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## Invertebrate Community Structure and Herbivory in a Tropical Rain Forest Canopy in Puerto Rico Following Hurricane Hugo<sup>1</sup>

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### ABSTRACT

The effect of hurricane disturbance on canopy invertebrate communities was studied at the Luquillo Experimental Forest in Puerto Rico. Invertebrate community structure and herbivory were compared among tree species co-occurring in intact forest (standing trees) and canopy gaps. Foliage-bearing branches were collected using a long-handled insect net fitted with a closeable plastic bag. Invertebrates were tabulated and foliage was dried, weighed, and measured for area missing. Lepidoptera, predaceous beetles, and decomposers were significantly more abundant in standing trees; whereas, some sap-sucking arthropods were more abundant in canopy gaps, indicating that these taxa responded to changes in microclimate and/or host condition resulting from disturbance. Herbivory (estimated as leaf area missing) and numbers of several taxa differed significantly among tree species, likely reflecting host preferences based on foliage nutritional quality. Species diversity and the gradient of disturbance may have masked disturbance effects.

*Key words:* disturbance; herbivory; hurricane; invertebrate community structure; Puerto Rico; species diversity.

FOREST CANOPIES ARE IMPORTANT interfaces for exchange of energy, water, and nutrients between the atmosphere and terrestrial ecosystems. Species interactions and processes such as herbivory influence canopy structure and function, through effects on foliage surface area, for example (Mattson & Addy 1975, Schowalter *et al.* 1986). Invertebrates are particularly abundant and diverse in forest canopies, affect canopy structure and processes, and respond to changes in forest conditions (Mattson & Addy 1975, Swank *et al.* 1981, Ohmart *et al.* 1983, Schowalter *et al.* 1986, Coley & Aide 1991, Fox & Morrow 1992). However, research on invertebrate effects on canopy structure and responses to environmental changes has been limited by the difficulty of canopy access.

In September 1989 Hurricane Hugo swept across the Luquillo Experimental Forest in eastern Puerto Rico, stripping foliage and toppling trees and initiating plant succession in canopy gaps (Walker *et al.* 1991). This disturbance provided an opportunity to study invertebrate community response to changes in canopy conditions in a tropical rain forest. This study was designed to compare invertebrate abundances, community structure, and herbivory among representative early and late successional tree species that co-occurred in lightly and severely disturbed patches of rain forest. Data were

used to test two hypotheses: that invertebrate taxa respond significantly to canopy disturbance in tropical forests; and, that herbivore effect on foliage area is related to plant status in intact forest or in gaps (*e.g.*, Coley 1983, Schowalter & Crossley 1987, Shelly 1988, Schowalter 1989).

### MATERIALS AND METHODS

**SITE DESCRIPTION.**—This study was conducted at the U.S. Forest Service El Verde Field Station, 10 km south of Rio Grande, Puerto Rico (18°10'N, 65°30'W) in the Luquillo Experimental Forest (LEF). The field station is located at 500 m elevation. Vegetation is dominated by tabonuco, *Dacryodes excelsa*, which composes 35 percent of the forest canopy below 600 m elevation (Brown *et al.* 1983). Canopy height averages about 20 m in undisturbed forests. Prior to Hurricane Hugo, small light gaps occurred infrequently in an otherwise closed canopy. Mean monthly temperatures range from 21°C in January to 25°C in September (Brown *et al.* 1983). Annual precipitation averages 372 cm and varies seasonally (McDowell & Estrada-Pinto 1988), with 20–25 cm per month from January to April (dry season) and about 40 cm per month during the remainder of the year (wet season).

Hurricane Hugo had an uneven effect on the forest canopy of the Luquillo Experimental Forest. The east side of the LEF experienced widespread treefall, with standing trees remaining only on sheltered slopes. The west side, including El Verde Field

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Station, was disturbed less severely, with 30–60 m diameter patches of standing trees interspersed with 30–60 m diameter patches of nearly complete tree-fall (gaps). Patches of standing trees did, however, sustain severe branch and foliage loss during the hurricane. Rapid refoliation and shoot replacement by surviving trees and seedling germination of early successional species began about nine months after the hurricane (Frangi & Lugo 1991). This study of canopy community recovery was initiated in February 1991, about 17 months after the hurricane (8 mo after initiation of recovery). Thickets of *Cecropia peltata* were developing in large patches of fallen trees.

**SAMPLING METHODS.**—I established six experimental blocks, each about 2000 m<sup>2</sup> and including a 500 m<sup>2</sup> patch of intact forest (standing trees) and a nearby 500 m<sup>2</sup> canopy gap. The blocks were distributed over 11 ha. Canopy closure above 2 m was 70–80 percent in plots of standing trees and 10–20 percent in gaps.

