

# Earthworm Abundance and Distribution Pattern in Contrasting Plant Communities Within a Tropical Wet Forest in Puerto Rico

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**ABSTRACT.**—Plant communities may impose strong control on soil fauna populations. We examined the abundance and distribution pattern of earthworms in two contrasting plant communities within a tropical wet forest in Puerto Rico. The *Dacryodes* community occurs in well-drained soils and is dominated by *Dacryodes excelsa*, *Manilkara bidentata*, *Guarea guidonea*, and *Sloanea berteriana*. The *Heliconia* community occurs in poorly-drained soils and is dominated by *Heliconia caribaea* and *Prestoa montana*. Earthworm biomass and density in the *Dacryodes* community were twice those in the *Heliconia* community. Earthworm distribution was clumped in both communities, but was more aggregated in the *Heliconia* community. Soil pH in the *Heliconia* community was higher than in the *Dacryodes* community and correlated negatively with earthworm density after pooling the data from both communities. However, soil pH alone could not explain the observed differences in worm abundance and fresh biomass across the Luquillo Mountains. Soil water content in the *Heliconia* community was higher than in the *Dacryodes* community, but did not correlate with earthworm density or biomass. Forest litter biomass did not differ between the two communities. *Pontoscolex corethrurus* dominated the density and biomass of earthworms on both communities, and these data are comparable to other wet tropical regions. Our results indicate that variation in plant species composition and soil properties between plant communities can trigger differences in earthworm abundance and distribution pattern within a tropical wet forest.

**RESUMEN.**—Las comunidades de plantas pueden imponer un control fuerte sobre las poblaciones de animales del suelo. Nosotros examinamos la abundancia y el patrón de distribución de las lombrices de tierra en dos comunidades de plantas en un bosque húmedo tropical en Puerto Rico. La comunidad de *Dacryodes* ocurre en suelos con buen drenaje y está dominada por *Dacryodes excelsa*, *Manilkara bidentata*, *Guarea guidonea* y *Sloanea berteriana*. La comunidad de *Heliconia* ocurre en suelos de pobre drenaje y está dominada por *Heliconia caribaea* y *Prestoa montana*. La biomasa y la densidad de las lombrices de tierra en la comunidad de *Dacryodes* fue el doble que en la comunidad de *Heliconia*. La distribución de las lombrices fue agregada en ambas comunidades, pero fue más agrupada en la comunidad de *Heliconia*. El pH del suelo en la comunidad de *Heliconia* fue más alto que en la comunidad de *Dacryodes*, y tuvo una correlación negativa con la densidad de las lombrices luego de unir los datos de ambas comunidades. Aun así, el pH del suelo solo no pudo explicar la diferencia observada en la abundancia y biomasa de las lombrices en el bosque de Luquillo. El contenido de agua del suelo en la comunidad de *Heliconia* fue más alto que en la comunidad *Dacryodes*, pero éste no correlacionó con la densidad o biomasa de las lombrices de tierra. La biomasa de la hojarasca del suelo no difirió entre las dos comunidades. *Pontoscolex corethrurus* dominó la densidad y abundancia de las lombrices en ambas comunidades de plantas; estos datos son comparables a los de otras regiones tropicales húmedas. Nuestros resultados indican que la variación en la composición de especies de plantas y las propiedades del suelo entre distintas comunidades de plantas pueden causar diferencias en la abundancia y en el patrón de distribución de las lombrices de tierra en un bosque lluvioso tropical.

## INTRODUCTION

Climate imposes strong control on the abundance and distribution of earthworms.

Under similar climate conditions, factors that determine earthworm abundance and distribution may depend on plant species composition and on the physical and chem-

ical properties of soils within a plant community (Lee, 1985; Berry, 1994; González et al., 1996). Previous information on earthworm abundance and distribution in tropical areas was mostly collected from agroecosystems, where management practices altered soil properties and plant communities. For example, increasing woody plant species richness during secondary succession in abandoned tropical pastures in Puerto Rico was associated with a decrease in worm abundance and an increase in the diversity of the earthworm community (Zou and González, 1997). Native worms preferred naturally regenerated forest to pine and mahogany plantations in abandoned croplands (González et al., 1996). Density of earthworms was positively correlated with inputs of organic nitrogen in *Albizia falcataria* (L.) Fosberg and *Eucalyptus saligna* Sm. plantations in Hawaii (Zou, 1993). Little information on earthworm abundance and distribution pattern is available from heterogeneous landscapes within humid tropical forests.

