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Soil communities and plant litter decomposition as influenced by forest debris: Variation across tropical riparian and upland sites

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Summary

Forest debris on ground surface can interact with soil biota and consequently change ecosystem processes across heterogeneous landscape. We examined the interactions between forest debris and litter decomposition in riparian and upland sites within a tropical wet forest. Our experiment included control and debris-removal treatments. Debris-removal reduced leaf litter decomposition rates in both the riparian and upland sites. Debris-removal also reduced soil microbial biomass C in the upland site, but had no effect on microbial biomass C in the riparian site. In contrast, debris-removal altered the density of selected arthropod groups in the riparian site. Litter decomposition rates correlated with both soil microbial biomass and the density of millipedes in a multiple stepwise regression model. Removal of forest debris can substantially reduce rates of leaf litter decomposition through suppressing soil activities. This influence can be further modified by landscape position. Forest debris plays an essential role in maintaining soil activities and ecosystem functioning in this tropical wet forest.

Introduction

Forest floor varies in the quantity of plant debris and this variation attributes to spatial heterogeneity of soil biota in forest ecosystems because forest debris provides them with food and shelter

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(Coleman and Crossley, 1996; Wardle and Lavelle, 1997). Soil biota plays an integral role in the decomposition processes. Recently, soil fauna has been shown to play an important role in plant litter decomposition in tropical forests (Heneghan et al., 1998, 1999; González and Seastedt, 2001; Liu and Zou, 2002). González and Seastedt (2000) demonstrated that litter decomposition rate (*k* value) was reduced by as much as 66% when arthropods were reduced using naphthalene. They further concluded that plant litter decomposition rates in tropical forests cannot be predicted in current models developed from temperate ecosystems that excluded soil biota as independent variables.

Plant litter can influence the activity of soil microbes and fauna by providing them with a food source and habitat (Zak et al., 1990, 1994; Ding et al., 1992; Bengtsson et al., 1998). Zimmerman et al. (1995) reported that the experimental removal of litter and woody debris 3 years after hurricane increased soil nitrogen availability and litterfall by 40% compared to unmanipulated control plots in a tropical wet forest of Puerto Rico. Li et al. (2005) suggested that litter removal in forests could reduce soil microbial activity and deplete the light fraction of labile carbon pools.

The influences of forest debris on leaf litter decomposition may be achieved through altering community structure and activities of soil biota as well as soil chemical and physical properties. These influences can be further modified by topography of land where ridge and slope areas are often most exposed to hurricane damages and valleys are relatively protected (Zimmerman et al., 1996). In addition, soil chemical and physical conditions may differ between ridges and valleys. In a tropical wet forest of Puerto Rico, ridge and slope areas are regarded as uplands that are typically dominated by an Oxisol, with low pH and cation concentration and with high carbon content, whereas valleys are represented by riparian soils with higher pH values and cation contents and with lower carbon levels (Scatena and Lugo, 1995; Soil Survey Staff, 1995). Compared to upland zones, riparian soils are often water-saturated, and periodically flooded. These differences in soil chemical and physical properties between riparian and upland sites may result in variations in soil activity (Badejo and Van Straalen, 1993; Willig et al., 1996). For example, Ettema et al. (1999) reported that soil microbial C and respiration in riparian sites were significantly higher than in upland sites. Riparian soils are recognized to provide ecosystem services disproportionate to their relatively small land area (Scatena, 1990; Frangi and Lugo, 1991; Fennessy and Cronk, 1997) and as ecological hot spots linking upland with aquatic systems (McClain et al., 2003).

We designed this study to examine the interactions between forest debris and leaf litter decomposition in riparian and upland sites within a tropical wet forest of Puerto Rico. Our overall hypothesis is that forest debris plays a central role in maintaining soil activity and ecosystem functioning. We predicted that removal of forest debris will result in reduction in the rates of plant litter decomposition through suppressing soil activity, and that the magnitude of this reduction in decomposition rates and soil biota will be greater in upland than in riparian sites because carbon and nutrient input can be supplemented through subsurface water in the latter. We further predict that plant litter decomposition rates will correlate with soil microbial biomass and litter fauna in the tropical wet forest.

