g., Hawaiian and Galapagos islands) where most extant land bird species evolved in situ, the establishment of appropriate source pools is problematic. For instance, in an analysis of the Tres Marias Islands, Grant (1966: 452) used the species from an "equivalent part of the [Mexican] mainland (same area and range of altitude), similar habitats, etc." as the source pool. The four Tres Marias Islands parallel the coastline and span some 80 km, the largest water gap being ca. 15 km between Maria Magdalena and Maria Cleofas. Nevertheless, Grant considered the four islands as a unit with identical source pools.

In a reappraisal of species/genus ratios of the Tres Marias avifauna, Simberloff (1970) included all species within 300 miles of the islands, excluding Baja California. Simberloff (1983) includes all species resident be-

low 3000 ft. elevation in Nayarit, Sinaloa, and Jalisco (the adjacent states).

These approaches are not wholly satisfactory. If distance between source pool and island affects colonization probabilities (MacArthur and Wilson 1967), then source pools for widely separated islands are not identical. This is especially true in speciose regions where many terminal range boundaries occur on the adjacent mainland. In other words, source pool species within the arbitrary distance of one island (300 miles in Simberloff's analysis) may be outside that limit for another island in the same archipelago. This problem is exacerbated in large archipelagos colonized from several mainland regions (e.g., West Indies, East Indies).

West Indian source pools have traditionally been constructed from West Indian species only (Simberloff and Connor 1978, Gotelli and Abele 1982). The substantially larger number of mainland colonists from nearby areas are excluded, in spite of their close proximity. For example, Grenada is over 2500 km from western Cuba, but less than 175 km from the diverse South American mainland, the fauna of which is excluded from the analysis. Colonization probabilities may be weighted by observed incidences (Connor and Simberloff's [1978] Type II null model), but this procedure does not alleviate the problem of distance. For example, two single island endemics, the Zapata wren (*Ferminia cerverai*) and St. Vincent's parrot (*Amazona guildingii*), are given equal membership in the source pool for Grenada. Yet, the distance from Grenada to St. Vincent is only 145 km, whereas the Zapata Swamp (Cuba) is over 2400 km away.

Another problem is that biogeographers have relied too heavily on faunal lists from irregularly shaped geopolitical units. Admittedly, county, state, and country lists are more easily obtained than those of circular, standardized areas. However, political states are rarely comparable on the basis of size or shape. For example, in studies of land-bridge island birds, Terborgh and Winter (1978) and Faaborg (1979) used handbooks and field guides for selected countries to calculate mainland source pools. Faaborg (1979) defined the mainland source pool for Coiba, Rey, and San Jose to be all of the land birds of Panama, even though parts of Costa Rica and Colombia are much closer to the islands than are parts of Panama.

In sum, there has been no attempt to construct independent and geometrically standardized source pools for birds on land-bridge islands and archipelagos.

### 1.2. Habitat preference

Habitat diversity is a well-known predictor of species richness in regional avifaunas (MacArthur 1972, Lack 1976). Components of habitat diversity such as the number of plant species, altitude, or number of habitat types are cited in scores of publications on species richness.

We argue that habitat availability on islands is of primary importance in determining what subset of the mainland avifauna could successfully colonize and persist on any given island. We further suggest that the distinction between the "total" pool and the "habitat" pool is real and important in determining whether island avifaunas are random or non-random subsets of mainland avifaunas. The "total" pool consists of all mainland and island species within a geometrically standardized area. However, the "habitat" pool (a subset of the total pool) would include only those species that breed in the spectrum of habitats present on the island. Thus, both total and habitat pool are viewed from the frame of reference of the island. Membership in either pool should be limited to breeding species. The distinction between total pool and habitat pool is especially important when considering the colonization potential of a habitat specialist. For example, a bird species restricted to montane cloud forest would not be expected to successfully colonize a nearby desert island. Likewise, there is little evidence that avian habitat specialists broaden their habitat preferences enough to resist extinction during periods of severe environmental instability (Pregill and Olson 1981). The numerical difference between the total pool and habitat pool of a habitat-depauperate island and a diverse mainland or archipelago may be several fold.

Of course, all of these factors have been discussed in other studies of island avifaunas (Connor and Simberloff 1978, Wright and Biehl 1982, Grant and Abbott 1980). Indeed, the call for biologically realistic source pools has become a platitude in biogeography. The same data sets are analyzed and reanalyzed without adequate consideration of habitat preferences and mainland community organization. This naive reliance on total pool calculations, with little regard to autecology of the organisms, may distort the analyses of structure in island communities.

### 1.3. Differences in colonization potential

Production of dispersing propagules per unit time, their probability of successfully colonizing an island, and longevity of subsequent populations are undoubtedly species specific. Unfortunately, these demographic parameters are not known for any bird species, much less all the species of an island's source pool. Incidence functions (Diamond 1975, Whittam and Siegel-Causey 1981) are often used to weigh a species probability of colonization (Simberloff and Connor 1978). Usually, these probabilities are generated from, and used to test, the same island distributions. This constraint generates a certain amount of nonindependence (Grant and Abbott 1980), which may or may not affect the power of statistical tests.

