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RESPONSE OF MAJOR SOIL DECOMPOSERS TO LANDSLIDE DISTURBANCE IN A PUERTO RICAN RAINFOREST

Yiqing Li[1], Honghua Ruan[2], Xiaoming Zou[3], and Randall W. Myster[4]

To understand the relationship between soil biota and soil disturbance, we sampled an upper and a lower transect within each of two landslides and their adjoining forests, during both the wet and dry season in Puerto Rico. We found that the distribution of earthworms and soil microbes (e.g., fungi and bacteria) showed considerable spatial difference in these tropical landslides. We also found that endogenic earthworms (*Pontoscolex corethrurus*) occurred in all habitats (upper landslide 9.5 ± 4 No. m^{-2}, lower landslide 43.8 ± 11 No. m^{-2}, upper forest 35.7 ± 8 No. m^{-2}, and lower forest 30.5 ± 14 No. m^{-2}), but anecic earthworms (*Amynthas rodericensis*) were only found in the undisturbed forests (3.4 ± 0.6 No. m^{-2}). Total bacterial and fungal biomasses were significantly higher in the forests than in the landslides. Active bacterial and fungal biomasses were significantly higher in the lower landslide area than in the upper landslide area. For all sampled soil parameters there was a dominance of microsite variation within landslides compared with seasonal changes or differences between landslides and adjacent forests. Earthworm density and biomass correlated positively with leaf litter, light-carbon fraction, and total bacteria and negatively with fine roots, suggesting that earthworm abundance and composition in landslides were regulated by carbon pools. Earthworm abundance and community structure as well as active and total fungal and bacterial biomass may reflect soil disturbance history and soil development processes over geological time in the Puerto Rican rainforest. (Soil Science 2005;170:202–211)

Key words: Earthworms, tropical landslides, soil organic carbon, tropical forests, fungal biomass, bacterial biomass.

TROPICAL forest ecosystems have increasingly excited the interests of ecologists not only because of the high biodiversity of these ecosystems but also because of the significant influences of tropical forests to global climate change. On a global scale, the size of the tropical forest sink for CO_2 is subject to constant change as a result of anthropogenic and natural disturbances to these forests (Davidson and Ackerman, 1993; Guo and Gifford, 2002; Malhi et al., 1999). The quantification of the effects of tropical forests on the global climate change is well dependent on the comprehensive understanding of the responses of the tropical forest ecosystems to changes in disturbance regimes (Schlesinger, 1990). Landslides are a common and recurrent natural disturbance, triggered by natural forces (e.g., heavy rains and earthquakes) or associated with human activities (e.g., road construction), in mountainous regions in wet tropics (Larsen and Torres-Sánchez, 1998; Scatena and Lugo, 1995; Walker et al., 1996). For example, Hurricane Hugo triggered more than 400 landslides in northeastern Puerto Rico in 1989 (Scatena and Larsen, 1991). Human activities accelerate landslide occurrences in the tropics. One analysis on the landslides in the Luquillo Experimental Forest found more than half of the landslides between

[1]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ. Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901-8551. E-mail: yiqingli@crssa.rutgers.edu

[2]Faculty of Forest Resources and the Environment, Nanjing Forestry University, Nanjing, China.

[3]Dr. Zou is corresponding author. Xishuangbanna Tropical Botanical Garden, Kunming, Yunnan, China; and Institute for Tropical Ecosystem Studies, University of Puerto Rico, San Juan, PR.

[4]Department of Biology, University of Central Oklahoma, Edmond, OK.

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1964 and 1989 were road-related, whereas the landslides associated with road construction accounted for only 2% of all landslides before 1964 (Guariguata and Larsen, 1990).

Landslides have important landscape and ecosystem-wide effects on nutrient availability by exposing nutrient-bearing weatherable saprolite (on the upper landslide) and transporting/redistributing material and nutrients (on the lower landslide; Myster et al., 1997; Swanson et al., 1982). Landslides then set up a spatial soil sequence (upper landslide ⟶ lower landslide ⟶ adjacent rainforest) that may reflect the geologic temporal soil developmental sequence in the tropical rainforests. Landslides create new microsites with increased light and redistributed plant and soil organic matter on which the soil and litter decomposer biota feed. Although landslides are very common and one of the most severe natural disturbances in the tropics, the studies on landslides mostly focused on landslide distribution (Larsen and Torres-Sánchez, 1998), the factors triggering landslides (Guariguata, 1990), nutrient availability (Scatena, 2001; Wilcke et al., 2003) and plant successions (Myster et al., 1997; Walker et al., 1996), and there is little information on soil decomposers, such as earthworms, fungi, and bacteria, on tropical landslides.