Canopy invertebrate communities in five major tree species representing early or late successional forests at the LEF were studied. *Dacryodes excelsa*, *Manilkara bidentata* (ausubo), and *Sloanea berteriana* (motillo) dominate closed canopy forests and persisted in patches of treefall as stump sprouts. *Cecropia peltata* and *Casearia arborea* (rabo raton) colonize large openings in the canopy, but also occur as scattered understory seedlings in closed canopy forests. Canopy invertebrate communities were compared among these tree species in patches of standing trees and in patches of fallen trees.

Canopies were sampled in February (dry season), May (early wet season), August (mid-wet season) and November (late wet season) during 1991 to account for life history variation. I used a long-handled insect net, fitted with a 50 liter plastic bag closeable by a drawstring, to collect foliage and branch samples at 8–12 m height above ground (Schowalter *et al.* 1981). The bag was slipped quickly over a foliage-bearing branch, closed, and clipped from the tree. Trees and branches were selected randomly, provided a sample was accessible. No effort was made to sample previously sampled trees. One tree per species per plot was sampled each time. Each sample was 10–30 g or about 1000 cm<sup>2</sup> of foliage material from 30–50 cm branch length.

This sampling technique may alarm some highly mobile arthropods. However, because most invertebrate herbivores and many predators are relatively sedentary and are collected with their foliage

food base, this technique is the most suitable for measuring population size and biomass of resident invertebrates (Majer & Recher 1988, Schowalter 1989). Other canopy sampling techniques, such as light traps, interception traps, and canopy fumigation, collect primarily mobile life stages dispersing from unknown sources.

Samples were fumigated with chloroform and sorted into invertebrate taxa and plant material. Invertebrates were counted by taxa, and representatives of each taxon dried at 50°C and weighed. All foliage was pressed, dried at 50°C and weighed. Foliage area with holes masked and without masking was measured on dried leaves with a LiCor® Leaf Area Meter (LiCor Inc., Lincoln, Nebraska). The proportion of leaf area occupied by holes provided an estimate of herbivore influence on leaf area. Leaf mining occurred infrequently only on *Manilkara*.

**DATA ANALYSIS.**—Invertebrate numbers were divided by foliage weight for each sample. Many taxa had too few individuals for separate analyses and were combined into functional groups. Numbers per foliage mass (intensity) were transformed to improve normality of data and constancy of variance. Transforming data to their ranks accomplished these objectives better than did natural logs.

A repeated measures analysis of variance was used to evaluate independence of data among sampling dates and to indicate significance of temporal trends. No autocorrelation was indicated. Therefore, data were pooled by sample date and analyzed by two-way analysis of variance (ANOVA) with treatment (gap vs standing trees) and tree species as main effects and blocks as replicates (Steel & Torrie 1980). The number of blocks (6) and sampling times (4) provided 24 replicates for each disturbance level × tree species combination. However, some tree species could not be located in some plots. All statistical analyses were performed using SAS software (SAS Institute, Inc. 1982). Differences were considered to be significant at the 0.05 level. For significant effects, means were compared using Fisher's Protected LSD Test with an experiment-wise error rate of 0.05.

## RESULTS

About 101 taxa were collected during this study. Particularly abundant taxa included a tree cricket (*Cyrtoxipha gundlachi*, Orthoptera), several Lepidoptera, several scale insects (especially *Vinsonia stellifera*, *Coccus acutissimus*, *Protospulvinaria pyr-*

TABLE 1. *Canopy invertebrate intensities (no./g foliage) by tree species in canopy gaps (G) or standing trees (S) following Hurricane Hugo (1989) during 1991 at El Verde Field Station, Luquillo Experimental Forest, Puerto Rico. Numbers in parentheses represent 1 standard error of the mean.*

