Nonsynchronous recovery of community characteristics in island spiders after a catastrophic hurricane

Thomas W. Schoener* and David A. Spiller

Section of Evolution and Ecology and Center for Population Biology, One Shields Avenue, University of California, Davis, CA 95616

Contributed by Thomas W. Schoener, December 1, 2005

We monitored spiders on 41 Bahamian islands for 4 years before and then 4 years after the catastrophic Hurricane Floyd passed directly over the site, inundating the study islands with its storm surge. The respective recoveries of major community properties after this annihilation were far from synchronous. Before the hurricane, the species-area relation was generally strong and the slope showed no temporal trend. After the hurricane, the slope increased from near zero (7 months later) to a value about equal to its prehurricane state. The lizard effect (difference in spider abundance or species richness between islands with and without the lizard Anolis sagrei) was generally strong before the hurricane; 7 months after, the lizard effect on abundance was weak and the effect on richness had vanished. In subsequent years, the lizard effect on abundance became strong again, but the effect on species richness remained weak. The strength of the lizard effect on both abundance and richness over the 8 years was strongly positively related to the density of lizards measured on a subset of the study islands. Twelve months after the hurricane, species richness averaged over all islands rebounded to the last prehurricane value, but abundance attained only about half that value; this finding was remarkably similar to results found in an earlier study of spiders impacted by Hurricane Lili (1996) in a different Bahamian region. Nonetheless, in the next 3 years, species richness failed to increase further, part of its long-term decline at the study site.

Rarely are ecologists able to document the refaunation of a well studied group of islands after a natural catastrophe. Even the famously (1), and sometimes controversially (2–5), documented recolonization of Krakatau has no “before” data available for comparison, surveys only being conducted after the volcanic eruption. This paper presents data on orb spider communities for 41 islands of varying area studied 4 successive years before, and then 4 successive years after, being struck by a catastrophic hurricane. The islands, located in the northern Bahamas near Great Abaco, were completely inundated when Hurricane Floyd, a Category IV hurricane, passed directly over them on September 14, 1999. It is doubtful that free-living spiders on any of these islands could have survived, so that extermination must have been virtually complete. Indeed, two months later, when we were first able to resurvey the islands after the hurricane, spider densities averaged only 1.7% of the last recorded values 7 months earlier.

These fortunate data provide a rare opportunity to ascertain to what extent and at what rate spider communities recovered from near-total destruction. In addition to following numbers of individuals and species, we document here the redevelopment of two community relationships, the species-area curve and the effect of a major predator, the lizard Anolis sagrei, on the abundance and species richness of its spider prey.

The species-area curve, giving the number of species as a function of area, has been described in an enormous variety of organisms and is nearly ubiquitous (e.g., refs. 1, 6–9). Rarely, however, is the progressive development of this relationship characterized from an initially empty environment. We are aware of only three such published studies: an experimental investigation of the colonization of hard substrata (artificial tiles) in the marine subtidal (10), a similar investigation by using wooden panels in the intertidal of an estuary (11), and the documentation of the restoration of the species-area relation for a single species, the lizard Anolis sagrei, also after Hurricane Floyd (12). How long does it take for the species-area relation, particularly its slope, to redevelop, and does this parallel recovery of the islands in number of individuals and species?

With regard to the second, predator-prey relationship, we have shown for a site in the central Bahamas (islands near Staniel Cay) that islands with lizards have markedly fewer individuals and species of spiders (13–15); we reproduced the direction and even the degree of that relationship by experimentally introducing lizards onto similar islands in the Abaco region (16, 17). When will islands with and without predators reach their characteristic differences, and how does the gradual recovery of lizards after hurricane devastation affect this timeline?

Results

“Normal” State Before the Hurricane. Spider abundance on no-lizard islands showed a steady, but small, decline over the 4 years before the hurricane (Fig. 1; analysis of adjusted means, \( r = -0.910 \)), whereas abundance showed no trend on lizard islands \( (r = 0.664) \). Abundance was lower on lizard than on no-lizard islands in each year, and abundance on lizard islands averaged 60% that on no-lizard islands \((P\text{ values given in Fig. 1)}\). The effect was weakest in April 1999, that census closest to the hurricane. Fig. 2 Left shows the abundance of spiders on each island in 1998 when the lizard effect was strong.

