Long-term entomological research on canopy arthropods in a tropical rainforest in Puerto Rico

T. D. Schowalter
LSU Agricultural Center

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Long-term research is critical to addressing effects of environmental changes, especially climate or land use, on ecosystems and their constituent species, because short-term studies yield incomplete or even misleading impressions (Adams 2001). For example, long-term studies have revealed that community and ecosystem responses to a disturbance event reflect the legacy of disturbances and other environmental changes over periods of decades to centuries (Harding et al. 1998, Summerville et al. 2009, Schowalter et al. 2017). In other words, community structure at a point in time depends on the history of environmental changes that filter community composition in different ways; i.e., species survival and response after successive events depends on their respective tolerances to each event. Short-term studies are incapable of revealing such legacy or contingency effects.

Insects provide valuable systems with which to study long-term effects of environmental changes. Insects represent the bulk of diversity (60-90% of all species) in terrestrial and freshwater ecosystems, have biomass often equal to or greater than that of more conspicuous vertebrates, and are highly responsive to changes in abiotic or host conditions (Schowalter 2016). Both above- and below-ground arthropods have considerable capacity to alter rates and patterns of primary production, decomposition, soil properties, and biogeochemical fluxes (Mattson and Addy 1975, Belovsky and Slade 2000, Schowalter et al. 2011). Outbreaks of herbivorous species are among the most dramatic biological processes, often triggered by disturbances (Mattson and Haack 1987, Schowalter 2012). Outbreaks are capable of altering ecosystem conditions and climate in ways that may contribute to ecosystem resilience (Chapman et al. 2003, Classen et al. 2005, Fonte and Schowalter 2005, Frost and Hunter 2007, Schowalter et al. 2011, Schowalter 2016), as well as the delivery of ecosystem services (Schowalter 2013, 2016).

Unfortunately, insects have received relatively little attention in long-term ecosystem studies. Entomologists traditionally have focused on the population dynamics of individual species and their associated hosts and natural enemies, whereas ecosystem ecologists tend to ignore insects or treat them as a single biotic pool (Hunter 2001).

Clearly, entomologists could contribute greatly to long-term studies of ecosystem responses to environmental changes. Research sites in the U.S. Long Term Ecological Research (LTER) Network, and collaborating networks in

Fig. 1. Differences in canopy cover in experimental gap (A) and non-gap (B) plots at Luquillo Experimental Forest, Puerto Rico, in 1991 following Hurricane Hugo (1989).

other countries, are often funded to conduct large-scale, long-term manipulative experiments. These platforms provide opportunities for entomologists to test hypotheses that would be impossible or impractical to conduct individually and to integrate their research within a broader ecosystem framework.

This paper describes an example of entomological research at one LTER site, the Luquillo Experimental Forest (LEF) LTER site in Puerto Rico, the only tropical forest site in the U.S. LTER network. Among other accomplishments, greater resolution of arthropod links within the food web at the LEF led to major revisions in hypotheses regarding food web properties (Reagan et al. 1996). Furthermore, entomological contributions to long-term, multidisciplinary research have demonstrated long-term responses of insects and other arthropods to various disturbances and environmental changes, as well as important roles in ecosystem processes. Engagement of
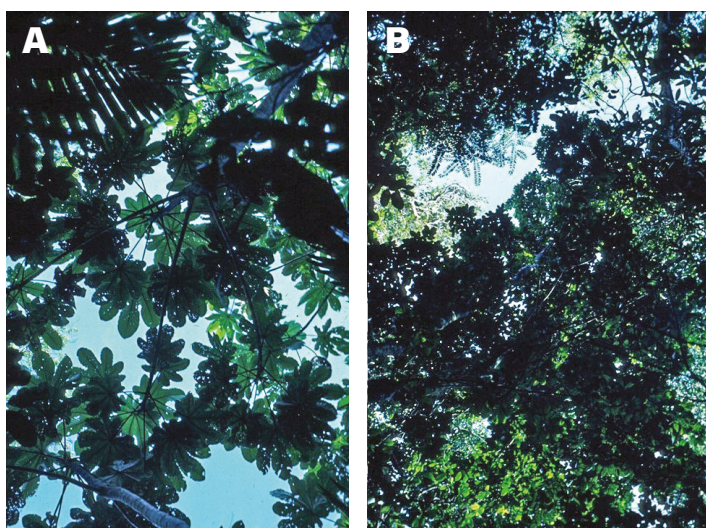

Fig. 2. Differences in canopy cover in experimental gap (A) and non-gap (B) plots at Luquillo Experimental Forest, Puerto Rico, in 1995. Note canopy dominance by *Cecropia schreberiana* in recovering gap.

entomologists in such studies is critical to understanding how environmental changes affect ecosystem structure, processes, and services.

Site Description

The LEF is located in the Luquillo Mountains of northeastern Puerto Rico and administered by the USDA Forest Service and the University of Puerto Rico. Mean monthly temperatures range from 25°C in January to 27°C in September (Waide et al. 2013). Precipitation averages 3,700 mm per year and varies seasonally, with 200-250 mm per month during January-April (dry season) and 350-400 mm per month during the remainder of the year (wet season) (Heartsill-Scalley et al. 2007, Waide et al. 2013). This site supports >468 native vascular plant species (>250 tree species), 78 vertebrate species, and >1,560 invertebrate species (Garrison and Willig 1996, Lawrence 1996, Reagan et al. 1996).

