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Determinants of plant species richness on small Bahamian islands

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Abstract

Aim I investigated the determinants of plant species richness in two archipelagos, comparing the predictive power of different explanatory variables. I evaluated both conventional variables and alternative variables not commonly used in such analyses. I also investigated the effect of island location in relation to neighbouring landmasses on plant species richness and the predictive ability of regression models.

Location Archipelagos of small islands in the central Exumas and near the north-east coast of Andros, Bahamas.

Methods I surveyed plant species richness and obtained measures of seven predictor variables: total island area, the ratio of perimeter to total area, vegetated area, the ratio of vegetated area to total area, distance to the nearest large island, elevation and protection from surrounding islands. All seven predictor variables were evaluated as determinants of plant species richness in simple and stepwise multiple linear regressions. Analyses were conducted for each archipelago overall, and then separately for three categories of islands in the Exumas. Total area, elevation, and distance were evaluated as predictors of vegetation incidence in simple and stepwise multiple logistic regressions for both archipelagos.

Results Some expression of insular area was always the best single predictor of plant species richness in the linear regressions. Total area was a relatively poor predictor compared with other expressions of insular area. Distance, elevation, and protection explained relatively little of the overall variation in plant species number, although all variables were selected as significant in some models. A greater amount of variation in plant species richness was explained by the linear regression models in the Exumas (69.0%) compared with Andros (60.9%). Different variables were entered into the models for the three categories of islands in the Exumas, and adjusted coefficients of multiple determination ranged from 68.9% to 85.7%. In the logistic regressions, the model including total area and distance yielded almost 90% correct classification of vegetation incidence in the Exumas; no significant variables were selected for Andros. A group of exposed, outer islands supported many fewer species than more sheltered islands, on the basis of total island area or elevation.

Main conclusions The three variables commonly used in studies of determinants of insular species richness – total island area, distance, and elevation – were relatively poor predictors in most analyses. Alternative expressions of insular area – indicative of disturbance or shape in combination with area – were usually better predictors than total area and may more realistically reflect habitable area. Alternative predictors explained similar amounts of variation in plant species richness compared with commonly used predictors, and combinations of all variables into a single stepwise model resulted in increased predictive power. The predictive power of the models tended to be higher for groups of islands that were more sheltered by neighbouring islands. Exposed islands,

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although separated by relatively small distances from nearby protected islands, may be impacted by storms much more severely and possess many fewer species. The location of small islands relative to large landmasses, as well as their geological histories, should be taken into account in such analyses.

Keywords
Bahamas, disturbance, insular species richness, island biogeography, linear regression, logistic regression, predictor variable.

INTRODUCTION

Biogeographers have long been fascinated by the factors influencing numbers of species on islands. The increase in species number with area is one of the oldest known ecological patterns, first documented by Watson and deCandolle in the mid-nineteenth century (Williams, 1964; Rosenzweig, 1995). Island biogeographers lacked a cohesive body of theory, however, until MacArthur & Wilson's (1963, 1967) work, which postulated that the number of species on an island was determined by an equilibrium between immigration and extinction, processes that are largely affected by insular area and distance to the mainland.

Many succeeding studies have examined area and distance, as well as island elevation or altitude, as determinants of species richness (reviewed by Williamson, 1981, 1988; Whittaker, 1998). Much variability in the predictive power of these variables has been documented, however, and in some cases even area was not found to be an important predictor of species number (Abbott, 1974; Gilbert, 1980). In addition to area, distance, and elevation, numerous other variables have been examined as potential predictors of insular species richness, such as habitat diversity (Rafe *et al.*, 1985; Deshaye & Morisset, 1988; Kohn & Walsh, 1994), latitude (Johnson *et al.*, 1968), rainfall (Heatwole, 1991), soil type (Johnson & Simberloff, 1974), temperature (Abbott, 1974), and energy (Wright, 1983).

Although classical island biogeographical theory has been questioned (Gilbert, 1980; Whittaker, 2000) and a call for a new paradigm of island biogeography has been issued (Lomolino, 2000a), area and distance still play primary roles in alternative theories (e.g. Heaney, 2000; Lomolino, 2000b). In general island area, and to a lesser degree isolation, can hardly be disputed as important determinants of insular species richness. Yet alternative expressions of insular area, or variables that measure some other aspect of insularity, may provide similar or greater predictive power.

Another important consideration in examining the determinants of insular species richness involves the degree of heterogeneity among the set of islands under study, in terms of their geological history or location relative to other landmasses. Separation of similar islands into categories based on such criteria may result in greater predictive power within categories, or indicate where stochastic variation makes prediction difficult (e.g. Heatwole, 1991).

To examine these ideas, I tested the predictive power of seven variables as determinants of plant species richness on small Bahamian islands. I evaluated three conventional variables often used in studies of determinants of insular species richness – area, distance, and elevation – along with three alternative expressions of insular area, and a measure of protection afforded to an island from neighbouring landmasses. I also categorized small islands based on their location relative to large mainland islands, to determine whether controlling for this source of heterogeneity within a group of islands would provide greater predictive power.

