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A Canopy Trimming Experiment in Puerto Rico: The Response of Litter Invertebrate Communities to Canopy Loss and Debris Deposition in a Tropical Forest Subject to Hurricanes

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Abstract

Hurricanes cause canopy removal and deposition of pulses of litter to the forest floor. A Canopy Trimming Experiment (CTE) was designed to decouple these two factors, and to investigate the separate abiotic and biotic consequences of hurricane-type damage and monitor recovery processes. As part of this experiment, effects on forest floor invertebrate communities were studied using litterbags. Canopy opening resulted in increased throughfall, soil moisture and light levels, but decreased litter moisture. Of these, only throughfall and soil moisture had returned to control levels 9 months after trimming. Canopy opening was the major determinant of adverse changes in forest floor invertebrate litter communities, by reducing diversity and biomass, irrespective of debris deposition, which played a secondary role. Plots subjected to the most disturbance, with canopy removed and debris added, had the lowest diversity and biomass. These two parameters were higher than control levels when debris was added to plots with an intact canopy, demonstrating that increased nutrient potential or habitat complexity can have a beneficial effect, but only if the abiotic conditions are suitable. Animal abundance remained similar over all treatments, because individual taxa responded differently to canopy trimming. Mites, Collembola, and Psocoptera, all microbiovores feeding mainly on fungal hyphae and spores, responded positively, with higher abundance in trimmed plots, whereas all other taxa, particularly predators and larger detritivores, declined in relative abundance. Litterbag mesh size and litter type had only minor effects

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on communities, and canopy trimming and debris deposition explained most variation between sites. Effects of trimming on diversity, biomass, and abundance of some invertebrate taxa were still seen when observations finished and canopy closure was complete at 19 months. This suggests that disturbance has a long-lasting effect on litter communities and may, therefore, delay detrital processing, depending on the severity of canopy damage and rate of regrowth.

Key words: canopy gaps; community composition; forest manipulation; fungi; litterbags; relative abundance.

Introduction

Tropical hurricanes, typhoons and cyclones are major perturbations that can have long-lasting effects on ecological processes and forest structure (Sanford and others 1991; Van Bloem and others 2005). In cases of extreme severity and frequency, such as typhoons in NE Taiwan, loss of nutrients through litterfall appears to limit tree growth and canopy height, and leaf regeneration is delayed (Lin and others 2003). In the Caribbean, where hurricanes are less severe and frequent, there is loss of leaves and wood, damage to branches and stems, and elevated mortality rates (Foster and Boose 1992; Lugo and Scatena 1996), but a rapid flush of new foliage and stem sprouts (Walker 1991). The magnitude of damage is strongly dependent on land-use history, and the effects of recent hurricanes (Boose and others 2004). Recovery can be rapid. Relative tree growth, after Hurricane Gilbert in a Mexican dry forest was higher than in the three pre-hurricane years (Wigham and others 1991), and in Puerto Rico, 5 years after Hurricane Hugo, regeneration and growth of survivors had increased the aboveground biomass to 86% of the pre-hurricane value (Scatena and others 1996). Pulses of litterfall from hurricane inputs rapidly disappear from the forest floor and are incorporated into forest nutrient cycles, which may be one reason for the resilience of these forests to wind disturbance (Ostertag and others 2003). It is not clear, however, if canopy opening and/or litter deposition stimulates decomposition.

This study simulates several effects of hurricane disturbance, based on observations of recent hurricanes in Puerto Rico. Hurricane Hugo (Category 3–4) struck Puerto Rico in September 1989 with sustained winds of over 166 km h^{-1}, causing severe defoliation of 56% of trees in study plots at El Verde (Scatena and Larsen 1991). Defoliation caused a large pulse in fine litter deposition of green leaves, small wood and miscellaneous debris, which was 1.2–1.9 times the normal annual litterfall throughout the Luquillo Experimental Forest (LEF) (Lodge and others 1991). In 1998 Hurricane Georges struck the LEF and caused 0.55–0.93 times the annual litterfall, and forest floor standing stocks were then 1.2–2.5 times greater than pre-hurricane values. Unlike regular litterfall, hurricane litter contains a high proportion of green leaves from which nutrients have not been translocated, thus altering litter quality. The input of phosphorus in total hurricane litterfall was 1.5–2.4 times normal annual input (Lodge and others 1991) and such a high magnitude of P transfer from canopy to forest floor may affect soil fertility and forest productivity (Sanford and others 1991). Fresh green leaves have significantly higher nitrogen concentrations and lower lignin to N ratios than senescent leaves, and significantly higher decay rates (Fonte and Schowalter 2004). Gaps and defoliation have a dramatic influence on light reaching the forest floor, resulting in growth of vines, and then of seedlings of pioneer trees and shrubs. These grow rapidly, reducing light intensity and the frequency of bright sun flecks (Fernández and Fetcher 1991).

The ecological effects of hurricanes have been particularly well documented in the LEF, a montane rainforest in eastern Puerto Rico. A long history of research on soils, climate, biota and ecosystem function (Odum and Pigeon 1970; Brown and others 1983; Reagan and Waide 1996) in this forest has allowed comparison with post-hurricane effects and subsequent recovery, for example, on landslide areas, groundwater chemistry, aboveground biomass, frog populations, freshwater shrimps and canopy arthropods.

In all these opportunistic studies of post-hurricane recovery of the forest ecosystem in Puerto Rico, it has been impossible to tease apart the consequences of the two major events: canopy opening and the pulse of litter to the forest floor. The experiment described here is part of a larger controlled experiment (the Canopy Trimming Experiment, CTE), designed to decouple the abiotic and biotic effects of hurricane-type disturbance, and to investigate their separate effects on the recovery of soils, biota and forest regrowth, in a multidisciplinary approach.

Hurricane litterfall amounts, litter decay rates and the chemistry of nutrient cycling have been extensively researched, but the effects of hurricanes on the agents of decay and recycling, microorganisms and litter fauna, have been under investigated. In this study, using litterbags sampled over a period of time, we ask what the effects of canopy opening and debris inputs are on forest floor litter faunal communities [micro- and mesofauna <2 mm (Ruiz and others 2008)], and whether they are affected by the quality of the litter and mesh size of the bags. Litterbag experiments, like all faunal exclusion studies, have limitations (Tanner 1981). For example, litterbags of different mesh sizes may provide different microclimates favoring different groups of organisms or, with very small mesh, become waterlogged. Litterbags were used, however, over whole-litter sampling because they allow treatment effects on colonization of new litter to be directly linked to effects on decay rates. Any change in the activity or biomass of the decomposer community in the bulk litter may affect faunal community composition, and colonization rates within the litterbags (Bradford and others 2002).

In this study, we tested the following hypotheses: (1) Canopy removal creates a harsher abiotic environment with adverse effects on litter invertebrate communities. (2) Increased litter deposition provides additional resources and habitat for invertebrates, and so increases invertebrate abundance, biomass and diversity. (3) Small mesh size of litterbags excludes certain invertebrates, and so changes taxonomic composition. (4) Litterbag invertebrate communities are similar in composition to those in bulk litter (compare Richardson and others 2005), and so provide a useful proxy for litter fauna. (5) All treatment effects are transient as the canopy regrows and detritus decomposes. For all hypotheses we assessed litter invertebrate communities in terms of abundance, biomass, diversity, taxonomic composition and trophic structure.