Soil organisms are critical to soil processes and nutrient cycles because they improve soil properties, accelerate decomposition of soil organic matter (Coleman and Crossley, 1996) and buffer nutrient fluxes from the external environment (Lugo and Scatena, 1995). Within the soil biota, earthworms may be particularly important because they 1) are dominate animals in the rainforest (38% of the animal biomass [112 kg ha] in the Puerto Rican rainforest, the most of any animal group; Odum and Pigeon, 1970), 2) are often positively correlated with productivity (Lavelle, 1988), and 3) affect soil organic matter turnover, nutrient availability, soil structure, water infiltration, and aeration (Edwards and Bohlen, 1995; Lee, 1985; Liu and Zou 2002). Microorganisms probably are the main agents responsible for soil humus formation in the tropics. Bacteria, although they are small in size, are especially prominent in soils because of their large numbers. The microbial biomass within the decomposing litter of forest soils is predominantly fungal, and fungi are probably the major agents of decomposition in all acidic environments (Fisher and Binkley, 2000). Bacteria and fungi play a major role in the degradation of vast amount of forest litter, roots, animal tissue, and cells of other microorganisms in the wet tropical forests.

Consequently, to understand the relationship between landslide disturbances and soil decomposer communities, we chose two landslides in Puerto Rico of similar topography, age, size, surrounding forest composition, climate, and parent material and sampled earthworms, fungi, bacteria, and soil factors, such as soil pH, soil moisture, and soil organic carbon (SOC), to address these questions: What are the differences between upper and lower landslides and between landslide and forest in the wet and dry seasons 1) for earthworm density, biomass, and species composition? 2) for fungal and bacterial biomass? and 3) for soil pH, moisture, light carbon fraction, total carbon, ground-litter, and root biomass?

MATERIALS AND METHODS

Study Site

The study site is the Luquillo Experimental Forest of northeastern Puerto Rico (18° 20′N, 65° 45′W). The Luquillo Experimental Forest is the tropical long-term ecological research site of the National Science Foundation (Waide and Lugo, 1992), consisting of subtropical wet forest characterized by tabonuco (*Dacryodes excelsa*), ausubo (*Manilkara bidentata*), and motillo (*Sloanea berteriana*) below 600 m, palo colorado (*Cyrilla racemiflora*) and palm (*Prestoea montana*) between 600 and 850 m, and cloud forest above 850 m (Ewel and Whitmore, 1973). Two landslides (ES1 and ES2) and their adjacent forest microsites (F1 and F2) were selected for this study. Both study landslides (ES1, ES2) are located in the Rio Espiritú Santo watershed of the Tabonuco forest and are of similar age (6 years and 5 years, respectively), area (2100 m^2, 1550 m^2), elevation (both 370 m), and slope (22°, 30°; Myster and Walker, 1997; Walker and Neris, 1993). Like all landslides in the tropics, these landslides have rock and bare soil (with lose soil profile) patches in the upper portion of the landslides and both plant and soil debris deposition in the lower portion of the landslides (Myster and Schaefer, 2003). Common plant species occurring on the landslides include the fern *Cyathea arborea* and *Gleichinia bifida* in the upper area and trees *C. schreberiana*, *Miconia racemosa*, *I. vera*, and *Nepsera acuatca* in the lower area (Myster, 2002). The sites were characterized by a wet tropical climate with mean annual precipitation of 3920 mm and mean annual air temperature of 22.3 °C (Lugo, 1992). The temperature was mild and stable, with diurnal and seasonal temperature ranges of 3–4 °C. Precipitation shows a seasonal variation, with a dry season from January to March and a wet season from May to September (Fig. 1).

Field Sampling

We established two transects (25 m) in each landslide (ES) and its adjacent forest (F) in June of 1994, one in the upper landslide area (10 m from the top slip-face) and the other (lower landslide area) 50 m from the top (Fig. 2). Eight 0.5 × 0.5-m plots were randomly assigned on each transect, four in the landslide and four in the surrounding forest. Ground litter biomass was collected from each plot. The ground litter was sorted into leaf litter and wood litter by hand. The upper 25 cm of the soil was removed, and earthworms in the soil were hand-sorted and stored in a cooler (Zou, 1993). All the roots (live plus dead) from each pit were separated from soil by washing in the field, stored in plastic bags, and brought to the laboratory. Finally, two cores of soils at a depth of 25 cm for measuring soil pH, soil moisture, microbial biomass, and SOC were taken, using a PVC pipe (4.5 cm in diameter) outside the left lower corner of each plot. These two soil cores were mixed, put into a labeled zip-bag, and stored in a cooler before taking to the laboratory. All plots were sampled in June of 1994 (wet season) and again in January of 1995 (dry season). The sampled items included root biomass, ground litter, soil samples for measuring microbial biomass, soil moisture, soil pH, and SOC.