METHODS

Study areas

This study was conducted on small islands in the central Exumas and off the north-eastern coast of Andros, Bahamas. In the Exumas, the study area included 154 small islands (114 vegetated and forty lacking vegetation) lying along the Exumas chain between O'Briens Cay and Bitter Guana Cay (Fig. 1). At Andros, I surveyed fifty-eight small islands (forty-eight vegetated and ten lacking vegetation) located off the north-eastern coast and inside the barrier reef, lying between Nicholls Town and Staniard Creek (see map in Morrison, 1997). Surveys were conducted in the Exumas in May 1998 and at Andros in April–May 1999.

Measurement of variables

Seven explanatory variables were used in the regression analyses: (1) total area (2) the ratio of perimeter to total area (P/A) (3) vegetated area (4) the ratio of vegetated area to total area (VA/A) (5) distance to the nearest mainland island (6) elevation, and (7) protection from surrounding islands. The response variable in all linear regression analyses was the total number of plant species on the island, or plant species richness (PSR).

Total area was the two-dimensional area of the island above the mean high tide mark, along which perimeter was measured. To accurately quantify the total area and perimeter of these small, irregularly shaped islands, in the Exumas I took aerial photographs from directly overhead at an altitude of 300 m in a small plane. The photographs were digitized, and analyses to calculate island areas and perimeters were performed on a Macintosh computer using the

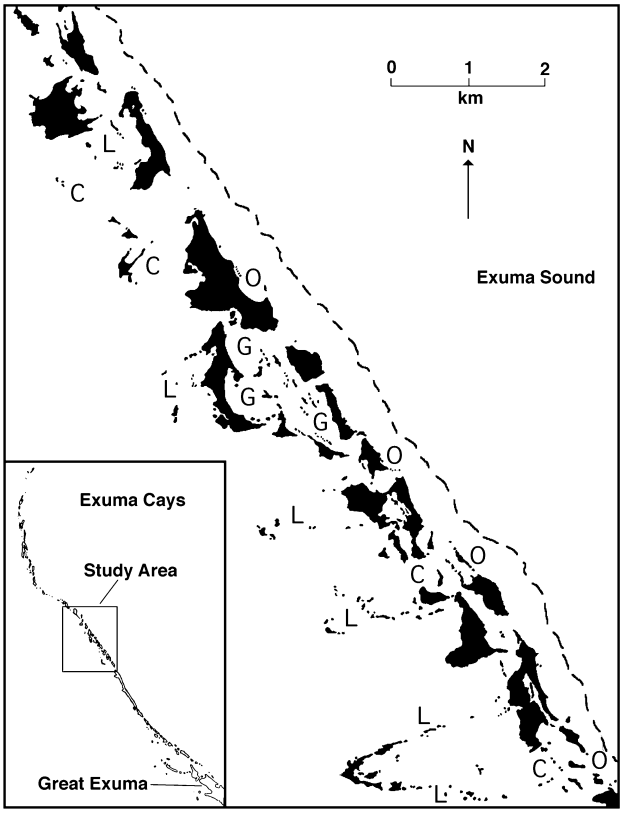

Figure 1 Map of the Exumas study area, showing approximate locations of the four different categories of small islands. C: channel islands, L: leeward islands, G: lagoon islands, O: outer islands. The dashed line marks the 100-fathom line (*c.* 182 m) separating the deep water Exuma Sound to the east from the shallow banks and islands to the west.

public domain NIH Image (developed at the US National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). At Andros, a fly over was not practical and areas and perimeters of the islands were determined from measurements taken on the islands using a tape measure. Most islands were elliptically shaped, and the formula for an ellipse was used to determine total area after measuring the long and short axes of each island.

Vegetated area was the two-dimensional area of the island covered by vegetation above the mean high tide mark. The measurements used to calculate vegetated area were made on the ground in both archipelagos with a tape or folding rule. Vegetation cover on some parts of some islands was patchy, and the percentage of actual cover was estimated. Three mangrove species (*Rhizophora mangle* L., *Avicennia germinans* [L.] L and *Laguncularia racemosa* [L.] Gaertn. f) grow primarily in the intertidal region and the areas covered by these species below the mean high tide mark were not included in the analyses. These three mangrove species were rare on the islands surveyed in the Exumas, but common in the archipelago at Andros.

Distance was measured to the nearest mainland island, which was considered to be the nearest source pool of the complete set of plant species found on the smaller islands. In the Exumas, mainland islands were classified as those islands > 46,580 m^2, which reflects a natural discontinuity in the distribution of island areas in the region (Schoener, 1987). In the archipelago near Andros, distance was measured to the main island of Andros. Elevation was measured as the vertical distance from the mean high tide mark to the highest point of the island.

