ALTERATION OF ISLAND FOOD-WEB DYNAMICS FOLLOWING MAJOR DISTURBANCE BY HURRICANES

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Abstract. Major abiotic disturbance can be an important factor influencing food-web dynamics, particularly in areas impacted by the recent increase in hurricane activity. We present a unique set of data on key food-web processes occurring on 10 small islands for three relatively calm years and then four subsequent years during which two hurricanes passed directly over the study site. Herbivory, as measured by leaf damage, was 3.2 times higher in the year after the first hurricane (2000) than in the previous year and was 1.7 times higher in the year after the second hurricane (2002) than in 2001. The effect of a top predator (the lizard, Anolis sagrei) on herbivory strengthened continuously after the first hurricane and overall was 2.4 times stronger during the disturbance period than before. Overall abundance of lizards was 30% lower during the disturbance period than before, and abundances of web spiders and hymenopteran parasitoids were 66% and 59% lower, respectively. We suggest that increased herbivory observed on all islands was caused, at least in part, by the overall reduction in predation by both lizards and arthropods, whereas magnification of the lizard effect on herbivory was caused by reduced compensatory predation by arthropods.

Key words: abiotic disturbance; Anolis sagrei; Conocarpus erectus; food webs; herbivory; hurricanes; leaf damage; parasitoids; spiders; trophic cascade.

INTRODUCTION

A trophic cascade occurs when predators at the top of a food web have a substantial impact, via organisms at intermediate levels, on basal organisms such as plants (Pace et al. 1999, Polis et al. 2000). Understanding how various factors influence the strength of trophic cascades is a central goal of current ecological research. The effects of productivity, food-web complexity, and ecosystem type have received much attention (Pace et al. 1999, Polis et al. 2000, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002). Abiotic stress or disturbance can also have profound effects on top-down control by predators (Menge and Sutherland 1987, Hunter and Price 1992, Power et al. 1996, Wootton et al. 1996, Preisser and Strong 2004). Disturbances associated with climate change may be responsible for the recent increase in widespread outbreaks of herbivorous insects (Logan et al. 2003). Stireman et al. (2005) suggest that one factor causing these outbreaks is a reduction in top-down control by parasitic wasps.

While conducting a long-term study of top-down effects by predatory lizards in island food webs, our study site in Abaco, Bahamas, was directly hit by the category four Hurricane Floyd in September 1999, the first major hurricane to strike that area since 1965 (Unisys 2004). The storm surge completely inundated all the study islands, and all free-living lizards apparently died or were washed away (Schoener et al. 2001). However, the islands were “repopulated” by hatchlings emerging from eggs that survived the storm surge (see Discussion). In November 2001, the study site was impacted by Hurricane Michelle, only a category one storm but having a surge that again completely or largely inundated the study islands (Schoener et al. 2004). To determine the effect of lizards on producers, we measured amounts of damage produced by herbivorous arthropods on large samples of buttonwood (Conocarpus erectus) leaves collected from six islands with lizards (Anolis sagrei) naturally present and from four islands without lizards. Previous experimental introductions demonstrated that lizards reduced buttonwood leaf damage on islands at the same site, but the strength of this indirect effect was weaker than the direct effect of lizards on web spiders (Schoener and Spiller 1999). Continuous sampling was conducted in 1997–2003, producing three years of data before Hurricane Floyd and four years after that enabled us to assess changes in overall levels of herbivory as well as in the top-down effect by lizards on herbivory.