Dominant vegetation includes tabonuco, *Dacryodes excelsa* Vahl (Burseraceae), which represents 35% of the forest canopy below 600 m elevation (Brown et al. 1983); *Manilkara bidentata* (A.DC.) A. Chev. (Sapotaceae) and *Sloanea berteriana* Choisy ex DC. (Elaeocarpaceae) in the overstory; and *Prestoea acuminata* (Willd.) H.E. Moore (Arecaceae), *Miconia prasina* (Sw.) DC. (Melastomataceae), *Casearia arborea* (Rich.) Urb. (Salicaceae), and *Psychotria brachiata* Sw. (Rubiaceae) in the understory. Canopy height averages 20 m (Weaver and Gould 2013), and small light gaps occur infrequently in the otherwise closed canopy of mature forests. *Cecropia schreberiana* Miq. (Urticaceae) is an important early successional tree species. *Heliconia bihai* (L.) L. (Heliconiaceae), *Piper* spp. (Piperaceae), and other understory shrubs, vines, and herbs form a dense understory in gaps.

Tropical forests often are thought to be relatively stable. However, many tropical forests, including the LEF, are subject to frequent hurricane and drought disturbances, which alter the structure and composition of forest communities (Van Bael et al. 2004, Scatena et al. 2012, Waide et al. 2013). Prior to 1989, Puerto Rico had not experienced a major hurricane (≥ Category 3, >178 kph wind speed) for 33 years (Betsy in 1956), and a closed canopy with little understory characterized the forest. However, during the past 27 years, this site was struck directly by two major hurricanes, as well as by many minor hurricanes, tropical storms, landslides, and droughts (Brokaw and Grear 1991, Walker 1991, Heartsill-Scalley et al. 2007, Walker et al. 2013). Hurricane Hugo (1989, Category 4) caused >50% defoliation and reduced mean canopy height and plant biomass by >50% at the LEF (Brokaw and Grear 1991, Walker 1991, Scatena et al. 1996), leaving severely damaged patches (30-60 m diameter) with extensive tree-fall (gaps) in a matrix of damaged standing trees (non-gaps) (Fig. 1). Rapid refoliation, shoot growth, and seedling recruitment began 6-9 months later (Frangi and Lugo 1991). Stands of *C. schreberiana* saplings and other early successional plants developed in gaps, and some later successional species resprouted from stumps and fallen trees (Fig. 2). *Cecropia schreberiana* was uncommon, except in gaps, by 1995 due to canopy

closure (Fig. 2), but increased again following Hurricane Georges (1998, Category 3). Hurricanes Marilyn (1995), Bertha and Hortense (1996), and Debby (2000) caused substantial defoliation and flooding but did not create appreciable gaps in the canopy. Hundreds of landslides occurred as a result of these hurricanes and rainstorms (Walker et al. 2013). In addition, significant droughts (>20% reduction in annual rainfall) occurred during 1994 (the second driest year on record), when precipitation was only 41% of the long-term annual average, 1997 and 2002, and minor droughts (at least 15 consecutive days without rain) occurred in 1991 and 2001 (Heartsill-Scalley et al. 2007, Scatena et al. 2012, Waide et al. 2013). By contrast, rainfall during 1996 and 1998 was 20% higher than the long-term average (Waide et al. 2013).

Arthropod Responses to Disturbances

Long-term studies have provided valuable insight into factors that affect arthropod populations (Morris 1964). Particularly long records include nearly 2,000 years for the Oriental migratory locust, *Locusta migratoria manilensis* (Meyen), in China (Stige et al. 2007, Tian et al. 2011); 1,173 years for the larch budmoth, *Zeiraphera diniana* (Guenee), in the European Alps (Esper et al. 2007); and 622 years for the Pandora moth, *Coloradia pandora* Blake, in western North America (Speer et al. 2001). Such long records aid greatly in identifying environmental factors responsible for population change (Morris 1964). Outbreaks are frequently triggered by drought or other host-stressing events (Mattson and Haack 1987; Van Bael et al. 2004; Stige et al. 2007; Schowalter 2012, 2016). On the other hand, intolerant species may be eliminated by disturbances or require long periods for population recovery (Willig and Camilo 1991). However, long-term studies of entire faunas and factors affecting assemblage composition and structure, as these affect food web dynamics and ecosystem processes, are rare.

Schowalter et al. (2017) studied changes in canopy arthropod assemblages in replicate gap and non-gap plots at El Verde over a 19-year period following Hurricane Hugo (1991-2009). Six tree species were sampled in all plots to represent dominant early (*C. arborea*, *C. schreberiana*, and *P. acuminata*) and late (*D. excelsa*, *M. bidentata*, and *S. berteriana*) successional species, as well as overstory (*D. excelsa*, *M. bidentata*, *S. berteriana*, and *C. schreberiana*) and understory (*C. arborea* and *P. acuminata*) trees. Overstory trees were sampled using a long-handled insect net with a closeable plastic bag inserted in the net (Fig. 3). This technique permits collection of samples from up to 12 m in height, representing the mid-canopy in tabonuco forest (Schowalter and Ganio 1999, 2003). The bag was slipped over a foliage-bearing branch, closed with a drawstring, and the branch clipped from the tree. Understory species and sprouts or saplings in gaps were sampled either by this method or by hand-bagging branches within 3 m of the forest floor. Foliage from samples was pressed and dried at 50°C to constant weight to provide a measure of sample mass for use as a covariate.

This sampling technique likely underrepresented highly

Fig. 3. Branch bagging, using a long-handled insect net and closeable plastic bag insert, of canopy foliage for measurement of canopy arthropods by U.S. and Taiwanese colleagues at the Luquillo Experimental Forest in Puerto Rico.

mobile arthropods (e.g., bees, wasps, flies) and, therefore, is not favored for biodiversity studies. However, this technique is particularly useful for representing density and biomass of resident arthropods that are associated with the sampled plant and that have the greatest effect on foliage turnover and nutrient fluxes (Majer and Recher 1988, Blanton 1990, Schowalter 2016). Most arthropod herbivores and many arthropod predators in this forest are relatively sedentary and were collected with foliage samples, and even some highly mobile species were captured. Alternative sampling techniques, such as interception traps or canopy fogging, typically represent more species but are biased toward flying insects that may or may not be associated with particular plants or experimental treatments (Southwood 1978, Leather 2005, Schowalter 2016).

