Ecosystems (2005) 8: 928–940
DOI: 10.1007/s10021-005-0047-0

ECOSYSTEMS

Plant Communities, Soil Microorganisms, and Soil Carbon Cycling: Does Altering the World Belowground Matter to Ecosystem Functioning?

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Abstract

Soil microorganisms mediate many critical ecosystem processes. Little is known, however, about the factors that determine soil microbial community composition, and whether microbial community composition influences process rates. Here, we investigated whether aboveground plant diversity affects soil microbial community composition, and whether differences in microbial communities in turn affect ecosystem process rates. Using an experimental system at La Selva Biological Station, Costa Rica, we found that plant diversity (plots contained 1, 3, 5, or > 25 plant species) had a significant effect on microbial community composition (as determined by phospholipid fatty acid analysis). The different microbial communities had significantly different respiration responses to 24 labile carbon compounds. We then tested whether these differences in microbial composition and catabolic capabilities were indicative of the ability of distinct microbial communities to decompose different types of litter in a fully factorial laboratory litter transplant experiment. Both microbial biomass and microbial community composition appeared to play a role in litter decomposition rates. Our work suggests, however, that the more important mechanism through which changes in plant diversity affect soil microbial communities and their carbon cycling activities may be through alterations in their abundance rather than their community composition.

Key words: biodiversity; microbial community; carbon cycling; decomposition; enzyme activity; PLFA; catabolic potential; tropics; La Selva Biological station.

Introduction

Land-use change and the associated loss of biological diversity is one of the largest threats to the world's ecosystems (Vitousek 1994; Chapin and others 1998). Many ecologists over the past decade have documented the potential effects of the loss of biological diversity on ecosystem processes (Naeem and others 1994; Tilman and Downing 1994; McGrady-Steed and others 1997; Wardle and others 1997; Chapin and others. 1998; van der Heijden and others 1998). It has become clear that plant diversity and species identity can influence the magnitude and stability of ecosystem processes over time, particularly at low levels of diversity (Hooper and Vitousek

Received 12 April 2004; accepted 11 October 2004; published online 28 November 2005.
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1997; Chapin and others. 1998; Tilman 1999; Wardle and others 2003).

Despite continued focus on the interaction between diversity and ecosystem processes, relatively little is known about the relationship between plant diversity and soil microbial diversity, nor whether plant-mediated changes in soil microorganisms influences ecosystem functioning. This is true despite the important role that microorganisms play in many critical ecosystem processes, including the decomposition of organic matter (Madigan and others 2000). Changes in plant communities often result in a change in the amount, quality, quantity, and timing of organic matter input to soil (Angers and Caron 1998; Hooper and others 2000). If those shifts in carbon input result in an alteration of the catabolic capabilities of soil microorganisms, rates of organic matter decomposition may in turn be affected. Thus diversity-driven changes in microbial community composition and function may have implications for nutrient cycling.

Although recent studies have found that land management, plant identity, and plant community type can affect the composition of soil microbial communities (Borga and others 1994; Waldrop and others 2000; Grayston and others 2001; Marschner and others 2001; Smalla and others 2001; Wieland and others 2001; Johnson and others 2003) few investigators have directly examined whether microbial communities vary with plant diversity (Broughton and Gross 2000; Naeem and others 2000; Stephan and others 2000; Zak and others 2003). The results from these studies are equivocal. Broughton and Gross (2000) examined microbial utilization of BIOLOG carbon sources along a productivity and plant diversity gradient in a successional field in Michigan. They found no shift in patterns of carbon resource utilization with plant diversity, but an increase in overall catabolic activity with productivity. Stephan and others (2000) found a significant increase in both overall microbial activity and the diversity of BIOLOG substrates used along a grassland plant diversity gradient in Switzerland. Naeem and others (2000) found that algal diversity had a significant, though not necessarily consistent or positive, influence on the number of substrates utilized by microbial communities in laboratory mesocosms that varied in both bacterial and algal diversity. Zak and others (2003) examined changes in microbial fatty acid composition and abundance as well as measures of microbial activity across a plant diversity gradient in a long-term experimental grassland system in Minnesota. They observed changes in microbial abundance and composition across the gradient, and concluded that these changes were more related to differences in plant productivity rather than plant diversity per se.

These studies offer some insight into how plant diversity affects the structure and function of microbial communities, but key issues remain unaddressed. First, two of the four studies above employed culture-dependent substrate utilization profiles (that is, BIOLOG plates). Although such studies offer an impression of microbial catabolism, culture-based assays are known to represent a scant proportion of natural microbial communities (Amann and others 1995; Konopka and others 1998). However, there is an alternative catabolic assay that avoids the biases of culturing by adding substrates directly to soil, which allows a more complete assessment of the catabolic activities of resident soil microorganisms (Degens and Harris 1997). This assay (referred to here as catabolic potential) has been used successfully to detect shifts in microbial catabolism across soil and land-use types and plant successional communities (Degens 1998; Degens and others 2000; Schipper and others 2001), but we know of no studies that have examined catabolic potential across a plant diversity gradient. Second, no studies to date linking plant diversity to microbial communities have been conducted in the tropics, where human alterations to species diversity are the most recent and dramatic. Finally, few studies have attempted to link differences in microbial catabolic assays directly to a real-world ecosystem function, such as plant litter decomposition (Degens 1998).

Here, we investigate whether plant diversity-mediated changes in microbial community composition in the tropics can influence soil carbon cycling. We hypothesized that: (1) microbial community composition would change across a plant diversity gradient, with each plant diversity level harboring a distinct microbial community; (2) soil catabolism (that is, the abilities of microbes to decompose a variety of organic compounds) would change across a plant diversity gradient, and microbial catabolic flexibility would increase with plant diversity; and (3) rates of litter decomposition would be correlated to differences in microbial community composition across the plant diversity gradient.

