Canopy arthropod responses to experimental canopy opening and debris deposition in a tropical rainforest subject to hurricanes

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ABSTRACT

We analyzed responses of canopy arthropods on seven representative early and late successional overstory and understory tree species to a canopy trimming experiment designed to separate effects of canopy opening and debris pulse (resulting from hurricane disturbance) in a tropical rainforest ecosystem at the Luquillo Experimental Forest Long-Term Ecological Research (LTER) site in Puerto Rico. We expected that either canopy opening or added debris would result in increased abundances of certain scale insects and other hemipterans, and thereby affect arthropod diversity.

Six of thirteen arthropod taxa tested showed significant responses to treatments as main effects or interactions. No taxon responded significantly to trim treatment alone. The red wax scale, *Ceroplastes rubens* (on *Manilkara bidentata*), was significantly less abundant in treatments with added debris than in treatments without added debris, and salticid spiders (on *Sloanea berteroana*) were significantly more abundant in treatments with added debris than in other treatments. Canopy trimming generally did not have a significant effect on assemblage diversity, whereas debris deposition significantly increased diversity on three late successional tree species. A number of significant treatment interactions were observed. Overall, the debris pulse had a greater effect on canopy arthropods than did canopy opening, suggesting that changes in plant condition resulting from nutrient availability associated with debris deposition have a greater effect on canopy arthropods than do the more direct and immediate changes in abiotic conditions resulting from canopy opening.

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1. Introduction

Cyclonic storms are a major factor affecting the structure and dynamics of forests in many parts of the world (Mabry et al., 1998; Whigham et al., 1999; Stork, 2007; Lee et al., 2008; Turton, 2008; Li and Duan, 2010). While such disturbances have obvious and widely-studied effects on vegetation (Brokaw and Grear, 1991; Walker, 1991; Scatena et al., 1996; Whigham et al., 1999; Stork, 2007), relatively few studies have addressed responses of forest fauna to direct and indirect effects of these disturbances.

Disturbances that open forest canopies directly alter gradients of light, temperature and moisture that affect abundance and distribution of arboreal arthropods (Gram et al., 2001; Schowalter, 1995, 2011, 2012; Marquis et al., 2002; Schowalter and Ganio, 2003; Madigosky, 2004; Grimbacher and Stork, 2007, 2009). In addition, foliage and branches stripped from trees add a pulse of detrital material to the forest floor (Lin et al., 2003; Richardson et al., 2010). This pulse has obvious effects on habitat conditions and resource availability for litter fauna (Richardson et al., 2010),

but decomposing litter also promotes primary production (Wood et al., 2009), thereby indirectly affecting habitat conditions and resource availability for canopy fauna. Canopy arthropod responses to disturbances have the capacity to alter patterns of biogeochemical cycling and ecosystem recovery, including adding pulses of detrital inputs to the forest floor during outbreaks (Schowalter et al., 2011; Schowalter, 2012).

A few manipulative studies in temperate forests have provided the opportunity to compare arboreal arthropod abundances before and after tree harvest in replicated experimental plots (e.g., Shure and Phillips, 1991; Gram et al., 2001; Marquis et al., 2002; Schowalter et al., 2005). However, tree harvest removes, rather than adds, much debris and thereby fails to imitate conditions created by natural disturbances, such as hurricanes that cause a pulse of treefall and other detrital input to the forest floor. Given the difficulty of anticipating where and when natural disturbances will occur, most research on effects of canopy disturbances on invertebrates has been restricted to comparisons of abundances among plots varying in post-disturbance severity (e.g., Schowalter and Ganio, 2003; Hirao et al., 2008; Grimbacher and Stork, 2009). Such research is potentially confounded by pre-disturbance spatial variation and post-disturbance spatial and environmental variation

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(e.g., topography, wind damage). Furthermore, no previous studies have separated the effects of canopy opening and debris deposition on forest canopy fauna.

In 2004, a canopy trimming experiment (CTE) was initiated in a hurricane-structured tropical rainforest ecosystem at the Luquillo Experimental Forest Long-Term Ecological Research (LTER) site in Puerto Rico. This experiment was designed to separate effects of canopy opening and debris deposition in replicated plots of sufficient size to simulate the effects of recent major hurricanes, e.g., Hugo in 1989 and Georges in 1998 (Brokaw and Grear, 1991; Walker, 1991; Schowalter and Ganio, 2003). Previous papers have reported treatment effects on plants and litter invertebrate communities (Richardson et al., 2010; Shiels et al., 2010).

This paper describes responses of canopy arthropods to experimental canopy opening and debris deposition treatments. Based on previous canopy arthropod responses to hurricane disturbance in this ecosystem (Schowalter and Ganio, 2003), we expected that either canopy opening or debris deposition would result in increased abundances of certain scale insects and other hemipterans.

2. Materials and methods

2.1. Site description

El Verde Field Station, Luquillo Experimental Forest LTER Site, is located 10 km south of Rio Grande, Puerto Rico (18°10′N, 65°30′W) at 500 m above sea level (McDowell et al., 2012). This site is administered by the USDA Forest Service Caribbean National Forest and Southern Forest Research Station and by the University of Puerto Rico. Mean monthly temperatures range from 21 °C in January to 25 °C in September (Brown et al., 1983). Annual precipitation averages 370 cm and varies seasonally, with 20–25 cm per month in January–April (dry season) and 35–40 cm per month in the remainder of the year (wet season) (McDowell and Estrada-Pinto, 1988; Heartsill-Scalley et al., 2007).

The forest is subject to frequent disturbances that alter the composition of forest communities (Scatena et al., 2012). During the past 25 years, this site experienced two major hurricanes (Hugo 1989 and Georges 1998) that broke or toppled trees on windward slopes over large areas, several moderate hurricanes (Luis and Marilyn 1995, Bertha and Hortense in 1996, Erika in 1997, Jose in 1999 and Debby in 2000) that caused substantial defoliation and flooding, a number of minor hurricanes and tropical storms (Heartsill-Scalley et al., 2007), and hundreds of landslides resulting from rainstorms. A significant drought occurred during 1994–95, when precipitation was only 41% of the long-term annual average, and minor droughts occurred in 1991, 1996, 2001 and 2003 (Heartsill-Scalley et al., 2007). Previous studies have shown similar responses by canopy invertebrates to hurricanes and droughts (Schowalter and Ganio, 2003), suggesting that abiotic changes resulting from experimental canopy opening should have significant effects.