The tropical wet forest in Puerto Rico (tabonuco forest) occurs between 300 and 600 m in the Luquillo Experimental Forest. Plant species composition varies across a heterogeneous landscape that differs in topographic positions and disturbance regimes within the tabonuco forest life-zone. Tree species composition in well-drained areas is dominated by *Dacryodes excelsa* Vahl., *Manilkara bidentata* (A. DC.) A. Chev., *Guarea guidonea* (L.) Sleumer, and *Sloanea berteriana* Choisy. Poorly drained areas are often associated with *Heliconia caribaea* Lam. and *Prestoea montana* (Graham) Nicholson (Soil Survey Staff, 1995).

González and Zou (in press) reported a lower earthworm density in areas close to *Heliconia caribaea* clones as compared to areas 3 m away from these clones. The study reported a lack of influence of *Dacryodes excelsa* on earthworm density in the same wet forest. The negative effect of *H. caribaea* may reduce the overall density of earthworms and alter their distribution patterns in areas dominated by this plant. Thus, we developed this study to examine the abundance and distribution of earthworms in a plant community dominated by

*H. caribaea* as compared with one dominated by *D. excelsa*. We asked these questions: (1) Does the *Heliconia* community support lower levels of earthworm density and biomass than the *Dacryodes* community?, (2) Is the distribution pattern of earthworms more aggregated in the *Heliconia* community than in the *Dacryodes* community?

## MATERIALS AND METHODS

### Study site

The study was conducted at El Verde (18°19'N, 65°49'W) in the Luquillo Long-Term Ecological Research (LTER) site, within the subtropical wet forest life zone. Elevation is 420 m and the mean annual precipitation is 3524 mm (García-Martinó et al., 1996). Mean annual air temperature is 22.3°C (Brown et al., 1983).

The soils of the LTER research area are developed from Cretaceous volcanic and sedimentary rocks (Seiders, 1971). The dominant soils are Oxisols classified as a very fine, kaolinitic, and moderately well drained (Soil Survey Staff, 1995). Plant communities within the Luquillo Mountains vary according to geomorphology, microclimate, land-use history, successional stage and disturbance (Crow and Grigal, 1979; García-Montiel and Scatena, 1994; Scatena and Lugo, 1995). The *Dacryodes* community typically occupies well-drained areas in uplands of the mature forest (Crow and Grigal, 1979), whereas the *Heliconia* community is located within the tabonuco forest but limited to disturbed riparian zones along poorly-drained soils in the valleys. Mature *D. excelsa* are canopy trees, 25-30 m tall, with small 50 × 100 mm leaves. This species has the highest basal area for a single species in the *Dacryodes* community (Zou et al., 1995). *Heliconia caribaea* is a monocot up to 4 m tall and grows aggregated as clones with 0.5 × 1.5 m leaves attached to their bases. It has the highest stem density (stem diameter > 1 cm) in the *Heliconia* community. When senescent, leaves fall to the forest floor in the *Dacryodes* community, but *H. caribaea* leaves die and decay attached to the plant base.

### Experimental Design

Field data were collected during the relatively dry season between November 10, 1994 to April 13, 1995. Earthworms were sampled in two grids randomly located in each community (*Dacryodes* and *Heliconia*). Each grid consisted of 16 quadrants (0.25 × 0.25 m each) at 3 m intervals within a 12 × 12 m area. Forest floor litter (mostly leaves, fruit, and twigs < 2 mm) in each quadrant was collected and stored in a paper bag. Biomass of forest floor litter was obtained after drying the plant material at 60°C for three days. Soil was removed to a depth of 0.25 m using a shovel, and earthworms were sorted by hand. Fresh biomass (weight) of earthworms was recorded in the laboratory after worms were rinsed with water and dried with paper towels. A soil sample (0-0.25 m) was taken from each quadrant for measuring soil pH and moisture content. Soil water content was calculated by oven drying 10 g of fresh sample at 105°C for 48 hours. Soil pH was measured using a paste of 1:1 ratio of fresh soil to deionized water.

