Natural Restoration of the Species-Area Relation for a Lizard After a Hurricane

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We document the decimation and recovery of the commonest lizard species, *Anolis sagrei*, on 66 islands in the Bahamas that were directly hit by Hurricane Floyd in September 1999. Before the hurricane, an island’s area was a better predictor of the occurrence of *A. sagrei* than was its altitude. Immediately after, altitude was a better predictor: Apparently all lizards on islands lower than about 3 meters maximum elevation perished in the storm surge. After about 1 year, area again became the better predictor. By 19 months after the hurricane, *A. sagrei* populations occurred on 88% of the islands they formerly occupied. Recovery occurred via overwater colonization and propagation from eggs that survived inundation, mechanisms that were enhanced by larger island area. Thus, natural processes first destroyed and then quickly restored a highly regular species-area distribution.

The community species-area relation, describing the increase of species number with increasing area, is one of ecology’s most pervasive regularities—even, perhaps, one of its few “laws” (1–6). This curve is itself composed of often quite regular occurrences for individual species: At the extremes, islands having or lacking a given species are entirely nonoverlapping in area, giving a steplike species-area relation for that species (7). A variety of causes for the species-area relation at both the community and individual species levels have been proposed (1–6). In the MacArthur-Wilson equilibrium model (1), for example, extinction rate is assumed to increase with decreasing population size, an assumption for which there is much evidence (8–11). Were population size less the smaller the area, individual species would tend not to occur on smaller islands, and fewer species would result there.

Other ways in which area might affect species occurrences can be more indirect. There is the possibility that larger areas might have greater maximum (or average) altitude. This may have two consequences. First, the greater the altitudinal range, the more kinds of habitats are likely to be found on the island, allowing more kinds of species to exist; many studies have explored this issue with correlation analysis, variously finding altitude, habitat diversity, or area to be most related to species number (12–14). Second, the higher the island, the more invulnerable are its populations to catastrophic inundations caused by natural events such as hurricanes and earthquakes. According to this line of reasoning, area is important because it is correlated with another variable, altitude, that is even more important. It would follow that were this correlated variable measured directly, the relation to species occurrences should be even more precise.

We have been studying the occurrences of lizard species on islands of the Bahamas for several decades. The turnover (the change in species occurrences via extinction and immigration) in the absence of major exterminating agents such as catastrophic storms is very low (15). Assuming a low immigration rate, one might expect the occurrences of lizards to be more strongly related to altitude than area; that is, to reflect the high-water mark of the major hurricanes that periodically devastate the Bahamas (16, 17). However, we have found area rather than altitude to be a better predictor of the occurrence of lizard species, both over large regions (6) and at specific sites. An example is given in Fig. 1 (top left: prehurricane). For 66 small islands from a site off Great Abaco measuring about 7 by 2 km, the occurrence of the commonest lizard species, *Anolis sagrei*, showed a stronger relation to area than to altitude (18). The figure also shows that area and altitude in this archipelago are strongly correlated (Pearson r = 0.85; P < 0.0001). In unifactorial logistic regression, each of area and altitude is significant by itself. However, in stepwise logistic regression, area is entered first and altitude is omitted, explaining no additional significant variation in occurrence (19). Given the arguments about the directly exterminating effect of inundation during natural catastrophes, how could area be more important than altitude?

Nature began a demonstration of how area attains its importance on 14 September 1999, when Hurricane Floyd, a category IV hurricane with maximum sustained winds ~250 km per hour, passed directly over the archipelago shown in Fig. 1. We were able to reach the islands about 2 months later and survey them for lizards. Surprisingly, only very small lizards (that is, no adults or near adults) were found on a substantial number of islands (20). Such lizards by their size can be surmised to have hatched from eggs since the hurricane (17). Experiments now under way show that, indeed, lizard eggs (at least those <10 days old) can survive submersion in sea water for up to 6 hours, which is approximately the maximum duration of the storm surge according to locals, with no detectable ill effects. We infer that when an island is completely inundated during high water, eggs can weather the storm, even though all hatched lizards are drowned, washed away, or otherwise perish.