Group (no. taxa)	Tree species									
	<i>Casearia</i>		<i>Cecropia</i>		<i>Dacryodes</i>		<i>Manilkara</i>		<i>Sloanea</i>	
	G N=19	S N=13	G N=24	S N=24	G N=24	S N=24	G N=23	S N=24	G N=21	S N=24
Chewing Phytophages	160 (150)	180 (79)	37 (15)	14 (14)	90 (28)	56 (19)	27 (8)	96 (42)	58 (13)	85 (5)
<i>Cyrtoxipha</i>	0	0	0	0	73 (27)	21 (7)	23 (7)	25 (8)	45 (15)	46 (12)
Other Orthoptera (2)	0	0	10 (10)	0	0	0	0	6 (4)	5 (4)	0
Lepidoptera (7)	0	100 (67)	15 (10)	14 (14)	13 (6)	24 (14)	0	14 (6)	0	34 (11)
Coleoptera (3)	160 (150)	76 (34)	10 (6)	0	0	12 (5)	0	50 (41)	0	5 (5)
Sucking Phytophages	320 (88)	450 (170)	180 (41)	840 (300)	610 (250)	510 (230)	880 (220)	540 (81)	250 (73)	64 (13)
<i>Vinsonia</i>	0	0	0	0	0	19 (16)	520 (210)	220 (61)	0	0
<i>Coccus</i>	0	0	0	0	110 (35)	40 (15)	2 (2)	0	18 (12)	3 (2)
<i>Ceroplastes</i>	0	45 (31)	0	0	180 (53)	150 (54)	250 (62)	260 (49)	11 (7)	0
<i>Protopulvinaria</i>	54 (40)	120 (120)	0	0	260 (180)	240 (220)	50 (25)	30 (21)	4 (3)	1 (1)
Other Coccoids (3)	98 (55)	100 (69)	11 (8)	120 (120)	6 (6)	0	0	0	3 (3)	0
<i>Sibovea</i>	43 (23)	7 (7)	24 (23)	270 (180)	0	0	8 (6)	0	130 (71)	0
Mirid sp.	0	0	110 (34)	99 (53)	0	0	0	0	0	0
Other Sap-suck. (19)	130 (42)	180 (83)	33 (14)	340 (150)	57 (16)	50 (22)	37 (10)	37 (10)	84 (29)	60 (13)
Omnivores	130 (55)	140 (69)	100 (46)	850 (300)	37 (21)	11 (6)	44 (34)	39 (28)	45 (17)	26 (15)
Formicids (3)	130 (55)	140 (69)	100 (46)	850 (300)	37 (21)	11 (6)	44 (34)	37 (28)	41 (17)	26 (15)
Molluscs (2)	0	0	0	0	0	0	0	2 (2)	4 (3)	0
Predators	260 (67)	300 (130)	120 (35)	420 (160)	96 (21)	88 (26)	65 (16)	72 (13)	45 (12)	98 (18)
Coleoptera (8)	76 (44)	73 (39)	6 (6)	42 (29)	10 (4)	12 (6)	0	7 (3)	0	13 (6)
Parasit. Hymen. (5)	14 (11)	36 (25)	8 (6)	120 (82)	11 (7)	0	6 (4)	0	11 (7)	6 (4)
Aranids (7)	130 (39)	140 (89)	100 (27)	100 (73)	69 (18)	69 (23)	45 (15)	55 (10)	34 (10)	73 (14)
Other Predators (12)	32 (17)	43 (44)	0	160 (140)	6 (5)	6 (3)	13 (9)	7 (4)	0	6 (3)
Detritivores	74 (31)	67 (33)	6 (6)	99 (57)	31 (11)	32 (10)	16 (9)	25 (8)	13 (6)	34 (8)
Blattids (2)	26 (15)	56 (33)	0	0	13 (9)	15 (6)	14 (8)	7 (4)	8 (5)	16 (6)
Other Detrit. (12)	48 (28)	11 (11)	6 (6)	99 (57)	18 (8)	17 (8)	0	18 (7)	5 (3)	18 (6)
Other Inverts. (9)	54 (29)	66 (33)	29 (20)	110 (75)	38 (17)	11 (5)	11 (6)	35 (24)	6 (5)	15 (6)

*iformis* and *Ceroplastes rubens*) and a cicadellid (*Sibovaea coffeacola*) (Homoptera), a mirid species (Heteroptera), ants (especially *Linepithema melleum*, Hymenoptera), two cockroaches (especially *Plectophora dorsalis*, Dictyoptera) and several spiders.

Disturbance intensity had a significant effect on the intensities of several taxa and functional groupings (Table 1). Lepidoptera ( $F = 6.1$ ;  $df = 1,42$ ;  $P = 0.017$ ), detritivores ( $F = 6.6$ ,  $df = 1,42$ ;  $P = 0.014$ ), and predaceous beetles, primarily coccinellids and lampyrids ( $F = 4.5$ ,  $df = 1,42$ ;  $P = 0.039$ ), were more abundant in standing trees; whereas, *Vinsonia* ( $F = 7.1$ ;  $df = 1,42$ ;  $P = 0.011$ ) and *Protospulvinaria* ( $F = 4.6$ ;  $df = 1,42$ ;  $P = 0.038$ ) were more abundant in gaps. A mirid sp. (Heteroptera) approached a significant response to disturbance ( $F = 3.4$ ;  $df = 1,42$ ;  $P = 0.07$ ), being more abundant in gaps. Total predators approached a significant response ( $F = 3.6$ ;  $df = 1,42$ ;  $P = 0.065$ ), being more abundant in standing trees.

