



Food Web Dynamics on Bahamian Islands

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Abstract

We here summarize and integrate findings in our studies of food-web interactions on Bahamian islands conducted over a 40-year timespan. Results obtained in a series of field experiments, taken together, provide compelling evidence that predatory lizards reduce herbivory and thereby have a positive indirect effect on plants, even though lizards also reduce web spiders which eat herbivores. Two exogenous factors, hurricanes and allochthonous resource pulses, play a significant role in structuring island communities and produce major temporal fluctuations in food-web dynamics. Following hurricanes, herbivory increased substantially on severely damaged plants due at least in part to enhanced susceptibility of resprouting foliage to herbivores. The top-down effect of lizards on herbivory was stronger after the hurricanes than before. Allochthonous resource pulses in the form of seaweed deposition events cause a sequential series of bottom-up and top-down effects that propagate throughout the food web. In the short-term, lizards shift from eating local prey (including terrestrial herbivores) to eating mostly marine detritivores, leading to increased herbivory and weakening the trophic cascade from lizards to plants. In the long-term, decomposing seaweed adds nutrients to plants, increasing their growth rate, and a numerical response by lizards to marine detritivores strengthens the trophic cascade.

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10.1 Introduction

Understanding how various factors influence species interactions in food webs is a central goal in ecology (Schoener 1989; Borer et al. 2005; Abdala-Roberts et al. 2019). One of the most influential concepts is the “trophic cascade” (Terborgh and Estes 2010), which can be broadly defined as the propagation of impacts by consumers on their prey downward through food webs (Estes et al. 2011). Indeed, many empirical studies have shown that the eradication of a single apex predator species caused dramatic changes in community structure and ecosystem functioning (Estes et al. 2011). The canonical theory for such trophic cascades assumes that consumers eat species in only the next level down, causing strong unimpeded top-down forcing (Oksanen et al. 1981). However, many food webs are reticulate, with consumers feeding on species in multiple trophic levels, and contain other complexities that can weaken trophic cascades (Polis and Strong 1996; Finke and Denno 2004; Cuny et al. 2021). Another theoretical assumption is that the system is at equilibrium or at least at a temporary steady state. Conversely, many studies have found that environmental perturbations can lead to substantial variation in the strength of trophic cascades, with important consequences for the food webs in which they are embedded (Piovita-Scott et al. 2017a).

Islands can serve as excellent model systems for studying food-web processes for three reasons. First, because they often vary in community composition, comparisons between islands with focal species present or absent can be used as replicated “natural experiments” (Diamond 1983) to test hypotheses on the functional role of those species in the food web. Second, island communities have fewer species and less spatial heterogeneity than mainlands, increasing the feasibility of identifying the key drivers of food-web dynamics (Wardle 2002). Third, islands are well-defined isolated areas and thus can be used as independent replicates in manipulative experiments designed to test food-web theory (e.g., Hambäch et al. 2004).

We have been studying food-web interactions on Bahamian islands for over 40 years. Our early studies focused on the top-down effects of predatory lizards on species in lower levels during a time period (throughout the 1980s and early 1990s) when no hurricane had a major impact on any of our study sites. Subsequently (1996 to present) hurricane frequency has increased substantially (Goldenberg et al. 2001; Kossina et al. 2020), and several hurricanes have passed directly over or close to our study islands, having devastating impacts on their communities. In the first section of this chapter, we will summarize our early studies on the basic structure and dynamics of our study system, focusing on how food-web complexity influences the cascading effects of lizards. The following sections will delineate the effects of hurricanes and allochthonous resource pulses on food-web dynamics, centering on how bottom-up processes associated with these environmental perturbations influence the trophic cascade at different time scales.

10.2 Food-Web Structure and Dynamics

To investigate the effect of predatory lizards on species in lower trophic levels, we used two complementary methods: (1) comparative studies on small islands with lizards present and absent and (2) experimental studies in which lizard densities were manipulated within enclosures on a large island and lizard introductions onto small islands initially without them. The most abundant lizard on our study islands is *Anolis sagrei*, a small species which eats a wide variety of arthropods, including carnivores, herbivores, and detritivores (Schoener 1968; Pringle et al. 2019). Observational and manipulative studies therefore centered on this species unless stated otherwise.

10.2.1 Comparative Studies

We began by counting annually the number of web spiders on approximately 100 islands with lizards either present or absent in the Exuma Cays, an archipelago in the central Bahamas consisting of approximately 50 relatively large islands surrounded by hundreds of smaller islands where we counted the spiders (Fig. 10.1). Analysis of the first two annual censuses showed that web-spider density was about ten times higher on no-lizard than on lizard islands (Schoener and Toft 1983; Toft and Schoener 1983), suggesting that lizards have a strong negative effect on spiders. Subsequent experimental work corroborated this causal link (Spiller and Schoener 1988, 1994), and long-term studies revealed that the interaction strength of lizards on spiders was related to island area (Schoener et al. 2016) and annual variation in the interaction strength was related to rainfall (Spiller and Schoener 1995, 2008).

These results prompted us to ask, does the top-down effect of lizards propagate further down the food-web? Because lizards feed on both carnivorous spiders and herbivorous arthropods and spiders eat herbivorous arthropods, lizards are “intraguild predators” (Polis et al. 1989). We proposed two different models in which the top-down effect of lizards on plants could be either positive or negative, depending on the relative interaction strength of lizards vs. spiders on herbivores (Fig. 10.2). In Model A the effect of lizards on herbivores is stronger than the effect of spiders on herbivores; the dominant pathway has two links connecting three trophic levels, and thereby the indirect effect of lizards on plants is positive. In Model B the effect of spiders on herbivores is stronger than the effect of lizards on herbivores; the dominant pathway has three links connecting four trophic levels, and thereby the indirect effect of lizards on plants is negative.