Study Site

The Luquillo Experimental Forest is part of El Yunque National Forest, in hurricane-prone NE Puerto Rico. The CTE plots are in mature lower montane rain forest, with tabonuco (*Dacryodes excelsa* Vahl), motillo (*Sloanea berteriana* Choisy) and sierra palm (*Prestoea montana* (Graham) Nicholson) as the dominants in the canopy, a lower canopy at 20 m, and an open understorey, with sparse forest floor vegetation. The plots are approximately 1 km northeast and east of El Verde Field Station (18.321°N, 65.820°W; Figure 1) at 340–470 m a.s.l. Annual rainfall is approximately 3.5 m (García-Martinó and others 1996), with approximately 97 rainless days per year. Rainfall is weakly seasonal, with a dry season between December and March (most commonly March) (http://lternet.edu/data/lterdb14/data/). Litterfall is also seasonal, with a main peak from March to June, a secondary peak in September, and minima from December to February (Zou and others 1995; Lawrence 1996;

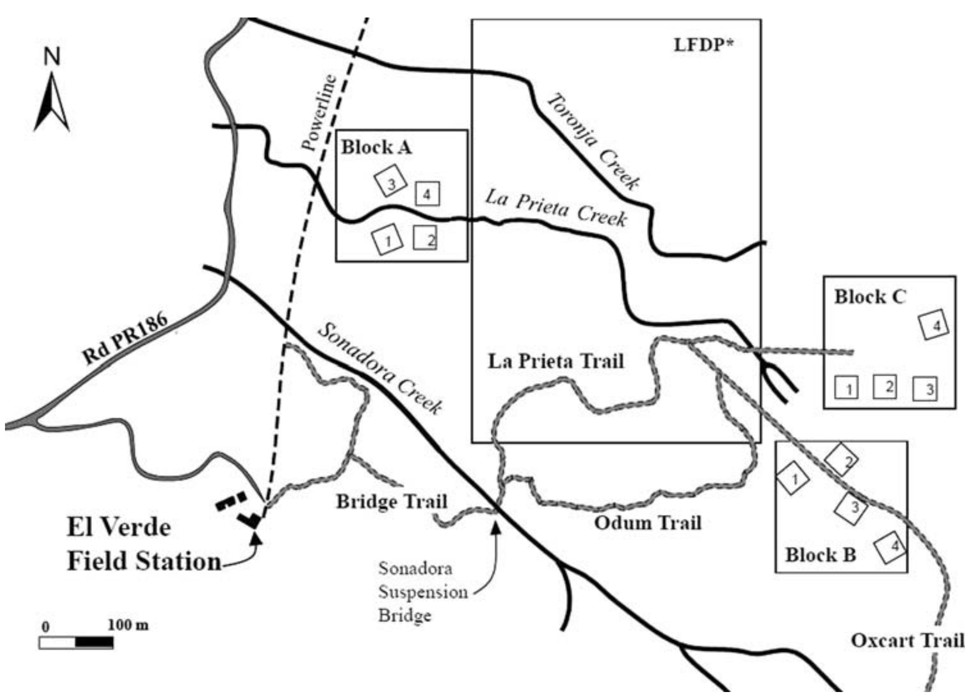

Figure 1. Location of CTE plots in the Luquillo experimental forest. Three blocks, *A*, *B* and *C*, each with four treatment plots. Road = *grey*, Trail = *grey with dashed edge*, Stream = *solid line*, * Luquillo Forest Dynamic Plot.

Zalamea and González 2008). Annual mean monthly temperatures (1975–2004) range between 20.6 and 25.8°C, with an annual mean of 23.0°C (SD = 1.9°C) (http://lternet.edu/data/lterdb16/data/).

Methods

Experimental Design

The experimental manipulations involved four randomized treatment plots in each of three blocks (Figure 1):

1. Canopy trimmed and trimmed biomass distributed on forest floor. This simulates the changes in microclimate and redistribution of biomass caused by a hurricane.
2. Canopy trimmed and trimmed biomass removed from the plot. This simulates the changes in microclimate openness created by the hurricane without the associated redistribution of biomass.
3. Canopy not trimmed but canopy biomass from a trimmed plot distributed on forest floor. This simulates the changes in redistribution of biomass created by the hurricane without the associated change in microclimate.
4. Canopy not trimmed and no canopy biomass added to forest floor. This maintains the forest unmodified by simulated hurricane disturbance.

Replicate blocks were in areas with similar land-use history, soil-type and vegetation. In all plots existing litter was left in place. Each plot was 30 × 30 m, with the interior 20 × 20 m of each plot used for measurements, and divided into 16 subplots. Litterbags (details follow) to be collected for invertebrate extraction were placed in sub-plots within each main plot. Two litterbag-level factors were considered in a factorial design: litterbag mesh size (large or small) and leaf litter type (dried green or senescent leaves). At each of 7 sampling dates, a litterbag for each litter treatment was collected from each of three sub-plots (1008 litterbags total).

Microclimatic Measurements

Daily rainfall totals were obtained from the National Atmospheric Deposition Program tower at El Verde, approximately 0.4–0.7 km from the experimental area (Figure 1). Funnels collected throughfall into bottles (3 per plot) and the volumes were recorded at 2-week intervals. The volume was converted to throughfall (mm^{-d}), using daily rainfall data from the NADP tower, by dividing the amount for any collection period into the same proportions as the daily rainfall recorded for the same period. This allowed the inclusion of rainless days in the throughfall record, because it was assumed that there would be no throughfall in the plots on days that the tower recorded no rainfall. Soil moisture and litter moisture content measurements from the plots were also made available (L Lebrón and DJ Lodge, respectively, unpublished data). Temperature was recorded using three Campbell 108 (Campbell Scientific) sensors per plot, connected to a Campbell data logger to give an hourly average. In the event, these proved unreliable, and there were many missing data. Canopy closure was monitored by using a Gap Light Analyzer (GLA, Frazer and Canham 1999) to analyze a series of hemispherical photographs taken at 1 m above the ground at each plot, both before trimming began and at intervals after trimming.

Canopy Trimming

Professional arborists carried out the canopy trimming. The trimming, weighing and replacement of

Table 1. Dates of Canopy Trimming of the Six Trimmed Plots, and Amounts of Material Removed, to be Returned to the 'Trimmed With Debris' Plots (TD) or Relocated from Trimmed Plots (TR) to the 'Untrimmed With Debris' Plots

Block	Treatment	Date of trim	Date of completion of debris redistribution	Amount of material removed [t (fw) per 900 m^2]			
				Leafy twigs	Wood	Palm frond	Total
A	TR	22 March–17 April 2005	16 June 2005[1]	3.08	4.86	0.99	8.93
A	TD	22 March–17 April 2005	16 June 2005	2.88	4.87	0.57	8.32
B	TD	26 October–2 December 2004	13 January 2005	5.60	6.89	0.29	12.78
B	TR	9 November–18 December 2004	20 January 2005[1]	4.65	5.49	0.52	10.67
C	TD	2 February–9 March 2005	17 March 2005	4.10	6.60	0.79	11.50
C	TR	24 January–9 March 2005	16 March 2005[1]	4.30	6.18	0.21	10.69

