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REVIEW

Recovery of food webs following natural physical disturbances

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The objective of our paper is to develop a mechanistic conceptual framework for how food webs recover from natural physical disturbances. We summarize our work on the effect of hurricanes on island food webs and review other studies documenting how other types of physical disturbances (including fires, floods, and volcanic eruptions) alter food–web interactions. Based on these case studies, we propose that four factors play an important role in food-web succession: (1) disturbance intensity, (2) sequential recovery/colonization of successively higher trophic levels, (3) tradeoffs between growth rate of organisms at different successional stages and susceptibility to consumers, and (4) detritus including autochthonous and allochthonous sources. Studies on river flooding and islands disturbed by hurricanes indicate that energy flow is higher and trophic cascades are stronger during recovery than when the food web is at a steady state. We suggest that as consumer species colonize during succession, they may change the species or phenotypic composition of their food supply from highly vulnerable to less vulnerable items, thereby weakening both bottom-up and top-down effects throughout the food web. High inputs of detritus caused by disturbances can amplify bottom-up effects during early succession, and subsequently alter top-down effects.

Keywords: disturbance; food webs; floods; hurricanes; islands; trophic cascades; volcanic eruptions

Introduction

The role of natural disturbances in structuring species interactions, species composition, diversity, and landscape dynamics has been well documented,[1–4] but studies on how disturbances affect whole food-web dynamics (changes in bottom-up and top-down effects from plants to predators) are rare.[5] There is a rich body of literature on food-web dynamics.[6–12] The underlying assumption in most food-web studies is that the system is at equilibrium or at least at a temporary steady state. However, food webs recovering from disturbances are clearly not at a steady state.

The objective of our paper is to develop a mechanistic conceptual framework for food-web succession. In their seminal paper on mechanisms of succession, Connell and Slatyer[13] recognized that traditional studies focusing only on producer species have ignored the top-down effect of consumers on producers which may play an important role in succession. We here extend their premise by addressing how food–web interactions among species in multiple trophic levels affect patterns of succession.

Groundbreaking studies by Mary Power and collaborators on reassembly of river food webs following floods have shown that maximum functional food-chain length (the number of trophic levels linked by strong interactions) occurs at intermediate stages of succession.[14–16] The mechanistic explanation for this phenomenon is that following flooding the riverbed is first colonized by rapidly growing, highly edible algae, followed by rapidly growing herbivores which are highly vulnerable to predators that devour the herbivores when they arrive, leading to a strong trophic cascade. Later in succession, the predators have eliminated the vulnerable prey leaving only slow-growing, well-protected

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Figure 1. Photograph of an exposed study island the week after Hurricane Lili. Before the hurricane, the top of the island was covered with 1–2 m tall *C. erectus* shrubs, which were mostly reduced to stumps by the storm surge. The person standing is Jonathan Losos.

prey not eaten by predators, causing the functional food-chain length to decline. These findings are supported by other studies showing that fast-growing early successional plant species are more susceptible to herbivory than slow-growing later successional species,[17–19] which may be linked to a resource allocation trade-off between growth rate and defense.[20] However, the generality of the entire suite of processes described by Power *et al.* has not been rigorously explored.

As discussed in detail below, our studies on recovery of island food webs following hurricanes show remarkable similarities to the findings of Power *et al.* for river food webs. To ascertain the generality of these processes, we review and compare the results in other studies on different types of major disturbances, including hurricanes, floods, fires, and volcanic eruptions. In addition, our review includes the effect of detritus, which did not seem to be important in the river food-web study mentioned above, but has been found to be the primary base of food webs immediately following disturbance in other studies.[21–23] We focus on major physical disturbances which typically have direct negative impacts on many species, not biological disturbances (e.g., disease, herbivore outbreaks, and invasive species) that typically have direct negative impacts on only certain species. We first discuss in detail the findings of our hurricane studies, followed by summaries of other studies of hurricanes, as well as floods, fires, and volcanic eruptions. Based on these case studies, we present graphical models of food-web trajectories during succession and identify key causal factors.

A major theme in our discussion is that the *strength* of trophic cascades varies during succession; this needs some clarification. A trophic cascade can be broadly defined as the propagation of impacts by consumers on their prey downward through food webs.[9] We define the *strength* of the cascade as the magnitude of the effect of the consumer population at the top of the food web on the resource population at the bottom.

The impact of hurricanes on Bahamian Island food webs

We have been studying food-web interactions on the Bahamian Islands for over 30 years. During the first half of this period (throughout the 1980s and early 1990s), no hurricane had a major impact on any of our study sites, whereas during the second half (1996 to the present) several hurricanes had passed directly over or close to the islands, having profound effects on their communities. This difference is linked to a recent increase in hurricane frequency.[24] During the 1980s and early 1990s, we conducted a series of observational and experimental studies that demonstrated that the most common lizard, *Anolis sagrei*, had a dramatic negative effect on web spiders,[25] as well as a significant positive effect on plants via reduced herbivory.[26] Although lizards reduced web spiders and both lizards and web spiders eat herbivorous insects, we found that web spiders (taken alone) did not have a significant effect