A more serious problem is that the use of incidence functions implies that all islands are available for colonization, when in reality, appropriate habitat is rarely

present on every site. This same criticism applies to the analysis of "checkerboard" distributions (Gilpin and Diamond 1982).

One indication of colonization potential is the extent of a species geographic range. We expect colonization potential to be roughly proportional to geographic range: widespread species have more dispersing individuals and are more likely to colonize and persist on islands than are species with very restricted distributions (see Hengeveld and Haeck 1981). We predict that source pool species with restricted distributions will be under-represented in island communities, everything else being equal.

Determination of widespread versus restricted distributions has been attempted for source pool species of Neotropical land-bridge islands (Faaborg 1979). Faaborg classified species that occur in both Panama and northeastern Venezuela as "widespread". These species occurring in either Panama or north-eastern Venezuela, but not both, were not discussed, but are implied to be "restricted". This classification technique is useful because one merely has to compare species lists. However, some species with tremendous ranges ( $>5 \times 10^6 \text{ km}^2$ ) are not classified as widespread by this criterion. Other species with relatively small areal ranges (e.g., *Phaethornis anthophilus*, *Melanerpes rubricapillus*) occur in both areas, and are classified as widespread. Ideally, the entire geographic range of each source pool species should be estimated, or assigned to a size class. Handbooks and field guides are usually unsuitable for this purpose.

Problems in the construction of realistic source pools and in the estimation of colonization probabilities make it difficult to evaluate the results of previous studies. This does not imply that null hypotheses are of no value, as has been suggested (Dunbar 1980, Diamond and Gilpin 1982, Roughgarden, in press). It does mean that source pools will have to be carefully designated with biologically realistic criteria.

Here we construct realistic source pools for seven Neotropical land-bridge islands. In this paper, we use these data to ask two questions:

- 1) At the family level, are island communities a non-random subset of adjacent mainland communities?
- 2) Are species with restricted mainland distributions under-represented on land-bridge islands?

## 2. Materials and methods

Present day avifaunas of land-bridge islands are often viewed as persisting subsets of the avifauna of the once connected mainland (Diamond 1972, Terborgh 1974, Faaborg 1979). These analyses assume that the avifaunas of the islands and mainland were identical at the time of disconnection by rising sea level. In this scenario, mainland communities have remained stable since disconnection, whereas the "super-saturated"

land-bridge islands relaxed to an appropriate equilibrium species number. All extant island species are presumed to have been continuous breeding residents since separation from the mainland. However, there is considerable evidence that the Caribbean coastal region of South America was much drier during the Pleistocene (Bradbury et al. 1981). If so, mesic vegetation and the associated avifauna may have recolonized land-bridge islands in the Holocene. Extinction of an island species and its subsequent recolonization cannot be detected.

Faaborg (1979) qualitatively analyzed avifaunas of four Neotropical land-bridge islands. His methods of source pool construction and categorization of widespread species were discussed in our introduction. In this paper, we analyze the distribution of families and widespread versus geographically restricted species on seven land-bridge islands (Fig. 1). Whereas Faaborg (1979) chose islands on the basis of habitat similarity, we purposely included islands with a diverse array of habitat types. Our aim is an overview of family distributions in a variety of habitat/island environments.

In our analysis we include only land bird families (Columbidae through Corvidae). Bird families ecologically dependent on water (Alcedinidae), those possibly exterminated or transported by Amerindians (Tinamidae, Cracidae, Phasianidae), or those whose breeding status is routinely questionable (Apodidae, Falconiformes) were excluded. We follow the arrangement of families and subfamilies and taxonomy of Morony et al. (1975), unless recent papers suggest otherwise.

We constructed source pools by the following method. Using the island location nearest the adjacent mainland as the center point, we drafted circles of various diameters on maps (map scales 1:1,000,000 to 1:250,000). Since Trinidad has the largest avifauna of the islands examined, it was used as the standard. If small radii circles are used (ca. 50–100 km), the resulting mainland source pool lacks many species found on Trinidad. On the other hand, if the radius is increased to

500 km, many habitats are included in the source pool which do not occur on Trinidad. This situation is more or less true for all seven islands. As an arbitrary compromise, we chose 300 km as an appropriate radius for source pool designation for this system. Source pools for the seven islands range from 399 species for Tobago to 560 species for San Jose and Rey (see Tab. 1). All land-bird species breeding within the source pool circle on the mainland and all adjacent land-bridge islands, were included in a particular source pool. For example, the breeding birds of Trinidad, Tobago, adjacent South America, and parts of Margarita were included in the source pool for Trinidad; birds of oceanic islands (e.g., Grenada) were excluded because they could have colonized only over water.

For this analysis we regard Aruba as a land-bridge island. Oceanographic charts suggest that during the lowest sea level (~130 m lower) of the Wisconsin glacial, Aruba was separated from the mainland by ca. 3–5 km water. Although this relatively narrow water barrier may have prevented colonization by some terrestrial species, we do not believe this greatly affected colonization by land-birds. Antbirds and tinamous regularly cross large water gaps to recolonize once-flooded islands in the Amazon River (Remsen and Parker 1983).