To quantify protection from waves and wind conferred by nearby islands (hereafter 'protection'), a circle was drawn around each island on a scale map, with the centre of the circle at the centre of the island. For every neighbouring island within the circle or in contact with the circumference of the circle, the arc of the circle that would be obstructed by the presence of the neighbouring island, from the centre of the focal island, was measured. The obstructed arcs due to all neighbouring islands within or on the circumference of the circle were then summed (see Fig. 2). The protection from surrounding islands could range from 0° (in the case where no other islands were near) to 360° (when the island in question was completely surrounded by islands or landmasses in all directions at the distance of the radius measured). This procedure was carried out three times, for circles with radii of 0.5, 1.0, and 1.5 km.

The numbers of plant species on each island were recorded in visual surveys in the Exumas in May 1998, and at Andros in April and May 1999. Every plant on every island was identified to species, as these islands are the subject of a long-term study of plant species turnover (Morrison, 1997,

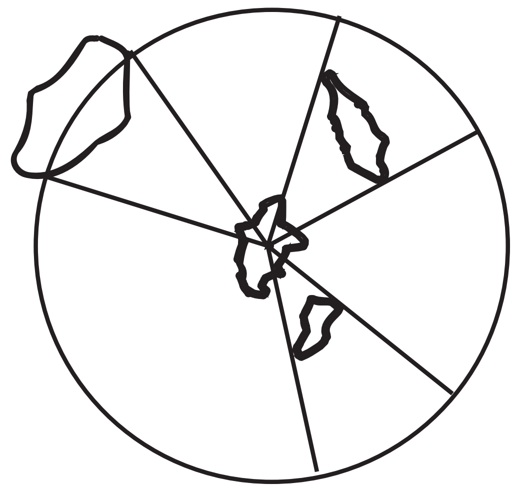

Figure 2 Method of determining angle of protection for the island in the centre of the circle. The arc of protection conferred by neighbouring islands lying within or on the circumference of the circle was determined by drawing lines from the centre of the focal island to a point on the circumference of the circle as shown, to quantify an arc of protection for each neighbouring island. The arcs were summed into a cumulative angle of protection. In this example, the angle of protection is *c.* 120°.

unpublished data). All cays surveyed had vegetated areas < 6000 m^2, small enough so that it was unlikely any species would be overlooked. Thus the survey methods used (explained in more detail in Morrison, 1997) produced a very accurate plant species richness data set. Species identifications follow Correll & Correll (1982). Voucher specimens have been placed in the J. M. Tucker Herbarium at U. C. Davis.

The distributions of all variables were plotted and examined prior to statistical analyses, and residuals were examined after models were constructed. Transformations were performed to normalize the distributions of variables when necessary. Total area, vegetated area, distance, and plant species richness were all $\log_{10}$ transformed. Elevation and protection from surrounding islands were square root transformed. The P/A ratio was reciprocal transformed, and the VA/A ratio was arcsine square root transformed.

In the Exumas, complete data were obtained for 102 of the 114 vegetated islands, and thus 102 islands were included in the linear regressions. At Andros complete data were obtained for all forty-eight vegetated islands, and all were used in the linear regression analyses. All 154 islands in the Exumas and all fifty-eight islands near Andros were included in the logistic regression analyses, where the focus was on presence or absence of vegetation on the islands.

Linear regression analyses

In preliminary analyses, plant species richness was regressed against the explanatory variable protection at the three different distances measured (circles of radii 0.5, 1.0, and 1.5 km, see above). Thus, three separate simple linear regressions were performed for each archipelago. In succeeding analyses, I used, the distance at which the explanatory variable protection explained the greatest amount of variation in plant species richness.

Correlation coefficients were calculated for each pair of explanatory variables, in each archipelago, to assess the degree of multicollinearity in the data. A series of simple linear regressions were performed, regressing plant species richness against each of the seven explanatory variables individually, for both archipelagos. Stepwise multiple regressions were then conducted for three sets of explanatory variables in both archipelagos. The first set included vegetated area, total area, elevation and distance. The latter three predictors represent variables that are commonly used in island biogeographical analyses and are relatively easy to obtain. Although not as commonly encountered, vegetated area has been used in a number of studies (e.g. Schoener & Toft, 1983; Morrison, 1998; Spiller *et al.*, 1998), and was included in the first set. The second set of predictors included VA/A, P/A, and protection. This set of predictors represents variables that have rarely or never been used in previous island biogeographical studies. The third set of predictors contained all seven explanatory variables (six for Andros; see Results).

In the stepwise regressions, predictor variables were entered or removed from the model based on their relative reduction of sums of squares, if their partial *F* exceeded the *F*-to-enter level or fell below the *F*-to-remove level. The minimum *F* acceptable to enter was 4.0 and the maximum *F* acceptable to remove was 3.9. This corresponds roughly to a significance level of $a = 0.05$ for any single test (Neter *et al.*, 1985). Both forward and backward stepwise regressions were performed for all analyses.

The islands in the central Exumas were subdivided into three categories according to their positions relative to larger mainland islands and surrounding ocean depths (Fig. 1). The first category, hereafter called 'channel' islands ($n = 20$), included islands that were located in relatively deep water channels (6–12 m) between mainland islands and were exposed to strong tidal currents, waves, and winds from both the east and west. The second category, hereafter called 'leeward' islands ($n = 57$), included islands that were located on relatively shallow banks (3–6 m), protected from the deep ocean and prevailing trade winds by mainland islands to the east, but were relatively exposed to the west. The third category, hereafter called 'lagoon' islands ($n = 25$), included islands that were in very shallow water (< 3 m) and protected on all sides by larger islands.