Laboratory and Data Analysis

Soil moisture contents were determined by oven-drying 10 g of fresh soil sampled at 105 °C for 48 h. Soil pH was measured with a Calomel electrode on a paste of 1:1 ratio of fresh soil and deionized water. The soil samples (100 g) used for determining C in light fraction and total C were wet-sieved through a 2-mm sieve, and stones and roots greater than 0.5 mm roots were picked out. The measurement of C in light fraction was conducted by using a density separation technique (Sollions et al., 1984). A 10-g subsample from each soil was dried in an oven at 50 °C and ground with a mortar and pestle. A 0.15-g subsample from the dried soils was analyzed for total C (Synder and Trofymow, 1984). A 1-g subsample from the dried soils was put into a beaker with 20 mL of sodium polytunstate, adjusted to a density of 1.85 g cm^{-3}. The subsamples were sonicated for 1 min and then evacuated for 10 min at −186 K pa to remove entrapped air from the soil pore space. After sitting overnight at room temperature, the light carbon fraction was removed by aspiration, trapped on a GF/A (Whatman Fiberglass) filter, and analyzed for organic C (Cambardella and Elliot, 1993).

Biomass of active and total fungi was estimated by using the agar film techniques (Lodge and Ingham, 1991). One gram of wet soil was placed in 9 mL of sterile tap water (1/10 dilution) and shaken by hand for 5 min. A 1/100 dilution was prepared by transferring 1 mL of the 1/10 dilution to 9 mL of sterile diluent. One-milliliter aliquots from each dilution (1/10 and 1/100) were transferred to test tubes and stained for 5 min by adding 1 mL of fluorescein diacetate in buffer. One milliliter of fresh molten agar was then mixed with the stained soil suspension, and an aliquot was transferred to the well of a coverslip well slide. Coverslip wells were prepared by taping two coverslips of known thickness to a microscope slide approximately 1 cm apart. A drop of agar suspension was placed on the slide between the two coverslips, and another coverslip was immediately pressed down on the agar to produce a film of known thickness. Active hyphal length was estimated on fresh agar film by using epifluorescent microscopy. The total length of hyphae was estimated on fresh films by using phase contrast microscopy. At least 20 fields were viewed along a vertical transect across the coverslip, and three transects were scanned on each slide. The hyphal length was calculated by multiplying the length of hyphae in one field by the number of fields needed to equal 1 cm^{-3} and then multiplying by the dilution of soil in the agar suspension

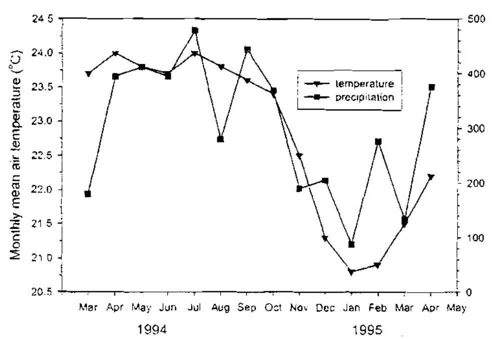

Fig. 1. Monthly precipitation and temperature in the Luquillo Experimental Forest in 1994 and 1995.

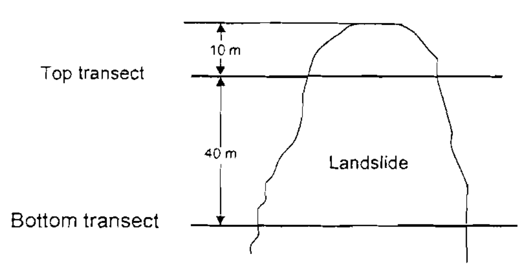

Fig. 2. Sampling strategy illustration on the two landslides in the Luquillo Experimental Forest.

