ORIGINAL ARTICLE

Patterns and processes in insular floras affected by hurricanes

Lloyd W. Morrison[1]* and David A. Spiller[2]

[1]*Department of Biology, Missouri State University, Springfield, MO and [2]Center for Population Biology and Section of Evolution and Ecology, University of California, Davis, CA, USA*

ABSTRACT

Aim To investigate species compositions, rates of species turnover, species–area and species–distance relationships and patterns of nestedness in the floras of small Bahamian islands, by comparing two groups of islands that had been differentially affected by two hurricanes.

Location Small islands occurring on either side of Great Exuma near Georgetown, Bahamas.

Methods We surveyed the plant species of 44 small islands over a 5-year period from 1998 to 2002. Hurricanes Lili and Michelle occurred in 1996 and 2001, respectively; both storms affected small islands on the more exposed south-west side of Great Exuma to a greater degree than small islands on the more protected north-east side. A set of 27 islands was surveyed in 1998 and 2002 to evaluate species turnover. Stepwise multiple linear regression analyses and an information-theoretic approach (the Akaike information criterion) were used to elucidate the importance of area and distance as predictors of plant species number. We compared a piecewise linear regression model with a simple linear regression of species number against area to determine whether a small island effect existed. Nestedness patterns were evaluated by Wilcoxon two-sample tests to analyse occurrence sequences.

Results Species turnover was low in an absolute sense (overall = 0.74% year^{-1}), yet was over three times higher than that documented in a nearby archipelago in the absence of hurricanes. Both vegetated area and distance were important predictor variables for exposed islands but not for protected islands. Some support was found for a small island effect for the exposed islands based on a piecewise linear regression model. Both island groups revealed significant nestedness at the level of the assemblage (both $P < 0.001$). On exposed islands, 65–79% (depending upon the method of calculation) of all species were significantly nested, but only 47% of all species were significantly nested on protected islands.

Main conclusions Overall, these insular floras seem highly resistant to hurricane-force disturbances. Species turnover was low ($< 1\%$ year^{-1}) in an absolute sense, particularly in comparison with rates for other taxa. Higher degrees of nestedness and significant species–area and species–distance relationships for exposed islands indicated stronger patterns of community assembly. It is likely that disturbance is a major structuring force for the exposed islands, although the type of disturbances that mediate these patterns may not be primarily hurricane-force storms.

Keywords

Akaike information criterion, Bahamas, disturbance, hurricane, insular floras, island biogeography, nestedness, plants, small island effect, species–area relationship.

*Correspondence: Lloyd W. Morrison, Department of Biology, Missouri State University, 901 South National Avenue, Springfield, MO 65897, USA.
E-mail: lloydmorrison@missouristate.edu

INTRODUCTION

The equilibrium theory of island biogeography (MacArthur & Wilson, 1967) stimulated great interest in the study of isolated populations, inspiring many studies of insular biotas (reviewed by Whittaker & Fernández-Palacios, 2007). Numerous criticisms have been levied against the simple equilibrium model (e.g. Gilbert, 1980; Williamson, 1989), however, and a number of refinements have been suggested, including the abandonment of the concept of a long-term balance, or equilibrium of immigration and extinction (e.g. Lomolino, 2000a,b). A crucial question in modern island biogeography theory is whether islands ever actually reach a state of equilibrium; in many cases disturbances may occur at a frequency or intensity that exceeds the biota's ability to completely recover (Whittaker, 1995, 2000). In such cases, a non-equilibrial or disequilibrial framework may represent a more informative approach (e.g. Lomolino, 2000b; Whittaker, 2000).

Recent hurricane activity coupled with long-term data sets has allowed the evaluation of hurricane disturbances on lizard and web spider populations inhabiting small islands in the Bahamas. The immediate impact of major hurricanes has included a dramatic reduction or extermination of species on some islands, although the overall effects on and long-term recovery of these taxa have varied depending upon a number of factors such as island location, area, elevation, season of the year and strength of the storm (Spiller et al., 1998; Schoener et al., 2001, 2004; Schoener & Spiller, 2006). Lizards and web spiders are relatively exposed to the high winds and waves of hurricanes, while the plants on these islands, which are firmly rooted in the limestone substrate and can survive limited inundation of seawater, may be less vulnerable.

Previously, one of us reported on the island biogeography and turnover dynamics of plants in an archipelago of small islands in the Exuma Cays (Morrison, 1997, 2003). This work revealed relatively low, consistent turnover rates over an 8-year period (1990–98) in the absence of any major disturbances. Here we examine the patterns and dynamics of plant communities inhabiting physically similar islands in nearby Great Exuma, which have been affected by two hurricanes, one before and one during this study. We address the following four questions: (1) how much turnover occurred in a 4-year period following Hurricane Lili and including Hurricane Michelle, and how does this turnover compare with that previously documented for nearby islands in the absence of hurricane force disturbances? (2) How well did area and distance predict species numbers, and how did this vary for small islands affected to different degrees by the hurricanes? (3) How nested were these floras, and how did patterns of species nestedness differ depending upon exposure to hurricanes? (4) What do the observed patterns indicate about the effects of disturbance on the floras of small Bahamian islands?

