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Plant and Litter Influences on Earthworm Abundance and Community Structure in a Tropical Wet Forest[1]

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ABSTRACT

Plant communities differ in species composition and litter input. To examine the influence of plant species on the abundance and community structure of soil fauna, we sampled earthworms in areas close to and away from the bases of *Dacryodes excelsa* and *Heliconia caribaea,* two distinct plant communities within a tropical wet forest in Puerto Rico. We also carried out a litter manipulation experiment to examine the short-term responses of earthworms to litter removal and litter addition treatments. We found that: (1) the density and biomass of both soil-feeding endogeic and litter-feeding anecic worms did not differ between areas close to and away from *Dacryodes* trees (in contrast, the density and biomass of anecic worms was higher in areas away from *Heliconia* plants despite the lack of differences for endogeic worms); and (2) total dry weight of earthworms tended to be higher in the litter addition treatment than in the control within the *Heliconia* community. Our results suggest that *Heliconia caribaea* has a strong negative influence on anecic earthworms and that earthworms in the *Heliconia* community are more sensitive to litter input than in the *Dacryodes* community.

RESUMEN

Las comunidades vegetales difieren en la composición de especies y en la introducción de hojarazca. Con el propósito de examinar la influencia de las especies de plantas sobre la abundancia y estructura de las comunidades de animales del suelo, nosotros muestreamos lombrices en áreas cercanas y lejanas a *Dacryodes excelsa* y *Heliconia caribaea,* dos especies de plantas que representan comunidades vegetales diferentes dentro del bosque lluvioso tropical en Puerto Rico. Se llevó a cabo un experimento de manipulación de hojarazca para examinar las respuestas a corto plazo de las lombrices a los tratamientos de remoción y adición de hojarazca. Se encontró que (1) la densidad o biomasa de dos tipos de lombrices, endogeica (comedora de suelo) y anecica (comedora de hojarazca) no difieren entre áreas cercanas y lejanas a los árboles de *Dacryodes;* en contraste, la densidad y biomasa de las lombrices anecicas fue mayor en áreas lejanas a las plantas de *Heliconia,* a pesar de que las lombrices endogeicas no mostraron diferencias, y (2) el peso seco de las lombrices en total tendió a ser mayor en los tratamientos de adición de hojarazca que en el control en la comunidad de *Heliconia.* Nuestros resultados sugieren que *Heliconia caribaea* tiene una fuerte influencia negativa sobre las lombrices anecicas y que las lombrices en la comunidad de *Heliconias* son más sensitivas a la introducción de hojarazca que en la comunidad de *Dacryodes.*

Key words: litterfall; plant-earthworm interactions; Pontoscolex corethrurus; *Puerto Rico; soil fauna.*

EARTHWORMS INGEST A VARIETY OF ORGANIC MATERIALS FROM SOILS (Hughes *et al.* 1994), that differ in quantity and chemical and physical palatability over a heterogeneous landscape. These include leaf litter, living and dead roots, microbial biomass, animal manure, leaf leachates, and root exudates (Lee 1985, Scheu 1987, Lavelle 1988, Cortez & Bouché 1992, James 1992). In tropical forests, canopy leaf litter has been suggested to be the major resource for decomposer communities (including earthworms) due to high carbohydrate content (Satchell & Lowe 1967, Martin & Lavelle 1992). Some studies have described the relationship between earthworm abundance and food resources by manipulating animal dung in agroecosystems (*e.g.,* James 1992, Hughes *et al.* 1994). Very few studies have dealt with the dynamics of earthworm communities as influenced by plant species and their litter input in tropical ecosystems.

