ture of late-onset non-insulin-dependent diabetes mellitus, it is possible that dysregulation of the HNF regulatory pathway, whether primary or secondary, can also contribute to this complex metabolic syndrome.

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18. The production of *HNF-3β* +/− ES cell lines, B13 and 4B1, has been described (*8*). Genotypes of *HNF-3β* mutant ES cell lines were analyzed by Southern blotting (*8*). *HNF-3β* −/− line B14 was derived from *HNF-3β* +/− line B13, and *HNF-3β* −/− lines 5.2 and 5.1 are from 4B1 as described in (*8*).
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Impact of a Catastrophic Hurricane on Island Populations

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Lizard and spider populations were censused immediately before and after Hurricane Lili on islands differentially affected by the storm surge. The results support three general propositions. First, the larger organisms, lizards, are more resistant to the immediate impact of moderate disturbance, whereas the more prolific spiders recover faster. Second, extinction risk is related to population size when disturbance is moderate but not when it is catastrophic. Third, after catastrophic disturbance, the recovery rate among different types of organisms is related to dispersal ability. The absence of the poorer dispersers, lizards, from many suitable islands is probably the result of long-lasting effects of catastrophes.

Major natural disturbances such as hurricanes and volcanic eruptions may be so catastrophic that biotas in exposed areas are scarred and even reshaped for years to come. Although major disturbances are potentially of such great importance (*1*), few precise field data are available to evaluate their impact. Reliable information on the biota before the disturbance is often absent, as is the case for the most lengthily monitored major disturbance of all, the eruption of Krakatoa's volcano in 1883 (*2*). Furthermore, because major disturbances are rare, the initial impact and the incipient stage of recovery are often missed because of the low probability of scientists being in just the right place at the right time.

In October of 1996, the highly improbable happened. We had just finished a census of lizard and spider populations on 19 islands (Fig. 1) near Great Exuma, Bahamas, as part of a long-term experimental study of the ecological effects of introducing two lizard species (*Anolis sagrei* and *A. carolinensis*) (*3*, *4*). Vegetation profiles of each island, which change little under normal conditions, had been determined 2 years previously (*5*). During the early morning of 19 October, Hurricane Lili, the first major hurricane to strike anywhere in the Exumas since 1932 (*6*), passed directly over our study site (Fig. 1) with sustained winds of 90 knots and a storm surge of nearly 5 m (*7*). The study islands are located on both sides of the very large island of Great Exuma. Because Lili's approach was westerly, the 11 islands on the southwest side were exposed to the full force of the storm surge, whereas the 8 islands on the northeast side were protected from this aspect of the hurricane. The next day, as soon as the storm subsided, and for 3 days thereafter, we recensused populations on all the islands. All populations were again censused about 1 year later (23 to 28 September 1997).

These unique data allow us to evaluate several propositions concerning the impact of disturbances on different types of organisms. First, that larger organisms may be more resistant than smaller ones to the immediate impact of a moderate disturbance (*8*, *9*). Second, that surviving smaller species may recover faster because their reproductive rate is higher than that of larger species (*9*). Third, that for moderate disturbances, the risk of extinction is a function of population size, whereas no such relationship exists for catastrophic disturbances (*10*). Fourth, that when all populations are exterminated by a catastrophic disturbance, the recovery rates of different species will be largely determined by their dispersal abilities (*11*). To evaluate

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these propositions, we compared the effect of the hurricane on lizards versus spiders and on protected versus exposed islands.

On the protected side, although effects were marked, a moderate number of individuals survived: The mean number of lizard individuals per island was 34% lower immediately after than before the hurricane, whereas the mean number of web-spider individuals was 79% lower (Fig. 2A). The change was statistically significant for lizards (P = 0.044) and for spiders (P = 0.002) and was significantly greater for spiders than for lizards (P = 0.032) (*12*). The mean number of web-spider species was reduced (P = 0.040), but the number of lizard species remained constant (Fig. 2B). Comparisons between censuses immediately after and 1 year after the hurricane showed that the numbers of lizard individuals were not significantly different (P = 0.401), whereas the number of spider individuals (P = 0.005) and species (P = 0.025) had increased. Thus, the data show that the larger lizards were more resistant than the smaller spiders to the immediate impact of the moderate disturbance on the protected side, which is in accordance with the first proposition above. Lizards may have been able to withstand the physical forces of the disturbance or to find protective cover better than spiders. On the other hand, spiders, which are generally more fecund and have shorter generation times, recovered faster than lizards, which is in accordance with the second proposition.

On the exposed side, all lizard and spider populations were exterminated (Fig. 2C). On 6 of the 11 islands, a few spider individuals were found immediately after the hurricane but these belonged to *Metazygia bahama*, a species completely absent on all the islands before the hurricane (*13*); spiders sustained a net 97% loss in total numbers (P = 0.001). One year later, no lizard was found on the study islands. In contrast, the numbers of spider individuals and species were higher the year after than immediately after the hurricane (P = 0.011 for individuals; P = 0.014 for species) (Fig. 2, C and D).

