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Post-Hurricane Successional Dynamics in Abundance and Diversity of Canopy Arthropods in a Tropical Rainforest

T. D. Schowalter,[1,2] M. R. Willig,[3] and S. J. Presley[3]

[1]Department of Entomology, Louisiana State University Agricultural Center, Baton Rouge, LA 70803 (tschowalter@agcenter.lsu.edu), [2]Corresponding author, e-mail: tschowalter@agcenter.lsu.edu, and [3]Center for Environmental Sciences and Engineering and Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269 (michael.willig@uconn.edu; steven.presley@uconn.edu)

Abstract

We quantified long-term successional trajectories of canopy arthropods on six tree species in a tropical rainforest ecosystem in the Luquillo Mountains of Puerto Rico that experienced repeated hurricane-induced disturbances during the 19-yr study (1991–2009). We expected: 1) differential performances of arthropod species to result in taxon- or guild-specific responses; 2) differences in initial conditions to result in distinct successional responses to each hurricane; and 3) the legacy of hurricane-created gaps to persist despite subsequent disturbances. At least one significant effect of gap, time after hurricane, or their interaction occurred for 53 of 116 analyses of taxon abundance, 31 of 84 analyses of guild abundance, and 21 of 60 analyses of biodiversity (e.g., richness, evenness, dominance, and rarity). Significant responses were ~60% more common for time after hurricane than for gap creation, indicating that temporal changes in habitat during recovery were of primary importance. Both increases and decreases in abundance or diversity occurred in response to each factor. Guild-level responses were probably driven by changes in the abundance of resources on which they rely. For example, detritivores were most abundant soon after hurricanes when litter resources were elevated, whereas sap-suckers were most abundant in gaps where new foliage growth was the greatest. The legacy of canopy gaps created by Hurricane Hugo persisted for at least 19 yr, despite droughts and other hurricanes of various intensities that caused forest damage. This reinforces the need to consider historical legacies when seeking to understand responses to disturbance.

Key words: Biodiversity, disturbance, hurricane, legacy, drought

Few investigations have documented long-term successional trajectories of insects or other animals to repeated, high-intensity disturbances (Schowalter and Ganio 2003; Turner et al. 2003; Bloch and Willig 2006; Willig et al. 2011, 2012; Schowalter 2012; but see Bloch et al. 2007, Prates et al. 2010). Because of logistic constraints, studies of responses to multiple, high-intensity disturbance events at the same site are rare (Turner et al. 1997) and typically focus on short-term responses (Lopez et al. 2003, Schoener et al. 2004). Long-term research is critical because short-term studies that represent before-and-after "snapshots" provide incomplete or even misleading impressions of the effects of disturbance on populations, communities, or ecosystem processes (Adams 2001). Moreover, the demographics of various species at the time of each event may influence the direction and magnitude of subsequent responses and vulnerability to future events (Willig et al. 2012, 2014). For example, past disturbances can influence responses to ensuing events (i.e., legacy effects), thereby confounding attempts to understand responses to disturbance. Legacy effects have been detected at least 50 yr after disturbances (Willig et al. 1998, 2007, 2012; Schowalter et al. 2003,

Summerville et al. 2009, Uriarte et al. 2009). Similarly, the effects of gaps created by one disturbance may be detectable even after subsequent disturbances, creating "gap legacy effects."

Cyclonic storms (i.e., hurricanes, cyclones, and typhoons) and droughts are major natural disturbances that affect the structure and dynamics of tropical and subtropical forests (Van Bael et al. 2004, Turton 2008, Li and Duan 2010, Scatena et al. 2012, Vogt et al. 2016). Hurricane-induced loss of forest canopy alters abiotic (e.g., understory light, temperature, and moisture) and biotic (e.g., changes in resource abundance and diversity) conditions (Shiels and González 2014). Faunal components of ecological systems are strongly affected by immediate impacts of a disturbance (e.g., mortality and redistribution of individuals), as well as by the subsequent changes in abiotic conditions (e.g., temperature and moisture) and attendant spatiotemporal variation in the composition and structure of plant assemblages (Walker et al. 1991, Willig and McGinley 1999, Schowalter 2012). In addition, environmental characteristics of nearby sites can influence succession by providing sources of colonists for disturbed areas (Willig et al. 2007). Arthropod responses to

disturbances, particularly outbreaks of herbivorous species, have the capacity to alter patterns of primary production, biogeochemical cycling, and ecosystem recovery (Mattson and Addy 1975, Belovsky and Slade 2000, Schowalter et al. 2011, Schowalter 2012). Post-disturbance outbreaks affect qualitative and quantitative responses of the community to ensuing disturbances (Knapp and Seastedt 1986, Jenkins et al. 2008, Taylor and MacLean 2009). Such contingency is a fundamental characteristic of ecological systems (Scheiner and Willig 2011). Understanding the effects of intense tropical storms on ecosystems is of increasing importance because such cyclonic storms are becoming more frequent as a consequence of global climate change (Webster et al. 2005, Villarini and Vecchi 2013). The Caribbean Basin is characterized by high cyclonic activity with the composition and structure of the biota molded by a disturbance regime dominated by hurricanes and high-energy storms (Scatena et al. 2012). In addition, the Caribbean is experiencing a drying trend that may be related to global warming (Neelin et al. 2006, Scatena et al. 2012). The Luquillo Experimental Forest (LEF) of Puerto Rico experiences multiple types of recurring disturbances, including hurricanes, droughts, and landslides (Scatena et al. 2012, Waide et al. 2013, Walker et al. 2013). Consequently, this system is ideal for testing predictions of contemporary succession theory (Pickett et al. 2011) in a tropical rainforest.