To calculate the habitat pool, we assume that source pool species that occur only in habitats not found on islands would not be expected to occur on the islands. This is not the same as saying that "if a species does not occur on an island, one wouldn't expect it to." There are certain species that for all intents and purposes have zero probability of colonizing a particular island lacking its preferred habitat. Furthermore, if the preferred habitat of a habitat specialist was eliminated by climatic change, the probability is zero that it would occur on the island today. For example, burrowing owls (*Speotyto cunicularia*) no longer occur in many areas in the Caribbean because the habitat has changed from savannah and xerophytic scrub to forest (Pregill and Olson 1981).

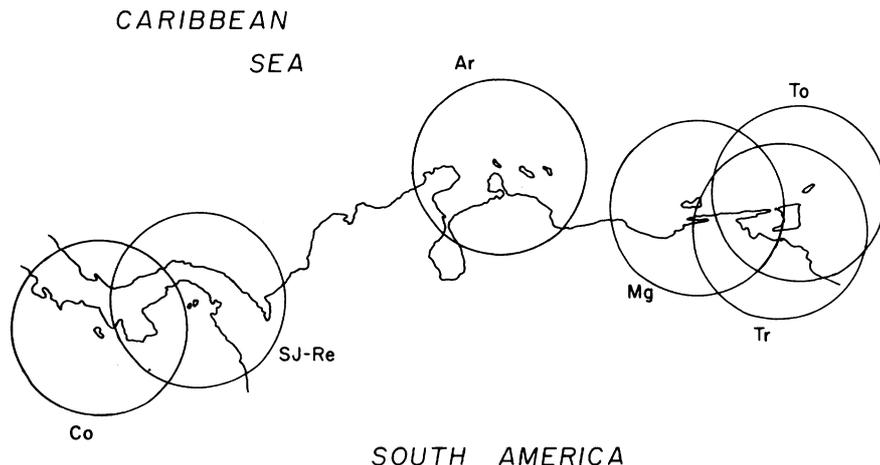


Fig. 1. Source pool circles for 7 Neotropical land-bridge islands. Co-Coiba; SJ = San Jose; Re = Rey; Ar = Aruba; Mg = Margarita; Tr = Trinidad; To = Tobago. The circles have a radius of 300 km and are drafted from the closest approach of the island to the mainland. The same circle was used for San Jose and Rey.

Tab. 1. Number of breeding land bird species in the total pool and habitat pool of seven land-bridge islands.

	Total pool	Habitat pool	Island
Trinidad .....	470	445	190
Tobago .....	399	342	77
Margarita .....	456	231	63
Coiba .....	513	348	64
Aruba .....	434	121	25
San Jose .....	560	390	36
Rey .....	560	390	38

A number of distinctive habitat types occur on the islands, such as mangroves, palm savannah, xerophytic scrub, columnar cactus, lowland rain forest, lower montane cloud forest, and grassland. A habitat was considered present on an island if the total area of the habitat exceeded ca. 50 ha. We considered the spectrum of habitats on each island. Then we compared habitat availability on the island with the habitat preferences of non-island species occurring within the source pool circle. We classified each species in the "total pool" or "habitat pool" on a case-by-case basis.

For islands with great habitat diversity, the difference between total pool and habitat pool is small (e.g., Trinidad, total pool 470 species; habitat pool 445 species). Other large, but habitat depauperate, islands have much smaller habitat pools (e.g., Aruba, total pool 434 species; habitat pool 121 species). For this system there is no significant correlation between island area and size of either total or habitat pools. Additionally, there is no correlation between distance from the mainland and the size of total and habitat pools. In this analysis, we include two of the Pearl islands, San Jose and Rey, in the Gulf of Panama. The distance between San Jose and Rey is less than 11 km. These islands were connected to each other since their separation from the mainland, so we assume they share an identical source pool, which was calculated from the closest point on Rey. Source pools for the remaining five islands were calculated separately (see Fig. 1). Lists of species for islands, habitat pools, and total pools are based on original technical literature (Appendix 1), gazeteers, maps, and the examination of museum specimens in the Louisiana State University Museum of Zoology, and the American Museum of Natural History.

To assess colonization potential, we categorized the geographical ranges of all 937 species occurring in the individual source pools. By definition, the terms "widespread" and "restricted" are arbitrary. Many species mentioned by Haffer (1974) as "Amazonian endemics" have ranges exceeding  $1 \times 10^6$  km<sup>2</sup>. Terborgh and Winter (1978) used the criterion of <50000 km<sup>2</sup> as a cut off point, although more than one of their examples exceeds that limit (e.g. *Leptosittaca branickii*).

A few mis-classifications are inevitable, and probably would not affect the results.

