Distributional Ecology of Selected Plants and Animals on Trinidad's Five Islands Archipelago

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Studies of the distributions of island-dwelling species have expanded our understanding of the factors that determine the structure and composition of island communities. Several generalities have emerged (Gorman 1979). All else being equal, there are fewer species on an island than on a comparable mainland area of the same size; the number of species on an island increases in a predictable way with increasing island area; the number of species on an island increases as habitat diversity on an island increases; the number of species on an island may be in a dynamic equilibrium; and the species found on islands are a non-random subset of the nearby continental biota.

In 1995, students from my class in "Caribbean Island Ecology" at the University of the West Indies assisted me in a survey of woody plants, land snails, ants, reptiles and land birds on the Five Island Archipelago. I report here on the results of those surveys and how well they conform to general theoretical predictions about island communities.

The Study Sites

The Five Islands (Nelson, Caledonia, Lenagan, Pelican, Rock and Craig), also known as The Cotorras, are a group of 6 small, low, arid, limestone islands in the Gulf of Paria (Figure 1). Two of the islands, Caledonia and Craig, are connected by a narrow isthmus at low tide, hence the seemingly inappropriate name for a group of 6 islands. They lie about 2.5 km south of the Chagaramas Peninsula of northwestern Trinidad. Prior to being disturbed by human activities, the parts of islands with soil were probably dominated by tropical semi-deciduous forests (Beard 1946). All of the islands have had permanent human dwellings on them in the past, but none has been inhabited on a regular basis since 1990. Table 1 summarizes some of the features of each island that could be estimated either in the field or from aerial photographs. It is habitat diversity.

A "mainland" site on Point Gourde on the south shore of the Chaguaramas Peninsula was used for some comparative studies. The 2.5-ha site was located in the Chaguaramas National Park about 4 km northwest of the Five Islands. It was similar to the Five Islands in its geology, climate and vegetation.

Methods

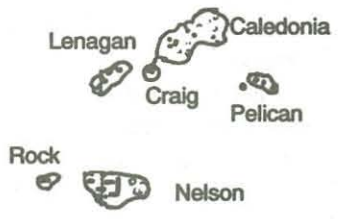
On February 10-11, 1995, a team of 30 investigators (see Acknowledgements) conducted surveys of five groups of relatively conspicuous organisms on the Five Islands: woody plants, land snails, ants, reptiles and land birds. Each island, except Craig Island, was surveyed with approximately equal effort, about 6-7 person-hours per island for each taxonomic group. Tiny Craig Island was surveyed for only 4.5 person-hours. During the surveys, investigators attempted to search as much of each island as possible. Woody plant surveyors collected samples of each species they encountered and preserved them in plant presses for subsequent identification . Snail surveyors searched for living terrestrial snails or their shells and collected specimens of each species they encountered for subsequent identification. Ant surveyors searched for ants, collected specimens of each species they encountered and preserved them in ethanol for subsequent identification. Reptile and bird surveyors identified specimens visually in the field and recorded the species they encountered. When constructing the bird lists, I excluded some wide-ranging species, such as vultures, shorebirds and swifts, that regularly visit the islands but do not reside on them.

For each taxonomic group and island, the surveyors recorded the time when they encountered each species. These times allowed me to construct species-accumulation curves that plotted the rate at which new species were discovered on each island. Two examples of such species-accumulation curves, for birds and reptiles on Caledonia Island, are shown in Figure2. Examination of these species-accumulation curves revealed whether or not the discovery of new species had reached an asymptote during the surveys. If an asymptote had been reached, I interpreted this to mean that all but the rarest and most inconspicuous species had probably been discovered. The 30 curves (for different combinations of islands and a taxonomic groups) suggested that the surveyors had found most of the snails, ants and birds on every island (e.g., see Figure 2A), but that they had not yet found all the woody plants and reptiles on some islands (e.g., see Figure 2B).