Materials and methods

Study sites and experimental design

This study was conducted in riparian and upland sites within a tabonuco forest at El Verde Field Station (18°20′N, 65°49′W) in the Luquillo Experimental Forest (LEF) of Puerto Rico. The vegetation was classified as a subtropical wet forest. The forest is dominated by tabonuco trees (*Dacryodes excelsa*). Elevation of the tabonuco forest ranges from 300 to 600 m above sea level. Mean monthly temperature varies from 20.8 to 24.4 °C with a mean annual precipitation of 3456 mm.

On September 21 of 1998, a category 2 hurricane, Georges, struck the LEF with a maximum wind speed of 185 km h^{-1}. We started our experiment 7 months after the passage of Georges. Freshly senesced leaves were collected in April of 1999. Leaf litterbags were constructed and placed in the field in May. We established a total of eight blocks with two plots (2 × 2 m in size) in each block along a slope from ridge top to stream bank in the tabonuco forest, of which four blocks were located in riparian sites near a stream and four in upland sites that include both ridge and slope areas (Ruan et al., 2004). Two treatments were randomly assigned to the two plots within each block: control and debris-removal. For the debris-removal plots, existing debris (averaged 450 g m^{-2}) from both pre-hurricane and post-hurricane input was removed on April 17, 1999. The removal of pre-hurricane debris represents the extreme bare soil conditions in heterogeneous landscape in the forest. To prevent

Table 1. Species composition and weight (g) of air-dried leaf litter in litterbags that represent the main tree species composition of natural litterfall in April 1999 from both the riparian and upland sites within a tropical wet forest of Puerto Rico.

Species	Riparian (g)	Upland (g)
Tabebuia heterophlla (DC.) Britton	0.5	
Prestoea montana (R. Grah.) Nichols.	0.4	
Byrsonima spicata (Cav.) HBK	0.4	
Inga laurina (Sw.) Willd.ex L.	0.2	
Sapium laurocerasus Desf.	0.2	
Buchenavia capitata (Vahl) Eichl.		0.6
Dacryodes excelsa Vahl		0.4
Homalium recemosum Jacq.		0.4
Guarea guidonia (L.) Sleumer		0.3
Sloanea berteriana Choisy		0.2
Other species	0.6	0.8
Total	2.3	2.7

The common mixed-species litterbags were used for a decomposition experiment in both riparian and upland sites.

post-hurricane debris input that remained in the canopy and the subsequent new litterfall, a tent of netting was built with PVC tubes 1.5 m above ground over the debris-removal plots.

Plots in the riparian area were established within 5–20 m from a perennial stream, the Quebrada Prieta. Soils in the plots are alluvial in origin, dominated by Inceptisols (Soil Survey Staff, 1995), and are poorly drained. Tree species composition in the riparian site is dominated by *Prestoea montana* (Graham) Nicholson, *Inga laurina* (L.), *Tabebuia heterophylla* (DC.) Britton, and *Byrsonima spicata* (Cav.) HBK (Table 1, see González and Zou, 1999).

Plots in the upland area were located at the upper slope above the stream. Soils of the area are a complex of Ultisols and Oxisols and are well-drained. The plots in the upland site were approximately 20–30 m above and at least 50 m away from the stream. Tree species composition was dominated by *Dacryodes excelsa* Vahl., *Buchenavia capitata* (Vahl) Eichl., *Homalium racemosum* Jacq., *Guarea guidonia* (L.) Sleumer, and *Sloanea berteriana* Choisy (Zou et al., 1995; Thompson et al., 2002).

Decomposition experiment

A common mixed-species litterbag (20 × 20 cm with 1.5 mm mesh openings) was used for the decomposition experiment in both riparian and upland sites. A total of 224 litterbags were constructed using plastic window screens, and filled with a mixture of air-dried and newly senesced fresh leaf litter collected from the riparian and upland areas (Zou et al., 1995). This fresh leaf litter represented the main tree species composition in natural litterfall in April (Table 1). Tree species composition of litterfall was determined using leaffall collected from the 4 m^2 tent above the debris-removal plots. Leaves of the five most common species from each of the riparian and upland sites, representing 81–85% of the total fresh leaf-fall 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 of 5 g air-dried leaf material (4.6 g mean oven-dried mass) in each litterbag. Initial leaf litter chemistry for C, N, and P contents was 51.3%, 1.57% and 0.57 mg g^{-1}, respectively (González and Zou, 1999; Liu and Zou, 2002).

