Making a virtue out of a necessity: Hurricanes and the resilience of community organization

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Most of us these days are all too aware of the disruptive impact of hurricanes in human affairs. Yet disturbances ranging from minor local disruptions to massive large-scale catastrophes are part-and-parcel of life in most natural ecosystems (1, 2). These disturbances often provide scientific opportunities, because sometimes one learns the most about how a system functions by watching it recover after it has been kicked by a major disturbance (e.g., ref. 3). Ecologists increasingly recognize that the structure of natural communities reflects the interplay of processes acting over a wide range of temporal and spatial scales (4) that are well beyond the scope of manipulative experiments. The article in this issue of PNAS by Schoener and Spiller (5) provides a deft testament to the insights that can sometimes be gleaned from ‘‘natural’’ experiments generated by large-scale disturbances, which permit an examination of system responses that could not be readily examined with manipulative experiments.

Responses to Disturbance

Schoener and Spiller (5) provide a portrayal of the impact on spider communities of a major hurricane (Floyd) that in 1998 slammed into a suite of 41 Bahamian islands, completely inundating them and driving multiple extinctions. Studies by Schoener, Spiller, and their associates before Hurricane Floyd provide a rich understanding of many aspects of this system and may indeed provide one of the better-understood terrestrial food webs. By comparing data collected from islands for several years before the hurricane, with an equal number of years after the hurricane, Schoener and Spiller (5) characterize key dimensions of community response to this disturbance. Both before and after the hurricane, some islands had lizards, and others did not. Earlier correlative and experimental studies (see references in ref. 5) found that lizards on these small islands act as effective top predators, limiting spider abundance and species richness. The spider communities on these islands also match a pervasive pattern in community ecology, the species-area relationship, which describes how species richness increases with increasing island area (6, 7). A useful statistic for describing the strength of this relationship is the z value, which is the slope of a regression of log species versus log area. The study by Schoener and Spiller (5) provides an analysis not only of different facets of community resilience to disturbance but also of how the effect of disturbance on the species–area relationship depends on trophic structure.

As Schoener and Spiller (5) note, by some measures these communities appear to be highly resilient, but by other measures, they are not. Within 4 years of the hurricane, average species richness had increased to its prehurricane value, but average abundance was still substantially depressed. The former result matches the findings of the celebrated defaunation study of Simberloff and Wilson (8) in the Florida Keys; arthropod communities contain many highly vagile species, and if islands are not too far from potential source areas, the dynamic colonization–extinction equilibrium predicted by the classical theory of island biogeography (9) can emerge relatively quickly after a major disturbance. Another indication of resilience at the whole community level is that the z value of these islands rebounded from near zero to approximately its predisturbance value. As Schoener and Spiller (5) note, few prior studies have permitted documentation of the temporal dynamics of the species-area relationship.

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The contrasting sluggish recovery in total abundance makes perfect sense. After a species recolonizes an island, it will initially be rare, and because of initial demographic stochasticity and exponential growth, there will be a lag before its abundance recovers to the carrying capacity defined by the interplay of resource availability and mortality factors. The lower resilience of spider abundance could reflect such demographic lags. In other systems, dominated by species with low vagility, one would expect to see much longer lags in recovery by species richness after a major perturbation than observed in these Bahamian spiders.

Schoener and Spiller (5) observe that the strength of the top-down effect of lizards on spider communities rebounded as well, when measured by the impact of lizards on spider abundance but not when measured by species richness. This pattern hints at a general message that goes beyond this study, namely that the influence of trophic interactions on community structure as assessed in field studies (e.g., using removal experiments) may itself strongly depend on the disturbance history of local systems. To me, an intriguing result reported by Schoener and Spiller but not emphasized by them is found in table 1 in ref. 5: the z value was greatly depressed after the hurricane, and then quickly rebounded, for islands free of lizard predation. By contrast, on islands that retained their lizards after the hurricane, the z values stayed comparable to their prehurricane values and showed no clear trend thereafter. The consistency through time of z values on islands with lizards suggests that top-down control of the species-area relationship in spider communities may be robust to major environmental perturbations, provided the top predator persists through the disturbance. Elucidating the mechanistic underpinnings of this effect will require a more detailed analysis of the interplay of predation and colonization–extinction dynamics at the level of individual spider species.

Future Directions

There are, of course, many questions left unanswered by Schoener and Spiller's study (5). For instance, in addition to direct mortality imposed by the hurricane, there could be a multitude of

Conflict of interest statement: No conflicts declared.

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impacts on island communities and ecosystems that influence the interaction between lizards and spiders. Direct structural impacts of wind and storm surges on vegetation could alter the palette of microhabitats suitable for orb-weaving spider occupancy (see ref. 10 for examples involving Hurricane Hugo on Puerto Rico), shift the availability of refuges from lizard predation, and alter microclimatic variables affecting both lizards and spiders. Storms can also provide a conduit for organic materials from oceans onto islands, with profound indirect consequences for island diversity and trophic interactions (11, 12), or conversely, a route for removal of accumulated resources to the ocean. Lizard predators and their spider prey are jointly sustained by an arthropod community, which itself would surely have experienced shifts in species richness and abundance in response to the hurricane. The exact relationship to be expected between trophic rank and the species-area relationship depends on many factors, including the degree of trophic generalization at each level and the magnitude of top-down effects of predation on extinction (13). Some lizard populations are found on islands without any spiders (see figure 2 in ref. 5), presumably because they are sustained by other species of arthropods; the population and community dynamics of this basal prey guild could influence the species-area relationship of the top and intermediate predators.

Ecologists increasingly recognize that analyzing the impacts of disturbance is central to interpreting many aspects of the structure and functioning of natural ecosystems, and that the "normal" is not a tidy equilibrium but incorporates variation and disturbance over a wide range of scales (14). This recognition is beginning to transform how ecologists view island ecology and biogeography. Many island systems are subject to recurrent hurricanes and tsunamis. The species that occur there can be expected to have evolved in the face of such perturbations, and the current structure of island communities surely reflects the long-term imprint of frequent disturbance (15). The results reported by Schoener and Spiller (5) suggest that some subsets of communities (e.g., spiders) rapidly rebound to a rough equilibrium after major disturbance, whereas others (e.g., lizards) have a much longer transient. They also note that other trends in the data may reflect longer-term climatic trends and the influence of less-intense hurricanes. Patterns revealed in a snapshot of a community will reflect the imprint of processes at many temporal scales. The interplay of temporal variation, disturbance regimes, dispersal, and food web interactions is a theme that has just begun to be addressed seriously by students of food web ecology (for steps in this direction, see, e.g., refs. 16–19), even though all of these factors are surely involved in determining the structure of most natural communities. A deeper understanding of this interface is increasingly urgent, given the worrisome likelihood that human-generated climate change may be spawning an upsurge in severe weather (20). The article by Schoener and Spiller (5) provides a timely case study that should help stimulate further theoretical and empirical studies of the interplay of time, space, disturbance, and trophic organization.

I thank Michael W. McCoy for commenting on a draft and the University of Florida Foundation for support.

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