METHODS

Study area

This study was conducted on 44 small islands occurring on both sides of the large island of Great Exuma in the region near Georgetown (Fig. 1). Fifteen of the islands were located on the north-east side of Great Exuma in Elizabeth Harbour, a natural harbour protected from the deep ocean by a long barrier island (i.e. the protected side). The other 29 islands were located on the south-west side of Great Exuma, on shallow water banks that are exposed to long stretches of open water to the south and west (i.e. the exposed side).

All islands surveyed had vegetated areas of < 1500 m², to allow the compilation of complete lists of plant species. Islands were composed primarily of marine limestone, with some islands consisting of small amounts of fossil sand deposits or loose sand. Very little soil was present on most islands, and organic matter accumulated in cracks and fissures in the limestone, where the vegetation was rooted. Because of their rocky composition, island size or shape does not vary over time as has been reported for sand islands (e.g. Flood & Heatwole, 1986). The perimeter of most islands, particularly
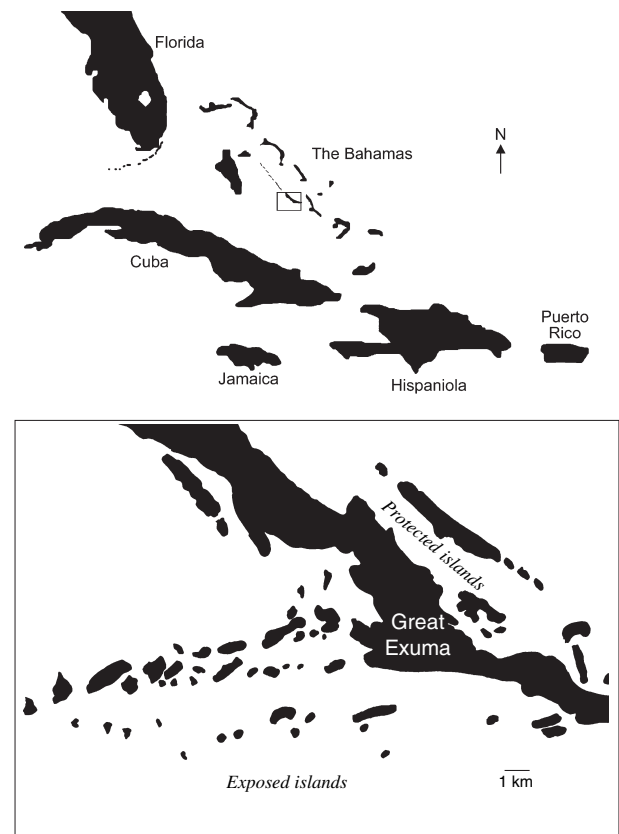

Figure 1 Map of the Georgetown region of Great Exuma, Bahamas, showing the general locations of the exposed and protected islands. The relatively tiny islands are not visible on the map.

those on the exposed side, is characterized by a swash zone – an area regularly disturbed by high tides and waves – that is usually barren of vegetation. Island elevations (vertical distance from the mean high tide mark to the highest point on the island) ranged from 0.41 to 3.25 m on the protected side, and from 0.61 to 3.66 m on the exposed side.

In October 1996, the eye of Hurricane Lili passed over Georgetown, resulting in a direct hit to these islands. Lili had sustained winds of 90 knots, and produced a storm surge of 5 m above mean sea level (Lawrence, 1996). In November 2001, Hurricane Michelle passed to the north of Great Exuma. Although Michelle was weakening as it moved over the Bahamas, it still produced sustained winds of 70–80 knots, and a storm surge of 1.6–2.6 m above mean sea level (Beven, 2002). Classification of islands on either the protected or exposed sides of Great Exuma reflects the paths of Hurricanes Lili and Michelle (both west to east), in that islands on the exposed (south-west) side were exposed to the full force of both hurricanes, particularly the impact of the storm surge (Spiller et al., 1998).

Field surveys

Surveys were conducted annually over a 5-year period from 1998 to 2002. Not all islands were surveyed in all years. A set of 27 islands (eight on the protected and 19 on the exposed side) was surveyed in 1998 and 2002 to evaluate species turnover. The 19 islands on the exposed side were also surveyed in 2000.

The 17 islands not evaluated for turnover were surveyed once or twice at some point during the 5-year period. Overall, 108 island visits were made over the 5 years of the study. All islands were visited in autumn; surveys in 1998 and 1999 were carried out in October, the 2000 survey was conducted in late September and the 2001 and 2002 surveys were carried out in early December.

Surveys were conducted by walking over each island in its entirety and recording the species present. On islands that were part of the turnover study, an additional search was conducted for missing species whenever a species known to have been present on that island previously was not found. The remains of extinct species were often discovered. When an apparent immigration was observed, the age of the individual(s) of the immigrating species was estimated to ensure it was a recent immigrant. Thus all observed extinctions and immigration events were verified for accuracy, to eliminate spurious turnover due to sampling error, or pseudoturnover (sensu Lynch & Johnson, 1974). Species identifications follow Correll & Correll (1982). Voucher specimens have been placed in the J. M. Tucker Herbarium at the University of California, Davis.

Calculation of species turnover

Turnover was calculated using the following formula:

$$\text{relative turnover} = \frac{I + E}{S_1 + S_2} \times 100$$

where I is the number of new species immigrating to the island between surveys, E is the number of species becoming extinct on the island between surveys, and S_1 and S_2 are the number of species on an island in surveys 1 and 2, respectively. Annual relative turnover was calculated by dividing relative turnover by the number of years intervening between surveys (Schoener, 1988).