Nearly 12,000 individuals representing 171 taxa were collected, including 40 identified species, 63 morphospecies, and specimens identified to family (62) or order (six). Only 25 taxa (including five family and four order designations) were sufficiently abundant for analysis. Gap type (gap plots versus closed canopy plots), time after hurricane (number of days) and temporal variation in precipitation (total rainfall during 28 days prior
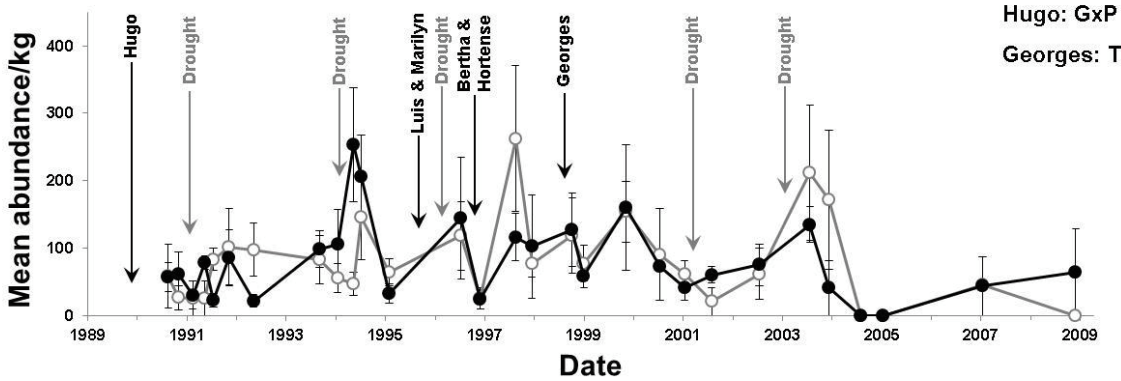
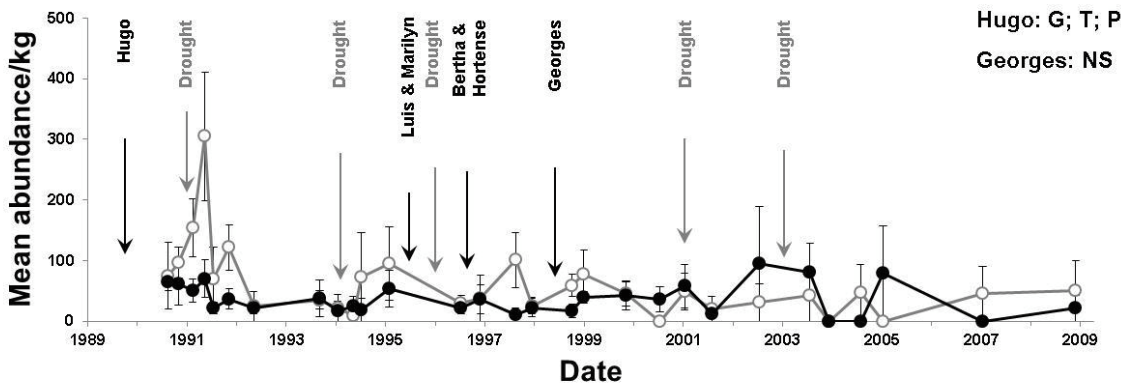## A) *Vinsonia stellifera* abundance on *Manilkara bidentata*
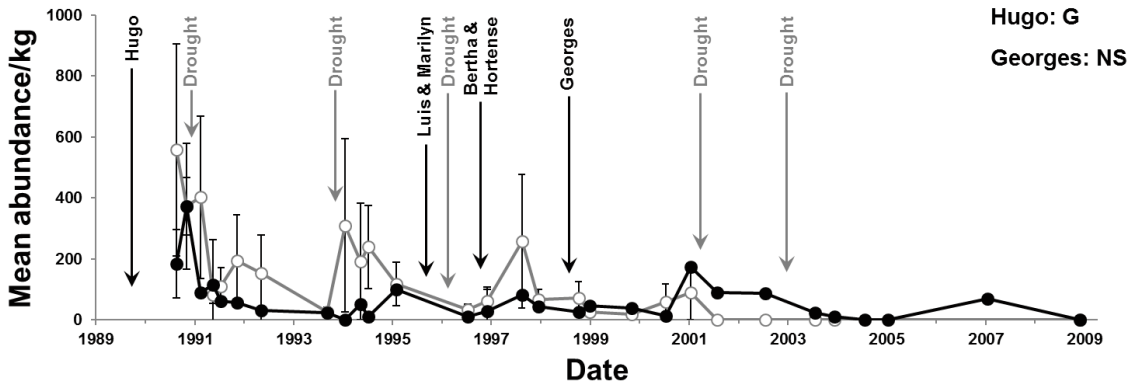
B) *Ceroplastes rubens* abundance on *Manilkara bidentata*
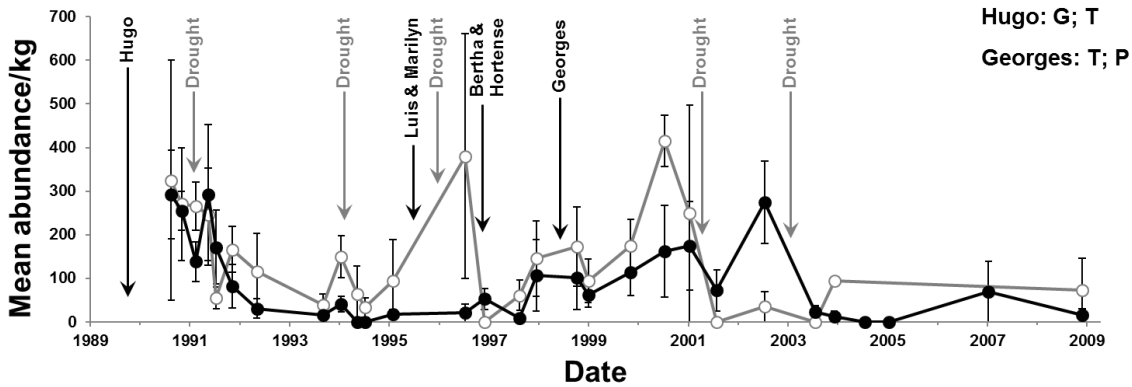
C) Detritivore abundance on *Sloanea berteriana*