For each category of islands, a series of simple linear regressions were performed, regressing the number of plant species against each of the seven explanatory variables individually. Stepwise multiple linear regressions were then conducted for each island category, regressing the number of plant species against all seven explanatory variables, using both forward and backward procedures. Analogous regressions were not conducted for categories of islands in the Andros archipelago, because the islands were all located between the mainland island of Andros to the west and a barrier reef to the east (*c.* 8 km offshore; see map in Morrison, 1997), and were not obviously separable into distinct categories.

StatView 4.0 was used for all linear regression analyses. Adjusted coefficients of determination (R_a^2) were used to make comparisons among the stepwise models. R_a^2 takes into account the number of parameters in the model through the degrees of freedom and increases only if the residual mean square decreases (Neter *et al.*, 1985), allowing for comparisons among models with different numbers of explanatory variables. When multiple comparisons were made within the same data set, the sequential Bonferroni method was used to control the type-I error rate (Rice, 1989).

Morrison (1997) presented a basic analysis of the determinants of plant species richness on Bahamian islands, which included fewer islands and evaluated fewer explanatory variables. The focus of this paper is not so much to identify the best predictor variables per se, but rather to compare among different types of predictor variables and among different types of islands.

Logistic regression analyses

Logistic regressions were employed to determine the variables that were the best predictors of vegetation incidence. The presence or absence of vegetation was regressed against three predictor variables: total island area, island elevation, and distance to the nearest mainland island. These variables were tested individually in simple logistic regressions, and simultaneously in a stepwise multiple logistic regression. SPSS 6.1 (SPSS, Inc.; Chicago, IL, USA) was used for these analyses. In the stepwise regressions, a forward procedure using the likelihood-ratio statistic was employed, which included a variable in the model at the $P = 0.05$ level and removed it if that variable's significance fell below 0.10. The percentage of islands classified correctly by the model, which is an indication of the power of the logistic regression (Norusis, 1994), was also calculated for all regressions.

Outer islands

To further elucidate the importance of island location and geological history in analyses of determinants of insular species richness, fourteen additional small islands on the eastern side of the larger islands of the Exuma Cays were surveyed in May 1999 (Fig. 1). The sea floor on the eastern side of the central Exuma Cays drops off steeply into the deepwater Exuma Sound, and the prevailing easterly trade winds result in much greater wave action impacting these small islands. The substrate of these outer islands also differed, consisting of a mixture of marine limestone and fossil sand deposits. Almost all of the 154 other islands surveyed in the Exumas were composed entirely of marine limestone. All plant species were identified, and total island area and island elevation were measured. Because most of these islands lacked vegetation, the sample size was too small for regression analyses of determinants of plant species richness, and data were plotted graphically.

RESULTS

A total of fifty-five plant species were recorded from the Exumas; thirty-eight plant species were recorded from the islands of the Andros archipelago. A list of species is available from the author.

Predictors of plant species richness

The preliminary analysis of the explanatory variable protection revealed low coefficients of simple determination for all radii distances evaluated ($r^2 < 0.06$ for the Exumas; $r^2 \leq 0.008$ for Andros). A radius distance of 1.0 km ($r^2 = 0.054$, $P = 0.019$) explained the greatest variation in plant species richness in the Exumas, and measurements at this distance were used in the succeeding analyses. At Andros, no significant relationships were observed at any distance and very small amounts of variation were explained. Thus this variable was not included in the stepwise regressions for the Andros archipelago.

Some of the predictor variables used in the regression analyses were significantly correlated with each other (Table 1). This was largely inevitable because five of the seven variables were related to insular size. Distance and protection were the exceptions, and these two variables had relatively few significant correlations with other explanatory variables. Because the same results were obtained in all but two analyses using both forward and backward stepwise multiple regression procedures (see below), multicollinearity in the predictor variables did not appear to be a serious problem.

In the Exumas, all seven explanatory variables were significant in simple linear regressions, whereas at Andros only five were significant. When significant, plant species richness was positively correlated with total area, vegetated area, VA/A, protection, and elevation, but was negatively correlated with P/A and distance, in both archipelagos (Table 2). The four expressions of insular area (total area, vegetated area, VA/A, and P/A) individually explained more of the variation in PSR than did the other variables, in both archipelagos.

In the Exumas, VA/A explained the greatest amount of variation in PSR of any single variable (55.1%). Vegetated area was the next best single predictor, explaining 50.3%. Although all variables were significant at $P < 0.05$, no others explained > 30% of the variation in the response variable. At Andros, vegetated area was the single best predictor, explaining 55.8% of the variation in plant species richness, followed by the P/A and VA/A ratios (explaining 45.9% and 43.7% of the variation, respectively). Because distance and protection were not significant in the simple linear regressions for Andros, these variables were not included in the succeeding stepwise analyses for that archipelago.