Table 1. Physical and ecological features of the Five Islands

Features of Islands	Caledonia Island	Nelson Island	Lenagan Island	Pelican Island	Rock Island	Craig Island
Area (ha)	2.50	1.68	0.45	0.20	0.12	0.06
Elevation (m)	40	15	15	5	5	20
Forest Cover(%)	80	8	60	40	80	30
Grass Cover(%)	3	60	5	2	0	0
Rock Cover(%)	10	15	30	70	20	70
Building Cover(%)	7	20	20	12	80	80
Number of buildings	7	10	5	3	1	1
Canopy Height(m)	15	1	10	3	3	5

Right: Figure 1- Map of the Five Islands Above : Table 1



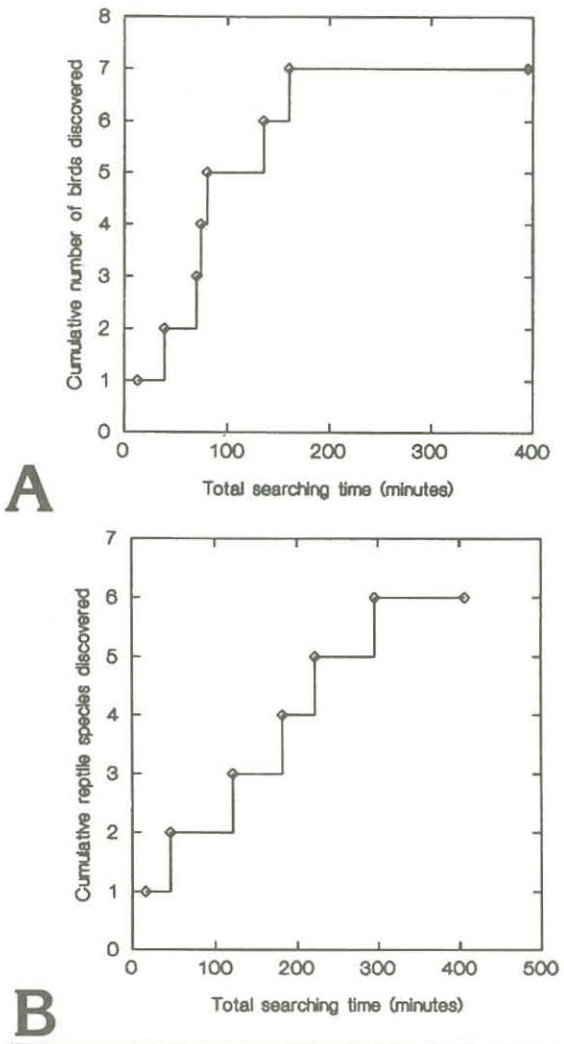


Figure 2. Species accumilation curves for bird species (A) and reptile species (B) on Caledonia Island

Specimens of woody plants, snails and ants were sorted into different "morphological types" that appeared to represent different species. Woody plants were subsequently identified to species with the assistance of the National Herbarium and appropriate references. Snails were not identified to species. Ants were sent to an ant specialist, Mark DuBois of the Illinois Natural History Survey, for specific identification.

When the species lists for each island were completed, I used correlation analyses to detect relationships between the number of species on an island and the island's features. I also created species-area curves that plotted the number of species on each of the islands against each island's area. I described the species-area curve for each taxonomic group using the power function equation, $S = cA^Z$, where S = number of species, A = island area, and c and z are constants that are taxa-specific. I used a computer program (SYSTAT) to fit curves to the points on each graph of species versus area. The values of "c" and "z" in the equation $S = cA^Z$ were determined by the SYTAT program.