### Data Analysis

A nested ANOVA was used to test for differences in earthworm density, earthworm fresh biomass, soil water content, soil pH, and biomass of forest floor litter (independent variables) between plant communities and grids within a community. Plots of residuals vs. predicted values indicated no obvious violation of the homogeneity assumption for the independent variables. An  $\alpha$  level of 0.05 was used for all tests. A simple linear correlation analysis was performed among earthworm density, earthworm fresh biomass, soil pH, soil water content, and biomass of forest floor litter.

Two indexes of dispersion for quadrant counts of earthworms were employed: the variance ( $s^2$ ) to mean ( $m$ ) ratio and Morisita's index of dispersion ( $I_d$ ) (Pielou, 1977; Krebs, 1989). The ratio ( $s^2/m$ ), named the index of dispersion ( $I$ ), is based on the observation that in a randomly distributed population the ratio of the variance to the mean of the number of individuals per sampling unit equals one. Uniform and clumped

distribution will give expected values for  $I$  of < 1 and > 1, respectively (Krebs, 1989). To test if the observed dispersion pattern was significantly different from a random distribution, the observed frequencies of the numbers of earthworms were compared with the expected binomial (random) frequency using the Kolmogorov-Smirnov test. This test is based on the absolute differences between observed and expected cumulative frequency distributions. These differences are expressed as differences between relative cumulative frequencies, and critical values decide whether the maximum difference between the observed and expected cumulative frequency distribution is significant (Sokal and Rohlf, 1995). The equation for the Morisita's index is:

$$I_d = n[(\sum x^2 - \sum x)/((\sum x)^2 - \sum x)]$$

where  $n$  = sample size; ( $x$  = sum of the quadrant counts (earthworms per quadrant) =  $x_1 + x_2 + x_3 + \dots$ ;  $\sum x^2$  = sum of quadrant counts squared =  $x_1^2 + x_2^2 + x_3^2 + \dots$  (Pielou, 1977; Krebs, 1989).  $I_d$  is a coefficient relatively independent of population density, and the rules that determine the distribution pattern of its expected values are the same as for  $I$ .

## RESULTS

Density and fresh biomass of earthworms in the *Dacryodes* community were twice those of the *Heliconia* community. *Pontoscolex corethrurus* Muller, a soil-feeding exotic earthworm, dominated both plant communities. *Amyntas rodericensis* Grube, a litter-feeding exotic earthworm, was also found in both plant communities. *Pontoscolex spiralis* Borges and Moreno, a soil-feeding native worm, was found only in the *Dacryodes* community. The density and fresh biomass of *Pontoscolex* sp. were significantly higher in the *Dacryodes* than in the *Heliconia* community. The fresh biomass of *Pontoscolex* sp. and the density of *A. rodericensis* were significantly different between the grids in the *Dacryodes* community (Table 1). Mean soil pH and water content were significantly higher in the *Heliconia* than in the *Dacryodes* community.

TABLE 1. Mean ( $\pm$  standard error), relative density, and fresh biomass (weight) of earthworm species. Results from nested ANOVA are included.

Plant community	Earthworm species	Density		Fresh biomass	
		(No. m <sup>-2</sup> )	%	(g. m <sup>-2</sup> )	%
<i>Dacryodes excelsa</i>					
Grid 1	<i>Pontoscolex corethrurus</i>	95 $\pm$ 14.2	97	21.6 $\pm$ 3.2	92
	<i>Pontoscolex spiralis</i>	1	1	0.6	3
	<i>Amyntas rodericensis</i>	2 $\pm$ 1.4	2	1.2 $\pm$ 0.8	5
Grid 2	<i>Pontoscolex corethrurus</i>	123 $\pm$ 19.1	90	39.8 $\pm$ 6.7	63
	<i>Amyntas rodericensis</i>	14 $\pm$ 4.1	10	23.6 $\pm$ 8.3	37
<i>Heliconia caribaea</i>					
Grid 1	<i>Pontoscolex corethrurus</i>	55 $\pm$ 15.3	95	15.9 $\pm$ 3.8	66
	<i>Amyntas rodericensis</i>	3 $\pm$ 2.2	5	8.0 $\pm$ 6.2	34
Grid 2	<i>Pontoscolex corethrurus</i>	73 $\pm$ 21.1	94	17.6 $\pm$ 3.3	76
	<i>Amyntas rodericensis</i>	5 $\pm$ 3.2	6	5.5 $\pm$ 4.1	24
A) Source [F (P)-values] <sup>1</sup>					
Plant community				9.57 (<0.01)	
Grid		6.64 (0.01)		4.90 (0.03)	
Plant community (Grid)		1.62 (0.21)		3.39 (0.07)	
		0.06 (0.80)			
B) Source [F (P)-values] <sup>1</sup>					
Plant community		1.91 (0.17)		1.01 (0.32)	
Grid		5.86 (0.02)		3.13 (0.08)	
Plant community (Grid)		2.99 (0.09)		4.97 (0.03)	