METHODS

The 10 study islands were 57–270 m² in vegetated area and were located in a protected “creek” waterway just south of Snake Cay, Great Abaco, Bahamas (details in Schoener et al. 2002). Vegetation on the islands consisted largely of shrubs that rarely exceeded 2 m in height. Herbivory was measured on Conocarpus erectus, one of the most common shrubs on the study islands.
Confirmed identifications of herbivores at the study site are Lepidoptera from the families Noctuidae (Collomena filifera and unknown species) and Gelechiidae (unknown species) and Coleoptera from the families Curculionidae (Artipus floridanus) and Chrysomelidae (Chaetocnema brunnescens). Leaves were collected on each island annually (at the end of April or beginning of May) from 1997 to 2003. To select shrubs for leaf collection, on each island we noted each C. eretctus shrub whose major and minor axes both exceeded 33 cm and ordered them around the circumference of the island (most C. eretctus were near the shoreline). We systematically selected every second to fourth shrub, depending on island area, to obtain 6–11 focal shrubs per island. To sample leaves we tossed a cardboard square haphazardly onto each focal shrub 1–5 times, depending on shrub size, and collected that branchlet closest to a marked corner of the square; this resulted in ~10–30 leaves collected per shrub each year. Total number of leaves collected over the entire study was 13 486. Sampled leaves were immediately pressed and then photographed. Total leaf and damaged areas were measured digitally from photographs using SigmaScan Pro Image Analysis System (SPSS, Chicago, Illinois, USA). Percentage leaf area damaged on each island in each year was computed by separately summing the damaged and total areas of all leaves sampled and dividing. For each island, the overall means for damage before and after Hurricane Floyd (September 1999) were computed as the average of the three annual values before and the average of the four annual values after, respectively. To test the effect of lizards (lizard islands vs. no-lizard islands) and time (before vs. after Floyd) we performed a repeated-measures analysis on the arcsine square-root transformed overall means for each island; the lizard × time term tested whether the magnitude of the lizard effect was different before vs. after Floyd. This analysis was followed by separate ANOVAs, before and after Floyd, of the overall means on lizard and no-lizard islands; the lizard-effect test was one-tailed because our previous field experiment at this site demonstrated that lizards reduced leaf damage on islands at the study site (Schoener and Spiller 1999).

We assume that the level of disturbance by hurricanes was the same on islands with and without lizards because these two different types of islands were interspersed across the study site. Because lizard islands tended to be larger (137–270 m²) than no-lizard islands (57–184 m²), we were concerned that the level of disturbance might have been greater on smaller islands and thereby influenced amounts of herbivory more on no-lizard islands. Therefore, we analyzed leaf damage with area as a covariate. ANCOVA showed that island area was not related to overall mean leaf damage ($F_{1,7} = 0.12, P = 0.744$), so the analysis without the covariate is presented in the results.

Lizard population sizes were estimated annually (April) using multiple-mark–recapture censuses (Heckel and Roughgarden 1979, Schoener et al. 2002); on three different days during the same week, lizards were censused and marked (a different color each day) with water-soluble latex paint administered long distance with Indico spraying devices (Forestry Suppliers, Jackson, Mississippi, USA). The procedure yielded a single estimate of population size on each island for each year; estimates are obtained using the multivariate-contingency-table method (Fienberg 1972, Schwartz and Seber 1999). Lizard density on each island in each year was computed as population size divided by vegetated area.

We monitored abundances of two common predatory arthropods on each island. Web-spider density was measured semiannually (April and November) by carefully searching the vegetation on the entire island and recording the number of spiders or fresh webs observed; density was computed as the total number divided by vegetated area. Relative abundance of hymenopteran parasitoids was measured annually (April) with sticky traps (22 × 14 cm sheets of clear plastic coated with Tangletrap adhesive on one side; Tanglefoot, Grand Rapids, Michigan, USA). On each island, 4–6 traps (depending on island area) were tied to the vegetation 0.2–0.5 m above the ground; numbers of individuals were recorded after 24 h. Traps were put in the same uniformly spaced locations each year. Our sticky traps capture a wide variety of parasitoids in the Bahamas (identities of 13 families are in Schoener et al. 1995), including both small (e.g., Platygasteridae and Eulophidae) and large (e.g., Braconidae and Pompilidae) species, suggesting that the traps provided a good estimate of relative abundance of all parasitoids. However, we note that this method for measuring parasitoid abundance may have been influenced by the particular weather conditions during the trapping days. Separate repeated-measures ANOVAs were performed on overall mean web-spider density and number of parasitoids per trap (both variables log-transformed) before and after Hurricane Floyd using the same model as described previously for leaf damage (without area as a covariate). For web spiders, the lizard-effect test was one-tailed because our previous field experiment at this site demonstrated that lizards reduced their densities (Schoener and Spiller 1999).