In the stepwise multiple regressions for the Exumas, vegetated area and distance were chosen as significant in the

Table 1 Correlation coefficients among explanatory variables used in regression analyses. Coefficients above the diagonal are for the central Exumas archipelago ($n = 102$ islands); coefficients below the diagonal are for the Andros archipelago ($n = 48$ islands). Bold entries represent significant correlations ($P < 0.05$) after correcting for multiple comparisons in each archipelago (Rice, 1989)

	Area	Veg Area	VA/A	P/A	Elevation	Distance	Protection
Area		0.753	**0.541**	**0.870**	**0.599**	0.107	**− 0.290**
Veg area	**0.801**		**0.890**	**0.707**	**0.519**	0.142	− 0.130
VA/A	**0.643**	**0.905**		**0.311**	**0.398**	0.010	0.047
P/A	**0.807**	**0.838**	**0.608**		**0.593**	− 0.085	− 0.188
Elevation	**0.923**	**0.749**	**0.554**	**0.761**		0.045	− 0.128
Distance	0.141	0.193	− 0.014	0.385	0.239		**− 0.412**
Protection	− 0.310	− 0.203	− 0.064	− 0.375	− 0.356	**− 0.552**	

Table 2 Results of simple linear regressions of plant species richness on seven different explanatory variables. Explanatory variables are listed in decreasing order of explanation of variation in plant species richness. 'Correlation' indicates the relationship (positive or negative) between plant species richness and the untransformed explanatory variables in significant regressions

Variable	Correlation	r^2	P
Exumas ($n = 102$)			
Vegetated area/total area	+	0.551	0.0001*
Vegetated area	+	0.503	0.0001*
Total area	+	0.273	0.0001*
Perimeter/total area	−	0.267	0.0001*
Elevation	+	0.079	0.0043*
Distance	−	0.062	0.012*
Protection (1.0 km)	+	0.054	0.019*
Andros ($n = 48$)			
Vegetated area	+	0.558	0.0001*
Perimeter/total area	−	0.459	0.0001*
Vegetated area/total area	+	0.437	0.0001*
Total area	+	0.362	0.0001*
Elevation	+	0.197	0.0016*
Protection (0.5 km)		0.008	0.55
Distance		< 0.001	0.96

* Significant ($P < 0.05$) using the sequential Bonferroni method (seven regressions for each archipelago) (Rice, 1989).

first model (Table 3). All three variables (VA/A, P/A, and protection) were chosen as significant in the second model. The amount of explained variation in PSR was slightly greater for the second set of predictors than the first (65.1% vs. 62.1%, respectively). In the analyses of all variables, four of the seven predictors were included in the final model, which explained 69.0% of the variation in plant species richness. Both forward and backward procedures selected the same set of variables for all three models.

At Andros, vegetated area was the only variable chosen in the first model (Table 3). Both PA/A and VA/A were included in the second model. The first model explained slightly more of the variation in plant species richness (54.9% vs. 51.8%). In the third model that evaluated six explanatory variables, the backward elimination procedure selected three variables whereas the forward selection procedure selected only one. Vegetated area was selected by both procedures. Overall, more of the variation in plant species richness was accounted for in the Exumas than at Andros, in all three models.

When the islands in the Exumas were divided into categories based on their location relative to mainland islands and explanatory variables were analysed individually with simple linear regressions, the best predictors varied somewhat among the three island categories (Table 4). The coefficients of simple determination for the four expressions of insular area (total area, vegetated area, VA/A and P/A) were still consistently higher than those of other variables. Greater predictive power was found for the lagoon islands (where four single variables explained > 60% of the variation in PSR) than the channel or leeward islands (where no single variable explained > 53% of the variation in PSR).

In stepwise multiple regressions for each island category, different sets of predictors were selected for each category. Overall, five of the seven explanatory variables were selected for at least one model (Table 5). Forward and backward procedures selected the same variables for the channel and leeward islands, producing models that explained 76.7% and 68.9%, respectively, of the variation in plant species richness. In the analysis of the lagoon islands the backward elimination process replaced vegetated area with total area, but the overall amount of variation explained by the two models was similar (84.9% vs. 85.7%). Comparing the final stepwise models for the three categories of islands vs. all islands grouped together, greater predictive power was achieved for the channel and lagoon islands, whereas a similar amount was achieved for the leeward islands.