[1]*Debris relocated to untrimmed plots with added debris.*

debris lasted from 26 October 2004 to 16 June 2005 (Table 1). Two plots in each block were trimmed and two were left untrimmed. Treatment implementation was slowed by adverse weather, and the extremely large amount of material that had to be collected, weighed and redistributed manually. All trees larger than 15 cm dbh had limbs and stems smaller than 10 cm diameter removed. All trees between 10 and 15 cm dbh were trimmed at 3 m height, and all limbs smaller than 10 cm removed. Palms had leaves reaching above 3 m trimmed, and the apical meristem was preserved. All material removed from the canopy of each trimmed plot (debris) was collected, segregated as leafy twigs, wood and palm, and weighed. Subsamples of each debris category were dried at 45°C, and reweighed to establish wet/dry weight ratios. In each block, after weighing, debris from one trimmed plot was returned to that plot, and evenly distributed. Debris from the other trimmed plot was removed and redistributed to one of the two untrimmed plots. Where there were large differences in amounts of material from the two trimmed plots in a block, the amount of debris returned to the two with-debris plots was evened out. We compensated for the unusually low amount of trimmed material in block A (Table 1) by using material from a nearby location. Approximately 10 t fresh weight of vegetation was removed from each plot ($\approx$111 t ha^{-1}), weighed and redistributed (Table 1, approximately 39% leafy twigs, 55% wood and 6% palm fronds initially, by fresh weight). Mass losses that occurred between trimming and redistribution were consistent across blocks for wood (11.6%) and palm (16.1%). An unexpected consequence of having piles of leafy litter on the forest floor awaiting processing (from 1 week to 2 months, Table 1) was that they were immediately attacked by invertebrate herbivores (mainly moth larvae). Green leaves degraded rapidly, and what was left for redistribution was mainly woody material, with minimal foliage (AS, unpublished data). Material had been stored and moved on tarpaulins, however, so nutrients in the form of frass were returned to the plots. The mass loss of leafy twigs varied from 23 to 33% among blocks, so there were differences in litter quality among blocks, but these differences are relatively small overall, as the main component of the debris was woody material. Overall, the relative proportions of the three components had changed to approximately 34% leafy twigs, 60% wood and 6% palm fronds (by fresh weight). The amount of detritus added to each of the six detritus addition plots was approximately 5.4 t dry weight, equivalent to 60 t ha^{-1}.

Litterbags and Invertebrate Collection

Litterbags (14.5 × 14.5 cm) were of large (1.8 mm) or small mesh (0.475 mm), filled with air-dried pre-weighed green or senescent leaves (approx. 5.5 g per bag), composed of a mixture of leaf species in the same proportion as their representation in natural litterfall (Zalamea and González 2008). The species were *Dacryodes excelsa*, *Manilkara bidentata* (A. DC.) Chev., *Cyrilla racemiflora* L. and *Prestoea montana* (R. Graham) Nichols (52%, on a dry mass basis), 19% of the 7 next most frequent species, and the remaining 29% a mixture of 19 less frequent species. The LEF is a seasonal wet tropical forest and in the 'dry' season has variable sequences of rainless days, which can dry out surface litter. The litterbags were put out at the same start period, after all canopy trimming was completed, to avoid confounding results with seasonal variations in replicate blocks cut at different times.

Litterbags were placed in all plots on 20–23 June 2005, and recovered after 2, 4, 7, 10, 13, 16 and 19 months in the field. Invertebrates from each bag were extracted using Tullgren funnels. The invertebrates collected were counted, measured and identified to morphospecies or species, and relative abundances were used to monitor changes in community composition and diversity indices. It was not practical to identify Acari (mites) or Collembola to morphospecies. Mites were identified as Oribatida, Mesostigmata or Prostigmata, and Collembola to family level. Morphospecies were assigned to broad trophic groups, based on the known biology of the taxa (for example, Merritt and Cummins 1984; Stehr 1987, 1991; Borror and others 1989). Trophic groups were defined for this study as: detritivores (comminuters of litter), microbiovores (feeding on fungi, bacteria, protozoa and small detrital particles), herbivores, parasitoids, predators and fluid feeders. This latter group was a mix of organisms known to feed on liquids from the final stages of decay, ants collecting honeydew from root-feeding Homoptera and adult flies (Diptera) which oviposit in litter. From information available for detritivores it was not always known, for example, whether an organism was feeding on detritus for its fungal and microbial content or decay products (panphytophagous), or consuming the detritus directly for its nutrients. Some oribatid mites are consumers of litter (detritivores), others are fungivores (microbiovores); similarly, some Prostigmata are predators, others microbiovores. In both cases the counts were apportioned 50/50 between the two trophic groups. Although Collembola are ecologically differentiated into many feeding guilds, those in tropical forest litters are characterized as specialist fungivores (hyphae and fungal spores), with only low densities of litter-shredding species (Rusek 1998). They were, therefore, all classified as microbiovores.

Biomass and Diversity

Biomass was estimated using length × dry weight relationships established for different groups of invertebrates obtained in earlier work with the fauna of bromeliad phytotelmata and forest floor litter (Richardson and others 2000, 2005). Additional weights were obtained during this study for mites, collembola and ostracods, archived at http://luq.lternet.edu/data/lterdb134/metadata/lterdb134.htm.

Diversity was compared among treatments and over time using Margalef's index of species richness and Simpson's reciprocal index ($1/D$), which takes relative species abundance into account. For a discussion of the advantages of these indices see Magurran (2004).

Statistical Analysis

Data were analyzed with mixed model ANOVAs. The ANOVAs examined four treatment effects (trim, debris, mesh, litter) over time, whilst controlling for random effects of block, plot and subplot. In the experimental design, subplot is nested within each of 4 plots per block, and plot is nested within each of three spatially distinct blocks. The trimmed and debris treatments were applied at the plot level, and the litter and mesh treatments at the subplot level. Thus, the four types of manipulation follow a split-plot design within a randomized block framework. All possible interactions between these four manipulated factors were considered. Date was examined only as a main effect, as temporal variance in the effects of manipulations was of minor interest. In addition, models that included interactions between date and manipulated variables failed to converge. In analyzing community parameters, the relative abundances of the main taxonomic groups were considered with reference to the effect of treatments and the passage of time.

The mixed effects linear model was fitted using maximum likelihood estimation (Package NLME, R Version 2.6.2), and significance of fixed effects was based on F tests ($\alpha = 0.05$). Residual plots were assessed for departures from normality and non-linearity. In many cases, the response variable needed to be transformed to conform to parametric assumptions of normality. Data were transformed back to their original scale for presentation of results. Response variables included community metrics (diversity, total abundance and biomass, and composition) and abundances of the six most common taxa. Biomass and total abundance were examined both with and without mites. Insufficient data existed for reliable univariate analysis of less abundant taxa. Instead, community composition was summarized by 3 PCA axes, using the software PRIMER (version 5.2.9, Plymouth Marine Labs), to provide information on treatment effects for all taxa. One outlier sample was identified by initial analyses and removed. Sample scores on the three PCA axes were used as response variables in the mixed model ANOVA, to examine treatment effects on community composition.

Results

Microclimate Changes

Analysis of the hemispherical photographs, using GLA, showed that canopy openness in the trimmed plots had declined from 15 to 20% immediately after trimming to just above the 5% level, which was similar to the untrimmed plots, after 18 months (Figure 2A). Canopy opening initially resulted in major differences in microclimate between trimmed and untrimmed plots that diminished as the canopy recovered.

Throughfall data (Figure 2B) show that canopy trimming increased the amount of precipitation reaching the forest floor directly, which was similar to the rainfall values when the canopy was first removed. Initially, throughfall in the intact canopy plots was approximately 60% of throughfall in trimmed plots. The difference in amount of throughfall in the trimmed and untrimmed treatments gradually decreased, so that by March 2006, 9 months after placing litterbags in the plots, the throughfall in canopy trimmed plots was similar to that in untrimmed plots. Similarly, soil moisture contents were approximately 10% higher in trimmed plots (L Lebrón and DJ Lodge, unpublished data), with the values again converging among treatments by March 2006. During the observation period there were four periods of high rainfall (>300 mm/month), October 2005, January, April and July 2006 (4, 7, 10 and 13 months), and one very dry month (March 2006, with <100 mm). Soil and litter moisture levels responded differently to canopy trimming. Soil moisture levels increased from the beginning to a peak in September 2005 (3 months), were lowest in October in both years