Determinants of species richness

To determine whether area and distance were informative predictors of the number of species present on an island, multiple linear regression analyses were performed, regressing the response variable, species number, against the predictor variables, island area and distance. For islands surveyed multiple times, species number represented the most 'stable state' for the years surveyed. For example, if an island was surveyed in three different years, and had 15 species present on two occasions and 14 on the other, 15 was used in the analysis. Vegetated area was used as a measure of the habitable size of the island. Distance was measured from Great Exuma. Vegetated area and distance were log-transformed to normalize the distributions.

A forward stepwise procedure was used, which selected predictor variables sequentially in order of their relative reduction of sums of squares if their partial F exceeded the F-to-enter level. After insertion of a variable, any variable could be removed if its partial F fell below the F-to-remove level. This procedure allowed for the elimination of unnecessary predictor variables. The minimum F acceptable to enter was set at 4 and the maximum F acceptable to remove at 3.9, corresponding roughly to a level of significance of 0.05 for any single test (Neter et al., 1996).

To determine whether a small island effect was present (i.e. a relative constancy in species numbers on the smaller islands, with the more typical increase in species numbers with area on larger islands), we compared a piecewise, or breakpoint, linear regression model with a simple linear regression. Species number was the response variable and vegetated area was the predictor variable in both models. The piecewise regression model contained an indicator variable that allowed for a change in slope of the regression line at a threshold value, although the line remained continuous (Neter et al., 1996). The model used was:

$$Y = B_0 + B_1 X + B_2[(X - T)I]$$

where Y is species number, X is vegetated area, T is the threshold value and

$$I = \begin{cases} 1, & \text{if } X > T \\ 0, & \text{otherwise.} \end{cases}$$

We evaluated both semi-log (taking the logarithmic transformation of the vegetated area only) and log–log (taking the logarithmic transformation of both species number and vegetated area) models.

We also used the Akaike information criterion (AIC, an information-theoretic approach; Burnham & Anderson, 2002) to evaluate the regression models. Because the sample size was small, we calculated AIC adjusted for small sample size (AIC_c) as:

$$AIC_c = AIC + 2K(K + 1)/(n - K - 1)$$

where K is the total number of parameters in the model (including the intercept and residual variance) and n is the sample size. Because AIC_c is on a relative scale, differences in AIC_c values were calculated as:

$$\Delta AIC_{ci} = AIC_{ci} - \text{minimum } AIC_c$$

for all candidate models, where i indicates the ith model. The best model was the one in which $\Delta AIC_c = 0$. Only models with $AIC_c \leq 2$ have 'substantial' support (Burnham & Anderson, 2002).

Quantification of nestedness

Wilcoxon two-sample tests (also known as Mann–Whitney U-tests) were used to analyse nestedness patterns. This approach was first used by Schoener & Schoener (1983) to measure the 'occurrence sequences' of species on islands, by ranking islands according to the magnitude of a particular variable (e.g. area), and then determining whether the associated presence/absence sequence of the species of interest was significantly non-random. This procedure has since been used to analyse nestedness patterns for individual species (Patterson, 1984; Simberloff & Levin, 1985; Simberloff & Martin, 1991; Kadmon, 1995; Nores, 1995; Hecnar & M'Closkey, 1997; Hecnar et al., 2002). While nestedness is, strictly speaking, a property of a species assemblage rather than an individual species, referring to individual species that have non-random occurrence sequences as being 'significantly nested' is usually done as a matter of convenience (e.g. Hecnar et al., 2002).

A nested matrix was constructed with species rank-ordered in terms of decreasing numbers of occupied islands, and islands rank-ordered in terms of decreasing numbers of species. If perfectly nested, all cells in the upper left-hand corner of the matrix would consist of 'presences' and all cells in the lower right hand corner would consist of 'absences'. The greater the departure from this pattern in the ordered matrix, the greater the departure from nestedness.

For each species, the Wilcoxon test (one-tailed) determines the degree to which the sequence of presences and absences is ordered, compared with a null hypothesis in which presences and absences occur at random. Species that are present on all islands do not provide evidence for or against nestedness, and cannot be analysed with this two-sample test. Statistical power to detect nestedness is low for species that are present on almost all, or very few, islands. This is taken into consideration when interpreting the results.

The degree of nestedness for entire species assemblages was determined by assuming that the species are independent and combining the tail probabilities of the individual species. The resulting statistic in this meta-analytic approach is chi-square distributed, with $2k$ degrees of freedom (k being the number of individual test probabilities) (Sokal & Rohlf, 1995). All species (except those that occurred on every island) were included in these meta-analyses, even those for which individual significant results could not be obtained due to lack of power. In the case of turnover, we used the occurrences that best represented the most 'stable state' for the years surveyed, as described above. We evaluated nestedness for individual species and entire species assemblages separately for islands on the exposed and protected sides. SPSS 11.0.4 for Mac OS X was used for all analyses.

RESULTS

Species overlap

A total of 34 species occurred in each of the island groups, on both the exposed and protected sides of Great Exuma, although almost twice as many islands were surveyed on the exposed side (29 vs. 15) (see Appendices S1 and S2 in Supplementary Material). The two groups shared 23 species, a 68% overlap. Two species (*Borrichia aborescens* and *Conocarpus erectus*) were almost ubiquitous, each occurring on all but one island overall. A third species (*Rhachicallis americana*) was also very common, occurring on 24 of 29 islands on the exposed side, and 13 of 15 islands on the protected side.

