

# The roles of island area *per se* and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups

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## Summary

1. We analysed the relationships between species richness, island area, and habitat diversity for birds, bats, butterflies, and reptiles and amphibians on 19 islands in the Lesser Antilles. Habitat diversity was quantified by Simpson's index based on the total areas of five vegetation types on each island. Island area varied over two orders of magnitude (13–1510 km<sup>2</sup>) and habitat diversity varied between 1 and 3.7 equivalents of equally abundant habitat types.
2. Because the Lesser Antilles consist of an inner arc of high, volcanic islands and an outer arc of low-lying islands formed of uplifted marine sediments, correlations between area and elevation ( $r^2 = 0.32$ ) and between area and habitat diversity ( $r^2 = 0.40$ ) were weak. Habitat diversity was, however, strongly correlated with maximum island elevation ( $r^2 = 0.85$ ).
3. Simple correlations of species richness with island area were significant for all four faunal groups, and simple correlations of species richness with elevation and habitat were significant for all groups except bats. In multiple regressions of species richness on area and habitat diversity together, area was a significant effect for birds and bats, and habitat diversity was a significant effect for birds, butterflies, and reptiles and amphibians.
4. These results suggest that the four Lesser Antillean taxonomic groups differ in their responses to area and habitat diversity. For butterflies and for reptiles and amphibians, the relationship of species richness to area is probably a fortuitous consequence of a relationship between habitat diversity and area. Bird species richness responds independently to both habitat diversity and area, and bat species richness is influenced by area but not by habitat diversity.
5. We suggest that this variation is related to differences in several biological traits of the different faunal groups. Strong habitat-diversity effects are likely in taxa with high degrees of habitat specialization, populations large enough to have a low probability of stochastic extinction, life-cycles that include a resistant resting stage that reduces vulnerability to catastrophic extinction, or a combination of these traits. In contrast, strong area effects are likely in taxa with weak habitat specialization, low population density, or both.
6. At least in Lesser Antillean birds, it is unlikely that immigration depends on island size. Therefore, the species–area relationship for birds is probably generated by island-size-dependent extinction. Among the four taxonomic groups we studied, only butterflies are likely to show a 'rescue effect' stemming from frequent between-island movement of individuals, as only butterflies exhibited low levels of endemism and lacked a unique area effect for species richness.

7. Considered in concert, these taxon-specific differences demonstrate that both biological characteristics of organisms and geographical features of island groups mediate the relative contribution of island area and habitat diversity to variation in species richness.

*Key-words:* area effects, habitat diversity, island biogeography, Lesser Antilles, species–area relationship.

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## Introduction

A positive relationship between island area and species richness has been so widely documented that it comes close to being a universal ecological ‘law’ (Preston 1948, 1960; Williams 1964; MacArthur 1972; Simberloff 1974; Schoener 1976; Abbott 1980; Williamson 1981, 1988; Rosenzweig 1995). The relationship has played an important role in the development of ideas in population biology (Hanski 1997; Hanski & Simberloff 1997), community ecology (Preston 1960; MacArthur 1972), and island biogeography (MacArthur & Wilson 1967). Nonetheless, the basis for the statistical effect of island area is poorly understood both theoretically and empirically. In particular, distinguishing between the direct and indirect effects of area on species richness has proven difficult (McGuinness 1984; Hart & Horwitz 1991; Kohn & Walsh 1994; Rosenzweig 1995). Although island area *per se* might directly affect species richness in several ways, the species–area relationship can also be generated indirectly by other factors that are fortuitously correlated with area.

Area might influence species richness directly in two ways: larger islands present larger targets for dispersing individuals and they generally support larger populations. Thus, island size may influence species richness by its effect on colonization rates or on the outcomes of several mechanisms that determine vulnerability to extinction (MacArthur & Wilson 1967). Less has been written about the dependence of colonization on island size and we will defer this issue until the discussion. Several mechanisms have been suggested for island-size-dependent extinction, which has received more attention. For example, larger populations tend to contain more genetic variation (Avice 1994), which may help them to respond to changes in environmental conditions; large population size also reduces vulnerability to stochastic extinction (Pielou 1977; Pimm, Jones & Diamond 1988; Dennis, Munholland & Scott 1991; Laurance 1991; Tracy & George 1992). Furthermore, the larger areas occupied by populations on larger islands, particularly islands with high productivity (Wright 1983), might mitigate the effects of catastrophic disturbances, such as hurricanes and volcanic eruptions, which

could devastate entire populations on smaller islands (Wiley & Wunderle 1994).

Area might also influence species richness indirectly via its correlation with other factors that affect diversity directly. Among the most plausible of such potentially confounding variables is habitat diversity, which is often presumed to increase in direct relation to island area (Kohn & Walsh 1994). If larger islands supported greater habitat diversity as a result of greater topographic and geological heterogeneity, this increased habitat diversity might promote increased species richness, particularly if the species involved tended to be habitat specialists (Hart & Horwitz 1991).

The relative influences of area *per se* and habitat diversity on island species richness have been addressed in few experimental studies. Simberloff (1976) examined the effect of area on species richness among mangrove islands lacking variation in habitat diversity and found area to be a significant effect. Douglas & Lake (1994) manipulated habitat diversity by cutting different patterns of grooves in tiles that were set in streams to be colonized by algae and freshwater invertebrates; in this case, habitat diversity exerted a significant effect on species richness. However, most studies have attempted to sort out the relationships between species richness, area and habitat diversity statistically, using multiple correlation and multiple regression to distinguish unique and confounded components of these relationships (see below). Nonetheless, in spite of dozens of such studies over three decades, the question, ‘To what extent is taxonomic diversity a function of island area *per se* or habitat diversity?’ remains largely unresolved.

Three factors have made the study of habitat diversity in species–area relationships problematic. The first is simply that habitat diversity is difficult to define (Simberloff 1976). Appropriate measures of habitat diversity are likely to differ from one type of organism to another. The most frequently employed diversity measure is maximum elevation, which was first used in a statistical assessment of area and habitat effects in T. H. Hamilton’s analyses of plant and bird species richness in the Galapagos Archipelago (Hamilton *et al.* 1963; Hamilton, Barth & Rubinoff 1964). Although elevation is an indirect and generally uncalibrated index of habitat diver-

sity, its statistical effects on species richness are often strong. An index related to maximum elevation is topographic diversity. Quantified as the number of arroyos per unit of area, or per unit of island perimeter, topographic diversity was not a significant effect in explaining variation in the diversity of orthopterans on the Channel Islands of California (Weissman & Rentz 1976). Other commonly employed measures of habitat diversity are number of vegetation types (Maly & Doolittle 1977; Dueser & Brown 1980; Kitchener *et al.* 1980a; Kitchener *et al.* 1980b; Reed 1981; Kitchener *et al.* 1982; Elmberg *et al.* 1994; Kohn & Walsh 1994), soil types (Johnson & Simberloff 1974; Buckley 1985), and structural habitat types (Tonn & Magnuson 1982). Another approach to the measurement of habitat diversity in terrestrial environments has been to quantify vegetation structure at many points within an area and use the standard deviation or other measure of dispersion of values as an index to habitat diversity (Opdam, Rijdsdijk & Hustings 1985; Freemark & Merriam 1986; Nilsson, Bengtsson & Ås 1988). Finally, several authors have used plant species richness as an index to the environmental diversity available to animal species. Although effects are often highly significant (Power 1972; Harris 1973; Case 1975; Power 1976; Brönmark 1985), plant diversity does not distinguish within-habitat and between-habitat components of diversity and therefore bears an unknown relationship to habitat diversity. In addition, because plant species richness itself might respond to both area and habitat diversity (Hamilton *et al.* 1963; Johnson, Mason & Raven 1968; Johnson & Simberloff 1974; Kohn & Walsh 1994), including it as an effect might confound statistical analyses of the interrelationship among animal species richness, area, and habitat diversity.

