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Correlation between earthworms and plant litter decomposition in a tropical wet forest of Puerto Rico

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Summary

Earthworms are recognized to play an important role in the decomposition of organic materials. To test the use of earthworms as an indicator of plant litter decomposition, we examined the abundance and biomass of earthworms in relation to plant litter decomposition in a tropical wet forest of Puerto Rico. We collected earthworms at 0–0.1 m and 0.1–0.25 m soil depths from upland and riparian sites that represent the natural variation in soils and decomposition rates within the forest. Earthworms were hand-sorted and weighed for both fresh and dry biomass. Earthworms were dominated by the exotic endogeic species *Pontoscolex corethrurus* Müller; they were more abundant, and had higher biomasses in the upland than in riparian sites of the forest. Plant leaf litter decomposed faster in the upland than riparian sites. We found that earthworm abundance in the upper 0.1 m of the soil profile positively correlated with decomposition rate of plant leaf litter. Ground litter removal had no effect on the abundance or biomass of endogeic earthworms. Our data suggest that earthworms can be used to predict decomposition rates of plant litter in the tropical wet forest, and that the decomposition of aboveground plant litter has little influence on the abundance and biomass of endogeic earthworms.

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Introduction

Scientists have long recognized that high levels of earthworm abundance are associated with faster plant litter decomposition in terrestrial ecosystems (Darwin, 1881; Lal, 1988; Edwards and Bohlen, 1996). However, few studies have tried to quantify the relationship between earthworm abundance and plant litter decomposition in tropical forests. Since earthworms compose the highest biomass among the tropical soil macrofauna, their role in plant litter decomposition may determine the structure and function of tropical forests (Fragoso and Lavelle, 1992). A few studies have demonstrated a positive correlation between earthworm abundance and soil C and N levels in tropical forests. For example, Zou and Bashkin (1998) and Gonzalez et al. (1999) showed that increases in earthworm density are associated with increases in concentrations of soil C and N. However, these studies did not explore the quantitative relations between earthworms and decomposition rates of plant litter. Liu and Zou (2002) found that by reducing earthworm numbers in tropical soils decomposition rates of plant litter decreased. A recent study found that earthworms in riparian zones were half as numerous as in upland zones within a tropical wet forest of Puerto Rico (Gonzalez and Zou, 1999). The riparian zones are dominated by a *Heliconia* plant community and located in valleys, usually near streambeds, whereas the upland zones are dominated by a *Dacryodes* plant community and are located along ridges and hillsides. We designed this study to examine the quantitative relationship between earthworm abundance and plant litter decomposition within a tropical wet forest under similar climate conditions. We also manipulated aboveground litter input to examine responses of earthworms to litter removal. We predicted that there are significant correlations between the abundance of earthworms and rates of plant litter decomposition. Because removal of plant litter does not drastically alter the decomposition potentials that are governed by climate, substrate quality, and soil activity (Swift et al., 1979), we further predicted that the abundance of endogeic earthworms would remain unchanged when surface litter was removed.

We conducted this study in upland and riparian zones within a tropical wet forest of Puerto Rico (Gonzalez and Zou, 1999). We chose to study this forest because it was dominated by endogeic earthworms. There are three ecological categories of earthworms among which the endogeic earthworms possibly contribute to the decomposition process of soil organic matter (Bouche, 1977; Lavelle, 1983) because endogeic earthworm species derive their nourishment from humified organic matter or root exudates and occasionally come to the surface to feed on dead organic materials beneath the litter layer (Lavelle, 1983; Edwards and Bohlen, 1996). In contrast, epigeic earthworms feed and live within the litter layer on surface mineral soils, and anecic earthworms live in mineral soils and feed mostly on surface litter materials. We selected the upland and riparian zones as study sites because they represent the largest variation in soil texture, decomposition rates of plant litter, and earthworm abundance within the tropical wet forest (Soil Survey Staff, 1995).

Methods

Study site

The study was conducted in the Luquillo Experimental Forest of Puerto Rico. The forest is a subtropical wet forest with an elevation of about 420 m above sea level (Zou et al., 1995). Annual litterfall averages 912.5 $g\,m^{-2}$ with a mean leaf litter decay rate of 1.42 yr^{-1} (Zou et al., 1995). The soils in the riparian zone of the forest are Inceptisols of alluvial origin, and the soils in the upland zone of the forest are Oxisols, developed from volcanic rocks and belonging to the Zarzal series with high clay content (Soil Survey Staff, 1995).

