

Root quality and decomposition environment, but not tree species richness, drive root decomposition in tropical forests

Nathaly R. Guerrero-Ramírez · Dylan Craven ·
Christian Messier · Catherine Potvin ·
Benjamin L. Turner · I. Tanya Handa

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Abstract

Background and aims Tropical forests contribute significantly to the global carbon cycle, yet the relative importance of tree diversity on key ecosystem processes such as root decomposition remains unknown.

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N. R. Guerrero-Ramírez · C. Messier · I. T. Handa
Département des Sciences Biologiques, Center for Forest
Research (CFR), Université du Québec à Montréal, C.P. 8888,
succ. Centre-Ville, Montréal, QC H3C 3P8, Canada

N. R. Guerrero-Ramírez (✉) · D. Craven
German Centre for Integrative Biodiversity Research (iDiv)
Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
e-mail: kirana1015@gmail.com

N. R. Guerrero-Ramírez · D. Craven
Institute for Biology, University of Leipzig, Johannisallee 21,
04103 Leipzig, Germany

C. Messier
Département des Sciences Naturelles, ISFORT, Université du
Québec en Outaouais, Gatineau, Canada

C. Potvin · B. L. Turner
Smithsonian Tropical Research Institute, Apartado 0843-03092,
Balboa, Ancon, Republic of Panama

C. Potvin
Department of Biology, McGill University, 1205 Dr Penfield,
Montréal, QC H3A-1B1, Canada

Methods We examined the influence of tree species richness on root decomposition over 485 days at two sites in Panama with contrasting soil fertility. Diversity effects on decomposition rates were calculated where 1) overstory tree species richness and composition matched that occurring inside root decomposition bags and 2) where roots of contrasting species richness decomposed under a common tree overstory. In addition, we tested 27 root traits to identify those that contribute to predict root decomposition in tropical forests. **Results** Tree species richness did not affect root decomposition rates, neither when species were manipulated within bags nor with varying tree overstory richness. Root carbon quality and micronutrient concentrations such as manganese explained 47 and 81 % of the variation in decomposition rates in the fertile and infertile site, respectively, demonstrating that the relative importance of traits was modulated by the soil environment. **Conclusions** Our results suggest that root decomposition in tropical forests is mediated by root functional composition and the soil environment rather than by species richness.

Keywords Biodiversity experiments · Belowground processes · Non-additive effects · Nutrient cycling · Functional traits · Soils

Introduction

Tropical ecosystems are known for their remarkable biodiversity and the vital role that they play in global

nutrient cycles (Malhi 2012). Approximately 40 % of the global carbon (C) stock is stored in tropical ecosystems (Soepadmo 1993). However, the belowground component of global C stocks has likely been underestimated due to methodological constraints of measuring root biomass and turnover (Robinson 2007). Despite the potential effects of loss of tropical tree species diversity on C storage (Bunker et al. 2005) and the urgent need for accurate estimates of the various components of the C cycle in tropical forests (Malhi and Grace 2000), there are relatively few studies that have examined belowground processes, such as the decomposition of tree roots, and even fewer that have included the interaction between tree diversity and root decomposition.

Organic matter decomposition is the reciprocal process of primary plant production in terrestrial ecosystems, whereby assimilated C retained in structural plant biomass is transferred to the soil as leaf, wood, or root litter and released by decomposer communities (Gessner et al. 2010). Decomposition rates, shown typically in studies on leaf litter, are understood to be driven by abiotic factors such as climate and the soil matrix or decomposition environment, and biotic factors that include the composition of decomposer communities and the quality of litter substrates (Bradford et al. 2014; Freschet et al. 2012b). Litter quality is considered particularly important in understanding 'species identity' effects that are frequently reported in decomposition studies (Cornwell et al. 2008).

An understanding of litter quality based on its chemical, structural and anatomical traits has provided further insights to the links between above- and belowground processes such as decomposition (Birouste et al. 2011; Cusack et al. 2009; Hobbie et al. 2010). For example, lignin:N and C:N ratio, reflecting important components of litter quality to decomposers, often contribute to predicting leaf litter decomposition (Freschet et al. 2012b) and are thus commonly included in biogeochemical models (Kucharik et al. 2000; Sitch et al. 2003). Nonetheless, an increasing number of studies on leaf litter decomposition suggest that other litter characteristics associated with C quality or the presence of particular micronutrients may also be important, particularly in tropical ecosystems (Hättenschwiler et al. 2011; Makkonen et al. 2012; Dale et al. 2015; García-Palacios et al. 2016). However, data on a wider set of relevant root traits that may contribute to our understanding of root decomposition remains limited.

Changing plant diversity within an ecosystem can influence decomposition by modulating litter quality and influencing the composition and activity of decomposer communities and their interactions (Gessner et al. 2010; Hättenschwiler et al. 2005). Studies on diversity and decomposition in the last decade (Gartner and Cardon 2004; Gessner et al. 2010; Handa et al. 2014) have been largely limited to leaf litter, and differences between leaves and roots, e.g. tissue composition and the decomposition environment, make it difficult to extrapolate the mechanisms involved in leaf decomposition to root decomposition (Hobbie et al. 2010). For example, the properties of the soil matrix may be of particular importance for root decomposition. Low soil fertility may slow decomposition rates (Wardle et al. 2004), while characteristics such as soil pH (Rousk et al. 2010), soil C:N ratio (Fierer et al. 2009) and soil texture (Gijsman et al. 1997) can affect decomposer communities, such as the composition and ratios of fungal and bacterial communities, or the activity and mobility of decomposers.

Species richness and composition of tree communities could influence soil biochemical processes by modifying the availability of resources (Cong et al. 2015) and microclimatic conditions (Brandtberg et al. 2000). Moreover, plant communities may affect belowground processes by influencing decomposer communities. For example, variability in plant nutrient supply could influence distribution and dispersion of decomposers (Ettema and Wardle 2002), while greater plant diversity may also increase the density and diversity of decomposer communities (Eisenhauer and Schädler 2011). Such effects may not be detected by a common garden approach to study decomposition, where the overstorey community does not match the litter composition within the decomposition bag.