In this analysis, we considered the global ranges of all source pool species. We use two classification types to categorize geographical range. Assuming that total areal range is important, but disregarding the shape of the range boundary, we estimated the number of 1° latitude × 1° longitude blocks in which a species occurs. By this classification (Type I), if a species occurs in 100 or more 1° × 1° blocks, it is considered "widespread". Type I "restricted" species occur in less than 100 1° × 1° blocks (Fig. 2). In a Type II classification, we also consider the shape of species range. If the entire world range of a species is contained in a centered 10° latitude × 10° longitude block, it is considered "restricted". If the geographical range cannot be fitted in a 10° × 10° block, the species is "widespread", regardless of the area of its distribution. We use the Type II classification because many Neotropical species have long and nar-

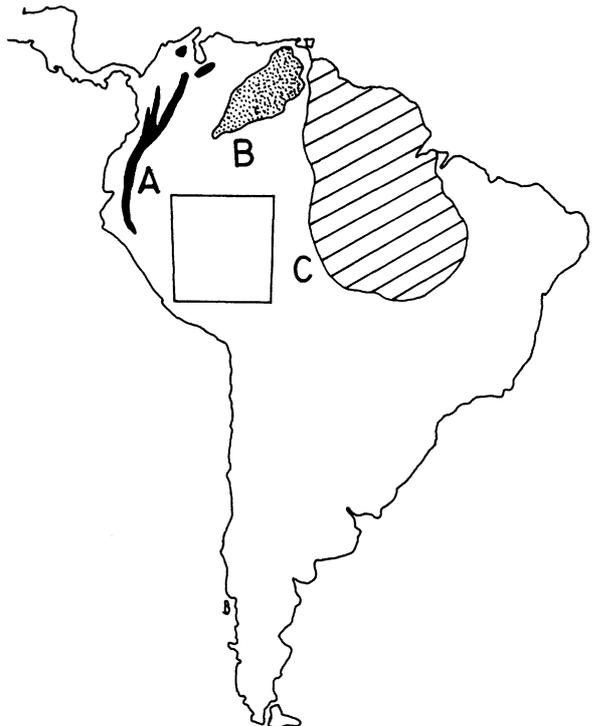


Fig. 2. Distributions of three hypothetical South American species: A, B and C. A 10° longitude × 10° latitude block is shown for comparison. Species A is considered "restricted" by Type I classification: its total areal range is less than 100 1° × 1° blocks. However, species A is considered "widespread" by the Type II classification. Its geographic range does not fit within a centered 10° × 10° block. Species B is "restricted" by both Type I and Type II classifications because its areal range is less than 100 1° × 1° blocks, and is encompassed by a centered 10° × 10° block. Species C is "widespread" by both classifications: its areal range is greater than 100 1° × 1° blocks.

row, or highly disjunct, geographical ranges, with small total areas. These species may be better colonists than the area of their geographic range would suggest.

### 3. Results

#### 3.1. The distribution of families on islands

We ask, are individual families over- or under-represented in island communities? We calculate the expected number of species in family I on island J as:

$$E(IJ) = F(I)N(J)/NN(J)$$

where NN(J) is the number of species in the source pool

for island J, and F(I) is the number of source pool species in family I. The total number of species on island J is given by N(J). In other words, we test the hypothesis that each family is represented on an island in the same proportion as in the source pool. Deviations from this expectation follow a hypergeometric distribution, sampling without replacement (Appendix 2).

For each family on each island, we calculated the exact tail probabilities for the observed species number, drawing from the habitat pools. Tab. 2 is a matrix of the significant tail probabilities. Only two negative deviations were extreme: parrots are under-represented on Tobago (expected = 4.4, observed = 1, p = 0.04), and antbirds are under-represented on Trinidad (expected = 15.1, observed = 9, p = 0.021). Ten of the 230 cells also showed significant positive deviations, mostly in the

Tab. 2. Significant deviations from the hypergeometric model, drawing from the habitat pool. A plus (+) means that more species in a family are present than expected by chance. A minus (-) indicates that fewer species are found than expected. A zero (0) means the family is not in the available habitat pool for the island. If no entry is given, the probability is >0.10 (0.05, 2-tailed) for that observation.

Family	Island						
	Tobago	Trinidad	Margarita	Aruba	Rey	San Jose	Coiba
Columbidae		++	+	+++			
Psittacidae	-						++
Cuculidae							
Tytonidae							
Strigidae							
Steatornithidae				0			0
Nyctibiidae				0			
Caprimulgidae							
Trochilidae							
Trogonidae			0	0			
Momotidae				0			
Galbulidae							
Bucconidae							
Capitonidae	0	0	0	0			
Ramphastidae			0	0			
Picidae							
Dendrocolaptidae							
Furnariidae							
Formicariidae		--					
Cotingidae				0			
Pipridae							
Tyrannidae					+	++	++
Hirundinidae							
Motacillidae				0			
Troglodytidae							0
Mimidae							0
Turdinae	+	++					
Poliophtilinae							
Vireonidae							
Emberizinae							
Thraupinae							
Tersininae							
Parulidae							++
Icteridae							
Corvidae							

\* p < 0.05.  
 \*\* p < 0.025.  
 \*\*\* p < 0.01.  
 0 not in habitat pool.

pigeons and flycatchers. The remaining observations did not differ significantly from the expected at the 0.10 level (0.05, two-tailed).