We used data on canopy arthropods from the LEF during a 19-yr period following Hurricane Hugo to evaluate responses of taxa, foraging guilds, and assemblages on particular host tree species to a complex disturbance regime that included two major hurricanes and multiple storms and droughts. Based on autecological knowledge of canopy arthropods in the LEF, we expected that taxon-specific performances would manifest as changes in either taxon or guild abundance. More specifically, we expected sap-sucking canopy arthropods to be more abundant in gaps than in closed canopy forest following hurricanes due to greater abundance of new vegetative growth. We expected canopy detritivores to be more abundant during dry conditions and soon after hurricanes due to pulses of litter caused by these events (Schowalter and Ganio 2003). We predicted that differences in conditions before each hurricane would result in hurricane-specific successional responses. Hurricane Hugo (hereafter Hugo, a Category 4 storm) was the first major hurricane (≥Category 3 storm) experienced by the LEF in 33 yr, whereas Hurricane Georges (hereafter Georges, a Category 3 storm) occurred only 9 yr after Hugo (Lomascolo and Aide 2001). Therefore, we expected arthropod responses to each hurricane to reflect differences in the number of large trees susceptible to hurricane damage, differences in the successional stage of the forest, and differences in species availability at the time of each hurricane. Finally, because the legacy of disturbance can last many decades (Thompson et al. 2002, Schowalter et al. 2003, Summerville et al. 2009), we expected the legacy of gaps created by Hugo to remain detectable following Georges.

Materials and Methods

Site Description

El Verde Field Station (18° 10′ N, 65° 30′ W) is 10 km south of Río Grande, Puerto Rico (McDowell et al.2012), in the Luquillo Mountains. It is administered by the USDA Forest Service, in association with El Yunque National Forest, and by the University of Puerto Rico. Mean monthly temperatures range from 25°C in January to 27°C in September (Brown et al.1983, Waide et al. 2013). Precipitation averages 3,668 mm per year and varies

seasonally, with 200–250 mm per month in January–April and 350–400 mm per month in the remainder of the year (McDowell and Estrada-Pinto 1988, Heartsill-Scalley et al.2007, Waide et al. 2013).

Vegetation surrounding the field station is dominated by tabonuco, *Dacryodes excelsa* Vahl (Burseraceae), which represents 35% of the forest canopy below 600-m elevation (Brown et al.1983). Other canopy dominants include *Manilkara bidentata* (A.DC.) A.Chev. (Sapotaceae) and *Sloanea berteriana* Choisy ex DC. (Elaeocarpaceae). *Prestoea acuminata* (Willd.) H.E. Moore (Arecaceae), *Miconia prasina* (Sw.) DC. (Melastomataceae), *Casearia arborea* (Rich.) Urb. (Salicaceae), and *Psychotria brachiata* Sw. (Rubiaceae) are major subcanopy species. 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.

The LEF is subject to frequent hurricanes, which alter the composition of forest communities (Scatena et al.2012). Before 1989, Puerto Rico had not experienced a major hurricane (≥Category 3 storms) for 33 yr (Betsy in 1956), and a closed canopy characterized the forest. However, during the past 27 yr, 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). Hugo (1989) caused 100% defoliation and reduced plant biomass by 50% at the LEF, leaving severely damaged patches (30–60 m in diameter) with extensive tree-fall (gaps), interspersed with areas where most or all trees remained standing (non-gaps). Rapid sprouting, refoliation, and seedling recruitment began 6–9 mo later, during early 1990 (Frangi and Lugo, 1991). Stands of *C. schreberiana* saplings and other early successional plants, particularly *H. bihai*, developed in gaps, and some later successional species resprouted from stumps and fallen trees. *Cecropia schreberiana* was uncommon at the site by 1995 because of canopy closure (Schowalter, personal observation), but it was common in new gaps created by Georges in 1998 caused substantial defoliation and flooding but did not create appreciable gaps in the canopy. Hundreds of landslides occurred because of these hurricanes and rainstorms (Walker et al. 2013). In addition, significant droughts (>20% reduction in annual rainfall) occurred during 1994 (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 1991and 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).

Experimental Design

Six blocks, each large enough to include one gap and one non-gap plots, were established in February 1991 (18 mo after Hugo, about 9 mo after recovery began) over an 11-ha area at about 380 m of elevation (Schowalter and Ganio 1999). Blocks were separated by at least 50 m. Each block included paired 30- to 50-m-diameter plots representing a gap and a nearby non-gap, with paired plots separated by 30- to 50-m distances (Schowalter and Ganio 1999). Gaps were defined as canopy openings, in which all or most trees fell or had the main stem broken during Hugo; non-gaps represented plots in which few, if any, canopy trees fell or were damaged severely. At

the beginning of this study, canopy coverage above 2 m in height above the ground was 10–20% in gaps and 70–80% in non-gaps. Foliage in non-gaps was largely concentrated along main boles and large branches, and small saplings of *C. schreberiana* and other early successional species occurred where sunlight penetrated the forest floor. All the plots established after Hugo were affected by subsequent hurricanes and droughts as part of a dynamic disturbance regime. Consequently, we continued to quantify successional trajectories of canopy invertebrates in these plots to assess legacy effects during secondary succession. Unfortunately, no data on community structure of canopy arthropods before Hugo are available.

Sampling Methods

Samples were collected from foliage (as described below) during 1991–1992, 1994–1995, 1997–2005, 2007, and 2009. During 1991 and 1992, samples were collected every 2–4 mo (February, June, September, and November) to represent seasonal differences in arthropod abundances. Through 2005, samples were collected during January–February and June–July. Because analyses indicated no significant seasonal differences in arthropod abundances (Schowalter and Ganio 2003), sampling was reduced to a single period, June–July, during the wet season. No samples were collected in 1993, 1996, 2006, or 2008.