The decomposition experiment was initiated in May 1999 and continued until May 2000. Litterbags were placed onto forest floor inside each plot. Two randomly selected litterbags were collected after 0, 60, 120, 180, 240, 300, 360 days in the field from each plot with a total of eight litterbags from the riparian or upland sites at each collection date for each of the control and debris-removal treatment. Fine live roots and soil that had entered the litterbags were carefully removed in the laboratory. The remaining litter in each litterbag was oven-dried at 70 °C for 72 h and weighed to determine dry mass loss.

Soil biota and physical properties

Soil microbial biomass was estimated using a modified chloroform-fumigation–incubation procedure (Jenkinson and Powlson, 1976; Liu and Zou, 2002; Ruan et al., 2004) each month from May 1999 to July 2000. Six cores (1.89 cm in diameter) were collected from each plot to a depth of 10 cm and combined to form a composite soil sample. The soil was homogenized by hand kneading of the sample bags. Small rocks, roots, macro-fauna, and plant roots were removed carefully. Two subsamples of 30 g each were obtained from each soil sample for the control and fumigation treatment. We fumigated the soils for 24 h under field moisture condition in ambient room temperature. A subsample of 10 g of soil was oven-dried at 105 °C for 24 h to determine soil moisture content.

Litter arthropods were extracted from litterbags collected after 120, 180, 240, 300 days in the field using Tullgren funnels (Crossley and Blair, 1991; Coleman et al., 1999). This extraction technique can remove mites and collembolans from the litterbags and allows for a conservative estimate of other arthropods such as Diplopoda, Chilopoda, Isopoda and Protura (González and Seastedt, 2001). Arthropods were classified into broad taxonomic units according to their ecological roles and for convenience (Heneghan et al., 1999; González and Seastedt, 2001).

Soil temperature was measured monthly with a digital soil thermometer that was vertically inserted 10 cm into soil in each plot. Soil bulk density was estimated using six soil cores collected to a depth of 10 cm from each plot. Soil moisture content was estimated monthly by oven-drying a 10 g subsample of field moist soil at 105 °C for 24 h. Soil pH was determined by an AB15 pH meter using a 1:1 ratio of fresh soil to deionized water (Liu and Zou, 2002).

Data analyses

Annual decomposition rates (k) were calculated using a single negative exponential decay model (Olson, 1963) for data averaged from two litterbags for each plot by treatment and location. Soil microbial biomass was calculated using the following formula (Jenkinson and Powlson, 1976) as $B = F/K$, where B is soil microbial biomass carbon in $mg\,C\,g^{-1}$ soil, F is CO_2-C evolved from the fumigated soil less that evolved from the unfumigated soil and $K = 0.45$, the fraction of the biomass C mineralized and absorbed as CO_2 during incubation.

A two-way repeated-measure MANOVA (GLM) was used to test for differences in mass remaining between treatments (control vs. debris-removal) and sites (upland vs. riparian) at each collection date (SAS Institute and Inc., 1990). Because of the large variation among blocks, we did not use the two-way ANOVA to examine for differences between sites or treatments on dependent variables. Instead, we used a paired comparison t-test to detect treatment effects at each site, and a one-way ANOVA to test for differences of between riparian and upland sites for each treatment. These dependent variables included soil microbial biomass, relative density and relative abundance of individual litter arthropod groups, soil bulk density, soil moisture, soil pH, and soil temperature. A linear regression analysis was performed between leaf litter decomposition rates and soil microbial biomass for each treatment at each site. To predict decomposition rates, we performed a multiple regression analysis using soil microbial biomass (annual means) and the relative density of litter millipedes (averaged from four collection dates) as independent variables. Relative density of millipedes was calculated as the ratio of millipede individuals to grams of litter mass remaining (González and Seastedt, 2001). Relative abundance of an arthropod group was defined as percent of individuals for that group to total individuals for all arthropod groups. Data were log-transformed when the assumption of normality was violated prior to statistics analysis; 0.05 was accepted α value.