Vegetation surrounding the field station is dominated by tabonuco, *Dacryodes excelsa* (Burseraceae), which comprises 35% of the forest canopy below 600 m elevation (Brown et al., 1983). Other canopy dominants include *Manilkara bidentata* (Sapotaceae) and *Sloanea berteroana* (Elaeocarpaceae). *Prestoea acuminata* (Palmaceae), *Miconia prasina* (Melastomataceae) and *Psychotria brachiata* (Rubiaceae) are major subcanopy species. Canopy height averages 20 m, and small light gaps occur infrequently in the otherwise closed canopy of mature forests. *Cecropia schreberiana* (Cecropiaceae) is an important early successional tree species. *Heliconia caribaea* (Heliconiaceae), *Piper* spp. (Piperaceae) and other understory shrubs, vines and herbs form a dense understory in gaps.

At this site, Hurricane Hugo (1989) left severely disturbed patches (30–60 m diameter), with nearly complete tree-fall (gaps),

interspersed with less disturbed patches where most or all trees remained standing but lost their foliage and smaller branches (non-gaps). Rapid sprouting, refoliation and seedling recruitment began during the wet season of early 1990 (Frangi and Lugo, 1991). Thickets of *C. schreberiana* saplings and other early successional plants, especially *H. caribaea*, developed in gaps, and some later successional species resprouted from stumps and fallen trees. *Cecropia schreberiana* largely disappeared from non-gaps by 1995, following canopy closure, but reappeared in gaps following canopy opening by Hurricane Georges in 1998. Hurricanes Bertha, Hortense, and Marilyn during 1996 and Debby in 2000 caused substantial defoliation but no significant canopy opening.

2.2. Experimental design

The CTE created replicate disturbed or undisturbed plots similar in severity and scale to disturbed patches resulting from Hurricanes Hugo and Georges at this site (see Schowalter and Ganio, 2003). Four 30 × 30 m plots with a 5 × 5 m grid designated by PVC pipe were established in each of three experimental blocks (Shiels et al., 2010). Each plot within a block was assigned randomly to one of four treatments: (1) canopy trimmed with debris removed, weighed, then redistributed throughout the plot to simulate conditions created by natural hurricanes (Trim + debris), (2) canopy trimmed, with trimmed material removed from the plot to simulate canopy opening without debris deposition (Trim + no debris), (3) canopy undisturbed, with trimmed material from treatment 2 weighed, then distributed throughout the plot to simulate debris deposition without canopy opening (No trim + debris), and (4) canopy undisturbed and no debris alterations occurred at the forest floor (No trim + no debris). Treatments were installed during October 2004–June 2005.

In trimmed plots, all non-palm trees ⩾15 cm diameter at 1.3 m height had branches <10 cm diameter removed (Shiels et al., 2010). For non-palm trees between 10 and 15 cm diameter, each tree was cut at 3 m height. For palms ⩾3 m tall (at the highest part of the leaf above ground), all leaves (fronds) were trimmed at the connection with the main stem, and the apical meristem was preserved. Therefore, except for some palms that had fronds attached to their stem below 3 m height, no vegetation of any type was trimmed below 3 m height. The trimming treatment reduced canopy cover and increased light levels at the forest floor by amounts similar to those caused by Hurricane Hugo (Shiels et al., 2010).

The debris from canopy trimming was sorted into three categories: wood (branches ⩾1.5 cm diameter), leaves and twigs (branches <1.5 cm diameter and all non-palm foliar material), and palm fronds (Shiels et al., 2010). Debris was immediately weighed to establish wet mass, then subsampled, weighed, dried at 45 °C to constant mass, and reweighed to establish wet–dry mass ratios. All debris was then piled by category outside of debris deposition plots until trimming and weighing in both plots within a block were completed. Therefore, debris experienced about one month of decomposition outside of plots before being placed in the treatment plots. Trimmed material totaled about 6500 kg dry weight per plot, similar to amounts deposited by Hurricane Hugo (Shiels et al., 2010).

2.3. Sampling methods

Canopy invertebrate abundances were measured as described by Schowalter and Ganio (1999, 2003). Briefly, seven tree species were selected for study to represent the dominant early (*C. schreberiana*, *P. acuminata*, *P. brachiata* and *M. prasina*) and late (*D. excelsa*, *M. bidentata* and *S. berteroana*) successional and overstory (*D. excelsa*, *M. bidentata*, *S. berteroana* and *C. schreberiana*) and understory (*P. acuminata*, *P. brachiata* and *M. prasina*) species

at this site. Schowalter and Ganio (1999, 2003) showed that invertebrates on these tree species responded significantly to hurricane disturbances. Canopy invertebrates were sampled prior to treatment during June (wet season) 2004. Following treatment application, all plots were sampled during June–July, 2005–2007 (post-treatment years 1–3) and 2009 (post-treatment year 5).

In each plot at each sampling time, one branch was collected from one tree of each species. 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 up to 12 m in height (Schowalter and Ganio, 1999, 2003), i.e., lower-to-mid canopy in this forest. The bag is slipped over a foliage-bearing branch, closed, and clipped from the tree. Understory species were sampled either by this method or by hand-bagging branches within 1–3 m height above the forest floor. Each sample represented 10–30 g dry weight or about 1000 cm^2 of foliage from a 30–50 cm branch length.

Our sampling technique probably under-represents highly mobile arthropods, (e.g., bees, wasps, flies), but it is particularly useful for representing density and biomass of resident invertebrates, i.e. those that feed on resources associated with the sampled plant over periods of weeks to months, and that have the greatest effect on foliage turnover and nutrient flux (Majer and Recher, 1988; Blanton, 1990). Most invertebrate herbivores and many predators are relatively sedentary and were collected with foliage samples, and even some highly-mobile species were captured. Other common sampling techniques, such as light traps, interception traps and canopy fumigation, are biased toward flying adult insects and do not capture important and abundant sedentary groups that respond significantly to disturbance in this forest, such as scale insects, leaf miners and gall formers and non-insect invertebrates, such as snails (Schowalter and Ganio, 1999, 2003). Furthermore, light traps, interception traps and canopy fumigation may yield more species, but branch bagging yields larger abundances of species that characterize sampled plants (Majer and Recher, 1988; Blanton, 1990).