Six tree species were selected for study 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. One tree of each species was sampled in each plot at each sample time. In gap plots, samples typically were taken from stump sprouts or saplings. Canopy invertebrates were sampled during 29 time periods from 1991 through 2009, resulting in a total of 1,395 samples from six host tree species. *Casearia arborea* had the fewest samples (183) and *S. berteriana* had the most (269).

Overstory trees were sampled using a long-handled insect net with a closeable plastic bag inserted in the net. 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, and the branch clipped from the tree. Understory species and sprouts or sapling in gaps were sampled either by this method or by hand-bagging branches within 3 m of the forest floor. In each plot at each sampling time, one accessible branch was collected from one randomly chosen tree of each host species (if present). Branches were usually ∼50 cm in length and no more than 1 cm in diameter at the point of excision. Although a particular tree could have been sampled more than once during the study for tree species with low abundance in a plot, samples were never taken from the same branch. This sampling phenomenon was most common for *C. schreberiana*, an early successional species that dies under closed canopies. 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 (see below).

Our sampling technique likely underrepresented highly mobile arthropods (e.g., bees, wasps, and flies). However, this technique is particularly useful for representing density and biomass of resident arthropods that feed over periods of weeks to months on resources associated with the sampled plant, and that have the greatest effect on foliage turnover and nutrient flux (Majer and Recher 1988, Blanton 1990). Most arthropod herbivores and many arthropod predators are relatively sedentary and were collected with foliage samples, and even some highly mobile species were captured.

Sampling regimes that use light traps, interception traps, or canopy fumigation are biased toward the capture of flying adult insects and do not capture important and abundant sedentary groups that respond significantly to disturbance, such as scale insects, leaf miners, and gall formers (Schowalter and Ganio 1999, 2003). Alternative sampling techniques often yield more species, but branch bagging yields greater abundances of species that characterize particular plants (Majer and Recher 1988, Blanton 1990). We emphasize that our objective was not to represent arthropod biodiversity of the forest exhaustively, but rather to evaluate the extent to which arthropods collected with a consistently used protocol revealed long-term successional responses to disturbance events in gap versus non-gap settings.

All invertebrates in each sample were identified to the lowest possible taxonomic rank. Abundant or well-known taxa were identified to genus or species by specialists at the USDA Systematic Entomology Lab in Beltsville, MD. Most taxa were identified to either genus or family by the senior author, using collections at El Verde Field Station, and by systematics colleagues at Oregon State University (for samples from 1991 to 2003) and Louisiana State University (for samples from 2003 to 2009). Many taxa could not be accurately identified owing to lack of reference material but were sorted into "morphospecies."

Quantitative Analysis

We evaluated the effect of hurricane-induced canopy loss (gaps vs non-gaps), time after hurricane, and variation in precipitation on various characteristics of the canopy arthropod fauna (i.e., abundances of taxa, abundances of foraging guilds, and taxonomic diversity of assemblages). Because droughts are not discrete events in time, but reflect temporal variation in precipitation, we used measured cumulative precipitation for 28 d before sampling as our treatment effect for analyzing arthropod responses to conditions that may reflect normal rainfall, elevated rainfall, or drought conditions.

Analyses were conducted separately for each host tree species because previous work (Schowalter and Ganio 2003) has shown that arthropod assemblages are relatively distinct among the selected host trees. We measured responses of each arthropod taxon that was sufficiently frequent and abundant (i.e., present in at least 10% of samples from a particular species of tree) to warrant statistical analysis. Analyses for taxa with lower frequencies of occurrence would have little statistical power. Morphospecies represented by one to three individuals were combined into higher taxonomic categories (e.g., family) for analysis of taxon or guild abundance. We did not conduct analyses for all trees combined for the following four reasons: 1) the aforementioned differences in temporal variation in sampling effort for each host tree, 2) most tree species in tabonuco forest were not sampled, 3) tree species were not sampled in the proportion of their occurrence in the forest, and 4) previous research has demonstrated significant differences in arthropod species' composition among tree species (Schowalter and Ganio 2003). Therefore, analyses of combined data would not accurately evaluate changes in either abundance or taxonomic diversity over time or at the forest level.

The amount of vegetation in a sample could affect the abundance or diversity of associated arthropods. Therefore, dry foliage mass was included as a covariate in all analyses to remove potential effects of variation in the sample volume before evaluation of the full factorial model. Gap was a model I treatment factor, time after hurricane and precipitation were continuous variables, and block was a model II treatment factor. We were not interested in block effects,

per se. Rather, experimental blocks controlled for unknown environmental variation in forest characteristics that were associated with geographic gradients and that might affect arthropod abundance or diversity. Inclusion of blocks as a random effect removed spatial variation associated with the blocks, and it is a recommended design to avoid pseudoreplication (Hurlbert 1984). Analyses were conducted in R (R Core Team 2015) using the nlme package (Pinheiro et al. 2014).

We used linear mixed-effects models (Pinheiro and Bates 2000) to evaluate the responses of taxon abundances, guild abundances, and taxonomic diversity to disturbance. Gap (gap plots vs closed canopy plots) and time after hurricane (number of days) estimated effects associated with intense hurricanes. In addition, we evaluated effects of temporal variation in precipitation (total rainfall during 28 d before each sample) and if responses to hurricanes are contingent on precipitation, as droughts may affect long-term patterns of response. Analyses were conducted separately for each hurricane, with data from 1991 to 1998 evaluating effects after Hugo and data from 1999 to 2009 evaluating effects after Georges. Because of our sampling design, an important distinction exists in the ecological interpretation of "gap effects" after Hugo versus those after Georges. Gaps sampled after Hugo were hurricane-induced openings caused by Hugo, which we interpret as gap effects. In contrast, gap plots sampled after Georges were not hurricane-induced openings created by Georges. Rather, gaps created by Hugo and closed before Georges thus represent an estimate of "gap legacy effects" that persist after the impact of Georges

Canopy arthropods represent multiple foraging guilds (Schowalter and Ganio 2003, Schowalter 2016), including folivores (orthopterans, lepidopterans, and coleopterans), sap-suckers (particularly hetmipterans), detritivores (arboreal blattids, psocopterans, collembolans, and oribatid mites, as well as taxa that migrate from the forest floor to the canopy), omnivores (primarily formicids), predators (coleopterans, hetmipterans, dipterans, hymenopterans, and arachnids), and miscellaneous foragers (dipterans and hymenopterans), as well as emergent aquatic species (plecopterans, dipterans, and trichopterans). At the guild level, abundances for all species belonging to a particular guild were summed to represent that guild's abundance.