<sup>1</sup>[F and (P)- values] refer to nested ANOVA results for comparison of means of A) *Pontoscolex* sp. and B) *A. rodericensis* between the plant communities, grids within a community, and the interaction of plant community and grid.

Soil pH was significantly different between grids within the *Heliconia* community. Biomass of forest floor litter did not differ between the two plant communities (Table 2). Earthworm density and biomass within each plant community were not correlated with soil pH, soil water content, or forest floor litter ( $-0.3 < R^2 < 0.02$ ;  $P > 0.14$ ). Earthworm density correlated with soil pH ( $r = -0.36$ ,  $P = 0.004$ ) after pooling the data from

both plant communities and did not correlate with soil water content or the biomass of forest litter (Fig. 1).

The distribution of earthworms was clumped in both grids of either *Dacryodes* or *Heliconia* communities (Table 3). Using combined data from both grids in each plant community, the Kolmogorov-Smirnov test still indicated a significant deviation from a random distribution. The

TABLE 2. Mean ( $\pm$  one standard error) of soil pH, water content, and biomass of forest floor litter (n = 16 per grid).

Plant community	Soil H <sub>2</sub> O (%)	Soil pH	Biomass of forest floor litter (g m <sup>-2</sup> )
<i>Dacryodes excelsa</i>			
Grid 1	67.0 $\pm$ 2.0	4.7 $\pm$ 0.09	428.3 $\pm$ 19.5
Grid 2	59.6 $\pm$ 1.7	4.9 $\pm$ 0.06	455.0 $\pm$ 32.2
<i>Heliconia caribaea</i>			
Grid 1	68.6 $\pm$ 4.8	5.9 $\pm$ 0.07	371.7 $\pm$ 81.8
Grid 2	72.8 $\pm$ 2.3	5.1 $\pm$ 0.04	446.1 $\pm$ 74.5
Source [F (P)-values] <sup>1</sup>			
Plant community	6.19 (0.02)	101.53 (<0.01)	0.31 (0.58)
Grid	0.29 (0.59)	31.82 (<0.01)	0.75 (0.39)
Plant community (Grid)	3.76 (0.06)	52.91 (<0.01)	0.17 (0.68)