Methods

Study Sites

We conducted this study within a long-term experimental system at La Selva Biological Station

in the Atlantic tropical lowlands of Costa Rica; a complete description of the experiment is presented in Haggar and Ewel (1995). The experiment was established to study the influence of plant species composition, plant diversity, and disturbance regime on the productivity and sustainability of tree plantations (Haggar and Ewel 1995). The sites are on an alluvial terrace that sustained cacao plantations for over 30 years prior to the experiment. In 1991, after all cacao vegetation was cut and the slash burned, plant communities were established that varied in species composition, diversity, and disturbance regime in a split-plot randomized block design (Russell and others 2004).

We sampled a subset of plant communities from the experimental system that spanned four levels of plant diversity. At the one-species level, *Cedrela odorata* was grown in monoculture (three replicate plots; 40 × 30 m). Three-species combinations consisted of *Cedrela*, an herb (*Heliconia imbricata*), and a palm (*Euterpe oleracea*; three replicate plots; 40 × 30 m). Five-species combinations consisted of *Cedrela*, two other hardwoods (*Hyeronima alchorneoides* and *Cordia alliodora*), and two palm species (*Euterpe macrospadix* and *E. oleracea*; two replicate plots; 40 × 40 m). Finally, two plots were allowed to regenerate naturally, resulting in high plant species diversity (>25 species; two replicates of irregular shape; sampled from 30 × 30 m within each plot). Thus, soil samples were taken from a total of ten plots.

The soils in the experiment are classified as mixed, isohyperthermic, andic, fluventic Dysotropept. Mean annual rainfall is 4 m, and mean annual temperature is 24°C. There is a short dry season between February and April, but mean monthly rainfall never falls below 0.1 m (Haggar and Ewel 1995).

Sampling

We carried out studies relating plant diversity, season, and microbial composition and activity throughout 2000 and 2001 (Carney 2003). For the study reported here, carried out in November 2001, we collected ten random samples of soil in each plot to 10 cm depth using a 2.5 cm diameter soil auger. We composited and homogenized the cores, and hand-sieved soil to remove large pieces of organic material (that is, ≥ 2 mm in size). We transported soils on ice to Stanford University, where we conducted soil nitrogen (N) analyses within 5 days of soil sampling and froze subsamples of soil for microbial community analysis at a later date. Subsamples of the remaining soil were either air dried for soil pH and phosphorus analyses, dried at 60°C for carbon analyses, dried at 105°C for soil moisture content, or used fresh in the carbon mineralization assays described below.

Microbial Community Analyses

We used phospholipid fatty acid (PLFA) composition to determine microbial community composition. We extracted 4 g lyophilized soil using a modified Bligh and Dyer extraction and identified and quantified individual fatty acids using gas chromatography (White and Ringelberg 1998). Peaks were identified using bacterial fatty acid standards and MIDI peak identification software (MIDI, Inc., Newark, DE).

We compared microbial community composition with the mole percent of the fatty acids identified in each soil, all of which were present in all soils. Bray–Curtis similarity matrices, a measure of community similarity that incorporates both the presence and relative abundance of marker fatty acids (Magurran 1988), were generated with fatty acid data. Using these similarity matrices, we performed a non-parametric two-way analysis of similarity (ANOSIM, Clarke and Warwick 2001) to test whether there were significant differences in microbial community composition among a priori defined treatment groups (that is, plant diversity levels). ANOSIM compares similarities within and among groups and tests these against a series of random simulations to evaluate the null hypothesis that there are no differences among groups. We visualized shifts in community composition among treatment groups using non-metric multidimensional scaling (MDS) of Bray–Curtis similarity matrices to produce two-dimensional ordination plots (Clarke and Warwick 2001). We report stress values, which reflect how accurately an MDS image represents the underlying data. Stress values of 0.05 or less indicate excellent representations of the underlying data and values of 0.1 or less are considered satisfactory (Clarke and Warwick 2001).

To determine which fatty acids accounted for observed differences in composition, we used the program SIMPER (Clarke and Warwick 2001). The program calculates the average dissimilarity among all pairs of intergroup samples (for example, it compares each plant diversity level to every other) and tabulates the average percent contribution of each fatty acid to the dissimilarity observed among the groups. In addition, we examined whether physiological status contributed to differences among treatment groups by examining whether the ratio of cyclopropyl fatty acids to their precur-

sors differed among treatment groups (Reichardt and others 1997); we found no trans fatty acids in our soils, so we did not calculate the ratio of cis to trans fatty acids, which is another indicator of microbial physiological status (Bossio and Scow 1998; Navarrete and others 2000). It is important to note here that microbial species often contribute to the abundance of many individual fatty acids, which constrains the interpretation of PLFA data (Haack and others 1994). For example, PLFA analysis of overall soil communities cannot be used to detect differences in species diversity, detect changes in the abundance of an individual species, or attribute differences in function to differences in the abundance of any one fatty acid or organism.

We also compared total microbial biomass among treatment groups; this was estimated as the sum of the quantity (nmol) of each of the fatty acid groups present in a given soil and is a measure that is highly correlated with other measures of microbial biomass (Baath and Anderson 2003; Leckie and others 2004).

We tested for differences in physiological status and microbial biomass using a generalized linear model (GLM, SAS 8.02). In all significance tests with GLM, we report significance values for the Type III Sums of Squares, which accounts for differences in sample size among predictor variables (Tabachnik and Fidell 1996).