Three categories of earthworm communities have been defined by Bouché (1977): (1) epigeic worms (pigmented) which live and feed in the surface litter above mineral soils; (2) anecic worms (pigmented) which burrow in soil and feed on surface litter; and (3) endogeic worms (unpigmented)

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which move close to the soil surface but feed on partially decayed litter and soil organic matter. A recent study has shown that the density and fresh weight of earthworms were twice as high in a *Dacryodes* community occurring along ridges than in a *Heliconia* community occupying valleys within a tropical wet forest in Puerto Rico (González 1996). Although both plant communities had a clumped distribution of worms, earthworms were twice as clumped in the *Heliconia* community than in the *Dacryodes* community. These differences in earthworm abundance and distribution pattern suggest possible differences due to plant influence and litter input between the two plant communities despite obvious contrast in their soil water regimes (González 1996). For example, when *Dacryodes* leaves senesce, they detach from the branches and fall in areas both close to and away from the base of the trees, but *Heliconia* fronds die and decay while still attached to the plant base, accumulating as clusters. In this study we tested the following hypotheses:

(H1) *Heliconia caribaea* has a more pronounced influence than *Dacryodes excelsa* on earthworm abundance and community structure. (a) Worm communities between areas close to and away from the base of *Dacryodes* trees do not differ because of similar quantity or chemistry of plant litter. (b) In contrast, earthworm communities differ between areas close to and away from the base of *Heliconia* plants because of differences in plant litter input.

(H2) Earthworm abundance is controlled by litter quantity and/or chemistry. Higher earthworm density in the *Dacryodes* community versus the *Heliconia* community is associated with higher litter input rate and/or higher litter quality (high N, P, and cation concentrations and low polyphenolics content).

(H3) Worm density rapidly decreases with litter removal and increases with litter addition in both communities.

METHODS

STUDY AREA.— The Luquillo Long-Term Ecological Research site is situated in the Luquillo Experimental Forest in Puerto Rico (18019'N, 65049'W) within the subtropical wet forest zone. The mature forest is dominated by tabonuco trees (*Dacryodes excelsa* Vahl) and is found mostly on well-drained ridges at 300 to 600 m elevation. Annual precipitation averages 3720 mm (Scatena 1989) with a period of reduced rainfall from January to April. Annual mean temperature is *ca* 22°C with little month to month variation (Brown *et al.* 1983).

Annual litterfall averages 912.5 g/m^2 with a mean annual leaf litter decay rate of 1.42 by the simple negative exponential equation (Zou *et al.* 1995). Soils are developed from Cretaceous volcanic and sedimentary rocks (Seiders 1971). The dominant soils in the ridges and hillsides are Ultisols and Oxisols; small areas of Inceptisols occur along streams. Soil water content is at field capacity throughout most of the year (Ewel & Whitmore 1973).

Two plant communities are particularly distinctive within the subtropical wet forest. One plant community is dominated by *D. excelsa, Manilkara bidentata, Guarea guidonea,* and *Sloanea berteriana* and is associated with ridges and hillsides. In valleys, the plant community is dominated by *H. caribaea* and *Prestoea montana.*

EXPERIMENTAL DESIGN.—Four trees of *D. excelsa* and four plants of *H. caribaea* were randomly selected within a 2-ha area. Litter production was monitored in 48 litter traps (0.50 m^2 in surface area, 0.65 m above ground) that were installed at two locations: three close to (0–2 m) and three away from (3–5 m) the bases of eight selected trees/plants (four for each species) beginning in October 1995. A distance of 3 to 5 m is based on 2.5 m as the maximum distance that *Heliconia* fronds extend away from the base. Three treatments (control, litter removal, and litter addition) were randomly assigned to three plots established underneath the litter traps of each selected tree/plant at each location. Individual trees/plants were at least 10 m apart.

Litter was collected biweekly, dried at 60°C, sorted into wood and fine litter (leaves, seeds, and flowers), weighed, and bulked by location (close and away) and by plant community (*Dacryodes* and *Heliconia*). The litter was then divided into 12 parts (3 treatments $\times$ 4 replicates) and replaced every two weeks in the experimental plots: one part for each of the control plots; two parts for each of the litter addition plots (double litter input rate); no litter was placed in the removal plots. A total of 48 plots were monitored for six months.

At the end of the experiment (May 1996), earthworms were sampled in plots (0.35 $\times$ 0.35 m) that were established in the center of each treatment plot. Ground litter (leaves and twigs < 2 mm) was collected from each plot and litter biomass was obtained after drying leaves and twigs at 60°C for at least 72 h. Earthworms were collected by hand-sorting the soils to a depth of 0.25 m. Fresh weights of the earthworms were obtained after the worms were rinsed with water and dried with absorbent paper on the same day they were collected. Dry weights of the earthworms were obtained after worms were freeze-killed and oven-dried at 70°C. Worms were separated based on abundance and biomass into three categories as defined by Bouché (1977): epigeic, anecic, and endogeic worms.