(mL g^{-1} soil). Biomass of active and total bacteria was obtained by using fluorescein isothiocyanate techniques (Babiuk and Paul, 1970; Zou and Bashkin, 1998). Twenty grams of soil samples were placed into a Waring blender containing 190 mL of sterile distilled water and shaken for 15 min by hand. Subsamples were removed for either plate counting or direct microscopy. Prepared soil smears were stained for 4 min with fluorescein isothiocyanate solution and then washed in 0.5 mol/L sodium carbonate buffer for 10 min and in 5% sodium pyrophosphate for 2 min. The smears were mounted in glycerol (pH 9.6) and observed with a microscope equipped with a mercury lamp and a barrier filter. The dispersed soil was diluted to a required dilution (10^{-4}, 10^{-5}, and 10^{-6} g of soil mL^{-1} water), and 0.1-mL portions were spread on the solidified agar. Five plates were used for each dilution. These plates were incubated for 2 weeks at 21 °C before counting the bacterial and actinomycete colonies.

Ground litter (leaves and twigs < 2 mm) was placed in an oven at 60 °C for 96 h. Root samples used for biomass determinations were washed again and separated into two diameter classes (>5 mm and < 5 mm), using the definition of fine root by Gower (1987). These root samples were placed in an oven at 75 °C for 1 week; afterward, the dry biomass was weighted. Earthworm number accounting and species identification were carried out at the same date as the field sampling occurred. Earthworms were rinsed, identified to species (Gonzalez et al., 1996; Zou and Gonzalez, 1997), and weighted after drying with paper towels. We used Scheffé's multirange test for significant differences in density and biomass of earthworms and soil variables in landslides and their adjacent forests. To examine any relationships between earthworms and the other factors, we computed Pearson product-moment correlation coefficients (SAS, 1999).

RESULTS AND DISCUSSION

Earthworms

Both the density and the biomass of earthworms in the upper landslide areas were significantly ($P \leq 0.05$) lower than in the lower landslide areas and in the upper and the lower areas of

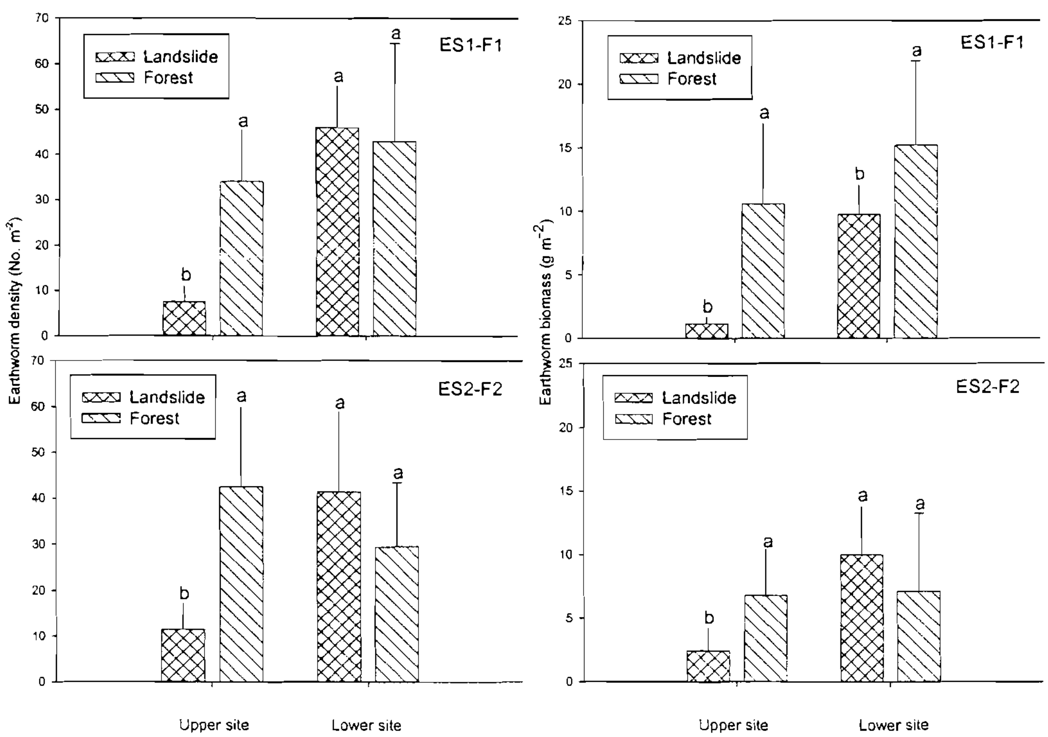

Fig. 3. Mean value (standard deviation) of earthworm density and biomass in landslides (ES1 and ES2) and adjacent forests (F1 and F2). Common letters within each topographical location (upper and lower site) indicate no significant difference between the landslide and the forest ($\alpha = 0.05$) by Scheffé's multiple range test. Means were averaged from the wet season and the dry season ($n = 8$). LF: soil organic carbon in light fraction.