Results

Leaf litter decomposition

For both riparian and upland sites, debris-removal reduced leaf litter decomposition rates, but the influence was more pronounced in the upland than in the riparian sites (Fig. 1). The control treatments had annual decay rates (k) that were 1.90- and 1.27-fold those of the debris-removal treatments in the upland and riparian sites, respectively. Mean leaf litter turnover time increased from 0.92 to 1.17 years after debris-removal in the riparian site, and from 0.75 to 1.42 years in the upland site. Annual mass losses of leaf litter were significantly higher in the control treatments at both sites. The significant treatment

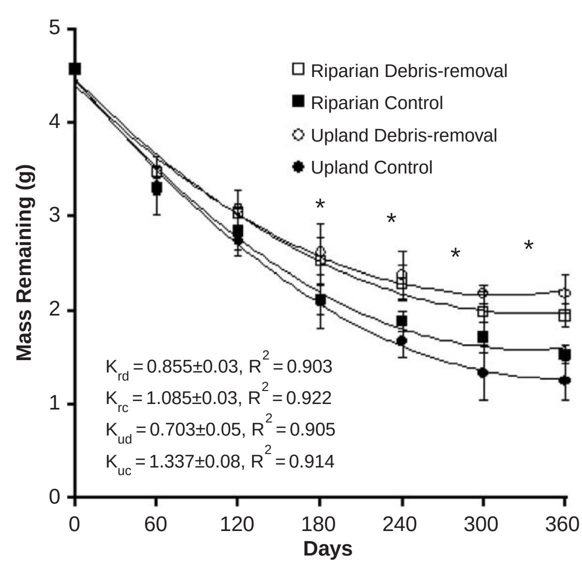

Figure 1. Leaf litter decomposition in a riparian and an upland site within a tropical wet forest of Puerto Rico. Values were averaged from four replicates. "*" indicates a significant difference in mass remaining between control and debris-removal treatments for both the riparian and upland sites (MANOVA, $P<0.05$). K values are for rd = riparian debris-removal; rc = riparian control; ud = upland debris-removal; and uc = upland control.

effects occurred after 180 days ($P = 0.006$ in upland and 0.046 in riparian) at both sites.

The mean percentage of annual mass loss of leaf litter was 5.0% higher in the riparian site than in the upland site for the debris-removal treatment, and was 5.9% higher for the control. Decomposition rates differed significantly between riparian and upland sites for both treatments. We did not find significant differences in soil temperature, soil moisture and soil bulk density either between sites or treatments. Soil pH in the riparian site was higher than in the upland site. However, there was no difference in soil pH between treatments for both riparian and upland sites (Table 2).

Soil biota

In the upland, debris-removal significantly reduced the annual mean values of soil microbial biomass C by 13.9% compared to the control. However, this was not the case in the riparian site (Fig. 2). Soil microbial biomass C did not differ between the control and debris-removal treatments in August 1999 for both the riparian and upland sites, but was consistently higher in the control than debris-removal plots after September 1999, 5 months after the initiation of the experiment. Soil microbial biomass C did not differ between riparian and

Table 2. Means (±standard error) of soil moisture, temperature, bulk density, and pH in a wet tropical forest of Puerto Rico.

Site	Treatment	Soil bulk density ($g\,cm^{-3}$)	Soil pH	Soil moisture (%)	Soil temperature (°C)
Riparian Site	Debris-removal	0.81±0.06	5.40±0.03Aa	70.08±10.41	22.08±0.12
	Control	0.83±0.05	5.38±0.04Aa	70.03±10.64	22.22±0.11
Upland Site	Debris-removal	0.77±0.02	5.06±0.01Ab	73.26±9.22	21.90±0.10
	Control	0.75±0.03	5.07±0.01Ab	75.09±9.89	22.08±0.15

Values for soil moisture, soil temperature and pH were derived from 12 collection dates averaged from four replicates (blocks), and for soil bulk density was derived from one collection date averaged from four replicates. Common upper-case letters within a column indicate no significant differences between control and debris-removal treatments, and different lower-case letters within a column indicate significant differences between riparian and upland sites for the same treatment ($\alpha = 0.05$).