Branch bagging has the additional advantages of permitting measurement of leaf area missing (LAM), a measure of the effect of herbivory on canopy porosity (foliage removal that increases fluxes of water and wind through the canopy), and of providing a standardized unit, either foliage area or mass, that permits comparison of invertebrate abundances as number per kg foliage among treatments differing in foliage structure. Previous studies in different forest types have demonstrated that the branch bagging technique can be used to distinguish treatment effects on invertebrate abundances and diversity (e.g., Schowalter et al., 1981; Schowalter, 1995; Schowalter and Ganio, 2003). Invertebrate density data also can be used to calculate invertebrate effects on nutrient flux rates, trophic interactions and other ecosystem processes (Schowalter, 2011).

For each branch-bagging sample collected in the CTE, all invertebrates were identified to the lowest possible taxonomic level. Foliage was pressed and dried at 50 °C to constant weight. Invertebrate numbers divided by foliage mass provided a standard unit of abundance (number per kg foliage) for comparison among tree species and treatments (Schowalter and Ganio, 2003), although this was not the unit used for statistical analyses (see Section 2.4). Dried, pressed foliage was measured for percentage leaf area missing, using a leaf area meter, as an indicator of herbivore effect on canopy processes.

2.4. Quantitative analysis

We evaluated the response of canopy arthropods to the CTE at the population and community levels. Population-level responses were evaluated based on abundance. Numbers of each taxon per sample were the unit of analysis. Because branch samples differed in size, branch mass was used as a covariate for statistical analyses. We analyzed responses of 13 arthropod taxa that were sufficiently frequent and abundant (i.e., present in at least five samples) on at least one tree species to warrant individual analysis. Analyses of species that occurred in fewer samples would have little statistical power to detect treatment effects, and limiting the number of taxa analyzed minimized the likelihood of obtaining significant responses purely by chance. For the 33 taxa × tree species combinations analyzed, we would expect 1–2 significant responses to occur by chance at the 5% level (e.g., see Progar et al., 1999).

Because biodiversity is a multidimensional concept that comprises multiple interrelated aspects, we estimated five taxonomic metrics of biodiversity for each sample as well as total abundance (i.e. total number of individuals regardless of species identity). These metrics included: (1) species richness (i.e., the number of captured species), (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, which was estimated as the number of species in a sample whose overall relative abundance for the entire data set was less than $1/S$, where S is the number of species obtained during both pre- and post-manipulation phases of the CTE. In a variety of contexts, these five metrics have been shown to estimate independent aspects of biodiversity and to effectively capture changes in biodiversity in response to geographic and environmental gradients (e.g. Stevens and Willig, 2002; Wilsey et al., 2005; Vance-Chalcraft et al., 2010).

To facilitate statistical analysis, each diversity metric was transformed into its effective number of species or Hill number (hereafter numbers equivalent). The numbers equivalent is the number of maximally dissimilar species with equal abundances that is required to produce the empirical value of a metric (Jost, 2006; Villéger et al., 2012). This transformation facilitates intuitive interpretation of differences between treatments because indices are expressed in the same units and have the necessary mathematical properties that facilitate logical comparison and statistical analysis (Jost, 2006). Metrics that represent species counts (e.g. species richness and rarity) are already expressed as numbers equivalents. Numbers equivalents for Shannon diversity, Camargo evenness, and Berger-Parker Dominance were quantified following Jost (2006) with functions written in Matlab 7.14.0.739. In numbers equivalents, larger values always indicate greater biodiversity. With respect to the numbers equivalent for dominance, larger values indicate greater biodiversity, but decreased dominance.

For population- and community-level characteristics, we evaluated the effects of time, canopy trimming, and debris deposition based on a linear mixed-effects model (Laird and Ware, 1982; Pinheiro and Bates, 1996, 2000). More specifically, we executed a three-way analysis (time [in years, including pre-treatment and post-treatment time periods] versus canopy trimming [trimmed or not trimmed] versus debris deposition [added or not added]) in a randomized block design with dry foliage mass of individual samples included as a covariate. Variation associated with foliage mass was removed prior to evaluation of the full factorial model. Time was a continuous variable, canopy trimming and debris deposition were Model I treatment factors, and block was a Model II treatment factor. Analyses were conducted separately for populations and communities of canopy invertebrates from each tree species. At the population level, we analyzed responses for each arthropod taxon that occurred in at least five samples from conspecific trees. Analyses were conducted in R (R Core Team, 2013). Use of rarefaction based on numbers of samples or numbers of individuals to control for sampling effects on diversity metrics was not possible or reasonable as individual samples were the unit of analysis and for each tree species the minimum sample size ranged

Table 1

Dependent variables by tree species in plots subjected to four combinations of canopy trimming and debris subsidy treatments in a tropical forest in Puerto Rico. All diversity metrics are given in their numbers equivalents (Jost, 2006).