Because biodiversity is a multidimensional concept, we estimated five taxonomic metrics that differ with respect to consideration of species abundances. These metrics included the following: 1) taxon richness (i.e., the number of captured taxa), 2) evenness estimated as the Camargo index (Camargo 1993), 3) dominance estimated as the Berger–Parker index (Berger and Parker 1970), 4) diversity estimated as the Shannon–Wiener index (Pielou 1966), and 5) rarity estimated as the number of taxa in a sample whose relative abundance was less than 1/S, where S is the number of taxa obtained from all samples from a particular tree species. All individuals from each sample were used to estimate diversity, including species that were not sufficiently common to be analyzed at the taxon level.

To facilitate statistical analysis, each diversity metric was transformed to its effective number of species (hereafter "numbers equivalent"). For the taxonomic dimension, the numbers equivalent is the number of species with equal abundance that is required to produce the empirical value of a metric (Jost 2006). This transformation facilitates intuitive interpretation of differences associated with treatments, because indices are expressed in the same units and have the necessary mathematical properties that facilitate logical comparison and statistical analysis. Metrics that represent taxon counts (e.g., taxon richness and rarity) are numbers equivalents and require no transformation. Numbers equivalents for Shannon diversity, Camargo evenness, and Berger–Parker dominance were quantified
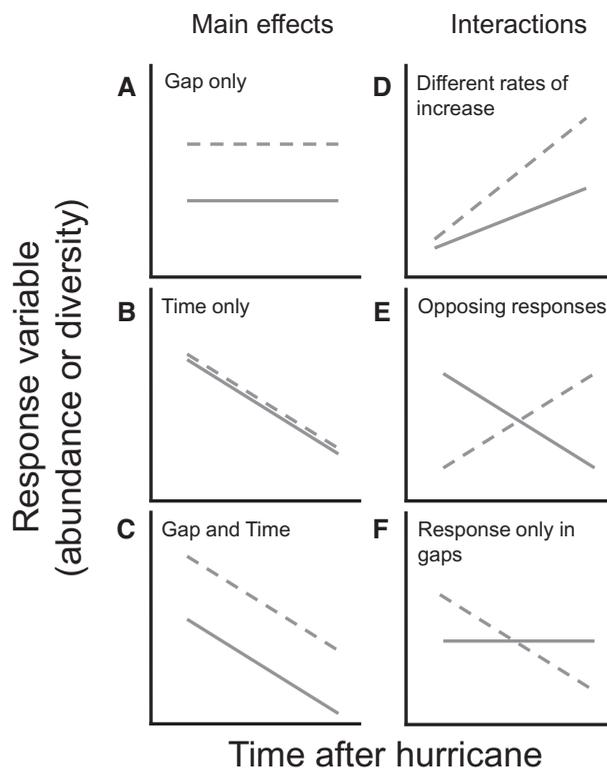

Fig. 1. Idealized examples of possible responses to hurricane-induced disturbances. Responses in gaps and closed canopy plots are represented by dashed and solid lines, respectively.

following Jost (2006) with functions written in Matlab 7.14.0.739 (MathWorks, Inc., Natick, Massachusetts) (Matlab 2012). In this context, greater values for numbers equivalents of dominance represent greater diversity (i.e., less dominance).

Our statistical approach facilitates the distinction of four general types of responses to hurricane disturbance (Fig. 1). First, a significant main effect for gap in the absence of an interaction with time suggests that consistent differences between gap and non-gap settings persist over time without evidence for any post-hurricane directional trajectory (Fig. 1A). Second, a significant main effect for time without an interaction with gap suggests that post-hurricane directional trajectories are consistent and independent of gap creation (Fig. 1B). Third, significant main effects may occur for gap and for time, with no interaction between them (Fig. 1C). This suggest that post-hurricane differences between gap and closed canopy plots persist over time, and that subsequent directional trajectories are the same in gaps and in non-gap settings (i.e., parallel trajectories). Fourth, a significant interaction involving gap and time suggests that the directional post-hurricane trajectories over time differ between gap and non-gap settings: these interactions can assume a number of forms (Fig. 1D–F). We used a chi-square contingency test (chisq.test function in R) with a Monte Carlo simulation (Hope 1968) based on 10,000 iterations to determine if the number of significant responses was contingent on hurricane identity (Hugo vs Georges). Chi-square tests were performed separately for taxon abundance, guild abundance, and taxon diversity.