Tree diversity could influence decomposition due to interactions of decomposers among litter comprised of co-occurring species within a plant community (Gartner and Cardon 2004; Handa et al. 2014; Hättenschwiler et al. 2005). Diversity effects related to litter mixtures can be explained by complementarity effects mediated by decomposer communities (Hansen and Coleman 1998). Other possible mechanisms include nutrient transfer (Lummer et al. 2012; Schimel and Hättenschwiler 2007) or the spread of inhibitory components by leaching or biological mediation (Coq et al. 2011; Fyles and Fyles 1993). As these mechanisms have been evaluated using mainly leaf litter mixtures, the

direct and indirect influences of diversity effects on decomposition of roots, particularly in the tropics, has yet to be determined.

Our study aimed to assess how the species richness of tropical trees influenced the decomposition rate of roots over 485 days. We tested a) the effect of low vs high species richness of overstory trees on root decomposition within experimental forest plots and b) the effect of low vs high species richness of tree roots within the decomposition bag under a common overstory. We hypothesized that tree species richness would influence decomposition rates in both cases, due to indirect effects on the abiotic and biotic decomposition environment at the plot level (Keller et al. 2013; Prescott and Grayston 2013) and variation of resource availability in the mixtures at the bag level (Hättenschwiler et al. 2005). In addition, we expected that the functional identity of species would be a key factor explaining root decomposition rates across sites. Thus, we tested tropical tree roots with varying traits to identify a range of potential drivers of root decomposition. Here, we use the expression “trait” to refer to morphological, physiological, or phenological characteristics of roots measurable at the individual level (Violle et al. 2007). Given that soil properties also may modulate the drivers of root decomposition (Silver and Miya 2001), the influence of plant species richness and functional identity was tested in two contrasting sites.

Materials and methods

Study sites

The study was conducted in two experimental forest sites in central Panama, Sardinilla (9°19' N, 79°38' W) and Agua Salud (9°13' N, 79°47' W), with annual precipitation of 2350 mm and 2300 mm, respectively (Scherer-Lorenzen et al. 2007; van Breugel et al. 2013). The Sardinilla site is a long-term diversity experiment consisting of a forest planted in 2001 on former pasture land with either one, three or six native tree species (Scherer-Lorenzen et al. 2005). The tree species used in the Sardinilla plantation were selected to have a gradient of relative growth rates (Table 1) from slow to fast: *Cedrela odorata*, *Tabebuia rosea*, *Anacardium excelsum*, *Hura crepitans*, *Cordia alliodora*, and *Luehea seemanii* (Scherer-Lorenzen et al. 2007). Mortality of one species, *Cordia alliodora*, was high

in the early years such that it is no longer considered to be represented within the tree diversity treatments at the site (Scherer-Lorenzen et al. 2007). After 10 years of growth, the Sardinilla plantation had a closed, stratified canopy and an understory vegetation dominated by grasses and herbaceous species. The site is underlain by Tertiary limestone (Stewart et al. 1980). Soils are Alfisols with vertic properties, including a high base status and clay texture, including shrink-swell clays (Potvin et al. 2004).

The Agua Salud forest sites include young native tree plantations established in 2008 on former cattle pastures and agricultural fields and secondary forests of different ages (van Breugel and Hall 2008; van Breugel et al. 2013). Agua Salud plantation plots are characterized by short, steep slopes with soils developed on pre-Tertiary basalt (Stewart et al. 1980). A subset of the planted native tree species (*A. excelsum* and *T. rosea*) in Agua Salud also occur in Sardinilla. After three years of growth, the canopy remains open with a vigorous understory dominated by exotic pasture grasses, as most individuals are less than ~2.5 m in height. In contrast to the plots in the Agua Salud plantation, the canopy in the secondary forest plots (abandoned approximately 50 years ago) is now closed and light availability is much lower (van Breugel et al. 2013).

Experimental design

Tree diversity effects on root decomposition were tested using low and high levels of overstory tree species richness within experimental plots and number of species of root within decomposition bag (Supplementary material Table S1). Root decomposition experiments were performed at two sites because they allowed for comparisons of decomposition dynamics between contrasting soil conditions (Table 2). To ensure a similar density of decomposition bags across plots, an area of 3 × 3 m in low richness and 3 × 6 m in high species richness plots was selected to establish the decomposition experiment within each experimental plot (45 × 45 m in Sardinilla and 45 × 39 m in Agua Salud). These areas were located in the center of plots to avoid edge effects and care was taken to avoid canopy gaps.

The low species richness level of tree overstory composition in Sardinilla consisted of monoculture plots of each tree species replicated twice: *A. excelsum*, *C. odorata*, *H. crepitans*, *L. seemanii*, and *T. rosea*

Table 1 Ecological characteristics of the studied native tropical tree species

Species	Family	Shade tolerance	Relative growth rate	Leaf phenology
<i>Anacardium excelsum</i>	Anacardiaceae	Intermediate-shade tolerant	Intermediate	Evergreen
<i>Cedrela odorata</i>	Meliaceae	Shade tolerant	Slow	Dry season deciduous
<i>Hura crepitans</i>	Euphorbiaceae	Intermediate- shade tolerant	Intermediate	Dry season deciduous
<i>Luehea seemanii</i>	Tiliaceae	Shade intolerant	Fast	Dry season deciduous
<i>Tabebuia rosea</i>	Bignoniaceae	Shade tolerant	Slow	Dry season deciduous

Family information from Coll et al. (2008) and Pérez (2008); shade tolerance from Scherer-Lorenzen et al. (2005); approximate relative growth rates from Scherer-Lorenzen et al. (2005); leaf phenology from Carrasquilla (2005), Pérez (2008) and Paul et al. (2012)