TABLE 1
Density (No. m^{-2}) and biomass (g m^{-2}) of earthworm *P. corethrurus* in landslides and forests in dry and wet seasons

	Density (No. m^{-2})	Biomass (g m^{-2})
Upper ES	9.5 (4) c	1.8 (0.7) c
Lower ES	43.8 (11) a	9.9 (3.5) a
Upper F	35.7 (8) b	6.4 (1.5) ab
Lower F	30.5 (14) b	6.1 (2.4) b

Common letters within a column indicate no significant difference ($P = 0.05$) by Scheffe's multiple range test ($n = 8$).

their adjacent forests in ES1-F1 and ES2-F2 study sites (Fig. 3). The density and biomass of earthworms did not significantly ($P \leq 0.05$) differ between the lower landslide areas and adjacent forests with the only exception in ES1-F1 site.

Because the density and biomass of earthworms performed the same patterns in the dry and wet seasons, we illustrated the results in the total by averaging the two sites in the wet and dry seasons (Table 1). We found that the density of the soil feeding endogenic earthworm species *P. corethrurus* in the lower landslide areas was significantly higher than in the upper landslide areas, in the upper forest areas, and in the lower forest areas. Earthworm biomass of *P. corethrurus* also showed significantly higher levels in the lower landslide areas than in upper landslide areas, in the upper forest areas, and in the lower forest areas. Earthworms of the litter feeding anecic species *A. rodericensis* were not found in the landslides. The density of *A. rodericensis* was significantly greater in the lower forest areas (8 ± 3.5 No. m^{-2}) than in the upper forest areas (2.5 ± 1.5 No. m^{-2}) by averaging the two sites and the wet and the dry season.

Earthworms play a critical role in the processes of soil development and fertility because of their burrowing and casting activity and the burial of organic materials, which enhance humus formation and differentiation of soil profiles (Feller et al., 2003). Although soil microorganisms are the primary agents of decomposition, breaking down plant and animal residues into useable nutrients for plants and other soil organisms, earthworms especially contribute to the breakup of larger plant organic matter by their feeding activities. In this study, earthworm abundance was lower in upper landslide areas than in lower landslide areas and undisturbed forests, suggesting that earthworm density may relate to plant and soil organic matter quantity in the disturbed soils. Our result that anecic earthworms were absent in landslide areas where the levels of ground litter mass and soil C were low and the ground litter (mostly ferns, grasses, and pioneer species) was different from the forests suggests that earthworm species distribution could be regulated by litter quantity and/or quality. A litter removal experiment in the same forest showed a decrease in anecic earthworm fresh weight within 6 months (Gonzalez and Zou, 1999). Annual litterfall in the rainforest reaches 912 g m^{-2} y^{-1} (Zou et al., 1995), but is an order of magnitude lower in ES2 (Myster and Schaefer, 2003). Whereas both kinds of earthworms feed on soil organic matter, anecic earthworms also feed on plant litter on the soil surface. The difference in earthworm species between landslide and forest (lack of anecic earthworms in landslides) is likely due to the low carbon input from aboveground plant communities that was destroyed by the severe landslide disturbance.

Microbial Biomass

Microbial biomass also showed significant differences between the upper and lower areas of the landslides and between the landslides and their adjacent forests in both ES1-F1 and ES2-F2 study sites (Table 2). Total fungal biomasses in the forests were

TABLE 2
Mean microbial biomass (standard deviation) in landslides (ES1 and ES2) and adjacent forests (F1 and F2)

Sites	Active fungi (mg kg^{-1} soil)	Total fungi (mg kg^{-1} soil)	Active bacteria (mg kg^{-1}soil)	Total bacteria (mg kg^{-1} soil)
ES1-F1				
Upper ES1	83.9 (34.1) ab	648.5 (77.5) c	17.2 (7.1) a	38.4 (11.8) b
Lower ES1	69.8 (29.2) b	881.5 (102.5) b	18.9 (3.3) a	34.3 (4.1) b
Upper F1	81.4 (27.5) ab	1046 (290.5) a	19.3 (5.2) a	72.9 (26.1) a
Lower F1	101.6 (33.1) a	1124 (263.7) a	18.4 (5.9) a	67.1 (11.0) a
ES2-F2				
Upper ES2	32.6 (17.1) b	451.4 (124) c	10.4 (1.9) b	37.0 (13.7) c
Lower ES2	55.4 (13.2) a	575.6 (154) b	21.5 (6.3) a	53.6 (12.4) b
Upper F2	61.4 (18.2) a	983.1 (208) a	16.6 (7.7) a	66.6 (20.5) ab
Lower F2	55.3 (23.3) a	981 (179.4) a	18.7 (5.2) a	70.3 (16.2) a

Common letters within a column in each site indicate no significant difference ($\alpha = 0.05$) by Scheffe's multiple range test ($n = 8$).