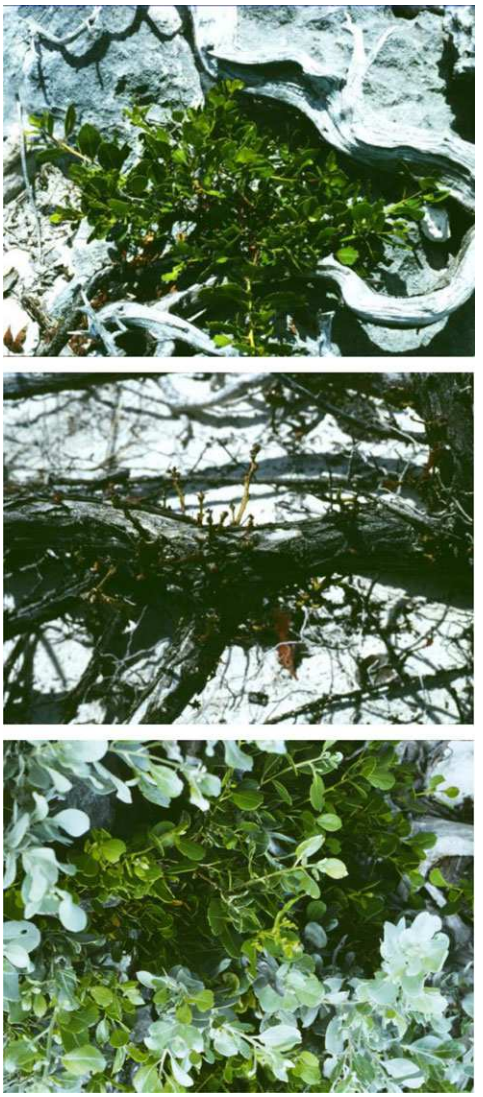

Figure 2. Photographs of *C. erectus* stumps on exposed study islands following Hurricane Lili. Top: A stump that is sprouting new vegetation, taken a few months after the storm. Note that all the leaves are green and many have been partially eaten by herbivores (probably lepidopterans). Middle: A stump several months after the hurricane. The plant had sprouted vegetation but all the leaves were eaten by herbivores. Bottom: Photograph of a stump with both green and silver leaves, taken about 18 months after the storm. The plant had initially sprouted green foliage, and then switched to sprouting silver foliage.

on herbivory.[27] Therefore, we concluded that our study system is functionally a three-trophic-level food web in which the web spiders can be excluded and still capture the trophic-cascade dynamics from top (lizards) to bottom (plants) of the food web. Hence, in the following summary of our work on the impact of disturbances, we will focus on the three-level system, but possible effects of other intermediate predators that eat herbivores, such as spiders and parasitoids, will also be mentioned.

In October 1996, we had just finished our annual survey of the biota inhabiting small islands located offshore of the north and south sides of the very large island Great Exuma when the eye of Hurricane Lili passed directly over the study site. A map of the study site showing the path of Lili and description of the study islands is in Spiller *et al.*[28] 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 (Fig. 1), whereas damage to the vegetation on the protected islands was minimal. 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.[28]

As part of an ongoing food-web study, we had measured amounts of leaf damage on *Conocarpus erectus*, a common seashore shrub, for 3 consecutive years before the hurricane.[29] The foliage color of *C. erectus* varies from green to silver, depending on the density of trichomes on the surface of the leaves. A previous study showed that green leaves (few trichomes) receive more herbivore damage than silver leaves (more trichomes), suggesting that the trichomes reduce herbivory.[30] During the hurricane, all study shrubs on exposed islands were reduced to stumps by the surge and regenerated by sprouting during the following year (Fig. 2, top). 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 that were defoliated repeatedly apparently died due to herbivory following the hurricane rather than by direct impact from the hurricane (Fig. 2, middle). We observed that on exposed islands *C. erectus* with silver leaves before the hurricane sprouted green leaves the year after and then reverted to producing silver leaves the following year (Fig. 2, bottom). 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. The 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.[29] 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.[29] The experiment showed that herbivory was significantly higher on pruned shrubs than on controls. 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 islands following Hurricane Lili was caused, at least in part, by increased susceptibility of the sprouted foliage to herbivorous arthropods; however, the reduction of predators may have also been important.

We also conducted long-term food-web studies on small islands in a semiprotected bay offshore of Great Abaco (located a few hundred kilometers north of Great Exuma) that 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 *C. erectus* was measured before and after the hurricane on islands that either had lizards present or absent continuously both before and after the hurricane.[31] The year after Floyd, leaf damage increased on both lizard and no-lizard islands, but the increase was greater on no-lizard islands (Fig. 3, top). In 2001, the site was hit by Hurricane Michelle and leaf damage increased again the following year. The negative effect size of lizards on herbivory increased after the first hurricane and overall was 2.5 times greater during the disturbance period (2000–2003) than before (Fig. 3, 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;[31] this increase could have also been caused by increased susceptibility of the foliage to herbivory (as found in our previous study[29]), 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.[31] 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.

In a third study, we focused on the effect of lizards on the moth *Achyra rantalis* feeding on the plant *Sesuvium portulacastrum* on small islands with and without lizards in the Exuma Cays, located about 100 km north of Great Exuma.[32] 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, the recovery rate following Floyd and Michelle was higher on lizard islands than on no-lizard islands.[32] We suggest that faster recovery was 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 very 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,[33] Gunderson[34]) of the plants.