A second problem in disentangling the effects of area and habitat diversity on species richness arises from the fact that most indices of habitat diversity are highly correlated with island area. This correlation renders it difficult to partition the independent statistical effects of habitat diversity and area *per se* on species richness (Simberloff 1976). Reasonable statistical power requires a large number of islands over which the correlation between area and habitat diversity is weak. Yet the islands included in such a sample should have similar access to colonization from a common species pool so as not to complicate statistical analyses by distance and regional effects (Hamilton *et al.* 1964; Johnson & Raven 1973; Ricklefs 1977). Some confusion also results from different interpretations of effects depending on the type of analysis applied. Early studies often reported only simple correlations of species richness with several attributes of islands (Johnson & Raven 1973; Power 1976; Dueser & Brown 1980; Haila 1983).

Simple correlations do not allow one to identify confounding effects due to correlations among independent variables. In some cases, analyses were restricted to simple correlations because the correlations among independent variables were so strong that multiple correlations were meaningless, particularly when the sample of islands was small, e.g. nine islands in the case of Dueser & Brown (1980), eight islands in the case of Power (1976).

Further confusion has arisen over the choice between stepwise (e.g. Reed 1981; Opdam *et al.* 1985) and multiple regression (e.g. Ricklefs 1977; Kitchener *et al.* 1982; Kohn & Walsh 1994). In stepwise regression, independent variables are usually entered in order of their correlation with the dependent variable, or their correlation with the residuals of the dependent variable from the regression on previously entered independent variables. As a result, a strong predictor variable in simple regression may be excluded from the stepwise regression model owing to its high correlation with some other, albeit stronger predictor variable. While this provides a locally valid descriptive equation for the data, it does not help to resolve the statistical interrelationships among the dependent (species richness) and independent (area, habitat diversity) variables. Multiple regression indicates the unique contribution of variation in independent variables to variation in the dependent variable. When several correlated independent variables are used, however, it may be difficult to identify unique significant relationships. A few studies have also applied path analysis in order to separate direct and indirect contributions of independent variables to variation in species richness (Power 1972; Kohn & Walsh 1994). This approach is based on models of causal relationship, and has generally shown that the influence of area on species richness has a direct component of unknown causation and an indirect component through the effect of area on habitat diversity.

A third problem in interpreting the potential influence of habitat diversity on island species richness is to understand how species respond to habitat heterogeneity. As Hart & Horwitz (1991, p.53) pointed out, 'Habitat diversity is irrelevant without some degree of species differentiation between habitats.' Presumably, habitat generalists are less sensitive to habitat diversity than are habitat specialists. One might therefore expect a greater statistical contribution of habitat diversity to the species richness of habitat specialists compared to habitat generalists. Biological interpretation of the statistical effects of habitat diversity depends on the degree of habitat specialization and beta diversity—the between-habitat component of diversity (Whittaker 1972; Cody 1975). This led Buckley (1982) to propose a habitat-unit model of island biogeography, in which spe-

cies–area relationships are calculated for each habitat type independently to ascertain the independent contributions of area and habitat diversity to species–area relationships.

We surveyed 35 studies of species–area relationships that included the contribution of habitat diversity. Of the 30 studies that used stepwise or multiple regression, 22 found a significant area component, 21 found a significant habitat-diversity component, and 10 found both (Appendix). Maximum number of species in these studies varied from 5 to 1008; number of islands, which were variously oceanic islands, islands in lakes, land-bridge islands, habitat fragments in altered landscapes, and aquatic ‘islands’ (ponds and lakes), varied from 7 to 263; maximum area varied from 4090 m<sup>2</sup> to 885 780 km<sup>2</sup>. The taxa and islands considered, the measurements of habitat diversity, and the statistical methods used in these studies were so varied that one can only conclude that area and habitat diversity may both have significant effects under various biogeographic scenarios. The lack of a clear trend in correlation studies suggests that experimental studies should be pursued actively. However, experimental studies of the processes that generate species–area relationships are not possible at the larger end of the temporal and spatial scale of island biotas, particularly when individual island floras and faunas have independent evolutionary histories and include endemic taxa. Therefore, multivariate statistical analyses will continue to play an important role in sorting out the determinants of island diversity.

In this study, we analyse the relationships of species richness to the area and diversity of major habitat types on 19 islands in the Lesser Antilles. Areas of five major habitat types were measured on each of the 19 islands, and the relative statistical contributions of island area and habitat diversity were determined by multiple regression. This group of islands presents a good opportunity to resolve the relationship of species richness to area and habitat diversity because of its relatively large sample size, large-scale habitat diversity assessment, relative independence of area and habitat diversity, and consideration of several faunal groups in a common geographical setting.

## Data and analysis

### THE ISLANDS

Our sample includes all the major islands in the Lesser Antilles, ranging from Anguilla in the north to Grenada in the south (Table 1). The only islands having areas greater than 10 km<sup>2</sup> that are not included are Desirade (27 km<sup>2</sup>), which is one of the satellite islands of Guadeloupe, and Bequia (19 km<sup>2</sup>), a small island in the Grenadines. Our sample does, however, include Marie Galante, a small

companion island to Guadeloupe, and Carriacou in the Grenadines. The Lesser Antilles are separated from the Greater Antilles (Puerto Rico and the Virgin Islands) in the north by the Anegada Passage, and from Trinidad and Tobago in the south by a wide gap. The islands in our sample range in size from Saba (13 km<sup>2</sup>) to Guadeloupe (1510 km<sup>2</sup>) (Lack 1976: Appendix 10), and thus vary in area over two orders of magnitude.

The 19 islands may be divided into two groups based on their geological origins and elevation (Donnelly 1985, 1988, 1989). The inner, volcanic arc consists of islands with elevations over 600 m and a broad range of habitats from dry scrub to cloud forest and high-altitude thickets. The outer islands (Anguilla, St. Martin, St. Bartholomew, Barbuda, Antigua, and Barbados) are composed of uplifted marine sediments and have elevations less than 500 m. These support primarily dry, scrubby vegetation. Guadeloupe is a composite island, with a volcanic portion to the west and an uplifted portion to the east. Attributes of the islands are presented in Table 1.

The major islands in the Lesser Antilles have probably been approximately in their present positions for at least 10 million years. Most of the Lesser Antilles are surrounded by deep water and have had no historical connection to other islands or to the mainland. Exceptions to this include several sets of islands that occupy shallow banks and which were connected during sea level lows at various times during the Pleistocene. These island groups include Nevis and St. Kitts, Antigua and Barbuda, the Grenadines (including Carriacou) and Grenada (Roughgarden 1995). Thus, most dispersal of land animals to, and within, the Lesser Antilles has been over water.

### THE ANIMAL TAXA

We included in our analysis four groups of animals with well-known distributions in the West Indies: birds, bats, reptiles and amphibians (also referred to as ‘herps’), and butterflies (‘leps’) (Table 1). Species richness values for birds were obtained from Bond (1956; supplements) and include all breeding land birds: raptors (Falconiformes), pigeons and doves (Columbiformes), parrots (Psittaciformes), cuckoos (Cuculiformes), owls (Strigiformes), nightjars (Caprimulgiformes), hummingbirds and swifts (Apodiformes), woodpeckers (Piciformes), and songbirds (Passeriformes). The avifauna of the Lesser Antilles is a mixture of species derived from South America (40%) and the Greater Antilles (27%), as well as Lesser Antillean species endemics of uncertain origin (33%) (Lack 1976; Bond 1979). In the case of the endemic thrashers (Mimidae), as many as four monotypic genera may have originated

Table 1. Area, elevation, and habitat diversity of Lesser Antillean islands included in this analysis