TABLE 3

Mean values (standard deviation) of biotic and abiotic environmental variables in landslides (ES1 and ES2) and adjacent forests (F1 and F2)

Sites	pH	Soil moisture (%)	LF g C kg^{-1} soil)	Total SOC (%)	Ground leaf litter (g m^{-2})	Ground wood litter (g m^{-2})	>5 mm root (g m^{-2})	<5 mm root (g m^{-2})
Dry season								
ES1-F1								
Upper ES1	5.12 (0.20) a	61 (1) a	0.38 (0.30) b	4.2 (0.6) b	55 (21) b	30 (20) a	8.8 (2.5) b	13.9 (3.5) c
Lower ES1	5.43 (0.06) a	63 (4) a	0.60 (0.70) b	8.8 (1.3) a	63 (16) b	34 (17) a	19.9 (4.1) b	33.7 (6.9) b
Upper F1	5.06 (0.26) a	52 (4) b	6.49 (2.80) a	9.7 (0.9) a	114 (15) a	15 (9) b	111.0 (30) a	59.0 (10.6) a
Lower F1	5.10 (0.30) a	55 (3) ab	6.85 (2.50) a	10.2 (1.6) a	117 (26) a	25 (5) a	109.0 (29) a	48.8 (18.0) a
ES2-F2								
Upper ES2	5.21 (0.50) b	58 (7) a	0.49 (0.06) b	3.1 (0.5) c	20 (8) b	5 (2) b	11.3 (7.2) b	38.0 (21.1) b
Lower ES2	5.82 (0.33) a	53 (2) a	0.36 (0.06) b	6.7 (0.7) b	69 (20) a	20 (8) a	18.0 (7.6) b	64.5 (20.0) a
Upper F2	4.40 (0.28) c	61 (2) a	9.68 (4.20) a	12.8 (1.9) a	104 (33) a	33 (14) a	116.0 (42) a	65.0 (16.3) a
Lower F2	4.73 (0.13) bc	56 (8) a	7.47 (4.80) a	11.3 (1.6) a	102 (29) a	28 (6) a	128.0 (43) a	75.0 (11.8) a
Wet season								
ES1-F1								
Upper ES1	5.22 (0.30) a	68 (14) a	0.56 (0.20) c	3.8 (0.7) b	38 (13) b	6 (2) b	8.4 (1.8) c	14.0 (9.6) b
Lower ES1	4.93 (0.14) a	67 (5) a	1.76 (0.30) b	8.4 (1.1) a	75 (23) a	24 (8) a	26.3 (12.0) b	36.4 (8.0) a
Upper F1	5.11 (0.08) a	56 (3) b	5.90 (2.10) a	10.8 (0.7) a	109 (22) a	32 (12) a	89.0 (12) a	44.3 (12.0) a
Lower F1	4.89 (0.40) a	58 (2) b	6.20 (1.90) a	13.2 (1.3) a	99 (15) a	27 (16) a	102.0 (42) a	45.6 (16.0) a
ES2-F2								
Upper ES2	4.51 (0.20) b	74 (5) a	0.43 (0.20) b	2.6 (0.8) b	34 (21) b	13 (4) b	21.0 (1.6) b	23.0 (12.1) b
Lower ES2	4.92 (0.10) a	68 (7) a	1.11 (0.40) b	8.9 (1.3) a	67 (18) a	14 (5) b	28.0 (2.4) b	18.0 (10.3) b
Upper F2	5.04 (0.08) a	56 (4) b	6.20 (2.40) a	11.2 (1.6) a	87 (32) a	29 (4) a	93.0 (32.0) a	44.0 (14.0) a
Lower F2	5.10 (0.30) a	58 (2) b	6.90 (1.30) a	10.5 (1.8) a	75 (34) a	33 (16) a	88.0 (26.0) a	36.9 (21.0) a

Common letters within a column in each site indicate no significant difference ($P = 0.05$) by Scheffe's multiple range test ($n = 4$). LF: soil organic carbon in light fraction.
a: Abiotic; b: biotic.