D) Sap-sucker abundance on *Sloanea berteriana*

to each sample), as well as interactions among factors, were evaluated. Note that gaps sampled after Hurricane Hugo were canopy openings caused by Hugo, whereas gaps sampled after Hurricane Georges were not created directly by Georges, but rather represented a legacy of Hugo that persisted through subsequent disturbances (Schowalter et al. 2017).

All of these ecological drivers influenced canopy arthropod abundances and guild structure. Significant ($P < 0.05$) effects of gap, time after hurricane, or interactions were seen for 46% of taxon analyses and 37% of guild analyses. Responses of arthropod populations and guilds following Hurricane Georges (1998) significantly ($P < 0.05$) reflected effects of Hurricane Hugo nine years earlier. Furthermore, arthropod responses to time after both hurricanes showed significant ($P < 0.05$) effects of variation in precipitation, indicating strong legacy effects, i.e., contingency on responses to earlier events.

Responses among arthropod taxa were idiosyncratic (Schowalter et al. 2017). Sap-sucking Hemiptera, especially *Ceroplastes rubens* Maskell and *Vinsonia stellifera* (Westwood) (Hemiptera: Coccidae), significantly ($P < 0.05$) increased in abundance following hurricanes or droughts, reflecting responses to rapidly resprouting vegetation, and declined over time following disturbance (Fig. 4). By contrast, a tree cricket, *Cyrtoxipha gundlachi* Saussure (Orthoptera: Gryllidae), and two spiders, *Lyssomanes portoricensis* Petrunkevitch (Araneae: Salticidae) and *Modisimus* sp. (Araneae: Pholcidae), increased ($P < 0.05$) in abundance through time following disturbance, especially in non-gaps. At the guild level, sap-suckers and detritivores were significantly more abundant following hurricanes and droughts and declined in abundance with time following disturbance.

Arthropod Responses to Experimental Manipulation of Hurricane Effects

Evaluation of biotic responses to natural disturbances suffers from infrequent and unpredictable recurrence for replication. Furthermore, hurricanes induce two potentially confounding changes in forest ecosystems. First, treefall, branch breakage, and defoliation open the canopy and permit penetration of sunlight and precipitation directly to the forest floor. This increases temperature and soil moisture but also evaporation, with obvious consequences for small organisms sensitive to changes in temperature and relative humidity (Schowalter 2012). Second, the mass of material falling to the forest floor represents a pulse of litterfall and nutrients that alter

Fig. 4. Examples of scale insect and guild responses to a complex disturbance regime at Luquillo Experimental Forest, Puerto Rico. Mean abundances (number of individuals) per sample per kg dry weight of foliage for A) *Vinsonia stellifera* on *Manilkara bidentata*, B) *Ceroplastes rubens* on *M. bidentata*, C) detritivore guild on *Sloanea berteriana*, and D) sap-sucker guild on *S. berteriana*. Data represent long-term trends (19 years) in abundance (±1 SE) in response to hurricanes (black text and arrows) and droughts (gray text and arrows) on trees located in gaps created by hurricanes (open circles and gray lines) or non-gaps (filled circles and black lines) during 1991-2009. Significant effects from general linear mixed-effects models are noted on each panel: G, gap, P, precipitation, and T, time after hurricane.

Fig. 5. Trimmed plot with canopy debris in the Canopy Trimming Experiment at Luquillo Experimental Forest, Puerto Rico. All branches and trees were trimmed at 10 cm diameter to simulate canopy-opening effects of major hurricanes. (Compare to Fig. 1A.) Note malaise trap centered in each plot.

forest floor habitat and soil fertility and can trigger dramatic changes in biotic interactions (Lodge et al. 1994, Fonte and Schowalter 2004).