A relatively large number of species occurred on only one island in each group ($n = 8$ on the exposed side and $n = 15$ on the protected side). If these rare species are excluded, more species were present on the exposed side (26 compared with 19). Excluding these rare species, 95% of the species occurring on the protected side were also present on the exposed side, whereas only 69% of the species present on the exposed side were also present on the protected side.

Species turnover

Species turnover for both protected and exposed islands combined for the 1998–2002 interval, although low in an absolute sense, was over three times higher than that documented in the Exumas Cays during two previous 4-year intervals, 1990–94 and 1994–98 ($P = 0.014$, $t = 2.49$, d.f. = 102; two-tailed t-test comparing all islands at Great Exuma to Exuma Cays islands for 1994–98) (Table 1). Turnover rates were similar for the protected and exposed groups of islands. Overall, immigration rates were two to three times higher than the rates previously determined from the Exuma Cays, and extinction rates were two to five times higher. Immigration rates were three times higher than extinction rates on the protected side; immigration rates and extinction rates were equivalent on the exposed side.

For islands on the exposed side, turnover rates were over twice as high in the interval 1998–2000 (after Lili but before Michelle) compared with the interval 2000–02 (after Lili and Michelle) (Table 1). Immigration rates were over three times higher than extinction rates in the interval 1998–2000, whereas only extinctions occurred in the interval 2000–02. Although the change in immigration–extinction dynamics between these intervals is striking, these rates are all relatively low in an absolute sense.

Table 1 Turnover, immigration, and extinction rates of plant species calculated on a per island basis. Turnover rates are given as mean ± SD. Immigration and extinction rates are absolute.

Archipelago/time period	Number of islands	Annual turnover (% $year^{-1}$)	Immigration rate (no. species per island yr^{-1})	Extinction rate (no. species per island yr^{-1})
Great Exuma				
All (1998–2002)	27	0.74 ± 1.15	0.074	0.056
Protected (1998–2002)	8	0.79 ± 1.10	0.094	0.031
Exposed (1998–2002)	19	0.72 ± 1.20	0.066	0.066
Exposed (1998–2000)	19	1.52 ± 2.40	0.184	0.053
Exposed (2000–02)	19	0.69 ± 1.58	0.0	0.132
Exuma Cays*				
1990–94	77	0.22 ± 0.72	0.036	0.029
1994–98	77	0.24 ± 0.80	0.026	0.010

*From Morrison (2003).

Determinants of species richness

On the exposed side, both vegetated area and distance were included in the stepwise multiple regression model. Plant species number was positively correlated with vegetated area and negatively correlated with distance. Vegetated area was the first variable selected and accounted for 28.5% of the explained variation in species number. When both variables were in the model, the overall coefficient of determination was 48.9%. The final model was:

$$\text{plant species number} = 23.19 + 4.45 \log(\text{vegetated area}) - 7.35 \log(\text{distance}).$$

The information theoretic approach yielded complementary results: the best model (lowest AIC_c; $\Delta AIC_c = 0$) was the model containing both vegetated area and distance (Table 2). The next best model, with only vegetated area as a predictor, had a relatively large ΔAIC_c (7.022).

Neither predictor variable was selected as significant in the stepwise regressions for islands on the protected side. The information theoretic approach was not used to evaluate the potential models because this approach, while selecting the best model in the set, is not useful if all models are poor (Burnham & Anderson, 2002).

Exposed islands appeared to accumulate species faster once they reached a certain threshold (c. 200 m^2), although there

Table 2 Models evaluated by the information theoretic approach. All models refer to the 29 islands on the exposed side of Great Exuma.

Model/variables	AIC_c	ΔAIC_c	K	R^2
Species–area relationships				
Vegetated area, distance	84.722	0	4	0.489
Vegetated area	91.744	7.022	3	0.285
Distance	96.756	12.034	3	0.150
Small island effect (semi-log)				
Piecewise model	90.219	0	4	0.391
Linear model	91.723	1.504	3	0.286
Small island effect (log–log)				
Piecewise model	−83.004	0	4	0.453
Linear model	−82.559	0.405	3	0.391

was much variability for the larger islands (Fig. 2). A similar pattern is not obvious for the protected islands, although sample size was smaller and the range of smaller islands was truncated. For the exposed islands, a piecewise linear semi-log regression model with a breakpoint at 200 m^2 explained more of the variability in species number than did a simple linear semi-log model (39.1% compared with 28.5%). The coefficient for the additional term in the model was significant ($t = 2.117$, $P = 0.044$). The piecewise model was somewhat better than the linear model based on the information theoretic approach ($\Delta AIC_c = 1.504$; Table 2), although the difference was not large and both models could be said to have substantial support.

For the log–log models, a piecewise linear regression explained 45.3% of the variability in species number compared with 39.1% for a simple linear regression. The coefficient for the additional term in the model was only marginally significant ($t = 1.716$, $P = 0.098$), however, and ΔAIC_c was only 0.405 (Table 2).

Nestedness

The island groups on both sides of Great Exuma revealed significant nestedness at the level of the assemblage (both $P < 0.001$). On an individual basis, two species on the protected side (B. aborescens and C. erectus) were present on all islands, and a significance test could not be done (Appendix S1). The same two species were present on all but one island on the exposed side, and due to low statistical power it was not possible to obtain a significant result (Appendix S2). On both sides, for species occurring on just one island, a significant result could only be obtained if that species was present on the most species-rich island.