Percent of fine litterfall by plant species in the *Dacryodes* and *Heliconia* communities were determined on one collection (April 1996). The fine litter category included leaves, flowers, fruits, and unidentified plant materials. A fresh litter sample from each tree or plant was oven-dried at 70°C for 72 h, compiled by location (close and away), and ground in a Wiley mill through a 0.85-mm (20 mesh) stainless steel sieve. The ground samples were then digested with H_2O_2 and concentrated HNO_3 (Luh Huang & Schulte 1985) and analyzed for P, K, Ca, Mg, Fe, Mn, Na, and Al using a plasma emission spectrometer (Beckman Spectra Span V). Nitrogen concentrations were determined using the semi-micro Kjeldahl method and H_2SO_4 digestion. Carbon and ash percentages were obtained after ashing 1 g at 490°C. Fine litter was analyzed for total extractable polyphenolics content using the Folin-Denis reagent (Horowitz 1970, Anderson & Ingram 1989) and reported as percent tannic acid equivalent (TAE %).

Data analysis.—Litterfall was calculated for each tree/plant by pooling data from both close and away locations (a total of six litter traps). One-way ANOVA was employed to test for differences in total litterfall, fine litterfall, and woodfall (dependent variables) between plant communities (SAS 1987). Within each plant community, we used one-way ANOVA to test for differences in earthworm density, fresh weight, dry biomass, and leaf elemental concentrations between two locations (close and away). Differences in earthworm density, fresh weight, and dry biomass among treatments (litter addition, removal, and control) within each plant community were also tested using one-way ANOVA. For the above ANOVAs, plant communities, locations, and treatments were treated as independent variables. Plots of residuals versus predicted values indicated no obvious violation of homogeneity assumptions for the independent variables. A simple linear correlation analysis was then performed between earthworm density, fresh weight, or dry weight and total litterfall, fine litterfall, woodfall, elemental concentrations, or litter C/N and C/P ratios (SAS 1987).

RESULTS

Earthworms.—Three earthworm species were found in the *Dacryodes* community and five in the *Heliconia* community. Two exotic earthworms, the endogeic species *Pontoscolex corethrurus* and the anecic species *Amynthas rodericensis,* occurred in both plant communities. The endogeic and native species *Estherella gatesi* and *E. montana* were only found in the *Heliconia* community, whereas *Pontoscolex spiralis* occurred only in the *Dacryodes* community. *Trigaster longissimus,* a native anecic species, was only found in the *Heliconia* community. No epigeic worms were found in either community.

Earthworm densities and the fresh and dry biomasses of the endogeic species in both plant communities and the anecic species in the *Dacryodes* community did not differ between close to and away from the tree/plant bases (Figs. 1a, b). In contrast, the densities and biomasses of anecic worms were significantly higher in areas away from the *Heliconia* plants than close to the *Heliconia* plants (Fig. 1b). Density of total earthworms was significantly higher in areas away from the *Heliconia* plants than in areas close to the *Heliconia* plants, although the biomass of total earthworms did not differ between the locations (Fig. 1c).

Earthworm densities and fresh and dry biomasses of endogeic or anecic species did not differ among control, removal and addition treatments in both plant communities (Figs. 2a, b). Total dry weight of earthworms in the *Heliconia* community, however, was marginally higher in the litter addition treatment than in the control or removal treatments at $P = 0.07$, although there were no significant differences in total worm densities and total fresh biomasses among the treatments (Fig. 2c).