In order to evaluate hypotheses concerning disturbance effects, and particularly to separate the effects of these two factors, LEF researchers established an ambitious Canopy Trimming Experiment in 2005 to replicate the effects of canopy opening and debris deposition represented by a Category 3 hurricane (Shiels and González 2014, Shiels et al. 2010). Three replicate blocks were divided into four 30 x 30 m treatment plots (untrimmed control, untrimmed control with added debris, trimmed with added debris, trimmed with no debris). Two plots in each block had all boles and branches cut at 10 cm diam. (Fig. 5). The two remaining plots in each block were untrimmed controls. Debris from trimmed plots in each block was removed, weighed and redistributed on the forest floor of one trimmed and one untrimmed plot in each block.
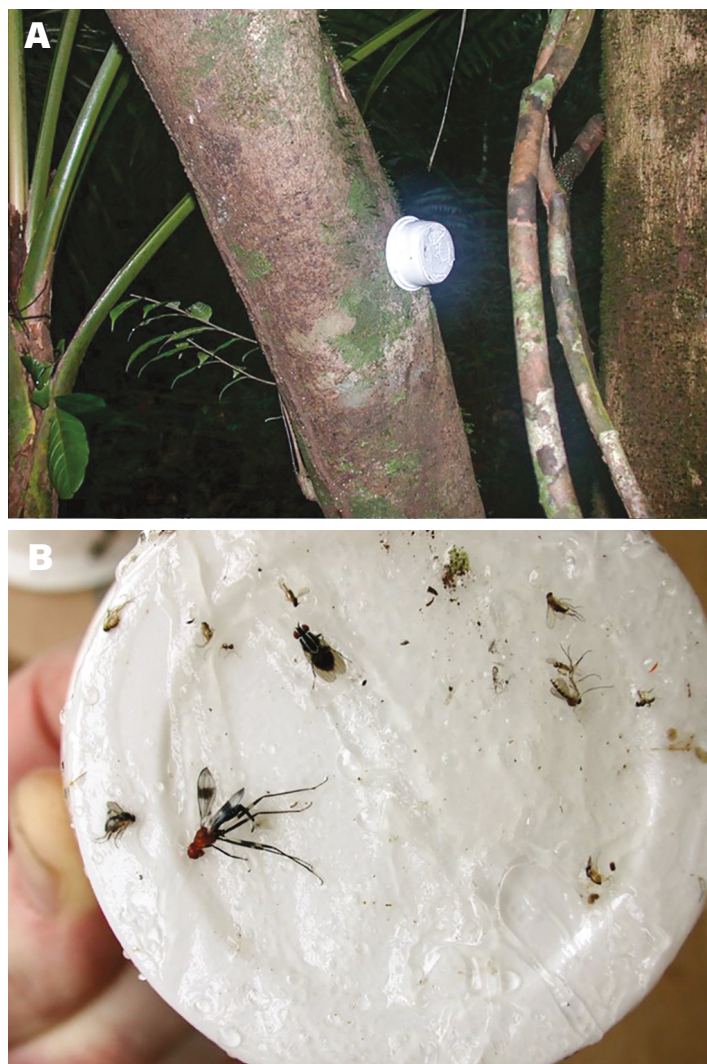
Fig. 6. Collection of arthropods in sticky traps at Luquillo Experimental Forest, Puerto Rico, for comparison with arthropod community in Dominican amber. A) Sticky trap used to simulate resin globules that trapped Miocene insects in amber; B) sticky trap with micropezid, phorid, mycetophilid and other Diptera collected over five days in January 2005.

Six arthropod taxa (three on *S. berteriana*, two on *M. bidentata*, and one on *D. excelsa*) showed significant (P < 0.05) responses to treatments as main effects or interactions (Schowalter et al. 2014). Only debris treatment had significant effects as a main factor. No significant responses were observed on early successional tree species. Leaf area removed, as a measure of herbivory, did not vary significantly by treatment.

Ceroplastes rubens on *M. bidentata* was three times more abundant in treatments with no added debris than in treatments with added debris, and *L. portoricensis* on *S. berteriana* was significantly more abundant in treatments with added debris than in other treatments. Abundance of *C. rubens* declined over time following treatment. Results for *C. rubens* seem anomalous compared to their responses to natural hurricane disturbance. Although the debris treatment was expected to increase nutrient availability for new shoot and foliage production (Wood et al. 2009), and thereby increase sap-sucking herbivore abundances

(Schowalter and Ganio 2003), several previous studies indicated that debris addition has the opposite effect at this site. Furthermore, the experimental debris pulse did not perfectly imitate that from a hurricane, given that debris removal, sorting, and weighing delayed debris redistribution in designated plots by about one month (Shiels et al. 2010), during which key nutrients such as nitrogen likely leached or were mineralized from decomposing litter. These data suggest that nutrient availability may have been limited in the debris pulse plots. Overall, the debris pulse had a greater effect on canopy arthropod abundances and diversity than did canopy opening, suggesting that changes in plant condition resulting from nutrient availability were more important for canopy arthropods than were the more direct and immediate changes in temperature and relative humidity.

In contrast, Richardson et al. (2010) reported that litter arthropods responded significantly to trimming but not to debris deposition. Their results indicated that the primary effect of hurricane disturbance on litter arthropods is through changes in habitat conditions resulting from canopy opening rather than from the pulse of debris to the forest floor.

Prather (2014) measured herbivory by insects on understory plant species in the same plots, using life table analysis of marked leaves, and found differential results for pioneer vs. non-pioneer plants. She concluded that pioneer plants experienced increased herbivory in trimmed plots as a result of their increased densities in response to canopy trimming, and that non-pioneer species experienced increased herbivory in debris addition plots as a result of their increased foliar quality in response to greater nutrient availability.

The plots were re-trimmed in 2015 to the same specifications as those in 2005, but without debris treatment. Continued sampling in these plots will address hypotheses regarding biotic responses to recurring disturbances.

Arthropods in Sticky Traps vs. Dominican Amber

Studies of arthropod assemblages in the fossil record can provide information on how assemblages have changed over evolutionary time (Boucot 1990). Studies at the LEF provide a unique opportunity to compare extant assemblages to those inferred from fossil amber deposits in the Caribbean.

Poinar and Poinar (1999) compiled data on inclusion of arthropod taxa in Dominican amber, representing a tropical hardwood forest from 25 million years ago. Their reconstruction of a Caribbean arthropod assemblage from a Miocene era tropical hardwood forest generally resembled canopy arthropod assemblages from the extant tropical hardwood forest at the LEF (see above), suggesting that forest arthropod assemblages in the Caribbean may have changed relatively little over this long time period.