Species richness over the 4 years preceding Hurricane Floyd showed downward trends on both no-lizard islands (Fig. 3; \( r = -0.879 \)) and on lizard islands \( (r = -0.692) \). Richness declined markedly on both types of islands in 1998. Richness on lizard islands averaged 66% that on no-lizard islands \( (P\text{ values in Fig. 3}) \). The lizard effect on richness was weakest in April 1999, that census closest to the hurricane, as found for the lizard effect on abundance. Fig. 2 Right shows the species richness on each island in 1998 when the lizard effect was strong.

The common slope [as determined by analysis of covariance (ANCOVA)] of the relation between species richness and log island area, the species-area curve, showed virtually no temporal trend before Hurricane Floyd \( (r = 0.004) \), giving a nearly horizontal regression line (Fig. 4). The slope attained its highest value in 1998, the year numbers of species declined markedly. The common slope \( (z) \) of log richness vs. log area also showed no temporal trend \((P\text{ Table 1})\). In each year, \( z \) values calculated for

Conflict of interest statement: No conflicts declared.

Abbreviation: ANCOVA, analysis of covariance.

See Commentary on page 2005.

*To whom correspondence should be addressed: E-mail: twschoener@ucdavis.edu.

© 2006 by The National Academy of Sciences of the USA
Hurricane Floyd, when the effects of both area and lizards were strong.

**Immediate Effect of the Hurricane.** Two months after the hurricane (mid-November), when we first were able to revisit the islands, all lizards large enough to be inferred as having hatched before the hurricane had disappeared. However, as described in refs. 12 and 18, we saw hatching lizards on a fair number of the islands then; these individuals must have survived inundation in the egg stage. We did not attempt to characterize which islands did and did not have hatchlings, as we feared such tiny lizards may be too rare and otherwise difficult to find for accurate representation. Thus, we do not present spider data on no-lizard vs. lizard islands for this date. Rather, we remark that mean density of spider individuals over all islands combined was 1.73% of the immediately preceding census (April 1999) and 1.65% of the 4-year average (1996–1999); the same figures for species richness are 24.6% and 20.9%, respectively.

Fig. 5 Upper (Abaco) shows values for the immediately preceding census and the 2-month-posthurricane census as open and closed bars, respectively; these results are very similar to those previously obtained for Hurricane Lili in Exuma (Fig. 5 Lower and Discussion). The comparison suffers from the fact that it is phenologically out-of-sync, as we have no November data before the hurricane. However, after the hurricane, no particular tendency for adjusted means to be higher or lower in November than in April exists for either individuals (November higher in four of six cases) or species (November higher in two of six cases).

In April 2000, the first posthurricane census at the traditional time, there were 11 lizard islands and 30 no-lizard islands (Table 1). Unlike all years before the hurricane, numbers of spider individuals were statistically indistinguishable between no-lizard and lizard islands (statistics in Fig. 1). Similarly, no significant difference existed for number of spider species (statistics in Fig. 3). Although the number of species on no-lizard islands was notably lower than the prehurricane average, it was about the same as that average for lizard islands. More striking still was the exceptionally low species-area slope (Fig. 4), very close to zero ($P = 0.349; P$ values for this slope were significant in all other years at $P < 0.05$ or better). In terms of the log-log regression, the slope ($z$) was 0.003 (Table 1).

**Temporal Trends After the Hurricane.** The species-area slope climbed over the posthurricane years in a nearly linear fashion ($r = 0.905$), achieving the prehurricane average by the third year (Fig. 4). Thus, the slope of the species-area relation showed essentially full recovery. As in the prehurricane years, log-log values of the species-area slope ($z$) were generally higher for lizard than for no-lizard islands (Table 1); the only exception is 2002, and the value was slightly negative for no-lizard islands in 2000.

Recovery of the lizard effect on spiders was different between abundance and species richness. For abundance, the gap between lizard and no-lizard islands was smaller than all prehurricane years only in the first posthurricane year; the gap increased almost monotonically, and by the fourth year, it slightly exceeded that for any prehurricane year (Fig. 1). For species richness, the gap was greater in three of the four prehurricane years than any gap after the hurricane. Correspondingly, during the last 3 years, the lizard effect on abundance was always significant ($P < 0.01$), whereas the lizard effect on species richness was only marginally significant ($P < 0.10$) in 2 years.
Mean species richness the first April census after Floyd was virtually identical to its value the previous year, the last census before Floyd struck (Fig. 5 Upper). Over the next 3 years, species richness rose slightly ($r = 0.794$) for no-lizard islands but never achieved the high values characterizing the first two prehurricane years (Fig. 3). Species richness for lizard islands showed no trend; the greatest change, a decline, was between the first and second years [Note that lizard populations are also recovering after the hurricane’s devastation (see Discussion)].