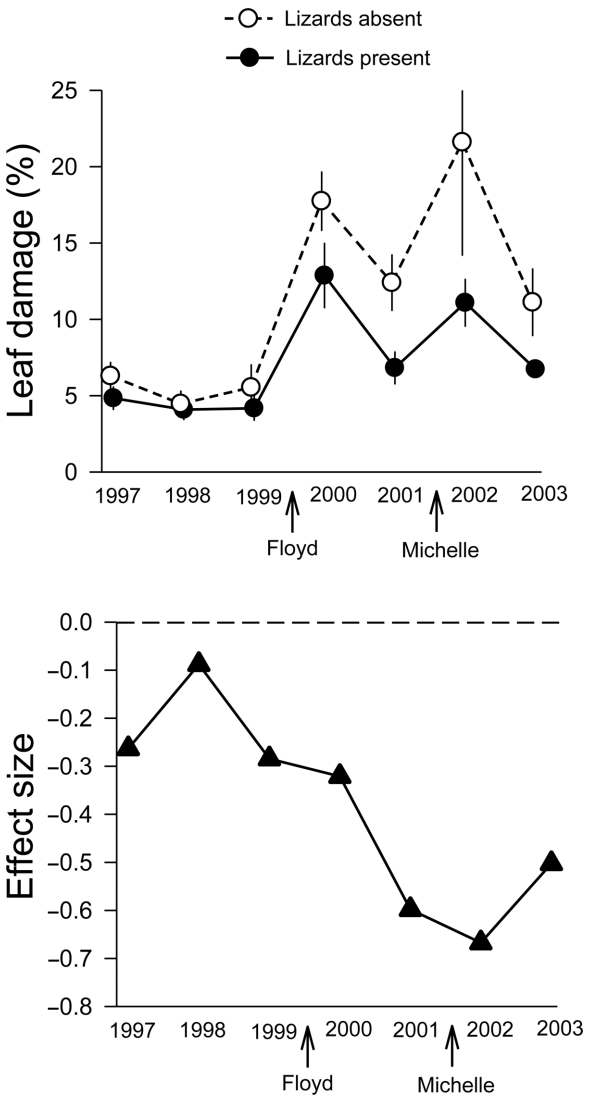

Figure 3. **Effect of lizards on herbivory measured on islands before and after disturbance by two hurricanes, Floyd and Michelle. Top: Leaf damage measure annually in April on islands with lizards present and absent (methods described in Spiller and Schoener[31]). Bottom: Effect size of lizards on herbivory each year, calculated as ln((mean leaf damage on islands with lizards present)/(mean leaf damage on islands with lizards absent)).**

During hurricanes, large amounts of seaweed are deposited on shorelines of islands. The seaweed represents a pulsed resource subsidy[35,36] that is consumed by detritivores, which are eaten by terrestrial predators; those predators also consume terrestrial herbivores. Additionally, seaweed washed high onshore 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 predators switch from eating herbivores to marine detritivores. In the long-term, we hypothesized that predators would respond numerically to marine subsidies and then switch back to eating mostly herbivores as the detritivores declined, leading to an *apparent trophic cascade* (sensu Polis *et al.*[37]) in which subsidies strengthen the positive effect of predators on plants. In short, we predicted that addition of marine subsidies would increase herbivory in the short term and decrease herbivory in the long term. To test

these hypotheses, we added seaweed to six shoreline plots and removed seaweed from six other plots for 3 months during the hurricane season (fall); all plots were repeatedly monitored for 12 months after the initial manipulation.[38] Lizard (*A. sagrei*) density responded rapidly and the overall average was 63% higher in subsidized than in removal plots. Stable isotope analysis revealed a shift in lizard diet composition toward more marine-based prey in subsidized plots. 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. Foliage growth rate was 70% higher in subsidized plots after 12 months. We suggest two causal pathways for the effects of marine subsidies on terrestrial plants: (1) 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 (2) the *fertilization effect* in which seaweed adds nutrients to plants, increasing their growth rate.[38] Because herbivory did not become lower in subsidized plots than in unsubsidized plots during the course of the experiment, there was no evidence of an apparent trophic cascade. Using path analysis on data collected in an observational study, Piovia-Scott *et al.*[39] revealed that the bottom-up fertilization effect was stronger than the top-down predator-diet-shift effect. This analysis also provided evidence that marine subsidies enhance the top-down effect of lizards on plants—seaweed increases lizard abundance which increases their effect on herbivory; this is consistent with the apparent trophic cascade hypothesis.

Other case studies of food webs impacted by disturbances

In this section, we summarize results found in other studies on food webs impacted by different types of disturbances. A large proportion of these studies involves hurricanes, the type of disturbance for which we are most familiar. Studies on other types of disturbances were gleaned from the literature, including only those that contained trophic interactions, mostly from plants to higher levels in the food web. We note that our literature review is not exhaustive and may be missing important papers. However, we contend that this review is novel and presents a good start for developing a general conceptual framework on how food webs recover following disturbance.

Hurricanes

Other comparative studies of herbivory following hurricanes produced mixed results. In September 1989, Hurricane Hugo passed directly over Puerto Rico, causing extensive damage to the rainforests. In April–May 1990, Torres[40] found outbreaks of lepidopterans, particularly *Spodoptera eridania*, feeding on mostly early successional plants growing in forest gaps. The outbreaks ended within a few months when most of the preferred host plants were decimated and parasitoids had increased. In contrast, another study in Puerto Rican rainforests following Hurricane Hugo by Schowalter and Ganio[41] showed that the abundance of defoliating insects and percentage of leaf area removed by chewing insects tended to be lower in heavily damaged areas (gaps) than in relatively undamaged sites, and herbivore abundances and leaf damage were not related to the concentration of nitrogen or other nutrients. Their study began more than a year after the hurricane, whereas intense herbivory found by Torres in Puerto Rico and in our study of Hurricane Lili in the Bahamas did not last more than 1 year. However, the year after Hurricane George struck Puerto Rico in 1998, Angulo-Sandoval *et al.*[42] found that levels of herbivory on understory plants were lower than before the storm, possibly caused by a habitat shift of vertebrate predators (birds and lizards) from the canopy trees, which were defoliated by the hurricane, to feeding on understory plants. Schowalter *et al.*[43] quantified long-term successional trajectories of arthropods in Puerto Rican rainforests from 1991 to 2009, finding that detritivores were most abundant immediately after hurricanes when litter resources were elevated, whereas sap-suckers were most abundant in gaps with rapidly growing new foliage; data on other guilds were inconclusive.