Results

The distribution of species among islands is presented in Table 2. The numbers of species on each island are summarized as follows: Caledonia (32 plants, 6 snails, 6 ants, 6 reptiles and 7 birds), Nelson (18 plants, 5 snails, 8 ants, 7 reptiles and 6 birds), Lenagan (15 plants, 5 snails, 5 ants, 6 reptiles and 5 birds), Pelican (13 plants, 3 snails, 7 ants, 2 reptiles and 3 birds), Rock (10 plants, 2 snails, 5 ants, 3 reptiles and 4 birds), Craig (5 plants, 2 snails, 5 ants, 1 reptile, and 2 birds). Correlation analyses revealed that there were several strong relationships between the number of species on islands and island features, especially island area . Table 3 summarizes the correlations that were statistically significant ($p < 0.10$).

Species-area curves for the Five Islands revealed that the number of species in each taxonomic group is a power function of island area (Figure 3). The values of z in the species-area equations for these curves, except for ants (see discussion below), fall within a typical and relatively narrow range of values: for plants (S = 19.71 A 0.378), for snails (S = 4.69 A 0.271), for ants (S = 6.44 A 0.077), for reptiles (S = 5.27 A 0.321), and for birds (S = 5.47 A 0.260).

During a 7-hour survey of the 2.5-ha site on the Chaguaramas Peninsula, I detected 21 bird species, and the species-accumulation curve for this survey suggested there were additional species that had not been detected. All 8 of the birds detected on the Five Islands were detected on the "mainland" site.

Discussion

These results can be interpreted in light of theoretical predictions and empirical results from other studies. This discussion focuses on 5 features of islands: the impoverishment of island biotas relative to continents, the species-area relationship on islands, the influence of habitat diversity on species diversity, the dynamic equilibrium of species numbers on islands, and the non-random sample of continental species on islands.

Impoverishment of island biotas.--The comparison of bird species on the Five Islands and the Chaguaramas Peninsula agrees with the general prediction that there are fewer species on an island than on a similar area of a mainland (for this comparison, Trinidad is considered a mainland). There were at least 3 times as many bird species on the 2.5-ha Chaguaramas site as on 2.5-ha Caledonia Island. There were 2.6 times as many species on the mainland site as on all 6 of the islands combined. Although not a strict area-for-area comparison, the mainland species pool of woody plants on the Chaguaramas Peninsula is several times the size of the woody plant community on the Five Islands (Beard 1946). Similarly, there are many reptiles on the Chaguaramas Peninsula that are absent from the Five Islands (H. E. A. Boos, personal communication).

Species-area relationships.--There is strong theoretical and empirical support for the mathematical relationship between island area and species diversity. In general, the value of z in the species-area equation is usually in the range 0.2 - 0.4. This means that a 10-fold increase in island area should result in an approximate doubling of the number of species. The data for most of the taxonomic groups in the Five Islands (plants, snails, reptiles and birds) are consistent with these generalities. But, ants are a conspicuous exception. There is relatively little variation in the number of ants per island, which ranges only from 5 to 8. Furthermore, 5 of the 8 species are found on every one of the islands. Perhaps these

Table 2. Distribution of woody plant, land snail, ant, reptile and land bird species on the Five Islands

Species	Caledonia Island	Nelson Island	Lenagan Island	Pelican Island	Rock Island	Craig Island
Plant (1)	x	x	x			x
Plant (2)	x	x	x	x	x	x
Plant (3)	x	x	x	x	x	x
Plant (4)	x	x	x	x	x	x
Plant (5)	x	x		x	x	
Plant (6)	x	x	x	x	x	
Plant (7)	x	x	x	x	x	
Plant (8)	x	x	x		x	
Plant (9)	x	x	x			
Plant (10)	x		x		x	
Plant (11)	x					
Plant (12)					x	
Plant (13)	x	x				
Plant (14)	x					
Plant (15)	x	x				
Plant (16)	x		x		x	
Plant (17)	x		x			
Plant (18)	x		x		x	
Plant (19)	x					
Plant (20)			x			
Plant (21)	x	x				
Plant (22)		x				
Plant (23)		x				
Plant (24)					x	
Plant (25)	x	x		x		
Plant (26)	x	x				
Plant (27)	x					
Plant (28)	x					
Plant (29)	x					
Plant (30)	x					
Plant (31)	x		x			
Plant (32)	x					
Plant (33)	x	x	x		x	
Plant (34)	x					
Plant (35)	x					
Plant (36)	x					
Plant (37)						x
Plant (38)				x		
Plant (39)				x		
Plant (40)	x	x				
Plant (41)				x		