Island	Area (km <sup>2</sup> )	Maximum elevation (m)	HD	Beard's HD	Area of vegetation zones (km <sup>2</sup> )					Number of species				
					Mangrove	Xerophytic	Mesophytic	Hygrophytic	Altitudinal	Birds	Bats	Herps	Leps	
Anguilla	90	300	1.00		0	90	0	0	0	0	13	5	12	11
St. Martin	85	410	1.22		0	77	9	0	0	0	14	6	9	24
Saba	13	860	1.80		0	9	3	1	0	0	17	3	7	13
St. Bartholomew	22	300	1.00		0	22	0	0	0	0	13	(1)	8	
St. Eustatius	20	600	1.22		0	18	2	0	0	0	18	5	9	
St. Kitts	170	1140	2.90	4.19	7	83	51	16	14	14	22	4	12	41
Nevis	130	1100	2.70	3.59	0	61	43	26	0	0	19	(1)	10	
Barbuda	160	300	1.00	1.91	0	160	0	0	0	0	22	6	6	
Antigua	280	400	1.14	1.22	0	261	19	0	0	0	21	7	12	32
Montserrat	100	910	2.61	2.57	0	49	34	17	0	0	23	11	13	39
Guadeloupe	1510	1500	3.73		210	576	314	367	44	44	34	10	16	44
Marie Galante	160	300	1.12		5	150	4	0	0	0	28	3	3	17
Dominica	751	1450	2.79	2.86	0	72	286	334	60	60	39	12	14	52
Martinique	1100	1340	3.08		19	405	417	234	25	25	38	10	11	38
St. Lucia	616	960	3.08	3.66	0	254	206	122	33	33	41	8	17	48
St. Vincent	350	1240	3.27	2.57	0	125	114	91	19	19	34	9	15	38
Barbados	430	340	1.22	1.83	10	388	32	0	0	0	18	9	8	24
Carriacou	34	300	1.00		0	34	0	0	0	0	23		5	23
Grenada	310	840	3.26	4.71	4	126	89	74	17	17	36	11	16	45

within the Lesser Antilles from a single ancestral taxon (unpublished data). Aside from this possibility, there is no strong evidence that speciation has caused increased species richness on individual islands within the Lesser Antilles; most of the species there were derived from outside the chain of islands.

Numbers of species of bats were available for 17 of the 19 islands (all but Marie Galante and Carriacou) (Baker & Genoways 1978). Only a single species of bat was reported from St. Bartholomew and from Nevis. Because nearby, topographically similar islands (St. Maartin and St. Kitts, respectively) have substantially more bat species (6 and 4), the bat faunal lists for St. Bartholomew and Nevis are almost certainly incomplete owing to poor sampling. Accordingly, we did not include St. Bartholomew or Nevis in our analysis of bat species richness; the deletion of these two islands had no qualitative effect compared to analyses in which these islands were included. Like birds, Lesser Antillean bats are derived from both the Greater Antilles (38%) and South America (38%), and show relatively low levels of species endemism within the Lesser Antilles (21%) (Jones 1989). Whether new species of bats have originated within the Lesser Antilles is open to question, as endemic species of the widespread genera *Sturnira*, *Myotis*, and *Eptesicus* are strictly allopatric to congeners elsewhere in the Lesser Antilles. The presence of *Chiroderma improvisum* Baker and Genoways and *Myotis martiniquensis* LaVal on more than one island suggests that these species may have undergone secondary expansions within the Lesser Antilles. There are no endemic genera of bats in the Lesser Antilles, nor have any bat taxa undergone an adaptive radiation within the archipelago.

Data on the species richness of reptiles and amphibians were assembled from Roughgarden

(1995, Table 3.2, Parts A and B) and Schwartz & Thomas (1975). Endemism levels among reptiles and amphibians are much greater than among birds and bats: 79% of all Lesser Antillean species are endemic to the archipelago, and 50% are single-island endemics. Only *Anolis* and *Eleutherodactylus* have more than one species per island.

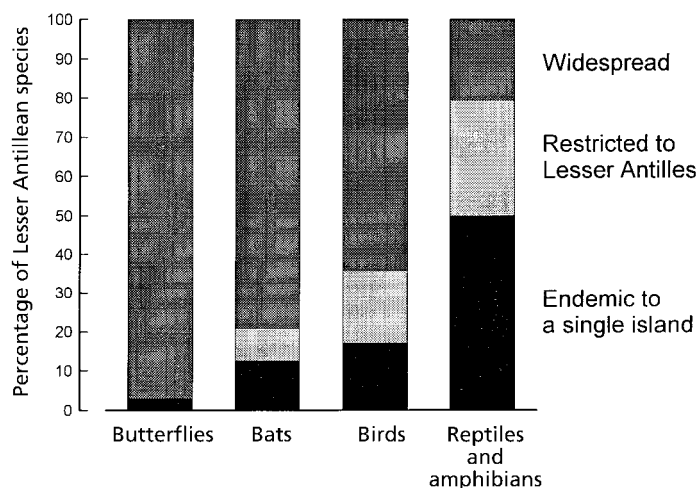
Data for butterfly species richness were obtained from an unpublished checklist provided by Neil Davies and based on Smith *et al.* (1994). Only two of 66 species are endemic to the Lesser Antilles (Riley 1975), the rest being widespread throughout the West Indies and, in most cases, continental areas surrounding the Caribbean Sea.

In Table 2, we estimate the relative vagility (colonizing ability), population sizes, and degree of habitat specialization among the four West Indian taxonomic groups. Few quantitative data are available to support these assessments. Vagility was judged to be high among Lepidoptera because of the small size and substantial flight capabilities of adult butterflies, and the low degree of endemism in Lesser Antillean butterflies. Birds and bats were judged to have moderate dispersal abilities, due in part to the moderate levels of endemism exhibited by these groups (Fig. 1). Vagility in reptiles and amphibians was assumed to be low due to their lack of flight and the high level of single-island endemism in Lesser Antillean reptiles and amphibians.

Population sizes are probably smallest for birds and bats, moderate for butterflies, and largest for reptiles and amphibians in the Lesser Antilles. The most abundant land bird in the West Indies, the bananaquit *Coereba flaveola* (Linnaeus), has population densities of 2–12 individuals per hectare on Grenada (Wunderle 1984) and about 2 ind. ha<sup>-1</sup> in rain forest on Puerto Rico (Recher 1970). In the Luquillo rain forest on Puerto Rico, all species of birds together had densities of 5–10 ind. ha<sup>-1</sup>

**Table 2.** Characteristics of four faunas of the Lesser Antilles. Species–area regression for bats based on 15 islands (see text)

	Birds	Bats	Herps	Leps
Islands	19	17	19	15
Species	70	24	68	66
Lesser Antillean endemics	25	5	54	2
(% of total species)	35.7	20.8	79.4	3.0
Single-island endemics	12	3	34	2
(% of total species)	17.1	12.5	50.0	3.0
Mean number of islands per species	6.76	4.92	3.00	7.41
(% of islands sampled)	35.6	28.9	15.8	49.4
Slope of species–area relationship	0.207	0.232	0.167	0.265
Standard error of slope	0.046	0.054	0.050	0.074
<i>F</i>	20.5	18.3	11.1	12.9
<i>P</i>	0.0003	0.0009	0.0040	0.0033
Vagility within the West Indies	Moderate	Moderate	Low	High
Relative population sizes	Small	Small	Large	Moderate
Habitat specialization	Moderate	Low	High	High



**Fig. 1.** Percentage of species of four faunal groups in the Lesser Antilles that are restricted to a single island, restricted to the Lesser Antilles, or widespread including the Greater Antilles or continental areas within the Caribbean Basin.

(Recher 1970), although densities may be up to three times greater in dry forests in the south-west of the island (Kepler & Kepler 1970). Population densities of bats are poorly known, although they are probably on the same order as those of birds, as indicated for one Panamanian bat community (Bonaccorso 1979) and for the most abundant member of that community, *Artibeus jamaicensis* Leach (2 ind ha<sup>-1</sup>; Leigh & Handley 1991).