**Results**

Total amounts of leaf damage before Hurricane Floyd (1997–1999) were relatively low, averaging ~5% (Fig. 1). In the first year after Floyd (2000), overall mean leaf damage on all islands was 3.2 times higher than in the previous year. In the following year (2001) leaf damage declined but was still higher than before Floyd. Hurricane Michelle then struck and leaf damage became...
1.7 times higher in the following year (2002) than in 2001. In the second year following Michelle (2003) leaf damage declined again, as it did the second year following Floyd. Overall mean leaf damage was higher during the four years after Floyd than during the three years before (repeated-measures ANOVA, time effect, $F_{1,8} = 120.56, P = 0.0001$).

The difference between lizard and no-lizard islands in amounts of leaf damage averaged over the three years before Floyd was not significant ($F_{1,8} = 1.07, P = 0.175$). In the first year after Floyd (2000) the difference between no-lizard and lizard islands was slightly larger than it was before (Fig. 1). This lizard effect became more pronounced during the following two years; in the year after Michelle (2002), mean damage on no-lizard islands was double that on lizard islands (22\% vs. 11\%). The difference between no-lizard and lizard islands averaged over the four-year period after Floyd was significant ($F_{1,8} = 8.71, P = 0.009$). Repeated-measures ANOVA showed that the difference between no-lizard and lizard islands was larger after Floyd than before (lizard × time effect, $F_{1,8} = 7.61, P = 0.025$). The magnitude of the lizard effect on herbivory (measured by the natural logarithm of the ratio of mean leaf damage on lizard to no-lizard islands) before and after Floyd was $-0.219$ and $-0.517$, respectively; therefore, the lizard effect was 2.4 times stronger after Floyd than before.

Lizard densities declined after each hurricane, particularly following Floyd (Fig. 2A). Overall mean density averaged over the four years after Hurricane Floyd was 30\% lower than mean density averaged over the three years before (paired $t$ test on mean densities before and after for each island: $t_3 = 3.94, P = 0.011$).

Web-spider densities declined gradually from 1997 to 1999 before they were decimated by Floyd (Fig. 2B). Spiders began to recover from Floyd only to be pounded again by Michelle; thereafter they began to recover again. Overall mean spider density was 66\% lower after Floyd than before (repeated-measures ANOVA, time effect, $F_{1,8} = 9.10, P = 0.0167$) and was 83\% lower on lizard than no-lizard islands (lizard effect, $F_{1,8} = 12.97, P = 0.0035$), but the lizard effect was not significantly different before vs. after (lizard × time, $F_{1,8} = 0.76, P = 0.4081$).

Hymenopteran parasitoid abundance fluctuated from 1997 to 1999 and declined steadily after Floyd (2000) until 2002 (Fig. 2C). Overall abundance was 59\% lower after Floyd than before (repeated-measures ANOVA, time effect, $F_{1,8} = 23.32, P = 0.001$). In contrast to web spiders, parasitoid abundance was 39\% higher on lizard than no-lizard islands (lizard effect, $F_{1,8} = 7.21, P = 0.028$); the difference was similar before and after Hurricane Floyd (lizard × time, $F_{1,8} = 0.20, P = 0.669$). To avoid confusion in the discussion, we note...
here that the positive effect of lizards on parasitoids appears to be caused by lizards reducing the abundance of spiders that catch parasitoids in their webs (Schoener et al. 2002). Therefore, the effect of web spiders on herbivorous arthropods could be both negative (direct predation) and positive (via predation on parasitoids that eat herbivores). This type of compensatory predation by parasitoids may explain why removing web spiders had no detectable effect on herbivory in a previous experiment (Spiller and Schoener 1994).

**Discussion**

The data in Fig. 1 document two changes in food-web processes following hurricane disturbance. First, consumption of plants by herbivorous arthropods increased dramatically on all islands after both hurricanes. Second, the indirect effect of a top predator (lizards) on plants, presumably caused by lizards eating herbivorous arthropods, also increased markedly (i.e., the disparity between herbivory on lizard and no-lizard islands increased).