Several taxa and functional groups differed in intensities among tree species (Table 1). *Cyrtoxipha* was more abundant on *Dacryodes*, *Sloanea*, and *Manilkara* than on the other two tree species ( $F = 14$ ;  $df = 4,42$ ;  $P = 0.0001$ ). *Vinsonia* was most abundant on *Manilkara* ( $F = 112$ ;  $df = 4,42$ ;  $P = 0.0001$ ), *Coccus* on *Dacryodes* ( $F = 12$ ;  $df = 4,42$ ;  $P = 0.0001$ ), and *Protospulvinaria* and *Ceroplastes* on *Manilkara* and *Dacryodes* ( $F_s > 10$ ;  $df = 4,42$ ;  $P = 0.0001$ ). Miscellaneous sap-sucking insects were most abundant on *Casearia* and least abundant on *Manilkara* ( $F = 3.2$ ;  $df = 4,42$ ;  $P = 0.021$ ). The mirid sp. was most abundant on *Cecropia* ( $F = 28$ ;  $df = 4,42$ ;  $P = 0.0001$ ). Formicids (ants), primarily *Linepithema*, were most abundant on *Cecropia* and *Casearia* ( $F = 7.1$ ;  $df = 4,42$ ;  $P = 0.0002$ ). Total sap-sucking invertebrates, omnivores and detritivores ( $F = 5.6, 7.1$  and  $3.2$ , respectively;  $df = 4,42$ ;  $P = 0.001, 0.0002$  and  $0.0214$ , respectively) differed in overall abundance among tree species. Sap-suckers were most abundant on *Manilkara* and least abundant on *Sloanea*; omnivores and predators were more abundant on *Casearia* and *Cecropia* than on the later successional species. Herbivorous beetles and total chewing phytophages approached a significant relationship to tree species ( $F = 2.3$  and  $2.5$ , respectively;  $df = 4,42$ ;  $P = 0.07$  and  $0.055$ , respectively).

*Vinsonia*, *Sibovaea*, the mirid sp. and total sap-suckers showed significant ( $F_s > 2.8$ ;  $df = 4,42$ ;  $P_s < 0.039$ ) treatment  $\times$  tree species interactions, indicating variable responses to disturbance severity among tree species. Total sap-sucker abundance on *Cecropia* was significantly higher ( $P = 0.007$ ) among

standing trees; abundance on *Sloanea* was higher in gaps ( $P = 0.055$ ). *Protospulvinaria* and molluscs (land snails, *Alcaldia striata* and *Gaeotis nigrolineata*) approached a significant interaction ( $F = 2.3$ ;  $df = 4,42$ ;  $P = 0.07$ ).

Numeric intensities multiplied by average weights for each taxon provided estimates of mass intensities (mg invertebrate/g foliage). Mass intensity is related to consumption rate and provides a better indication of ecological importance than does abundance. Functional group comparison (Fig. 1) indicated that mass intensities of detritivores and predators generally were larger in standing trees than in gaps. Mass intensities of sap-sucking phytophages were larger in gaps for late-successional trees and standing trees for early successional trees. Mass intensities of chewing herbivores were influenced disproportionately by large Orthoptera.

Relatively few taxa showed significant temporal trends in abundance. Herbivorous beetles and Lepidoptera showed significant third order polynomial patterns, with peak abundances ( $F_s > 4.2$ ;  $df = 1,36$ ;  $P_s < 0.048$ ) in August (mid-wet season), indicating seasonal patterns. Ants were least abundant at this time ( $F = 10$ ;  $df = 1,36$ ;  $P = 0.003$ ). *Sibovaea* showed a significant linear increase in abundance during the year ( $F = 9.0$ ;  $df = 1,36$ ;  $P = 0.005$ ), suggesting continued population growth or recovery.

Leaf area missing as a result of herbivory varied significantly ( $F = 7.9$ ;  $df = 4,36$ ;  $P = 0.0001$ ) among tree species (Fig. 2) but not between disturbance levels ( $P = 0.41$ ) nor as a result of interaction ( $P = 0.13$ ). The late successional and more numerous *Manilkara* and *Sloanea* tended to have more leaf area missing than did the early successional and less numerous *Casearia* and *Cecropia*. *Dacryodes* showed intermediate values.

## DISCUSSION

Invertebrate abundances and community organization showed significant responses to disturbance intensity and/or tree species. Only one taxon (*Sibovaea*) showed a linear temporal trend that suggested population recovery from disturbance during the year. Herbivore effects on foliage area were not significantly related to disturbance intensity or clearly related to herbivore abundance.