We found adult or nearly adult lizards, individuals that had not been killed or washed away, on 12 of the 66 islands 2 months after the hurricane. These 12 islands tended to be both higher and larger than those having no adult lizards, but the threshold of separation for altitude was visibly more precise than that for area (Fig. 2). Stepwise logistic regression confirmed this impression, with only altitude entering the model [although both variables again were significant in unifactorial regression (21)]. Islands with and without adult lizards overlapped in altitude over the range from 2.6 to 3.2 m, as compared to a range for all islands of 0.4 to 6.1 m. This rather precise threshold, about half a meter wide, which coincided with substantial reductions of leaf litter and topsoil, can be inferred to correspond to the height of the storm surge; that is, to the maximum rise in sea level resulting from the hurricane.

Seven months after the hurricane (April 2000: Fig. 1, top right), islands showed a less precise altitudinal threshold than 2 months after the hurricane (compare to Fig. 2) but also a less precise areal threshold than before the hurricane (compare to Fig. 1, top left). As for 2 months after the hurricane, stepwise logistic regression again selects altitude as the only significant variable, although both area and altitude are significant in unifactorial analyses (21). This state of affairs reverses 14 months after the hurricane (November 2000: Fig. 1, bottom left), when it is area, not altitude, that is solely selected by the regression. The latter situation persists at the final survey (April 2001: Fig. 1, bottom right), 19 months after the hurricane (21). Again in these analyses, both variables are significant in unifactorial regression. Hence, altitude loses its primacy over area rather quickly as time elapses after the hurricane.

For islands where *A. sagrei* was the only
lizard species, lizard establishment was permanent: Once an island was found to have those lizards, it was never found without them. The only island having a second species of lizard, *Leiocephalus carinatus* (predatory on *A. sagrei*), was the only exception to the trend: Although a few *A. sagrei* were seen on that island after the hurricane, at the last census it had no *A. sagrei* and was the largest previously inhabited island by far to be in that state (Fig. 3, bottom right). Elsewhere (17), we showed that other islands of its area on which *L. carinatus* were artificially introduced mostly also lost *A. sagrei*. Although post-hurricane colonization and then extinction were thus generally not observed as part of the reconstitution of lizard-inhabited islands, unobserved colonization followed by unobserved extinction (or vice versa) is, of course, always possible during an interval between two surveys [for example, see (22)]. However, if in-and-out events were common, we should have detected more with our rather frequent censuses.

The reconstitution of islands having *A. sagrei* lizard populations before the hurricane is shown in Fig. 3. After ~2 months, we found adult or near-adult lizards on 12 of 49 islands; after 7 months, we found such lizards on 33 of 50 islands; after 14 months, we found such lizards on 43 of 50 islands. By the last survey, 19 months later, we found adult or near-adult lizards on 12 of 49 islands. Founders could have been supplemented by natural colonists. Further, the islands on which we saw no hatchlings still may have had them, because such islands can be quite large, so that one is then looking for needles in haystacks (see also caption of Fig. 2). Survival as eggs was doubtless a significant part of the reconstitution of lizard populations on islands (17). On the other hand, distributional gains between the second and third post-hurricane censuses and between the third and fourth censuses (10 islands and 2 islands, respectively) are most likely due to overwater recolonization. This is a rather large amount of species immigration when compared to the natural magnitude as estimated in a previous study at a different site (15), in which only one immigration of any lizard species was observed on 89 islands in 2 years, but of course a different and much larger set of islands was available after the hurricane than during “typical” times.

No evidence exists that the hurricane itself transported lizards: We found no island inhabited by lizards immediately (2 months) after the hurricane that was not inhabited before [but see (18)]. One island known not to have lizards immediately before the hurricane had lizards after it. This island was apparently colonized between 14 and 19 months after the hurricane; it was continuously uninhabited by lizards for at least 11 years before the hurricane struck. Its colonization exemplifies the low but finite natural turnover characterizing this system (15).

The rapid and fairly complete reconstitution of lizard occurrence found in this study is in some contrast to the only other such data in existence, those collected 3 years before in the wake of Hurricane Lili (16). On 19 October 1996, Lili passed directly over another of our study sites, a set of islands in the central Bahamas off Great Exuma, also terminating an experiment. Although of lower wind speed than Hurricane Floyd (the hurricane of the present study), Hurricane Lili generated a substantially higher storm surge, attaining about 5 m and largely devastating vegetation on exposed islands. All lizards perished, and thorough searches immediately after the hurricane as well as ~3 months later produced no hatchlings (or lizards of any kind) on any of the experimental islands. Of the five similarly sized islands at that site...
known to have *A. sagrei* lizards naturally. Lizards were found on only one after a 12-month interval, and lizards have been seen on three of the five up to the present, 4 years later. We suggest that the physical force of the storm surge, much greater at the Exuma site, was much more devastating to the egg stage there; indeed, the vegetation at the site, was much more devastating to the egg later. We suggest that the physical force of lizards were found on only one after a 12–