Tree species	Variable	Control	Untrimmed + debris	Trim + removal	Trim + debris
Cecropia schreberiana	Number of samples	5	5	12	4
	Total foliage mass (kg)	50	32	94	40
	Leaf area missing (%)	2.0	1.5	3.1	1.8
	Collembola (No./kg)	60	63	85	25
	Wulfila tropicus (No./kg)	60	63	53	0.0
	Total abundance (No./kg)	660	1400	750	570
	Richness	4.0	3.4	3.0	2.5
	Shannon-Wiener diversity	3.3	3.0	2.7	2.2
	Carmargo evenness	2.9	2.7	2.4	1.9
	Berger-Parker dominance	1.9	2.5	2.0	1.6
	Rarity	2.8	1.4	1.5	1.3
Dacryodes excelsa	Number of samples	5	10	12	16
	Total foliage mass (kg)	130	190	270	340
	Leaf area missing (%)	1.0	1.4	2.0	1.3
	Protopulvinaria pyriformis (No./kg)	7.9	52	26	32
	Cyrtoxipha gundlachi (No./kg)	56	31	56	59
	Collembola (No./kg)	7.9	10	19	0.0
	Wasmannia auropunctata (No./kg)	7.9	0	23	18
	Wulfila tropicus (No./kg)	0.0	0.0	3.8	12
	Miscellaneous moths (No./kg)	7.9	10	3.8	15
	Total abundance (No./kg)	220	290	240	320
	Richness	4.0	3.1	3.1	4.6
	Shannon-Wiener diversity	3.6	2.6	2.8	4.1
	Carmargo evenness	3.3	2.3	2.5	3.7
	Berger-Parker dominance	2.4	1.7	2.3	2.7
	Rarity	2.4	1.8	1.0	2.8
Manilkara bidentata	Number of samples	8	11	8	11
	Total foliage mass (kg)	150	220	190	260
	Leaf area missing (%)	10	6.3	7.8	5.5
	Ceroplastes rubens (No./kg)	120	45	140	42
	Vinsonia stellifera (No./kg)	20	9.0	54	57
	Cyrtoxipha gundlachi (No./kg)	34	40	11	38
	Collembola (No./kg)	40	4.5	5.4	3.8
	Wasmannia auropunctata (No./kg)	47	4.5	16	27
	Salticids (No./kg)	6.7	9.0	0.0	7.7
	Total abundance (No./kg)	900	520	620	490
	Richness	4.4	3.7	4.0	4.6
	Shannon-Wiener diversity	3.0	3.0	2.7	3.8
	Carmargo evenness	2.5	2.7	2.3	3.3
	Berger-Parker dominance	1.7	2.1	1.7	2.3
	Rarity	3.1	2.1	2.5	2.6
Miconia prasina	Number of samples	6	8	10	14
	Total foliage mass (kg)	57	67	61	81
	Leaf area missing (%)	2.7	3.5	2.7	6.2
	Ceroplastes rubens (No./kg)	160	300	50	160
	Bothriocera sp. (No./kg)	87	75	33	12
	Cyrtoxipha gundlachi (No./kg)	52	60	50	25
	Collembola (No./kg)	110	90	99	37
	Wasmannia auropunctata (No./kg)	17	30	180	25
	Wulfila tropicus (No./kg)	0.0	45	33	75
	Total abundance (No./kg)	770	1300	1000	1900
	Richness	2.7	4.5	2.8	4.4
	Shannon-Wiener diversity	2.3	3.7	2.5	3.5
	Carmargo evenness	2.0	3.2	2.3	3.1
	Berger-Parker dominance	1.8	2.3	1.9	2.3
	Rarity	1.0	3.0	1.4	3.0
Prestoea acuminata	Number of samples	8	11	12	16
	Total foliage mass (kg)	100	150	140	160
	Leaf area missing (%)	1.9	3.5	3.4	2.3
	Cyrtoxipha gundlachi (No./kg)	49	21	35	62
	Collembola (No./kg)	10	14	7.0	19
	Wasmannia auropunctata (No./kg)	39	260	220	25
	Total abundance (No./kg)	380	690	720	820
	Richness	2.6	2.6	2.5	3.1
	Shannon-Wiener diversity	2.3	1.8	1.7	2.7
	Carmargo evenness	2.1	1.6	1.6	2.4
	Berger-Parker dominance	1.8	1.3	1.2	2.1
	Rarity	1.0	1.6	1.5	1.3
Psychotria brachiata	Number of samples	6	7	10	11
	Total foliage mass (kg)	30	27	49	36
	Leaf area missing (%)	6.3	6.9	6.1	6.5

Table 1 (continued)

Tree species	Variable	Control	Untrimmed + debris	Trim + removal	Trim + debris
	Petrusa sp. (No./kg)	170	480	180	56
	Cyrtoxipha gundlachi (No./kg)	34	37	140	84
	Collembola (No./kg)	67	190	100	84
	Wasmannia auropunctata (No./kg)	100	0.0	230	200
	Total abundance (No./kg)	2300	3000	2400	3000
	Richness	4.2	3.1	4.3	3.6
	Shannon-Wiener diversity	3.4	2.4	3.5	2.6
	Carmargo evenness	2.9	2.0	3.0	2.3
	Berger-Parker dominance	2.4	1.6	2.3	1.7
	Rarity	2.2	1.9	2.7	2.4
Sloanea berteroana	Number of samples	8	10	13	16
	Total foliage mass (kg)	180	180	290	350
	Leaf area missing (%)	8.6	4.5	6.4	7.8
	Cyrtoxipha gundlachi (No./kg)	38	49	21	51
	Miscellaneous moths (No./kg)	5.4	5.5	3.5	20
	Collembola (No./kg)	5.4	16	7.0	5.7
	Wasmannia auropunctata (No./kg)	27	33	7.0	26
	Wulfila tropicus (No./kg)	0.0	27	21	8.5
	Salticids (No./kg)	0.0	16	3.5	14
	Total abundance (No./kg)	530	450	440	660
	Richness	3.4	3.9	3.9	5.9
	Shannon-Wiener diversity	2.4	3.0	3.1	4.3
	Carmargo evenness	2.1	2.6	2.7	3.8
	Berger-Parker dominance	1.6	1.9	1.9	2.3
	Rarity	2.1	2.6	2.8	4.1

from 0 to 2 individuals. It is important to note that we controlled for sample size by including dry mass of the vegetation associated with each sample as a covariate, removing variation associated with sample mass prior to evaluation of effects associated with the CTE. Given the structure of the data and focal unit of analysis, this is the best option to control for potential sampling effects.

3. Results

3.1. Population responses

Few individual invertebrate taxa had sufficient abundances for statistical analyses. Of 105 taxa collected, 58 were represented by <5 specimens, and only 13 were represented by >30 specimens. Individual statistical analyses of treatment effects were conducted only for the 13 taxa on the particular host trees on which they occurred with sufficient abundances (Table 1).

Six taxa (three on *S. berteroana*, two on *M. bidentata*, and one on *D. excelsa*) showed significant responses to treatments as main effects or interactions (Table 2). No taxa responded significantly to trim treatment alone. No significant responses were observed on early successional tree species.