On the exposed side, 65% (22 of 34) of all species were significantly nested (69% if one excludes the two species for which a significant result could not be obtained). Only 47% (15 of 32) of all species (excluding the two ubiquitous species) were significantly nested on the protected side. Excluding species that occurred on only one island (and the two species on the exposed side for which a significant result could be obtained), the percentage of significantly nested species was
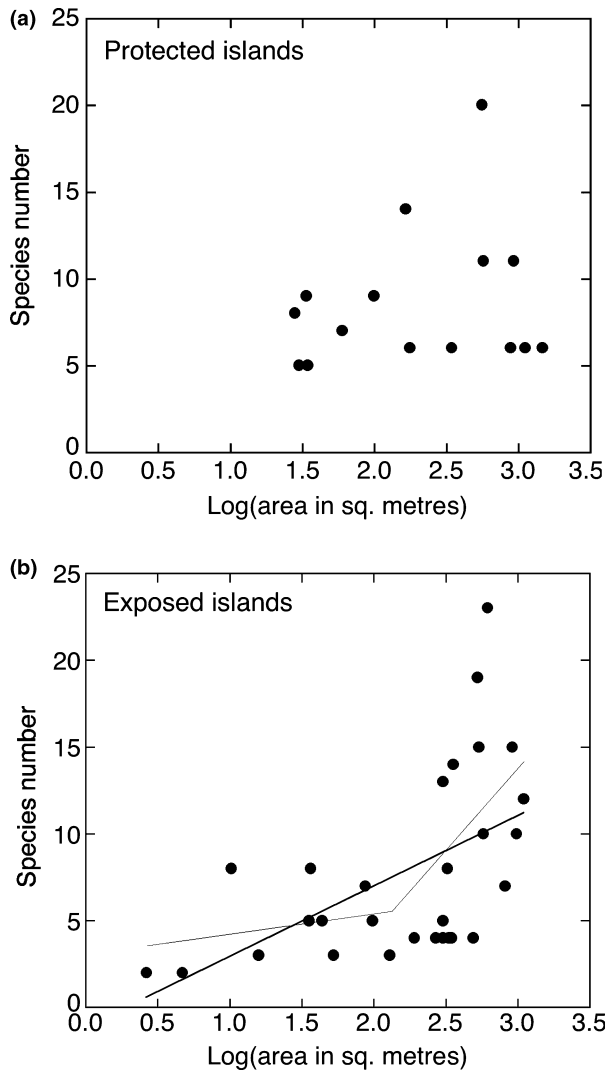
Figure 2 Species–area relationships for small islands on (a) the protected and (b) the exposed sides of Great Exuma. In (b) the straight line represents the line of best fit by a simple linear regression, whereas the broken line represents a piecewise linear regression with a threshold at a vegetated area of 200 m^2. The simple linear regression model was: plant species number = −1.115 + 4.058 log(vegetated area). The piecewise regression model was: plant species number = 3.166 + 0.934 log(vegetated area) + 11.503 [(log(vegetated area)−2.3) × I], where I = 1 if log(area) > log (200), and 0 otherwise.

79% for the exposed side and 47% for the protected side (exposed vs. protected: χ^2 = 4.56, P = 0.033, d.f. = 1).

DISCUSSION

Species turnover

Overall, these insular floras seem to be highly resistant to hurricane-force disturbances. Species turnover rates for the islands surveyed were over three times higher than rates observed in a nearby archipelago in previous years lacking

hurricanes, yet were still low in an absolute sense. No data were available before Hurricane Lili, and it is possible that an extinction pulse occurred during or directly after this storm. Immigrations did exceed extinctions for a 2-year period 2 years after Lili, and extinctions exceeded immigration events in the wake of Hurricane Michelle.

These findings are in marked contrast to the effects of Lili on the lizards and web spiders of many of these same islands. All lizards and web spiders were exterminated on islands on the exposed side; populations of lizards and web spiders were reduced by 34% and 79%, respectively, on the protected side (Spiller *et al.*, 1998).

A number of methodological inadequacies that may result in inaccurate turnover estimates for insular floras have been identified, including comparison of surveys compiled by different investigators, spending varying amounts of time on the islands on different survey dates, conducting surveys at different seasons of the year, or attempting to survey islands that are too large (Abbott, 1977, 1983; Nilsson & Nilsson, 1985). In one well-documented study (Nilsson & Nilsson, 1982, 1983) the majority of apparent turnover was found to be pseudoturnover (i.e. spurious turnover due to sampling error). Annuals that may be present only in the seed bank, or in general any species possessing no aboveground part that can be seen during the survey, also create problems (Höner & Greuter, 1988).

The turnover estimates presented here are largely free from these sources of error, as all surveys were conducted in a standardized method by the same observer (L.W.M.) in the same season, and only islands small enough to be thoroughly surveyed were included. All species present were long-lived perennials. Furthermore, most comparisons were made based on survey intervals of 4 years. Thus, even though the documented differences in turnover rate between the islands of this study and the Exuma Cays surveyed in previous years are small in an absolute sense, they are likely to represent a real difference rather than variability due to sampling error.

