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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 m^2 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.

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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 Chysomelidae (*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. erectus* shrub whose major and minor axes both exceeded 33 cm and ordered them around the circumference of the island (most *C. erectus* 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 a previous field experiment demonstrated that lizards reduced leaf damage on islands at the study site (Schoener and Spiller 1999). To obtain quantitative estimates of the magnitude of the lizard effect on herbivory before and after Floyd we computed the natural logarithm of the ratio of mean leaf damage on lizard islands to the mean leaf damage on no-lizard islands (as in Schoener et al. 2002).

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 m^2) than no-lizard islands (57–184 m^2), 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

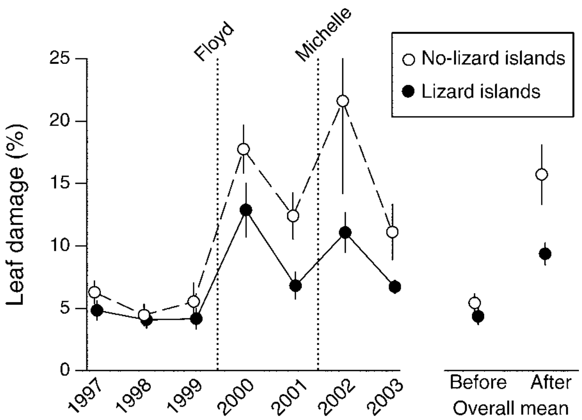

FIG. 1. Mean percentage of leaf area damaged in *Conocarpus erectus* (±SE) on six islands near Snake Cay, Great Abaco, Bahamas, having lizards and on four islands not having lizards before and after disturbance by Hurricanes Floyd and Michelle. "Before" and "after" overall means are the means of the three annual measures before Floyd and the four annual measures after Floyd.

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: $t_5 = 3.94$, $P = 0.011$).

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

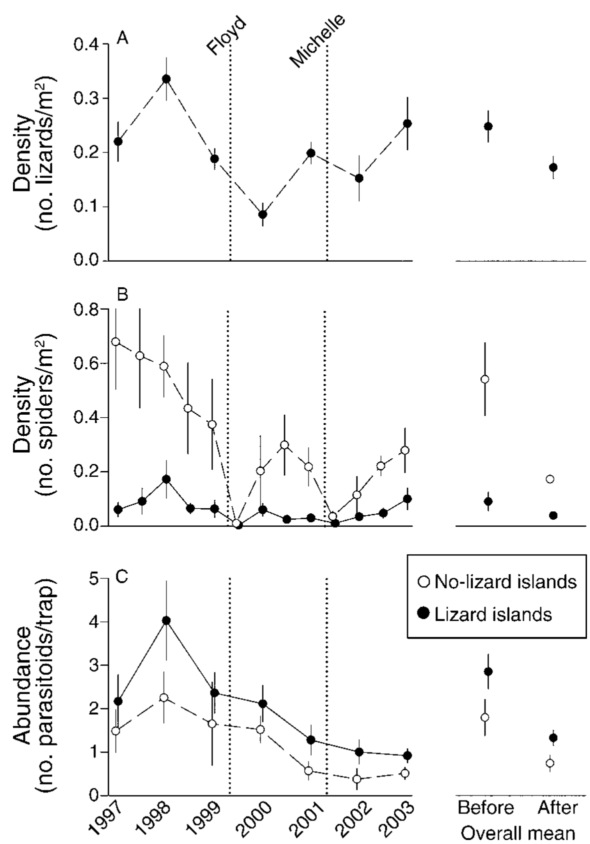

FIG. 2. (A) Mean lizard density (estimated by a multiple-mark–recapture method) on six islands before and after hurricane disturbance. (B) Mean web-spider density and (C) mean number of hymenopteran parasitoids caught in aerial sticky traps on six islands having lizards and on four islands not having lizards before and after hurricane disturbance. Overall means and error bars are as in Fig. 1. The error bars for overall mean web spiders after Floyd are too small to detect on the graph; standard errors for the lizard and no-lizard islands are 0.011 and 0.016, respectively; some of the date-specific error bars also do not show at this resolution.

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 hatchling 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 (Emanuel 2005, but see Landsea 2005), increased herbivory, as reported here, may become more widespread in the affected regions.