We chose four blocks in each of the riparian and upland zones. A randomized block design with two treatments within each block was established in each of the riparian and upland sites beginning May 1999. The two treatments were control and litter removal. A tent 1.5 m in height was built with PVC tubes (diameter 3.5 cm) and netting to exclude litter input from the litter-removal plots. Each plot was 2×2 m in size. A total of eight plots were set up with four replicates per treatment in each of the riparian and upland zones.

Earthworm sampling

Earthworms were sampled between 17 and 21 June 2001 from eight 0.3×0.3 m sites located randomly in each of the control and litter-removal plots in both upland and riparian sites, about 2 years after the litter exclusion treatment. Soil was removed from the control plot (normal leaf litter input) and the experimental plot (leaf litter removed by litter traps) in each site. Soil was removed in two steps: soil in the upper 0.1 m was removed first, and then soil was removed to a depth of 0.25 m. Both were removed using a shovel onto plastic sheets. Earthworms were hand-sorted and stored in plastic bags. In the laboratory, earthworms were sorted and counted according to type (endogeic vs. anecic species) and species (Gonzalez et al., 1996; Borges and Alfaro, 1997; Sanchez-de Leon et al., 2003). Fresh weight of earthworms was acquired after the worms were rinsed with water and dried with paper towels on the same day of sampling. Dry weight of earthworms was obtained using a freeze-dryer. Two-way ANOVA was performed to examine differences in earthworm density, fresh weight, and dry weight between the control plot and the experimental plot, between riparian and upland forests, and between 0–0.1 m and 0.1–0.25 m depths.

Table 1. Leaf litter species composition and air-dried weight (g) in litterbags that represent the natural litterfall in April 1999 in the riparian and the upland areas of a tropical wet forest, Puerto Rico

Species	Upland	Riparian
Buchenavia capitata (Vahl) Eichl.	1.2	
Dacryodes excelsa Vahl	0.8	
Homalium recemosum Jacq.	0.8	
Guarea guidonia (L.) Sleumer	0.6	
Sloanea berteriana Choisy	0.4	
Philodendron giganteum Schott	0.2	
Prestoea montana (R. Grah.) Nichols.		1.1
Tabebuia heterophlla (DC.) Britton		1.1
Byrsonima spicata (Cav.) HBK		0.9
Inga laurina (Sw.) Willd.ex L.		0.5
Sapium laurocerasus Desf.		0.3
Marcgravia rectiflora Triana and Planch		0.2
Mixture of other species	1.0	0.9
Total	5.0	5.0

Decomposition experiment

To reflect the variation in decomposition rate, we used two types of leaf litter for the upland and riparian sites. Leaf decomposition rates were measured using litterbags (20×20 cm) made of plastic window screens with 1.5 mm mesh openings. A total of 112 litterbags were constructed, of which 56 were filled with newly senesced fresh leaf litter collected from the riparian forest and incubated in the control plots of the riparian forest, and another 56 were filled with leaf litter from the upland forest and incubated in the control plots of the upland forest. This fresh leaf litter represented the main tree species composition in natural litterfall in April 1999 (Table 1). The species composition of litterfall was determined using leaffall in the 4 m^2 randomly established PVC-tent in each plot. Leaves of the six most common species from each forest, representing 81–85% of the total fresh leaf mass, were placed in litterbags in proportion to their biomass in litterfall (Table 1). Leaves of the remaining species were randomly selected to obtain a total 5 g air-dry leaf material (4.6 g mean oven-dry mass) in each litterbag. Leaf chemical composition was 1.02% N, 0.33 mg g^{-1} P, with a C/N ratio of 41.5 for the upland sites, and 1.23% N, 0.51 mg g^{-1} P, with a C/N ratio of 34.3 for the riparian sites (Gonzalez and Zou, 1999). The decomposition experiment was initiated in June 1999 and continued until June 2000. Two randomly selected litterbags were collected after 0, 60, 120, 180, 240, 300, and 360 days (two-monthly intervals) in the field. Fine live roots and soil which had entered the litterbags were carefully removed in the laboratory. The remaining litter of each litterbag was oven-dried at 70 °C for 72 h and weighed to determine dry mass. Annual decomposition rates (k) were calculated using a single negative exponential decay model (Olson, 1963) by regressing the natural logarithm of the mean percent of mass remaining per plot vs. time. We tested for difference in decomposition rates (k) between riparian and upland zones using one-way ANOVA. We also examined correlations between the natural logarithm of total earthworm density, fresh or dry biomasses within total and upper 0.1 m soil depths and decomposition rate of plant litter using a regression analysis (SAS, 1987).