($n = 10$). In Agua Salud, monoculture plots of *A. excelsum* and *T. rosea* were replicated three times ($n = 6$). The high species richness level of tree overstory composition differed at both sites. In Sardinilla, it consisted of three plots that had a five-species mixture in the tree overstory ($n = 3$), while in Agua Salud, it consisted of three plots of secondary forests older than 50 years with 155 species 0.2 ha^{-1} ($n = 3$, Supplementary material Table S1). In total, 22 experimental plots were used. Within decomposition bags, the low and high species richness levels refer to the number of species of roots inside each bag. The low species richness level consisted of single-species roots for each of the five studied tree species, while the high species richness level consisted of a five-species root mixture containing all five of the studied species. Despite very high diversity in tropical forests, the number of species contained in the high richness levels were similar to the number of co-occurring litter species found at the spatial scale of an experimental litter bag, i.e. seven species (Handa et al. 2014). To avoid confusion, we will use “low” and “high richness” to refer to tree overstory species richness within the plot and “single-species” and “five-species root mixture” to refer to low and high root richness within the bag.

In each low tree richness plot, decomposition bags with roots matching the composition of the tree overstory and decomposition bags with the five-species root mixture were installed (4 bags with single-species roots + 4 bags with five-species root mixtures \times 10 plots = 80 bags in Sardinilla and 4 bags with single-species roots + 4 bags with five-species root mixtures \times 6 plots = 48 bags in Agua Salud). For the high richness plots in both Sardinilla and Agua Salud, 72 decomposition bags were installed per site (20 bags with single-species roots (4 bags per species) + 4 bags with five-species root mixture \times 3 plots = 72 bags). In total, 272 decomposition bags

were installed, i.e. decomposition rates values (k annual) were based on four temporal points, each with 68 independent replicates (Supplementary material Table S1 and Fig. S1). This design allowed us to assess not only the effects of tree species richness on root decomposition but also any potential diversity effects (Loreau 1998) associated with species richness of roots inside the bag (single-species vs five-species root mixture) under heterogeneous biotic and abiotic conditions. Variation in abiotic conditions are attributed especially to differences in soil phosphorus (P) availability, i.e. lower P availability on the basalt soils in Agua Salud and higher P availability in Alfisols in Sardinilla.

The influence of tree species richness (plot and decomposition bag levels) on diversity effect was tested in two ways (Fig. 1). First, single-species and five-species root mixture bags were installed in plots with the same overstory richness and composition (i.e. *T. rosea* roots in *T. rosea* plots, Fig. 1a) to calculate the diversity effect integrating the effect of tree overstory species richness and composition (plot level) with that of root and decomposer interactions inside the root decomposition bags (decomposition bag level). This contrast was possible only in Sardinilla where the five species were represented in low and high richness plots. Secondly, single-species and five-species root mixtures were installed under the same high richness tree overstory at both sites (Fig 1b) to evaluate if diversity effects due to decomposer interactions at the decomposition bag level varied across sites (e.g., Wardle et al. 1997).

Root selection, installation, and harvest

Root material for the five tree species (Table 1) was manually excavated in non-experimental plots only in the Sardinilla plantation to control for differences in root quality between sites. At the moment of the excavation,

Table 2 Soil characteristics in tree richness plots at the Sardinilla and Agua Salud sites

Soil variable Mean \pm SE	Plot richness (Tree overstory)			
	Sardinilla		Agua Salud	
	Low	High	Low	High
Water content (%)	44.4 \pm 2.3	43.5 \pm 1.7	45.5 \pm 2.8	46.0 \pm 3.8
pH (H ₂ O)	5.7 \pm 0.04	5.4 \pm 0.03	5.5 \pm 0.07	-
Carbon (%)	5.5 \pm 0.2	6.2 \pm 0.7	3.1 \pm 0.2	3.5 \pm 0.2
Nitrogen (%)	0.5 \pm 0.01	0.6 \pm 0.06	0.3 \pm 0.01	0.3 \pm 0.03
Extractable phosphorus (mg kg ⁻¹)	3.53 \pm 0.38	3.53 \pm 0.38	1.1 \pm 0.05	1.5 \pm 0.1

Sardinilla: total carbon, nitrogen and pH from Healy et al. (2008); extractable phosphorus from Zeugin et al. (2010), and clay loam texture (Abraham, 2004). Agua Salud: pH, total carbon, nitrogen, and phosphorus (Hall & van Breugel, personal communication). Soil texture in Agua Salud varied between silty clay to clay (Hassler et al., 2011)

trees were ten years old (DBH ranged between 10.1 to 19.8 cm in the plantation depending on the species). Soil particles were removed while leaving the roots intact to determine root orders for each species based on the classification proposed by Pregitzer et al. (2002). A digital caliper was used to measure the diameter of each root order to the nearest 0.01 mm. Root order determination was done on two root branches per tree and for ten trees per species. These same trees were subsequently used to collect roots for decomposition experiments. Roots were removed from the soil, washed, and air dried at 40 °C for four days. Specific root orders were selected to standardize root quality, which can vary more among root orders than among species (Goebel et al. 2011; Guo et al. 2008). We selected the 4th and 5th root orders because they have the same function, i.e. transport and storage of nutrients. Additionally, these root orders also represent a significant proportion of plant biomass; between 22 and 40 % of total plant biomass was located in roots greater than 2 mm in Sardinilla (Coll et al. 2008). After roots were selected, they were cut to 10 cm in length. Decomposition bags (10 cm \times 20 cm) were made using a 2 mm nylon mesh to permit entry of meso-fauna, which contribute to decomposition in the tropics (Yang and Chen 2009; Handa et al. 2014). Although absolute values may have been underestimated due to accidental loss of material, any litter loss was likely random across treatments and minimal due to the coarse size of roots. A total of 5 g dry weight (40 °C) of material was placed carefully in the bags and closed by a manual heat sealer. Aluminum identification tags were placed inside and outside decomposition bags. For species mixtures, equal proportions of root from each species were used.