For each linear mixed-effects model, we did not interpret a lower-order term if it was contained in significant higher-order terms (e.g., if the gap × precipitation interaction was significant, a main effect for gap or precipitation was not interpreted). To understand effects associated with succession after hurricanes while

Table 1. Number of significant responses to gap creation by Hugo (G), legacy of gap creation after Georges (G), time after hurricane (T), and precipitation (P) by taxon abundance, guild abundance, or taxonomic biodiversity of canopy arthropods (Suppl. Tables 1–3 [online only])

	Number of analyses	Number of nonsignificant analyses	Results of linear mixed-effects models									
			Main effects			Two-way interactions				Effect categories		
			G	T	P	G × T	G × P	T × P	Three-way	Gap effects	Time effects	Contingency
Hugo												
Taxon abundance	58	22	8	12	5	3	2	9	2	10	21	5
Guild abundance	42	21	6	7	6	3	2	2	2	8	9	5
Taxonomic biodiversity	30	18	0	2	5	4	2	2	0	2	4	4
Georges												
Taxon abundance	58	38	5	6	2	2	4	3	2	9	9	4
Guild abundance	42	28	2	5	1	0	1	3	2	3	8	2
Taxonomic biodiversity	30	18	0	6	1	4	4	0	1	4	6	5
Hugo	130	61	14	21	16	10	6	13	4	20	34	14
Georges	130	84	7	17	4	6	9	6	5	16	23	11
Taxon abundance	116	60	13	18	7	5	6	12	4	19	30	9
Guild abundance	84	49	8	12	7	3	3	5	4	11	17	7
Taxonomic biodiversity	60	36	0	8	6	8	6	2	1	6	10	9

Gap effects represent consistent effects of canopy loss regardless of time (G or G × P), time effects represent consistent successional trajectories regardless of gap creation (T or T × P), and contingency represents temporal trends that are gap-dependent (G × T or G × T × P).

controlling for effects of variation in precipitation, we categorized statistical responses into three groups: 1) gap effects that do not vary over time (i.e., significant gap effect or gap × precipitation interaction); 2) time effects that are independent of gap (i.e., significant time effect or time × precipitation interaction); and 3) contingencies in which the effect of time depends on gap (i.e., significant gap × time or gap × time × precipitation interactions).

Results

We collected 11,626 individuals representing 171 taxa, including 40 identified species, 63 morphospecies, and specimens identified to family (62) or order (6). Only 25 taxa (including five families and four orders; Suppl. Table 1 [online only]) were sufficiently abundant for analysis (40–900 individuals each). All taxa could be assigned to a functional group. Diversity indices would be affected to the extent that multiple, indistinguishable species in combined taxa would not be represented individually. Although taxa at the rank of family or order comprised 1,880 occurrences (out of 5,588 total occurrences), 1,473 were represented by a single individual and 244 by only two individuals. Therefore, of all occurrences, only 2.9% represented three or more individuals in a combined taxon and likely had little effect on estimates of biodiversity.

The large number of taxa analyzed in this study increases the probability of Type I error (Progar et al. 1999), i.e., on average, we would expect one taxon per 20 analyzed to show significant responses erroneously ($\alpha = 0.05$). We were more concerned about the consequences of ignoring results that have biological implications than about the potential for Type I errors. In general, adjustments to maintain experiment-wise error rates at 0.05 increases the number of Type II errors more quickly than it corrects potential Type I errors (Hurlbert and Lombardi 2003, Moran 2003). Therefore, we interpreted results based on exact *P*-values without application of overly conservative and controversial *P*-value adjustments, with the understanding that a few significant results contributing to overall patterns may represent Type I errors.

Evaluation of multiple taxa in this study has the advantage of indicating the degree of consistency of responses to treatments among taxa (Moran 2003). Furthermore, analyzing multiple taxa should reduce the probability of Type II error, i.e., some taxa should show nonsignificant responses erroneously, but if treatments have general effects among taxa or functional groups, then some should show significant responses. Proportions of significant responses are given below only to indicate the extent of significant responses above the expected 5% error rate. As expected, some responses were positive and some negative for each factor, depending on tolerances of species to changes in abiotic conditions or resulting changes in resource characteristics.

Results of analyses are summarized in Table 1. At least one significant gap, time, or interaction effect occurred for 53 of 116 (46%) analyses of taxon abundance (Suppl. Table 1 [online only]), with such effects occurring more frequently after Hugo (33 of 58 analyses) than after Georges (20 of 58). Similarly, at least one significant gap, time, or interaction effect occurred for 31 of 84 (37%) analyses of guild abundance (Suppl. Table 2 [online only]), with effects occurring more frequently after Hugo (18 of 42 analyses) than after Georges (13 of 42). Finally, at least one significant gap, time, or interaction effect occurred for 21 of 60 (35%) analyses of taxonomic biodiversity (Suppl. Table 3 [online only]), with effects occurring less frequently after Hugo (9 of 30 analyses) than after Georges (12 of 30). Only three taxonomic analyses, four guild analyses, and three biodiversity indices showed significant responses to precipitation alone.

The proportion of significant effects on taxon abundance ($\chi^2 = 5.87$, $P = 0.024$) after Hugo (57%) was significantly greater than that after Georges (34%). In contrast, the proportion of effects on guild abundance ($\chi^2 = 1.29$, $P = 0.364$) or taxon diversity ($\chi^2 = 0.66$, $P = 0.587$) was not significantly different between hurricanes. In addition, the frequency of significant effects was similar for taxa at both low and high ranks ($\chi^2 = 1.11$, $P = 0.409$). The difference in the number of significant responses between hurricanes was associated with precipitation (Table 1).