Predictors of vegetation incidence

In the Exumas, all three predictor variables were significant in the simple logistic regressions (Table 6). The stepwise

Table 3 Explanation of variation in plant species richness by predictor variables selected by stepwise multiple linear regression analyses. Three different models were tested. Model no. 1 included the variables vegetated area, total area, distance, and elevation. Model no. 2 included the variables VA/A, P/A, and protection. Model no. 3 included all seven explanatory variables (six for Andros). Predictor variables are listed in the order of selection. Numbers in parenthesis after each selected variable represent adjusted coefficients of multiple determination (R_a^2) for the model containing that variable and any others selected before it, for the forward selection procedure

Exumas ($n = 102$)

1. PSR = 0.537 + 0.350 vegetated area (0.498) – 0.274 distance (0.621)
2. PSR = −0.512 + 0.013 VA/A (0.547) + 0.038 protection (0.626) + 0.034 P/A (0.651)
3. PSR = −0.642 + 0.012 VA/A (0.547) – 0.125 distance (0.629) + 0.033 protection (0.651) + 0.249 total area (0.690)

Andros ($n = 48$)

1. PSR = 0.332 + 0.269 vegetated area (0.549)
2. PSR = 0.308 + 0.066 P/A (0.447) + 0.006 VA/A (0.518)
3. (forward selection) PSR = 0.334 + 0.264 vegetated area (0.522)

(backward elimination) PSR = 0.303 + 0.269 vegetated area – 0.192 elevation + 0.374 total area (0.609)

Table 4 Results of simple linear regressions of plant species richness on seven explanatory variables for each of three categories of islands in the central Exumas. The explanatory variables are ranked for each category by their ability to explain variation in the response variable

	Channel islands ($n = 20$)			Leeward islands ($n = 57$)			Lagoon islands ($n = 25$)		
Variable	Rank	r^2	P	Rank	r^2	P	Rank	r^2	P
Vegetated area	1	0.518	0.0003*	2	0.527	0.0001*	1	0.830	0.0001*
Total area	2	0.495	0.0005*	4	0.270	0.0001*	3	0.713	0.0001*
Perimeter/area	3	0.374	0.0041*	3	0.330	0.0001*	4	0.620	0.0001*
Vegetated area/area	4	0.231	0.032	1	0.561	0.0001*	2	0.810	0.0001*
Distance	5	0.223	0.035	6	0.029	0.21	6	0.080	0.17
Elevation	6	0.182	0.061	5	0.056	0.08	5	0.335	0.0025*
Protection	7	0.110	0.15	7	0.009	0.48	7	0.040	0.34

* Significant at $P < 0.05$ by the sequential Bonferroni method (Rice, 1989). Seven regressions were conducted within each island category.

Table 5 Models selected by stepwise multiple linear regression analyses for the three different categories of islands in the Exumas. Predictor variables are listed in order of selection. Numbers in parenthesis after each selected variable represent adjusted coefficients of multiple determination (R_a^2) for the model containing that variable and any others selected before it, for the forward selection procedure

Island group	Best model
Channel islands	PSR = –1.226 + 0.876 total area (0.466) – 0.448 distance (0.767)
Leeward islands	PSR = 0.618 + 0.011 VA/A (0.556) – 0.192 distance (0.653) + 0.057 P/A (0.689)
Lagoon islands	(forward selection) PSR = –0.156 + 0.283 vegetated area (0.822) + 0.010 VA/A (0.857)
	(backward elimination) PSR = –0.558 + 0.290 total area + 0.014 VA/A (0.849)

Table 6 Results of simple logistic regressions of the occurrence of vegetation against three predictor variables in the Exumas. % Correct, correct classification of islands by the model containing the indicated variable. All variables are significant predictors after correction for multiple comparisons (Rice, 1989)

Variable	Coefficient	χ^2	P	% Correct
Total area	+	72.92	< 0.0001	87.16
Elevation	+	25.93	< 0.0001	70.78
Distance	–	4.87	0.0274	74.03

procedure for the Exumas produced the following model ($\chi^2 = 79.124$, $P = < 0.0001$):

$$\text{Vegetation incidence} = -6.807 + 4.928 \text{ total area} - 1.447 \text{ distance}$$

Thus, the probability of occurrence (p) of vegetation was positively related to total area and negatively to distance. Correct classification for this model was 89.86%. No predictor variables were significant in the logistic regressions for Andros.

Outer islands

The exposed, outer islands supported far fewer plant species per unit area than the more sheltered islands ($F = 9.72$, $P = 0.0023$, ANCOVA with total area as a covariate; Fig. 3). The increase in plant species richness as a function of increasing island area (the slope in a simple linear regression model) was greater for the sheltered islands than the outer islands ($y = 5.57x - 9.70$ vs. $y = 2.75x - 7.01$, respectively). This was also true if the regression was forced through zero ($y = 1.84x$ vs. $y = 0.45x$, sheltered vs. outer islands, respectively). Outer islands that lacked vegetation were much larger than the more sheltered islands that lacked vegetation [831.2 ± 656.7 ($n = 10$) vs. 134.9 ± 131.3 ($n = 40$) m^2 [mean ± SD], respectively; $P = 0.0002$, Mann–Whitney test].

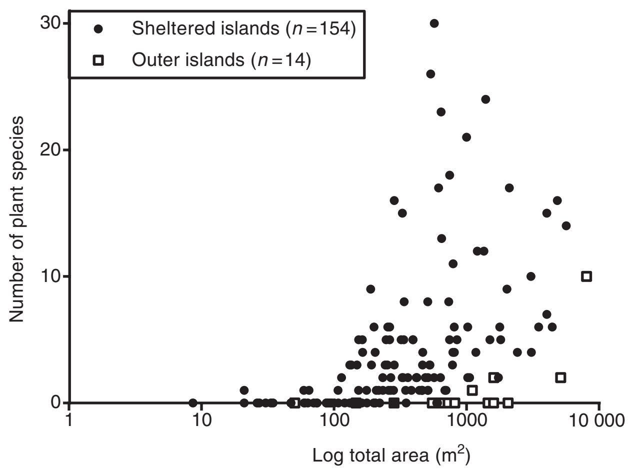

Figure 3 Number of plant species as a function of total island area for all small islands in the Exumas.