To investigate the indirect effect of lizards on plants (via herbivory), in 1984, we measured the amount of leaf damage on *Conocarpus erectus* (buttonwood), one of the most common species on our study islands. Buttonwood occurs as two different color morphs with “silver” or “green” leaves, containing high and low density of trichomes, respectively. Silver and green morphs are often intermingled on the same island. We collected large samples of leaves on 74 islands with lizards either present



Fig. 10.1 *Top*: Aerial photograph of the Exuma Cays, an archipelago in the central Bahamas consisting of approximately 50 relatively large islands surrounded by hundreds of smaller islands. *Bottom*: A closer view of a segment of the Exuma Cays. Lizards were present on all large islands and were present or absent on small islands. Photographs taken by David Spiller

or absent and measured percent of leaf area damaged in the lab (Schoener 1988). Results showed that leaves were 1.5 times more damaged on no-lizard islands than on lizard islands, supporting Model A (Fig. 10.2), and green leaves were 1.4 times more damaged than silver leaves, indicating that the top-down effect of lizards and plant defense are equally important factors controlling herbivory. Web-spider

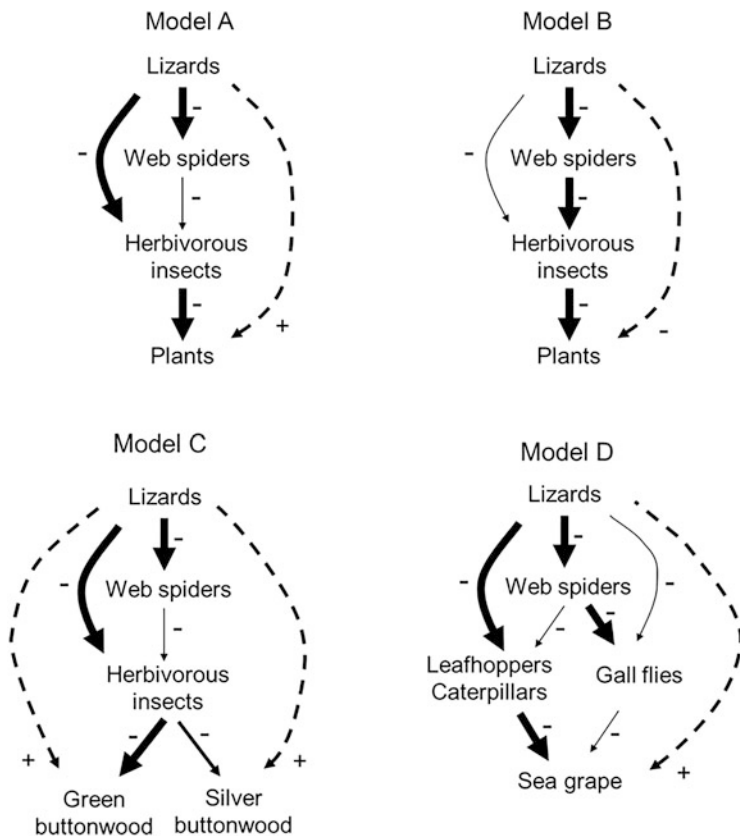


Fig. 10.2 Food-web interaction modules with intraguild predation in which lizards eat web spiders, and both lizards and web spiders eat herbivorous insects. Solid lines represent direct effects proportional to their thicknesses. Dashed lines represent the indirect effect of lizards on plants. In Model A the effect of lizards on herbivores is stronger than the effect of web spiders on herbivores, and thereby the indirect effect of lizards on plants is positive. In Model B the effect of lizards on herbivores is weaker than the effect of web spiders on herbivores, and thereby the indirect effect of lizards on plants is negative. Model C represents our interpretation of the comparative study on small islands of buttonwood leaf damage for green and silver color morphs containing leaves with low and high densities of trichomes, respectively. Model D is our interpretation the enclosure-experiment results in which the effect of lizards on leafhoppers and caterpillars is strong, whereas the effect of web spiders on gall flies is strong (see text for more explanation)

density was not correlated with leaf damage (Schoener 1988), indicating that the effect of lizards on herbivory is stronger than that for spiders, as in Model A. Model C (Fig. 10.2) is our interpretation of this study showing that the negative direct effect of herbivores is stronger for green than for silver morphs. Analysis of variance showed that the effect of lizards on leaf damage did not differ significantly between color morphs, indicating the positive indirect effect of lizards was the same magnitude for the two morphs. In addition to the study of leaf damage, Schoener (1987)

found that the frequency of the silver morph was higher on no-lizard islands than on lizard islands, suggesting that chronically greater herbivory on no-lizard islands selected for silver morphs, or induced the production of trichomes. Later lab experiments (Agrawal and Spiller 2004) showed that silver leaves were less damaged than green leaves by two different herbivorous arthropods common on our study islands, an adult flea beetle (*Chaetocnema brunnescens*) and a bagworm lepidopteran (*Biopsyche* sp.).

10.2.2 Field Experiments

We conducted a series of controlled field experiments designed to test the top-down effect of lizards on spiders and plants and to elucidate the mechanisms. In the first experiment, we manipulated lizard density within six enclosures on a large island (Staniel Cay); three enclosures were selected randomly to have lizards removed and the other three had lizards present at their natural density serving as controls. The study site was located on a sandy bluff covered with dense scrubby vegetation 0.5–1.5 meters high, predominately *Coccoloba uvifera* (sea grape). During the experiment (May 1985 to November 1988), we counted numbers of web spiders at about 3-month intervals and measured amounts of damage that accumulated on large samples of sea grape leaves tagged each year.