In the first survey year (1998), *c.* 10% of all populations had characteristics of recent immigrants, judging from the amount and age of aboveground foliage. A population is defined here as all the individuals of a species existing on an island; often this was only one or a few plants. All other populations had obviously been present before Hurricane Lili (1996). Surveys in succeeding years, however, revealed that much more growth had occurred in most of these populations than would be expected in the case of arriving colonists (i.e. seeds or vegetative propagules). The observed growth was consistent with a large, established root biomass. Thus no extinctions were recorded based only on the first year's data. The rocky substrate of the islands is likely to protect plant roots from scouring by both wind and water, and the roots of many plants probably survived even though all or most aboveground biomass was lost. Lili reduced the overall volume of vegetation on small islands of the exposed side by 42%, and a 15% reduction was documented for islands on the protected side (Spiller *et al.*, 1998).

There was evidence of damage to aboveground biomass by Hurricane Michelle in 2001, although qualitatively the damage was less than that due to Lili. Surveys in 2001 were conducted in December, 1 month after Michelle. The prevalence of immigrations compared with extinctions from 1998–2000 is consistent with species colonizing the islands after the impact of Hurricane Lili, which is likely to have caused some extinctions. The relatively high extinction rate from 2000–02 is most probably attributable to the impact of Hurricane Michelle. Thus, these insular floras appeared to be in a state of recovery from 1998–2000, followed by a decline in 2000–02, rather than a true state of equilibrium.

Determinants of species richness

Island area was a significant predictor of species numbers on the exposed side. While this may not be a very unique finding, the interesting facet of this system is that area was not a significant predictor on the protected side (where variation in vegetated area explained only 4.4% of the variation in species number). A likely mechanism is that disturbance events (e.g. storms, winds, waves) affect the species compositions of these islands, and the impacts of such events are a function of island size. For example, larger islands have a greater perimeter and wider swash zone over which the energy of breaking waves is dissipated. Islands on the exposed side typically have broad swash zones, while vegetation grows right up to the edge of islands on the protected side, where small islands are shielded by nearby large islands. Protected islands, in some ways (e.g. exposure to storm driven winds and waves), represent habitat similar to the interior of much larger islands. A larger pool of species may be able to inhabit these protected islands, and the number of species actually present may be determined by various factors (e.g. dispersal abilities) which overall exert weaker control than the disturbance effect on the exposed islands.

Species numbers on islands of the exposed side increased at a faster rate with increasing area after the vegetated area reached c. 200 m^2, although there was much variability in species numbers among the larger islands. Other studies of insular floras have reported a relative constancy in species numbers over a range of smaller island areas, with the more typical increase in species numbers with area evident on larger islands (i.e. the 'small island effect'; Whitehead & Jones, 1969). Although frequently ignored in many species–area analyses, a small island effect has been found to be a common feature of many data sets (Lomolino & Weiser, 2001). Lomolino & Weiser (2001) found the small island effect to be more prevalent when archipelagos were analysed with semi-log regression models compared with log–log models. Accordingly, the small island effect was more obvious for the exposed islands of this study when a semi-log model was used. This may be due to the general tendency of a log–log transformation to linearize the data to a greater degree than a semi-log transformation.

MacArthur & Wilson (1967) hypothesized that very small islands may be unstable, and their entire floras or faunas affected by storms. This idea, refined into the disturbance hypothesis by McGuinness (1984), postulates that very small islands are susceptible to disturbance events that could cause area-independent extinction rates. Most formulations of this hypothesis seem to imply disturbances that are stochastic in nature, resulting in high species turnover and relatively large variation in species richness, obliterating species–area relationships. Yet the small island effect in this case may be due more to smaller-scale chronic disturbances. The species found on the smaller islands on the exposed side may be better able to tolerate harsh conditions, and floras there persist with low turnover and little variation in species richness or composition. Thus the small island effect in this system could result from a deterministic, rather than a stochastic, process.

Distance was negatively associated with species numbers on the exposed side, but was not a significant predictor for islands on the protected side. Distance could also be an indicator of the impacts of disturbance. Islands farther from the main island of Great Exuma are more likely to experience higher waves and winds because they are more likely to be in deeper water and lack the protective shelter of nearby islands (Morrison, 2002). The range of island distances involved, however, may also play a role: islands on the protected side were relatively close to Great Exuma (20–1100 m), whereas islands on the exposed side covered a much greater range of distances (615–11,700 m).

Nestedness

Nestedness occurs when the species composition of each island represents a subset of the species assemblage on more speciose islands. A high degree of nestedness implies that the geographical distribution of species is a deterministic (and predictable) function of physical, biological or anthropogenic processes, rather than a random assortment of the available species pool (e.g. Patterson & Atmar, 1986; Simberloff & Martin, 1991; Cook, 1995; Cook & Quinn, 1995; Kadmon, 1995; Hecnar & M'Closkey, 1997; Wright et al., 1998; Hecnar et al., 2002).

A number of indices that generate a single statistic to measure the nestedness of an entire biotic assemblage have been proposed (Cook, 1995). The advantages of the method used here are that it allows the assessment of nestedness for individual species as well as the biotic assemblage as a whole, and aspects of its statistical properties are well known (Simberloff & Martin, 1991). Most biotic assemblages as a whole, when tested for nestedness, have been shown to exhibit significant nestedness patterns (Cook & Quinn, 1995). Yet when species are tested individually, only a relatively small number may be significantly nested. In a study of plants on islands in a reservoir, for example, Kadmon (1995) found that while the entire assemblage was significantly nested, only a relatively small fraction of the individual species (< 20%) displayed significant nestedness.