Outer islands supported fewer species although they tended to be higher than the more sheltered islands (Fig. 4). Outer islands that lacked vegetation were much

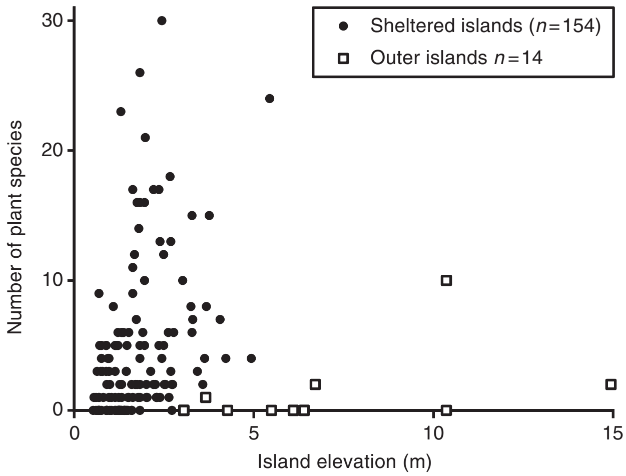

Figure 4 Number of plant species as a function of island elevation for all small islands in the Exumas.

higher than the more sheltered islands that lacked vegetation [5.4 ± 2.3 ($n = 10$) vs. 1.2 ± 0.4 ($n = 40$) m (mean ± SD), respectively; $P = 0.0001$, Mann–Whitney test].

DISCUSSION

Evaluation of predictor variables

The three variables commonly used in studies of determinants of insular species richness – total island area, distance, and elevation – were relatively poor predictors in most analyses. Of the four expressions of insular area evaluated independently in simple regressions, total area was the third best in the Exumas (all islands considered together) and the worst at Andros. Distance and elevation always ranked among the worst three predictors overall in simple regressions for all archipelagos and island groups.

Vegetated area was frequently among the best single predictors, and entered into many of the stepwise regressions. Vegetated area is probably a better indicator of 'habitable area' than total area on these islands. A swash zone extends around the perimeter of most islands, where vegetation is rare to non-existent. These zones vary in width, and appear to result from wave action, inundation by extreme high tides, or storm events. Vegetation may also be absent from areas in the interior of the islands, perhaps because not enough soil is present for plant growth.

The ratio of vegetated area to total area was also a good predictor, and in some cases was superior to vegetated area. VA/A represents an effect of both island size and disturbance. VA/A will generally increase as island size increases, particularly if the width of the swash zone remains relatively constant. This ratio will decrease as the swash zone increases in width, for islands of a similar size.

The ratio of perimeter to total area was the second best single predictor at Andros and was selected in the second model for both archipelagos in the stepwise regressions. P/A will increase as islands of a similar size become more irregularly shaped. (For example, an elliptical island with the same total area as a circular island will have a larger P/A ratio.) This ratio will decrease, however, as island size increases for islands of a similar shape. Thus this metric is sensitive to variation in both island size and shape. P/A has been shown to be an important predictor for oceanic islands where the input of marine energy or biomass is important (Polis & Hurd, 1995, 1996; Polis *et al.*, 1998), and for habitat islands where edge effects are important (Helzer & Jelinski, 1999). Blouin & Connor (1985), however, found that, after accounting for the effect of area, island shape (quantified by three alternate measures) did not explain a significant amount of residual variation in species number in more data sets than expected by chance alone.

A measure of protection from surrounding islands has not been used previously in island biogeographical studies, to my knowledge. In theory, neighbouring islands or landmasses in close proximity to the island in question should offer some degree of protection from waves or winds. A higher incidence of emergent land in the vicinity is also usually indicative of shallower seas in the region, which are usually associated with smaller waves. The degree of protection from surrounding islands as measured here was not a good single predictor in either archipelago. Although protection was positively correlated with plant species richness, this variable explained < 6% of the variation in plant species richness in the Exumas (all islands considered together), and < 1% of the variation in PSR at Andros. Protection did enter into the multiple regression models as a significant variable for all islands considered together in the Exumas, however, and was not highly correlated with most other explanatory variables.

Predictive power of the models

In the stepwise regressions, both in Exumas and at Andros, the model containing the three variables rarely used in such analyses (VA/A, P/A, and protection) explained similar amounts of variation in plant species richness as the model containing the four commonly used variables (vegetated area, total area, distance, and elevation). In the Exumas, the model containing all variables explained more variation in PSR than was possible using only the commonly used predictors (69.0% vs. 62.1%). At Andros, the backward elimination model containing all variables explained more variation than was possible using only the commonly used predictors (60.9% vs. 54.9%).