Soil Characteristics

We measured extractable NH_4–N and NO_3–N, Bray's phosphorus (P), Organic P, moisture, pH, C:N and %C in each soil composite. For extractable nitrogen, 15 g subsamples of field-moist soil were extracted with 100 ml 2N KCl by shaking for 1 h. The extract was passed through Whatman #1 filters, and the filtrate was analyzed for NH_4–N and NO_3–N colorimetrically with an autoanalyzer (Alpkem Flow Solution IV). We determined available P from air-dried soil using the Bray P1 method (Olsen and Sommers 1982) followed by colorometric analysis using a Hitachi U-2001 spectrophotometer. We measured organic P using the Saunders and Williams ignition method (Olsen and Sommers 1982), again followed by colorometric analysis. Soil gravimetric moisture content was determined by oven drying 100 g subsamples of field moist soil at 105°C for 48 h. Soil pH was measured on air-dried soil in 0.01M $CaCl_2$, using a 1:2 (w/v) soil:liquid ratio (Accumet Dual Channel pH/Ion/Conductivity Meter). Percent C and C:N were determined with oven-dried soil (60°C) using a Carlo Erba NA1500 Series II elemental analyzer fitted with a thermal conductivity detector. Soil nutrient concentrations were expressed on an oven-dry basis and analyzed using GLM (SAS 8.02).

Catabolic Potential Assay

Soil catabolic potential, an assay that measures the capability of soil microbes to mineralize a diverse suite of organic compounds, was assessed using a technique described in detail elsewhere (Degens and Harris 1997; Degens and others 2001). Briefly, soils from each plot were conditioned for 7 days at 40% moisture and 25°C. The respiration responses of the conditioned soils were measured after the addition of 22 different labile carbon substrates. Specifically, the substrates consisted of 2 amines (glucosamine, glutamine), 6 amino acids (arginine, asparginine, glutamic acid, histidine, lysine, serine), 1 aromatic compound (urocanic acid), 2 carbohydrates (glucose, mannose), and 14 carboxylic acids (ascorbic acid, sodium citrate, fumaric acid, gluconic acid, α-ketovaleric acid, malic acid, malonic acid, pantothenic acid, quinic acid, succinic acid, tartaric acid). Solutions of 15 mM were added for amines, amino acids, and aromatic chemicals; 75 mM for carbohydrates; and 190 mM for carboxylic acids (Degens and Harris 1997; Degens and others 2001). The response of each soil to each substrate was determined using a separate, individual vial. The substrates were added in solution, at a ratio of 2 ml to 1 g equivalent dry weight soil; controls consisted of an equivalent amount of deionized water. Soils were incubated at 25°C in 30 ml sealed Wheaton vials for 4 h. After incubation, soil CO_2 efflux was determined using an infrared gas analyzer (Shimadzu GC-14A). Soil slurries were vortexed for 15 s halfway through the incubation and just before sampling at the end of the incubation.

We used these data to determine whether soils from different plant diversity levels have distinct catabolic talents (hereafter referred to as catabolic fingerprints). We analyzed the catabolic data using Bray–Curtis similarity matrices as described above. Prior to statistical analysis, the baseline respiration rates of each soil (measured in control soils) were subtracted from the respiration responses of each soil to the 24 substrates. We then generated Bray–Curtis similarity matrices using all 24 substrate responses, and tested for differences among soil treatment groups (that is, plant diversity levels) with ANOSIM. We visualized differences in catabolic fingerprints using nondimensional scaling.

We also compared the relative catabolic flexibility of the microbial community in each plot by calculating the catabolic evenness (E) of each soil we assayed as per Degens and others (2001). E was calculated using the Simpson–Yule diversity index: $E = 1/\Sigma p_i^2$, where p_i is the respiration response to an individual substrate as a proportion of the total respiration responses of the soil summed across all substrates. The use of other diversity indices did not qualitatively alter the results.

Litter Decomposition Assay

We measured litter decomposition among plant diversity treatments in laboratory mesocosms (that is, mason jars) with soils kept at constant soil moisture (40%) and temperature (25°C) to control for as many factors as possible other than microbial community composition. After conditioning each soil for 14 days at 40% moisture and 25°C, we added litter (see below) to soils in a factorial array, such that litter from each plant diversity treatment was decomposed in soil from each treatment. Soils were collected from each replicated site in the four diversity treatments ($n = 10$; see Study Sites), and litter was pooled across replicate sites within the diversity treatments ($n = 4$). Thus, there were a total of 40 soil/litter combinations. For each soil/litter combination in the factorial design, 15 g field moist soil were incubated with 200 mg ground litter (see below) in triplicate; there were also three replicate jars for control soils where no litter was added. CO_2 mineralization was determined with 10 ml NaOH traps that were changed regularly over 80 days. Hereafter, the diversity level from which the soil was sampled will be referred to as ''soil type'', and the diversity level from which the litter was collected will be referred to as ''litter type''.

Litter used in the decomposition experiment was collected from field plots biweekly from 1.73×0.50 m traps in each of the monoculture, three-species combination, and five-species plots as part of ongoing monitoring of the long-term field experiment. In these plots, the litter was separated by species, dried at 70°C, and ground in a Wiley mill with 40 mm mesh. After grinding, we created litter mixtures for each plant diversity level that roughly reflected the estimated litter contribution of each species in the plantations to ensure that laboratory amendments would mimic actual litter inputs. In the secondary succession plots, no long-term litter traps were present; to capture litter in these plots, two temporary mesh traps were placed in each plot for four months and litter was collected biweekly. Litter was dried and ground as above without separating species. We combined litter across individual plots in each plant diversity treatment such that we had a total of four litter types: monoculture litter, three-species combination litter, five-species litter, and secondary succession litter.