significantly greater than in the landslides in both the sites. There was also a significant difference between the lower landslide areas and the upper landslide areas, with a higher value in the lower landslide areas. Active fungal biomass between landslides and forests and between the upper landslide areas and the lower landslide areas were not as consistent as the total fungal biomass. However, the value of active fungal biomass in upper landslide area was significantly lower than the lower landslide area and the forests in ES2-F2. Total bacterial biomass was significantly greater in the forest than in the landslide in ES1-F1, whereas it did not differ among the lower landslide area and the forests in ES2-F2 site. Active bacterial biomass in the upper landslide area was significantly lower than the lower landslide area and the forests in ES2-F2, but there was no difference in ES1-F1. We did not find clear seasonal patterns of microbial biomass in the two sites.

Soil microorganisms were particularly important to increasing soil fertility and accelerating the revegetation process in disturbed soils (Veblen, 1989; Walley et al., 1996). Higher microbial biomass in the lower areas than in the upper areas of the landslides suggests that landslide disturbance altered the composition of microbial biomass, as suggested by Singh et al. (2001) in a study of the disturbed soils in a tropical forest in Nepal Himalaya. A number of studies have shown that newly formed landslides exhibit low soil nutrients, absence of advance regeneration due to impoverished seed bank, and possibly a lack of mycorrhizal inoculum (Dalling and Tanner, 1995). Wilcke et al. (2003) reported that lower areas of landslides had greater concentration of most nutrients than those in the upper areas of landslides, based on a study of the landslides in montane rainforest, Ecuador. Our result of lower microbial biomass in the upper landslides suggests that microbial biomass might closely relate to carbon and nutrient availability. The result that total fungal biomass was higher in the lower landslide areas, where earthworms were also abundant, suggests that earthworms may prefer feeding on other decaying organic substances to feeding on fungi in disturbed soils.

Soil Properties

The upper landslide areas in both ES1-F1 and ES2-F2 study sites in the two seasons had significant lower values in total SOC, C in light fraction, ground leaf litter, ground wood litter, roots greater than 5 mm, and roots greater than 5 mm (Table 3). Soil pH in the upper landslide areas did not show patterns similar to the other variables except in ES2 in wet season, with a significant lower value than the lower landslide area and the upper and the lower areas of the forest. Soil moisture in the upper landslide areas in both ES1-F1 and ES2-F2 in the wet season was significantly greater than in the forests. The lower landslide areas did not differ from the forests in total SOC, with the only exception in ES2-F2 in the dry season, whereas the C in light fraction in the lower landslide areas was significantly smaller than the upper and the lower areas of the forests (Table 3). The root biomass greater than 5 mm in the lower landslide areas was significantly lower than the forests but did not differ from the upper landslide areas in both ES1-F1 and ES2-F2 study sites. Soil moisture in the lower landslide areas in ES1-F1 and ES2-F2 in the wet season was significantly greater than the forests, whereas the soil pH did not differ from the upper landslide areas and the forests except in the ES2-F2 in dry season, with a significantly greater value than the upper landslide areas and the forest.

The disruption of soil-plant systems caused by landslides in the tropics resulted in loss of suface soil organic matter and decline in the concentration of available nutrients (Singh et al., 2001). Our results of soil properties within a landslide and between the landslides and the forests suggest that landslides exhibit a strong environmental heterogeneity in tropical zones. Our finding on SOC in the landslides and the adjacent forests is consistent with the some other observations by Dalling and Tanner (1995), Walley et al., (1996), Singh et al., (2001), and Wilcke et al. (2003) that SOC and/or nutrients are generally higher in the adjacent forests than the landslides and also higher in the lower areas than in the upper areas of the landslides.

Correlations

Both the density and biomass of earthworms of the two species were positively and significantly correlated with total SOC, ground leaf litter, and total bacteria in the landslides and the forests in ES1-F1 and ES2-F2 with a few exceptions, whereas no correlations were found between the earthworms (in both density and biomass) and soil pH, soil moisture, and total fungal biomass (Table 4). Negative correlations were observed between the earthworm (in density and biomass) of *P. corethrurus* and fine roots (<5 mm) in the wet season. Carbon in light fraction was positively correlated with the density and biomass of species *A. rodericensis* but did not correlate with the density and biomass of species *P. corethrurus*, regardless of season.