Overall, more of the variation in plant species richness was explained by the stepwise linear regressions in the Exumas than at Andros. Of particular interest in this respect were the logistic regressions, in which the stepwise model correctly predicted the presence of vegetation on small islands in the Exumas almost 90% of the time, whereas no variables were found to be significant predictors at Andros.

Between 60% and 70% of the variation in PSR was explained by the best stepwise models for the Exumas and

Andros. When the islands in the Exumas were categorized, the best model explained > 75% of the variation in PSR for the channel islands and > 85% of the variation in PSR for the lagoon islands. The remaining variation may be partially explained by other, yet unidentified variables not included in the analyses. A certain amount of unpredictable, stochastic variability probably exists in these insular systems, and may be associated with storm-induced disturbances. The leeward islands are the most exposed to long stretches of open ocean, and the lagoon islands receive the most protection from neighbouring landmasses. Exposure to storm-induced disturbances may result in a less predictable pattern of species richnesses.

The greater predictive power of the models for the Exumas compared with Andros may also result from such forces. Although all the islands at Andros were located within the barrier reef, at high tide the reef is submerged and large waves originating in the deep water to the west and driven east by the trade winds may impact the low-lying islands.

Identification of other explanatory variables that could be potentially important predictors for these archipelagos is not obvious. Habitat diversity has been found to be an important predictor in a number of studies (Buckley, 1982, 1985; Rafe *et al*., 1985; Deshaye & Morisset, 1988; Kohn & Walsh, 1994) and area has often been considered to be primarily a surrogate for habitat diversity. The islands surveyed, however, displayed little discernible habitat diversity.

The importance of scale and island location

The best predictors of species richness may vary among archipelagos due to effects of scale (Whittaker, 1998). Some variables may simply not encompass enough variation relative to colonization or survival ability of the taxa in question. For example, although distances ranged over two orders of magnitude at Andros and over three orders of magnitude in the Exumas, the most distant islands in both archipelagos were only 2.4 km from the nearest mainland island. Most plant species may easily disperse this far, and it is possible that no islands were truly remote enough for isolation to be an effective barrier.

Likewise, elevation may not have been an important predictor because most of the islands surveyed were relatively flat, reaching a maximum elevation of only 5.4 m in the Exumas (excluding outer islands) and 1.8 m at Andros. Yet in a study of the determinants of plant species numbers on coral cays of the Great Barrier Reef, Australia, Heatwole (1991) found island elevation to be the most important predictor, although 'almost all cays' in his study were 'relatively flat'.

The best predictors may also vary with island location or geological history. For example, in Heatwole's (1991) study the variables explaining the most variation in plant species richness differed between coral cays and continental islands, as did the total amount of variation explained by regression models. In the Exumas, the ranking of most explanatory variables varied among the three different categories of islands, as did the amount of explained variation in PSR. These islands all have similar geological histories, and appear to differ primarily in the degree to which they are surrounded by larger mainland islands and in the depth of the surrounding ocean. Although protection was a poor predictor, VA/A may have captured some of the potential exposure effect. Additionally, some other measure of exposure to stormy seas may explain additional variation in PSR. Identification and measurement of the factors involved, however, is not trivial.

Species richness on a per area (or elevation) basis for the fourteen outer islands was much lower than that for the other, more sheltered small islands in the Exumas archipelago. The major difference characterizing the outer islands was that they were located in the deep water side of the Exumas chain, receiving no protection from the larger, mainland islands. Thus variation in island location over a relatively small spatial scale (hundreds of meters) may have relatively large impacts on species richness.

Disturbances by infrequent but major storms may strongly affect species numbers on small islands. The magnitude of the effects may depend in large part on location of the islands with respect to neighbouring landmasses and relative ocean depth, which will in turn affect winds and waves impacting the islands. At nearby Great Exuma, for example, a hurricane exterminated all lizard and spider populations on exposed islands, although all lizard and most spider populations survived on sheltered islands located only some kilometres away (Spiller *et al*., 1998).

Implications

As in many other studies of islands or habitat fragments, area was found to be an important determinant of species richness. A number of mechanisms have been proposed to explain the correlation between species number and insular area (Connor & McCoy, 1979; McGuinness, 1984; Kelly *et al*., 1989). Expressions of insular area other than total physical area, however, may commonly be better predictors of species richness. While my results further confirm the primacy of area in determining insular species richness, they also indicate a need to consider not only the total physical area of an island, but also the 'habitable' area. This consideration will be probably more important for smaller islands and more irregularly shaped islands.

Although island elevation and distance were not found to be important predictors in this system, they have been documented as such in other studies (e.g. Diamond, 1972; Heatwole, 1991), further illustrating that the factors shaping species richness may vary with geography and the taxa in question.

Finally, the geological history of an island, along with its location relative to other islands, large landmasses, variation in ocean depth, and prevailing winds should be taken into account. Islands in close proximity may be very different in relation to one or more of these variables. Unfortunately, such influences may not be easy to quantify in a simple variable.

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