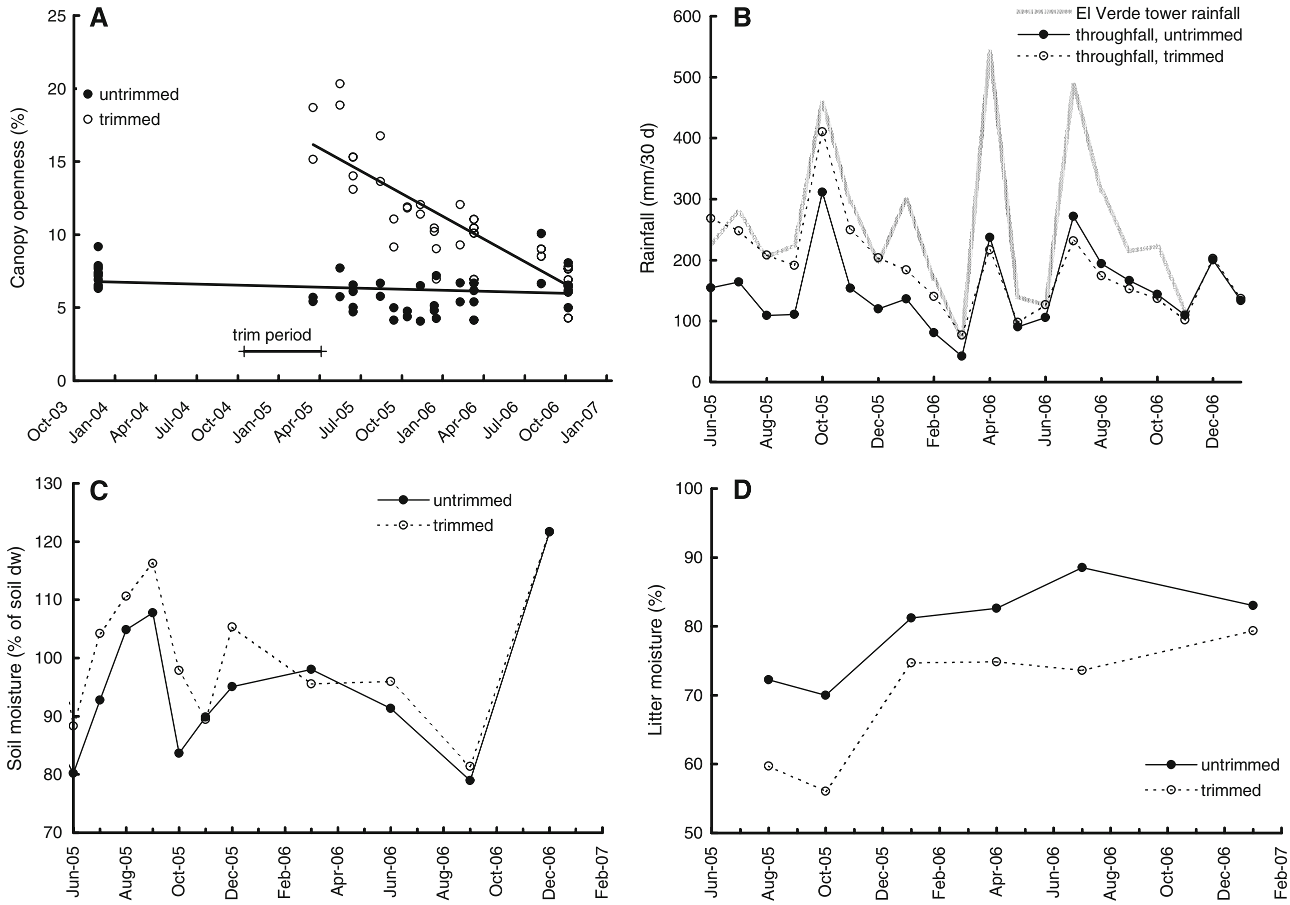

Figure 2. Aspects of canopy closure. **A** Levels of canopy openness before and after trimming, in trimmed and untrimmed plots. **B** Rainfall recorded at the El Verde meteorological tower, and throughfall recorded from untrimmed and trimmed plots. **C** Soil moisture levels. **D** Litter moisture levels.

(4 and 16 months), and peaked in December 2006 (Figure 2C), and were higher in the trimmed plots during the early stages of the experiment. Litter moisture, however, was lower in trimmed plots than in untrimmed plots (DJ Lodge, unpublished data; Figure 2D).

Temperature records from the plots were incomplete, and none were obtained from October 2005 to April 2006, because of unreliable equipment. Data were, however, sufficient to show that there was little difference in mean temperature, 1 m above the ground in shaded cups, between trimmed and untrimmed plots. Untrimmed plots were slightly warmer than plots with the canopy removed (mean daily temperature difference +0.6°C, range 0.1–1.2°C in any month). Maximum daily temperatures were, however, higher in trimmed plots (difference +1.1°C, range 0.4–2.4°C in any month) before canopy closure. Seasonally, the warmest period was May–September (monthly mean 24.5–25°C), and the coldest January (21°C).

Animal Abundance, Biomass, and Diversity over Time

All community parameters changed significantly during the experiment (Table 2). Abundance increased initially (colonization) and then declined (Figure 3A) along with a decrease in amount of litter remaining in the litterbags. Overall, only approximately 26% of the original litter remained after 19 months in the field, and the percentage of litter mass remaining was higher in trimmed than in untrimmed plots (GG, unpublished data). Total animal counts peaked in the first three sample periods (August 2005–January 2006), and then declined to approximately 35% of the initial level by January 2007 (Figure 3A). Numerically, mites dominated the fauna throughout the experiment, with 66% of the 52,035 animals collected comprising mites but, as time progressed, they became numerically less important, both in relative terms (from 75 to 55%) and in absolute numbers (from

Table 2. Significance of Fixed Effects and Interactions (Mixed Model ANOVA) for Abundance of Invertebrates Recovered from Each Litterbag, Total Biomass (dry wt, mg per litterbag), Diversity Indices, Abundance of Organisms of the Main Taxonomic Groups Recovered from Each Litterbag, and PCA Scores

	Main effects					Significant interactions
	Time	Trim	Debris	Mesh	Litter type	
Animal abundance	**0.001**	0.096	0.330	**0.010**	0.719	None
Animal abundance—exc. mites	**0.001**	0.413	0.369	**0.027**	0.230	T × L
Animal biomass	**0.002**	**0.027**	**0.023**	**0.026**	0.974	None
Animal biomass—exc. mites	**0.003**	**0.016**	**0.042**	**0.014**	0.852	T × L
Simpson 1/*D*	**0.000**	**0.001**	0.621	0.976	0.130	M × L; T × D
Margalef	**0.000**	**0.001**	0.110	0.423	0.576	T × D
Formicidae	**0.000**	0.965	0.585	0.271	**0.047**	None
Acari	**0.000**	**0.016**	0.552	0.179	0.472	None
Collembola	**0.000**	**0.039**	0.202	**0.012**	0.880	T × D × M
Isopoda	**0.000**	0.170	0.778	0.901	0.488	T × D; T × M; M × L
Hemiptera and Homoptera	**0.000**	0.079	0.546	**0.023**	0.670	T × M
Coleoptera	0.364	**0.001**	**0.008**	0.224	0.854	T × D; T × D × M
PCA 1	**0.000**	**0.005**	**0.016**	0.533	0.960	T × D
PCA 2	**0.000**	**0.001**	**0.047**	0.768	0.110	None
PCA 3	**0.000**	0.766	0.818	0.146	**0.023**	T × M

Bold type highlights significant values (P < 0.05). Data from 144 litterbags from each of 7 sampling periods, from 2 to 19 months in the field. Significant interactions are indicated in the right hand column.
T trim, D debris, M mesh size, L litter type.