Because the earliest stages of decomposition consist mainly of the mineralization of soluble sugars, a function we suspect is ubiquitous among microbial communities (Gartner and Cardon 2004), we preleached the litter to remove soluble sugars prior to adding it to soil. Although this removed potential differences in litter types (that is, different litter types may have different amounts of soluble sugars), we wanted to focus on latter stages of litter decomposition, where microbial community composition is more likely to influence this process. We soaked the litter in a 2 mm mesh bag for 5 min in 500 ml of water and repeating the soaking five times. The litter was again dried at 70°C and sterilized with 12 h of gamma-irradiation prior to amendment. Subsamples of this litter were analyzed at the Center for Water and the Environment (Natural Resources Research Institute, University of Minnesot, US) for total N and P using Kjeldahl digestion and for lignin with acetyl bromide digestion (Hobbie 1996). Litter was also analyzed for carbon fractions following forest product techniques (Fernandez and others 1999). Fractions included non-polar extractives (NPE: fats, oils and waxes), water solubles (WS: amino acids, simple sugars, soluble phenolics), acid solubles (AS: cellulose, himicellulose, starch, polypeptides, nucleic acids), and acid insolubles (AIS: primarily lignin; Hobbie 1996). Fractions are percents of ash-free dry mass.

To examine differences in decomposition rates, we used GLM (SAS 8.02) and tested for the effects of soil type, litter type, and their interaction on total CO_2 mineralization rates for the 80-day experiment.

Relating Microbial Communities to Carbon Cycling

In each of our two carbon mineralization assays, we tried to control for environmental factors known to influence carbon cycling in soils (that is, temperature and soil moisture). However, soils differed in initial microbial biomass, extractable ammonium, and net N-mineralization rates (see Results), all factors that are known to have an effect on carbon mineralization rates.

We used simple and partial Mantel tests to examine the correlation between each of our response variables (that is, catabolic potential, cata-

bolic evenness, and decomposition rate) and each of the variables known to vary significantly across soils (that is, microbial community composition, microbial biomass, initial soil NH_4 concentrations, and net N-mineralization). Simple Mantel tests are based on similarity matrices and determine whether sites that are similar in one aspect (that is, catabolic potential) are also similar in another (for example, microbial community composition). Partial Mantel tests determine the relationship between two variables while holding the effects of other variables constant (for example, a partial Mantel determines the relationship between soil catabolic potential and microbial community composition while controlling for the effects of microbial biomass and soil NH_4 concentration). In these tests, we used Bray–Curtis measures of dissimilarity for microbial community composition and soil catabolic potential. The remaining variables were converted to Euclidean distance matrices; for decomposition rates, we used the average rate across all litter types. We first conducted simple Mantel tests that correlated soil catabolic potential, soil catabolic evenness, and litter decomposition rate with each of the soil biotic and abiotic variables. We then used partial Mantel tests to determine the partial correlation between each of the three response variables and each of the soil biotic and abiotic variables. We did not include net N-mineralization in the analyses involving soil catabolic potential, as this was a short-term assay conducted over 4 h and differences in N-mineralization over this time frame are not likely to affect carbon mineralization rates; inclusion of this variable in the partial Mantel tests did not qualitatively alter the results. We also examine whether catabolic potential was related to litter decomposition with a simple Mantel test.

Results

Plant diversity had a significant effect on microbial community composition ($P < 0.01$, ANOSIM; Figure 1). Shifts in composition occurred between each diversity level; the starkest differences occurred among the monocultures, three-species combinations and secondary succession plots. Differences in microbial composition between each pair of sites were due to differences in the relative abundance of a number of fatty acids, the vast majority of which are indicative of bacteria; fungal biomarkers did not play a substantial role in discriminating treatments (Table 1). We found no significant difference in the ratio of cyclopropyl to precursor fatty acids across the plant diversity gradient ($F_{3,9} = 1.568$, $P = 0.292$, GLM). Plant diversity marginally affected microbial biomass (Table 2), with soils in the one- and five-species plots supporting lower biomass than soils in the three-species and secondary succession plots.

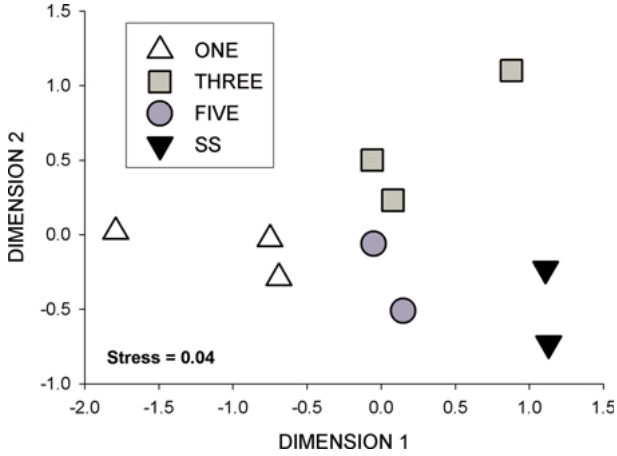

Figure 1. Multi-dimensional scaling plots of microbial community composition across a plant diversity gradient. *ONE*, monocultures; *THREE*, three-species combinations; *FIVE*, five-species combinations; *SS*, secondary succession plots. Axes are arbitrary and scaled in units of Bray–Curtis similarity; the closer points are on the graph, the more similar they are in composition.

Soil characteristics were generally very similar across the plant diversity gradient, but there were significant differences in extractable NH_4 and net N-mineralization (Table 2). Five-species plots and secondary succession plots had the highest levels of extractable NH_4, while net N-mineralization in the secondary succession sites was higher than in all other plots.

The catabolic fingerprints of microbial communities varied significantly with plant diversity ($P < 0.01$, ANOSIM; Figure 2). Three-species combinations and five-species plots were indistinguishable, but monoculture and secondary succession sites were distinct from these plots and from one another. There was also a significant effect of plant diversity on catabolic evenness ($F_{3,9} = 14.67$, $P < 0.01$, GLM; Figure 3), which increased along the plant diversity gradient.