Litterfall.—Total litterfall in the *Heliconia* community did not differ from that of the *Dacryodes* community, which averaged 2.07 and 1.79 g/m^2/d, respectively (Table 1). Total litterfall and fine litterfall (leaves, flowers, and fruits) were significantly higher in areas close to than away from the tabonuco trees (Table 1). Woodfall was highly variable and did not differ between locations in the *Dacryodes* community. Total litterfall was not significantly different between areas close to and away from the *Heliconia* plants, which averaged 2.21 and 1.92 g/m^2/d, respectively (Table 1). No correlations

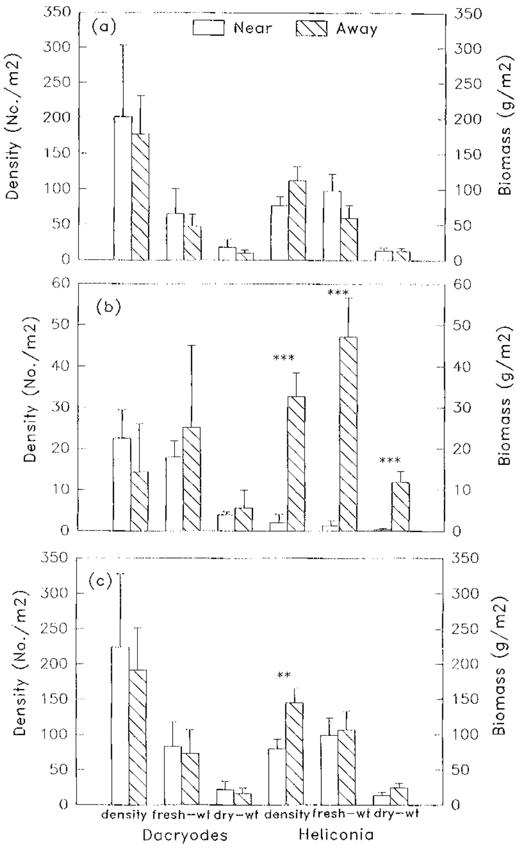

FIGURE 1. Means of earthworm density, fresh weight, and dry weight from Control treatment of (a) endogeic, (b) anecic, and (c) total worms in areas close to and away from bases of *Dacryodes* or *Heliconia* in a subtropical wet forest of Puerto Rico. Bars represent means ± 1 SE ($N = 4$). Significance levels are: * $0.1 > P > 0.05$; ** $0.05 > P > 0.01$; *** $P < 0.01$.

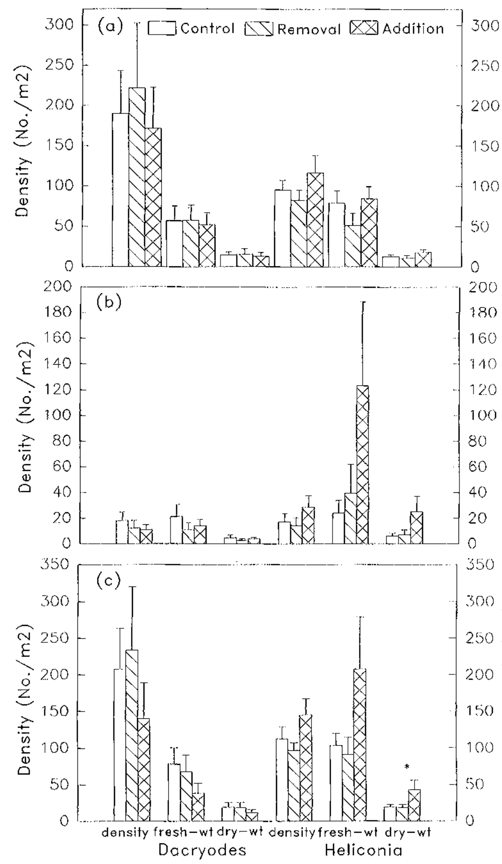

FIGURE 2. Means of earthworm density, fresh weight, and dry weight of (a) endogeic, (b) anecic, and (c) total worms in control, litter removal, and litter addition treatments in *Dacryodes* and *Heliconia* communities. Bars represent means ± 1 SE ($N = 4$). Significance levels are: * $0.1 > P > 0.05$; ** $0.05 > P > 0.01$; *** $P < 0.01$.