Decomposition bags were randomly selected from a well-mixed box and installed in the center of each experimental plot. Each decomposition bag was inserted at a depth of 20 cm in a diagonal position and separated from the next bag by a distance of 40 cm. Because understory vegetation could reach more than a meter in height, it was cut and removed before installation of decomposition bags.

Root bags were installed in August/September 2011 and collected four times at 50, 160/195 (Agua Salud/Sardinilla), 310 and 485 days. Mass loss at each collection was determined by washing roots carefully over a 2 mm or 250 μ m mesh sieve depending on the decomposition stage and oven-drying samples at 65 °C for four days. Initial dry weight values at 40 °C were converted to dry mass at 65 °C based on conversion factors calculated for each species ($n = 5$ per species).

Root trait measurements

We made various quantitative measurements of root litter quality or traits potentially related to root decomposition (Aulen et al. 2012). These included structural, anatomical, and chemical characteristics and were measured on the 4th and 5th root orders for each of the five species at the beginning of the experiment (initial root quality). Root diameter, specific root length (SRL), root density, and root dry matter content (RDMC) were measured with a segment of fresh root material on five trees per species. For each replicate, four measurements of roots from the same tree, but different branches, were taken. Root diameter was measured three times at different points using a caliper. SRL is the relationship

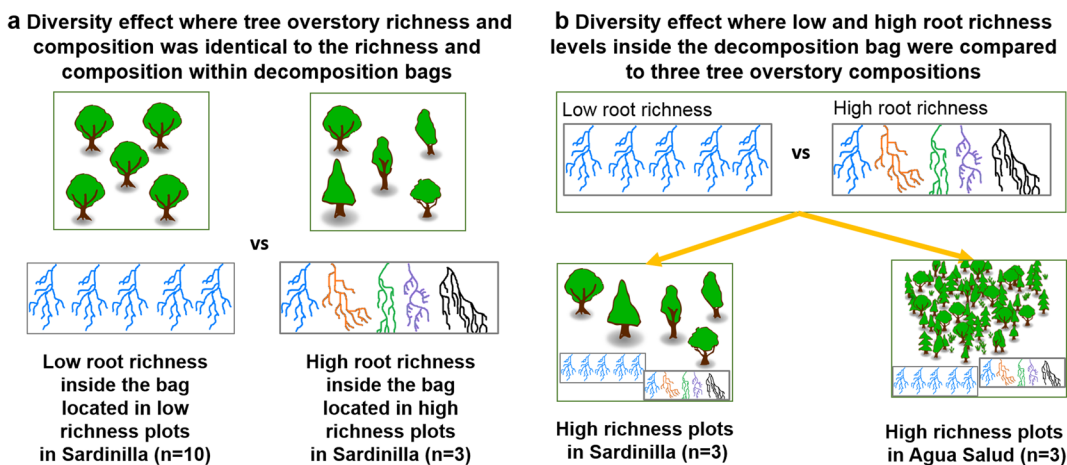


Fig. 1 Experimental design for testing diversity effects on root decomposition associated with root and tree overstory species richness and composition. Note that for the sake of simplicity only

one single-species root combination is shown, but all five single-species decomposition rates were used for the calculation of tree richness effects

between root length and dry weight (cm g^{-1}). Root length was measured with ImageJ (Abramoff et al. 2004) using scanned digital images, while root weight was determined after being oven dried at 65°C for 48 h. Root volume was measured using the water-displacement method (Chave et al. 2006). Root density was calculated by dividing the 65°C oven dried weight by the volume. RDMC was measured using a modified method from leaf dry matter content (LDMC) using partial rehydration (Vaieretti et al. 2007).

Anatomical measurements were made using fresh material collected in the field from three different trees per species and transported to the laboratory immediately. Samples were cut manually, slides were mounted, and images were taken by an Olympus FV1000 confocal microscope using auto-fluorescence. Images were analyzed using ImageJ (Abramoff et al. 2004) to determine: the percent area of xylem, cortex or parenchyma, epidermis (including peridermis), and proportion of cross-sectional vessel area in the xylem (Chave et al. 2009; Poorter et al. 2010). Anatomical root traits were included because root decomposition is likely associated with traits that are correlated with wood decomposition rates (Cornwell et al. 2009; van Geffen et al. 2010).

For root chemical traits, C and nitrogen (N) concentrations were determined with a Flash 1112 Elemental Analyzer (Thermo Fisher Scientific, USA) using five replicates per species. Concentrations of phosphorus (P), aluminum (Al), boron (B), calcium (Ca), copper

(Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na), and zinc (Zn) were determined by digesting 200 mg of oven-dried ground root material in 2 mL of concentrated nitric acid at 180°C under pressure in PTFE vials for 6 h. Five replicate root samples were analyzed for each species, with detection by inductively-coupled plasma optical-emission spectrometry (ICP-OES) (Optima 7300 DV, Perkin Elmer, Inc., Shelton, CT, USA). Water-soluble compounds, hemicelluloses and lignin (van Soest method) were quantified using a fiber analyzer system using four replicate samples per species (ANKOM Technology, NY, USA). Samples were enclosed in a bag and treated with a series of aggressive extractants to determine 1) neutral detergent fiber percent (% NDF- total fiber), 2) acid detergent fiber percent (% ADF – cellulose, lignin, insoluble ash) and lignin and insoluble ash percent (Alvarez-Clare and Kitajima 2007).