In contrast to mean species richness, mean abundance the first April census after Floyd did not fully attain the last prehurricane value but was only about half (Fig. 5 Upper). Yearly abundances after the hurricane for both lizard and no-lizard islands are lower than all of the prehurricane values (Fig. 1). In both cases, little temporal trend existed after the hurricane.

**Discussion**

**Prehurricane Variation in Community Characteristics.** The 4 years preceding Hurricane Floyd, 1996–1999, give some picture of normal variation in the slope of the species-area relation, the effect of lizards on spiders, and the number of spider individuals and species.

The slope of the species-area relation showed no temporal trend before the hurricane; it was least in 1998, the year the lizard effect was strongest (note, however, that statistical computations of the species-area slope and the lizard effect for a particular year comes from the same ANCOVA model). Prehurricane slopes of the species-area relation on a log-log plot ($z$, Table 1) fall well within the range of those reported by Connor and McCoy (7) for 90 species-area data sets. The average prehurricane overall slope is 0.24, as compared to Connor and McCoy’s mean of 0.31.

Although ANOVAs never show a significant slope heterogeneity, values of $z$ for lizard islands are always higher than for no-lizard islands; however, this trend is not significant by a binomial test (one-tailed $P = 0.063$). Holt (20) predicted that $z$ should increase with trophic rank if predator extinction rates declined with area or if predator colonization rates increased with area; data supporting this prediction are summarized by Hoyle (21). In our system, both of Holt’s conditions have been shown for Bahamian spiders, the former repeatedly (22–24); the former condition was also shown for Bahamian lizards (25). Holt’s theory is meant to apply to trophic levels in the same archipelago and to absolute, not relative, trophic rank. Nonetheless, from Holt’s (20) treatment one might expect an intermediate predator, such as spiders, to have a smaller slope when being predated upon than otherwise, but this pattern is not true of the present data. In a later treatment, however, Holt et al. (26) suggested that a trophic level suffering a strong depressing effect from a higher level might have its species-area slope increased, because differential extinction is expected on smaller islands. Thus, the strong lizard effect on their spider prey could shift expectations toward a steeper species-area slope on lizard islands. Data for the central Bahamas have greater $z$’s or $r$’s for no-lizard islands (13, 27), contrasting with the present result for Abaco, so there is no overall regional trend.

The lizard effect was weak only in the fourth year (1999), and no temporal trend existed. The most likely explanation for the weak lizard effect in 1999 was the action of Tropical Storm Mitch, which generated substantial rainfall and high water in the Abaco region when it struck in November 1998. The lizard census after Mitch gave the lowest densities of any prehurricane year (1999; see below). Thus lizard and no-lizard islands differed the least in lizard density in 1999, producing the weak lizard effect.

Number of species for both lizard and no-lizard islands dropped sharply between the second and third year, and the decline continued into the fourth year for the latter (Fig. 3). Number of individuals either declined weakly (≈20%) and nearly monotonically for no-lizard islands or (if anything) slightly increased for lizard islands (Fig. 1). Such declines may have been associated with rainfall (unpublished data), because correlations with days of rain become progressively more negative with increasing length of the interval (up to 12 months) before the census. Rainfall may have a disruptive effect, either directly or because it can be accompanied by wind and high sea-water levels. Such an effect would be exacerbated, of course, when the abundant rainfall is associated with cyclonic storms. Although Tropical Storm Mitch was not associated with a short-term drop in spider species richness and abundance, long-term, cumulative effects of this and other major storms could gradually attenuate species richness. Relevant here is that two category I hurricanes, Erin and Bertha, impacted the study region in 1995 and 1996, the

### Table 1. Slope of log number of species vs. log island area each year for all islands combined and for no-lizard and lizards islands

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Island type</td>
<td>All islands</td>
<td>0.231</td>
<td>0.120</td>
<td>0.417</td>
<td>0.208</td>
<td>0.003</td>
<td>0.157</td>
<td>0.352</td>
</tr>
<tr>
<td></td>
<td>No-lizard islands</td>
<td>0.140</td>
<td>0.063</td>
<td>0.400</td>
<td>0.117</td>
<td>-0.050</td>
<td>0.136</td>
<td>0.366</td>
</tr>
<tr>
<td></td>
<td>Lizard islands</td>
<td>0.270</td>
<td>0.144</td>
<td>0.427</td>
<td>0.263</td>
<td>0.261</td>
<td>0.211</td>
<td>0.289</td>
</tr>
</tbody>
</table>

Data reflect $z$ values computed by using ANCOVA for all islands and separate simple regressions for lizard and no-lizard islands. Censuses were conducted April–May each year. hurricane Floyd passed directly over the study site in September 1999 between the 1999 and 2000 censuses.
year before and the first year of the study, and may have had delayed effects (see below).