Species	Caledonia Island	Nelson Island	Lenagan Island	Pelican Island	Rock Island	Craig Island
Snail "A"	x	x	x	x	x	
Snail "B"	x	x	x			
Snail "C"	x	x	x	x	x	
Snail "D"		x				
Snail "E"	x	x	x			
Snail "F"			x		x	x
Snail "G"						x
Snail "H"	x					
Snail "I"	x					
Ant "A"	x	x	x	x	x	x
Ant "B"	x	x	x	x	x	x
Ant "C"	x	x	x	x	x	x
Ant "D"	x	x	x	x	x	x
Ant "E"	x	x	x	x	x	x
Ant "F"	x	x			x	
Ant "G"		x			x	
Ant "H"		x				
Iguana iguana	x	x	x	x		
Hemidactylus mabouia		x	x			
Thecadactylus rapicaudus		x				
Gonatodes vittatus	x	x	x	x	x	
Anolis aeneus	x	x	x	x	x	x
Gymnophthalmus underwoodi	x	x	x			
Ameiva ameiva	x	x	x			
Mastigodryas boddaerti	x					
Leptotila verreauxi	x	x	x	x		
Amazilia chionopectus	x	x				
Amazilia tobaci	x	x				
Elaenia flavogaster	x		x	x	x	x
Mimus gilvus	x	x	x	x	x	x
Coereba flaveola	x		x			
Thraupis episcopus	x	x	x	x	x	
Tiaris bicolor		x				

small, dry islands provide few habitats for ants, and only a small number of "super tramp" species (Diamond 1974) can successfully colonize. Once those super tramps are present, there will be few additions to the ant fauna.

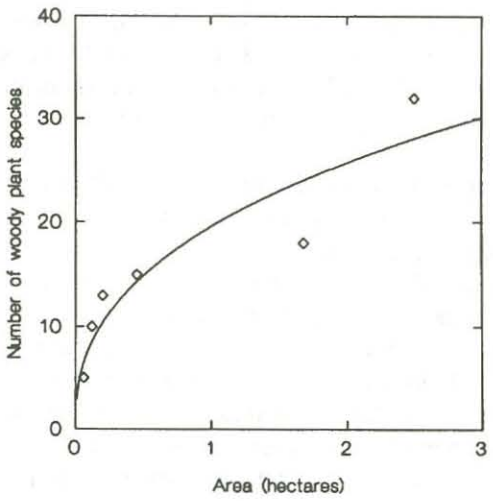
The species-area equations for the Five Islands can be used to "predict" the number of species on larger islands on the basis of their areas. In the Gulf of Paria, there are several other larger islands that have been surveyed for birds and reptiles (Boos 1983, 1990;Boos & Quesnel 1993; ffrench 1965, 1967a, 1967b, 1969). On 454-ha Monos Island, 45 species of land birds (of the types we considered) have been recorded; the species-area equation predicts 37 . On 108-ha Huevos Island, 36 species of land birds have been recorded; the species-area equation predicts 23 . On 409-ha Chacachacare Island, 42 species of land birds have been recorded; the species-area equation predicts 36. These three larger islands probably have more species than the species-area equation predicts because they have more habitat diversity than the Five Islands (see below).