In the factorial litter decomposition experiment, decomposition rates increased significantly and monotonically across soils with increasing plant diversity levels ($F_{3,9} = 12.93$, $P < 0.0001$, GLM; Figure 4). However, there was no litter type effect nor a litter type by soil type interaction. Although plant litter amended to the mesocosms varied in species composition and diversity, the characteristics of the litter added were relatively similar (Table 3).

Table 1. The Three Most Important Fatty Acids Discriminating Microbial Composition Among Plant Diversity Levels, based on Average Dissimilarity between all Pairs of Inter-Group Samples

Plant diversity[1] level comparison	Fatty acid	Taxonomic affiliation	Contribution %[2]	Cumulative[3]
ONE vs. THREE	18:1ω7c	Gram − Bacteria	14.3	14.3
	i15:0	Gram + Bacteria	10.0	24.3
	16:1 ω7c	Unknown	9.7	34.0
ONE vs. FIVE	18:1ω7c	Gram − Bacteria	17.8	17.8
	10Me16:0	Gram + Bacteria	9.2	27
	16:0	Bacteria	6.8	33.8
ONE vs. SS	18:1ω7c	Gram − Bacteria	19.7	19.7
	10Me16:0	Gram + Bacteria	15.9	35.6
	i15:0	Gram + Bacteria	8.9	44.5
THREE vs. FIVE	a15:0	Gram + Bacteria	13.0	13.0
	16:0	Bacteria	11.0	24.0
	16:1 ω7c	Unknown	8.7	24.7
THREE vs. SS	10Me16:0	Gram + Bacteria	18.3	18.4
	16:0	Bacteria	13.5	31.8
	18:1ω7c	Gram − Bacteria	12.3	44.1
FIVE vs. SS	10Me16:0	Gram + Bacteria	18.3	18.3
	18:1ω7c	Gram − Bacteria	16.2	34.5
	i15:0	Gram + Bacteria	9.3	43.8

[1]ONE = monocultures, THREE = three species combinations, FIVE = five-species combinations, SS = secondary succession plots.
[2]Contribution % = the percent of difference between diversity treatments for which the fatty acid accounts.
[3]Cumulative % = the cumulative percent of the difference accounted for by each additional fatty acid.

Table 2. Soil Chemical and Microbiological Properties across the Plant Diversity Gradient

	Plant diversity level[1]				
Soil property	ONE	THREE	FIVE	SS	Significance[2]
Microbial biomass (PLFA nmol/g)	33.87^{a}	47.61^{a}	37.66^{a}	55.82^{a}	NS ($P = 0.0507$)
NO_3–N (mg^{-1} kg^{-1})	3.43^{a}	3.43^{a}	3.30^{a}	5.68^{a}	NS
NH_4–N (mg^{-1} kg^{-1})	3.39^{a}	2.04^{ab}	7.79^{c}	5.83^{bc}	**
Net N-mineralization (mg^{-1} kg^{-1} d^{-1})	0.247^{a}	0.384^{a}	0.354^{a}	0.599^{b}	*
Bray's P (mg^{-1} kg^{-1})	30.22^{a}	19.40^{a}	28.34^{a}	22.50^{a}	NS
Organic P (mg^{-1} kg^{-1})	842.99^{a}	875.99^{a}	902.49^{a}	935.80^{a}	NS
pH (in calcium chloride)	5.64^{a}	5.50^{a}	5.41^{a}	5.65^{a}	NS
%C	2.75^{a}	3.16^{a}	3.25^{a}	3.35^{a}	NS
C:N	10.95^{a}	11.81^{a}	12.15^{a}	12.12^{a}	NS

P Values are from a generalized linear model.
Values presented here are treatment means.
[1]ONE, monocultures; THREE, three species combinations; FIVE, five-species combinations; SS, secondary succession plots.
*[2]Values are significant at * $P < 0.05$, ** $P < 0.01$, ns, not significant; Letters denote differences in pairwise means.*

Catabolic potential was most highly correlated to differences in microbial community composition (Table 4). This relationship remained strong even when the effects of the other soil variables (that is, microbial biomass and soil NH_4 concentrations) were statistically controlled with a partial Mantel test (Table 4). Microbial biomass was also highly related to differences in catabolic potential in the simple and partial Mantel tests (Table 4). Soil catabolic evenness, on the other hand, was most highly related to microbial biomass with the simple Mantel tests, and was the only factor significantly related to catabolic evenness when using partial Mantel tests (Table 4). Catabolic evenness was also highly correlated to microbial community composition in the simple Mantel test, but this relationship disappeared when the effects of other factors were taken into account (Table 4). Decomposition rates were significantly correlated to microbial community composition, microbial biomass, and net N-mineralization rates using simple Mantel tests (Table 4). Partial Mantels showed that when

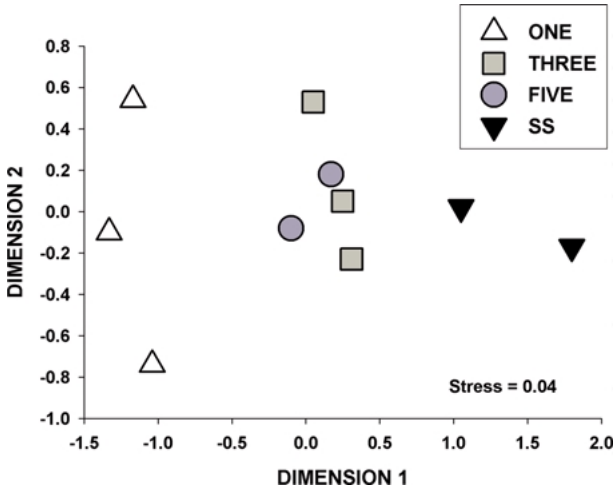

Figure 2. Multi-dimensional scaling plots of catabolic potential across a plant diversity gradient. *ONE*, monocultures; *THREE*, three-species combinations; *FIVE*, five-species combinations; *SS*, secondary succession plots. Axes are arbitrary and scaled in units of Bray–Curtis similarity; the closer points are on the graph, the more similar they are in catabolic potential.