Presence and Absence of Posthurricane Temporal Trends in Community Characteristics. The slope of the species-area relation increased during the 4 years after Hurricane Floyd, eventually attaining its average prehurricane value (Fig. 4). Hence, recovery of the species-area relation was rapid and essentially complete in 3–4 years. Another study documenting the ontogeny of the species-area relationship entirely from a tabula rasa beginning is an experiment on a marine subtidal “fouling” community in Puget Sound, WA (10). In that study, artificial islands of textured Formica having six areas spanning three orders of magnitude were submerged (from a floating dock) in an otherwise undisturbed site and their colonization by sessile organisms observed. The species-area slope went from very small values to near its maximum ($z = 0.24–0.29$) in ~10 weeks, the same time on average that the numbers of species on the panels took to approach equilibrium and about the same time that most panels achieved near 100% cover. It is not surprising that a kind of stasis was simultaneously achieved in the number of species and the species-area slope at the same time as empty space for colonization had nearly run out. Data on these community characteristics for natural hard-substrata in the subtidal do not exist (nor might they have been fully comparable to those from the panels), so one cannot speak of “recovery” in this example. But despite the subtidal study being rather different, there is no question that the concordance it showed between numbers of species and the species-area slope does not occur in the present study (compare Figs. 3 and 5). Data from the other experimental study of the development of the species-area relation (11) are not entirely comparable to ours because only three areas were used, and the Pearson $r$ rather than $z$ measured the strength of the relation. The latter increased during one season of the year and decreased during another, apparently providing yet another empirical pattern.

That the recovery of the lizard effect on spider species was less complete than the recovery of the species-area effect can be related to the varying density of the lizards, which on those very small islands are, in large part, top predators. Indeed, a plot of the magnitude of the lizard effect on spider species as a function of lizard density shows a positive correlation, both as a whole ($r = 0.669$, one-tailed $P = 0.035$) and before and after Floyd taken separately (Fig. 6). Correlations for the lizard effect on spider individuals were even stronger [$r = 0.837, P = 0.005$; we checked for first-order autocorrelation but it was low (−0.21 and 0.13, respectively), for species and individuals], so we did not include autocorrelation in the statistical models (cf. ref. 28)]. On the subset of islands used in this analysis, lizards were less dense in the first three years after Floyd than in any prehurricane year except 1999, the year after Tropical Storm Mitch (see above). Moreover, lizards were far less dense the first year after Floyd (year 2000 in Fig. 6) than any other year. Correspondingly, on lizard islands, spider species richness the first year after Floyd was slightly higher than the prehurricane mean, and even slightly higher than on no-lizard islands (Fig. 3). The number of spider individuals showed less difference between lizard and no-lizard islands in the first year after Floyd than in any prehurricane year, but unlike the number of species, the difference eventually increased in the fourth year to a value slightly exceeding that of any prehurricane year. Variation in lizard numbers was not, of course, the only kind of variation induced by the hurricane’s effect on lizards: The number of lizard islands also dropped substantially, from 25 to 28 before the hurricane to 11 to 16 after the hurricane (the maximum was reached just before Michelle, which was a very late-season hurricane that exterminated some lizard populations surviving Floyd, probably because it struck after the hurricane-resistant egg stage was no longer being produced; ref. 29). This change in state of island from one year to the next could have varying influences on the relative recovery of the lizard effect. A likely one was that some islands especially favorable for spiders that lost lizards as a result of Floyd became no-lizard islands, increasing the lizard effect.