Responses After Hugo

As a main effect or via an interaction with time, gaps created by Hugo affected taxon abundance in 15 of 58 (26%) analyses, guild
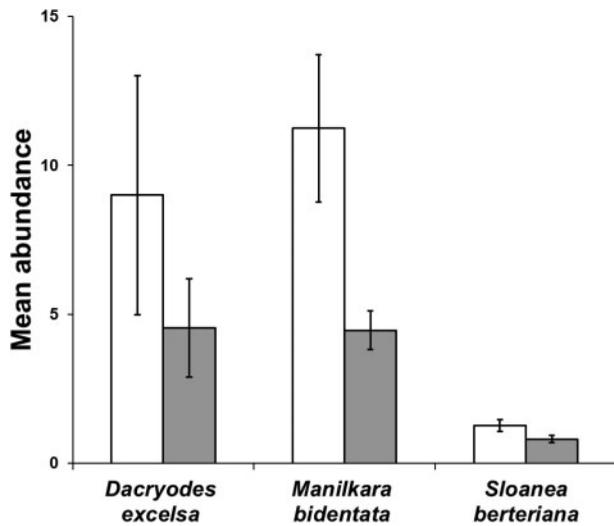
Fig. 2. Mean number of detritivores per sample in gaps (white) and non-gaps (gray) after Hugo on each of three dominant canopy tree species. Error bars represent ±1 SE. The error bars are for descriptive purposes and do not represent the basis for significance in the linear mixed-effects models (Suppl. Table 2 [online only]), which controlled for variation in sample mass and for block effects.

abundance in 13 of 42 (31%) analyses, and taxonomic biodiversity in 6 of 30 (20%) analyses. Taxon and guild abundances were consistently different between gaps created by Hugo and forest that did not exhibit canopy loss, regardless of variation over time or in precipitation, in eight and six cases, respectively (Table 1). Only sap-suckers (particularly *Ceroplastes rubens* Maskell, *Coccus acutissimus* Green, *Protopulvinaria pyriformis* (Cockerell) and *Vinsonia stellifera* (Westwood) (Hemiptera: Coccidae)) exhibited the same response to gap creation on different species of host tree (Fig. 2), being more abundant in gaps than in non-gaps on each of the dominant canopy tree species (*D. excelsa*, *M. bidentata*, and *S. berteriana*). No main effects of gap occurred for taxonomic biodiversity (Table 1).

As a main effect or as an interaction with gap, time affected taxon abundance in 26 of 58 (45%) analyses, guild abundance in 14 of 42 (33%) analyses, and taxonomic biodiversity in 8 of 30 (27%) analyses (Table 1). Only sap-suckers exhibited the same response to time on different species of host tree (Fig. 3), decreasing during succession on each canopy tree species (*D. excelsa*, *M. bidentata*, and *S. berteriana*).

In many cases, successional responses after Hugo were contingent on precipitation, as rainfall during the 28 d before sampling affected taxon abundance, guild abundance, or taxon biodiversity as a main effect or as an interaction with gap or time in 18 of 58 (31%), 12 of 42 (29%), and 9 of 30 (30%) analyses, respectively. Significant effects of interaction between gap and time (successional trajectories dependent on gap creation) after Hugo occurred in five cases for taxon abundance, five cases for guild abundance, and four cases for taxonomic biodiversity (Table 1).

Responses After Georges

As a main effect or via an interaction with time after Georges, the legacy of gaps affected taxon abundance in 13 of 58 (22%) analyses, guild abundance in 5 of 42 (12%) analyses, and taxonomic biodiversity in 9 of 30 (30%) analyses. Taxon and guild abundances were significantly different between plots that represented the legacy of gap formation and those that did not in five and two cases,
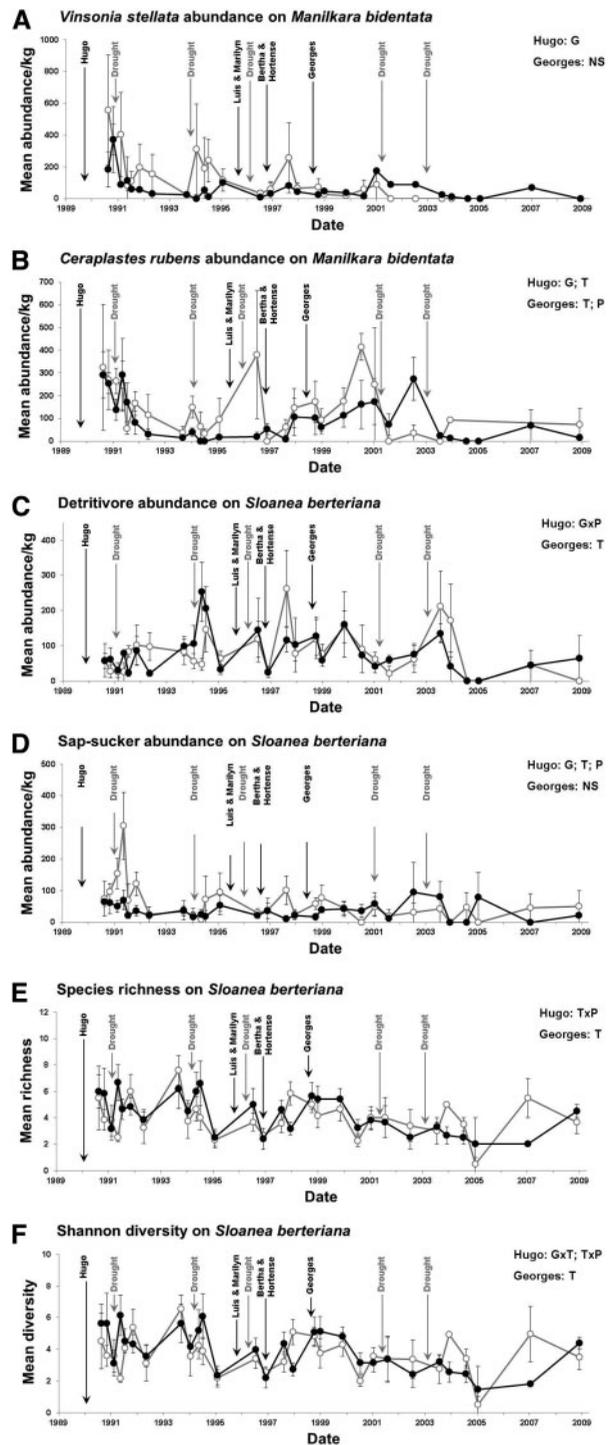