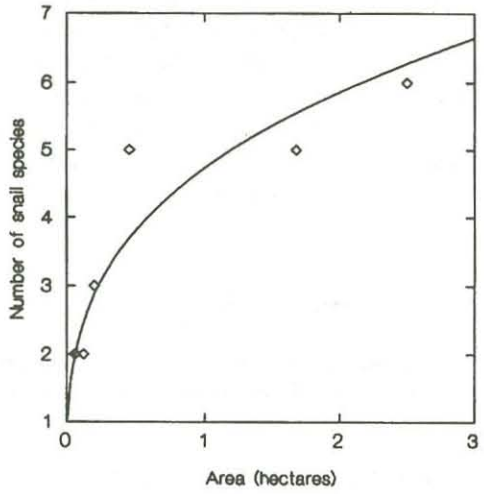
For reptiles, the recorded and predicted number of species on larger islands are: Monos (18 vs. 26), Chacachacare (15 vs. 36), Huevos (13 vs. 23), 158-ha Gaspar Grande (11 vs. 26). These comparisons suggest that there may be more reptile species still to be discovered on these larger islands, which is not surprising in view of the few brief surveys that have taken place.

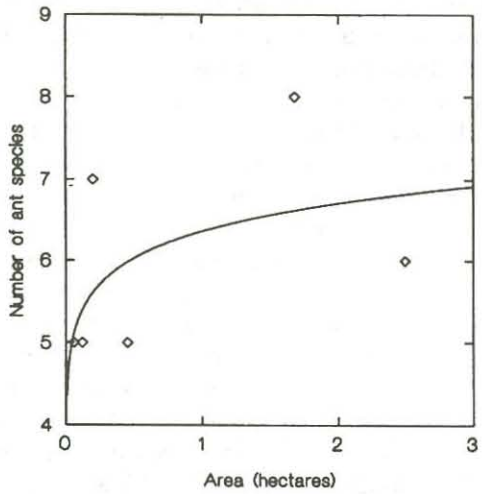
Influence of habitat diversity.--All else being equal, islands that have more types of habitats should have more species than islands with more uniform habitats. On the Five Islands, most of the habitat diversity has been generated by past human disturbances. For example, buildings and open grassy areas, conspicuous habitat features on Nelson Island, are human artifacts. The presence of these habitats is an important prerequisite for successful colonization by some species. Indeed, several species seem to be restricted only to the island or islands that have their specific habitat. Seed-eating birds, for example, are found only on Nelson Island, which has large grassy areas. And, ant diversity is strongly coorelated with grass cover.

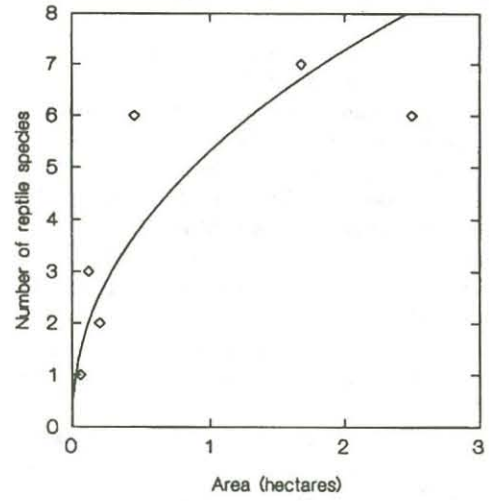
Table #3. Correlations between species numbers and island features; only statistically significant correlalations (r> 0.725, p< 0.10) arte presented

Features of islands	Numbers of ant species	Numbers of bird species	Numbers of plant species	Numbers of reptile species	Numbers of snail species
Area		+ 0.894	+ 0.928	+ 0.746	+ 0.847
Elevation			+ 0.739		
Forest cover					
Grass cover	+ 0.779				
Rock cover		-0.892		-0.892	
Building cover			-0.735		-0.823
No. of buildings		+ 0.825		+ 0.893	+ 0.863
Canopy Height					