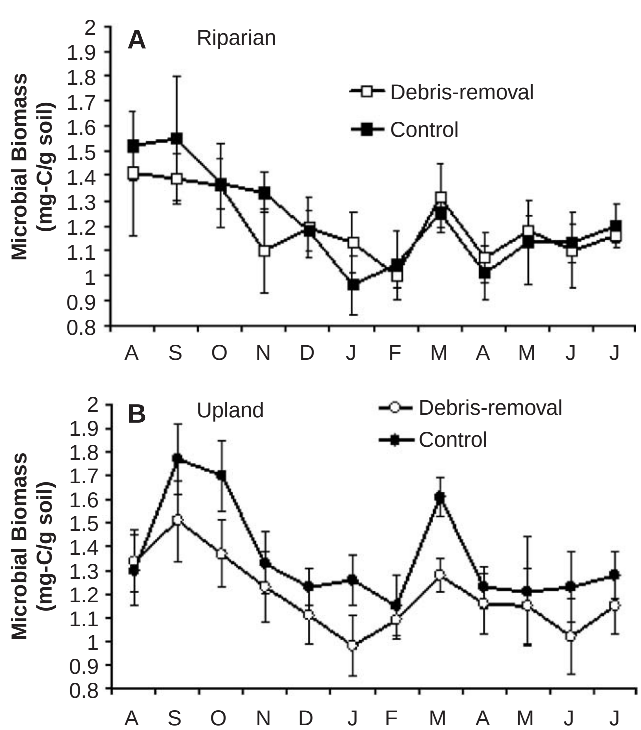

Figure 2. Annual variation in soil microbial biomass of (A) riparian and (B) upland soils within a tropical wet forest of Puerto Rico. Bars indicate ±1 standard error.

Table 3. Mean (±standard error) relative density (ind. g^{-1} dry litter) of litter fauna in litterbags in riparian and upland sites within a tropical wet forest of Puerto Rico.

Taxonomic unit	Riparian		Upland	
	Debris-removal	Control	Debris-removal	Control
Arachnid-Acari	7.17±2.13a	3.71±0.93b	5.74±2.59	7.14±2.54
Arachnid-others	2.98±0.93	2.45±0.97	2.67±1.01a	1.76±0.76b
Diplopoda	0.56±0.21a	1.36±0.73b	0.43±0.14a	1.27±0.13b
Chilopoda	0.05±0.04	0.04±0.02	0.07±0.03	0.01±0.01
Crustacea-Isopods	0.06±0.03	0.95±0.75	0.16±0.10	0.43±0.19
Crustacea-Others	0.02±0.02	0.19±0.16	0.00±0.00	0.00±0.00
Collembolla	0.42±0.20	0.35±0.15	0.13±0.07	0.69±0.32
Protura	0.29±0.18	0.73±0.25	0.04±0.03	0.22±0.11
Diptera	1.62±0.55	0.83±0.27	1.44±0.75	1.38±0.57
Coleoptera	0.09±0.03	0.14±0.01	0.01±0.02	0.19±0.16
Hymenoptera	1.65±0.46	0.75±0.01	0.74±0.24	0.72±0.21
Homoptera	0.05±0.02	0.11±0.04	0.06±0.04	0.13±0.05
Hemiptera	0.06±0.04	0.07±0.04	0.00±0.00	0.00±0.00
Others*	0.14±0.06	0.40±0.18	0.35±0.13	0.29±0.10
Total	15.16±3.46	12.08±2.45	11.84±4.25	14.23±4.20

Values were derived from four collection dates averaged from four replicates. Different letters within the same site represent significant difference in relative density between treatments ($n = 16$, $\alpha = 0.05$).
*Unknowns and immatures.

upland sites for either the control or debris-removal treatments.