To assess the overall distribution of each family, we combined probabilities across islands using Fisher's test (Sokal and Rohlf 1969), which has a Chi-square distribution (Tab. 3). By this criterion, pigeons, flycatchers and warblers are consistently over-represented on islands. All other families are found in about the same proportions as their mainland source pools. Thus, no family is consistently under-represented.

Again, the results are similar using both total pools and habitat pools. However, tail probabilities are generally more extreme for the total pool than for the more realistic habitat pool. Using the habitat pool, the correlation ( $R^2$ ) between observed and expected species number for each family is 0.67 (Fig. 3). However, using the total pool expected values, the correlation between observed and expected is only 0.62. The difference between these two models is significant ( $p < 0.01$ ); as anticipated, values from the habitat pool are a superior predictor of species richness in each family. At the family level, some of the differences between island and mainland avifaunas are directly attributable to differences in available habitat.

### 3.2. Number of families on islands

One indicator of taxonomic diversity is the species/genus ratio which has often been used to compare island and mainland avifaunas (Järvinen 1982). Species/genus and species/family ratios have been traditionally interpreted as indicators of interspecific competition, although other mechanisms could also produce non-randomness (Dillon 1981). Here, we used rarefaction (Simberloff 1978b) to estimate the expected number of families per island, relative to the mainland habitat pools. The number of families on each island is consistent with the expected value (Fig. 4); deviations from the expected are uncorrelated with island area. Thus, these islands are not depauperate in families, relative to adjacent mainland communities. The rarefaction results for habitat pools and total pools are nearly identical.

### 3.3. Rare and missing families

Of the forty families in our mainland source pools, eight families are present on no islands, and four families are found on only one of the seven islands. Here, we test whether these distributions are anomalous. For five of the eight missing families, appropriate habitats are absent on all islands. These missing families require no statistical explanation. For the remaining seven families, we used the hypergeometric model to estimate  $P(OI)$ , the probability of the family being absent from island  $I$ . The probability of occurrence is thus  $1 - P(OI)$ . Joint probabilities for the observed number of occurrences

Tab. 3. Fisher's combined probabilities for overall family distributions ( $-2 \sum \ln(p) = \chi^2$ ,  $df = 2n$ ). Fisher's test for combining probabilities was used to evaluate the tail probabilities for each family, across all islands. These tail probabilities are from the hypergeometric model, sampling without replacement from the habitat pool (see Appendix 2).

Family	Observed < expected	Observed > expected
Columbidae	0.48	41.27**
Psittacidae	10.73	13.34
Cuculidae	4.97	9.63
Tytonidae	1.06	12.10
Strigidae	7.54	6.34
Steatornithidae	0.91	1.72
Nyctibiidae	2.71	2.60
Caprimulgidae	1.93	15.43
Trochilidae	7.03	9.24
Trogonidae	6.06	3.27
Momotidae	3.79	4.65
Galbulidae	6.48	2.02
Bucconidae	14.94	0.98
Capitonidae	0.79	0.00
Ramphastidae	7.46	0.24
Picidae	12.70	2.51
Dendrocolaptidae	15.05	3.35
Furnariidae	10.09	2.35
Formicariidae	16.39	3.27
Rhinocryptidae	—	—
Cotingidae	16.45	0.31
Pipridae	10.72	2.32
Tyrannidae	8.38	27.25*
Oxyruncidae	—	—
Hirundinidae	3.98	10.21
Motacillidae	3.04	0.00
Ptiligonatinae	—	—
Cinclidae	—	—
Troglodytidae	12.48	3.42
Mimidae	1.28	8.36
Turdinae	1.44	20.26
Poliophtilinae	2.56	7.21
Vireonidae	3.57	14.35
Emberizinae	10.19	10.37
Catamblyrhynchinae	—	—
Thraupinae	9.71	9.42
Tersininae	0.92	1.73
Parulidae	2.39	26.12*
Icteridae	8.17	8.39
Corvidae	6.50	0.00

\*  $p < 0.05$ .

\*\*  $p < 0.01$ .

can be calculated directly as products of the  $P$ 's and  $1 - P$ 's (Feller 1968). Thus, the probability of seven absences is the product of the seven  $P(OI)$ 's. The probability of one or fewer occurrences is the probability of seven absences plus the seven combinations of the probability of occurrence on each island. These tail probabilities are given in Tab. 4, using both total pools and habitat pools to estimate the  $P(OI)$ 's.