Following Hurricane Opal in a North Carolina forest, Hunter and Forkner[44] found that herbivory was substantially higher in damaged than in undamaged sites, even though their study was conducted more than a year after the hurricane. Concentrations of putative defensive compounds (foliar astringency and tannins) measured by Hunter and Forkner were higher in damaged than undamaged sites. Therefore, some other factor caused higher herbivory in damaged sites by overcoming higher astringency

and tannins. It is possible that intense herbivory the year after the hurricane induced the trees to produce more chemical defenses the next year.[45]

Koptur *et al.*[46] studied herbivory on plants immediately following Hurricane Andrew in south Florida, which was a Category 5 storm that caused catastrophic damage. They found that levels of herbivory were very low 1 month after the storm and increased precipitously the following 2 months. This study suggests that the catastrophic disturbance devastated herbivore populations over a large area, providing the plants with herbivore-free time for a while until herbivores recolonized the study area. Similarly, Pascarella[47] found that seed production of the tropical shrub *Ardisia escallonioides* increased markedly for 2 years after Hurricane Andrew. Populations of a specialist flower galling moth (*Periploca* sp.) were very low the year after Andrew and increased markedly during the next 2 years. Hence, decimation of the moth populations, along with other factors caused by the hurricane, resulted in a window of opportunity for seed production.

Floods

Studies by Nakamura *et al.*[48,49] of willow trees on the bank of a river in Japan damaged by floods during a typhoon produced results similar to our findings on Bahamian island plants damaged by hurricanes.[29] Nakamura *et al.*[48] found that the number of sprouting shoots was significantly greater on severely damaged trees than on lightly damaged trees, and the abundance of leaf beetles and levels of herbivory were higher on the rapidly growing, damaged trees. These results support the plant vigor hypothesis,[50] which states that herbivores preferentially feed on rapidly growing plants. Furthermore, predatory arthropods were also more abundant on heavily damaged plants, indicating that increased herbivores had a positive bottom-up effect on predators. The results of an experimental study on cut and uncut (control) willow trees were consistent with the comparative study after the flood.[49] They showed that on cut trees, shoots grew faster, leaves contained more nitrogen and water, abundance of leaf beetles and levels of herbivory were higher, and abundance of predatory arthropods was higher than on uncut trees. We note that in our study on small islands devastated by Hurricane Lili,[29] we did not observe a rapid increase of predators on heavily damaged plants because the hurricane apparently exterminated all arthropods on the islands (observations made by D. Spiller a few days after the storm). Arthropods recolonizing the small study islands must have come from distant larger islands, where populations survived the storm. We suggest that the high dispersal ability of moths combined with their attraction to the lush foliage sprouting on the damaged plants enabled them to recolonize islands before the predators. In the studies by Nakamura *et al.*, both herbivorous and predatory arthropods were able to rapidly recolonize heavily damaged trees from nearby lightly damaged trees.

The most comprehensive studies of how disturbance affects food-web processes were conducted by Mary Power and her collaborators working in the Eel River in California.[14–16] Eighteen years of field observations and five summer field experiments revealed that year-to-year food-web structure was highly variable. In typical years with scouring winter floods, which flush out the system, the river is first colonized by *Cladophora*, a filamentous green algae. The floods provide the algae with a consumer-free window of time in which large mats can form on the riverbed. Later in the spring, reassembly of the food web can vary, depending on the species composition of the consumers. In their first experiment in 1989,[51] *Cladophora* was consumed by *Pseudochironus*, a tuft-weaving midge capable of devouring most of the algal mats. Experimental manipulations showed that without fish, predatory insects (odonates) ate most of the midges and the algal mats persisted during the summer, whereas when fish were present they consumed most of the odonates, which increased the midges and consequently reduced the algae. Thus, the experiment revealed a four-trophic-level cascade. In drought years without disturbance (1990 and 1991), the dominant primary consumer was *Dicosmoeus*, a predator-resistant armored caddisfly. Experiments during drought years showed that predators had no effect on armored caddisflies, indicating that the food web had only two functional levels. Taken together, these studies indicate that disturbance increases the functional food-chain length. Detailed analysis of food-web processes in flood years indicated that energy flow from producers to predators was highest at intermediate stages of recovery from disturbance, and thereby the trophic cascade was strongest at that time.

Fisher *et al.*[21] studied the recovery of a desert stream in Arizona after an intense flash flood which virtually eliminated all the biota. The flood deposited a large amount of detritus (dead leaves and wood) on the riverbed. Initially, macoinvertebrates (all taxa taken together) fed nearly exclusively on the allochthonous detritus, then switched to diatoms which grew rapidly, and later consumed mostly autochthonous detritus.

Rocky intertidal disturbances

Sousa[18] studied succession of intertidal algae species on boulders in southern California. The major form of natural disturbance in this system is the overturning of boulders by wave action, particularly during the winter. Disturbed boulders are rapidly colonized by a mat of green algae (*Ulva* spp.), followed by the accumulation of perennial red algae species (*Gigartina* spp.) that dominate the boulders as the abundance of green algae declines. Field experiments demonstrated that without further disturbance the green algae persists and inhibits the recruitment of perennial red algae, supporting the inhibition model of succession proposed by Connell and Slatyer.[13] Selective grazing on *Ulva* by the crab *Pachygrapsus crassipes* is a mechanism that opens space, allowing the recruitment of red algae. Similarly, Lubchenco[19] showed in Massachusetts that periwinkle snails (*Littorina littorea*) preferentially consumed early successional algae (*Ulva, Enteromorpha, Porphvra*), enabling the recruitment of later successional algae (*Fucus*). Both studies indicate that the top-down effect of herbivory decreases later in succession when the community consists of more resistant algal species. They also show that herbivores increase the rate of succession by removing the early successional species. However, Farrell[52] showed that in Oregon, where barnacles were the early successional species, herbivorous limpets delayed the establishment of later successional macroalgae and thereby impeded succession.

Wootton[53] studied the effect of bird predation on the succession of sessile invertebrates in Washington. He showed that goose barnacles (*Pollicipes polymerus*) colonized disturbed areas before mussels (*Mytilus californianus*), and that the barnacles inhibited the recruitment of mussels. Predation by gulls on goose barnacles enhanced mussel recruitment and thereby increased the rate of succession. Further studies by Wootton[54] on more species in the community revealed that early successional species with smaller adult body size were more susceptible to predation than later successional larger species. Hence, as succession proceeds, predator-susceptible species are replaced by predator-resistant species.