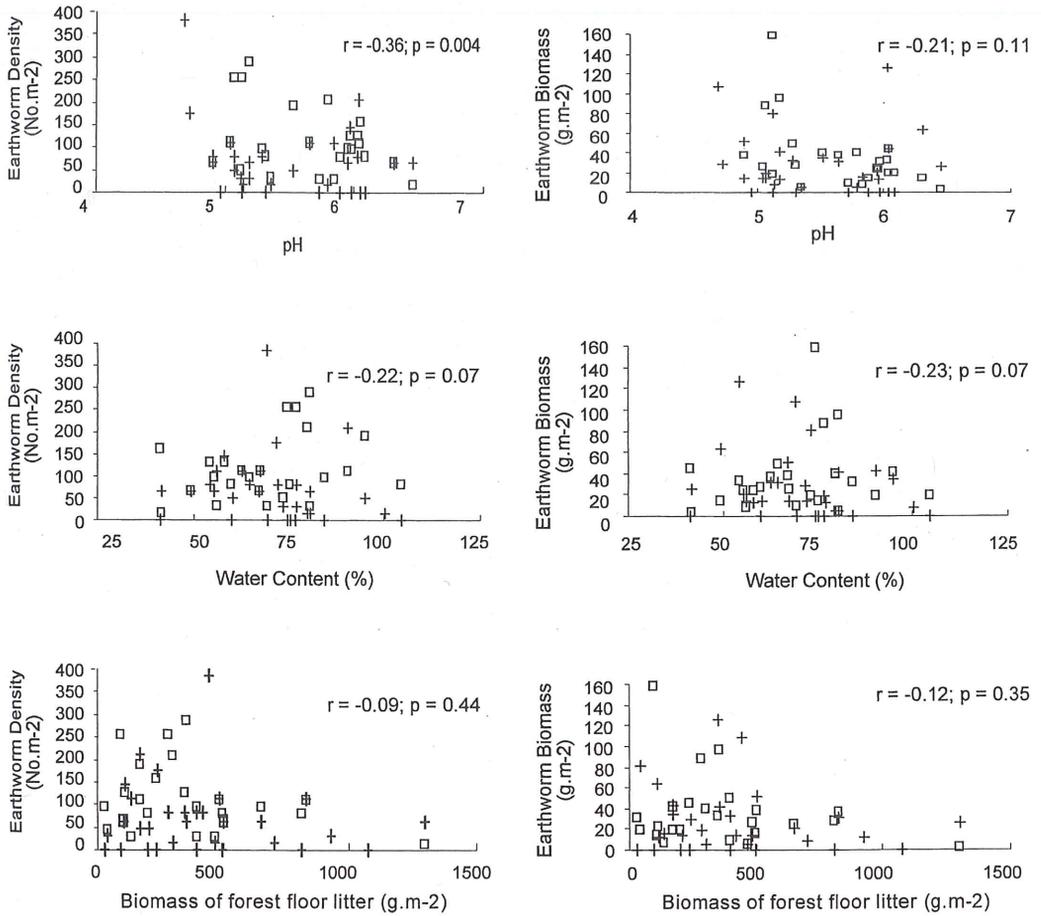


FIG. 1. Correlation between earthworm density or biomass (fresh weight) and soil pH, water content (%), or biomass of forest floor litter (g. m<sup>-2</sup>) in *Dacryodes* (□) and *Heliconia* (+) communities within a tropical wet forest in Puerto Rico.

variance-to-mean ratio ( $I$ ) and the Morisita's index of dispersion ( $I_d$ ) of the *Heliconia* community were twice those of the *Dacryodes* community.

#### DISCUSSION

Earthworms can use a wide variety of organic materials for food. Even in adverse conditions they can extract sufficient nourishment from soil to survive (Edwards and Bohlen, 1996). Satchell (1967) suggested that the most important factors determining earthworm abundance and biomass are the quantity and quality of food. Many studies have demonstrated that worm abundance is affected

by the quantity of litter input (e.g., Abbott and Parker, 1981; Cuendet, 1984; Lee, 1985; Hendrix et al., 1992). Although *Dacryodes* and *Heliconia* communities differed in plant species composition, the quantity of litter input did not differ, and averaged 1.79 and 2.06 g m<sup>-2</sup> d<sup>-1</sup> for the two communities, respectively (González and Zou, in press). These data indicate that differences in above-ground litter quantity cannot explain the observed differences in earthworm abundance and fresh biomass between these two plant communities.

Soil pH was significantly different between the two plant communities, but it alone could not explain the observed difference in worm abundance and fresh bio-

TABLE 3. Earthworm distribution pattern, Variance-to-Mean Ratio (I), and Morisita's Index of Dispersion ( $I_d$ ).

Plant community	Indexes of Dispersion		Kolmogorov-Smirnov test			Spatial Pattern
	I	$I_d$	$d_{max}^1$	CV <sup>2</sup>	P	
<i>Dacryodes excelsa</i>						
Grid 1	4.26	1.16	0.227	0.164	0.01	Clumped
Grid 2	6.11	1.23	0.296	0.154	0.01	Clumped
Combined	5.23	2.03	0.195	0.106	0.01	Clumped
<i>Heliconia caribaea</i>						
Grid 1	2.10	1.87	0.288	0.222	0.01	Clumped
Grid 2	2.96	2.03	0.275	0.262	0.02	Clumped
Combined	2.61	2.01	0.286	0.140	0.01	Clumped

<sup>1</sup>The maximum absolute difference between the cumulative frequencies;

<sup>2</sup>Critical value.

mass because it also varied between grids within a plant community (Table 2). Zou and González (1997) reported a higher fresh biomass of earthworms in abandoned pastures (175 g m<sup>-2</sup>) than in the *Dacryodes* community (41 g m<sup>-2</sup>) despite soil pH being similar (4.7 vs. 4.8). Mahogany plantations with soil pH values similar to those of the *Dacryodes* community sustained a lower fresh biomass (30 g m<sup>-2</sup>) of earthworm (González et al., 1996). On the other hand, naturally regenerated secondary forest with soil pH values similar to those of the *Dacryodes* community supported higher fresh biomass (61 g m<sup>-2</sup>) of earthworms (González et al., 1996). These data show an inconsistent pattern between soil pH and fresh biomass of earthworms.