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Literature Cited

Agrawal, A. A., and D. A. Spiller. 2004. Polymorphic buttonwood: effects of disturbance on resistance to herbivores in green and silver morphs of a Bahamian shrub. American Journal of Botany 91:1990–1997.

Angulo-Sandoval, P., H. Fernandez-Marin, J. K. Zimmerman, and T. M. Aide. 2004. Changes in patterns of understory leaf phenology and herbivory following hurricane damage. Biotropica 36:60–67.

Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436:686–688.

Fienberg, S. E. 1972. The multiple-recapture census. Biometrika 45:591–603.

Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Nunez, and W. M. Gray. 2001. The recent increase in Atlantic hurricane activity: causes and implications. Science 293:474–479.

Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? American Naturalist 157:262–281.

Heckel, D. G., and J. Roughgarden. 1979. A technique for estimating the size of lizard populations. Ecology 60:966–975.

Hirsh, H., and T. Marler. 2002. Damage and recovery of *Cycas micronesica* after Typhoon Paka. Biotropica 34:598–602.

Hunter, M. D., and R. E. Forkner. 1999. Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. Ecology 80:2676–2682.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724–732.

Koptur, S., M. C. Rodriguez, S. F. Oberbauer, C. Weekley, and A. Herndon. 2002. Herbivore-free time? Damage to new leaves of woody plants after Hurricane Andrew. Biotropica 34:547–554.

Landsea, C. W. 2005. Hurricanes and global warming. Nature 438:E11–E12.

Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and Environment 1:130–137.

Losos, J. B., T. W. Schoener, and D. A. Spiller. 2003. Effect of immersion in seawater on egg survival in the lizard *Anolis sagrei*. Oecologia 137:360–362.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.

Nakamura, M., S. Utsumi, T. Miki, and T. Ohgushi. 2005. Flood initiated bottom-up cascades in a tritrophic system: host plant regrowth increases densities of a leaf beetle and its predators. Journal of Animal Ecology 74:683–691.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483–488.

Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. What makes a trophic cascade a trophic cascade? Trends in Ecology and Evolution 15:473–475.

Power, M. E., M. S. Parker, and J. T. Wootton. 1996. Disturbance and food chain length in rivers. Pages 286–297 *in* G. A. Polis and K. O. Winemiller, editors. Food webs: integration of pattern and dynamics. Chapman and Hall, New York, New York, USA.

Preisser, E. L., and D. R. Strong. 2004. Climate affects predator control of an herbivore outbreak. American Naturalist 163: 754–762.

Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. American Naturalist 155: 141–153.

Schoener, T. W., and D. A. Spiller. 1999. Indirect effects in an experimentally staged invasion by a major predator. American Naturalist 153:347–358.

Schoener, T. W., D. A. Spiller, and J. B. Losos. 2001. Predators increase the risk of catastrophic extinction of prey populations. Nature 412:183–186.

Schoener, T. W., D. A. Spiller, and J. B. Losos. 2002. Predation on a common *Anolis* lizard: Can the food-web effects of a devastating predator be reversed? Ecological Monographs 72:383–407.

Schoener, T. W., D. A. Spiller, and J. B. Losos. 2004. Variable ecological effects of hurricanes: the importance of seasonal timing for survival of lizards on Bahamian islands. Proceedings of the National Academy of Sciences 101:177–181.

Schoener, T. W., D. A. Spiller, and L. W. Morrison. 1995. Variation in the hymenopteran parasitoid fraction on Bahamian islands. Acta Oecologica 16:103–121.

Schowalter, T. W., and L. M. Ganio. 1999. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. Ecological Entomology 24:191–201.

Schwartz, C. J., and G. A. F. Seber. 1999. A review of estimating animal abundance III. Statistical Science 14:427–456.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Boitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Spiller, D. A., and A. A. Agrawal. 2003. Intense disturbance enhances plant susceptibility to herbivory: natural and experimental evidence. Ecology 84:890–897.

Spiller, D. A., and T. W. Schoener. 1994. Effects of top and intermediate predators in a terrestrial food web. Ecology 75: 182–196.

Stireman, J. O., III, et al. 2005. Climatic unpredictability and parasitism of caterpillars: implications of global warming. Proceedings of the National Academy of Sciences 102:17384–17387.

Unisys. 2004. Atlantic tropical storm tracking by year. ⟨http://weather.unisys.com/hurricane/atlantic/index.html⟩

Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. Science 273:1558–1560.