Dean and Connell[55] studied the effects of successional algal changes on the assemblage of small invertebrate animals living in the algae at the same California boulder field studied by Sousa. They found that abundance and diversity of invertebrates increased during succession. Trophic structure changed markedly during succession. The proportion of the total number of individuals that were grazing herbivores decreased, while the proportion that were filter feeders increased; individuals in other trophic categories were relatively rare and no significant change in their proportions occurred. The reduction in grazing herbivores during succession is consistent with Sousa's study showing that herbivores prefer early successional algal species more than late successional ones. Dean and Connell[56] showed that increased abundance and diversity of small invertebrates during succession was linked to greater structural complexity in later successional algal species that reduced predation by fish and crabs and physical stress. Hence, the vulnerability of small invertebrates to predation decreased during succession.

Fires

Many perennial plants species resprout vigorously following fire,[57] possibly due to increased light and rapid assimilation of nutrients in the soil from ash. Stein *et al.*[58] demonstrated experimentally that herbivory by both grasshoppers and elk was higher on burned than on unburned willows in Arizona. Knapp *et al.*[59] found that bison grazed preferentially within burned watersheds at the Konza Prairie, Kansas. Similarly, Pearson *et al.*[60] showed that grazing intensity by bison and other ungulates was higher at burned than at unburned sites following the Yellowstone National Park fires in 1988. Studies in Amazon forests by Massad *et al.*[61] and semiarid sand dunes in Australia by Giljohann *et al.*[62] showed that overall herbivory was higher following fires for a variety of plant species. These studies also indicated that the effect of fires on herbivory may be contingent on nutrients and rainfall. Massad *et al.*[61] found that adding nutrients to burned plots increased herbivory. Giljohann *et al.*[62] found that fire increased

herbivory in dry years but not wet years. Knight and Holt[63] showed that fires in Floridian pine forests generate spatial gradients in herbivory. Grasshopper abundance and herbivory were higher on plants around the edge of recently burned areas than in the middle, probably because grasshoppers colonized the edge before middle regions.

Volcanic eruptions

In May 1980, a cataclysmic eruption occurred at Mount St. Helens, Washington, leaving an extensive barren area of pumice plains on the north slope.[64] The area was initially colonized by lupines (*Lupinus lepidus*) in 1981 which spread rapidly during the next decade, forming dense patches of vegetation.[65] Herbivory on lupines was rare until 1993 when they started to become conspicuous.[66] Boring tortricid moths became very abundant, causing 100% mortality of lupines in several patches, and gelechiid and pyralid leaf miners also caused extensive damage. The initially high growth rate of the lupine population measured in the 1980s was dramatically reduced in the 1990s. Fagan and Bishop[67] provided convincing evidence that herbivory impeded the spread of lupines on the pumice plains. Interestingly, herbivory was much higher on the edges of patches than in core areas, whereas predatory arthropods were more common in core areas, suggesting the accumulation of predators in the older core areas reduced herbivory. However, Bishop *et al.*[68] found no evidence that top-down effects by predators controlled herbivores in the core areas. Instead, chemical analysis and manipulative experiments showed that plant competition for phosphorous in high-density core areas lead to low-quality plants, and thereby lower herbivory than in low-density edge areas.[69]

Kasatochi Island, a small volcano in the central Aleutian Archipelago of Alaska, erupted violently in August 2008.[70] Most of the island was covered with a thick layer of ash and pyroclastic flow. Surveys of plants and animals on Kasatochi were conducted before and after the eruption. Before the eruption, Talbot *et al.*[71] found that the island was covered with a lush green carpet of low-lying vegetation comprising 86 species. Their survey in 2009 (Ref. 71) showed that eradication of the flora throughout the island was nearly complete, except for some areas where heavy rain eroded the ash, exposing remnants of live plant material which formed patches of vegetation containing a total of 18 species. During the next few years, Walker *et al.*[72] discovered viable plant propagules that had apparently been buried under ash for at least 3 years; they documented a continuous increase in plant species richness on the island. In a survey of arthropods before the eruption, Sikes and Slowik[73] collected a diverse assemblage of species, including herbivores, predators, and detritivores, that occurred throughout the island. One year after the eruption, they found arthropods on the beach associated with wrack (dead kelp) and in a cave containing bird carcasses. All specimens collected were saprophagous species or predators of those species; no herbivores were found. Surveys during the next few years by Walker *et al.*[72] indicated that most of the arthropods on Kasatochi Island were associated with a marine-based food web dominated by flies that ate wrack or carrion on the beach. The lack of herbivores during early succession on Kasatochi Island is consistent with the findings in the Mount St. Helens studies described above. Auklets and other seabirds were abundant on Kasatochi before the eruption and recolonized the island the following year.[74] Renner *et al.*[75] suggest that soil development will be accelerated by auklets bringing large quantities of marine-derived nutrients to their nest sites, which enhances the recovery of plants.

Toward a conceptual framework on food-web succession

In this section, we present a conceptual framework for the redevelopment of food webs following disturbances. Figure 4 contains schematic diagrams of temporal changes in food-web structure following intense and moderate disturbances. These diagrams are based primarily on the results of our studies on the recovery of food webs on Bahamian islands following hurricanes, but we will also discuss how other studies on a variety of other types of disturbances fit the patterns.