By this test, puffbirds are absent more often than expected. The only island puffbird, *Hypnellus ruficollis*, occurs on Margarita; the probability of this one occurrence is 0.007. No jays (Corvidae) are found on

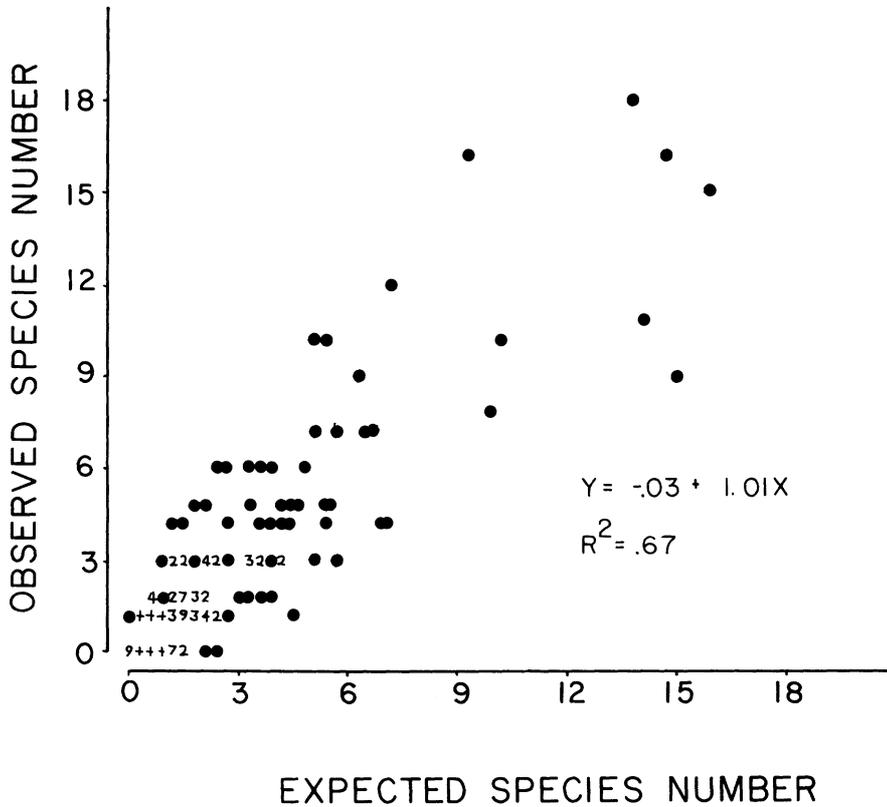
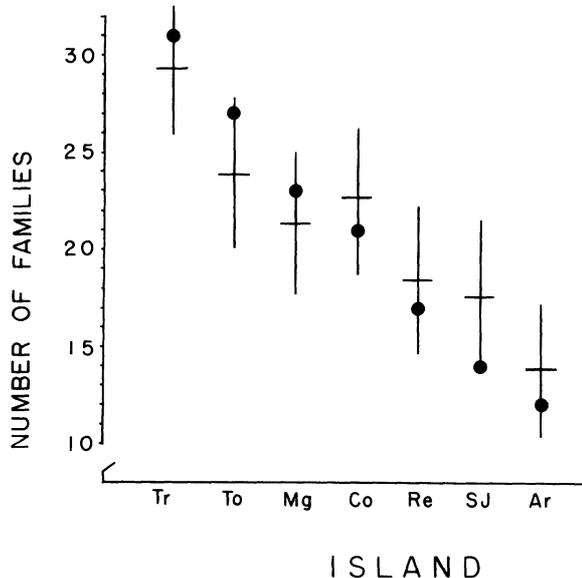


Fig. 3. Observed and expected species number on all islands. Each point is a family on an island. A plus (+) indicates 10 or more points. The expected values are generated from Eq. 1, using the habitat pool. The regression line was fitted through all points ( $n = 226$ ) although they are not truly independent. We calculated a weighted-least squares regression, using the variances from the hypergeometric model (Eq. 2) as the weights. This procedure compensates for nonuniform scatter of the data. One outlier was omitted (Trinidad flycatchers obs. = 31, exp. = 32.5), which did not affect the calculations.



any of these islands. However, the probability of this event is not too extreme ( $p = 0.039$ ). If Trinidad is excluded from the calculation, the probability of no occurrences on the other six islands is only 0.203. Except for the puffbirds, these families are not missing more often than one would expect by chance. In par-

Tab. 4. Tail probabilities for uncommon families. Probabilities are given for the observed number of occurrences or fewer on the 7 islands. For 5 families, no habitat was available on the island; otherwise, tail probabilities are calculated using both total pool and the habitat pool.

Family	no. of occurrences	Tail probability	
		Total pool	Habitat pool
Steatornithidae	1	0.778	0.695
Bucconidae	1	0.014	0.007
Capitonidae	0	0.423	0.674
Ramphastidae	1	0.056	0.081
Rhinocryptidae	0	0.246	-
Oxyruncidae	0	0.766	-
Motacillidae	0	0.316	0.218
Ptilonotinae	0	0.670	-
Cinclidae	0	0.723	-
Catamblyrhynchinae	0	0.816	-
Tersininae	1	0.779	0.817
Corvidae	0	0.043	0.039

Fig. 4. Observed and expected number of families on each island. The horizontal bar is the expected number calculated by rarefaction from the habitat pools. The vertical line is a 95% confidence interval. Circles are the observed number of families on each island. Abbreviations are in Fig. 1. Order of islands is arbitrary.

ticular, note that lack of preferred habitats on the islands is directly responsible for five of the eight absences. Again, the results are quite similar if total pools rather than habitat pools are used to estimate the  $P(OI)$ 's.