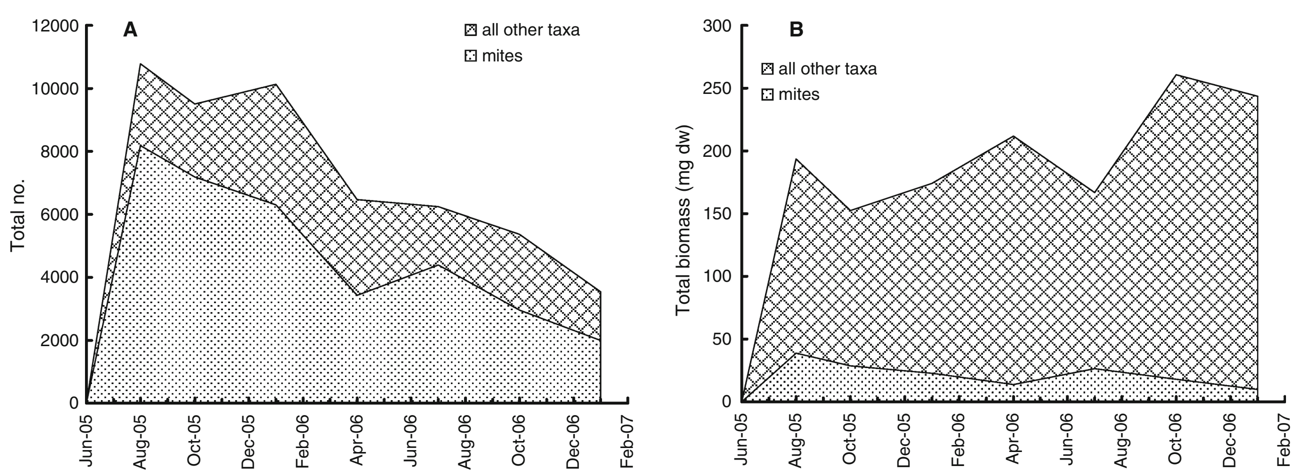

Figure 3. Community differences. **A** Total abundance, and **B** biomass of mites and all other taxa, summed over all treatments.

approximately 8,200 to 2,000 per collection) (Figure 3A). When biomass is considered, however, they comprised a much smaller proportion of the fauna, about 20% initially and 4% at the last collection. When mites were excluded from the counts, all other organisms combined showed a maximal abundance, peaking at 7 months (January 2006) (Figure 3A). Although abundance declined throughout the experiment, many taxonomic groups showed an increase in October 2006, irrespective of time of initial trimming, which differed among blocks. This suggests a seasonal pattern of abundance, also recorded in the LEF by Pfieffer (1996).

Total animal biomass differed between dates and, unlike abundance, did not decline over the period of the experiment (Table 2; Figure 3B). Consideration of biomass is important, as individual animals varied in dry weight by a factor of about 75×10^4 from the smallest (mites) to the largest (millipedes). Due to their relative infrequency large organisms can, however, have a disproportionate effect on some of the data. Relative abundance calculations are important, to monitor changes in community composition.

Effect of Treatments on Animal Community Parameters

The major plot treatments of canopy trimming and debris deposition significantly affected animal diversity and biomass (Table 2). Animal diversity was significantly lower in trimmed plots than in untrimmed plots, irrespective of debris treatment (Figure 4). There was, however, a significant interaction between the two treatments, with the most disturbed plots (trimmed + debris) having the lowest diversity, whereas untrimmed plots + debris had the highest diversity (Figure 4). Animal biomass was significantly lower in trimmed plots irrespective of debris treatment (Figure 5), but the effect of debris in plots with intact canopy was unclear, because of the high variability due to the occasional occurrence of single large animals which had grown in a few bags.

Treatments at the sub-plot level, mesh size and litter type had fewer significant effects (Table 2). Animal abundance and biomass were significantly affected by mesh size, with higher abundance and lower biomass in the small mesh bags. Litter quality had no direct effect on community parameters, but excluding mites from abundance and biomass sums allowed a trimmed × litter interaction to be revealed; abundance and biomass were higher for dried green litter in trimmed plots and for senescent litter in untrimmed plots. Three and four-way

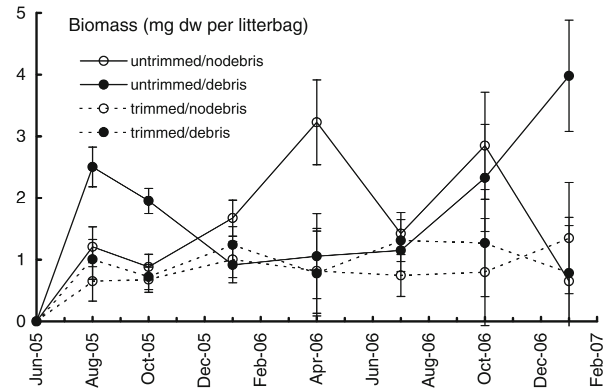

Figure 5. Significant effects of canopy trimming and debris deposition on invertebrate biomass. *Error bars* ± 1 S.E.

interactions were never significant for any of these response variables.

Effect of Treatments on Community Composition

Overall changes in community composition between samples were captured by a PCA, whose first three axes represented 27% of between-sample variation in composition (Tables 2, 3). The first and second PCA axes are significantly driven by trim and debris manipulations (either alone or in combination), suggesting that most of the variance in invertebrate composition is due to these two plot-level factors (mixed model ANOVA, Table 2). The first axis (11.6% total variance) separated Psocoptera from isopods and millipedes, whereas the

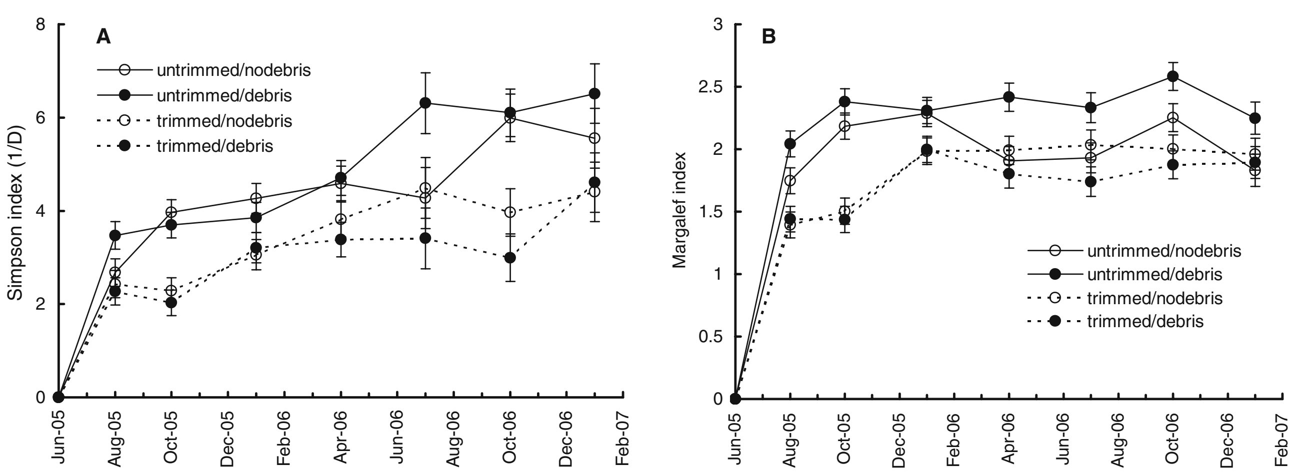

Figure 4. Significant effects, over time, of canopy trimming and debris deposition on diversity. **A** The reciprocal Simpson (1/*D*), and **B** Margalef's indices. *Error bars* ± 1 S.E. Each point is the sum of data from 36 litterbags. Simpson $D = \Sigma$ (n_i (n_i − 1))/(*N* (*N* − 1)), where n_i = abundance of the $_i$th species and *N* = total abundance. Margalef $D_{Mg} = (S - 1)/\log_n N$, where *S* = no. of species and *N* = the total no. of individuals in the sample.