Mites dominated the density of litter arthropods in both riparian and upland sites and contributed up to 68% of the total individuals (Table 3). Other arthropod groups included litter fragmentors (Diplopoda and Isopoda), predators (some species in Hymenoptera), and grazers such as Collembola (Table 3). The mean total density of litter arthropods in litterbags at the riparian site was 15.2 and 12.1 individuals per gram dry litter, and at the upland site was 11.8 and 14.2 individuals per gram of dry litter for the debris-removal and the control treatments, respectively. These values were lower than those reported by González and Seastedt (2001) probably due to variations in extraction techniques or changes after hurricane Georges. There were no significant differences in total arthropod density in the litterbags between the treatments or sites. However, Diplopoda density was significantly reduced by debris-removal treatment for both riparian and upland sites (Table 3). Its relative abundance decreased from 11% in the control plots to 2.5% in debris-removal plots in the riparian site, and from 8% in the control plots to 3% in the debris-removal plots in the upland site. In contrast, Acari increased significantly from 31% in the control plots to 47% in the debris-removal plots in the riparian site, and from 13% in the control plots to 22% in the debris-removal plots in the upland site. There was no significant difference in the total number of individuals of litter arthropods between the riparian and the upland sites for either control or debris-removal treatments.

Correlation between decomposition rates and soil biota

When data were pooled for both control and debris-removal treatments from both riparian and upland sites, leaf litter decomposition rates (k) were significantly correlated with both soil microbial biomass C (X_1 in $mg\,C\,g^{-1}$ of soil) and the relative density (X_2 in ind. g^{-1} litter) of millipedes averaged from the four collections:

$$k = 0.38 + 0.58\,X_1 + 1.04\,X_2 \quad (n = 16,\ R = 0.765,\ P < 0.05) \tag{1}$$

and

$$M = e^{-(0.38+0.58X_1+1.04X_2)t}, \tag{2}$$

where M is the percent of leaf litter mass remaining after t years.

In this multiple stepwise regression model, litter millipedes and soil microbial biomass C explained 40% and 19% of the variance in leaf decomposition rates, respectively. The interaction between millipedes and soil microbial biomass C contributed only

2% to the variation in decomposition, thus were not included in this model.

Discussion

Forest debris effects

Decomposition is an integrative process that reflects climate and microclimate conditions, litter chemistry, and soil activity. In this study, the removal of existing forest floor mass followed by exclusion of subsequent litterfall reduced plant litter decomposition rates in both upland and riparian sites, but had little influence on soil physical and chemical properties. We used the same leaf litter in both upland and riparian sites with similar climate conditions. The reduction in litter decomposition rates in response to removal of forest debris and subsequent litterfall reflects changes in soil biological activities.

In the upland site, soil microbial biomass was significantly reduced by debris-removal treatment. Litter decomposing white-rot basidiomycete mycelia dominate the upland site (Lodge et al., 1994; Lodge, 1996) where soils are Oxisols with high clay content (Soil Survey Staff, 1995). The removal of forest debris is likely to reduce the abundance of these litter decomposing fungi. Furthermore, upland soils are relatively low in soil nitrogen and phosphorus contents (Scatena and Lugo, 1995; Soil Survey Staff, 1995). The reduced plant litter input can affect soil microbial biomass through decreased nutrient availability in soils as commonly observed in agricultural systems. Ding et al. (1992) showed that fuel collection of plant leaf litter in a subtropical forest of China significantly reduced soil microbial biomass. Li et al. (2005) reported that removal of debris decreased soil microbial biomass in secondary forests and tree plantations (*Pinus caribeae*) of Puerto Rico.

In contrast, soil microbial biomass was not affected by forest debris-removal treatment in the riparian site. Riparian soils are dominated by an Inceptisol with fine to coarse texture, and are relatively rich in nitrogen and phosphorus. These soils are often flooded and saturated with water and subsequently with additional input of carbon and nutrient from subsurface water. Thus, limiting factors for microbial growth may shift from nutrients in the upland site to soil texture and anaerobic conditions in the riparian site. Silver et al. (1999) reported that oxygen contents in soil atmosphere were reduced from 20% in upland soils to $<3\%$ in riparian soils. Furthermore, litter decomposing white-rot basidiomicete mycelia are less abundant or absent in riparian site (Lodge, 1994, 1996). With the consistent supply of dissolved organic carbon and nutrients in subsurface water (McDowell and Asbury, 1994), microbial growth might be relatively less affected by the removal of forest debris.