Densities of many reptiles and amphibians are several orders of magnitude higher than those of populations of birds and bats. For small reptiles, density estimates include 175 ind. ha<sup>-1</sup> (Heatwole & Sexton 1966) and 325 ind. ha<sup>-1</sup> (Turner & Gist 1970) for mainland tropical rain forest species, 2000–5600 ind. ha<sup>-1</sup> for *Anolis acutus* Hallowell on St. Croix (Ruibal & Philibosian 1974), up to 1850 ind. ha<sup>-1</sup> for six species of lizards in xeric habitats in the Dominican Republic on Hispaniola (Powell, Parmerlee & Smith 1996), up to 379 ind. ha<sup>-1</sup> for *Ameiva fuscata* Garman, 751 ind. ha<sup>-1</sup> for *Mabuya mabouya* Lacépède, and 2148 ind. ha<sup>-1</sup> for *Anolis oculatus* Cope on Dominica (Bullock & Evans 1990), 1420–5480 ind. ha<sup>-1</sup> for six species of *Anolis* in the West Indies (Bennett & Gorman 1979; Schoener & Schoener 1980; Pacala & Roughgarden 1984), 9700 ind. ha<sup>-1</sup> for *Anolis sagrei* Duméril and Bibron in the Bahamas (Schoener & Schoener 1980), up to 20000 ind. ha<sup>-1</sup> for *Anolis pulchellus* Duméril and Bibron in grassy lowlands of Puerto Rico (Gorman & Harwood 1977), and 21000–26000 ind. ha<sup>-1</sup> for the canopy anole, *Anolis stratum* Cope, at El Verde, Puerto Rico (Reagan 1996). Estimates for amphibians include 100–800 ind. ha<sup>-1</sup> each for five species of *Eleutherodactylus* at El Verde, Puerto Rico (Reagan 1996) and 70–5000 ind. ha<sup>-1</sup> for populations of four species of

*Eleutherodactylus* at several locations in Puerto Rico (Joglar & Burrowes 1996).

Population densities of some butterflies must be high but few direct estimates have been made. Species of *Passiflora*-feeding *Heliconius* butterflies, which have uncommon larval host plants, have densities in the range of up to only 6–8 adult ind. ha<sup>-1</sup> (Gilbert 1984); peak densities of two species of *Euphydryas* butterflies in California serpentine grasslands were 123 and 485 ind. ha<sup>-1</sup> (Murphy *et al.* 1986), with numbers of the first species as high as 900 ind. ha<sup>-1</sup> in some years (Ehrlich, Launer & Murphy 1984). Neither of these estimates is likely to give a good indication of population densities of Lesser Antillean species.

Habitat specialization is also difficult to quantify. Habitat distributions of Lesser Antillean birds have been measured by Cox & Ricklefs (1977), Wunderle (1985), and Lovette (unpublished data) who determined that birds of Dominica, St. Lucia, Grenada, and St. Kitts, are distributed through an average of 4.2–5.4 of nine distinct habitats sampled. Compared to birds, we judged that both reptiles and amphibians and butterflies are more specialized with respect to habitat, and bats are less specialized, although few data address these points. Butterflies tend to be food-plant specialists (Owen 1971; DeVries 1987) and many plants have restricted habitat distributions. However, habitat distributions of flying adult tropical butterflies tend to be broad (DeVries, Murray & Lande 1997) and in one study were similar to those of birds (Lawton *et al.* 1998). Reptiles and amphibians may also have narrow habitat distributions (Rodríguez & Cadle 1990; Powell *et al.* 1996; López-González & González-Romero 1997), particularly with respect to breeding sites, although many also have dormant or resistant

stages that may insulate them from variations in the environment (Duellman & Treub 1986). Bullock & Evans (1990) censused three species of lizards in dry scrub woodland, littoral woodland, lowland rain forest, montane rain forest, and elfin woodland on the island of Dominica. *Anolis oculatus* occurred at high densities in all these habitats; *Mabuya mabouya* and *Ameiva fuscata* were restricted to dry scrub woodland and littoral forest.

#### HABITAT DIVERSITY

We used vegetation maps produced by Henri Stehle (1945) to estimate the habitat diversity of 19 islands in the Lesser Antilles (Table 1). Stehle distinguished five habitat types: mangrove, xerophytic, mesophytic, hygrophytic, and altitudinal. These correspond approximately to vegetation types classified by Beard (1949) as mangrove, dry scrub woodlands (a secondary community), secondary rainforest, lower montane rainforest plus rainforest, and elfin woodland. Additional vegetation types recognized by Beard, but occupying relatively small areas or areas of high disturbance, were montane thicket and palm brake. Values of habitat diversity (see below) for 10 Lesser Antillean islands calculated from Tables III in Beard (1949: p. 95) were generally higher and more variable among islands owing to the greater number (eight) of natural, uncultivated habitats tabulated. Nevertheless, over all the islands indices to habitat diversity based on Beard's and Stehle's data are broadly comparable ( $r_s = 0.72$ ,  $P = 0.018$ ,  $n = 10$ ). This congruence largely reflects the disparity in habitat diversity between the inner arc of high volcanic islands and the outer low-lying islands.

Areas of habitat were obtained from Stehle's vegetation maps using a Numonics 2210 (Numonics, Montgomeryville, PA) digitizing tablet and SigmaScan™ Version 3.9 (Jandel Scientific, Corte Madera, CA) software. To quantify habitat diversity, we used the inverse of Simpson's index (Simpson 1949; Magurran 1988)

$$HD = HD = \frac{1}{\sum_{i=1}^n p_i^2}$$

where  $p_i$  is the proportion of the total area occupied by the  $i$ th of  $n$  vegetation types. Simpson's index,  $D = \sum p_i^2$ , is the probability that any two randomly placed points will fall in a different habitat type. Because this index emphasizes differences between locations within an island, the value of  $D$  is sensitive to the degree of evenness in the proportions of habitat areas. This is a suitable property because the value of a habitat for maintaining diversity presumably varies in relation to its relative area. The inverse of Simpson's index ranges from 1, when there is only one habitat, to the total number of vegetation types ( $n$ ) which is attained when all vege-

tation types occupy equal areas. Thus, in this study, the maximum possible habitat diversity is 5. In fact, however,  $HD$  varied from a low of 1 (Anguilla, St. Barts, Barbuda, and Carriacou) to a high of 3.73 (Guadeloupe). Islands fell into two distinct groups with respect to habitat diversity corresponding to low ( $HD < 1.3$ ) and high ( $HD > 2.6$ ) islands; only Saba, a small (13 km<sup>2</sup>) but relatively high (860 m) island, was intermediate ( $HD = 1.8$ ). Both habitat diversity groups included both large and small islands, however, raising the possibility of distinguishing statistically between the effects on species richness of island area and habitat diversity.

In addition to habitat diversity, we also tabulated the number ( $N$ ) of habitat types present on each island, total island area, and the maximum elevation. Island areas and species richnesses were log<sub>10</sub>-transformed prior to all analyses. The log-transformed area was given the variable name *LOGAREA*.

#### STATISTICAL METHODS

Simple linear regressions were used to characterize the relationships between island and habitat variables, and between these variables and the species richness of each taxonomic group. We used multiple regression analyses to investigate the relationship between the species richness of each taxonomic group (dependent variable) and the pair of independent variables, *LOGAREA* and  $HD$ . As we were interested in the unique contributions of variation in area and variation in habitat diversity to species richness, we report  $F$  statistics and  $P$ -values for Type III sums of squares.

All analyses were performed using the SAS statistical package (SAS Institute Inc. 1988), using the GLM and STEPWISE procedures.