The response of the canopy community to hurricane disturbance was consistent with, but less pronounced than, responses to large-scale harvest of temperate forests (Schowalter & Crossley 1987, Schowalter 1989). Lepidoptera were more abun-

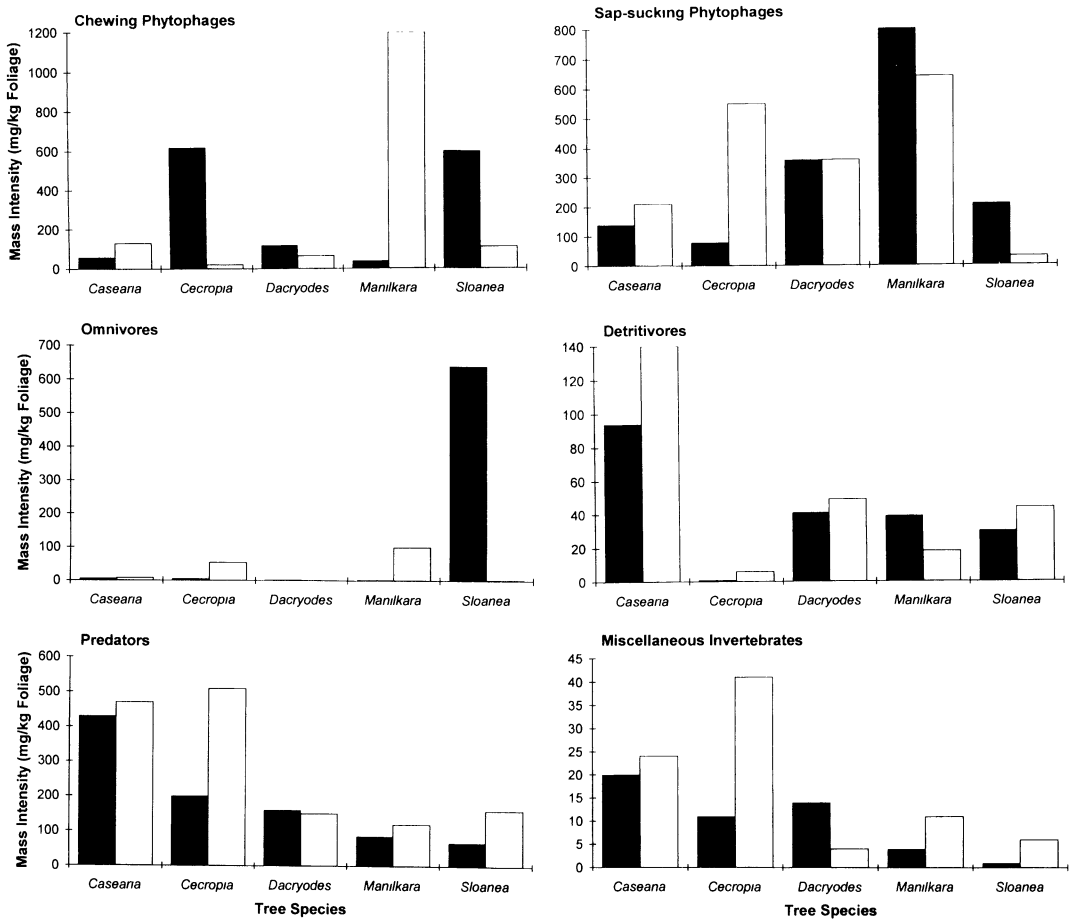


FIGURE 1. Mass intensities of invertebrate functional groups by tree species in gaps (solid bars) and standing trees (open bars) following Hurricane Hugo (1989) at El Verde Field Station, Luquillo Experimental Forest, Puerto Rico, during 1991.

dant in the closed canopies of standing trees, while several sap-sucking phytophages were more abundant in gaps. These taxa dominate temperate forests, but this tropical forest showed a greater diversity of taxa and responses to disturbance. The variable responses of canopy invertebrate taxa were similar to the responses of frogs (Woolbright 1991), lizards (Reagan 1991), birds (Waide 1991), and understory invertebrates (Willig & Camilo 1991, Alvarez & Willig 1993) to hurricane disturbance at this site, and of insects to treefall gaps in Panama (Shelly 1988).