The complete recovery after one year of mean number of spider species to its last value before Hurricane Floyd, but the only partial recovery of mean number of individuals, parallels in pattern and even magnitude results for spiders after Hurricane Lili (1996) (compare Fig. 5 Upper and Lower). We pointed out for the Lili study (15) how a rapid return to a species equilibrium (1) is suggested, just as was found for experimental defaunation of Lili (1996) (compare Fig. 5 Upper and Lower). Why did spider abundance not increase monotonically during the four posthurricane years? A major consideration was probably the fact that another hurricane, Michelle, struck the Abaco area in November 2001, between the second and third posthurricane years. Abundance (Fig. 1) declined between April 2001 and April 2002 (although this phenomenon was not reflected in species richness; Fig. 3). Michelle was a Category I hurricane, and its storm surge was not nearly as high (~1 m at our site (29), as compared to 3 m during Floyd). A 1-m increase in sea level would have completely submerged or nearly (high water level >90% of the total altitude) submerged only 18 of the 41 islands.
in the present study; of course, the lower parts of even the highest islands would have been covered as well. This effect compares to that of the potentially much more destructive Hurricane Floyd, during which all islands of the present study were apparently completely submerged. More generally, all posthurricane years had greater-than-average rainfall for the 8-year study period, the two highest values being the periods including Floyd or Michelle (unpublished data). Hence, the very destructive immediate effects of hurricanes may be embedded in a long-term pattern of lesser destruction associated with increased rainfall, contributing to the explanation of why spiders did not achieve high densities or diversities during the 4 years after Floyd.

A related reason for a slow recovery of a biota after a catastrophic disturbance is less local: Any extensive hurricane that passes over a particular site must also cause severe destruction to certain adjacent regions. As a well documented example, Hurricane Joan destroyed the rainforest canopy over an area of 500,000 hectares in southeastern Nicaragua and apparently also diminished substantially bird and bat population numbers (refs. 32 and 33). Such an effect, were it to have occurred in our system, did not mitigate the immediate rebound after Floyd in the number of species, although it may have contributed to the long-term gradual decline over the entire 8-year study period. Indeed, 1995 marked the beginning of the abrupt rise in frequency of “major” (Category III or greater) Atlantic hurricanes (http://weather.unisys.com/hurricane/atlantic/index.html), and the possible disappearance of certain species over large surrounding areas would have reduced immigration rates to our study archipelago, diminishing over time its species richness. This overall drop would also contribute to the failure of the lizard effect on species richness to become very large toward the end of the study.

In conclusion, although ecologists have long been interested in the effects of physical disturbance on communities (34–38) and are now increasingly turning their attention to the effects of chronic climatic variation (39–41), few data on the community effects of catastrophic climatic events, such as hurricanes, are available. The dramatic increase in hurricanes over the past decade means that such data are becoming increasingly common (e.g., refs. 12, 18, 29, 32, 33, 42–44). This increase could continue if the elevated North Atlantic sea-surface temperatures were to be resulting, in part, from long-term climate change (ref. 45; but see refs. 46 and 47). Given the rarity of such data until recently, it is unsurprising that community-ecological theory for expectations from major catastrophes is just beginning to be developed (44, 48). We suggested elsewhere (42) that a specific top predator (in this case lizards) was less affected in the short term by moderate climatic disturbance than a specific intermediate predator (in this case spiders), because the former are larger. Further, we suggested that the intermediate predator, because of higher rates of increase, could recover sooner from such disturbance. Although such arguments could contribute toward a portion of a general theory of how climatic catastrophes affect ecological communities, even theory for the effects of chronic climatic variation is scarce (49). Thus, very recently Voight et al. (41) reported that sensitivity to climatic variation (as encapsulated in PCA variables) in a north temperate grassland community over 20 years was greater the higher the trophic level, yet offered no explanatory hypotheses. Similarly, we had no general explanation for the temporal discordance of the respective recoveries from climatic catastrophe of the species-area slope vs. overall species richness. Perhaps unusually for the science of ecology, here is a topic for which now at least data may be leading the development of theory.

**Materials and Methods**

**Sites, Species, and Census Procedures.** Study islands were located off Great Abaco, Bahamas, in protected “creek” areas near Snake Cay/Buckaroo Bay. We censused 41 islands ranging in vegetated areas from 13 to 270 m². Censuses were performed each year in late April–early May (the end of the dry season) for the interval 1996–2003 (two islands were inadvertently missed in April 2003). In addition, for the 4 years after Hurricane Floyd, we censused the same islands in late fall.