The red wax scale, *Ceroplastes rubens*, was 3-fold more abundant on *M. bidentata* in treatments that received no added debris (Fig. 1), compared to debris deposition treatments ($p = 0.009$, $n = 38$, $F = 8.01$). Salticid spiders (on *S. berteroana*) were significantly more abundant in debris deposition treatments than in treatments that received no additional debris ($p = 0.048$, $n = 47$, $F = 4.18$; Fig. 1). An anyphaenid spider, *Wulfila tropicus*, showed a significant trim × debris interaction ($p = 0.010$, $n = 47$, $F = 7.43$) on *S. berteroana*. Treatments did not show significant effects for any folivore species or for leaf area removed, a measure of the effect of herbivory. *Ceraplastes rubens* on *M. bidentata* also showed a significant response to time ($p = 0.021$, $n = 38$, $F = 5.97$; Fig. 1). Collembola on *D. excelsa* ($p = 0.021$, $n = 43$, $F = 5.94$), an unidentified lepidopteran on *S. berteroana* ($p = 0.040$, $n = 47$, $F = 4.56$) and *W. tropicus* on *M. prasina* ($p = 0.050$, $n = 38$, $F = 4.20$) showed significant trim × time interactions. In addition, a tree cricket, *Cyrtoxipha gundlachi*, on *D. excelsa* showed a significant trim × debris × time interaction ($p = 0.029$, $n = 43$, $F = 5.23$).

3.2. Community responses

Diversity indices revealed significant treatment effects at the community level (Tables 1 and 2). Five of six diversity metrics on *D. excelsa* ($n = 43$; richness, $p = 0.009$, $F = 7.70$; diversity, $p = 0.013$, $F = 6.99$; evenness, $p = 0.018$, $F = 6.26$; rarity, $p = 0.011$, $F = 7.39$; abundance, $p = 0.021$, $F = 5.91$) and on *M. bidentata* ($n = 38$; richness, $p = 0.001$, $F = 13.21$; diversity, $p = 0.008$, $F = 8.09$; evenness, $p = 0.009$, $F = 7.89$; dominance, $p = 0.043$, $F = 4.50$; rarity, $p = 0.001$, $F = 15.55$) were significantly related to sample size as a covariate. Again, most significant treatment effects were observed for arthropods on late successional tree species (*D. excelsa*, *M. bidentata* and *S. berteroana*); none were observed on early successional tree species (*C. schreberiana* or *P. brachiata*).

Canopy trimming significantly affected dominance on *D. excelsa*. Moreover, debris treatment significantly affected diversity and rarity on *D. excelsa*; total abundance on *M. bidentata*; species richness, diversity, evenness, rarity and total abundance on *M. prasina*; dominance on *P. acuminata*; and richness, diversity, evenness, rarity and total abundance on *S. berteroana*. Time was a significant factor for species richness, diversity, rarity and total abundance on *D. excelsa* (Fig. 2), richness on *M. bidentata* and total abundance on *P. acuminata*. A trim × debris interaction was significant for rarity on *D. excelsa*, evenness and dominance on *P. acuminata*, and total abundance on *S. berteroana*; a trim × time interaction was significant for species richness, diversity, evenness and dominance on *S. berteroana* (Fig. 2); a time × debris interaction was significant for diversity and dominance on *M. bidentata* and dominance on *P. acuminata*. Finally, a trim × debris × time interaction was significant for diversity and evenness on *M. prasina*.

4. Discussion

The CTE was designed to indicate the relative importance of canopy opening and a pulse of debris to the forest floor as factors affecting biotic responses to hurricane disturbance. Our results

Table 2
Probability table for variables analyzed (by linear mixed effects model (ANCOVA) – Yi + sample mass as a covariate) by tree species (number of samples) in plots subjected to four combinations of canopy trimming and debris subsidy in a tropical forest in Puerto Rico. See Table 1 for generic names. An asterisk (*) indicates significance.