Other factors might have affected the measured differences between disturbance levels. More pronounced invertebrate responses might have been observed immediately after the hurricane or in more discrete treatments. This study began after about eight months of canopy recovery, during which

greater initial differences in community structure might have disappeared. Hurricane disturbance at this site was expressed as a fine-scale mosaic of severity levels across the forest landscape, in contrast to the discrete pattern of 10–20 ha harvested vs undisturbed patches in comparable studies of temperate forests (Schowalter & Crossley 1987, Schowalter 1989). Many tropical invertebrate species (such as *Cyrtosipha*) may be adapted to producing sufficient dispersants to colonize sparse hosts, spreading individuals widely among disturbance levels and tree species, thereby masking disturbance effects. Aphids, which have shown the most dramatic responses to disturbance in temperate forests (Schowalter & Crossley 1987, Schowalter 1989), are poorly represented in the tropics (Dixon 1985) and were virtually absent from samples in Puerto Rico.

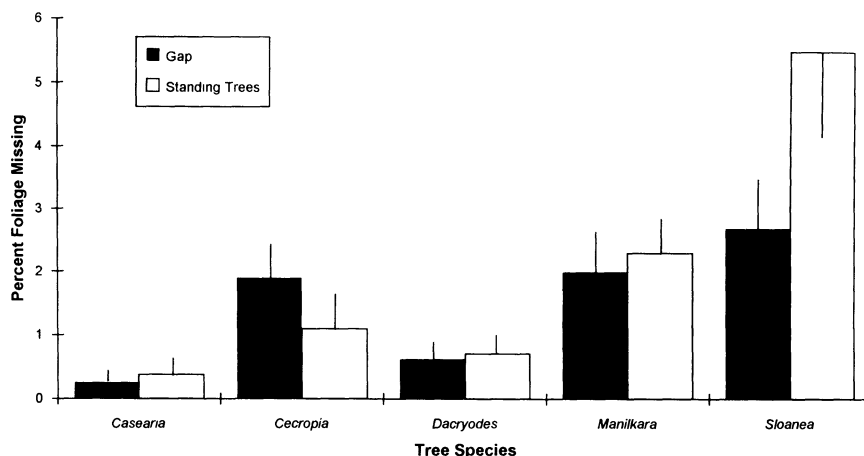


FIGURE 2. Leaf area missing by tree species in gaps and standing trees following Hurricane Hugo (1989) at El Verde Field Station, Luquillo Experimental Forest, Puerto Rico, during 1991. Vertical lines represent 1 standard error of the mean.

Significant differences in invertebrate abundances and canopy community structure between disturbance levels likely reflect altered environmental conditions. Forests with relatively closed canopies maintain more stable temperatures, higher humidities, and lower wind speeds compared to nonforested areas (e.g., Franklin *et al.* 1989). These conditions may permit survival of many species (such as detritivores) that are intolerant of extreme temperatures or desiccation. Disturbances such as hurricanes that open the canopy over large areas create extreme environmental conditions and alter plant physiological processes. Invertebrate species promoted by exposure, reduced competition, or reduced predation often show dramatic population growth. Sap-sucking insects often are favored by reduced predation and increased nitrogen transport in sap of rapidly sprouting plants, especially when tended by ants (Dixon 1985).

Herbivory, estimated as leaf area missing, did not differ significantly between disturbance levels. However, the late successional *Manilkara* and *Sloanea* showed the highest rates of foliage loss, suggesting that increasing importance of these species during ecosystem recovery could increase overall herbivory and nutrient turnover rates.

Tree species characteristics apparently outweighed effects of disturbance intensity in this study. Given that the entire forest was defoliated by the hurricane, regrowth foliage may have been qualitatively similar among disturbance levels, emphasizing among-tree variation but masking disturbance effects. Responses to disturbance were most pronounced in the later successional trees, *Dac-*

*ryodes*, *Manilkara*, and *Sloanea* (Table 1), which likely were altered most by breakage and defoliation. Invertebrates associated with the two early successional tree species may not have responded yet to the altered condition and/or increased abundance of these hosts.

The estimates of herbivory in this study do not account for leaves entirely consumed or abscised from the tree (Lowman 1992, Risley 1993). Examination of leaf scars and patterns of leaf consumption on sampled branches ( $N = 220$ ) indicated that leaves were shed progressively from the proximal ends of branches, and that leaf area missing did not increase in this direction. Therefore, leaf disappearance apparently occurred primarily through shedding of senescent leaves, regardless of herbivory. The estimated level of herbivory (1–6%) is within the nominal range of foliage removal by herbivores in other forest ecosystems (Schowalter *et al.* 1986, Coley & Aide 1991).