Results showed the mean number of web spiders was three times higher in lizard-removal enclosures than in controls with lizards (Spiller and Schoener 1988). Dietary analysis of lizards and web spiders in the enclosures showed a moderate overlap in the size distribution and taxonomic composition of arthropods, but there were significant differences. Lizard diets contained larger arthropods and more Homoptera and Lepidoptera (which are predominantly herbivorous) than web-spider diets (Spiller and Schoener 1990a). Araneae (spiders) were frequently eaten by lizards, but not by web spiders. Lizards reduced food consumption by *Metepeira datona* (the most abundant web-spider species), and the reduction was stronger for large prey (>4 mm body length) than for small prey (≤ 4 mm). Lizards also reduced the biomass of large arthropods caught in aerial sticky traps, but not the biomass of small arthropods. These results revealed that lizards are both predators and competitors of web spiders and thereby intraguild predators, having both direct and indirect negative effects on web spiders. We suggest that the direct effect of predation by lizards is stronger than competition because they greatly reduced short-term survivorship of web spiders (Spiller and Schoener 1988, 1990a).

We analyzed three different categories of leaf damage: scars (necrotic areas), holes (entirely missing areas), and galls (Spiller and Schoener 1990b). In the field we observed scars produced by homopterans (leafhoppers) and holes produced mostly by caterpillars; galls were produced by the cecidiomyiid midge *Ctenodactylomyia watsoni*. Scar damage was 2.2 times higher in lizard-removal enclosures than in controls. Hole damage was 1.7 times higher in lizard-removal enclosures than in controls. In contrast, gall damage was 1.7 times higher in controls with lizards than in lizard-removal enclosures. Total leaf damage was 2.0 times higher in

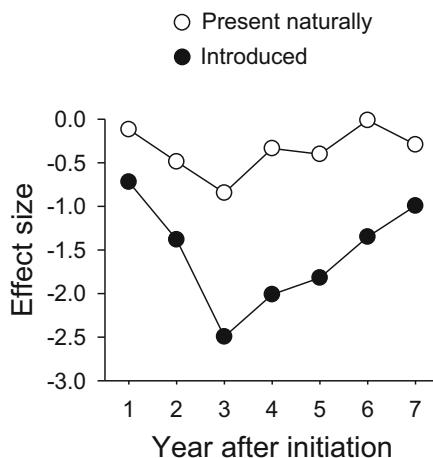
lizard-removal enclosures than in controls. We suggest that the effect of lizards on leafhoppers and caterpillars was strong relative to the effect of spiders because these relatively sedentary herbivores are easily caught by lizards, but not in spider webs, whereas the effect of web spiders on gall flies (searching for oviposition sites) was stronger because they are frequently caught in spider webs but not by lizards. We propose that because web-spider density was higher in lizard-removal enclosures than in controls, reduced gall damage in removals was caused by higher predation by web spiders. Our experimental results can be delineated by a composite of Models A and B (Model D, Fig. 10.2). Because scars and holes accounted for most of the total leaf damage, lizards reduced total herbivory, thereby having a positive effect on sea grape.

To tease apart the effects of lizards and web spiders, we conducted a 2×2 factorial enclosure experiment with four treatments ($n = 3$ for each): (1) Controls with lizards and spiders unaltered (natural densities), (2) lizards removed and spiders unaltered, (3) spiders removed and lizards unaltered, (4) both lizards and spiders removed (Spiller and Schoener 1994). This experiment was conducted on Staniel Cay, the large island where the previous experiment was performed. The experiment ran from 1989 to 1992 and data collection followed the same procedures as described for the previous experiment. Results showed that spider density was 1.5 times higher in lizard-removal enclosures than in controls. Web spiders reduced the biomass of small arthropods (mostly flies) caught in aerial sticky traps. Hence, by reducing web-spider density, lizards had an indirect positive effect on small flies. Total leaf damage was 3.3 times higher in treatments with lizards removed than in those with lizards unaltered. We found no significant effect of web spiders on any type of leaf damage. An objective of the experiment was to test the direct negative effect of web spiders on gall flies, as depicted in Model D (Fig. 10.2). However, galls were extremely rare during this experiment, making it unfeasible to detect the effect of web spiders.

We used a system of small islands located in the Abacos (northern Bahamas) to conduct a seven-year experiment to test the direct and indirect effects of introducing the lizard *A. sagrei* on the food web (Schoener and Spiller 1996, 1999). Eight islands without lizards were blocked into four pairs, according to vegetated area (amount of land covered by vegetation), and lizards were introduced onto one island (selected randomly) from each pair. The experiment included four other islands containing lizards naturally (one in each block) that were used to ascertain if and when the food-web elements on the introduction islands converged to those with lizards present naturally. Lizard introduction caused a rapid and devastating effect on web-spider density; within 2 years web-spider density on introduction islands converged to about the same level as on islands with lizards present naturally and remained there until the end of the experiment (Schoener and Spiller 1996). During the last 6 years of the experiment, mean web-spider density was 80% lower on islands with lizards introduced than on no-lizard islands and was 86% lower on islands with lizards present naturally than on no-lizard islands.