Tree species	Variable	Sample mass (as covariate)	Time (as covariate)	Trim	Debris	Time × trim	Time × debris	Trim × debris	3-Way
Cecropia schreberiana (26)	Leaf area missing	0.26	0.91	0.40	0.51	0.65	0.61	0.79	0.55
	Collembola	0.51	0.57	0.86	0.48	0.53	0.86	0.89	0.84
	W. tropicus	0.09	0.57	0.28	0.14	0.43	0.61	0.15	0.98
	Total Abundance	0.31	0.55	0.34	0.82	0.65	0.89	0.57	0.91
	Richness	0.99	0.83	0.26	0.57	0.27	0.79	0.75	0.43
	Diversity	0.69	0.99	0.29	0.67	0.31	0.40	0.90	0.39
	Evenness	0.54	0.95	0.31	0.73	0.33	0.29	0.91	0.33
	Dominance	0.22	0.82	0.50	0.41	0.65	0.11	0.43	0.33
	Rarity	0.61	0.85	0.32	0.22	0.39	0.84	0.51	1.0
Dacryodes excelsa (43)	Leaf area missing	0.09	0.31	0.53	0.35	0.16	0.39	0.55	0.58
	P. pyriformis	0.13	0.64	0.81	0.42	0.61	0.29	0.44	0.99
	C. gundlachi	0.00	0.62	0.38	0.74	0.74	0.20	0.56	0.03*
	Miscellaneous moths	0.64	0.22	0.94	0.44	0.17	0.95	0.56	0.40
	Collembola	0.02*	0.89	0.86	0.12	0.02*	0.61	0.24	0.62
	W. auropunctata	0.88	0.12	0.24	0.72	0.98	0.30	0.97	0.92
	W. tropicus	1.0	0.88	0.11	0.30	0.92	0.45	0.48	0.70
	Total abundance	0.02	0.02*	0.81	0.07	0.92	0.65	0.47	0.12
	Richness	0.01*	0.03*	0.43	0.05	0.86	0.54	0.15	0.26
	Diversity	0.01*	0.04*	0.22	0.05*	0.94	0.69	0.12	0.39
	Evenness	0.02*	0.09	0.15	0.07	0.99	0.64	0.14	0.38
	Dominance	0.09	0.28	0.05*	0.17	0.69	0.97	0.47	0.46
	Rarity	0.01*	0.05*	0.91	0.05*	0.87	0.49	0.04*	0.42
Manilkara bidentata (38)	Leaf area missing	0.26	0.09	0.41	0.18	0.99	0.20	0.95	0.36
	C. rubens	0.24	0.02*	0.59	0.01*	0.51	0.08	0.70	0.31
	V. stellifera	0.49	0.35	0.18	0.96	0.53	0.64	0.90	0.93
	C. gundlachi	0.50	0.50	0.71	0.34	0.76	0.44	0.65	0.60
	Collembola	0.46	0.61	0.21	0.11	0.99	1.0	0.20	0.78
	W. auropunctata	0.10	0.97	0.96	0.35	0.37	0.70	0.09	0.90
	Salticids	0.17	0.50	0.48	0.35	0.22	0.60	0.49	0.97
	Total abundance	0.16	0.12	0.58	0.05*	0.62	0.88	0.24	0.47
	Richness	0.00*	0.03*	0.83	0.98	0.77	0.21	0.21	0.92
	Diversity	0.01*	0.11	0.58	0.30	0.43	0.04	0.23	1.0
	Evenness	0.01*	0.15	0.72	0.22	0.42	0.05	0.27	0.97
	Dominance	0.04*	0.21	0.83	0.10	0.38	0.02*	0.61	0.95
	Rarity	0.00*	0.06	0.86	0.49	0.79	0.50	0.17	0.81
Miconia prasina (38)	Leaf area missing	0.12	0.27	0.61	0.09	0.18	0.77	0.25	0.40
	C. rubens	0.89	0.81	0.20	0.51	0.66	0.64	0.98	0.88
	Bothriocera sp.	0.76	0.19	0.06	0.49	0.14	0.87	0.54	0.54
	C. gundlachi	0.00*	0.26	0.97	0.71	0.98	0.29	0.68	0.18
	Collembola	0.74	0.18	0.12	0.32	0.93	0.77	0.71	0.85
	W. auropunctata	0.30	0.87	0.68	0.10	0.35	0.26	0.36	0.74
	W. tropicus	0.30	0.57	0.87	0.27	0.05*	0.49	0.56	0.48
	Total abundance	0.26	0.06	0.67	0.02*	0.55	0.87	0.81	0.40
	Richness	0.73	0.18	0.98	0.00*	0.85	0.23	0.68	0.08
	Diversity	0.69	0.44	0.83	0.02*	0.67	0.24	0.94	0.04*
	Evenness	0.66	0.51	0.99	0.03*	0.68	0.28	0.87	0.04*
	Dominance	0.89	0.45	0.76	0.28	0.95	0.54	0.84	0.10
	Rarity	0.57	0.46	0.56	0.00*	0.90	0.43	0.89	0.19
Prestoea acuminata (47)	Leaf area missing	0.94	0.14	0.92	0.97	0.87	0.09	0.26	0.74
	C. gundlachi	0.57	0.21	0.58	0.70	0.59	0.86	0.25	0.68
	Collembola	0.35	0.46	0.88	0.53	0.24	0.88	0.70	0.60
	W. auropunctatus	0.085	0.62	0.91	0.91	0.12	0.27	0.23	0.97
	Total abundance	0.56	0.02*	0.55	0.59	0.29	0.80	0.32	0.73
	Richness	0.46	0.59	0.56	0.26	0.98	0.27	0.73	0.92
	Diversity	0.19	0.74	0.56	0.09	0.70	0.10	0.05	0.55
	Evenness	0.19	0.57	0.61	0.08	0.62	0.05	0.05*	0.49
	Dominance	0.37	0.31	0.50	0.04*	0.40	0.03*	0.01*	0.42
	Rarity	0.50	0.27	0.74	0.68	0.94	0.60	0.38	0.72
Psychotria brachiata (34)	Leaf area missing	0.07	0.96	0.74	0.64	0.77	0.72	0.92	0.18
	Petrusa sp.	0.16	0.41	0.40	0.75	0.76	0.98	0.37	0.92
	C. gundlachi	1.00	0.29	0.11	0.12	0.83	0.12	0.24	0.48
	Collembola	0.87	0.69	0.56	0.99	0.78	0.94	0.24	0.20
	W. auropunctata	0.30	0.57	0.13	0.40	0.45	0.88	0.93	0.67
	Total abundance	0.84	0.77	0.85	0.40	0.88	0.91	0.99	0.37
	Richness	0.89	0.19	0.63	0.49	0.63	0.51	0.92	1.0
	Diversity	0.52	0.09	0.72	0.29	0.73	0.43	0.93	0.46
	Evenness	0.55	0.12	0.69	0.25	0.69	0.48	0.97	0.42
	Dominance	0.71	0.25	0.98	0.13	0.84	0.76	0.99	0.29
	Rarity	0.97	0.30	0.30	0.97	0.63	0.59	0.99	0.75

Table 2 (*continued*)

Tree species	Variable	Sample mass (as covariate)	Time (as covariate)	Trim	Debris	Time × trim	Time × debris	Trim × debris	3-Way
Sloanea berteroana (47)	Leaf area missing	0.19	0.74	0.56	0.59	0.72	0.84	0.06	0.11
	C. gundlachi	0.41	0.49	0.91	0.44	0.33	0.45	0.24	0.12
	Miscellaneous moths	0.25	0.05	0.27	0.07	0.04[*]	0.20	0.09	0.23
	Collembola	0.55	0.79	0.52	0.84	0.33	0.28	0.29	0.70
	W. auropunctata	0.24	0.62	0.45	0.40	0.21	0.98	0.43	0.52
	W. tropicus	0.91	0.56	0.77	0.91	0.71	0.79	0.01[*]	0.96
	Salticids	0.50	0.61	0.85	0.05[*]	0.88	0.89	0.71	0.27
	Total abundance	0.80	0.65	0.48	0.53	0.19	0.76	0.04[*]	0.16
	Richness	0.42	0.21	0.08	0.02[*]	0.03[*]	0.76	0.10	0.06
	Diversity	0.39	0.19	0.08	0.05[*]	0.03[*]	0.82	0.28	0.12
	Evenness	0.45	0.17	0.06	0.03[*]	0.04[*]	0.75	0.32	0.15
	Dominance	0.68	0.50	0.17	0.16	0.05[*]	0.70	0.91	0.72
	Rarity	0.69	0.12	0.06	0.04[*]	0.09	0.70	0.15	0.06

[*] Significant at *P* < 0.05; note that some *p*-values of 0.05 were rounded up, others down.

indicated that debris treatment had a more pervasive effect on canopy arthropods than did canopy removal. This is most likely due to indirect effects of debris on the availability of nutrients for new foliage production on host trees (e.g., Zimmerman et al., 1995; Wood et al., 2009), because only a few flying beetles and flies are known to move between canopy and forest floor environments.

4.1. Population responses

Although few taxa showed significant responses to the treatments, the same scale insect species (*C. rubens*) that showed significant responses to disturbances in earlier studies (Schowalter and Ganio, 1999, 2003) also responded significantly in this study. However, abundances of this insect were significantly lower in debris deposition treatments (Fig. 1), contrary to increased abundance in response to previous natural disturbances (Hurricanes Hugo and Georges and the 1994–95 drought) that added debris to the forest floor (Schowalter and Ganio, 2003). The highest abundance of this insect (though non-significant) was in the trim + no debris treatment.