fore the hurricane are marked “present.” Shortly after the hurricane (~2 months), such islands include most of the islands over 3 m high but are rather variable with respect to area. As time progressed, both lower and smaller islands were filled in, and area became a better and better predictor of which islands had lizard populations restored. At the end of the study, 19 months later, *A. sagrei* lizard populations that included adult or near-adult individuals were found on 88% of the islands, as compared to 24% of the islands immediately after the hurricane. The island marked with a cross in a circle (lower right panel) at ~19 months after the hurricane was the only island with a second species of lizard, the larger predatory *L. carinatus*. Sample sizes are as follows: ~2 months after the hurricane = 49 islands; on other dates ~50 islands.

Fig. 3. Restoration of lizard distribution over the archipelago in relation to island area and altitude. Only islands found to naturally have *A. sagrei* before the hurricane are shown (see (18) for elaboration). Adult or near-adult individuals were found on islands marked “present.” Shortly after the hurricane (~2 months), such islands include most of the islands over 3 m high but are rather variable with respect to area. As time progressed, both lower and smaller islands were filled in, and area became a better and better predictor of which islands had lizard populations restored. At the end of the study, 19 months later, *A. sagrei* lizard populations that included adult or near-adult individuals were found on 88% of the islands, as compared to 24% of the islands immediately after the hurricane. The island marked with a cross in a circle (lower right panel) at ~19 months after the hurricane was the only island with a second species of lizard, the larger predatory *L. carinatus*. Sample sizes are as follows: ~2 months after the hurricane = 49 islands; on other dates ~50 islands.
Role of Erv29p in Collecting Soluble Secretory Proteins into ER-Derived Transport Vesicles

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Proteins are transported from the endoplasmic reticulum (ER) in vesicles formed by coat protein complex II (COPII). Soluble secretory proteins are thought to leave the ER in these vesicles by “bulk flow” or through recognition by hypothetical shuttling receptors. We found that Erv29p, a conserved transmembrane protein, was directly required for packaging glycosylated pro-α-factor (gpαf) into COPII vesicles in Saccharomyces cerevisiae. Further, an Erv29p-gpαf complex was isolated from ER-derived transport vesicles. In vivo, export of gpαf from the ER was saturable and dependent on the expression level of Erv29p. These results indicate that membrane receptors can link soluble cargo proteins to the COPII coat.

In eukaryotic cells, secretory proteins are packaged into COPII-coated vesicles at the ER for transport through the early secretory pathway. The mechanisms by which secretory proteins are segregated away from ER resident proteins during vesicle formation are still a matter of debate (1). Certain portions of integral membrane cargo appear to bind directly to subunits of the COPII coat (2, 3), allowing for their concentration into ER-derived vesicles (4, 5). It is less clear how soluble secretory cargo proteins are exported from the ER, and evidence supporting bulk flow (5) and receptor-mediated export mechanisms (2, 6) exists. One difficulty with the receptor model has been the failure to identify integral membrane proteins that could fulfill this function.

In S. cerevisiae, COPII-coated vesicle formation has been reconstituted in cell-free reactions using ER membranes and purified COPII components: Sar1p, Sec23p complex, and Sec13p complex (7). COPII vesicles have been isolated and several of the abundant integral membrane constituents have been characterized in an effort to identify proteins involved in sorting during vesicle formation (8). One such ER-vesicle protein of 29 kD (hence Erv29p) is conserved across species (9), is selectively packaged into COPII vesicles (8), and contains multiple membrane-spanning domains with a terminal dilysine sorting signal (10).

Haploid erv29Δ strains are viable and display no observable growth defects (8, 10). To test whether ERV29 deletion influenced protein transport between the ER and Golgi, we performed a reconstituted cell-free assay that measures transport of [35S]gpαf to the Golgi complex (11). Surprisingly, no transport of gpαf was detected in membranes lacking Erv29p, although translocation of [35S]pre-pof into ER membranes was unaffected. Specifically, the defect in gpαf transport occurred at the COPII-dependent budding step. Budding of gpαf in wild-type membranes was efficient (33% of total), whereas only minor amounts (4% of total) were budded from erv29Δ membranes (Fig. 1A). To distinguish whether this result was due to a general decrease in COPII budding or a fail-