The top diagram in Figure 4 depicts food-web succession following an intense disturbance that removes virtually all the biota in an area isolated from undisturbed areas. In many cases, the plants may not be killed, but the standing biomass of green matter is virtually gone. In the first stage, the plants recolonize the area, or resprout from roots and stumps, which grow rapidly during this herbivore-free time period, as found in studies of catastrophic

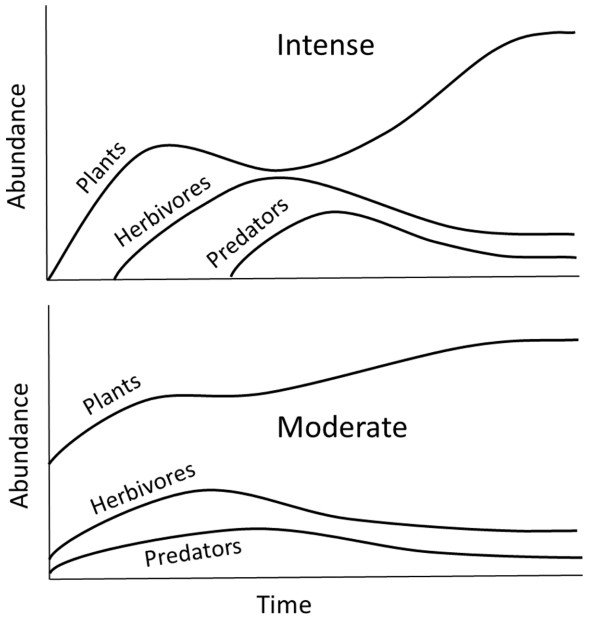

Figure 4. **Schematic diagrams of temporal changes in food-web structure following an intense disturbance (top) and a moderate disturbance (bottom). See text for explanation. The absolute scale on the *y*-axis is not intended to be the same for all trophic levels.**

hurricanes[46,47] (D. S., personal observations), river floods,[14–16] and volcanic eruptions.[66,72,73] In the second stage, herbivores colonize the area, their populations grow rapidly, and they begin to impede plant population growth rate,[66,67] or in some cases reduce plant abundance,[40] as depicted in the diagram and as shown in the middle photograph of Figure 2. The strong top-down effect by herbivores may be caused by two factors: (1) high susceptibility to herbivores of early succession plants or resprouted foliage and (2) the lack of predators. In the third stage, predators colonize the area and begin to reduce herbivores more and more as the predator populations grow, and thereby the plant populations begin to grow again. Eventually, the reduction of herbivores leads to a reduction in predators and the system reaches a steady state if the area is not disturbed again.

The dynamics following a single moderate disturbance is depicted in the bottom diagram of Figure 4. In this case, recovery dynamics are less pronounced than those following an intense disturbance. This is because the disturbance does not remove all the organisms, eliminating the sequential colonization of successively higher trophic levels that drives the pronounced dynamics following an intense disturbance. Although herbivore populations may have declined during a moderate disturbance, there is no herbivore-free period. Herbivore populations increase but their growth rate is reduced by growing populations of the surviving predators, so the increase in herbivory is not dramatic and the effect of herbivory on plant abundance is less noticeable. This diagram may fit studies of terrestrial plants severely damaged by a river flood surrounded by plants with less damage[48,49] and studies of fires which do not burn all plants in the study area.[59–62]

Table 1 lists four factors found in the studies reviewed above that may in general affect food-web succession. We will discuss the mechanisms and processes by which each of the factors plays a role in food-web redevelopment.

Factor 1

Disturbance intensity has been shown to be important in various ways in many studies of succession in plants and sessile marine animals.[2–4] Power *et al.*[16] revealed that reassembly of river food webs only occurs during years with scouring winter floods, but not in drought years with little disturbance. Years without scouring floods do not have enough discharge to turn over most of the cobble on the river bottom, and consequently do not restructure the food web. Our study on the effect of Hurricane Lili showed that

Table 1. Factors affecting food-web dynamics following disturbance

Factor	Effects, mechanisms, and processes	Refs.
1. Disturbance intensity	Strong disturbance causes more profound effects than weak	16,29
2. Sequential recovery/colonization of successively higher trophic levels	Creates herbivore-free time for rapid plant growth and subsequent predator-free time for herbivores	14–16,29,46,47,66,72,73
3. Tradeoffs between successional stage and susceptibility to consumers	Early successional species (or phenotypes within a species) are more susceptible than later successional species (or phenotypes)	14–16,18,19,29,40,44,48,49,53–56,58–62,66,67
4. Detritus	Can initially be the primary base of food webs instead of producers	21,38,43,72,73

food-web effects were much stronger on exposed islands devastated by the storm surge than on protected islands.[29]

Factor 2

Sequential recovery/colonization of successively higher trophic levels creates herbivore-free time for rapid plant growth and subsequent predator-free time for herbivores. Evidence for herbivore-free time is found in studies of plants following a catastrophic hurricane,[46,47] colonizing algae following river flooding,[14–16] and plants following volcanic eruptions.[66,72,73] We found that herbivores colonized exposed islands devastated by Hurricane Lili before predators did, giving them a period of predator-free time that resulted in major damage on plants.[29] This process could be caused by two mechanisms: (1) successively lower dispersal rates of species in higher trophic levels and (2) consumers in a given trophic level cannot colonize an area until the abundance of their food supply in the next lower trophic level is high enough to support them.[76,77] In accordance with the exploitation ecosystems hypothesis of Oksanen *et al.*,[7] increasing productivity during succession enables the colonization of higher trophic levels.