We measured herbivory on buttonwood which occurred on all the study islands (Schoener and Spiller 1999). The trajectory of total leaf damage on introduction

Fig. 10.3 Effect sizes of lizards on leaf damage computed as $\ln(\text{mean damage on islands with lizards present [naturally or introduced]}/\text{mean damage on islands without lizards})$



islands was intriguing. Three years after initiation of the experiment, leaf damage plummeted on introduction islands and was 92% lower than on no-lizard islands; surprisingly, at this time leaf damage was 57% lower on introduction islands than on islands with lizards present naturally. Towards the end of the experiment, leaf damage in the two treatments with lizards (present naturally and introduced) started to converge. Figure 10.3 shows the stronger effect size of lizards on introduction islands than on islands with lizards present naturally, which maximized 3 years after initiation of the experiment. We posit that initially islands without lizards contained herbivorous insects that lacked antipredator traits and thereby were more vulnerable to lizards than those on islands with lizards present naturally where the vulnerable herbivores had been depleted by lizards. We suggest that when lizards were first introduced onto no-lizard islands they feasted on the vulnerable herbivores, causing amounts of leaf damage to drop below the level on islands with lizards present naturally (which contained fewer vulnerable herbivores). Then after several years most of the vulnerable herbivores were depleted on the introduction islands, which were replaced by less-vulnerable herbivores, and leaf damage converged to the level on islands with lizards present naturally.

The number of large arthropods (>4 mm body length) caught in aerial sticky traps did not differ significantly between treatments, but the number of small arthropods (≤ 4 mm) was significantly higher on islands with lizards than those without lizards. A separate analysis of hymenopteran parasitoids, which were predominantly small (usually 1–2 mm), showed they were significantly more abundant on islands with lizards than those without lizards (Schoener et al. 1995). In a later experiment at the same site (Schoener et al. 2002), we found a negative correlation between parasitoid abundance and web-spider density, suggesting that higher web-spider density on no-lizard islands reduced parasitoid abundance. Hence, because parasitoids often prey on herbivorous insects, web spiders may have both a direct negative effect on herbivorous insects and an indirect positive effect via their negative effect on

parasitoids. This may be one reason why the effect of web spiders on total herbivory is weak.

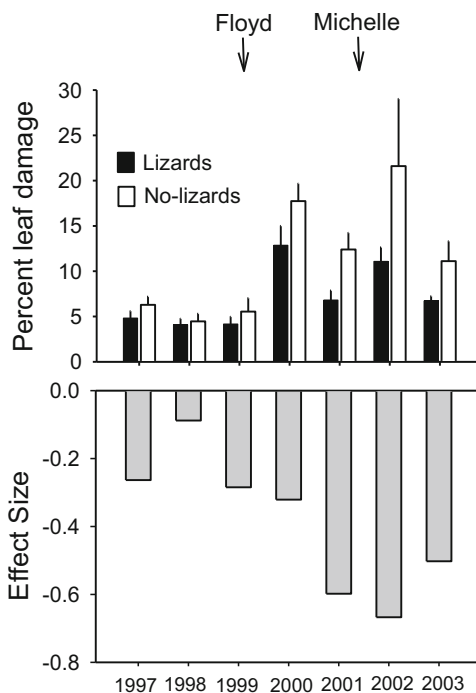
10.3 Hurricanes

In October 1996, we had just finished our annual survey of the biota inhabiting small islands located offshore the north and south sides of the very large island Great Exuma, when the eye of Hurricane Lili pasted directly over the study site (Spiller et al. 1998). Because Lili's approach was from the southwest, islands on the south side of Great Exuma were exposed to the full force of the storm surge, the most destructive component of the hurricane, whereas islands located on the north side were much more protected. The surge removed most of the standing biomass of vegetation on the exposed islands, whereas damage to the vegetation on the protected islands was minimal. In the week following the storm, we found that all lizard and spider populations were exterminated on exposed islands; in contrast, no lizard population and only small populations of spiders were exterminated on protected islands.

As part of an ongoing food-web study, we had measured amounts of leaf damage on buttonwood for three consecutive years before the hurricane (Spiller and Agrawal 2003). During the hurricane, all study shrubs on exposed islands were reduced to stumps by the surge and regenerated by sprouting during the following year. Damage on the sprouted foliage was high and we frequently found moth larvae (*Collomena filifera* and other unidentified species) consuming the leaves. Some shrubs were completely defoliated, and a few which were defoliated repeatedly apparently died due to herbivory following the hurricane rather than by the direct impact from the hurricane. We observed that on exposed islands buttonwood with silver leaves before the hurricane sprouted green leaves the year after and then reverted to producing silver leaves the following year. In addition, the sprouted foliage appeared to be very lush, possibly because the leaves were larger, more tender or contained more nitrogen. Measurements of leaf damage before and after the hurricane showed that herbivory increased on devastated islands exposed to the storm surge but not on relatively undamaged shrubs on protected islands, suggesting that foliage sprouting on severely damaged shrubs was more susceptible to herbivores than new foliage on undamaged shrubs. Abundance of moths caught in sticky traps on exposed islands was very low a few months following the hurricane and then increased markedly after 12 months. We hypothesized that increased herbivory on exposed islands was caused by two factors: low predator abundance and increased susceptibility to herbivory of leaves on damaged shrubs.

To test the second factor, we conducted a controlled field experiment: Hurricane damage was simulated by pruning shrubs on replicated islands (Spiller and Agrawal 2003). The experiment showed that herbivory was significantly higher on pruned shrubs than on unaltered control shrubs. Leaf size was larger, percent nitrogen was higher, and leaf toughness and trichome density were lower on pruned shrubs than on controls. The experimental results indicate that enhanced herbivory on exposed

Fig. 10.4 *Top:* Mean percent of total leaf area damaged on islands with and without lizards before and after hurricanes Floyd and Michelle struck the study site. Error bars are standard errors. *Bottom:* Effect sizes of lizards on leaf damage computed as in (mean damage on islands with lizards/mean damage on islands without lizards)



islands following Hurricane Lili was caused, at least in part, by increased susceptibility of the sprouted foliage to herbivorous arthropods, but the reduction of predators may have also been important.