This hypothesis was tested at the LEF using sticky traps (Fig. 6) designed to resemble resin globules that eventually could become amber. Seven small plastic cups (7 cm diameter x 5 cm tall) were coated with adhesive and placed on lower tree boles or on logs at one non-gap

Table 1. Frequency of inclusion of arthropod taxa in Dominican amber[1] (25 mybp) and sticky traps from the Luquillo Experimental Forest (LEF) in Puerto Rico (2004-2007).

Taxon	Amber	LEF
Diptera	0.31	0.52
Anisopodidae	0.004	0.006
Cecidomyiidae	0.07	0.05
Ceratopogonidae	0.03	0.006
Chironomidae	0.03	0.04
Chloropidae	0	0.006
Dolichopodidae	0	0.05
Drosophila	0	0.02
Micropezidae	0	0.01
Mycetophilidae	0.04	0.10
Phoridae	0.01	0.06
Psychodidae	0.03	0.01
Sarcophagidae	0	0.06
Scatopsidae	0.04	0
Sciaridae	0.02	0.02
Tachinidae	0	0.02
Tephritidae	0	0.006
Acalyptrate Diptera	0.05	0.08
Hymenoptera	0.37	0.18
Chalcidoidae	0.06	0.03
Formicidae	0.26	0.08
Apidae	0.05	0
Coleoptera	0.07	0.09
Curculionidae	0.04	0.03
Other Coleoptera	0.03	0.06
Lepidoptera	0.02	0.01
Trichoptera	0.006	0
Orthoptera	0.006	0.01
Blattaria	0.03	0
Thripidae	0.002	0
Hemiptera	0.03	0.02
Cicadellidae	0.01	0
Fulgoroidae	0.02	0.02
Collembola	0.007	0.04
Psocoptera	0.06	0.01
Myriopoda	0.002	0
Crustacea	0.001	0
Onycophora	0	0.006
Araneae	0.03	0.01
Acari	0.001	0.06

[1] Data from Poinar and Poinar (1999)

site at the LEF for five-day periods during June 2004, January and July 2005, July 2006, and July 2007 (total: 35 samples). Samples were dominated by Diptera (89% of specimens), with phorids representing 60%, mycetophilids 16%, dolichopodids 4%, sarcophagids 2%, cecidomyiids and chironomids 1% each, and other Diptera 5%. Other collected taxa included Hymenoptera (6% of specimens), with chalcidoid wasps 4%, *Wasmania auropunctata* (Roger) (Hymenoptera: Formicidae) ants 1%, and other Hymenoptera 1%; Coleoptera (2% of specimens), with curculionids 1% and other Coleoptera 1%; and a variety of other insects, spiders, and mites representing 3%. Two small *Anolis* lizards and a small *Eleutherodactylus* frog also were captured. Arthropod compositions in sticky traps from the LEF and in Dominican amber were similar (Table 1).

Arthropod Effects on Ecosystem Processes

Arthropods are capable of controlling rates of ecosystem processes such as primary production, succession, decomposition, and nutrient fluxes (Hunter et al. 2012, González et al. 2014, Hunter 2016, Schowalter 2016). Changes in arthropod assemblages, especially during outbreaks, have consequences for ecosystem processes. For example, Torres (1992) reported that a sequence of Lepidoptera species appeared and defoliated a corresponding sequence of early successional host plant species during the first six months following Hurricane Hugo (1989) in Puerto Rico, but disappeared after depleting their resources, thereby advancing succession during recovery from this disturbance. Schowalter (unpubl. data) observed this process following Hurricane Georges, with *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae) rapidly defoliating *Phytolacca rivinoides* Kunth & Bouché, *Urera baccifera* (L.) Gaudich. ex Wedd., and other early successional hosts, and *Cosmosoma myrodora* Dyar (Lepidoptera: Erebidae) rapidly defoliating *Mikania cordifolia* (L. F.) Willd. (Fig. 7). Reduced groundcover allowed later successional species to flourish in the wake of these outbreaks. Herbivore-induced alteration of vegetation structure affects nutrient fluxes and microclimate (Chapman et al. 2003, Classen et al. 2005, Schowalter 2016).

Folivorous Lepidoptera, Coleoptera, and Orthoptera that dominate mature forest communities cause turnover of foliage material to the forest floor as solid foliage fragments (greenfall), insect feces and carcasses, and enriched throughfall (precipitation augmented with nutrients leached from chewed foliage during percolation through vegetation) (Fonte and Schowalter 2005, Frost and Hunter 2007). Nutrients are mineralized from these materials through a relatively slow processes of decomposition that facilitates uptake by plants (Christenson et al. 2002, Frost and Hunter 2007, Wood et al. 2009). By contrast, sap-sucking Hemiptera that dominate early successional communities cause turnover primarily as liquid honeydew that is quickly immobilized by microorganisms before reaching the ground (Stadler and Müller 1996, Stadler et al. 1998, 2001).