Results

Earthworms were dominated by the endogeic species *Pontoscolex corethrurus* Müller, whose densities and fresh and dry biomass were significantly higher in the 0–0.1 m depth than in the 0.1–0.25 m depth (Fig. 1a–c). Densities and fresh and dry biomass of anecic species, including the native species *Estherella gatesi* Borges and Moreno and exotic species *Amynthas rodericensis* Grube, did not differ between 0–0.1 m and 0.1–0.25 m depths, but earthworm densities and fresh biomass for the total number of earthworms were significantly higher in 0–0.1 m depths than in 0.1–0.25 m depths. Densities and fresh and dry biomass were significantly higher for *P. corethrurus* in upland

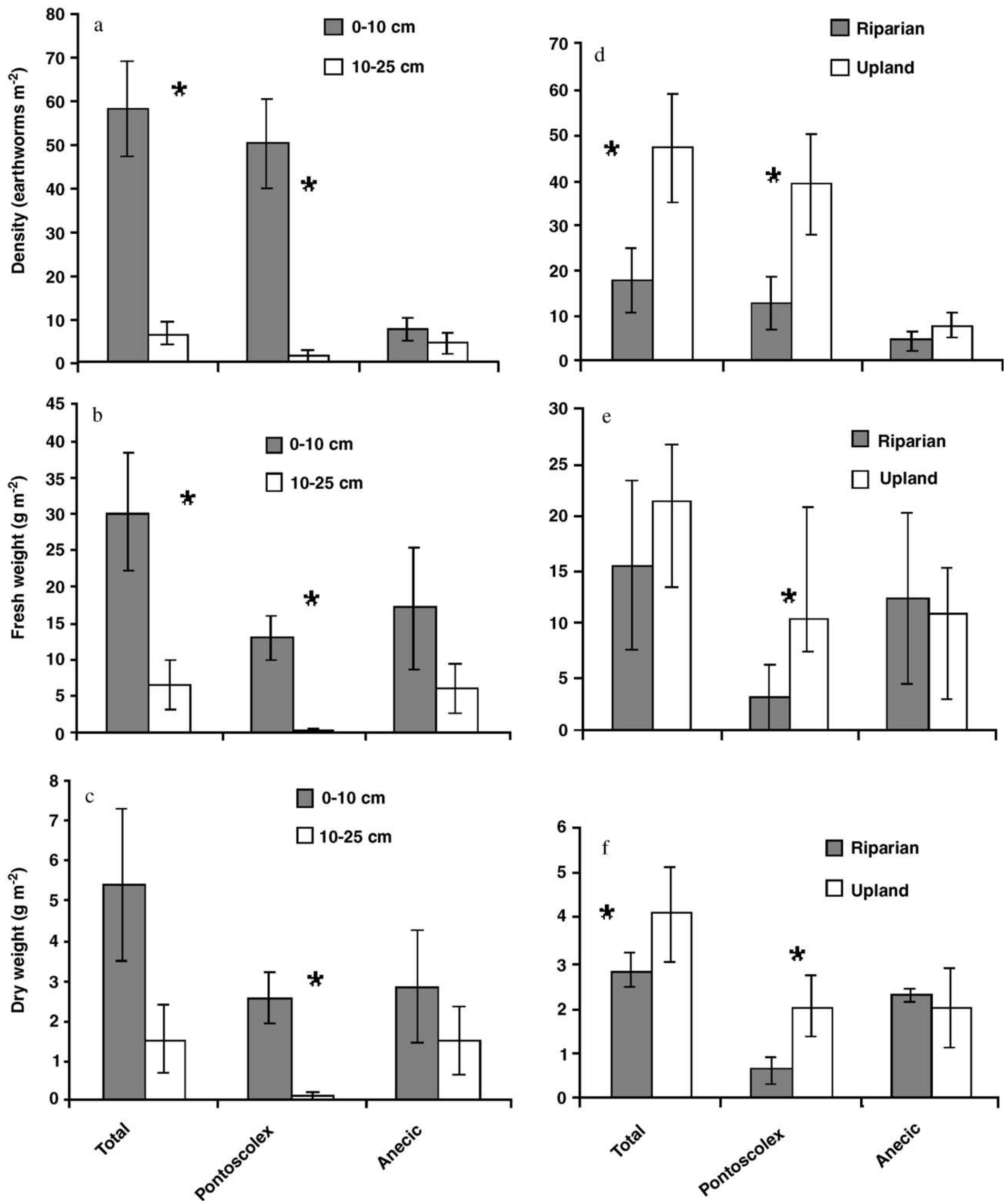

Figure 1. Means of earthworm density, fresh weight, and dry weight from both control and litter-removal treatments of total earthworms, *P. corethrurus*, and anecic earthworms in 0–0.1 m and 0.1–0.25 m depths (a–c) and between riparian and upland zones (d–f). Bars represent means with confidence intervals of 95%. Significance level: *$P<0.05$.

sites than in riparian sites (Fig. 1d–f). In contrast, densities and fresh and dry biomass of anecic species did not differ between upland and riparian sites. The density and dry biomass of the total number of earthworms were also significantly higher in upland sites than in riparian sites. Earthworm density was 77 and 64 individuals m^{-2} in the control and litter-removal treatments, respectively. Fresh and dry biomasses of earthworms