The sampling period (November to April) is the season with the lowest precipitation in the tabonuco forest (García-Martín et al., 1996). An on-going study showed little variation in earthworm population abundance between the dry and the wet seasons in the tabonuco forest (Liu and Zou, unpublished data). Soil water content in the *Dacryodes* community was lower than in the *Heliconia* community, but *P. corethrurus* density and fresh biomass were higher in the former, implying that soil moisture regimes are not the driving factor affecting worm abundance in the *Heliconia* community.

González and Zou (in press) report that earthworm density averaged 79 individuals m<sup>-2</sup> in areas close to *H. caribaea* clones and 145 individuals m<sup>-2</sup> in areas 3 m away from these clones. The latter number was

greater than the 118 individuals m<sup>-2</sup> found in the *Dacryodes* community from this study, suggesting that *H. caribaea* plays an important role in reducing earthworm density. This negative effect of *H. caribaea* is most likely achieved through reducing below-ground food availability and altering other soil chemical properties. There is no information on root productivity and root exudates for this plant species. However, earthworm abundance has been correlated positively with soil C and N levels (e.g., Lee, 1985; Fragoso and Lavelle, 1992; Zou and Bashkin, 1998). Soil organic C and N contents from the top 25 cm of soil profile in the *Dacryodes* community (C: 3.46%; N: 0.36%) were higher than in the *Heliconia* community (C: 2.99%; N: 0.28%) (data from Soil Survey Staff, 1995), indicating that the altered soil properties may have produced the differences in earthworm abundance between the two plant communities.

Both plant communities also differ in landscape position and stand age. The *Dacryodes* community occupies soils on ridges and under older stands than the *Heliconia* community. The *Heliconia* community occupies soils along riparian valleys that are constantly disturbed. Therefore, *Heliconia* community soils are relatively young and contain less organic matter (131 vs. 210 Mg ha<sup>-1</sup>) (Scatena and Lugo, 1995). Earthworms can ingest a large proportion of soil organic matter in many ecosystems; consequently differences in soil organic matter could have produced the differences in earthworm abundance between the two plant communities.

The highly clumped spatial pattern of earthworms in the *Heliconia* community might also result from the strong negative effect of *H. caribaea* on earthworm density (González and Zou, in press). The reduced earthworm density in areas surrounding *H. caribaea* clones, as compared with areas 3 m away from these clones, can enhance the aggregation of worms in the *Heliconia* community. In contrast, *D. excelsa* did not have a significant effect on earthworm abundance between areas close to and away from its bases. Thus, it has limited influence on the aggregation of earthworms.

Our data on earthworm density are comparable to data from other moist and wet tropical sites, but are higher than the 12 worm m<sup>-2</sup> reported in an earlier study in the same forest (Borges and Alfaro, 1997). Earthworm density in two tropical forests from Mexico varied from 79 to 132 worm m<sup>-2</sup> (Lavelle, 1983). Fragoso and Lavelle (1992) reported an average of 68 worms m<sup>-2</sup> and 12.9 g m<sup>-2</sup> (fresh biomass) in tropical rain forest communities of Mexico. In Hawaii, earthworm density in undisturbed rain forests was 21 worms m<sup>-2</sup> (Aplet, 1990). Average density of earthworms in tropical forests was not significantly different from that of temperate deciduous and cold coniferous forests (Lee, 1985; Fragoso and Lavelle 1992).

In our study, *P. corethrurus* dominated the density and biomass of both plant communities. Earthworm density and biomass in the Central American forests of Mexico and Costa Rica are also dominated by the exotic worm *Pontoscolex corethrurus* (Fragoso and Lavelle, 1992). Higher earthworm density in the *Dacryodes* community than in the *Heliconia* community suggests that plant species and soils have a strong influence on the abundance and distribution of earthworms under similar climate conditions.

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