Pulses in the availability of soil nitrogen are particularly distinct in seasonally dry, tropical rainforests such as
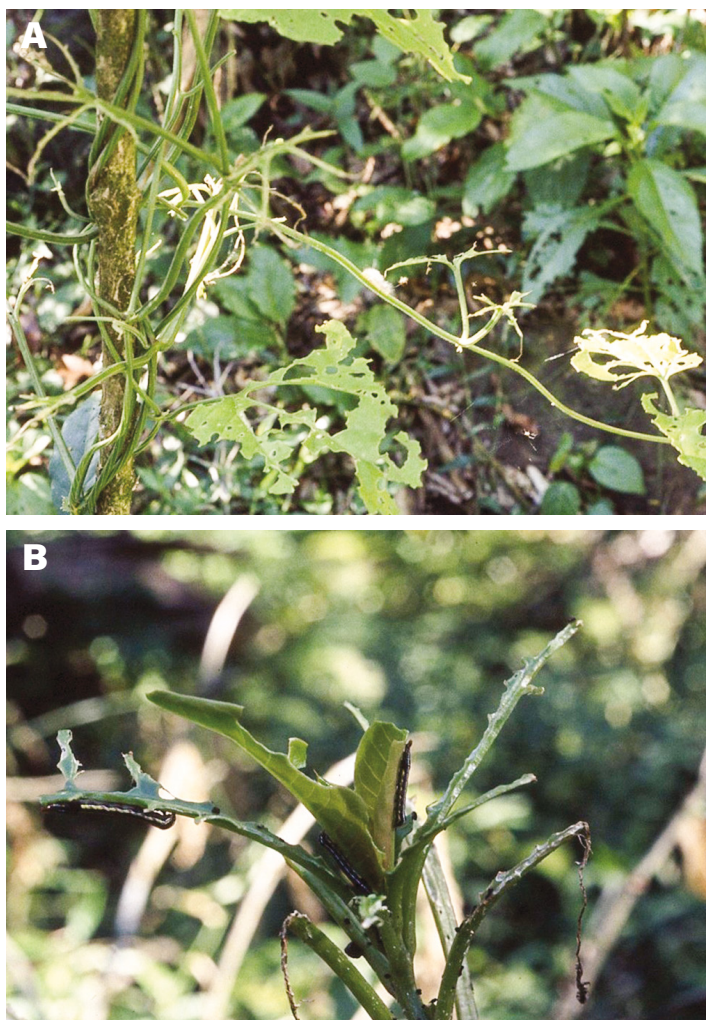
Fig. 7. Examples of Lepidoptera outbreaks on early successional plants following Hurricane Georges in early 1999. A) *Cosmosoma myrodora* **on** *Mikania cordifolia*; **B)** *Spodoptera eridania* **on** *Phytolacca rivinoides*.

the LEF and may be instrumental in disrupting microbial immobilization of nutrients, permitting greater plant uptake and productivity but potentially increasing nutrient export (Lodge et al. 1994). Insect outbreaks also create pulses in nutrient fluxes that can alter biotic interactions (Christenson et al. 2002, Frost and Hunter 2007, Schowalter et al. 2011).

Fonte and Schowalter (2005) established replicated inclusion/exclusion cages to measure the effect of herbivory by walkingsticks, *Lamponius portoricensis* Rehn (Phasmida: Pseudophasmatidae), on understory *Piper glabrescens* (Miq.) C. DC. at the LEF. Forty *P. glabrescens* of similar size (1 m height) and foliage density were enclosed in cages (60 cm x 60 cm x 60 cm, 3.2 mm nylon mesh) suspended above the ground from a 2 m PVC pole (Fig. 8). Cages were assigned randomly to four treatments: high and low levels of herbivory, herbivore exclusion, and control. The controls had large (25 cm x 25 cm) openings cut in the underside of the cage to allow free access by herbivores, while the upper portion and sides were left intact in order to maintain microclimatic

and shading conditions similar to the other treatments. The low-herbivory treatment contained one adult male *L. portoricensis* in each cage, and the high-herbivory treatment had one adult male and one adult female *L. portoricensis* in each cage. Total leaf area and leaf area missing were measured for five randomly chosen leaves of each plant prior to treatment, after one month, and after two months.

Total herbivory, expressed as leaf area removed, was subdivided into two components of herbivore inputs: greenfall (green leaf fragments larger than 5 mm x 5 mm) and frass (calculated as the difference between total leaf area removed and greenfall, although this component also could include fine greenfall). The portion of leaf area removed in the form of greenfall was measured by collecting fallen leaf fragments trapped in the enclosures every two to four days.

Ion-exchange resin bags were used to measure nutrient flux to the soil under each cage (Binkley and Matson 1983; Binkley et al. 1986). Resin bags were constructed from nylon stockings and contained one compartment each of positively and negatively charged resin beads. Each compartment was approximately 16 cm^2 and filled with 10 g of resin. Each resin bag was placed on the forest floor surface, centered directly under each cage. Resin bags placed in this manner provided relative comparisons of nutrient inputs to the soil from above. Resin bags were collected after 64 days and analyzed for NO_3, NH_4, and PO_4.

Litterbags were used to measure leaf decomposition rates under each cage. Recently senesced leaflets of *D. excelsa* were collected, air-dried for 48 hours, and thoroughly mixed before weighing. Litterbags (10 cm x 10 cm, 1 mm nylon mesh) were filled with 2.5 g ± 0.1 g air-dried litter. Subsamples collected during litterbag construction were used to obtain an oven-dry (50ºC) weight conversion for the air-dried leaves. Four litterbags were placed beneath each cage and collected after nine, 18, 47, and 76 days in the field. All litterbags were oven-dried at 50ºC for seven days upon collection.

As expected, herbivory treatments caused significantly ($P < 0.05$) different levels of leaf area removal (Fonte and Schowalter 2005). Leaf area removed was lowest in the herbivory exclusion treatment (< 6%) and highest in the high-herbivory treatment (>90%), with many plants experiencing complete foliage removal. Greenfall accounted for 46% of the total leaf area lost. Nitrate flux was significantly ($P < 0.05$) positively related to leaf area removed, greenfall, and frass input (Fonte and Schowalter 2005). Litter decomposition rate was significantly positively related to frass input (Fonte and Schowalter 2005).