We also conducted long-term food-web studies on small islands in a semi-protected bay offshore Great Abaco which took a direct hit by Hurricane Floyd in September 1999. Lizards were exterminated on some but not all of the study islands. Leaf damage on buttonwood was measured before and after the hurricane on islands which either had lizards present or absent continuously both before and after the hurricane (Spiller and Schoener 2007). The year after Floyd, leaf damage increased on both lizard and no-lizard islands. In 2001 the site was hit by Hurricane Michelle and leaf damage increased again the following year (Fig. 10.4, top). The negative effect size of lizards on herbivory was 2.5 times stronger during the disturbance period (2000–2003) than before (Fig. 10.4, bottom). Overall abundance of lizards was 30% lower during the disturbance period than before, and abundances of web spiders and hymenopteran parasitoids were respectively 66% and 59% lower. 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; increased herbivory could have also been caused by increased susceptibility of the foliage to herbivory (as found in Spiller and Agrawal 2003), but that factor was not tested in the study. We hypothesize that magnification of the lizard effect on herbivory following disturbance was caused by reduced compensatory predation by arthropods

on islands without lizards. A second hypothesis is that herbivores colonizing islands following the disturbances were more vulnerable to lizard predation than those present before the disturbances. The generality of the second hypothesis will be discussed below (Sect. 10.5.2).

In a third study, we focused on the effect of the moth *Achyra rantalis* feeding on the plant *Sesuvium portulacastrum* on small islands with and without lizards in the Exuma Cays (Spiller et al. 2016). The plant is a fast-growing prostrate vine inhabiting shorelines, and consequently moths are highly vulnerable to being consumed by lizards which frequently forage close to the ground. Measurements of moth abundance were on average > 4 times higher on no-lizard than on lizard islands. The site was impacted by Hurricanes Floyd and Michelle; the centers of the storms passed nearby causing moderate disturbance. Lizards were not exterminated on any study islands, but large proportions of the study plants growing on shorelines were washed away. Immediately following each hurricane percent cover over the ground by *S. portulacastrum* was reduced to about the same low level on all islands. However, regrowth rate following Floyd and Michelle was significantly higher on lizard islands than on no-lizard islands, presumably caused by lizards controlling moths after the hurricanes. Moths were much more abundant on no-lizard islands and were observed infesting plants following the hurricanes, apparently impeding regrowth of vines on the damaged plants. In fact, on some no-lizard islands where moths were exceptionally abundant, percent cover decreased further the second year after the disturbances, which was evidently caused by intense herbivory on the remaining vines. Hence, lizards increased the recovery rate (“ecological resilience” sensu Pimm 1991, Gunderson 2000) of the plants.

10.4 Marine Subsidies

The influence of resource subsidies (the flow of nutrients and organisms across habitat or ecosystem boundaries) on recipient food webs has received a burgeoning amount of attention (Polis et al. 1997, 2004; Marczak et al. 2007; Leroux and Loreau 2008; Subalusky and Post 2019; Scherer-Lorenzen et al. 2022). Resource subsidies may vary temporally, arriving in pulses (Yang et al. 2008, 2010), which can produce a variety of effects on recipient food webs (Anderson et al. 2008; Holt 2008; Takimoto et al. 2009; Leroux and Loreau 2012).

In the Bahamas, large amounts of seaweed are deposited on shorelines in the fall following tropical storms and early cold fronts. We hypothesized that this seaweed deposition represents a pulsed resource subsidy (sensu Sears et al. 2004, Yang et al. 2008) that is consumed by detritivores, which are eaten by predatory lizards; those predators also consume terrestrial herbivores. Additionally, seaweed washed high onshore during storms may decompose directly into the soil and fertilize plants. We hypothesized that the marine-based resource pulse would enhance terrestrial herbivory in the short-term when the lizards switch from eating herbivores to marine detritivores, weakening the trophic cascade from lizards to plants. In the long-term, we hypothesized that lizards would respond numerically to marine subsidies

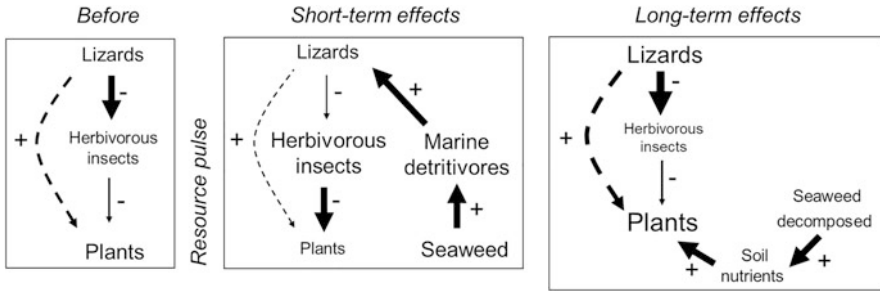


Fig. 10.5 Food-web modules showing the hypothesized short-term and long-term effects of a resource pulse (seaweed deposition). Solid lines represent direct effects proportional to their thicknesses. Dashed lines represent the indirect effect of lizards on plants (a trophic cascade). For each food-web element, the change in font size is proportional to its change in abundance over time. *Before the pulse:* A moderate top-down effect by lizards on herbivorous insects leads to a moderate trophic cascade. *Short-term effects:* Lizards switch to eating mostly marine detritivores, leading to increased herbivores, and thereby weakening the trophic cascade. *Long-term effects:* Lizards proliferate due to a delayed reproductive response, caused by consumption of copious detritivores in the past. The seaweed becomes decomposed and marine detritivores die off, and subsequently the lizards switch back to eating mostly herbivores, strengthening the trophic cascade. Also, the decomposed seaweed adds nutrients to the soil, fertilizing the plants

and then switch back to eating mostly herbivores as the marine detritivores decline, strengthening the trophic cascade. These hypotheses are depicted in Fig. 10.5.