Factor 3

Trade-offs 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) are a factor. Plant susceptibility to herbivores can be higher following disturbance in two different ways. (1) Variation among species: Early successional species may be more vulnerable to herbivores than late successional species, as found in studies of terrestrial plants[17] and intertidal algal species.[18,19] Hence, there may be a life-history tradeoff between dispersal ability and herbivore susceptibility in plant species. This is supported by studies reviewed above documenting outbreaks of herbivorous insects on early successional plants following a hurricane[40] and following a volcanic eruption.[66,67] (2) Phenotypic changes within species: Many studies showed that terrestrial plants heavily damaged by disturbance are more susceptible than undamaged plants, including resprouting plants on islands following a catastrophic hurricane,[29] resprouting plants on the bank of a river following a major flood,[48,49] and resprouting plants following fire.[58–62] The most pervasive mechanism increasing herbivory seems to be the higher nitrogen content of resprouted leaves,[29,48,49] although decreased defense mechanisms (reduced leaf toughness and trichomes) may also be important.[29] These findings are relevant to field experiments investigating the effect of browsing by moose on birch,[78] rabbits on willows,[79] and beavers on cottonwood:[80] Pruning or clipping apical buds resulted in increased susceptibility of the foliage to herbivorous arthropods. In the birch study, increased nitrogen, larger leaves, and other chemical and morphological changes were purportedly caused by a breakdown in apical dominance, which regulates the allocation of resources and other physiological processes throughout the plant.[78] In our study,[29] virtually all of the apical meristems were removed by the hurricane and experimentally on pruned shrubs. Thus, breaking

apical dominance may have caused the pruned shrubs to produce vigorously growing shoots of foliage that are rich in nutrients and sugars and poor in proteinaceous material, making them more susceptible to herbivorous insects.[81] Another mechanism in which plant vulnerability may decrease during succession was revealed in studies of lupines on Mount St. Helens;[68,69] in later stages of succession, when plants attain high densities, depletion of nutrients may lead to low-quality hosts, thereby reducing herbivory.

There may also be a trade-off between dispersal ability and vulnerability to predators among herbivore species or phenotypes. The studies of river food webs by Power *et al.*[14–16] 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. In years with scouring floods, rivers are quickly colonized by tuft-weaving midges or mayflies, whereas in drought years caddisflies persist throughout the year and into the next season, dominating the food web. Hence, when predators colonize an area in this system, the abundance of early arriving vulnerable prey species decreases as the abundance of later arriving invulnerable prey increases. Similarly, Wootton's[54] findings in a rocky intertidal system revealed that as succession proceeds, predator-susceptible species are replaced by predator-resistant species. Evidence for this process comes from our experimental introductions of lizards onto islands, showing that the lizards quickly exterminated vulnerable web-spider species that built their webs close to the ground and remained in their web during the day when the diurnal lizards are foraging, whereas the most common species persisting generally built webs higher in the vegetation and remained concealed in the vegetation during the day.[82] The results of this experiment also showed that introduced lizard populations initially had a stronger effect on herbivores than later on, possibly because lizards initially exterminated (or greatly reduced) highly vulnerable species, so later on only less vulnerable species persisted.[83] We hypothesize that in some systems, recolonization by predators facilitates a decrease in the relative abundance of early arriving vulnerable prey and an increase in the relative abundance of later arriving invulnerable prey.

In addition to a change in species composition, when predators colonize an area they may cause a change in herbivore traits within a species that decreases their vulnerability (e.g., they spend more time avoiding predators and less time feeding); this is known as a *trait-mediated indirect effect.*[84,85] Ontogenetic changes in prey species during succession may also be important. For example, species that escape predation by growing large enough to be invulnerable to predation will take time to grow that large, and thereby are more vulnerable after disturbance when they are primarily present at early life stages. 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.[86]

Factor 4

Detritus can initially be the primary base of food webs (instead of producers) following disturbance, as found in studies of a hurricane,[43] a river flood,[21] and a volcanic eruption.[72,73] Manipulation of seaweed on island shorelines, simulating deposition by hurricanes, showed that detritivores living in seaweed became the major prey of predatory lizards, which had indirect effects throughout the food web.[38] Figure 5 is a schematic representation of how a resource pulse of detritus affects food-web dynamics following a moderate disturbance. Details are based on the results of our studies of seaweed deposition,[38,39] but we suggest that inputs of detritus caused by disturbance may affect other systems similarly. Amounts of detritus and detritivores are initially high and rapidly decline during early stages of succession. Predators (lizards, in our studies) respond rapidly by switching from foraging in the vegetation on herbivores to foraging on the ground on detritivores,[87] leading to a short-term increase in herbivores and a decrease in plant abundance, depicted at time 1. At time 2, detritivores have decreased precipitously, while predator populations have increased, mainly from feeding on copious amounts of detritivores.[88] At this point, predators have switched back to foraging in the vegetation on herbivores, decreasing herbivory and increasing plant abundance. This process is referred to as an apparent trophic cascade[37] in which the addition of detritus leads to an increase in the top-down effect of predators on plants. In addition, nutrients are being assimilated by plants at time 2, increasing their growth rate. Thereafter, the food supply of predators is low and their population declines,

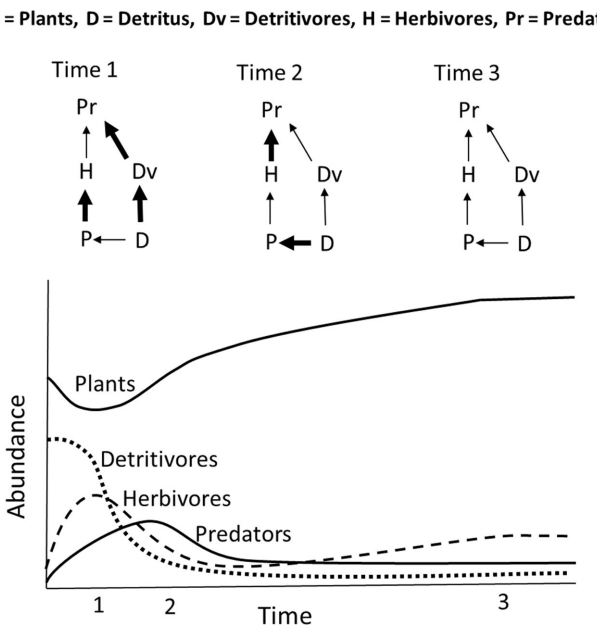

Figure 5. Schematic representation of how a resource pulse of detritus affects food-web dynamics following a moderate disturbance. See text for explanation. The absolute scale on the *y*-axis is not intended to be the same for all trophic levels.

leading to a slight increase in herbivores, and the system reaches a steady state at time 3. In summary, high inputs of detritus caused by disturbances can amplify bottom-up effects during early succession, and subsequently increase the strength of top-down effects during the mid-succession period.