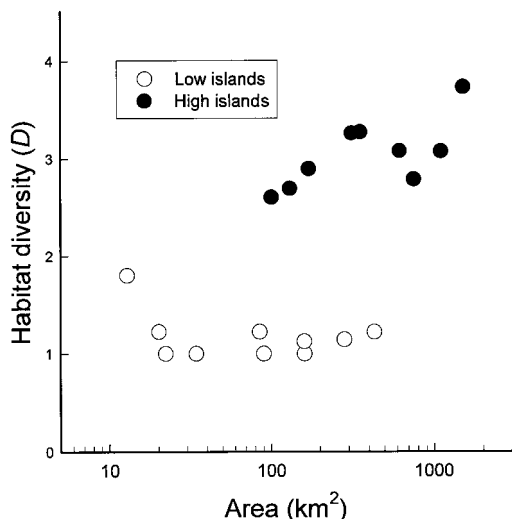
#### Results

##### GENERAL PATTERNS

The areas of the 19 islands included in this study varied over two orders of magnitude, from 12.8 to 1510 km<sup>2</sup> (Table 1). Island area and maximum island elevation were significantly correlated ( $r^2 = 0.32$ ,  $P < 0.05$ ), with the largest islands tending to have the greatest maximum elevation.

The number of habitats represented on each island varied from 1 to 5 (Table 1). All islands had substantial areas of xerophytic habitat, and all but the four low islands of Anguilla, St. Bartholomew, Barbuda, and Carriacou had mesophytic habitat. Mangroves occupied measurable areas only on St. Kitts, Guadeloupe, Marie Galante, Martinique, Barbados, and Grenada. Hygrophytic habitat was present only on islands having elevations above 800 m, and altitudinal forest was restricted to a smaller



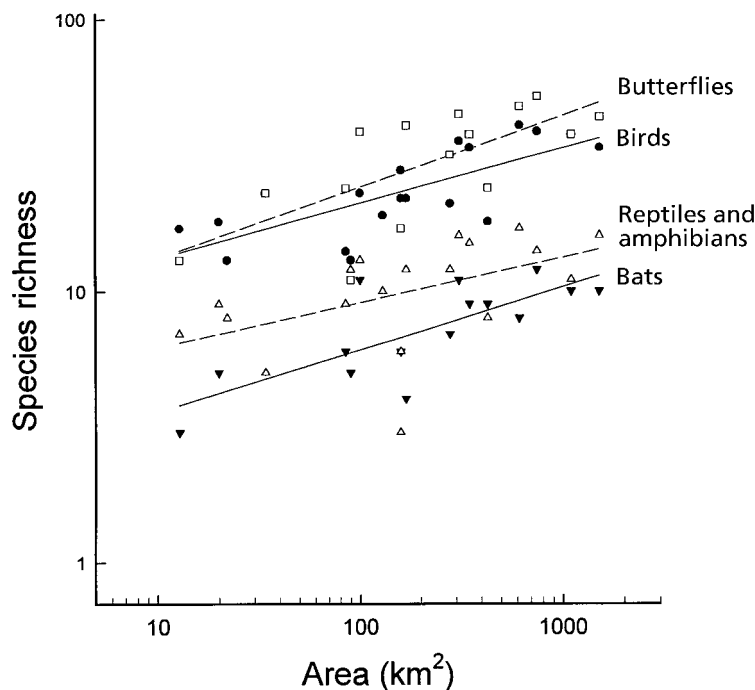


**Fig. 2.** Relationship of habitat diversity ( $D$ ) to area among islands in the Lesser Antilles. Islands having maximum elevations exceeding 800 m and with low to moderate  $HD$  (range 1.00–1.80) among which habitat diversity was not significantly correlated with island area ( $r^2 = 0.14$ ,  $P > 0.3$ ). The second comprised nine medium to large islands with maximum elevations exceeding 800 m and with greater  $HD$  (2.6–3.7). Among these islands, area and habitat diversity were positively associated ( $r^2 = 0.47$ ,  $P < 0.05$ ). Over the entire sample of 19 islands, habitat diversity was significantly correlated with maximum island elevation ( $r^2 = 0.85$ ,  $P < 0.001$ ). When elevation and log-transformed area were entered into a multiple regression model of their influence on  $HD$ ,

number of larger islands generally having yet higher elevation.  $N$ , the number of habitats, was significantly correlated with island area ( $r^2 = 0.45$ ,  $P < 0.005$ ), and with maximum elevation ( $r^2 = 0.69$ ,  $P < 0.0001$ ). Together, the combination of island area and maximum elevation accounted for much of the variation in number of habitats ( $R^2 = 0.75$ ). Number of habitats was highly correlated with the

habitat diversity index  $HD$  ( $r^2 = 0.80$ ), suggesting that variation in the evenness of the proportion of habitat areas among islands makes a smaller contribution to  $HD$  than does the number of habitats. Thus, the inverse of Simpson's index provides a measure of habitat richness that is not unduly influenced by differences in dominance in area among habitats between islands.

$HD$  varied from a minimum of 1.00 on four small islands where only a single habitat type was present to a maximum of 3.73 on Guadeloupe, the largest island included in the survey, which supported all five habitat types (Table 1). Habitat diversity was significantly and positively correlated with island area ( $r^2 = 0.40$ ,  $P < 0.01$ ). Despite this general relationship, however, two qualitatively different subsets of islands were apparent (Fig. 2). The first comprised 10 small- to medium-sized islands with maximum elevations under 800 m and with low to moderate  $HD$  (range 1.00–1.80) among which habitat diversity was not significantly correlated with island area ( $r^2 = 0.14$ ,  $P > 0.3$ ). The second comprised nine medium to large islands with maximum elevations exceeding 800 m and with greater  $HD$  (2.6–3.7). Among these islands, area and habitat diversity were positively associated ( $r^2 = 0.47$ ,  $P < 0.05$ ). Over the entire sample of 19 islands, habitat diversity was significantly correlated with maximum island elevation ( $r^2 = 0.85$ ,  $P < 0.001$ ). When elevation and log-transformed area were entered into a multiple regression model of their influence on  $HD$ ,



**Fig. 3.** Relationship of log-transformed species richness to log-transformed island area for four faunal groups within the Lesser Antilles. Butterflies, open squares and dashed line; birds, filled circles and solid line; reptiles and amphibians, open triangles and dashed line; bats, filled triangles and solid line.

**Table 3.** Coefficients of simple correlation ( $r$ ) between species richness of four animal groups and island area, elevation, and habitat diversity. Species richness and island area were log-transformed. Note: NS indicates  $P > 0.05$ ; \*  $0.05 > P > 0.01$ ; \*\*  $0.01 > P > 0.001$ ; \*\*\*  $P < 0.001$

Taxonomic group	Island area	Elevation	Habitat diversity (HD)
Birds	0.740 ***	0.664 **	0.741 ***
Bats	0.636 **	0.238 NS	0.353 NS
Herps	0.499 *	0.640 **	0.712 ***
Butterflies	0.706 **	0.693 **	0.779 ***

only elevation was a significant unique effect ( $F = 60$ , d.f. = 1,16,  $P < 0.0001$ ; for *LOGAREA*,  $F = 2.5$ , d.f. = 1,16,  $P = 0.14$ ; multiple  $R^2 = 0.87$ ).

#### PATTERNS OF SPECIES RICHNESS

Simple correlations showed that in all four taxa the logarithm of species richness was significantly correlated with the logarithm of island area ( $r^2 = 0.39$ – $0.58$ ; Fig. 3), with island elevation ( $r^2 = 0.44$ – $0.64$ ; except bats,  $r^2 = 0.16$ , NS), and with habitat diversity ( $r^2 = 0.55$ – $0.74$ ; except bats,  $r^2 = 0.26$ , NS) (Table 3).

Slopes of the logarithmic species–area relationships (Table 2) varied between  $0.165 \pm 0.070$  SE for reptiles and amphibians and  $0.265 \pm 0.074$  SE for butterflies. Birds ( $0.207 \pm 0.046$  SE) and bats ( $0.233 \pm 0.055$  SE) were intermediate. In pairwise comparisons of regression slopes, none of the slopes differed significantly from one another.