Our results showing a correlation between earthworms and the soil light carbon fraction coupled with past results that showed a correlation be-

TABLE 4

Correlation coefficients for earthworms and soil biotic and abiotic variables in wet and dry season (n = 32)

Sites	pH	SM (%)	LF (g C kg^{-1} soil)	Total SOC (%)	Ground leaf litter (g m^{-2})	<5 mm root (g m^{-2})	Total fungi (mg kg^{-1})	Total bacteria (mg kg^{-1})
Dry season								
P. corethrurus								
Density	−0.09	−0.08	0.17	0.4*	0.27	0.36*	0.17	0.06
Biomass	0.15	−0.15	0.02	0.36*	0.2	0.4*	0.19	0.41*
A. rodericnesis								
Density	−1.1	−0.22	0.36*	0.27	0.45*	0.36*	−0.09	0.58†
Biomass	−0.02	−0.26	0.36*	0.22	0.5*	0.28	−0.04	0.59†
Wet season								
P. corethrurus								
Density	0.09	−0.1	0.24	0.47*	0.46*	−0.48*	0.18	0.26
Biomass	0.16	−0.27	0.28	0.41*	0.51†	−0.51*	0.08	0.34*
A. rodericnesis								
Density	−1.11	−0.11	0.46*	0.45*	0.95†	0.03	0.13	0.21
Biomass	0.1	−0.26	0.31*	0.47*	0.43*	0.02	0.04	0.39*

Statistics incorporate data from both landslides and forests at both locations. SM: soil moisture, LF: SOC in light fraction. Significant level, * 0.01< $P \leq 0.05$; † ≤ 0.01.

tween earthworm biomass and amount of litter (Gonzalez and Zou, 1999), fine roots (Sanchez et al., 2003), or SOC levels (Zou and Bashkin, 1998) point to the potential importance of landslide litter decomposition and landslide soil carbon availability. Myster and Schaefer (2003) found in a ES2 litter decomposition study that organic matter declined to near 50% levels in 16 weeks with these significant species differences found after 4 weeks (*Miconia sp.* < *Cecropia schreberiana* < *Dacroydes excelsa*). In addition, total soil carbon levels (ranging from 0.29 to 7.11% of soil mass) were significantly smaller in the upper ES2 landslide plots compared with lower ES2 plots (Myster and Fernández, 1995). Indeed, the development of soil organic matter during landslide succession may be the dominant process controlling nutrient availability (Zarin and Johnson, 1995) and, consequently, the results showing earthworm interactions with carbon may be reflecting general processes of soil development and fertility. Further in the humid tropics, earthworms may have a predominant effect of regulation of soil organic matter (Lavelle et al., 1993). For example, earthworms create structures, casts, and galleries, which modify the circulation and accumulation of water and gasses in soils that may further affect the decomposition of soil organic matter in the long term (Tisdall and Oades, 1982).

Barois and Lavelle (1986) reported that microorganisms were stimulated in tropical endogeic earthworm gut and casts due to the addition of intestinal mucus. In this study, earthworms (both in density and biomass) of the two species were highly correlated with total bacterial biomass. This finding might reflect the strong interactions between earthworms and bacteria in the soil decomposition processes. To our surprise, we did not find any correlations between earthworms (in density and biomass) of the two species and the fungal biomass in both wet and dry seasons in this study. This observation may indicate that bacteria play a more important role in the interaction with earthworm activity than the fungi in the Neotropical forests and landslides.

The community structure of earthworms also indicated past disturbance history in this tropical wet forest. Anecic earthworms were present only in the undisturbed areas of the forest and were absent in landslide areas even 6 years after disturbance. However, the invasive endogeic earthworm *P. corethrurus* was a rapid colonizer in the disturbed landslides. Other disturbance studies suggested that the recovery of anecic earthworms in abandoned tropical pastures often took more than 20 years (Sanchez et al., 2003; Zou and Gonzalez, 1997).

CONCLUSIONS

We studied the landslides only in the dry and the wet season within a year, and this limited observation prevented us from drawing a general conclusion on biotic and abiotic changes of tropical landslides. However, our finding that landslides performed large spatial difference in earthworm species composition, density, biomass, and correlations with other biotic and abiotic factors implies that landslide positions may illustrate different stages of soil disturbance in tropics. Landslides removed most soil organic materials at the upper landslide and redeposit plant and soil organic matter at the lower landslide, though some residual organic matter from plant primary production before the landslide event would be incorporated into soil subsurface layers. This results in considerable differentiation in the activities of earthworms and microbes within a landslide or between landslide and forest suggest that landslides in tropics could possibly be an indicator of soil development over geological time.

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