Table 3. Species Scores on the First Three Principal Components Axes, Each Arranged in Descending Order

PCA 1		PCA 2		PCA 3	
Psocoptera	0.07	Acari	0.49	Araneae and Opiliones	0.42
Chilopoda	−0.09	Collembola	0.40	Hemiptera and Homoptera	0.38
Ostracoda	−0.14	Diptera larvae/pupae	0.39	Formicidae	0.37
Formicidae	−0.16	Psocoptera	0.25	Ostracoda	0.35
Diptera larvae/pupae	−0.17	Lepidoptera larvae	0.12	Coleoptera larvae	0.17
Pseudoscorpiones	−0.20	Araneae and Opiliones	0.07	Isopoda	0.14
Diplura	−0.22	Formicidae	0.00	Collembola	0.13
Lepidoptera larvae	−0.23	Diplopoda	−0.04	Acari	0.04
Hemiptera and Homoptera	−0.24	Ostracoda	−0.06	Diptera larvae/pupae	0.02
Acari	−0.25	Isopoda	−0.07	Diplura	0.00
Coleoptera adults	−0.27	Coleoptera larvae	−0.11	Psocoptera	−0.13
Araneae and Opiliones	−0.28	Coleoptera adults	−0.13	Pseudoscorpiones	−0.17
Collembola	−0.32	Chilopoda	−0.15	Coleoptera adults	−0.21
Coleoptera larvae	−0.34	Hemiptera and Homoptera	−0.29	Diplopoda	−0.25
Diplopoda	−0.35	Pseudoscorpiones	−0.32	Lepidoptera larvae	−0.29
Isopoda	−0.41	Diplura	−0.35	Chilopoda	−0.49
Variation explained (%)	11.6		8.5		7.3

Note that Coleoptera larvae and adults were treated separately in the PCA.

Table 4. Relative Abundance (% of Counts or Dry Wt) of Taxonomic Groups in Complete Forest Floor Litter and Litterbags at Various Stages of the CTE

	Whole tabonuco forest litter[1]		In counts from litterbags—after *n* months in the field								
	Count	Dry wt	2	4	7	10	13	16	19	Mean Count	Mean Dry wt
Acari	47.3	1.8	71.8	68.6	56.0	40.9	49.7	60.0	65.8	**59.0**	**8.9**
Formicidae	17.4	2.8	16.0	12.5	20.9	34.3	28.7	7.0	8.1	18.2	**16.0**
Collembola	7.2	1.3	7.8	8.3	11.1	11.3	8.7	9.1	5.6	8.8	**4.9**
Hemiptera and Homoptera	5.7	4.0	0.5	1.4	3.3	5.3	3.7	8.0	6.0	4.0	2.8
Isopoda	**3.8**	3.5	0.5	1.8	1.4	0.9	0.8	1.5	2.1	1.3	2.7
Coleoptera adult	**3.4**	**6.4**	0.2	0.3	0.4	0.1	0.6	1.1	1.5	0.6	2.7
Coleoptera immature	1.6	0.1	0.5	1.3	1.0	0.8	1.0	1.1	1.2	1.0	0.5
Diptera adults	3.0	**1.8**	0.7	1.4	1.5	1.0	2.1	3.1	2.9	1.8	0.3
Isoptera	**2.4**	**33.4**	0	0	0.1	0	0	0.1	0	<0.1	0.2
Diptera immature	2.0	0.3	0.7	1.4	1.5	1.0	2.1	3.1	2.9	1.8	**1.6**
Araneae and Opiliones	**1.7**	**12.7**	0.5	0.6	0.7	0.9	0.3	1.0	1.1	0.7	2.1
Pseudoscorpiones	**1.6**	0.9	0.5	1.2	0.8	1.7	0.5	0.9	0.7	0.9	1.5
Diplopoda	1.1	11.8	0.3	1.3	1.2	1.6	1.5	2.4	2.1	1.5	15.3
Blattaria	**0.3**	**2.3**	<0.1	0	<0.1	0	<0.1	0	0	<0.1	0.2
Lepidoptera larvae	0.2	0.1	0.3	0.3	0.4	0.1	0.2	0.3	0.4	0.3	**14.7**
Lepidoptera adults	0.1	0.7	0	0	0	0	0	0	0	0	0
Chilopoda	0.1	3.0	0	0.1	0.0	0.1	0.2	0	0	0.1	**22.6**

Values in bold identify results with large relative differences between results from whole litter and from litterbags (columns 2 and 11 and 3 and 12).
[1]Data from 4 × 0.25 m^2 litter samples from tabonuco forest at El Verde in each of the years 1999, 2000 and 2001 (Richardson and others 2005).

second axis (8.5%) separated mites and Collembola from Diplura (Table 3). By contrast, effects of mesh and litter are only apparent on the third, more minor (7.3% total variance), axis (mixed model ANOVA, Table 2). This axis separated the very rare centipedes from ants, and Homoptera and Hemiptera (Table 3). The results of the PCA are corroborated by individual analyses of the six most common taxa, which together account for 94% of all animals recovered during the study. All except ants showed significant responses to trimming or debris treatments, either directly or through interactions (Table 2).

Individual taxa responded differently to the trimming of the canopy, causing a major shift in community composition. Mites, Collembola and Psocoptera (maximum scores in PCA 1 and 2 axes) responded positively, with higher abundance in trimmed plots, whereas Homoptera and Hemiptera, isopods and millipedes (minimum scores on PCA axes 1, 2 and 3) responded negatively (Figure 6), as did all other taxonomic groups. The opposing responses explain the lack of any effect on overall abundance at the community level. Effects of debris additions often occurred in combination with trimming treatments (Table 2). For example, debris additions increased Coleoptera abundance most noticeably in the untrimmed plots (Figure 7). Collembola and isopods also responded positively to debris addition, as did rarer taxa such as millipedes and ostracods. Ants were unusual in showing a significant response to litter type only, reaching high abundances in bags with senescent litter. Four taxa responded to mesh size in combination with other factors (Table 2), for example, collembola were significantly more abundant in small mesh bags and Hemiptera and Homoptera in bags of larger size mesh.

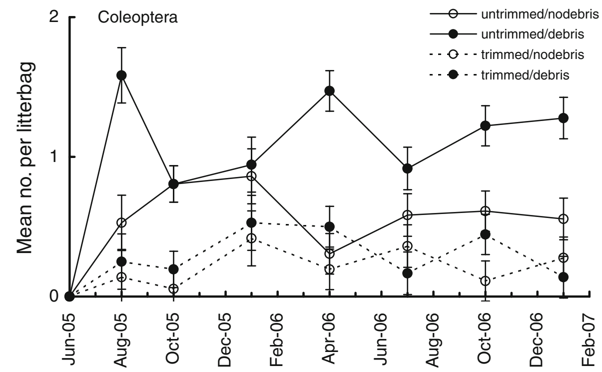

Figure 7. Effects of canopy trimming and debris deposition on abundance (mean no. per litterbag) of Coleoptera, over time. *Error bars* ± 1 S.E.

Litterbag Fauna Versus Whole-Litter Fauna

Most taxonomic groups found in whole litter in the LEF (Richardson and others 2005) were also found in the litterbags, though they were smaller species or instars of the meso- or macro-fauna in natural litter of the forest floor (Table 4). The relative biomass of mites was approximately five times higher in litterbags than in bulk litter (Table 4). Litterbags also tended to favor ants and collembolans, whereas counts of isopods, adult flies and beetles, termites, cockroaches, spiders, opilionids and pseudoscorpions were relatively less abundant.