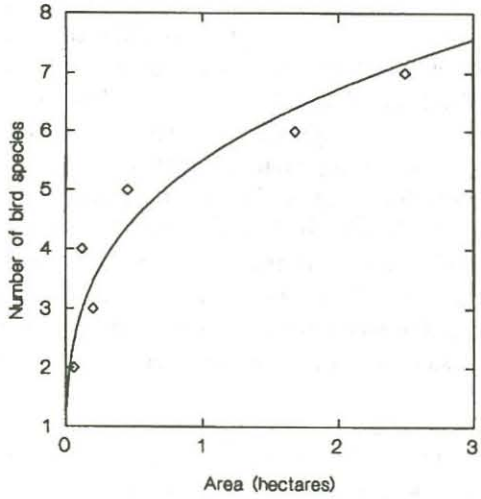


Figure 3. Species-area plots for woody plants, land snails, ants, reptiles and land birds on the Five Islands; power-function corves ($s = cA^Z$) were fitted to the points in each graph.

Correlation analyses suggest that not all habitat features have a positive effect on species diversity. Rock cover and buildling cover, which are largely non-habitats, were negatively correlated with the numbers of species in all 5 groups, and 4 of those negative correlations were statistically significant.

Evidence for a dynamic equilibrium.--The equilibrium theory of island biogeography (MacArthur and Wilson 1967) predicts that the number of species on an island is the outcome of a dynamic equilibrium between the arrival of new species and the extinction of species already present, with the equilibrium point influenced by island area. A correlate of this equilibrium is "species turnover" in which the number of species on an island remains fairly constant over time, but the species composition changes (Diamond 1980). Turnover rates are expected to be very high on islands as small as the Five Islands, especially among short-lived, vagile species.

In 1974 and 1987 previous Zoology Department expeditions to the Five Islands surveyed the flora and fauna, though not as thoroughly and systematically as in 1995 (Department of Zoology, unpublished records). There have also been other visits by naturalists who produced species lists. Comparisons of the species lists from these surveys with the 1995 lists provide evidence that turnover has been occurring. None of the reptile species previously recorded since 1974 was absent in 1995, but several new species were added to the lists for each island, except Nelson. Whether these were overlooked on previous surveys or are recent colonists cannot be determined since the efforts involved in previous surveys are unknown, but likely less than in 1995. For birds, it is almost certain that every species present was recorded during each survey, and turnover was more conspicuous. Four birds recorded on Nelson Island in 1987 were definitely absent in 1995, and 2 species present in 1995 were not recorded in 1987. This change represents a 40% turnover rate (extinctions +colonizations / 1987 species +1995 species), a fairly high rate that would be expected for a group like birds on a small island.

Non-randomness of colonization.--The species that occur on islands are typically a non-random subset of the pool of potential colonists from mainland source areas. The species found on the Five Islands comprise only a small portion of the species found on the Chaguaramas Peninsula, and some types of species that are abundant and well represented on the mainland are absent from the Five Islands. For example, among birds, frugivores, flycatchers and foliage-gleaning insectivores are important components of the bird community on the Chaguaramas Peninsula but absent or under-represented on the islands. This condition is known as "disharmony" and results in island communities that are ecologically incomplete and have many open niches. Some absences are the result of inabilities to disperse across water, but others are the result of failures to maintain viable populations on islands.

Some species reach islands as a result of deliberate or inadvertent introductions by human beings. Owing to their human history, the Five Islands have undoubtedly had many opportunities for introductions. Among woody plants, at least five species, such as mango and West Indian cherry, are probably introductions (Chaboo 1990). Among reptiles, geckoes may have been introductions.

Summary

Surveys of woody plants, land snails, ants, reptiles and land birds on the Five Islands revealed differences among the islands and between the islands and the Chaguaramas Peninsula. There are fewer species on the islands than on a comparable area on the mainland. The number of species on the islands increases with island area. Habitat diversity on the islands influences species composition. There has been a substantial turnover of species over the past 8 years. And, the compositions of the communities on the islands show disharmony.

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