### 3.4. Range distributions

Null models which assume all species are equiprobable colonists are unrealistic, because species vary in their ability to disperse, invade, and persist on islands (Baker and Stebbins 1958).

Using the hypergeometric model, we tested whether species with restricted distributions (Type I or Type II) are represented on islands in the same proportion as on the mainland. For this analysis, we ignored familial status, and simply considered the total numbers of widespread and restricted species. Again, the statistics were calculated using both the total pool and the habitat pool as reference distributions. We conducted separate analyses for Type I and Type II classifications.

For Type I distributions, we reject the null for four of seven islands; Trinidad, Coiba, San Jose, and Rey have significantly fewer Type I restricted species than expected (Fig. 5). Aruba also has fewer restricted species than expected, whereas Margarita and Tobago have slightly more. Surprisingly, the results are nearly identical for Type II restricted species: Coiba, San Jose, and Rey have fewer Type II restricted species than expected; Trinidad is marginally nonsignificant ( $p = 0.058$ ). Although Type I and Type II distributions are similar for total species number, differences may exist at the family level.

If these analyses are repeated using the total pool, the deviations are more extreme. For Type I restricted species, for example, we reject the null on all seven islands. Using the more realistic habitat pool, we reject on only four of the seven islands. Using the total pools artificially inflates the expected number of restricted species on these islands. But even after taking account of habitat, there is still a strong tendency for species with restricted mainland distributions to be under-represented on islands.

In summary, land-bridge island communities appear to be a random subset of the mainland habitat pool, at the family level, with a few exceptions. When geographic range is considered, island communities do not appear to be a random subset; species with widespread mainland ranges are disproportionately common on several islands.

## 4. Discussion

Interspecific competition has been suggested as a mechanism limiting the number of confamilial species occurring on islands (Terborgh 1973, Lack 1976). Implicit in these studies is the assumption that species in a

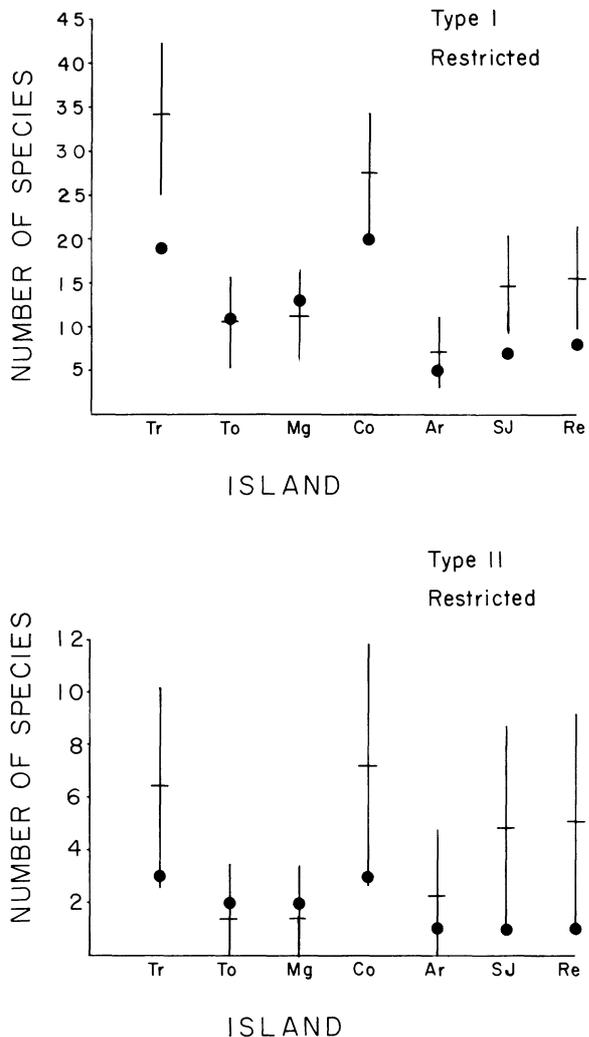


Fig. 5. Observed and expected numbers of species with "restricted" mainland distributions. The horizontal bar is the expected value from the hypergeometric model, drawing from the habitat pools. Total numbers of "restricted" species are shown on each island, using the Type I and Type II classifications (see text).

family behave like a guild: "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967). Several null hypotheses have been constructed at the family level with the hope of detecting such competitive effects (Connor and Simberloff 1979, Gotelli and Abele 1982). Gilpin and Diamond (1982) have criticized this approach; they correctly observe that bird families are rarely equivalent to ecological guilds. Their analyses of New Hebrides bird distributions are based on a "group of ecologically related species that share food resources and foraging technique . . ." (Diamond and Gilpin 1982: 65).

Unfortunately, Diamond and Gilpin's groupings also

fail to meet Root's original criterion. Namely, guilds must not be defined by taxonomic units but by resources (Jaksić 1981, MacMahon et al. 1981). For example, the New Hebrides fruit eating guild should include, among others, all fruit eating bats, rodents, insects and birds in the community. Fruit eating birds, do not in themselves constitute a true guild, only an assemblage (sensu Jaksić 1981). Assemblages may represent groups of species most likely to be competing, but this is not the same thing as a guild.