TABLE 1. *Mean (SE) litterfall rates in* Dacryodes *and* Heliconia *communities. Common letters within each plant community indicate no significant differences between areas close to and areas away from* Dacryodes *trees or* Heliconia *plants at* $\alpha = 0.05$ *by Scheffe's multiple range test* (N = 4). *There are no significant differences in the average wood, fine litter, and total litterfall rates between the plant communities at* $\alpha = 0.05$ *by Scheffe's multiple range test.*

Community	Location	Wood ($g/m^2/d$)	Fine litter ($g/m^2/d$)	Total ($g/m^2/d$)
Dacryodes	Close (0–2 m)	0.28 a (0.05)	1.66 b (0.09)	1.93 b (0.10)
	Away (3–5 m)	0.28 a (0.08)	1.40 a (0.09)	1.65 a (0.07)
	Average	0.28 a (0.04)	1.53 a (0.07)	1.79 a (0.07)
Heliconia	Close (0–2 m)	0.33 a (0.09)	1.88 a (0.34)	2.21 a (0.39)
	Away (3–5 m)	0.30 a (0.06)	1.63 a (0.26)	1.92 a (0.29)
	Average	0.32 a (0.05)	1.76 a (0.26)	2.07 a (0.22)

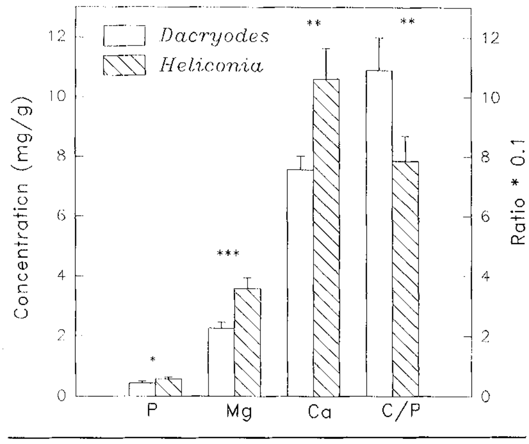

FIGURE 3. Mean concentrations of P, Mg, Ca, and C to P ratio in fine litter of *Dacryodes* and *Heliconia* communities in a subtropical wet forest of Puerto Rico (N = 4). Significance levels are: * 0.1 > P > 0.05; ** 0.05 > P > 0.01; *** P < 0.01.

were observed between litterfall and earthworm density or between litterfall and fresh or dry biomass.

Fine litterfall was dominated mainly by *D. excelsa* and *M. bidentata* in the *Dacryodes* community. *Dacryodes excelsa* represented 47 percent of the total fine litterfall in areas close to the tabonuco trees. *Dacryodes excelsa* (20.1%), *Manilkara bidentata* (18%), *Alchorneopsis floribunda* (4%), *Sloanea berteriana* (3.6%), and *Casearia arborea* (3.5%) dominated the fine litterfall in areas away from the tabonuco trees. Plant species composition of fine litterfall close to the *Heliconia* plants was dominated by *H. caribaea* (27.8%), *Cecropia scheberiana* (8.5%), and *A. floribunda* (1.1%), whereas *P. montana* (13.6%), *Philodendrum giganteum* (10.6%), *M. bidentata* (5.8%) dominated the fine litterfall in areas away from the *Heliconia* plants.

LITTER CHEMISTRY.—Of all the elements analyzed, only the concentrations of litter P, Mg, and Ca were significantly different between the two plant communities. P, Mg, and Ca were significantly higher in the *Heliconia* community than in the *Dacryodes* community (Fig. 3). The C/N ratio did not differ between plant communities, but the C/P ratio was significantly higher in the *Dacryodes* community than in the *Heliconia* community, averaging 109.81 and 78.5, respectively. Although there were no significant differences in nutrient concentrations between areas close to and away from the tree/plant bases in either plant community (Table 2), concentrations of litter P correlated significantly with fresh biomass of anecic worms (P = 0.02), and concentrations of litter N correlated significantly (P = 0.01) with the fresh and dry weight of anecic worms. Fresh weight of endogeic and all earthworms correlated negatively with percent tannic acid equivalent (Table 3). The significance levels for correlations between earthworm density, fresh weight, or dry biomass and K, Fe, Mn, Na, or C/N were all > 0.10.