Fig. 3. Empirical examples of complex long-term patterns of taxon abundance, guild abundance, and taxonomic biodiversity for canopy arthropods in response to a complex disturbance regime in the Luquillo Mountains of Puerto Rico. Mean abundances (number of individuals) per sample per kilogram dry weight of foliage for (**A**) *Vinsonia stellifera* on *Manilkara bidentata*, (**B**) *Ceroplastes rubens* on *M. bidentata*, (**C**) detritivores on *Sloanea berteriana*, and (**D**) sap-suckers on *S. berteriana*. Mean taxonomic biodiversity per sample based on (**E**) species richness on *S. berteriana* and (**F**) Shannon diversity on *S. berteriana*. Data represent long-term trends (19 yr) in abundance or biodiversity (±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 located under closed canopy forest (filled circles and black lines). Significant effects from general linear mixed-effects models are noted on each panel: G, gap, P, precipitation, and T, time after hurricane.

respectively. No main effects of gap legacy occurred for taxonomic biodiversity (Table 1).

As a main effect or via an interaction with gap legacy, time after Georges affected taxon abundance in 13 of 58 (22%) analyses, guild abundance in 10 of 42 (24%) analyses, and taxonomic biodiversity in 11 of 30 (37%) analyses. Main effects of precipitation after Georges were infrequent for taxon abundance (significant in 2 of 58 cases), for guild abundance (significant in 1 of 42 cases), or for taxonomic biodiversity (significant in 1 of 30 cases). In contrast, responses to time after Georges or to gap legacy were frequently dependent on precipitation (Table 1). Significant interaction between gap and time (successional trajectories dependent on gap legacy) after Georges occurred in four cases for taxon abundance, two cases for guild abundance, and five cases for taxonomic biodiversity.

Discussion

Disturbance and plant successional dynamics have pervasive effects on canopy arthropods in the LEF. Nonetheless, long-term data can be "noisy," particularly during secondary succession in a system with a complex disturbance regime (see Fig. 3 for illustrative examples of long-term trends in abundance and biodiversity). Such variability arises because multiple factors shape successional trajectories for plants and insects, including legacies from previous land use or previous disturbances (Willig et al. 1998, 2007, 2012; Thompson et al. 2002; Uriarte et al. 2009). The "noisy" nature of long-term data in disturbance-mediated tropical forests decreases the power to detect responses to hurricanes and enhances statistical conservatism. Consequently, significant responses likely reflect particularly strong effects, as weak effects would not be distinguishable from background noise. We detected significant responses for a large proportion of analyses of taxon abundance, guild abundance, and taxonomic diversity because of hurricane-induced disturbances (Suppl. Tables 1–3 [online only]). In addition, complex responses were common (e.g., abundance or diversity increased with time in gaps but decreased with time in closed canopy forest; trajectories of abundance or diversity during succession were contingent on precipitation or canopy closure). These results indicate that: 1) differential performance of taxa, guilds, and assemblages during recovery of tropical forest from hurricanes is typical and 2) environmental context affects the direction and magnitude of responses. Contrary to expectations, temporal trajectories were comparable after each hurricane. Abundance or diversity increased with time in 4–6% of cases, decreased with time in 8–10% of cases, and exhibited complex responses in 13–21% of cases. Rather, the greatest difference in responses between hurricanes was associated with precipitation (Table 1), likely because more droughts and more severe droughts occurred after Hugo than after Georges.

Responses of Species and Guilds
A combination of processes (e.g., colonization, survival, reproduction, competition, facilitation, abiotic filtering, and habitat matching) likely contribute to responses during hurricane recovery, with the relative importance of mechanisms being taxon-, guild-, or assemblage-specific. In general, responses of canopy arthropods to hurricanes were idiosyncratic, consistent with unpredictable successional dynamics of trees in neotropical forests (Norden et al. 2015). For arthropods, this likely reflects a combination of differential responses of taxa and guilds, differential responses by host tree species, and variation in conditions at the time of each disturbance (Walker and Willig 1999).

A common characteristic of disturbances that initiate succession is that they cause mortality of structurally or functionally dominant organisms, and alter the distribution of resources or environmental characteristics (White and Jentsch 2001). Intense hurricanes cause physical damage that changes abiotic conditions, forest structure, and/or resource availability, thereby changing relative proportions of available niche types in the forest (Walker and Willig 1999, Scatena et al. 2012). Canopy arthropods represent folivores, sapsuckers, detritivores, omnivores, predators, and aquatic species, with each group relying on a different resource base. For example, folivores chew foliage tissues, sap-suckers siphon phloem or xylem fluids, and detritivores feed on detrital material collecting on leaf surfaces or branches (Schowalter 2016). In addition, arthropod assemblages were sampled from trees that represent early and late successional species, as well as canopy and subcanopy species. Consequently, effects of canopy opening, drought, host tree species' identity, source-sink dynamics, initial local conditions, and interactions between trophic levels all represent sources of ecological complexity that contributed to variation in responses to disturbance.

Only sap-suckers and detritivores exhibited consistent responses to hurricane-induced disturbance, at both taxonomic and guild levels, suggesting that a single mechanism may drive successional responses of these guilds. The taxa represented by these groups typically are smaller insects with high reproductive rates that would reflect an r strategy best suited for rapid responses to changing environmental conditions compared with larger species with annual life cycles that would reflect a K strategy better adapted to more stable conditions in later successional forests (Schowalter 2016).

Sap-suckers, particularly *C. rubens* and *V. stellifera* (both scale insects), were more abundant in gaps than in closed canopy forest and declined with time following hurricanes on each of the three dominant canopy tree species (*D. excelsa*, *M. bidentata*, and *S. berteriana*). Each of these responses reflects the association of sapsuckers with the rapid growth of new foliage and shoots that support a high rate of nutrient translocation to the tissues on which these insects feed (Schowalter 2016). Similar conditions likely occurred in the upper canopy of intact forest following hurricanes. Samples collected from the upper crowns of *D. excelsa* and *M. bidentata* accessible from a 20-m canopy walkway at the LEF suggested higher abundances of sap-suckers immediately after Hugo and declining thereafter, although sampling was insufficient for statistical analysis (T. D. S, personal observation).