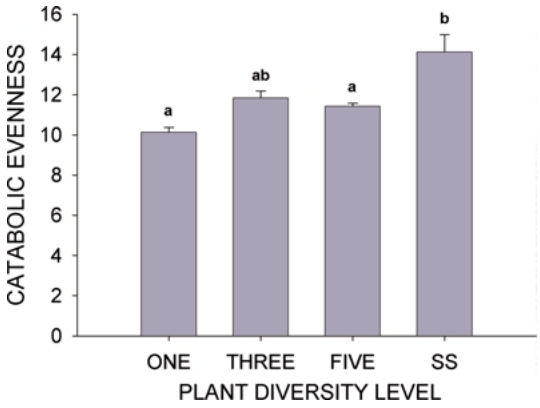

Figure 3. Soil catabolic evenness across a plant diversity gradient. *Bars* with different superscripts are significantly different at $P < 0.05$. Values are means + SE.

the effects of the other soil variables were removed, microbial biomass, net N-mineralization, and initial soil NH_4 concentrations were all correlated to decomposition rates (Table 4). Catabolic potential and decomposition rates were highly related in a simple Mantel test ($r = 0.689$, $P < 0.001$).

Discussion

We found that microbial community composition varied among all levels of a plant diversity gradient, a pattern closely mirrored by soil catabolic fingerprints and litter decomposition rates. We also found that microbial community composition was the

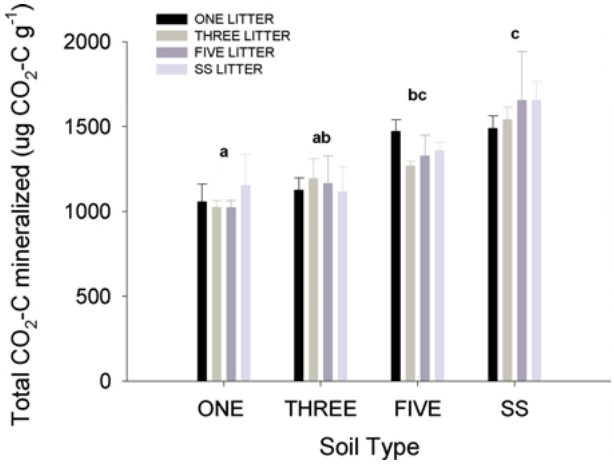

Figure 4. Total CO_2 mineralized over the 80-day litter decomposition assay after subtraction of basal respiration values. Letters denote differences in pairwise means at $P < 0.05$.

factor most strongly related to the differences in soil catabolic potential, while microbial biomass was the factor most strongly and consistently related to all three measures of carbon mineralization across the soils in our study.

Our finding that plant diversity had a significant effect on microbial community composition (Figure 1) corroborates another study done at this site that examined how microbial community composition shifted along a larger set of plant diversity plots and between wet and dry seasons (Carney 2003). In that study, we explored the potential mechanisms behind microbial community changes (such as plant-mediated changes in soil characteristics). Soil %C was most often associated with changes in microbial community composition across sites. This suggests that differences across the plant diversity gradient in belowground plant productivity, which has been shown to be correlated with soil %C in these sites (Russell and others 2004), is a potential mechanism driving microbial community differences.

In this paper, we focus on understanding the potential implications of changes in microbial communities for ecosystem processes rather than the mechanisms underlying those microbial patterns. Organic matter decomposition is a major determinant of carbon flux in ecosystems, and is a critical pathway by which nutrients are made available to plants for growth (Schlesinger 1997). It is carried out by many microorganisms (as well as invertebrates and vertebrates), many of which often work in concert to mineralize carbon from organic material (Coyne 1999). If changes in the

Table 3. Chemistry of Litter Amended to Soils in the Decomposition Assay

Litter nutrients (%)			Litter carbon fractions (%)[2]						
Litter type[1]	C	N	NPE	WS	AS	Lignin	Tannin Equivalent	WS GE	AS GE
ONE	52.77	1.43	0.51	4.94	48.97	45.58	1.34	0.61	21.85
THREE	48.39	1.36	1.49	6.21	56.66	35.64	1.24	0.52	32.59
FIVE	53.76	1.79	0.82	7.69	48.39	43.09	1.97	0.90	22.17
SS	54.77	1.37	1.66	7.03	43.68	47.63	1.92	1.07	22.40

[1]*Litter type, the plant diversity level from which the litter was collected.*
[2]*NPE, nonpolar extractives; WS, water soluble; AS, acid soluble; GE, glucose equivalent.*

Table 4. Results of Simple (r) and Partial (ρ) Mantel tests[1] relating Characteristics that Varied across Soil Types to Catabolic Potential, Catabolic Evenness, and Litter Decomposition Rates

	Catabolic potential[2]		Catabolic evenness		Litter decomposition	
	r	ρ	r	ρ	r	ρ
Microbial composition	0.588**	0.435*	0.418*	ns	0.411*	ns
Microbial biomass (PLFA nmol g^{-1})	0.556**	0.352*	0.756***	0.681**	0.487**	0.428*
$[NH_4]$ (mg^{-1} kg^{-1})	ns	ns	ns	ns	Ns	0.516**
Net N-mineralization (mg^{-1} kg^{-1} d^{-1})	–	–	–	–	0.560*	0.424*

[1]*Simple Mantel tests determine whether sites that are similar in one aspect are also similar in another. Partial Mantel tests determine the relationship between two variables while holding the effects of other variables constant. See Methods for a full explanation of the analyses presented here.*
[2]*Values are significant at * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = not significant.*

composition of microorganisms alter catabolic capabilities of the decomposer community, decomposition rates may be affected.