Figure 3 shows the numbers of individuals (population size) of each species recorded on each island before the hurricane that were determined as extinct and extant immediately after. On the protected side, none of the five introduced lizard populations became extinct, even though two populations were very small (fewer than five individuals). In addition to the introduced populations, the presence of natural lizard populations (*A. sagrei*) was ascertained before the hurricane on five small islands on the protected side (*4*); no such population became extinct. In contrast, 9 of 22 web-spider populations became extinct. The proportion of populations becoming extinct was significantly higher for spiders than for the introduced and natural lizard populations combined (P = 0.018; Fisher's exact test, one-tailed), which again supports the first proposition. Spider populations becoming extinct were significantly smaller than those remaining extant (P =

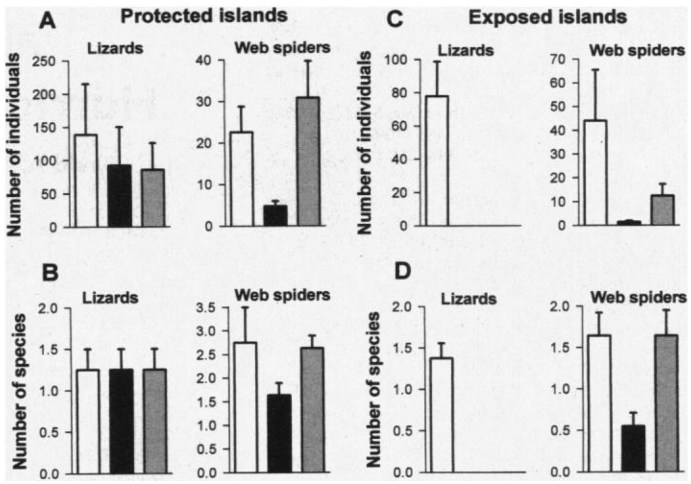

Fig. 2. Mean numbers of individuals and species of lizards and web spiders on protected (**A** and **B**) and exposed (**C** and **D**) islands immediately before (9 to 17 October 1996; white bars), immediately after (20 to 23 October 1996; black bars), and ~1 year after (23 to 28 September 1997; gray bars) Hurricane Lili. Error bars indicate standard errors.

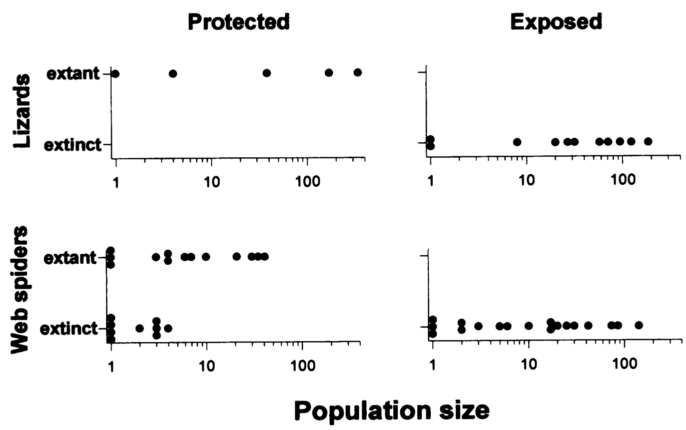

Fig. 3. Relationship between population size recorded immediately before and extinctions recorded immediately after Hurricane Lili for each species of lizard and web spider on protected and exposed islands.

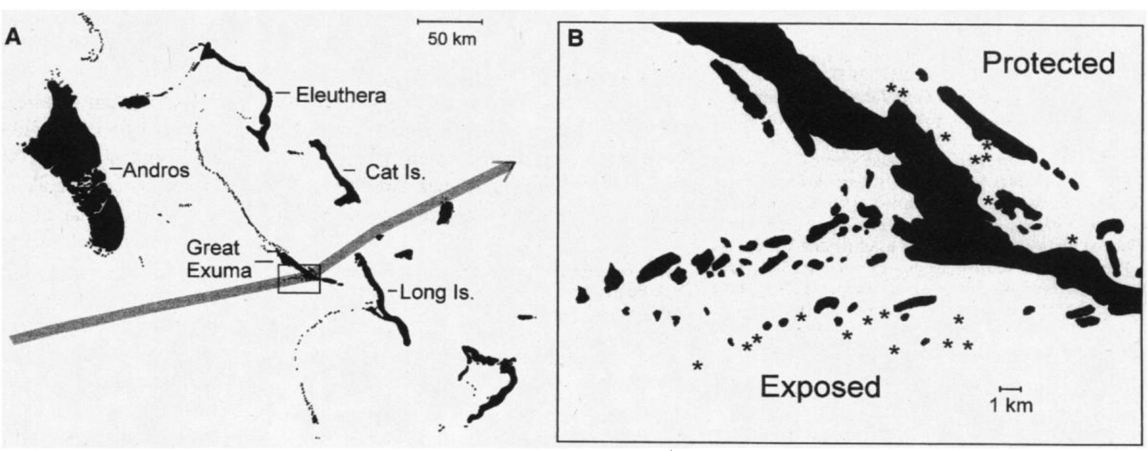

Fig. 1. (**A**) Map of the central region of the Bahamas showing the path of Hurricane Lili. (**B**) Asterisks indicate the locations of the study islands.