DISCUSSION

In hypothesis 1, we expected to find little difference in earthworm communities between areas close to and away from the bases of *D. excelsa* trees due to similar litter quantity or chemistry. In fact, the

TABLE 2. *Mean elemental concentration (SE) of fine litter (leaves, flowers, and fruits) in* Dacryodes *and Heliconia communities. There are no significant differences in fine litter elemental concentrations between areas close (0–2 m) to and away (3–5 m) from plant bases at* α = *0.05 by Scheffé's multiple range test within each plant community* (N = *4).*

Site	C (%)	N (%)	P (mg/g)	K (mg/g)	Ca (mg/g)	Mg (mg/g)	Fe (mg/g)	Mn (mg/g)	Al (mg/g)	Ash (%)	TAE (%)
Dacryodes											
Close	42.33	1.02	0.33	3.01	7.68	2.02	0.17	0.59	1.21	8.46	5.85
	(0.28)	(0.02)	(0.01)	(0.40)	(0.86)	(0.29)	(0.03)	(0.04)	(0.91)	(0.62)	(0.98)
Away	43.07	1.29	0.52	3.70	7.45	2.47	0.29	0.46	1.64	6.87	6.52
	(0.25)	(0.14)	(0.10)	(0.66)	(0.49)	(0.30)	(0.08)	(0.07)	(1.18)	(0.53)	(2.0)
Heliconia											
Close	42.24	1.23	0.51	6.29	8.95	3.48	0.45	0.93	0.56	8.66	1.25
	(0.53)	(0.15)	(0.06)	(2.15)	(1.45)	(0.49)	(0.07)	(0.25)	(0.04)	(1.16)	(0.6)
Away	42.89	1.64	0.66	4.35	12.3	3.68	0.24	0.59	2.21	7.25	4.45
	(0.36)	(0.2)	(0.08)	(0.64)	(1.03)	(0.59)	(0.08)	(0.11)	(1.83)	(0.78)	(3.26)

TABLE 3. *Correlation coefficients (significance level) among litterfall chemistry, tannin, and earthworm density and biomass in* Dacryodes *and* Heliconia *communities* (N = 4).

	Endogeic			Anecic			Total		
Variable	Density (no./m^2)	FW[a] (g/m^2)	DW[b] (g/m^2)	Density (no./m^2)	FW (g/m^2)	DW (g/m^2)	Density (no./m^2)	FW (g/m^2)	DW (g/m^2)
N (%)	−0.15 (0.57)	0.06 (0.83)	0.13 (0.63)	0.36 (0.17)	0.55 (0.03)*	0.58 (0.02)*	−0.09 (0.73)	0.31 (0.24)	0.36 (0.17)
P (mg/g)	−0.13 (0.63)	0.12 (0.66)	0.04 (0.88)	0.39 (0.14)	0.59 (0.01)*	0.61 (0.01)*	−0.07 (0.80)	0.38 (0.14)	0.29 (0.26)
C/P	0.21 (0.44)	−0.13 (0.62)	−0.02 (0.95)	−0.28 (0.29)	−0.48 (0.06)	−0.50 (0.045)*	0.16 (0.56)	−0.34 (0.20)	−0.22 (0.39)
Ca (mg/g)	−0.01 (0.97)	0.06 (0.82)	0.19 (0.48)	0.28 (0.30)	0.41 (0.11)	0.47 (0.07)	0.03 (0.91)	0.25 (0.35)	0.36 (0.17)
Mg (mg/g)	−0.13 (0.61)	0.36 (0.17)	0.08 (0.77)	0.14 (0.60)	0.36 (0.17)	0.41 (0.11)	−0.11 (0.68)	0.48 (0.06)	0.24 (0.36)
Al (mg/g)	0.44 (0.08)	0.31 (0.24)	0.42 (0.10)	0.30 (0.26)	0.44 (0.09)	0.44 (0.09)	0.47 (0.07)	0.48 (0.06)	0.54 (0.03)*
TAE (%)	−0.00 (0.98)	−0.55 (0.02)*	−0.32 (0.23)	0.02 (0.93)	−0.11 (0.68)	−0.13 (0.63)	−0.00 (0.99)	−0.53 (0.03)*	−0.32 (0.22)

[a] FW: Fresh weight; [b] DW: Dry weight; * indicates significance level at 0.05.