Data analyses

Tree species richness effects on root decomposition

Decomposition was evaluated using decomposition rates (k) that were calculated using a first order, exponential decay model proposed by Olson (1963) and fitted with a nonlinear least squares regression (nls) with untransformed data (Adair et al. 2010). Effects of tree species richness at the plot and the decomposition bag

level on root decomposition rates ($k \text{ year}^{-1}$, Supplementary material Fig. S1) were analyzed using a linear mixed effect model using ‘lme4’ (Bates et al. 2015). Specifically, site (Sardinilla vs Agua Salud), tree overstory species richness at the plot level (low vs high richness plots), tree richness at the decomposition bag level (single-species vs five species root mixture), and their interactions were included as explanatory variables (fixed effects). To account for variation in root decomposition rates within richness levels at the decomposition bag level, species composition of the roots inside the decomposition bag was treated as a random intercept. Subsequently, likelihood ratio tests using maximum likelihood estimation (Zuur et al. 2009) were used to assess the statistical significance of individual fixed effects and their interactions. Model assumptions were checked by visually inspecting residuals for homogeneity and Pearson residuals for normality. To evaluate model variation explained by fixed and random effects, marginal and conditional R^2 were calculated using ‘MuMIn’ (Nakagawa and Schielzeth 2013); marginal R^2 represents model variation explained by fixed effects in the final model and conditional R^2 represents model variation explained by random and fixed effects together.

To determine whether diversity effects on root decomposition occurred, proportional deviance was calculated (Loreau 1998) from single-species and mixtures using the following equation:

$$D_t = \frac{(O_t - E_t)}{E_t}$$

where the tree overstory species richness and species composition matched species richness and composition inside the decomposition bag (diversity effect integrating plot and decomposition bag levels, Fig. 1a). D_t was the proportional deviance of decomposition rates of the root mixture located in the high tree richness plot in Sardinilla, O_t was the observed decomposition rates taken from the root mixture located in the high tree richness plot in Sardinilla, and E_t was the expected value of decomposition rates of the root mixture, estimated from the sum of decomposition rates of single-species roots decomposing in their respective low richness plot in Sardinilla. Where single-species roots and five-species root mixtures were installed under the same tree overstory in both Sardinilla and Agua Salud (diversity effect at decomposition bag level only, Fig 1b), D_t was

the proportional deviance of decomposition rates of the root mixture, O_t was the observed decomposition rates taken from the root mixture, and E_t was the expected value of decomposition rates of the root mixture, estimated from the sum of decomposition rates of single-species roots located at sites with the same tree overstory composition.

To test whether D_t differences in each scenario were significant, 95 % confidence intervals were calculated using 10,000 bootstrap replicates (adjusted percentile bootstrap). If the 95 % CIs did not include zero, this would indicate significant non-additive effects.

Species functional identity effects on decomposition

Variation among species based on their root traits was visualized using a principal component analysis (PCA) in the “vegan” package (Oksanen et al. 2013). Ratios of C, N, and P were included due to their stoichiometric importance in the decomposition process (Manzoni et al. 2010). Due to the number of root traits measured and possible multi-collinearity, partial least squares regression (PLSR) was used to determine 1) which root traits best explained decomposition and 2) if the effects of these traits were consistent across sites. In the final models, root diameter and density, epidermis area, and concentration of Cu, Fe, Mg, and Zn were excluded because of their similarity with other traits (based on a correlation matrix, Supplementary material Table S2). PLSR models using root traits at each site were fit using the “pls” package (Mevik and Wehrens 2007). To evaluate model fit, cross validation was used. The best model was selected based on low values of mean squared errors of prediction (MSEP) and root mean square errors (RMSE) using leave-one-out (LOO) cross-validated predictions. After that, a Jackknife approximate t test of regression coefficients was performed to assess the significance of estimated effects (Martens et al. 2001). In addition, response ratios (k value in Agua Salud divided by k value in Sardinilla) were used to calculate the magnitude of the difference in decomposition rates between sites. The response ratios were then related to the initial root lignin concentration using standard major axis (SMA) regression in the ‘smatr’ package, as both contain measurement error (Warton et al. 2012). All statistical analyses were performed using R 3.1.0 (R Core Team 2015).

Results

Tree species richness effects on root decomposition

Decomposition rates of roots varied between 0.4–1.1 g year⁻¹ in Sardinilla and between 0.5–2.6 g year⁻¹ in Agua Salud (Supplementary material Fig. S1). However, we found no evidence for direct (bag level) or indirect (plot level) richness effects on root decomposition rates on decomposing roots. While the fixed and random effects explained 76 % of model variation (conditional R²), neither the interactions among fixed factors or tree species richness (low and high) at plot and decomposition bag levels were significant predictors of root decomposition rates (p -value < 0.05, Supplementary material Table S3). The only significant fixed factor in the model was site, which indicated strong differences in decomposition across sites (marginal R² = 20 %). On average, decomposition rates at Agua Salud were 40 % higher than those at Sardinilla (Supplementary material Fig. S1). No significant diversity effects (Dt) were observed either when tree species richness matched root species richness (Figs. 1a and 2a) or when decomposing under the same tree overstory (Figs. 1b and 2b).

Species functional identity effects on decomposition

Species varied markedly in their root traits (Fig. 3), with the first two axes of the principal component analysis explaining 77 % of variation. The first principal component (PC1) was largely determined by chemical traits (e.g. Al, Mn, Na), as well as some structural (diameter, and SRL) and anatomical (epidermis, vessel and xylem areas) traits. The second principal component (PC2) was defined principally by structural (lignin and RDMC) and chemical traits (e.g., Mg and Zn concentrations, hemicelluloses, and cellulose). Some anatomical traits, such as xylem area, also contributed to PC2; C:P ratio was an important trait associated with both axes, while N:P ratio was associated with PC2. The water soluble fraction of tissue was associated with both axes. Roots of *A. excelsum*, *H. crepitans*, and *T. rosea* were strongly associated with the first axis (PC1) and roots of *C. odorata* and *L. seemanii* with the second axis (PC2).

PLSR models showed which root traits explained significant amounts of variation in root decomposition rates (Fig. 4). Across sites, 39 % of the variation in decomposition rates were predicted significantly by

Al, lignin, Mn, RDMC, SRL, vessel area proportion and water soluble compounds ($p < 0.05$, Fig. 4, Supplementary material Table S4 and S5). Separate PLSR models per site explained 47 % and 81 % of the variation in k values in Sardinilla and Agua Salud, respectively (Supplementary material Table S4). The best PLSR model for Agua Salud also included C:N and C:P, while that for Sardinilla included cortex and xylem area proportion and K and Na concentrations as significant variables. Root Ca significantly predicted variation in k in Sardinilla and Agua Salud when considered individually, but not in the model considering both sites. While some root traits significantly explained root decomposition rates in all models, the magnitude (but not the direction) of the size effect varied for traits between sites (Fig. 4, Supplementary material Table S5).