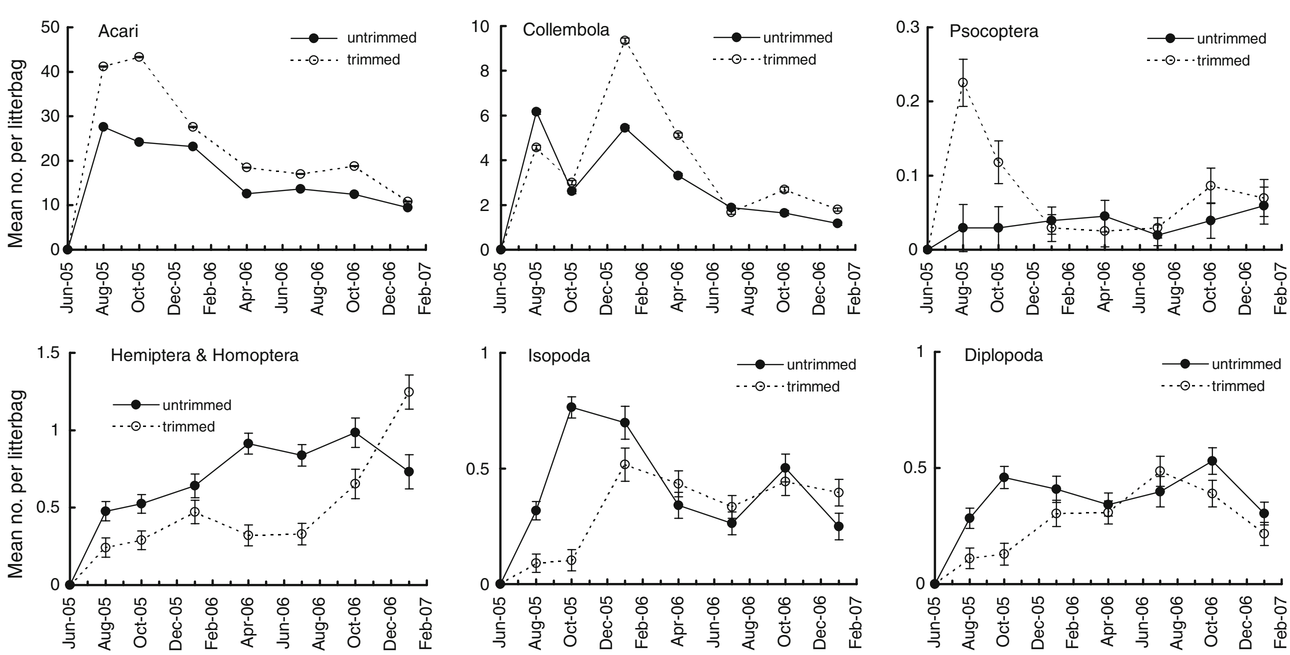

Figure 6. Effects of canopy trimming on the abundance (mean no. per litterbag) over time of invertebrates most affected by canopy trimming. *Error bars* ± 1 S.E.

This may be an artefact of mesh size for some groups, for instance only minute spider species were found, whereas the commonest species in whole litter, *Modisimus montanus* Pet. (a small spider but with extremely long legs) was almost never found in litterbags, and the same applied to beetle species, where large forms were excluded. Two species of ant, *Solenopsis corticalis* Forel and *Wasmannia auropunctata* (Roger), nested in litterbags, and biomass was increased by the presence of larvae. Termites were underrepresented, as wood, their food, was not included in the litterbags (Table 4). Scolytid beetles and larvae, which are woodborers, were also scarce. Cockroaches are light aversive and only found in deep litter, and even small instars were only rarely found in the litterbags on the surface.

Trophic Specialization

Microbiovores and detritivores, mainly mites and collembola, were the most abundant trophic groups, together comprising 70% of all organisms, and much more abundant in trimmed than untrimmed plots (Figure 8). There was a general decline in relative abundance over time. Predator relative abundance was 23% overall, increased slightly over time, and was much higher in the plots with intact canopy, although the difference decreased over the period. These three groups made up 93% of the total fauna. The other trophic groups were relatively small, and showed slight increases with time, but no clear effects of treatment, except for the herbivores (homopteran root feeders), which increased markedly in the trimmed plots over the final 6-month period.

Discussion

In forests, storm damage or anthropogenic impacts such as logging provide large amounts of organic matter to be processed by the biota as part of the ecosystem response to disturbance. Canopy loss, however, can cause abiotic changes, which may affect the biota and interfere with recovery processes. The CTE, because of its long time-scale, allowed the relative importance of canopy opening and debris deposition on invertebrate decomposer communities to be distinguished. It also allowed dynamic processes of litterbag colonization and seasonal changes in litter invertebrate populations to be distinguished from treatment effects.

Treatment Effects

Canopy Trimming

Canopy trimming resulted in abiotic changes: more throughfall, which in the early stages of the experiment was almost as high as rainfall; higher soil moisture levels; higher light levels (canopy openness) and lower litter moisture. Although throughfall returned to pre-disturbance levels in trimmed plots within 9 months, canopy closure was not complete until 19 months.

Canopy opening was the major determinant of community change, by reducing overall invertebrate diversity and biomass, with fewer large detritivores (for example, Coleoptera and Diplopoda), and in bringing about changes in community composition, with fungivores (for example, mites, Collembola and Psocoptera) dominant in cut plots. These changes were independent of debris treat-

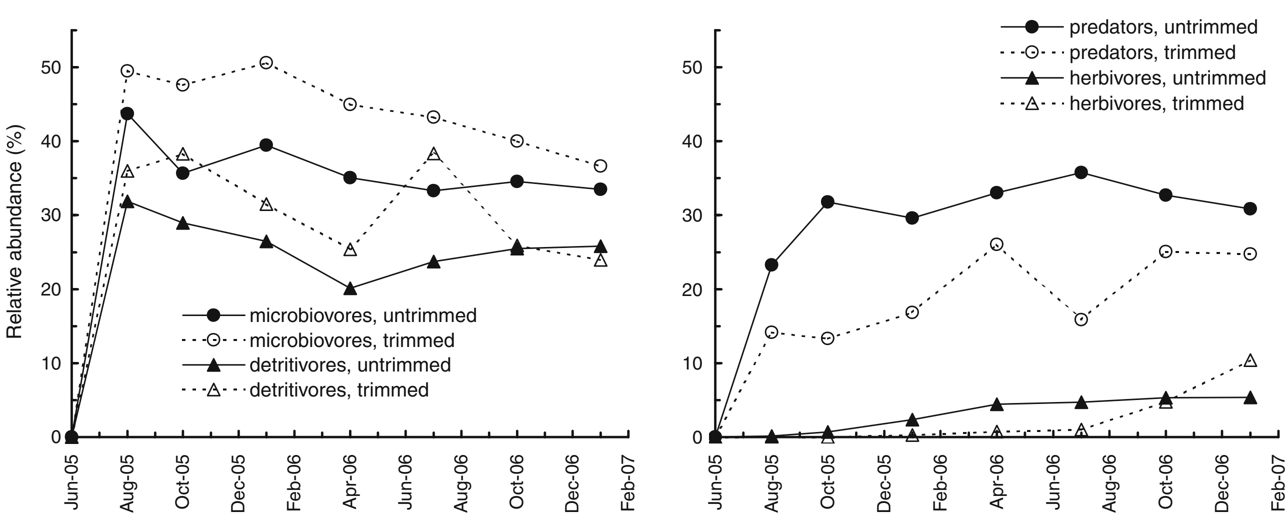

Figure 8. Relative abundance (%) of trophic groups over time, in trimmed and untrimmed plots. Fluid feeders and parasitoids occurred at low frequency and are omitted.

ments, which played a secondary and interactive role. Litterbags in cut plots had the highest litter-mass remaining after extraction of the organisms (GG, unpublished), indicating lower decomposition rates. The first hypothesis, that canopy trimming has an adverse effect on litter communities is confirmed.