The reasons for the significant increase in abundance of *C. rubens* in the no debris treatments are unknown but may be related to unmeasured differences in plant condition due to debris manipulation. 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 indicate that debris addition has the opposite effect at this site. Zimmerman et al. (1995) found that debris removal in experimental plots following Hurricane Hugo increased soil nitrogen and above-ground productivity. Lodge et al. (2008) reported that nitrogen addition to the forest floor in the Luquillo Experimental Forest inhibited growth of basidiomycete fungi, the primary decomposers in this ecosystem. Furthermore, Treseder (2008) conducted a meta-analysis of nitrogen addition studies and found that nitrogen addition typically reduced microbial biomass and soil respiration, thereby reducing nitrogen flux for plant use, when nitrogen availability is high relative to carbon availability. Fresh litter, such as that resulting from the manipulated debris pulse, has a lower carbon:nitrogen ratio than does senescent litter (Fonte and Schowalter, 2004) and, therefore, should have an effect similar to nitrogen addition. Accordingly, the debris deposition treatment likely reduced nitrogen availability for new shoot production, which is an important resource for herbivores such as *C. rubens*.

Alternatively, differences in timing of debris deposition between this study and natural hurricane disturbances may have affected nutrient fluxes and biotic responses. Shiels et al. (2010)

reported that debris for this study decomposed for about one month outside the deposition treatment plots. Indeed, stem basal area (a measure of above-ground primary productivity) showed no significant responses to trimming but was significantly higher in debris deposition treatments than in treatments without added debris, suggesting differences in debris effects from those reported by Zimmerman et al. (1995) following Hurricane Hugo.

Spiders did not respond significantly to previous hurricane or other disturbances at this site (Schowalter and Ganio, 2003), and reasons for their significant responses to debris treatment (Fig. 1) or interactions in this study are unknown. Spiders are relatively mobile and might be capable of moving between canopy and forest floor. If so, changes in the forest floor environment could explain spider responses to the CTE treatments. The small number of replicates (three) in this study may have reduced the ability to detect population-level responses by taxa that responded strongly and significantly to hurricane disturbances, e.g., *Vinsonia stellifera* on *M. bidentata* and *Itacoris* sp. on *C. schreberiana* (Schowalter and Ganio, 1999, 2003).

In a concurrent study at the same study site (Richardson et al., 2010), litter arthropods responded to trimming, but not to debris deposition. The results from their study indicate 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.

4.2. Community responses

In general, there were three types of community-level responses to the canopy trimming experiment. No treatment effects on arthropod communities were associated with *C. schreberiana* and *P. brachiata* (which became two of the most abundant species in trimmed plots during the first 3 years post-treatment (Shiels et al., 2010)); few and inconsistent effects on communities were associated with *M. bidentata* and *P. acuminata*; and numerous similar effects for multiple metrics were associated with *D. excelsa*, *M. prasina* and *S. berteroana*.

For *D. excelsa*, diversity increased with time after treatment for most metrics (Fig. 2). This appears to be due primarily to an increase in abundance of rare species, which increases richness and, in the absence of increases in abundance of more common species, explains increases in diversity and evenness. In general, diversity was greater in debris deposition treatments, regardless of metric. Diversity based on dominance was greater (i.e. less dominance) in trimmed treatments.