To assess whether the differences in microbial communities we observed mattered to soil carbon cycling, we first measured soil catabolic potential, an assay that estimates the catabolic capabilities of soil microorganisms (Degens and Harris 1997). Catabolic fingerprints closely mirrored the changes in microbial community composition across the plant diversity gradient, suggesting that each microbial community had distinct catabolic talents (Figure 2). Indeed, catabolic potential was most highly correlated with microbial community composition (Table 4) and these variables remained highly correlated when differences in soil NH_4 concentrations and microbial biomass were statistically controlled for (Table 4).

We also found that catabolic evenness, an indicator of overall microbial catabolic flexibility, increased along the plant diversity gradient, with the highest plant diversity plots having the highest catabolic evenness (Figure 3). Microbes residing in a diverse plant community are likely confronted with a diverse array of plant secondary compounds from which they can derive energy (Bardgett and Shine 1999; Hooper and others 2000). This high number of substrates may lead to high niche diversity, whereby microorganisms specialize in degrading particular compounds (Sugai and Schimel 1993). A microbial community that produces enzymes capable of degrading a wide range of compounds should be able to readily decompose a greater variety of organic compounds when compared to a microbial community originating from a monoculture, where a lower diversity of enzymes may be needed.

Although we found an increase in catabolic evenness with plant diversity that was correlated to differences in microbial community composition (Table 4), the partial Mantel tests reveal that increases in microbial biomass across the plant diversity gradient may be responsible for these changes in catabolic evenness (Table 4). Other investigators have found that catabolic evenness increases with soil carbon (Degens and others 2000), and differences in microbial biomass in our system are correlated with changes in soil carbon ($R^2 = 0.416$, $P < 0.05$). Thus, changing plant diversity may indirectly affect the catabolic diversity of soil microorganisms by changing the amount of soil carbon available to soil heterotrophs. We can-

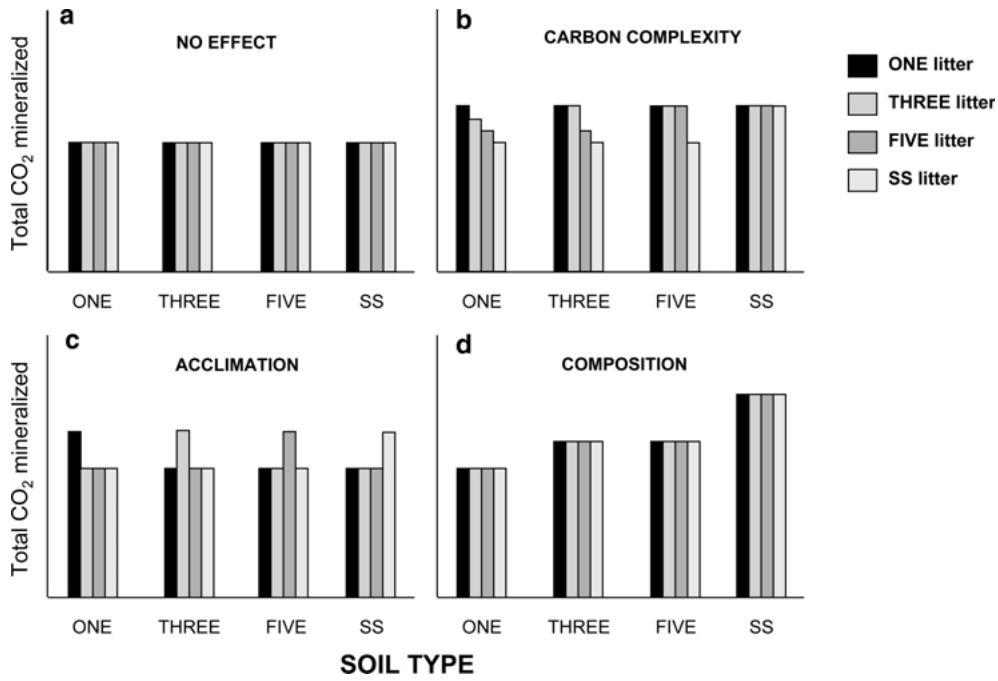

Figure 5. Four alternative hypotheses regarding the outcome of the litter decomposition assay (see Discussion for explanation of each). ''Soil type'' refers to the plant diversity treatment level from which the soil was sampled. Each bar represents a different litter type amended to each soil type.

not be certain why this link exists, but higher amounts of energy may enable the persistence of a higher diversity of soil heterotrophs (Rosenzweig 1995), leading to a more catabolically diverse microbial community. Because phospholipids incorporate information from many species, we cannot directly test this hypothesis in this study.

The relationship between microbial community composition and their catabolic capabilities suggests that plant-mediated differences in soil microorganisms may affect soil carbon cycling rates. To more fully explore this, we conducted a fully factorial litter decomposition experiment, where each soil from across the plant diversity gradient was exposed to plant litter from across the same gradient.

We had four alternative hypotheses regarding the outcome of our litter decomposition assay. (1) No effect: no differences across soils in litter decomposition rate (Figure 5A). One might expect differences in microbial community composition to be unimportant to decomposition rates because there are potentially thousands of species of microbes per gram of soil (Torsvik and others 1990); even very distinct microbial communities may produce all the enzymes necessary to degrade a given litter type (Schimel 1995). (2) A ''carbon complexity effect'': soil microbes from less diverse plant communities are increasingly poor decomposers of litter from higher plant diversity plots (see reasoning behind catabolic evenness above; Figure 5B). 3) An ''acclimation'' effect: soil microbes are able to decompose litter from their plot of origin more rapidly and completely relative to foreign litter sources (Figure 5C). Evidence of microbial acclimation to their carbon environment has been demonstrated in a bioreactor, in peat bogs, and in broad-leaved forests of Central and North America (Sugai and Schimel 1993; Karthikeyan and others 1999; Gholz and others 2000). This is presumably due to the specificity of particular enzymes, which can be associated with particular microorganisms, in the degradation of organic compounds. For instance, degradation of recalcitrant organic compounds is carried out primarily by lignases found in fungi and actinomycetes (Hammel 1997). Less is known about the pathways through which less recalcitrant organic compounds are processed. (4) A ''composition'' effect: litter decomposition rates mimic patterns we found in microbial community composition and catabolic potential (Figure 5D). If this were true, the starkest differences would be among monocultures, three-species combinations, and secondary succession plots, while there would be little to no difference between the three-species combinations and 5 species plots (see Figures 2 and 3).