Dacryodes community did not differ in the density and biomass of either endogeic or anecic earthworms between areas close to and away from the tabonuco trees. Although litterfall was higher in areas close to the tabonuco trees, litter chemistry did not differ between the two locations. This suggests that litter quality may play a more important role than litter quantity in controlling earthworm abundance in this forest. Therefore, we accept Hypothesis 1 for the *Dacryodes* community. In contrast, we predicted a difference in earthworm communities between areas close to and areas away from the *Heliconia* plants because of differences in litter input. We found a higher abundance of anecic worms in areas away from these *Heliconia* plants. We observed no difference in litterfall or litter chemistry between the two locations, however, suggesting that *Heliconia* plants influence earthworm communities through altering soil properties rather than litter quantity or chemistry. Thus, we partially accept hypothesis 1 for the *Heliconia* community.

In hypothesis 2, we predicted that higher quantity and/or quality of litterfall would contribute to a higher earthworm density in the *Dacryodes* community than in the *Heliconia* community. The data showed that both plant communities had the same rate of litterfall. Furthermore, higher concentrations of litter P, Mg, and Ca, and a lower ratio of litter C/P were found in the *Heliconia* community in which lower earthworm density was observed. These data suggest that neither the quantity nor the quality of litter as assessed by variables studied here explains the observed difference in worm abundance between the two plant communities. Therefore, we reject Hypothesis 2.

Alternative mechanisms that might affect the earthworm density between the two plant communities include chemical and physical properties of the soils (González *et al.* 1996), belowground organic inputs, and top-down control from predators. Soil C and N concentrations (Soil Survey Staff 1995) from the top 25 cm of the profile in the *Dacryodes* community (C: 3.46%; N: 0.36%) were higher than those of the *Heliconia* community (C: 2.99%; N: 0.28%). Shortage of one or both of these elements sometimes may limit earthworm populations (Lee 1985). Information on belowground organic inputs is not available for either plant community. Our personal observations suggest that lizards, and potentially frogs, are likely to be the predators of earthworms when worms feed or cast on the soil surface.

In hypothesis 3, we anticipated a higher earthworm density in the litter addition treatment and a lower earthworm density in the litter removal treatment than in the control treatment. Densities and fresh and dry biomasses of both endogeic and anecic earthworms did not differ among control, removal, and addition treatments in the *Dacryodes* community. Dry biomass of total worms was marginally higher in the addition treatment than in the control or removal treatments for the *Heliconia* community ($P = 0.07$). This implies that absolute amounts of resources do not have strong controls on earthworm densities or, more likely, a longer period of time and/or a higher number of replicates than those used in this study would show a significant difference among treatments. Conversely, there was no effect of litter removal treatment on earthworm communities, again suggesting that the presence or absence of organic matter does not stimulate rapid changes in earthworm densities. Thus, we must reject the third hypothesis.

Judas (1990) manipulated leaf litter input in a beechwood growing in limestone soil in Germany, finding that both anecic and endogeic populations decreased with the augmentation of leaf litter input after a five-year experiment. He concluded that endogeic and anecic populations in the beechwood could be restricted by factors connected with the thick litter layer that influenced the O_2 supply or the bacterial/fungal ratios. In the present study, the litter addition treatment did not trigger a decrease in worm abundance in both *Dacryodes* and *Heliconia* communities and tended to increase worm abundance in the latter, suggesting that the effect of litter addition on earthworms may differ between temperate and tropical forests and among plant communities within tropical forests. Earthworms in the *Heliconia* community appeared to be more sensitive to changes in resource availability than in the *Dacryodes* community.

Our results have two implications. First, the strong negative effect of *H. caribaea* on anecic earthworms may explain the observed highly clumped distribution pattern of earthworms in the *Heliconia* community (González 1996). Second, hurricane disturbances that produce pulses in plant litter input (Lodge *et al.* 1991) cannot cause rapid changes in earthworm abundance and community structure in the *Dacryodes* community, but could increase earthworm biomass in the *Heliconia* community.

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