Interspecific variation in root traits reflected differences in decomposition rates between sites. For example, lignin concentration explained 61 % of the difference in decomposition rates between sites (Supplementary material Fig. S2). In other words, while roots with less poor C quality decomposed up to ~60 % faster in Agua Salud than in Sardinilla, poorer C quality material decomposed ~30 % faster in Sardinilla than in Agua Salud.

Discussion

This study is the first to our knowledge to assess the effect of varying both species richness within the tree overstory and that within decomposition bags on the decomposition of tropical tree roots. With the exception of *A. excelsum* (1.4 k annual) and *H. crepitans* (2.6 k annual) in Agua Salud, our values for root decomposition rates were similar to those reported for root decomposition in other neotropical forests (0.4 to 1.1 k annual, Cusack et al. 2009). Contrary to our hypotheses, we found no significant diversity effects on root decomposition rate either at the plot level with matching tree overstory (Fig. 2a) or at the decomposition bag level in the common garden experiment (Fig. 2b). Instead, patterns of decomposition were strongly modulated by species' functional identity within root decomposition bags and the different decomposition environments (assessed by soil fertility, Table 2) at both sites. This result is consistent with that from an earlier leaf litter mixing decomposition experiment at the Sardinilla site where only species-specific responses were found

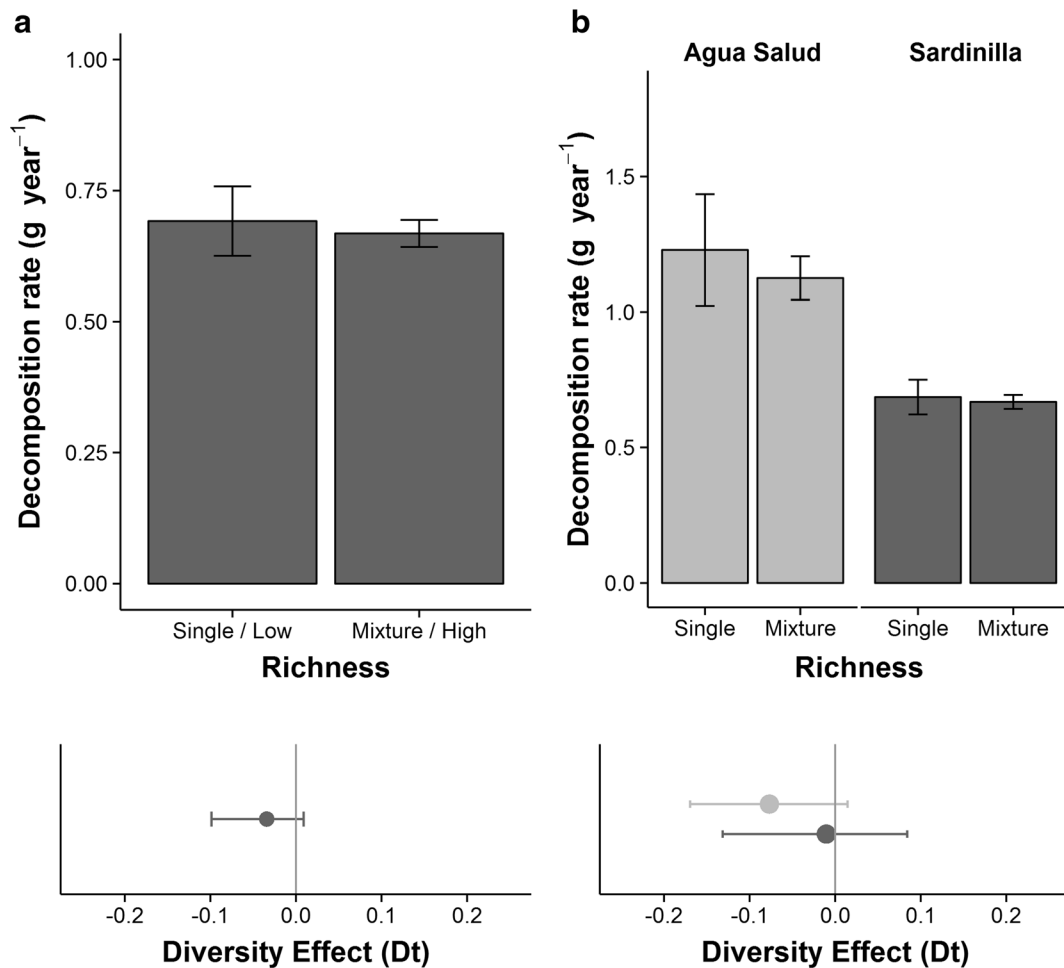


Fig. 2 Mean decomposition rates (upper panel; +SE) and diversity effects (95 % Confidence Intervals below panel) for annual k where a) tree species richness and composition matched root richness and composition inside the decomposition bag in Sardinilla, i.e. single species roots located in low richness plots

and five-species root mixtures located in high richness plots and b) single-species and five-species root mixtures were installed under the same tree overstory composition (Diversity effects inside the decomposition bag). Tree overstory compositions were used in Agua Salud (gray) and Sardinilla (dark gray)

(Scherer-Lorenzen et al. 2007). It also supports broader and more recent evidence that the effects of diversity on decomposition, if present at all, are of smaller magnitude than effects on primary productivity (Cardinale et al. 2011; Hooper et al. 2012) and may be explained by the presence of particular plant functional types within litter mixtures (Handa et al. 2014).