The lack of any soil type by litter type interaction terms in the two-way ANOVA from our experi-

ment excluded our ''carbon complexity'' and ''acclimation'' hypotheses. The fact that litter across the diversity gradient was surprisingly similar in chemistry (Table 3) likely contributed to the lack of a litter effect or soil by litter interaction. There was, however, a significant effect of the plant diversity level from which the soil was collected on decomposition rate (Figure 4), one that closely resembled the ''composition'' hypothesis (Figure 5D).

We attempted to experimentally control for all factors known to influence decomposition rate other than microbial community composition, but differences in nutrient availability and microbial biomass across soils likely contributed to the variation in decomposition rates (Table 2). Indeed, although we found that microbial community composition was significantly related to differences in litter decomposition rates (Table 4), this relationship disappeared when accounting for differences in microbial biomass and nitrogen. In fact, we found that background net N-mineralization rates were the most highly correlated with decomposition rates, and that this factor remained significant when accounting for the effect of other factors on decomposition rates. We also found that microbial biomass was related to decomposition rates in both the simple and partial Mantel tests. These factors interact and influence one another (that is, a larger microbial pool will likely lead to higher rates of soil N turnover), and thus we cannot attribute the differences in decomposition rate to any individual factor alone. However, the fact that microbial biomass was highly correlated to decomposition rates (Table 4) suggests that the plant diversity-mediated changes in the overall abundance of microorganisms were more important to decomposition rates than changes in microbial community composition.

We also found that catabolic potential was highly correlated to litter decomposition rates, which suggests that catabolic potential assay may be a reasonable indicator of relative rates of decomposition among soils, at least under the optimal and controlled conditions under which we ran the decomposition assays. Our findings agree with another study, where fumigation-induced changes in catabolic potential were related to rates of wheat straw decomposition under optimal moisture (Degens 1998); however, in that study, the relationship disappeared under sub-optimal moisture conditions (Degens 1998). Another study found that patterns of BIOLOG substrate utilization profiles did not match patterns of ryegrass residue decomposition (Griffiths and others 2000). The discrepancy between this and the former studies may be due to either the different substrate utilization techniques used or differences in the conditions under which the decomposition assays were run (soils in the latter study were incubated at lower temperatures and unknown soil water content).

Before concluding, we must point out that, like other studies attempting to relate the species diversity to ecosystem function (for example, productivity), we cannot unequivocally state that the shifts in microbial community composition and catabolic activity we observed were due to the number of plant species alone (Tilman and Downing 1994; Tilman 1996; Hooper and Vitousek 1997; Huston 1997; Lawton and others 1998). As plant diversity increased in this study, so did the likelihood that a study site contained a species that had a strong effect on each of these measures (that is, the sampling effect; Wardle 1999). Put simply, plant species identity may have been as likely as the number of plant species to influence soil microbial community composition, abundance, and activity (see Borga and others 1994; Marschner and others 2001; Carney 2003). Regardless of the mechanism driving the differences we observed, we found evidence that plant community-mediated changes in microbial community composition and abundance can influence soil carbon processes.

Conclusion

Although the links among plant communities, microbial communities, nutrient availability and ecosystem processes are never unidirectional and rarely simple (Naeem 2000; Hooper 2000), our study demonstrates the potential for human alteration of aboveground plant communities to affect soil microorganisms and the processes they mediate. We found some evidence that changes in microbial community composition associated with changes in plant diversity can exert a significant influence on soil carbon processing, but the most consistent factor affecting carbon mineralization in our soils was microbial biomass. Although the importance of microbial community composition to constraining specific microbially-mediated processes has been reported for nitrification, denitrification, and specific enzyme activity (Carney and others 2004; Cavigelli and Robertson 2000; Waldrop and others 2000; Griffiths and others 2001), our results suggest that, in this system, variation in the abundance of soil microorganisms resulting from plant community differences may be more important to soil carbon processes than those related to microbial community composition. The importance of these varied relationships among

plant diversity, soil composition, and ecosystem processes may be particularly important to understand in the tropics, where the vast majority of the world's biodiversity and productivity resides.

ACKNOWLEDGEMENTS

We thank Jack Ewel for his generosity in sharing his field sites, staff, equipment, knowledge, and guidance throughout this project. We also thank Brendan Bohannan and Peter Vitousek for aiding the direction of the research, Alex Reich and Ricardo Bedoya for field and logistical support, and the Huertos crew for help in the field. Thanks also to Steven Allison, Teri Balser, Peter Jewett, Ryan King, Ian Monroe, Zenobia Moore, and Martha Roberts for help with laboratory and statistical analyses. The manuscript greatly benefited from suggestions made by Kathleen Boomer, Aimee Classen, Claire Horner-Devine, Amy Luers, Pat Megonigal, Stephen Porder, and Taylor Ricketts. The National Science Foundation Graduate Fellowship Program, NSF Doctoral Dissertation Improvement Grant No. 0205959, NSF awards DEB 90318403 and DEB 9623969, the Stanford University School of Earth Sciences McGee Fund, and a grant from the A. W. Mellon Foundation to Pamela Matson supported this research.

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