Schowalter et al. (2011) subsequently manipulated inputs of foliage fragments, frass, and throughfall in small (0.11 m^2) experimental plots to evaluate their independent effects on nutrient fluxes, measured as nutrient absorption in resin bags and litter decomposition rates in each plot. Background rates of greenfall and frass were measured monthly using litterfall collectors and augmented in designated plots the following month by adding 10-fold greenfall (Fig. 9) or 10-fold frass (collected from walkingsticks and

Fig. 8. Exclosure/enclosure used to evaluate effects of walkingsticks, *Lamponius portoricensis*, on foliage loss and nutrient fluxes from *Piper glabrescens* at the Luquillo Experimental Forest, Puerto Rico.

grazing on microfungi controls the rate of litter decomposition and mineralization.

Cross-Site Comparison

A benefit of working with the LTER or similar networks is opportunities to compare data among sites and networks with similar or contrasting environmental conditions. For example, comparison of canopy arthropod responses to canopy-opening disturbances among three contrasting forest types—tropical rainforest at the LEF (Schowalter et al. 2017), temperate deciduous forest at the Coweeta Hydrologic Laboratory LTER site in North Carolina (Schowalter and Crossley 1988), and boreal coniferous forest at the H.J. Andrews Experimental Forest LTER site in Oregon (Schowalter 1995)—indicated that Lepidoptera consistently decrease in abundance and Hemiptera consistently increase in abundance following canopy-opening disturbances. Similarly, manipulation of herbivore abundance or herbivore inputs to litter at these three sites indicated similar effects on nutrient fluxes (Seastedt et al.1983, Schowalter et al. 1991, Reynolds and Hunter 2001, Fonte and Schowalter 2005, Frost and Hunter 2007).

Globally, comparable sites in other networks provide replicate sites within biomes. The Fushan LTER site, the oldest site in the Taiwan Ecological Research Network (TERN), is similar to the LEF in latitude (24° N), climate (mean annual temperature 18°C, mean annual precipitation 4,000 mm), forest structure, and cyclonic storms (typhoons) (Lin et al. 2011). However, the forest at Fushan is dominated by temperate species belonging to the Lauraceae, rather than tropical species, and major storms (>157 kph) occur more frequently (8-12 years) at Fushan (Mabry et al. 1998, Lin et al. 2011) than at the LEF (50-60 years) (Scatena 1995). Consequently, the canopy is shorter at Fushan (10 m vs. 20 m), tree species show less

caterpillars in the lab). Throughfall fluxes of NH_4, NO_3, and PO_4 (but not water) were doubled in treatment plots, based on published rates of fluxes of these nutrients in throughfall at the LEF (McDowell 1998). These treatments simulated the turnover expected from a low to moderate outbreak of folivores in this forest. Control plots received only background flux rates for these compounds but the same minimum amount of distilled water. Frass addition significantly increased NO_3 and NH_4 fluxes, and frass and throughfall additions significantly reduced decay rate compared to controls. Reduced decay rate suggests that nitrogen flux was sufficient to inhibit microbial decomposition activity, a result consistent with that in the Canopy Trimming Experiment (see above, Schowalter et al. 2014). These results demonstrated that herbivores, at low to moderate outbreak levels, would be expected to increase ecosystem-level N and P fluxes by >30% at the LEF.

Litter invertebrates are instrumental in controlling decomposition rates. González et al. (2014) reported that litter invertebrates can be responsible for up to 66% of litter decomposition rate in tabonuco forest at the LEF and were significantly correlated with decomposition and mineralization processes in the Canopy Trimming Experiment. They suggested that the rate of collembolan

Fig. 9. Experimental plot to evaluate effects of manipulated greenfall (shown here), frassfall, and throughfall on nutrient fluxes on the forest floor at the Luquillo Experimental Forest, Puerto Rico.

variation in susceptibility to wind damage, and gaps are less frequent and typically limited to fall of individual taller trees (Lin et al. 2011). Comparison of canopy arthropod responses to major storms at the two sites indicated that arthropod guild structure showed much less variation in response to gap formation at Fushan than at the LEF (W.-J. Wu, J.-T. Chao, H.-K. Luh, M.R. Willig, S.J. Presley and T.D. Schowalter unpubl. data). Comparative sampling in Louisiana following Hurricane Katrina (2005) suggested that these differences in arthropod responses reflect the phylogeny of sampled forest trees more than they do differences in disturbance frequency (TDS unpubl. data). González and Seastedt (2001) compared litter decomposition and soil fauna at tropical wet (LEF), tropical dry (Guánica Biosphere Reserve, Puerto Rico), and north- and south-facing subalpine (Niwot Ridge LTER site, Colorado) sites and found that soil fauna had a disproportionately larger effect on litter decomposition at the tropical wet site, compared to the subalpine and tropical dry sites.

Conclusions

Insects respond dramatically to changes in environmental conditions and are capable of engineering additional changes in ecosystem structure and function. The Luquillo Experimental Forest LTER site provides an example of the contributions of entomological research to understanding arthropod responses to storm and drought disturbances and their effects on primary production and nutrient fluxes. Future plans include research on climate change, using the natural climatic variation along an elevation gradient, to predict how arthropod communities will change as climate becomes warmer and drier (González et al. 2013).

Long-term studies are necessary to evaluate factors that affect arthropod responses and to demonstrate how the history of disturbance events can shape arthropod assemblages and their effects on ecosystem structure and function at a site. Entomologists clearly can contribute substantially to these studies and can benefit from integration of entomological data with broader ecosystem variables. For more information on the U.S. LTER network and to explore opportunities for collaborative research, visit www.lternet.edu.

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T.D. Schowalter, Entomology Department, Louisiana State University Agricultural Center, Baton Rouge, LA 70803