Miconia prasina had significantly more total arthropods in the debris deposition treatments and had significant 3-way
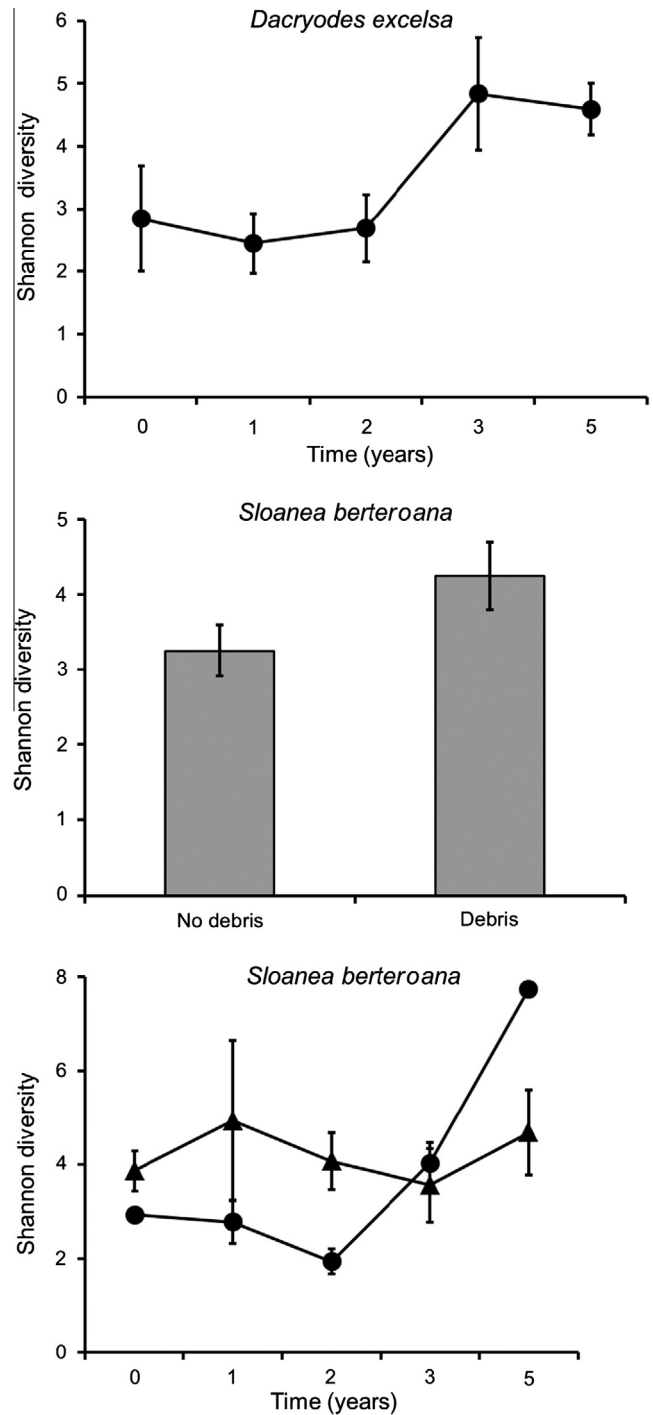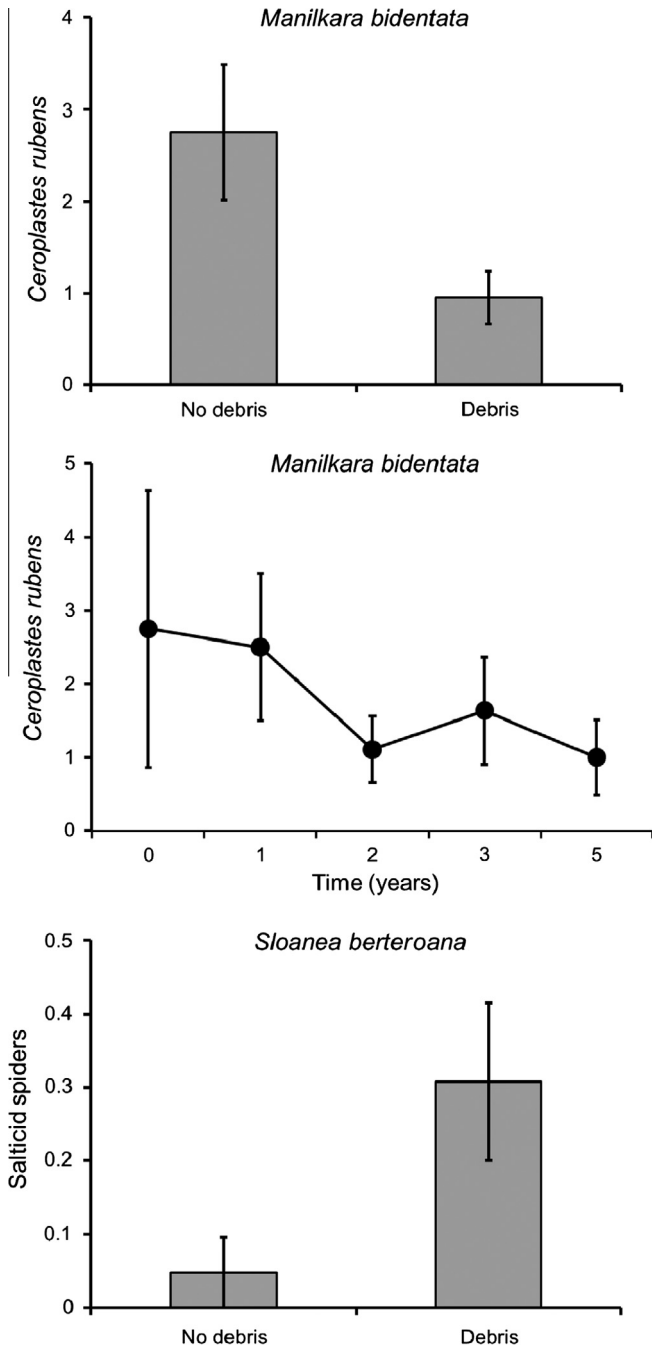
Fig. 1. Mean abundances (±1 standard error) showing responses to debris treatments for *Ceroplastes rubens* on *Manilkara bidentata* and for salticid spiders on *Sloanea berteroana* and response to time since treatment application for *Ceroplastes rubens* on *Manilkara bidentata*.

Fig. 2. Mean Shannon diversity (±1 standard error) in numbers equivalents (Jost, 2006) showing changes in diversity over time on *Dacryodes excelsa* after application of treatments, response to debris treatments on *Sloanea berteroana*, and an interaction between time after treatment and trim (no trim treatments are indicated by ● and trim treatments are indicated by ▲) on *Sloanea berteroana*.

interactions for diversity and evenness, which do not allow for interpretation of lower order effects, e.g., 2-way interactions or main treatment effects. Similar to our results for *D. excelsa*, diversity metrics generally were greater in debris deposition treatments compared to treatments receiving no added debris.

For *S. berteroana*, richness, diversity, evenness, and dominance showed time × trim interactions. In each case, these community metrics increased over time for the untrimmed treatments, but did not change in trim treatments (Fig. 2). This is interesting because communities in trim treatments were more diverse initially than were those in untrimmed treatments, and in year 3 communities in the untrimmed treatments became (and stayed) more

diverse than did those in the trim treatments (which did not change in diversity over time). This could be due to random variation in specific trees related to some unmeasured event(s), as sample sizes were small. Consistent with results for *D. excelsa* and *M. prasina*, diversity metrics generally were greater in debris treatments.

Overall, the debris pulse had a more pervasive effect on canopy arthropod populations and communities than did canopy

opening. These results indicate that changes in plant growth (Shiels et al., 2010) or condition resulting from nutrient availability in added debris may have a greater effect on canopy arthropods than do more direct changes in abiotic conditions resulting from canopy opening. Arthropod taxa- and assemblage-level responses were specific to, and varied among, particular host trees, e.g., significant but opposite effects of debris deposition on total arthropods on *M. prasina* and *M. bidentata*. We suggest that the greater effect of treatments on canopy fauna associated with late successional, compared to early successional, tree species reflects a differential effect of treatment on responses among tree species representing successional stages, e.g., greater degree of injury to late successional species. Loss of canopy cover generally did not have a significant effect on assemblage diversity, contrary to earlier studies (Schowalter and Ganio, 2003; Grimbacher and Stork, 2009), whereas debris deposition significantly affected abundances of several taxa and increased diversity of assemblages on three late successional tree species. Debris effects on diversity generally were not driven by strong responses of common species (which would have appeared in the population-level analyses), but rather were driven primarily by similar responses by many species, most of which were uncommon.

These results suggest that changes in arthropod communities are likely to become more frequent, given predictions that the frequency and severity of hurricanes and droughts will increase as global temperatures rise (Schowalter, 2011, 2012). Because changes in canopy insect abundances affect nutrient fluxes from canopy to forest floor in this and other forests (Schowalter, 2011; Schowalter et al., 2011), effects of hurricane disturbance are likely to cascade through ecosystems in ways that will alter future structure and function.

Acknowledgments

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