Multiple logarithmic regressions of species richness on habitat diversity and island area showed strikingly different patterns in the four faunal groups (Table 4). The  $F$  statistics for type III sums of squares assess the unique statistical contributions of each independent variable to variation in the dependent variable, taking into account the correlations among the independent variables. These results indicate a unique statistical effect of habitat diversity in the case of birds, butterflies, and especially rep-

tiles and amphibians. Area *per se* exerted a unique statistical effect only in birds and bats. The same pattern appeared when number of habitats was used in the place of habitat diversity (results not reported). In summary, area and habitat contributed about equally to species richness of birds and butterflies; number of bat species was sensitive to variation only in island area; and number of reptile and amphibian species was strongly correlated only with habitat diversity.

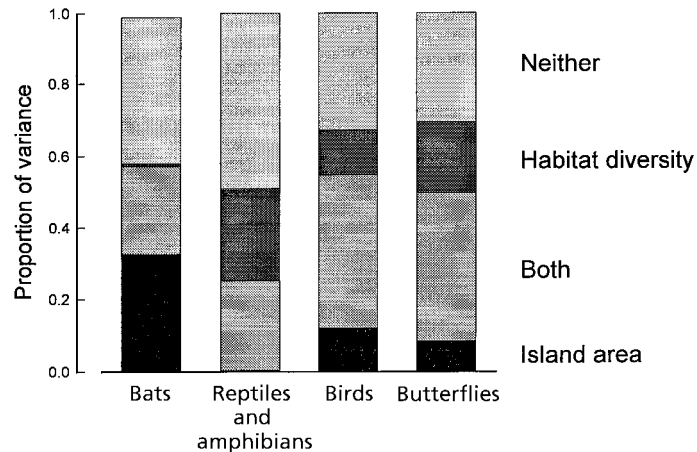
The contributions of area and habitat diversity to variation in species richness cannot be fully separated because of the correlation between the two independent variables. The total variance in species richness among islands has four components, one uniquely related to island area, one uniquely related to habitat diversity, a third related to correlated variation in area and habitat diversity, and the fourth comprising the remainder, or unexplained variation. The relative magnitudes of these variance components are shown in Fig. 4. Variation in species richness related to the correlation between area and habitat diversity was greatest in birds and butterflies, and least in bats and reptiles and amphibians. This component of the variation cannot help to resolve the relative contributions of habitat diversity and island area to species richness. Where this component is large, however, both habitat diversity and area make separate unique contributions to the total variance in species richness. Where the unique variance was dominated by either habitat diversity (reptiles and amphibians) or area (bats), the influence of correlated variation in habitat diversity and area was smaller. The unexplained variance was relatively large for reptiles and amphibians, but the extent that this might be due to inadequate collecting is not clear.

#### Discussion

In spite of correlations among the independent variables, this analysis had enough statistical power in terms of sample size and independence of variables to discern unique contributions of both area and habitat diversity to species richness. These contribu-

**Table 4.** Results of multiple regressions of the logarithm of species richness on island area and habitat diversity. Note: NS indicates  $P > 0.05$ ; \*  $0.05 > P > 0.01$ ; \*\*  $0.01 > P > 0.001$ ; \*\*\*  $P < 0.001$ . RMSE (root mean squared error) is the standard deviation of the data about the regression line

Group	$N$	$F$ -ratio		Area		Habitat diversity		RMSE	$R^2$
		Area	HD	Slope	SE	Slope	SE		
Birds	19	5.9 *	6.0*	0.126	0.052	0.074	0.030	0.100	0.671
Bats	17	6.7 *	0.1 NS	0.375	0.145	0.087	0.272	0.407	
Herps	19	0.1 NS	8.5 ***	0.026	0.075	0.128	0.044	0.144	0.510
Leps	15	3.4 NS	7.7 *	0.139	0.075	0.116	0.042	0.126	0.694



**Fig. 4.** Proportion of variance in species richness among islands related uniquely to island area (black portion of bars), uniquely to habitat diversity (dark grey), to correlated variation between area and habitat diversity (medium grey), and unexplained by either or both factors (light grey).

tions differed strikingly among the four faunal groups considered. At one extreme, species richness of bats was sensitive to area but not habitat diversity; at the other extreme, the diversity of reptiles and amphibians was correlated only with habitat diversity. Birds and butterflies were intermediate in that their species richnesses were related statistically to both island area and habitat diversity. The different responses of the faunal groups to the independent variables presumably reflect differences in the biology of these taxa, including dispersal qualities that influence rate of spread through the Lesser Antilles and local ecological characteristics that influence the persistence of established island populations.

In Table 5, we have summarized five considerations that might influence the effects of area *per se*

and habitat diversity on species richness in these taxa.

1. Between-island movement could lead to the rescue of populations on the verge of extinction and presumably keep the slope of the species–area curve low (Ricklefs & Cox 1972; Brown & Kodric-Brown 1977). In this way, vagility might reduce the effect of area on species richness. Conversely, it might enhance the effect of habitat diversity if highly vagile habitat specialists are able to colonize most, or all, suitable habitat areas within the archipelago. One indication of inter-island movement is a low prevalence of endemism in individual island populations. Among the four groups included in this study, however, endemism does not parallel the slope of the species–area relationship (Table 5). Reptiles and amphibians have very high endemism in the Lesser

**Table 5.** Attributes of four groups of animals that might influence the relationship of species richness to the area and habitat diversity of islands

	Bats	Birds	Butterflies	Herps
<b>Patterns</b>				
Contribution of area to species richness	Moderate	Moderate	Low	Low
Contribution of habitat diversity to species richness	Low	Moderate	Moderate	High
Slope of species–area relationship	High	Moderate	Moderate	Low
Endemism in Lesser Antilles	Moderate	Moderate	Low	High
<b>Processes</b>				
Vagility	Moderate	Moderate	High	Low
Area-dependent colonization	Unknown	No	Unknown	Unknown
Habitat specialization	Low	Moderate	High	High
Population size	Small	Small	Moderate	Large
Resting states	Low	Low	High	Moderate

Antilles but the species–area regression for them has a low slope; conversely, butterflies exhibit low endemism the Lesser Antilles but their species–area regression has the highest slope of the four taxa considered. However, although simple regressions of species richness on area alone revealed a relatively steep slope in butterflies, in multiple regressions of species richness on both area and habitat diversity, the slope of the relationship with respect to area was insignificant for butterflies. Thus, while there is no indication that the rescue of island populations by migration of individuals between islands plays a general role in modifying the species–area relationship, it might be an important factor for such taxa as butterflies.

2. Habitat specialization would tend to make species richness more sensitive to habitat diversity and perhaps less sensitive to area *per se*. Although a high degree of habitat specialization should result in a low contribution of area *per se* to species richness, it might lead to high species richness per unit of island area on islands with multiple habitats. Table 5 shows that the rank ordering of the four faunal groups with respect to habitat specialization is consistent with the relative contribution of habitat diversity to the species richness of islands. Unfortunately, no direct evidence is available on habitat specialization with respect to the vegetation types used in this study to quantify habitat diversity. Species of bats found in the Lesser Antilles are mostly generalized feeders, including 10 species of aerial insectivores, 4 nectarivores, and 7 canopy frugivores out of 24 species (Jones 1989). Conspicuously absent in comparison with continental localities are species that glean insects from vegetation (Findley 1993). The habitat distributions of these bats remain poorly understood. However, Fleming *et al.* (1972) and Arita (1993, 1997) have shown that Central American bats tend to be widespread with respect to habitat and geography, even though some species are sensitive to habitat disturbance (Fenton *et al.* 1992). The butterflies of the Lesser Antilles belong primarily to the families Nymphalidae, Lycaenidae, Pieridae, and Hesperidae, all of which are food plant specialists (Riley 1975). How this translates into habitat specialization is not known. Locally, adult butterflies tend to be habitat generalists in their flight areas (DeVries *et al.* 1997; Lawton *et al.* 1998). However, the butterflies of Costa Rica are relatively specialized with respect to six recognized faunal zones; the 543 species occur in an average of 2.3 faunal zones per species (DeVries 1987). Possibly the smaller number of species in the Lesser Antilles exhibit ecological release, as Cox & Ricklefs (1977) have demonstrated for birds. West Indian birds (Cox & Ricklefs 1977; Wunderle 1985) and reptiles (Bullock & Evans 1990; López-González & González-

Romero 1997) exhibit a broad range of habitat breadths but these cannot be compared directly with other groups. Although habitat specialization may have an important influence on the way in which habitat diversity influences species richness, we have no empirical basis for evaluating this idea beyond the subjective categorization presented in Table 5. Most importantly, our characterization of habitat diversity based on major vegetation types may be more relevant to some faunal groups than to others.