Changes in invertebrate communities in trimmed plots may be explained by three mechanisms: (a) migration away from adverse conditions, (b) differential mortality of taxa sensitive to disturbance and (c) interactions with fungal groups.

(a) Strong physical gradients, particularly between soil and litter moisture, may explain the lower diversity in cut plots. Many litter organisms are strongly light and drought aversive and move to deeper layers, for example, small cockroach nymphs (strongly negatively phototactic) were almost completely absent from litterbags. It is likely that light has the strongest effect, as litterbags did not appear to dry out, and Tanner (1981) found that their litter water content was higher than that of forest floor litter in a dry period. As long as there is a gradient, however, moisture sensitive animals will respond.

(b) Lower diversity in disturbed plots may also be explained by differential mortality, with many species sensitive to changes in their natural habitat, and consequential changes in community composition. After Hurricane Hugo in the LEF one species of ant, *Wasmannia auropunctata* (an introduced 'tramp species'), became the dominant ant species, representing 94% of all ants found 6 months after the hurricane (Perfecto and Camilo, in Garrison and Willig 1996). Pre-hurricane sampling had yielded 18 ant species, with two endemics the most common. Forestry operations have disturbance effects similar to hurricanes (Miller and Lodge 2007), and total arthropod abundance was lower in intact or salvaged log gaps and greater in forested controls (Greenberg and Forrest 2003). Niemela and others (1993) showed changes in relative abundance with disturbance, and Turner and Foster (2009) found reduced biomass and abundance of mesoarthropods in all compartments of a Malaysian forest in conversion of primary forest to oil palm. Species with a narrow distribution and small local populations are doubly vulnerable. Collembolan communities had lower population densities in managed forests than in semi-natural forests, with a severe decrease in species richness of the endemic component (Cassagne and others 2006). Conversely, any species with a high tolerance of disturbance, such as *W. auropunctata*, highly abundant and nesting in litterbags in this experiment, is at a competitive advantage, and this ant spreads rapidly after logging operations (Walsh and others 2004). Disturbance, therefore, has major effects in changing food webs.

(c) Many litter organisms are fungivores, usually specialists feeding on either white rot basidiomycetes (Newell 1984) or microfungi that colonize litter surfaces (Visser and Whittaker 1977; Schneider and Maraun 2005). Fungal biomass in litter in the LEF changes rapidly in response to moisture (Lodge 1996), with longer-term declines and large fluctuations thought to be due to grazing by invertebrates. Different fungal groups may respond differently to environmental conditions. We suggest that changes in some invertebrate populations may be explained by the changes in fungal communities, found by other researchers in parallel studies in the same treatments and sub-plots. In these plots, fungal biomass in litter was similar between trimmed and untrimmed plots (estimated by fatty acids, Rivera-Figueroa 2008), but fungal community composition was not. Trimmed plots with lower litter moisture had lower basidiomycete white rot activity (responsible for lignin breakdown), suggesting a shift to micro-fungi in trimmed plots (Rivera-Figueroa 2008; DJ Lodge, personal communication). Trimmed plots had significantly higher populations of mites, Collembola and Psocoptera and these are precisely the taxa known to have many species that are specialist grazers of microfungi on litter surfaces. Greater growth of microfungi, both in litterbags and bulk litter, could promote increased abundance of these invertebrate taxa. Holler and Cowley (1970), also working in the LEF, recorded higher microfungal populations in plots in which the canopy had been removed than in control plots. They suggested that increased exposure resulted in higher litter temperatures, which in turn resulted in better growth or sporulation conditions for these fungi.

Debris Deposition

Addition of debris may have been expected to increase invertebrate density and diversity because of increased nutrient provision from both green and woody litter, increased habitat complexity and physical effects of woody litter (increased humidity and shelter). Debris additions interacted significantly with canopy trimming. Under a closed canopy, diversity, biomass, and abundance of certain groups, for example, coleoptera, isopods and millipedes were highest. With trimmed canopy plus debris (the most disturbed plots) they were at their lowest. Thus, the second hypothesis is only partially true, and debris stimulates litter communities only when the abiotic conditions are suitable. Presumably, in terms of forest recovery after hurricanes, this is when canopy gaps close and there is deposition of new litterfall. In the CTE there were unavoidable differences in litter quality among blocks, because of some herbivory before redistribution, so the experiment did not exactly reflect hurricane conditions. As wood was the major component of debris, however, it may be that the relatively small differences in proportion of leafy twigs among blocks would not have resulted in large differences in response. The overwhelming response of litterbag communities was to canopy opening, rather than to litter deposition, albeit rather woody litter. Sayer and others (2006) in Panama also found that, although litter removal from the forest floor was associated with lower abundance of mesoarthropods in litterbags, abundance did not differ significantly between controls and litter-addition plots. They suggested that this was due to reduced diffusion of oxygen in the denser forest floor, increases in the number of predators, and greater amounts of phytochemicals.

Litterbag Factors

Mesh size and litter type were unimportant in determining community composition in litterbags, and differences were significantly driven by plot-level manipulations, as shown by PCA. Differences in mesh size only influenced abundance and biomass by excluding larger organisms, and did not cause changes in taxonomic composition, so hypothesis 3 is invalid.

Successional stages of colonization showed that litterbag fauna is at first dominated by mites that, together with Collembola and Psocoptera, feed on fungal hyphae, spores and bacteria (Dindal 1990). Non-fungus feeding mites have cellulases in their guts derived from symbiotic fungi, and fungivores have trehalase, enabling them to use trehalose in fungi (Dindal 1990). Thus mites as a group are primed for colonization of both the initial air-dried litter and the early stages of its colonization by fungi. Their abundance and biomass was considerably higher than previous measurements in bulk litter in the LEF (Richardson and others 2005) but, because of their small size, some authors (Franklin and others 2004; Illig and others 2008) do not consider them to be directly important in decomposition processes. Millipedes and isopods occurred later in the succession and are known to prefer well-decayed litter (Pfieffer 1996) and, as mites declined in relative abundance, the diversity of the larger detritivores and predators increased. Hemiptera/Homoptera were also abundant towards the end of observations, but this was mainly due to ensign coccids (Ortheziidae) feeding on fine roots permeating the bags, not to organisms feeding on the litter, particularly in trimmed plots. Although litterbags were favorable to mites and some species of ant, which used them as nesting sites, and lacked wood feeding species, the taxonomic groups responsible for comminuting leaf litter in the litterbags were similar to those in bulk litter. Litterbags can, therefore, provide a useful proxy for studying litter fauna directly responsible for decay processes (hypothesis 4), but do not provide the evidence of litter food-web structure that can be obtained from bulk sampling.

Litterbag experiments have a limited life span, because bags deteriorate and nutrient resources decline. Although there was some convergence of data, effects of trimming on diversity, biomass and abundance of some taxa, particularly the coleoptera, could still be detected when canopy closure was complete after 19 months. This suggests that effects are not merely transient (hypothesis 5) and there may be long-lasting consequences for food webs and ecosystem function after canopy damage.

Conclusions

Litterbags are essential for measuring loss of leaf litter biomass during the decay process. We demonstrated that they could also be successfully used to discriminate between animal communities in different experimental treatments. In this forest, canopy trimming had major effects in stimulating populations of specialist micro-fungus feeders, decreasing the abundance of larger taxa, many of which are major comminuters of litter, and in decreasing overall animal diversity and biomass. Additional disturbance through debris deposition further decreased diversity and biomass. In the natural environment, through complex interactions of the invertebrate and fungal biota, hurricane damage may, therefore, delay litter breakdown and return of nutrients to the ecosystem, at least through the early recovery period. The expected time of this delay would be dependent on the severity of canopy damage, which may increase with the predicted rise in frequency and severity of hurricanes in the Caribbean region.

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