Both changes can be explained by reductions in predator abundances (Fig. 2). Web-spider densities declined on all islands after each hurricane, and their overall density was 66% lower after Floyd than before. Parasitoid abundance declined steadily following Floyd, and the overall mean on all islands was 59% lower after than before. On islands with lizards present, lizard densities declined after each hurricane, particularly after Floyd, and the overall mean was 30% lower after Floyd than before. Abundance of other types of predatory arthropods (e.g., wolf and jumping spiders, large wasps, ants) may have been reduced as well. The overall reduction in predator abundances could have also been part of a longer-term trend that began before Floyd. The noticeable drop between 1998 and 1999 may have been caused by Mitch, a storm that passed close to the study site during that time interval, suggesting that this longer-term decline of predators was also related to tropical storm activity. The devastation caused by Floyd (a category four hurricane) was very obvious when we visited the site six weeks after; no web spider was found on one-half of the islands and mean density was 3% the level of the previous census. Furthermore, only hatching lizards were found on all islands six weeks after Floyd (Schoener et al. 2001); this and subsequent observations (Schoener et al. 2004) and experiments (Losos et al. 2003) indicated that all free-living lizards were killed or washed away by the storm surge and only the eggs survived.

We suggest that higher levels of herbivory observed on all islands (the first change in food-web processes) was caused, at least in part, by the overall reduction in predation by both arthropods and lizards. This is generally consistent with the Menge-Sutherland Hypothesis (Menge and Sutherland 1987) that abiotic stress (or disturbance) reduces the top-down effect of predators on their prey. However, magnification of the indirect effect of a top predator (lizards) on plants (the second change) requires a different explanation. We suggest that reduced compensatory predation by arthropods caused the second change as follows. Before the disturbances, relatively high abundances of predatory arthropods compensated for the absence of lizard predation; consequently, herbivory levels were about the same on islands with and without lizards. After the disturbances, relatively low predation by arthropods did not compensate for lizard predation, so herbivory increased more on no-lizard than on lizard islands, magnifying the lizard effect. In addition, the reduction in predatory arthropods might have caused a dietary shift by lizards in which they ate more herbivores in place of predatory arthropods, thereby increasing the per capita predation rate by lizards on herbivores. This change in the per capita effect would contribute to the magnification of the lizard effect, but reduced compensatory predation by arthropods could have magnified the lizard effect even if the per capita effect remained constant.

Previous studies have also found evidence for increased herbivory following hurricanes (Hunter and Forkner 1999, Hirsh and Marler 2002, Spiller and Agrawal 2003, Agrawal and Spiller 2004, Nakamura et al. 2005), suggesting that this pattern may be fairly common (for exceptions see Schowalter and Ganio 1999, Koptur et al. 2002, Angulo-Sandoval et al. 2004). Studies by Spiller and Agrawal (2003) and Agrawal and Spiller (2004) on the same subject species (C. erectus) as the present study, but in a different region of the Bahamas (Exuma), revealed that following Hurricane Lili both herbivore abundance and leaf damage were higher on severely damaged than on undamaged plants and that enhanced herbivory was associated with increased leaf nitrogen and other traits that may increase foliage susceptibility to herbivores. Nakamura et al. (2005) found similar evidence for increased foliage susceptibility to herbivores following hurricane disturbance in Japan. We did not measure leaf traits relating to herbivore susceptibility for the present study, but we note that this mechanism could have also been partially responsible for the overall increase in herbivory presented here. In contrast, Hunter and Forkner (1999) found that concentrations of putative defensive compounds (foliar astringency, tannins) were higher in hurricane-damaged sites with higher herbivory than in undamaged sites, suggesting that increased herbivory was not caused by higher foliage susceptibility.

The results in this study complement findings by Stireman et al. (2005), suggesting that climatic variability disrupts top-down control by parasitoids on host populations. They predict that herbivore outbreaks will increase as climate becomes more variable due to global warming. Both the present study on the effects of Hurricanes Floyd and Michelle in 1999 and 2001 and a previous study conducted ~400 km farther south in the Bahamas (Exuma) on the effect of Hurricane Lili in 1996 (Spiller and Agrawal 2003) showed that herbivory
increased markedly following each hurricane. Such major disturbance is continuing as part of the recent upsurge in Atlantic hurricane activity (Goldenberg et al. 2001): Hurricanes Frances and Jeanne impacted a large portion of the Bahamas in 2004. Were hurricane activity intensified further by global warming (Emmanuel 2005, but see Landsea 2005), increased herbivory, as reported here, may become more widespread in the affected regions.

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