Environmental heterogeneity (biotic and abiotic) may have contributed to mitigating or overshadowing hypothesized diversity effects, as well as explaining the strong site differences in our study. At the plot level, this heterogeneity may have been linked to the soil environment that buffers micro-climatic conditions (Silver and Miya 2001), such that inherent soil properties may have

affected root decomposition more strongly than soil changes resulting from varying overstory tree species richness. Variability between sites may have affected soil properties, such as fertility and pH, which can influence decomposer communities (Wardle et al. 2004; Fierer & Jackson, 2006, Lauber et al., 2008). Strong site differences in decomposition rates were presumably related to the differing nutrient status between sites (Table 2), mostly related with available P (63 % higher in Sardinilla than in Agua Salud). There were also differences in the tree overstory richness of high diversity plots and the age of forest establishment (3 vs 10 yrs., Agua Salud and Sardinilla) in the low diversity plots, although, with no significant diversity effects

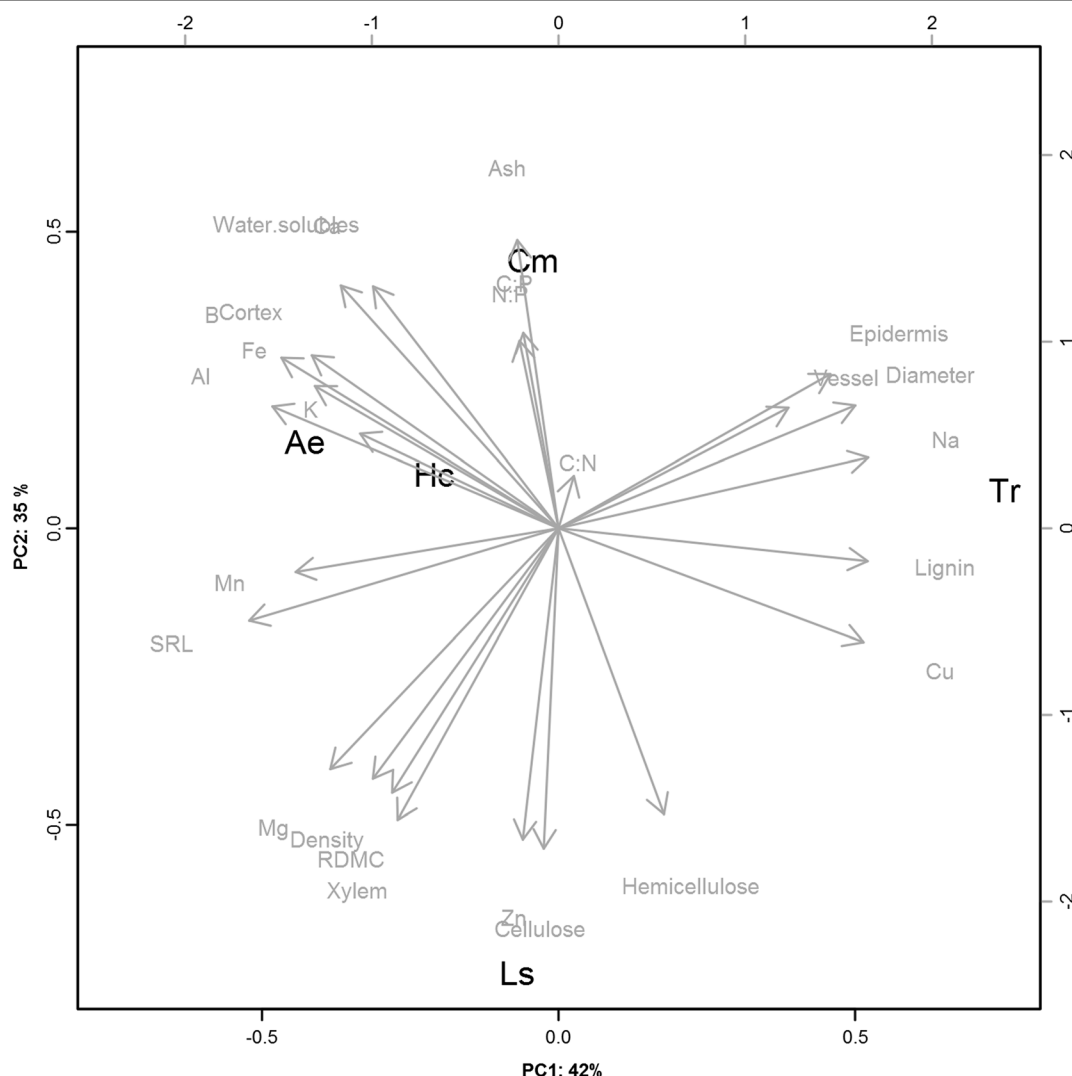


Fig. 3 Principal component analysis using all measured root functional traits. Five species used: *Anacardium excelsum* (Ae), *Cedrela odorata* (Cm), *Hura crepitans* (Hc), *Luehea seemanii* (Ls) and *Tabebuia rosea* (Tr). Root functional traits were: specific root length (SRL), root dry matter content (RDMC), vessel

proportion related to xylem area (Vessel), carbon (C), nitrogen (N), phosphorus (P), aluminum (Al), boron (B), calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na) and, zinc (Zn)

reported, these varying factors within the tree overstory diversity treatment conditions seem less important than more intrinsic decomposition environment characteristics to explain root decomposition results.