We tested our hypotheses on large islands in the Exumas where we added seaweed to six shoreline plots and removed seaweed from six other plots for 3 months during fall 2006; all plots were repeatedly monitored for 12 months after the initial manipulation (Spiller et al. 2010). Three months after the initial manipulation, biomass of amphipods (the major marine detritivores) was 79 times higher in plots with seaweed added than in plots with seaweed removed, and lizards were observed eating the amphipods. Stable isotope analysis revealed a shift in lizard diet composition toward more marine-based prey in subsidized plots. Wright et al. (2013) showed that lizard individual growth rate was higher in subsidized plots. Buttonwood leaf damage was 70% higher in subsidized than in removal plots after 8 months, but subsequent damage was about the same in the two treatments. After 12 months, buttonwood leaf nitrogen content was 18% higher and foliage growth rate was 70% higher in subsidized plots. We suggest two sequential causal pathways for the effects of marine subsidies on terrestrial plants: (1) *The predator-diet-shift effect:* Lizards shift from eating local prey (including terrestrial herbivores) to eating mostly marine detritivores, leading to increased herbivory and thereby weakening the trophic cascade from lizards to plants and (2) *The fertilization effect:* Seaweed adds nutrients to plants, increasing their growth rate (Spiller et al. 2010). Because herbivory did not become lower in subsidized plots than in unsubsidized plots during the course of the experiment, there was no evidence that marine subsidies strengthened the trophic cascade in the long-term (as depicted in Fig. 10.5), possibly because the experiment needed to run for a longer period of time. Predatory arthropods also

increased in the subsidized plots, including the large ant *Camponotus tortuganus*. Buttonwood petioles contain extrafloral nectaries that attract ants which in turn eat herbivorous arthropods (Piovia-Scott 2011). Hence, reduced leaf damage in subsidized plots may have been caused by both lizards and ants switching to eating mostly marine detritivores.

To test the interactive effects of marine subsidies on predation by lizards and ants, we conducted an experiment (Piovia-Scott et al. 2011) on 12 small islands in the Exumas. Lizards were present on six islands and absent from six islands, and seaweed treatments (added or removed) were assigned to half the islands with and without lizards. On each island, 11–12 buttonwood branches were randomly assigned to have ants excluded with Tanglefoot® adhesive or unaltered. After 7 months, the experiment showed that on islands without marine subsidies, the effect of only lizards or only ants on leaf damage was weak, but with both together leaf damage was markedly reduced. The effect size of both predators together was three times the additive effects of each one alone, making the interactive effect of lizards and ants synergistic (Sih et al. 1998). We suggest that the synergistic effect was linked to temporal partitioning of activity time by the two predators; lizards (*A. sagrei*) are diurnal whereas the dominant ants (*C. tortuganus*) are nocturnal. Hence, herbivores could avoid *A. sagrei* by feeding at night and avoid *C. tortuganus* by feeding during the day, but they could not allocate activity times to avoid both types of predators. Lizards did not affect the abundance of ants, implying that temporal partitioning may reduce the frequency of antagonistic interactions between the different predators. On islands with marine subsidies, lizards and ants alone tended to reduce leaf damage, but the synergistic effect on herbivory was eliminated, presumably because both lizards and ants switched from eating herbivores to eating marine detritivores, as found in the previous experiment. In this experiment there was no evidence that marine subsidies strengthened the trophic cascade in the long-term (as depicted in Fig. 10.5), but again this experiment may have not run long enough to reveal this process.

To test the short and long-term effects of marine subsidies, we conducted a 5-year experimental study on 32 small islands in Abaco (Piovia-Scott et al. 2019; Wright et al. 2020). In this experiment, we manipulated the frequency and magnitude of pulses of seaweed deposition on islands with or without experimentally introduced populations of lizards. There were four seaweed input treatments: (1) a single large addition in the first year, (2) three small annual additions (adding up to the same total as the single large addition), (3) three large annual additions, and (4) controls with no seaweed input. In the short-term (the first year of the experiment), inputs of marine subsidies weakened the effect of lizards on buttonwood leaf damage and growth, presumably associated with a lizard diet shift from herbivores to marine detritivores. This short-term weakening of cascading effects on plants was more pronounced in treatments with higher subsidy magnitude (1 and 3). However, in the long-term (after the first year), inputs of marine subsidies strengthened the lizard effect on leaf damage and growth. This long-term effect was more pronounced in the high frequency input treatments 2 and 3. We posit the long-term effect operates via two pathways: (1) a numerical response by lizards (Wright et al. 2020) and (2) plant

fertilization, whereby increased quality of foliage for herbivores leads to increased herbivory on no-lizard islands, but not on islands with lizards. This occurs because herbivores are free to respond numerically to fertilization on no-lizard islands, but not on islands with lizards which keep herbivores at a low level. Note that this explanation is consistent with the exploitation ecosystems hypothesis (Oksanen et al. 1981).