By contrast, the tree cricket, *Cyrtoxipha gundlachi* Saussure (Orthoptera: Gryllidae), and two spiders, *Lyssomanes portoricensis* Petrunkevitch (Araneae: Salticidae) and *Modisimus* sp. (Araneae: Pholcidae), tended to increase in abundance through time, particularly in non-gaps. These responses suggest a more K-adapted strategy and/or increased prey availability for predators.

During drought in the LEF, some trees lose their leaves because of water stress (Beard et al. 2005). Resultant increases in litterfall create pulses of resources for detritivores, potentially accounting for the consistent negative association between precipitation and abundance of the detritivore guild, in addition to increased abundances of detritivores following hurricanes. Canopy arthropods exhibit similar short-term responses to hurricanes and to drought in the LEF (Schowalter and Ganio 2003). Both types of disturbance initiate changes in the abiotic environment (e.g., increase temperature and evapotranspiration) and cause pulses of litter input. The movement of resources from the canopy to the forest floor and the creation of hotter and drier conditions may dominate short-term responses (Schowalter et al. 2014, Shiels and González 2014); however, long-term trajectories are less consistent than short-term responses.

Initial Conditions and Differential Responses to Hurricanes

Taxon abundance, guild abundance, and biodiversity each responded more often to time after hurricane than to gap creation or variation in precipitation, indicating that temporal changes in habitat associated with succession had a stronger effect on canopy arthropods than was the loss of forest canopy during a hurricane or temporal variation in precipitation. Differences in the extent and intensity of forest damage between hurricanes (Lomascolo and Aide 2001, Ostertag et al. 2003) resulted in more effects associated with succession after Hugo (34 time effects and 14 interaction effects) than after Georges (23 time effects and 11 interaction effects). However, these differences were not as great as expected. In concert, these results show the priority of successional trajectories after disturbance over other factors (i.e., creation of canopy openings and drought) associated with the disturbance regime, but recognizing that disturbance events initiate those successional changes. In general, temporal changes in plant conditions (e.g., nutrient availability) may have a greater effect on canopy arthropods than do more direct and immediate changes in abiotic conditions associated with canopy opening (Lodge et al. 1991, Scatena et al. 1996, Schowalter et al. 2014) or with precipitation (this study).

The number of significant responses by canopy arthropods after Hugo was 1.5 times greater than that after Georges, with significant responses by more taxa, guilds, and assemblages after Hugo than after Georges (Table 1). Hugo was more intense than Georges, producing more damage to the canopy and depositing more debris on the forest floor (Lomascolo and Aide 2001, Ostertag et al. 2003). These differences in the physical effects on the forest between the two hurricanes could explain the greater influence of Hugo on the abundances of canopy arthropods. However, it is not possible to disentangle the potential contributions of differences in hurricane intensity from the differences in initial conditions at the time of each hurricane. Because of differences in the time since a major hurricane had affected the LEF, the number of large trees that were susceptible to hurricane-induced damage was greater during Hugo than during Georges, creating greater potential for forest damage and, therefore, greater effects on the flora and fauna. In contrast, the forest was still in the relatively early stages of recovery from Hugo when Georges occurred, with a canopy arthropod fauna that was already characteristic of a recovering forest, resulting in less potential for responses to Georges.

Legacy Effects

Because the locations of plots were identical after both Hugo and Georges, the designation of gap and non-gap plots was independent of canopy loss caused by Georges. Gaps in the canopy created by Hugo in 1989 were largely filled by vegetation by 1994, although these gaps were reopened to various degrees by Georges, depending on the abundance of easily broken *C. schreberiana* (Schowalter and Ganio 1999). Nonetheless, differences in canopy arthropod abundance and diversity between gap and non-gap plots continued throughout the 19-yr study period, with nearly as many gap legacy effects observed after Georges (16) as those observed after Hugo (20). Perhaps this should not be surprising, as the legacy of human land use practices in the LEF can be detected in tree species' composition over 50 yr after cessation of logging and agricultural activities (Willig et al. 1997, 2007, 2012; Thompson et al. 2002, Uriarte et al. 2009). However, the spatial scale of hurricane-induced gap creation was much smaller than that of historical land use activities, and canopy arthropods are more vagile and characterized by much shorter

generation times than are trees. These factors reduce the expected duration of legacy effects for canopy arthropods in gaps. Nonetheless, legacy effects persist for multiple decades, representing scores of generations for canopy arthropods.

In conclusion, canopy arthropod communities in hurricane-mediated systems are temporally dynamic, and changes are difficult to predict, given a large number of contingencies (Schowalter 2012, 2016), as well as the multiple interacting disturbance events (Willig and Walker 1999). Disturbances can increase environmental heterogeneity, which can increase arthropod biodiversity during early stages of succession. Thereafter, biodiversity decreases as the structure of the forest and associated environmental conditions more closely resembled the pre-disturbance state. Many taxa and guilds exhibited differential responses, with different species (e.g., sapsuckers vs tree crickets) performing similar functions in different contexts (e.g., open vs closed canopy). Deposition of large amounts of litter and subsequent growth of new shoots temporarily increased resources for detritivores and sap-suckers, respectively. These time-dependent changes in resource abundance result in relatively predictable changes to forest quality through time, such that their effects take priority over those associated with forest physiognomy or short-term variation in precipitation. Finally, legacy effects are important for understanding responses to disturbances, as effects from previous disturbances may affect responses to ensuing disturbances.

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