Foliar nutrient concentrations measured in earlier studies (Ovington & Olson 1970, Scatena *et al.* 1993) did not appear to explain patterns of invertebrate abundance among tree species in this study. *Cecropia* has high concentrations of nitrogen (1.8%), phosphorus (1.1 mg/g), potassium (8.8–13 mg/g) and calcium (9.6–12 mg/g); *Casearia* has the highest foliar nitrogen concentration (2.2%), but intermediate concentrations of other nutrients (0.7–0.8, 6.0–10, and 4.0 mg/g, respectively) (Ovington & Olson 1970, Scatena *et al.* 1993). These two species had small herbivore biomasses and low rates of herbivory. *Dacryodes* and *Sloanea* have the lowest concentrations of potassium and

calcium (5–7 mg/g K and 3.8–7.9 mg/g Ca) and intermediate concentrations of nitrogen and phosphorus (1.2–1.4% N and 0.63–0.71 mg/g P), but had low and high rates of herbivory, respectively, and large biomasses of herbivores. *Manilkara* has the lowest concentrations of nitrogen and phosphorus (1.1% N and 0.57 mg/g P) and intermediate concentrations of potassium and calcium (11 mg/g K and 8.2 mg/g Ca) (Ovington & Olson 1970, Scatena *et al.* 1993) and had high rates of herbivory.

*Dacryodes* foliage (and other tissues) is characterized by conspicuous amounts of aromatic terpenoids (T. D. Schowalter, pers. obs.) that likely limit defoliator biomass and herbivory (Harborne 1982). *Manilkara* produces a white, sticky sap that flows from foliar wounds (T. D. Schowalter, pers. obs.), but nevertheless supported an abundant and diverse fauna. The other tree species may have high lignin content or produce other chemical defenses, *e.g.*, alkaloids by the nitrogen-rich *Casearia* and *Cecropia*. Bloomfield (1993) reported that senesced *Cecropia* foliage had significantly higher lignin content than did senesced *Dacryodes* or *Manilkara* foliage.

Variation in invertebrate biomass and herbivory generally was positively related to the abundances of these tree species (*Dacryodes* > *Manilkara* = *Sloanea* > *Cecropia* > *Casearia*, Ovington & Olson 1970), as predicted by the resource concentration hypothesis (Root 1973, Coley 1983, Kareiva 1983). *Dacryodes* was a notable exception, with a low rate of herbivory, perhaps because of low nutrient and high terpene concentrations. Herbivory was higher in standing trees for the later successional species, and was higher in gaps for *Cecropia*, where it formed dense thickets.

Seasonal variation in invertebrate abundances also was apparent in this study, as reported also by Janzen (1973), Wolda (1978), and Shelly (1988).

However, this study was not designed to evaluate seasonal changes or causal factors.

## CONCLUSIONS

The invertebrate community structure in this tropical rain forest canopy differed between disturbance levels and among tree species. Sap-sucking invertebrates tended to be more abundant in gaps; whereas, Lepidoptera were more abundant in standing trees, as found in studies in temperate forests. However, disturbance effects were less pronounced in the tropical rain forest, perhaps reflecting the less discrete disturbance pattern and greater species diversity at this site. Differences in invertebrate abundances and rates of foliage loss among tree species may have reflected the relative abundance and nutritional quality of foliage. The extent to which these data reflect nominal conditions on this island, or in mainland tropical forests, is unknown.

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## LITERATURE CITED

- ALVAREZ, J., AND M. R. WILLIG. 1993. Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 25: 100–110.
- BLOOMFIELD, J. 1993. Nutrient dynamics and the influence of substrate quality on the decomposition of leaves and fine roots of selected tree species in a lower montane tropical rain forest in Puerto Rico. Yale University Ph.D. Dissertation, New Haven, Connecticut.
- BROWN, S., A. E. LUGO, S. SILANDER, AND L. LIEGEL. 1983. Research history and communities in the Luquillo Experimental Forest. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. SO-44. South. For. Exp. Stn., New Orleans, Louisiana.
- COLEY, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53: 209–233.
- , AND T. M. AIDE. 1991. A comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson (Eds.). *Plant-animal*