In addition to these experiments, we conducted a comparative study of natural variation in seaweed deposition and terrestrial food-web components using 29 shoreline plots located on large islands in the Exumas. Results of this study showed lizard density, leaf damage and nitrogen content, and foliage growth were significantly higher in plots with high amounts of subsidies than in those with low amounts of subsidies (Spiller et al. 2010). The natural variation in seaweed deposition appeared to be habitual, linked to topographical features of the shoreline plots. Hence, in this case the seaweed deposition “treatment” occurred more like a continuous long-term press than a pulse. A path analysis on leaf damage provided evidence that marine subsidies enhanced the top-down effect of lizards on plants (seaweed increases lizard abundance which increases their effect on herbivory); however, the bottom-up fertilization effect was stronger than the top-down lizard effect (Piovia-Scott et al. 2013).

10.5 Discussion

10.5.1 Food-Web Structure of the Study System

The results of our studies, taken together, provide compelling evidence that predatory lizards reduce herbivory and thereby have a positive effect on plants, even though lizards also reduce web spiders which eat herbivores. We conclude that the effect of lizards on herbivores is stronger than the effect of web spiders on herbivores because the major herbivores are more vulnerable to lizards than to web spiders. Dial and Roughgarden (1995) studied the effects of *Anolis* lizards on a large, complex food web of arthropods and associated herbivory in a Puerto Rican rain forest. They removed several arboreal *Anolis* species (mostly *A. evermanni* and *A. stratulus*) from the canopy of seven tabonuco trees (22–29 meters in height!); seven similar tabonuco trees with *Anolis* present at their natural densities were the controls. The experiment showed that lizards reduced the abundance of both predacious and herbivorous arthropods and reduced the frequency of leaf damage. Several lines of evidence indicate that higher herbivory in lizard-removal trees was caused by greater abundances of large herbivorous arthropods which were eaten more frequently by lizards than by predatory arthropods which typically ate smaller prey. The results obtained in Dial and Roughgarden’s field experiment are remarkably similar to our findings, even though their study was conducted on a much larger island with a more complex food web.

Mooney et al. (2010) performed a meta-analysis on 113 experiments (predominantly on mainlands) documenting the effects of insectivorous vertebrates on

predacious arthropods, herbivorous arthropods, and plants. They predicted that because insectivorous vertebrates are intraguild predators, feeding on both predacious and herbivorous arthropods and predacious arthropods feed on herbivores, the effect of the vertebrate predators on predacious arthropods should be stronger than their effect on herbivores. However, they found that the effect of vertebrate predators was on average about the same for predacious and herbivores arthropods, and they indirectly reduced plant damage and increased plant biomass. This and other analyses indicated that intraguild predation does not weaken the trophic cascade, as expected according to some theory (Mooney et al. 2010). We contend that effects of insectivorous vertebrates on predacious arthropods, herbivorous arthropods, and plants are generally consistent with Model A (Fig. 10.2).

Body size appears to play an important role in structuring food webs (Schoener 1989; Petchey et al. 2008; DeLong et al. 2015). We posit that top-down effects of vertebrate predators are usually stronger than arthropod predators because vertebrate predators are larger, and thereby can eat a broader range of herbivorous arthropods, including those that are too big for most predacious arthropods. In addition, because they are generally smaller than vertebrates, arthropod predators are eaten by a wider range of predators and are more susceptible to physical disturbances caused by the weather which frequently reduce their abundance, weakening their top-down effect (Schoener and Spiller 2003). Social ants may be the exception that proves the rule (Mooney 2007; Piovia-Scott 2011). Cooperative foraging may enable ants to capture prey larger than those captured by solitary predatory arthropods and group defense may protect them from predators.

We did find evidence that intraguild predation by lizards on web spiders caused an indirect positive effect on gall-making flies and other small insects caught in sticky traps which may have slightly weakened the trophic cascade. In addition, Piovia-Scott et al. (2017b) found that lizards reduced the abundance of other predatory arthropods. However, intraguild predation may not always dampen the trophic cascade. We found evidence that web spiders reduced the abundance of hymenopteran parasitoids which often prey on herbivores; therefore, lizards may indirectly increase parasitoids by eating web spiders. This four-level interaction chain (lizards-spiders-parasitoids-herbivores) within the food web may strengthen the trophic cascade from lizards to plants.

Furthermore, interactions between different types of predators may not always be antagonistic, dampening the trophic cascade. We found that the effects of diurnal lizards and nocturnal predatory ants on plants were synergistic (Piovia-Scott et al. 2011), possibly because herbivorous arthropods had no “escape in time” from predation. Synergistic effects of multiple predators on prey may also be caused by different predators foraging in different places within the prey’s habitat (Sih et al. 1998). We suggest that on our study islands overall levels of herbivory are controlled by a suite of predator species preying upon multiple herbivore species.

10.5.2 Temporal Variability in Food-Web Dynamics

Numerous abiotic and biotic factors can change food-web dynamics at different time scales (Piovia-Scott et al. 2017a). We found that food webs on Bahamian islands were profoundly impacted by two exogenous factors, hurricanes and allochthonous resource pulses. Both of these factors can play a major role in structuring island communities (Whittaker 1995, 2000; Polis et al. 1997, 2004; Fukami et al. 2006) and as discussed below can produce major temporal fluctuations in food-web dynamics.

Following hurricanes, herbivory increased substantially in all of our studies (Spiller and Agrawal 2003; Spiller and Schoener 2007; Spiller et al. 2016). We propose that these high levels of herbivory following hurricanes were caused by two factors. The first is increased susceptibility to herbivorous arthropods of resprouted foliage on severely damaged plants, which is linked to increased nitrogen and reduction of defensive traits (Spiller and Agrawal 2003). Other studies have found that plants heavily damaged by physical disturbances were more susceptible to herbivory, including resprouting plants on the bank of a river following a major flood (Nakamura et al. 2005, 2006) and resprouting plants following fire (Stein et al. 1992; Knapp et al. 1999). The second factor causing higher herbivory following hurricanes is a reduction in predators. Following catastrophic disturbance by Hurricane Lili on exposed islands, all predators were exterminated (Spiller et al. 1998), giving the colonizing herbivores a “predator-free window in time.”