were 53.9 and 13.6 g m^{-2} for the control plots and 30.5 and 5.0 g m^{-2} for the litter-removal plots, respectively. Density and fresh and dry biomass of *P. corethrurus*, anecic earthworms and total earthworm species did not differ between the litter-removal and control plots, although the dry biomass of anecic earthworms in the control plots (10.34 g m^{-2}) was three times that in the litter-removal plots (2.79 g m^{-2}). A larger sampling size may have detected the influence of litter removal on anecic earthworms.

There was a significant difference between mean annual decay rates in the riparian and upland forest sites (Fig. 2a). Upland sites ($k = 1.47$, $R^2 = 0.92$, $P < 0.05$) had a significantly higher mean annual decay rate than riparian sites ($k = 0.94$, $R^2 = 0.95$, $P < 0.05$). Litter mass decreased faster in the upland than in the riparian forest sites, especially after 180 days. The correlation between the natural logarithm of earthworm density at a depth of 0–0.1 m and decomposition rate of leaf litter was positive and linear (Fig. 2b). Upland sites had significantly higher mean annual decay rate, percentage mass loss, and earthworm densities and biomass than riparian sites.

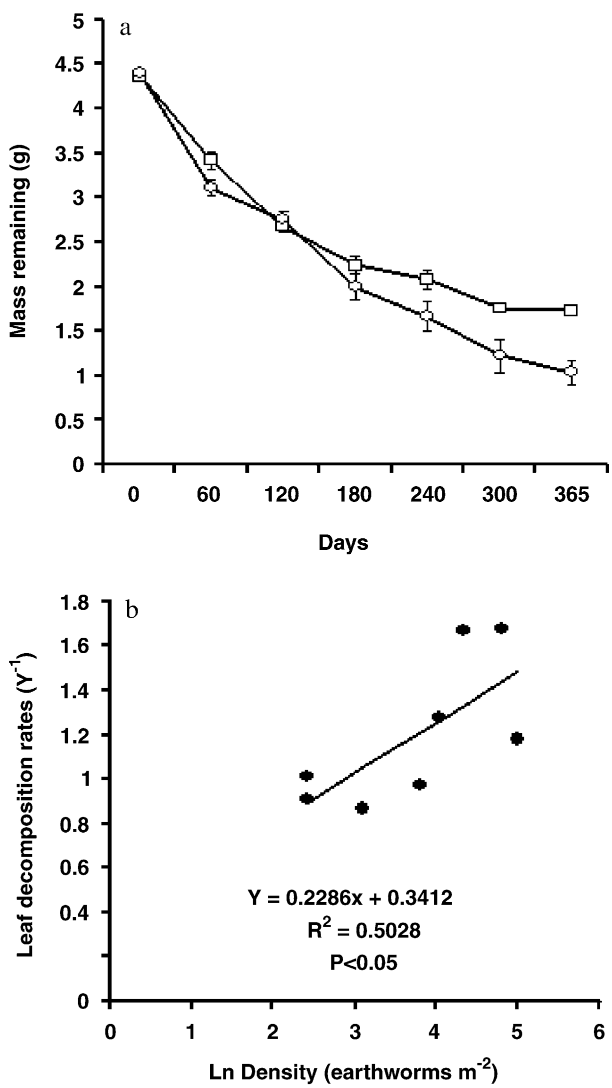

Figure 2. (a) Leaf litter decomposition in a riparian (squares) and an upland forest (circles) within a tropical wet forest of Puerto Rico, and (b) correlation between the natural logarithm (ln) values of earthworm abundance and rates of plant litter decomposition.