A relatively large percentage of species displayed significant nestedness on these small islands. Moreover, significantly more species on the exposed side displayed nested patterns compared with those on the protected side. A larger pool of species may be able to inhabit these protected islands, as described above, and the identity of those species actually present may result from random chance to a greater degree than for exposed islands, which may only be suitable for a smaller pool containing species that are well adapted to disturbance. Previous studies in the Bahamas have revealed the percentage of significantly nested species to be 77% for small islands in the Exuma Cays and 79% for small islands off the north-east coast of Andros (Morrison, 1997).

Effects of disturbance on community assembly

Higher degrees of nestedness and significant species–area and species–distance relationships for islands on the exposed side indicate stronger patterns of community assembly. Lower degrees of nestedness and the lack of significant effects of area or distance on the protected side reveal more randomization in insular species compositions. It is likely that disturbance is a major structuring force affecting islands on the exposed side. Given an island of similar size, a species may be able to survive on the protected side but not on the exposed side. Hurricanes approaching from a different direction could be expected to have different effects on the two sides of Great Exuma, although the small islands in Elizabeth Harbour (i.e. on the protected side) are in general much more shielded by surrounding larger islands than are small islands on the south-west (i.e. the exposed) side.

Yet the type of disturbances that mediate these patterns may not primarily be hurricane-force storms. In fact, most populations seemed to do well in the aftermath of a direct hit by a major hurricane. Instead, numerous smaller storms that occur on an annual basis may represent the primary structuring forces. Because these islands are small and low-lying, relatively small disturbance events will affect them, and the degree of impact of larger disturbance events may not be much greater (i.e. submersion by a few centimetres of water may not be that much different from submersion by several metres). Thus, these small islands may remain close to an equilibrium number of species over the long term because chronic disturbance plays a major role in structuring the communities, at least on the exposed side, and acute major disturbances do not exterminate many species.

For example, near ubiquitous species such as *B. aborescens* and *C. erectus* appear to be very tolerant of chronic disturbances and thus survive on almost all islands. Species that are less tolerant to such disturbances survive only on islands on the protected side or in the interior of larger islands on the exposed side. The mechanism by which such disturbance operates may be related to salt tolerance. These small, low-lying islands receive much salt spray, particularly on the exposed side. The physiological effects of salinity on plants have been documented in many studies (summarized in Waisel, 1972; Reimold & Queen, 1974; Sen & Rajpurohit, 1982; Khan & Weber, 2005).

With the exception of the last decade, major hurricanes have rarely struck the Exumas since records have been kept; the last major hurricane before Lili occurred in 1932 (Spiller *et al.*, 1998). Given the longevity of many of these plant species and the evolutionary forces at work, however, the importance of hurricane disturbances cannot be ignored. Additional work in other archipelagos, involving before and after surveys, is under way to further evaluate their effects (L.W.M., unpublished data).

REFERENCES

Abbott, I. (1977) Species richness, turnover and equilibrium in insular floras near Perth, Western Australia. *Australian Journal of Botany*, **25,** 193–208.

Abbott, I. (1983) The meaning of *z* in species/area regressions and the study of species turnover in island biogeography. *Oikos*, **41,** 385–390.

Beven, J. (2002) *Tropical cyclone report: Hurricane Michelle.* National Hurricane Center, Miami, FL.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer, New York.

Cook, R.R. (1995) The relationship between nested subsets, habitat subdivision, and species diversity. *Oecologia*, **101,** 204–210.

Cook, R.R. & Quinn, J.F. (1995) The influence of colonization in nested species subsets. *Oecologia*, **102,** 413–424.

Correll, D.S. & Correll, H.B. (1982) *Flora of the Bahama Archipelago*. J. Cramer, Vaduz, Germany.

Flood, P.G. & Heatwole, H. (1986) Coral cay instability and species-turnover of plants at Swain Reefs, Southern Great Barrier Reef, Australia. *Journal of Coastal Research*, **2,** 479–496.

Gilbert, F.S. (1980) The equilibrium theory of island biogeography: fact or fiction? *Journal of Biogeography*, **7,** 209–235.

Hecnar, S.J. & M'Closkey, R.T. (1997) Patterns of nestedness and species association in a pond-dwelling amphibian fauna. *Oikos*, **80,** 371–381.

Hecnar, S.J., Casper, G.S., Russell, R.W., Hecnar, D.R. & Robinson, J.N. (2002) Nested species assemblages of amphibians and reptiles on islands in the Laurentian Great Lakes. *Journal of Biogeography*, **29,** 475–489.

Höner, D. & Greuter, W. (1988) Plant population dynamics and species turnover on small islands near Karpathos (South Aegean, Greece). *Vegetatio*, **77,** 129–137.

Kadmon, R. (1995) Nested species subsets and geographic isolation: a case study. *Ecology*, **76,** 458–465.

Khan, M.A. & Weber, D.J. (eds) (2005) *Ecophysiology of high salinity tolerant plants*. Springer, Dordrecht, The Netherlands.

Lawrence, M.B. (1996) *Preliminary report: Hurricane Lili*. National Hurricane Center, Miami, FL.

Lomolino, M.V. (2000a) A call for a new paradigm of island biogeography. *Global Ecology and Biogeography*, **9**, 1–6.