In addition to increased herbivory, we found that following moderate disturbances by hurricanes, when lizards were not exterminated, the top-down effect of lizards on leaf damage was stronger after hurricanes than before (Fig. 10.4). We suggest that herbivores colonizing islands following the disturbances were more vulnerable to lizard predation than those present before the disturbances. There may be a trade-off between dispersal ability and vulnerability to predators among herbivore species. For example, studies of river food webs following scouring floods (Wootton et al. 1996; Power et al. 2008) showed that early herbivorous colonizers, such as tuft-weaving midges and mayflies, are more vulnerable to predators than later arriving herbivores, such as armored caddisflies; subsequently, when predators arrive they deplete the vulnerable herbivore species and the river becomes dominated by the protected herbivore species. In addition to a change in species composition, when predators colonize an area they may cause phenotypic changes in herbivore traits within species that decrease their vulnerability (e.g., they spend more time avoiding predators and less time feeding), known as a trait-mediated indirect effect (Schmitz et al. 2004; Schoener and Spiller 2012). Furthermore, natural selection may favor herbivore individuals that are less vulnerable to predators but also less efficient at consuming plants, leading to a rapid eco-evolutionary response (Schoener 2011). These processes may also be applicable to the results of our lizard introduction experiment on small islands in which the effect size of introduced lizards on leaf damage was initially much stronger than the effect size of lizards naturally present (Fig. 10.3). We suggest that before introduction these islands contained naïve herbivores vulnerable to lizard predation, which were devoured by lizards within a few years, and subsequently the effect size decreased.

Spiller et al. (2018) proposed a mechanistic conceptual framework for how food webs recover from natural physical disturbances, based on our island studies and empirical studies on other types of physical disturbances (including fires, floods, and volcanic eruptions). We found evidence for a general pattern of island food-web succession generated by two processes: 1) Sequential recovery/colonization of successively higher trophic levels. This creates “herbivore-free time” for rapid plant growth and subsequent “predator-free time” for herbivores and 2) tradeoffs between successional stage and susceptibility to consumers in which early successional species (or phenotypes within a species) are more susceptible than later successional species (or phenotypes). Thus as consumer species colonize an island, they may change the species or phenotypic composition of their food supply from highly productive and vulnerable items to less productive and vulnerable items, thereby weakening both bottom-up and top-down effects in the food web.

Allochthonous resource pulses in the form of seaweed deposition events have multiple temporally varying effects on Bahamian island food webs. In the short-term, all of our experiments found evidence for the “predator-diet-shift effect” in which lizards shift from eating local prey (including terrestrial herbivores) to eating mostly marine detritivores, leading to increased herbivory and thereby weakening the trophic cascade from lizards to plants (Spiller et al. 2010; Piovia-Scott et al. 2011, 2019). In the long-term, we found evidence for two other mechanisms: 1) The “fertilization effect” in which seaweed adds nutrients to plants, increasing their growth rate (Spiller et al. 2010), as well as increasing herbivory (Piovia-Scott et al. 2013) and 2) a numerical response by lizards to marine subsidies strengthens the trophic cascade from lizards to plants (Piovia-Scott et al. 2019). Hence, allochthonous resource pulses can cause a sequential series of bottom-up and top-down effects that propagate throughout the food web.

In the Bahama Islands, the most significant seaweed deposition events occur during hurricanes when massive amounts of seaweed are washed high upon the shoreline into the vegetation. By providing nutrients to the plants and prey subsidies to the secondary consumers, such events occurring at a low frequency may have a favorable impact on island communities in the long term. However, in the short term, we have found that herbivory increases following hurricanes via increased susceptibility to herbivores of the foliage on severely damaged plants and following seaweed deposition when predators switch from eating herbivores to marine detritivores. In addition to the recent increase in hurricane frequency and intensity, which is expected to continue due to climate change (Kossina et al. 2020), during the last decade there has been a dramatic increase in the amount of *Sargassum* seaweed in the Atlantic Ocean with unprecedented amounts washing ashore more and more frequently (Rafael et al. 2019; Wang et al. 2019). Hence, the compounding effects of increasing frequency of hurricanes and seaweed deposition may lead to chronic intense herbivory on islands, particularly when hurricanes reduce predator abundances.

During this time of increasing frequency of many types of disturbances, strategies for sustainable management of ecosystems should focus on maintaining resilience (Pimm 1991; Gunderson 2000; Pace et al. 2015). We have found that predators

increase the recovery rate of producers following disturbance, implying that maintaining key species interactions embedded within food webs may mitigate the negative impacts of global change on island ecosystems.

10.6 Conclusions

We have found that predatory lizards reduce herbivory and thereby have a positive indirect effect on plants on Bahamian islands. Food-web complexity can influence the cascading effects of lizards. For example, intraguild predation by lizards on spiders (which also eat herbivores) may weaken the cascade. However, interactions between different types of predators may not always be antagonistic, dampening the trophic cascade. We found that the positive effects of diurnal lizards and nocturnal predatory ants on plants were synergistic, possibly because herbivorous arthropods had no “escape in time” from predation. Two exogenous factors, hurricanes and allochthonous resource pulses, play a significant role in structuring island communities and produce major variation in food-web dynamics.

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