Discussion

Decomposition rate is determined by climate, litter chemistry, and soil biota (Swift et al., 1979; Lavelle et al., 1993). Soil biota was shown to be the main variables determining the decomposition rate in an experiment conducted in the same forest as investigated in the present study by Liu and Zou (2002). Since earthworms have the highest biomass of soil macrofauna they are one of the main contributors to soil activities in tropical wet forests (Fragoso and Lavelle, 1992). In addition to the direct consumption, earthworms accelerate plant litter decomposition through elevating soil microbial activity and enhancing the inoculation of soil microbes in worm casts to the fresh plant leaf materials (Liu and Zou, 2002). Our study found higher mean annual decay rates and percent mass lost of plant litter in the upland forest than the riparian forest. We also found that the density of earthworms in upland sites was about three times as high as in the riparian sites for both *P. corethrurus* and total number of earthworms.

We predicted that the decomposition coefficient would be positively correlated with earthworm density in the tropical wet forest. Our data support the prediction that the decomposition rate is faster in the upland than in the riparian forests and that there is a significant correlation between earthworm density in the upper 0.1 m of the soil profile and rates of plant litter decomposition. Liu and Zou (2002), by removing most earthworms from study plots, found that exotic endogeic earthworms *P. corethrurus*, the most common earthworm species found in our study, accelerate leaf decomposition. They also found that soil microbial activity was elevated by this endogeic earthworm although soil microbial biomass did not change between the earthworm reduced and control plots. Their results suggested that endogeic earthworms accelerate plant litter decomposition through elevating soil microbial activity or enhancing microbial inoculation through the production of surface earthworm casts. Direct consumption of plant litter by endogeic earthworms may be ignored because endogeic worms mostly feed on materials within mineral soil layers, not plant litter on soil surface. In a parallel study, Ruan et al. (2006) found that litter removal significantly reduced plant litter decomposition. The reduction in litter decomposition rate was accompanied by reduced soil microbial biomass in the upland area and reduced numbers of litter arthropods in the riparian area. However, both the present study and that of Ruan et al. (2006) did not examine whether litter removal altered surface cast production by endogeic earthworms. There is still a lack of direct evidence that endogeic earthworms accelerate plant litter decomposition through their production of surface worm casts.

The possible effect of the litter removal on endogeic earthworms were insignificant, because both endogeic and total earthworm densities did not differ between treatments, suggesting that short-term removal (less than 2 years) of aboveground litter has little effect on endogeic earthworm biomass and densities although litter may provide protection from sunlight, predation and soil water loss. Similar studies by Gonzalez and Zou (1999) and Sanchez-de Leon and Zou (2004) also found that endogeic earthworm densities and fresh and dry biomass did not differ significantly between control and litter-removal plots 6 and 12 months after the treatment, respectively. However, both these studies showed a tendency of reduction in anecic earthworm fresh and dry weight after litter-removal treatments. These studies suggest that the abundance of endogeic earthworms is not controlled primarily by the aboveground litter input, but more likely affected by below ground net primary productivity and soil physical and chemical properties.

Earthworms were more abundant in the upland than in the riparian zones. *Heliconia* plants were found to alter soil properties that contribute to lower densities and biomasses of earthworms in riparian zones than in upland forests dominated by *Dacryodes* trees (Gonzalez et al., 1999; Gonzalez and Zou, 1999). Furthermore, riparian soils are young Inceptisols that contain high fraction of sand and silt (Soil Survey Staff, 1995). The riparian area is frequently flooded and its soils are covered with less floor mass than upland soils. Both the high levels of sand content and frequent flooding may reduce surface casting activities by the endogeic earthworms, resulting in slow decomposition rates of plant litter in riparian areas.

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