For the sake of argument, we assume that Diamond and Gilpin have correctly identified assemblages of potential competitors. This approach may work for a few well defined groups, but will fail for complex Neotropical avifaunas. There are too many species with poorly known feeding habits to define resource-based groups. Moreover, many species are opportunistic feeders with catholic diets, which may vary seasonally and regionally. This makes it nearly impossible to define feeding assemblages for entire avifaunas, except perhaps on the basis of crude dietary categories (e.g. fruits, seeds, nectar), that may not represent true resource overlap.

Consequently, we have limited our analysis to families. We do not believe families represent units of interspecific competition. However, species within a family are usually ecologically and morphologically similar; therefore non-randomness of island avifaunas may be detected at the family level.

Using a simple null model which assumes all source pool species are equiprobable colonists, we find that three families are unusually common on land-bridge islands: pigeons, flycatchers, and warblers. In contrast to other studies (Terborgh and Winter 1978, Faaborg 1979) our analysis did not reveal many 'extinction-prone' families. Only one family of 40, the *Bucconidae*, was present less often than expected. These results suggest that the proportional representation of most families on islands is consistent with mainland source pools. But in terms of absolute numbers, many species and families are missing from these islands.

Terborgh (1973) and Faaborg (1979, 1980), have used linear regressions to examine the problem of missing families on islands. Faaborg (1979) regressed species number in a family versus total species number on an island or mainland community. He considered the  $x$  value at the point  $y = 1$ , to be the minimum community size in which a given family will persist. Faaborg does not present confidence bands for these estimates, although such intervals are notoriously broad for these sorts of data (Haas 1975, Gilbert 1980, Boecklen and Gotelli in press). A more serious statistical problem is that total family size puts a constraint on these regressions. In fact, for Terborgh (1973) and Faaborg's (1979) analyses, the regression slopes are highly correlated with family size (Gotelli and Abele 1982). This problem complicates any comparison of regression lines among families. Our null models avoid these problems by directly incorporating family size.

An important constraint in our model is the total number of species on the island. If this variable is influenced by species interactions, then we have incorporated competitive effects into our null model (Diamond and Gilpin 1982). However, we are not addressing species interactions with this test; instead, we are examining whether island avifaunas appear to be a random subset of adjacent mainland communities. Thus, we are emphasizing patterns in the data, rather than mechanisms that have produced them. Island data could indicate no deviations from randomness, even though the mainland source pools are highly structured by deterministic mechanisms. Interspecific competition could influence habitat use on islands (Ricklefs and Cox 1978), as well as determine mainland range boundaries (Terborgh and Weske 1975). However, these problems require more data and cannot be addressed with an analysis of species lists.

Although we are unsure about competitive effects, we have shown the importance of two factors on land-bridge avifaunas: available habitat and mainland geographic ranges. Results from total and habitat pools are qualitatively similar for all analyses. This is reassuring, because it means the conclusions are robust to minor changes in the source pool. However, a statistical comparison of total and habitat pools shows that the habitat pool is a superior predictor of species richness in each family. Thus, the presence of available habitat is one factor which contributes to differences between island and mainland bird communities. If available habitat were not an important variable, then the total pool would have served just as well. Accordingly, we are suspicious of faunal collapse models for land-bridge islands, because these models imply that habitat changes since the Pleistocene have not affected extinction or recolonization.

We have also shown that geographic range is correlated with persistence of species on islands. Namely, species with restricted mainland distributions are under-represented on land-bridge islands. Although area of a species range is an important factor, we were surprised to find that shape of the range is not. The Type I and Type II distributions were nearly identical with respect to the expected values. Although the shape of the range may be important, we did not detect differences.

In summary, our methods attempt to correct some of the deficiencies of previous work. Our results suggest that available habitat and mainland geographic ranges affect the colonization potential of individual species. These autecological factors, which must be studied on a species by species basis, are probably the most important determinants of island community structure. The excessive attention devoted to inferences of interspecific competition from species lists is unlikely to reveal much more about island communities. Future studies should focus on the autecological characteristics of colonizing species, and on the available habitats and resources of islands.

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**Appendix 1.** Principle literature sources for the construction of source pools

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**Appendix 2.** Consider a source pool of N equiprobable colonizing species, and a single family in the pool with F species. For a community of n species drawn from this pool, the expected number of species in the family is:

$$E = \frac{nF}{N} \quad (1)$$

and the variance is:

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

The probability of drawing X or fewer species is:

$$P(X \leq c) = \sum_{x=0}^c \frac{\binom{F}{x} \binom{N-F}{n-x}}{\binom{N}{n}} \quad (3)$$

We used Eq. 3 to test whether the observed number of species in any family deviated from the expected. A rough confidence interval about the expected value is given by  $\pm 2$  sd. We graphed this confidence interval in Fig. 5, although we used exact tail probabilities in all statistical tests.

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