3. Population size may influence the sensitivity of island populations to stochastic or catastrophic extinction. Presumably, lower population density should make species more prone to extinction on small islands and thus enhance the influence of island size on diversity. Probability of extinction is inversely related to population size among birds on small islands (Pimm, Jones & Diamond 1988) although stochastic extinction only becomes a high probability in populations under 1000 individuals (Pielou 1969). Ricklefs & Cox (1972) showed that extinction of Antillean populations of birds during the last 150 years is also inversely related to island size above a certain threshold. Bats and birds presumably have lower densities and therefore lower population sizes on average than either butterflies or reptiles and amphibians. This contrast is consistent with the relative influence of island size *per se* on species richness, which is higher in birds and bats, and lower in reptiles and amphibians and butterflies. Thus, it is plausible that the species–area relationships exhibited by birds and bats are partly generated by island-size-dependent extinction related to small population size.

4. Area-dependent colonization, resulting from larger islands being better targets for dispersing individuals, could enhance the relationship of species richness to area *per se*. The contributions of colonization and extinction to species–area relationships can be tested by comparing species–area curves for recent colonists to those for old populations. If area-dependent colonization is important, then recent colonists should show strong species–area relationships. If recent colonists have lower species–area slopes than older species, then extinction has played a strong role. Ricklefs & Cox (1972) presumed that the relative ages of island populations could be judged by the degree of taxonomic differentiation among island populations. This assumption has now been verified by analyses of DNA sequence divergence among West Indian birds (Ricklefs & Bermingham 1999). Applying this logic to birds in the West Indies, Ricklefs & Cox (1972) found that the species–area relationship had a much lower slope among recent colonists than among older populations, suggesting that area-dependent extinction is more important than area-dependent colonization in shaping the species–area relationship of

Lesser Antillean birds. Nothing is known about the relative ages of island populations in the other three taxa considered in this analysis.

5. Resting or resistant stages would enhance the ability of a species to avoid catastrophic extinction and thereby reduce the influence of island area on species richness. Of the groups included in this study, dormancy is potentially most prominent in Lepidoptera (Owen 1971), which may pass through unfavourable seasons as diapausing eggs and pupae. These resting stages are highly resistant to drought and, presumably, to catastrophic events such as hurricanes and volcanic eruptions. Reptiles and amphibians may also persist for long periods in protected microenvironments without having to feed. This may be particularly important to amphibians that breed in ephemeral sources of water. In this analysis, the species richness of neither butterflies nor reptiles and amphibians was influenced by island area.

In summary, we might expect to see strong effects of habitat diversity when: (a) species are specialized with respect to habitat; (b) when populations are dense enough that they are above the critical demographic threshold for viability on islands of the smallest size; (c) when inter-island movement can rescue populations from extinction; or (d) when resting stages help populations resist catastrophic extinction. We expect to see strong effects of island area when (a) the size of the target for colonists is important and (b) when population densities are low enough that small island size can bring numbers of individuals into the range for stochastic extinction.

The analyses in this study combined with estimates of vagility, habitat specialization, and population density for each of the four faunal groups suggest that vagility and size of island as a target for colonization are not important factors in this system. Thus, it would appear that the species–area relationship is established by differential extinction of island populations with respect to island size or by differential establishment of populations with respect to habitat diversity. Birds and bats appear to be more vulnerable to extinction on smaller islands because of their low population densities and lack of resistant resting stages. The diversity of each of these faunal groups is controlled primarily by the area of the island *per se*, which sets an upper limit to the size of populations. Because the species richness of butterflies and that of reptiles and amphibians primarily reflect habitat diversity independently of island area, the diversity of these groups would appear to be related to the presence of suitable habitat for each of the species in the pool of potential colonists. This presumes that these species colonize suitable habitats directly from similar habitats on other islands or on the mainland.

Ricklefs & Cox (1972) outlined a scenario for the development of island avifaunas in the West Indies.

Colonists are primarily birds of open, coastal scrub habitats, which become established in similar habitats in the Antilles. On large, high-elevation islands with a high diversity of habitats, these colonizing populations may expand into wetter, montane areas of the islands and exhibit broad habitat distributions, a pattern originally described by Wilson (1961) for ants on islands in Melanesia. Most islands within the Antilles have suitable coastal habitat for avian colonists and even the smallest islands in the group are populated. Following establishment, however, risk of extinction is inversely related to island size and, over time, a species–area relationship is established (Ricklefs & Cox 1972). Greater habitat diversity may prolong population persistence if montane habitats provide refuges for established populations from competition from, or pathogens brought by, new colonists. This has been evident in the avifauna of the Hawaiian Islands, where native birds have been virtually extirpated from the lowlands following the introduction of avian malaria and its mosquito vector (Van Riper *et al.* 1986). It may explain why bird species richness is influenced by both island area and habitat diversity.

If butterflies and reptiles and amphibians were habitat specialists, then establishment of populations of these taxa would depend on the availability of suitable habitat. Accordingly, the species–area relationship would be established at the colonization phase by habitat filters. This also implies that colonization of each habitat type occurs directly from the corresponding habitat in the source area. That is, for example, montane specialists arrive from montane habitats on source islands or the continent. Such patterns of dispersal have been identified through molecular phylogenetic analyses of high elevation species of mammals (Smith & Patton 1993) and birds (Fjeldså 1992) in the Andes Mountains and in upper-elevation plants in the Canary Islands (Franciscoortega, Jansen & Santosguerra 1996). This is less likely to be the case in birds of the West Indies because few widespread species are restricted to montane habitats. The relatively weak dispersal abilities of montane endemics also apparently applies to birds of forest interiors, even at low elevations, because most such taxa (e.g. antbirds, ovenbirds, woodcreepers, woodpeckers) are absent from suitable habitats in the West Indies (Ricklefs & Cox 1972). The model of habitat-specific colonization also does not apply to *Anolis* in the Greater Antilles because diversified island *Anolis* faunas are produced primarily by adaptive radiation within islands (Irschick *et al.* 1997; Losos *et al.* 1998).

## Conclusions

The species richness of a taxon on a particular island is the outcome of many processes affecting

the colonization, evolution, and persistence of island populations. The expression of these processes is likely to differ among taxa because of variation in biological attributes related to vagility, habitat specialization, population density, and resistance to environmental variation. These processes may also vary in their outcome among island groups because of differences in the range of island area, habitat diversity and spacing. Although studies of the relationship between species richness and island area have been important to the development of many areas of ecology, evolution, and conservation biology, understanding how the species–area relationship is generated requires a closer look at its underlying processes. In particular, we were struck by the paucity of available information on density and habitat specialization of populations, and of habitat distributions on islands. Separating species according to age, based on DNA sequence divergence, will permit an assessment of the relative roles of island-size-dependent colonization vs. extinction in generating the species–area relationship. Such genetic approaches, which we are applying to West Indian birds in collaboration with E. Bermingham, also will allow us to appraise inter-island movement, which may be important in masking local extinctions and reducing the dependence of species richness on island size. Comparison of different taxa in the same island setting offers the potential for controlling island attributes while assessing the effects of differences in species attributes. Conversely, comparing the same taxon in different island groups might show how island-group attributes themselves influence species richness. Although we have been able to make progress in this analysis using data available in the literature, it is clear that new information gathered in the context of the issues that surround the species–area relationship is required to fully explore the area *per se* vs. habitat diversity issue.