Lomolino, M.V. (2000b) A species-based theory of insular zoogeography. *Global Ecology and Biogeography*, **9**, 39–58.

Lomolino, M.V. & Weiser, M.D. (2001) Towards a more general species–area relationship: diversity on all islands, great and small. *Journal of Biogeography*, **28**, 431–445.

Lynch, J.F. & Johnson, N.K. (1974) Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. *The Condor*, **76**, 370–384.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.

McGuinness, K.A. (1984) Equations and explanations in the study of species–area curves. *Biological Reviews*, **59**, 423–440.

Morrison, L.W. (1997) The insular biogeography of small Bahamian cays. *Journal of Ecology*, **85**, 441–454.

Morrison, L.W. (2002) Determinants of plant species richness on small Bahamian islands. *Journal of Biogeography*, **29**, 931–941.

Morrison, L.W. (2003) Plant species persistence and turnover on small Bahamian cays. *Oecologia*, **136**, 51–62.

Neter, J., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. (1996) *Applied linear statistical models*. Irwin, Chicago.

Nilsson, I.N. & Nilsson, S.G. (1982) Turnover of vascular plant species on small islands in Lake Mockeln, South Sweden 1976–1980. *Oecologia*, **53**, 128–133.

Nilsson, S.G. & Nilsson, I.N. (1983) Are estimated species turnover rates on islands largely sampling errors? *The American Naturalist*, **121**, 595–597.

Nilsson, I.N. & Nilsson, S.G. (1985) Experimental estimates of census efficiency and pseudoturnover on islands: error trend and between-observer variation when recording vascular plants. *Journal of Ecology*, **73**, 65–70.

Nores, M. (1995) Insular biogeography of birds on mountain-tops in north western Argentina. *Journal of Biogeography*, **22**, 61–70.

Patterson, B.D. (1984) Mammalian extinction and biogeography in the southern Rocky Mountains. *Extinctions* (ed. by M.H. Nitecki), pp. 247–293. University of Chicago Press, Chicago.

Patterson, B.D. & Atmar, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological Journal of the Linnean Society*, **28**, 65–82.

Reimold, R.J. & Queen, W.H. (eds) (1974) *Ecology of halophytes*. Academic Press, New York.

Schoener, T.W. (1988) On testing the MacArthur–Wilson model with data on rates. *The American Naturalist*, **131**, 847–864.

Schoener, T.W. & Schoener, A. (1983) Distribution of vertebrates on some very small islands. I. Occurrence sequences of individual species. *Journal of Animal Ecology*, **52**, 209–235.

Schoener, T.W. & Spiller, D.A. (2006) Nonsynchronous recovery of community characteristics in island spiders after a catastrophic hurricane. *Proceedings of the National Academy of Sciences USA*, **103**, 2220–2225.

Schoener, T.W., Spiller, D.A. & Losos, J.B. (2001) Natural restoration of the species-area relation for a lizard after a hurricane. *Science*, **294**, 1525–1528.

Schoener, T.W., Spiller, D.A. & Losos, J.B. (2004) Variable ecological effects of hurricanes: the importance of seasonal timing for survival of lizards on Bahamian islands. *Proceedings of the National Academy of Sciences USA*, **101**, 177–181.

Sen, D.N. & Rajpurohit, K.S. (eds) (1982) *Contributions to the ecology of halophytes. Tasks for Vegetation Science 2*. Dr. W. Junk Publishers, The Hague, The Netherlands.

Simberloff, D. & Levin, B. (1985) Predictable sequences of species loss with decreasing island area – land birds in two archipelagoes. *New Zealand Journal of Ecology*, **8**, 11–20.

Simberloff, D. & Martin, J.-L. (1991) Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. *Ornis Fennica*, **68**, 178–192.

Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*. W. H. Freeman and Company, New York.

Spiller, D.A., Losos, J.B. & Schoener, T.W. (1998) Impact of a catastrophic hurricane on island populations. *Science*, **281**, 695–697.

Waisel, Y. (1972) *Biology of halophytes*. Academic Press, New York.

Whitehead, D.R. & Jones, D.E. (1969) Small islands and the equilibrium theory of insular biogeography. *Evolution*, **23**, 171–179.

Whittaker, R.J. (1995) Disturbed island ecology. *Trends in Ecology and Evolution*, **10**, 421–425.

Whittaker, R.J. (2000) Scale, succession and complexity in island biogeography: are we asking the right questions? *Global Ecology and Biogeography*, **9**, 75–85.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

Williamson, M. (1989) The MacArthur and Wilson theory today: true but trivial. *Journal of Biogeography*, **16**, 3–4.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A. & Atmar, W. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia*, **113**, 1–20.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Occurrences of species on the 15 islands on the protected side of Great Exuma.
Appendix S2 Occurrences of species on the 29 islands on the exposed side of Great Exuma.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-

2699.2008.01910.x (This link will take you to the article abstract).

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

BIOSKETCHES

Lloyd Morrison has studied Bahamian ants and plants since 1989. His research interests include island biogeography, metapopulation dynamics, invasion ecology, and the resistance and resilience of insular communities in relation to disturbance.

David Spiller has studied Bahamian lizards, spiders, insects and plants since 1983. His research interests include species interactions, food-web structure, metapopulation and metacommunity dynamics and the impact of hurricanes on island communities.

Editor: Jon Sadler