Islands could change their state (“lizard” vs. “no-lizard”) from one year to the next. We used the following set of rules to designate lizard vs. no-lizard for a particular island in a particular census period. Islands on which only a single adult male was observed in at least 3 visits per census period were considered no-lizard, because one individual known to be male could not have found a viable population (lizards smaller than adult males cannot be sexed by sight and so could be male or female, and a single female could have found a population if it has stored sperm or fertilized eggs). An island initially without lizards was designated lizard in the second and subsequent consecutive censuses that lizards were first observed, but no-lizard for the first such census because lizard density then was probably substantially lower than equilibrium. An island having lizards for 3 consecutive years (before or after the hurricane taken separately) was counted as lizard in the fourth year as well, even if lizards were not seen; only one such island fit this rule, and lizards were seen on it again the next year.

During each spider census, all orb webs were examined on each island, and their occupants, if any, were noted as to species. The entire island could be searched without disturbing the vegetation, as the latter was never prohibitively dense. Vegetation rarely exceeded 2 mi in height, so that we were able to inspect easily virtually all foliage for webs. We believe we found nearly all of the diurnally existing orb webs, with nearly all of the diurnally active spiders, on each island; in a different region of the Bahamas, recounts of particular islands a few days apart gave little difference (details in refs. 13 and 50).

Sixteen species of spiders occurred in orb webs on the islands monitored during the 8 years of the study; nine in the Araneidae (Metepeira datona, Metepeira sp., Eustala caziert, Argiope argentata, Argiope trifasciata, Eriophora ravilla, Gasteracantha cancriformis, Cyclosa walckenaeri, Gei sp., two in the Uloboridae (Uloborus trilineatus, Philoponella semiplanulosa) and four in the Tetragenathidae [Philpha clavipes, Plustometra argyra, Leucauge sp., and a species unidentified to genus (probably Tetragnathidae)]. In addition, because of its occurrence in the webs of orb spiders, we included the kleptoparasitic theridiid, Argyrodes elevatus, in the counts.

**Statistical Analyses.** The main analysis for each census period was an ANCOVA in which the factor was presence or absence of lizards on the island and the covariate was log_{10} island area. The analyses were first run with the area × lizard interaction included. If that interaction was not significant (at $P = 0.05$), the model was run without it and the resulting statistics used; in fact, no analysis had a significant interaction in this study or even one for which $P < 0.20$, the cutoff recommended by Winer (51) for inclusion of the interaction. The main summary statistics were three parameters estimated from the ANCOVA: the (common) slope of the species vs. area relationship, the adjusted (= least-squares) mean of the dependent variable for lizard islands, and the same quantity for no-lizard islands. Two $P$ values from the ANCOVA, that for the common slope (the “area effect”), and that for the difference between adjusted means on lizard vs. no-lizard islands (the “lizard effect”), were used to assess statistical significance for a given census year. Because we had clear directional hypotheses, one-tailed $P$’s were used for these tests.

For spider abundance (number of individuals for all species combined) as the dependent variable, ANCOVAs were performed after log transformation. For spider species richness as...
the dependent variable, we ran ANCOVAs with both untransformed and log transformed values, as species-area data sets from the most comprehensive literature review (including 90 cases) were almost equally divided as to which gives the better fit (7). In our study, both species-area slopes and lizard effects tended to be slightly more significant for the untransformed dependent variable than for the transformed dependent variable, but overall the results of both analyses were quite similar. In addition to the ANCOVAs, we ran simple regressions on log(species richness) vs. log(island area) separately for no-lizard and lizard islands, to compare slopes (z’s) for spiders that would have different average trophic positions, a topic of recent interest (21, 26). Because the interaction of area and lizard/no-lizard was not significant for any year (see previous paragraph), we evaluated (in a binomial test) only whether the number of years in which z for lizard islands exceeded z for no-lizard islands was significant.

We computed Pearson correlation coefficients between time and abundance, species richness, or the species-area slope. These coefficients were calculated separately for the four-year sequence before and the four-year sequence after the hurricane; the coefficients are used only descriptively and are not used formally for hypothesis testing.

To compare data from this study (in Abaco) to those from a previous study (in Exuma; ref. 42) after another hurricane (Lili), we present before and after means and standard deviations for numbers of individuals and species (see Results: Immediate Effect of the Hurricane).

Lizard population size on each island was estimated from censuses over 3 consecutive days, during which all lizards seen were marked long-distance with a specific color of paint (52). Log-linear capture-recapture models were used to generate the estimates statistically (53–56; further details in ref. 19).

We thank J. Losos for comments, B. Pinder for logistical assistance, and the Bahamas government for permission to conduct research. The project was funded by the National Science Foundation.