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**Appendix: Part A**

A literature survey of studies relating species richness to the area and habitat diversity of islands. SR = range of species richness; NG = information not given

Study	Source	Taxon	SR	Islands	Areas
1.	Abbott (1974)	Plants	2–186	Islands in Southern Ocean	1–11960 km <sup>2</sup>
2.	Buckley (1985)	Plants	1–45	Mudflat islets	1–4090 m <sup>2</sup>
3.	Hamilton <i>et al.</i> (1963)	Plants	7–325	Galapagos Archipelago	0.2–2249 mi <sup>2</sup>
4.	Harner & Harper (1976)	Plants	24–87	Nested quadrats	1, 10, 100, 1000, 10000
5.	Johnson <i>et al.</i> (1968)	Plants	4–420	California Channel Islands	0.02–134 mi <sup>2</sup>
6.	Johnson & Raven (1973)	Plants	3–444	Galapagos Archipelago	0.01–4669 km <sup>2</sup>
7.	Johnson & Simberloff (1974)	Plants	62–1008	British Islands	0.5–2137 km <sup>2</sup>
8.	Kohn & Walsh (1994)	Plants	0–71	Shetland Islands, U.K.	0.031–99.6 ha
9.	Nilsson <i>et al.</i> (1988)	Plants	18–32	Islands in Lake Mälaren, Sweden	0.6–74.3 ha
10.	Rydin & Borgegård (1988)	Plants	0–115	Islands in Lake Hjälmaren, Sweden	50–25170 m <sup>2</sup>
11.	Brönmark (1985)	Snails	2–14	Ponds	0.003–2.33 ha
12.	Maly & Doolittle (1977)	Snails	3–10	Bahama Cays	1–101 ha
13.	Nilsson <i>et al.</i> (1988)	Land snails	9–27	Islands in Lake Mälaren, Sweden	0.6–74.3 ha
14.	Abbott (1974)	Insects	2–300	Islands in Southern Ocean	1–11960 km <sup>2</sup>
15.	Nilsson <i>et al.</i> (1988)	Carabid beetles	4–28	Islands in Lake Mälaren, Sweden	0.6–74.3 ha
16.	Weissman & Rentz (1976)	Orthoptera	5–39	California Channel Islands	2.6–249 km <sup>2</sup>
17.	Tonn & Magnuson (1982)	Fish	1–10	Wisconsin lakes	2.4–89.8 ha
18.	Kitchener <i>et al.</i> (1980a)	Lizards	3–34	Nature reserves, Australia	34–7808 ha
19.	Losos (1986)	Geckos	1–4	Indian Ocean islands	0.004–2512 km <sup>2</sup>
20.	Case (1975)	Lizards	2–11	Islands in Gulf of California	0.6–1430 km <sup>2</sup>
21.	Abbott (1974)	Birds	1–9	Islands in Southern Ocean	1–11960 km <sup>2</sup>
22.	Blake & Karr (1987)	Birds	9–43	Woodlots	0.0018–6 km <sup>2</sup>
23.	Reed (1981)	Birds	1–79	British islands	0.0008–10.7 km <sup>2</sup>
24.	Elmberg <i>et al.</i> (1994)	Waterfowl	1–11	Finnish lakes	2–48 ha
25.	Haila <i>et al.</i> (1983)	Land birds	1–60	Sweden, Åland Archipelago	0.5–582 ha
26.	Hamilton <i>et al.</i> (1964)	Birds	Up to 500	Three groups of islands	Up to 885 780 km <sup>2</sup>
27.	Kitchener <i>et al.</i> (1982)	Birds	18–56	Nature reserves, Australia	34–7808 ha
28.	Freemark & Merriam (1986)	Birds	NG	Ontario woodlots	3–7620 ha
29.	Opdam <i>et al.</i> (1985)	Birds	1–10	Netherlands woodlots	1–20 ha
30.	Harris (1973)	Birds	7–20	Galapagos Islands	1–2249 mi <sup>2</sup>
31.	Power (1972)	Birds	2–32	California Channel Islands	0.2–134 mi <sup>2</sup>
32.	Power (1976)	Birds	6–37	California Channel Islands	2.9–249 km <sup>2</sup>
33.	Dueser & Brown (1980)	Mammals (rodents)	0–5	Virginia barrier islands	29–2197 A
34.	Kitchener <i>et al.</i> (1980b)	Mammals	1–10	Nature reserves, Australia	34–7808 ha
35.	Burbidge <i>et al.</i> (1997)	Mammals	NG	Coastal islands, Australia	NG

## Appendix: Part B

A literature survey of studies relating species richness to the area and habitat diversity of islands. N = number of islands; R = type of correlation or regression; SIM = simple correlation; STW = stepwise regression; MUL = multiple regression; NS = effect not significant.

Study	N	R	Area	Habitat diversity	Measure of habitat diversity
1.	19	SIM	21%	NS	Elevation
		STW	33%	NS	
2.	61	SIM	85–93%	No <sup>1</sup> , yes <sup>2</sup>	<sup>1</sup> sediment type; <sup>2</sup> elevation (= salinity heterogeneity)
3.	17	MUL	NS	Yes	Elevation
4.	30	SIM	Yes	Yes	Heterogeneity (soil irregularity, aspect, water holding capacity)
		MUL	Yes	Yes	
5.	18	MUL	Strong	Weak	Elevation
6.	29	SIM	88%	72%	Elevation
		MUL	Yes	NS	
7.	42	STW	Yes	Yes	Soil types (1–6 per island)
8.	45	MUL, path	Yes (19%)	Yes (29%)	Habitat diversity (14 types, 1–13 per island)
9.	17	STW	58%	NS	Standard deviation of vegetation variables among plots
10.	40	STW	84%	3%	Ten habitat types
11.	115	STW	15%	15%	Plant (macrophyte) diversity
12.	7	MUL	NS	Yes (70%)	Six habitat types
13.	17	STW	43%	NS	Standard deviation of vegetation variables among plots
14.	19	SIM	NS	77%	Land plant species; elevation (NS)
		STW	8%	73%	
15.	17	STW	51%	NS	Standard deviation of vegetation variables among plots
16.	8	STW	Strong	NS	Elevation, topographic diversity
17.	18	SIM	Yes	Yes	Diversity of qualitative habitat categories combining depth, substrate, and vegetation
18.	23	STW	No	Yes	Vegetation associations (4–45 per reserve)
19.	48	STW	NS	Yes (14%)	Elevation
20.	24	STW	Strong	Weak	Elevation, plant species, plant volume diversity
21.	19	STW	NS	70·9%	Land plant species; elevation (NS)
		SIM	37%	71%	
22.	15	STW	88–98%	NS	Forest structure variation
23.	73	STW	4%	76%	Number of habitats (26); elevation
24.	31	SIM	Yes	Yes	Habitat structural diversity (SIM); vegetation types (NS);
		STW	Weaker	Stronger	number of prey taxa (SIM, STW)
25.	44	SIM	89%	84%	Habitat types (1–10)
26.	12–25	MUL	Yes	NS	Elevation
27.	23	STW	Strong	yes	Vegetation associations (4–45 per reserve)
28.	21	STW	50%	17%	Structural classes diversity
29.	68	STW	Stronger	Weaker	Structural classes diversity
30.	15	MUL	NS	Yes	Plant species richness, elevation
31.	16	MUL	NS	Yes	Plant species richness, elevation
32.	8	SIM	88–92%	93–98%	Plant species richness
33.	9	SIM	Yes	Yes	Elevation, plant associations, soil types
34.	23	SIM	72%	55%	Vegetation associations (4–45 per reserve)
		STW	Yes	No	
35.	92–263	STW	Yes	No	Elevation, precipitation