Discussion

Studies on river flooding[14–16] and islands disturbed by hurricanes[29,31] indicate that energy flow is higher and trophic cascades are stronger during recovery than when the food web is at a steady state. This can be seen in Figure 4 (top diagram): in the middle time period of the graph, herbivore and predator populations have built up to high levels and each is having a strong effect on the trophic level below. Hence, both bottom-up and top-down effects for consumers are strongest at intermediate stages of succession. At later stages, predators have reduced the number of herbivores so their populations decline as they deplete their food supply, thereby reducing top-down effects on plants. As consumer species colonize the disturbed area, they may change the species or phenotypic composition of their food supply from highly vulnerable to less vulnerable species, thereby weakening both bottom-up and top-down effects throughout the food web.

High levels of herbivory on damaged terrestrial plants resprouting new foliage seem to be common, as found in studies on islands following hurricanes[29,31,44] (but see, Refs. 41 and 42), on a river bank following flooding[48,49] and on forests following fires.[58–62] These findings are relevant to a world-wide increase in herbivory on forest trees caused by global warming.[89] Although gradually increasing temperature and decreasing precipitation in areas associated with global warming may be classified as chronic stress, extreme weather events are disturbances which have become more and more common.[90] Hence, increased frequency of a variety of disturbances linked to climate change, including fires, hurricanes, and floods, may be having pronounced negative effects on plants via food-web processes.

Detritus may play a major role in food-web succession during the initial stage of recovery. The source of detritus may be autochthonous, as in studies finding large amounts of leaf litter in a rainforest following hurricanes,[22,23] or allochthonous as in a study on river flooding finding large amounts of detritus deposited by the disturbance.[21] Marine

macrophytes (seaweed) deposited on shorelines support a rich array of primary and secondary consumers in many regions of the world.[91–94] Deposition of large amounts of seaweed following tropical storms is probably very common.[95] Our experimental study in the Bahamas showed that this allochthonous resource pulse has multiple effects on shoreline food webs.[38] Deposition of other allochthonous materials caused by disturbances may be common in a variety of different ecosystems. In addition to the deposition of detritus found on riverbeds,[21] river floods may deposit nutrient-rich sediments onto surrounding terrestrial areas that fertilize plants, leading to strong bottom-up effects followed by strong top-down effects. Landslides may also transport nutrient-rich soils onto disturbed areas, promoting the regrowth of vegetation. Of course, some disturbances may actually remove nutrient-rich sediments, for example, during scouring floods and storm surges. Furthermore, high detritus deposition may bury some low-lying plants, having direct negative effects, as found in salt marshes.[96] Hence, effects of detritus and sediment deposition on food-web dynamics may be quite variable.

We note that at this point the general processes specified here need to be taken with caution. We realize that the presented trajectories and key factors may not apply to many systems due to other complicating factors not taken into consideration. Idiosyncrasies inherent in different systems, along with climatic variation during recovery, may often make it difficult to assess general patterns.[43,90] We contend that this review did find similar patterns in the recovery of food webs following a variety of disturbances and suggest that it serves as a good start toward the development of a conceptual framework for food-web succession.

Finally, most theoretical and empirical studies of trophic cascades focus on steady-state equilibrium abundances of producers and consumers. However, we need to focus on nonequilibrium conditions as well, in which populations may fluctuate dramatically due to disturbances. We suggest that food-web interactions are stronger during recovery following disturbance than when the system is in a steady state. Our studies show that predators can increase the recovery rate of producers following disturbance.[31,32] During this time of increasing frequency of many types of disturbances, strategies for sustainable management of ecosystems should focus on maintaining resilience.[97] A mechanistic understanding of how food webs are impacted and recover from disturbances may be used to make good management decisions. The findings of our studies imply that preserving viable predator populations may mitigate the negative impacts of global change on ecosystems.

Future directions

More studies on how entire food webs (from plants to predators) recover following disturbance are needed. Long-term studies are the best method for revealing the impacts of disturbance in nature.[98,99] Food-web studies in progress should make contingent plans on how to proceed, in the event that a disturbance does occur, to reveal the trajectories and identify key causal factors. Documenting the response by all species and trying to find patterns would be difficult and probably unfruitful. We suggest focusing on species that have previously been shown to be, or seem to be, major players in the food web, and performing manipulative experiments on those species, along with long-term surveys documenting the natural recovery process.

Development of dynamic mathematical models based on the trajectories and key processes presented in this paper may lead to the development of a formal theory on food-web succession. Such models, complemented by empirical studies, could be used to address a variety of important questions. For example, how does variation in colonization rates among trophic levels affect the food-web trajectories? What is the relative importance of differential colonization rates and temporal variation in vulnerability to consumers in changing the strength of food-web interactions during succession? How do different amounts of detritus affect food-web dynamics after disturbance? What is the effect of eco-evolutionary processes during succession on food webs? How do multiple disturbances affect food webs, and at what point does the system shift to a new regime?[100]

Our review focuses on processes that occur within a certain area, overlooking some processes that occur at the landscape level in which metacommunity dynamics may be important in determining food-web assembly.[101–104] Landscape dynamics can be quite complicated and addressing this issue is beyond the scope of this review, which we consider to be the first step toward understanding how food

webs redevelop following disturbance. In the future, a thorough treatment of food-web succession at the landscape level would be useful.

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Competing interests

The authors declare no competing interests.

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