- interactions: evolutionary ecology in tropical and temperate regions, pp. 25–49. John Wiley & Sons, New York, New York.
- DIXON, A. F. G. 1985. Aphid ecology. Blackie Academic & Professional, London, England.
- FOX, L. R., AND P. A. MORROW. 1992. Eucalypt responses to fertilization and reduced herbivory. *Oecologia* 89: 214–222.
- FRANGI, J. L., AND A. E. LUGO. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica* 23: 324–335.
- FRANKLIN, J. F., D. A. PERRY, T. D. SCHOWALTER, M. E. HARMON, A. MCKEE, AND T. SPIES. 1989. Importance of ecological diversity in maintaining long-term site productivity. In D. A. Perry, B. Thomas, R. Meurisse, R. Miller, J. Boyle, P. Sollins, and J. Means (Eds.). *Maintaining long-term productivity of Pacific Northwest forest ecosystems*, pp. 82–97. Timber Press, Inc., Portland, Oregon.
- HARBORNE, J. B. 1982. Introduction to ecological biochemistry. 2nd edition. Academic Press, London, England.
- JANZEN, D. H. 1973. Sweep samples of tropical foliage insects: description of study sites, with data on species abundances and size distributions. *Ecology* 54: 687–708.
- KAREIVA, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. In R. F. Denno and M. S. McClure (Eds.). *Variable plants and herbivores in natural and managed systems*, pp. 259–289. Academic Press, New York, New York.
- LOWMAN, M. E. 1992. Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphora sassafras* (Monimiaceae). *Biotropica* 24: 263–272.
- MAJER, J. D., AND H. F. RECHER. 1988. Invertebrate communities on Western Australian eucalypts—a comparison of branch clipping and chemical knockdown procedures. *Aust. J. Ecol.* 13: 269–278.
- MATTSON, W. J., AND N. D. ADDY. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515–522.
- MCDOWELL, W. H., AND A. ESTRADA-PINTO. 1988. Rainfall at the El Verde Field Station, 1964–1986. U.S. Dep. Energy, Tech. Rep. CEER-T-228. Center for Energy and Environmental Research, San Juan, Puerto Rico.
- OHMART, C. P., L. G. STEWART, AND J. R. THOMAS. 1983. Leaf consumption by insects in three *Eucalyptus* forest types in southeastern Australia and their role in short-term nutrient cycling. *Oecologia* 59: 322–330.
- OVINGTON, J. D., AND J. S. OLSON. 1970. Biomass and chemical content of El Verde lower montane rain forest plants. In H. T. Odum and R. F. Pigeon (Eds.). *A tropical rain forest, a study of irradiation and ecology at El Verde, Puerto Rico*, pp. H53–H77. U.S. A.E.C., National Tech. Info. Serv., Springfield, Virginia.
- REAGAN, D. P. 1991. The response of *Anolis* lizards to hurricane-induced habitat changes in a Puerto Rican forest. *Biotropica* 23: 468–474.
- RISLEY, L. S. 1993. Effect of simulated insect herbivore damage on survival of tree leaves. *Environ. Entomol.* 22: 57–61.
- ROOT, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43: 95–124.
- SAS INSTITUTE, INC. 1982. SAS user's guide: statistics. SAS Institute, Inc., Cary, North Carolina.
- SCATENA, F. N., W. SILVER, T. SICCAMA, A. H. JOHNSON, AND M. J. SANCHEZ. 1993. Biomass and nutrient content of the Bisley experimental watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. *Biotropica* 25: 15–29.
- SCHOWALTER, T. D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. *Can. J. For. Res.* 19: 318–322.
- , AND D. A. CROSSLEY, JR. 1987. Canopy arthropods and their response to forest disturbance. In W. T. Swank and D. A. Crossley, Jr. (Eds.). *Forest hydrology and ecology at Coweeta*, pp. 207–218. Springer-Verlag New York Inc., New York, New York.
- , W. W. HARGROVE, AND D. A. CROSSLEY, JR. 1986. Herbivory in forested ecosystems. *Annu. Rev. Entomol.* 31: 177–196.
- , J. W. WEBB, AND D. A. CROSSLEY, JR. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology* 62: 1010–1019.
- SHELLY, T. E. 1988. Relative abundance of day-flying insects in treefall gaps vs. shaded understory in a Neotropical forest. *Biotropica* 20: 114–119.
- STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics. 2nd edition. McGraw-Hill Publishing Company, New York, New York.
- SWANK, W. T., J. B. WAIDE, D. A. CROSSLEY, JR., AND R. L. TODD. 1981. Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia* 51: 297–299.
- WAIDE, R. B. 1991. Summary of the response of animal populations to hurricanes in the Caribbean. *Biotropica* 23: 508–512.
- WALKER, L. R., D. J. LODGE, N. V. L. BROKAW, AND R. B. WAIDE. 1991. An introduction to hurricanes in the Caribbean. *Biotropica* 23: 313–316.
- WILLIG, M. R., AND G. R. CAMILO. 1991. The effect of Hurricane Hugo on six invertebrate species in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 23: 445–461.
- WOLDA, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J. Anim. Ecol.* 47: 369–381.
- WOOLBRIGHT, L. L. 1991. The impact of Hurricane Hugo on forest frogs in Puerto Rico. *Biotropica* 23: 462–467.