Forest debris-removal also changed the community structure of litter arthropods. Debris-removal significantly reduced the abundance of millipedes, dominated by small-sized species less than 2 mm in diameter, in the upland site. This reduction was even more pronounced in the riparian site. Other litter fragmentors such as Isopoda also tended to decrease with the debris-removal treatment. The removal of forest debris exposed our litterbags to the ambient atmosphere and may have reduced litter moisture levels, resulting in reduction of moisture-sensitive litter fauna. In July 1999, water contents in these litterbags were 215.6% and 184.7% in the upland site control and debris-removal treatments and 253.2% and 197.9% in the riparian site control and debris-removal treatments, respectively.

Millipedes play a major role in the fragmentation of plant litter in this forest. They are dominated by small-sized species (less than 2 mm in diameter). Reduction in the millipede population can slow down litter fragmentation process, thus reducing the surface area for microbial inoculation during litter decomposition. For example, Bonkowski et al. (1998) reported that exclusion of millipedes significantly reduced plant litter decomposition in a beech forest in Germany. Furthermore, earthworm density in the upland site was twice as high as in the riparian site (González and Zou, 1999; González et al., 1999). High earthworm abundance was shown to increase plant litter decomposition rates in this tropical wet forest (Liu and Zou, 2002). In general, reduction in the abundance of litter and soil fauna has shown to reduce plant litter decomposition rates in this tropical forest (Heneghan et al., 1998, 1999; González and Seastedt, 2001; Liu and Zou, 2002).

Difference in the responses of soil biota to forest debris manipulation between the riparian and upland sites has management implications. McDowell et al. (1992) and Bowden et al. (1992) demonstrated that nitrogen loss was greater in riparian than upland sites. Nitrogen loss is mainly regulated by soil microbial activity. Our data show that the removal of forest debris in riparian soils did not alter microbial biomass. Therefore, removing of forest debris after hurricane disturbance from riparian site and depositing them to bare soils in the upland site may increase microbial immobilization of nutrients in the upland, thus reducing the relatively large loss of nitrate observed in streams after hurricane Hugo in 1989 (Schaefer et al., 2000). The export of nitrate and ammonium in streams increased by 180% and 100% during the first post-hurricane year after hurricane Hugo struck the LEF in 1989.

A model for litter decomposition at local landscape scale

While landscape position can impose influence on soil edaphic and microclimate conditions (Lavelle et al., 1993) and the levels of hurricane damages on forests (Zimmerman et al., 1996), hurricane disturbance alters plant litter decomposition rates mainly through regulating soil microbial and arthropod activities. We constructed a multiple regression model Eq. (1) to predict plant litter decomposition using soil microbial biomass and millipede relative density for the tropical wet forest in Puerto Rico including both riparian and upland sites. This regression model is further incorporated into a new decomposition model (Eq. (2)). Our analyses revealed that millipede relative density reflected 40% of the variation in litter decomposition constant (k) in the tropical wet forest, whereas soil microbial biomass explained 19% of the variation. The remaining 41% of variation reflects contribution of other soil biota on the decomposition such as earthworms (Liu and Zou, 2002). This model did not incorporate independent variables associated with climate and litter chemistry as they do not vary drastically within the wet forest.

In summary, our experiment demonstrated that forest debris plays an important role in maintaining soil microbial activity and litter arthropod diversity. While soil microbial biomass was sensitive to forest debris manipulation in upland sites, litter arthropods were more responsive to litter input in riparian sites. Reduction in microbial biomass or litter millipede density was correlated with reduction in the decomposition rates of plant litter. Our data showed that soil microbial biomass and relative millipede density were good indicators of plant litter decomposition in this tropical wet forest.

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