0.001; one-tailed t test on log-transformed population size) (*14*).

On the exposed side, all lizards and spiders became extinct even though the population sizes of some were large; the maximum lizard and spider populations had 186 and 143 individuals, respectively. In addition, all of the five natural lizard populations (*A. sagrei*) we found before the hurricane on small exposed islands also became extinct. This extinction versus population-size relationship was used by Pimm *et al.* (*10*) to characterize "catastrophic" extinction, but apparently no illustrative data were available until now. Moreover, the results for spiders on the protected and exposed islands, taken together, provide the first precise demonstration of the third proposition.

What feature of the hurricane was responsible for the catastrophic extinction on the exposed islands? Because most of Great Exuma lies below an altitude of 10 m, wind velocity during the hurricane over its protected satellite islands was probably equal to, or only slightly less than, that over its exposed islands. However, Great Exuma did substantially impede the effect of the storm surge on the protected islands—immediately after the hurricane, we observed much scouring by water (for example, erosion and sand deposition) even on the highest surfaces of all exposed islands, but no such damage was present on protected islands. Moreover, the volume of vegetation was much more reduced on exposed than on protected islands, averaging 42% (SE = 5.1) versus 15% (SE = 7.1), respectively. Thus, the storm surge appeared to be the aspect of the hurricane that was responsible for catastrophic extinction on the exposed islands. Similar differential effects of hurricanes were found for corals in protected and exposed areas located on opposite sides of Heron Island on the Great Barrier Reef (*15*). Other studies of lizards (*16*) and birds (*17*) in different areas on very large West Indian islands have also shown substantial differences in hurricane damage. Thus, marked spatial heterogeneity appears to be a common feature of the impact of hurricanes on natural populations.

The results on the exposed islands 1 year after the hurricane are in accordance with the fourth proposition. Although the number of spider individuals averaged about one-third of the prehurricane value, the mean number of spider species rebounded to exactly the same value as before the hurricane. A rapid return to a dynamic species equilibrium (*18*) is suggested, just as has been found in experimental defaunation studies of collective arthropod biotas on small islands (*19*). Hence, although hurricanes may exterminate spider populations, many small islands are quickly recolonized, including some without lizards, where spiders can reach extraordinarily high densities (*20*). The excellent over-water dispersal abilities of such arthropods seems clearly responsible. Indeed, the first known colonist of the denuded Krakatoa was a spider (*2*)! In contrast to spiders, recolonization by lizards was minimal (*21*). Bahamian lizards have been experimentally introduced, repeatedly and successfully, onto small islands where they do not naturally occur (*22*, *23*). Because these islands were united with much larger ones when sea levels were lower 8000 to 10,000 years ago (*24*), it is reasonable to conclude that they did at one time have lizard populations. This suggested to us (*22*) that infrequent catastrophic hurricanes exterminated lizards on such islands. We now have an actual demonstration of the hypothesized mechanism. Immediately after the hurricane, lizards were found on a large exposed island, but only in the highest area. Hence, catastrophic extinction of lizards may have occurred only on islands small enough to be inundated completely during the hurricane. Thus, given the poor dispersal abilities of lizards, their absence from most small islands may literally represent the high-water mark of previous hurricanes. More generally, this study illustrates that after a catastrophic disturbance, the recovery rate among different types of organisms increases strongly with dispersal ability.

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12. The proportional changes in numbers of lizards and spiders between two censuses on each island were shown to be statistically greater than zero by performance of a paired t test on log-transformed numbers. The P values are one-tailed because numbers were expected to decrease from immediately before to immediately after the hurricane. The difference between lizards and spiders in the proportional change was analyzed with a t test; the P value is one-tailed because the numbers of spiders were expected to decrease more than the numbers of lizards. The P values for changes from immediately after versus 1 year after the hurricane are two-tailed.
13. This surprising observation suggests that the hurricane transported the species beyond its normal range of dispersal. Although these spiders might have come from Great Exuma, *M. bahama* was previously recorded on only Andros and Bimini, located >100 km from the study islands [H. W. Levi, *Bull. Mus. Comp. Zool.* **154**, 81 (1995); H. Levi, personal communication]. One year after the hurricane, *M. bahama* was absent on all islands, as it was in each of our four annual censuses before the hurricane.
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