With 39 % of decomposition explained by traits across both sites and up to 81 % explained at the Agua Salud site (Fig. 4, Supplementary material Table S4 and S5), our results provide a basis for selecting a wider array of root functional traits that could capture key dimensions of interspecific variation relevant for predicting decomposition and nutrient cycling. Two

broad groups of traits emerge from our analyses: the first associated with C quality (e.g. structural toughness) of the roots, and the second, with micronutrient concentrations. Roots associated with poorer C quality for decomposers as measured here included high lignin and high RDMC, and proportion of cross-sectional vessel area in the xylem that correlated negatively with root decomposition (Fig. 4, Supplementary material Table S5). Greater vessel area could limit decomposer mobility when interstitial spaces are plugged with tyloses, gum, or resin (van Geffen et al. 2010). This

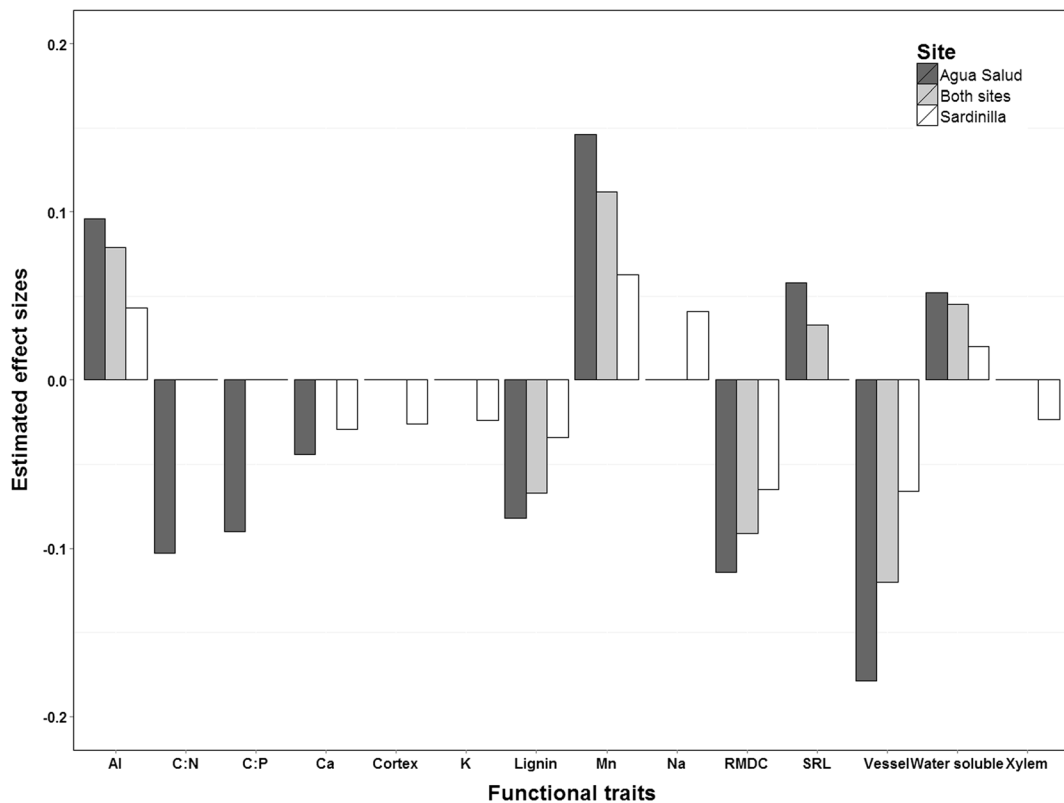


Fig. 4 Significant effect sizes ($\alpha < 0.05$) of fitted PLSR models testing relationships between root functional traits and root decomposition rates using Jackknife approximate regression coefficients test. The percent of decomposition rate variation explained by functional traits varied among 39, 47 and 81 % in both sites, fertile site (Sardinilla) and infertile site (Agua Salud), respectively.

Abbreviations of functional traits include aluminum (Al), carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), potassium (K), manganese (Mn), sodium (Na), root dry matter content (RDMC), specific root length (SRL), and vessel proportion related to xylem area (Vessel). R^2 values show the percent of variation explained by each model

group of traits are associated generally with slower ecosystem process rates reflecting poorer litter quality for decomposers (Hättenschwiler et al. 2011). The second group of traits reflected the micronutrient concentrations of litter and points to a newly emerging functional understanding of decomposition that shows the importance of these micronutrients to decomposer communities (e.g. Mg: Makkonen et al. 2012, Ca and Mg: García-Palacios et al. 2016, Hobbie 2015). In our study, the concentration of Mn was a strong positive predictor of root decomposition (Fig. 4). Mechanisms explaining the positive link to decomposition may include the role of Mn in regulating the activity of enzymes involved in degradation (Baldrian and Snajdr 2011; Hobbie 2015). In addition, a potential toxin, Al, was also a positive predictor of root decomposition. Aluminium is known to have anti-fungal properties such that only highly adapted fungal taxa are associated with leaves having high Al concentrations (Kembel and Mueller 2014).

Possibly, such specialization may also occur on root tissue and Al-resistant taxa may be particularly efficient at organic matter decomposition.

Interestingly, the relative importance of individual root traits varied across decomposition environments (sites), thus illustrating the relevance of substrate-quality matrix interactions (Freschet et al. 2012a). Substrate-quality interactions, i.e. the interaction between litter quality and the decomposition environment, could be linked to differences in the nutritional requirements between decomposer communities and nutrient limitations in the ecosystem (Kaspari et al. 2008; Hobbie 2015). For example, C:P was a significant variable for predicting decomposition rates in the infertile (Agua Salud) site but not in the fertile (Sardinilla) site. Such a difference could be explained by the association of the infertile site with P-poor soil, which are common on old, stable landscapes in the tropics (Vitousek and Sanford 1986). Clearly, studies focusing on the

mechanisms underlying such interactions and in understanding other factors that could explain root decomposition across sites are required. Nonetheless, an understanding of which traits are relevant in particular soils, especially in tropical forests that demonstrate large spatial variation in soil nutrients (Condit et al. 2013; John et al. 2007), will enable us to arrive at better large-scale predictions about nutrient cycling.

Our results show that tropical tree communities do not influence root decomposition through tree species richness at either the plot or decomposition bag levels, but rather through functional identity associated with root quality. As a result, changes in tree overstory composition in tropical regions that alter functional composition, e.g., land-use change or drought, could have significant repercussions on ecosystem processes such as root decomposition. Although we did not observe significant effects of tree species richness on root decomposition at the levels that we studied, our approach to quantify diversity effects at decomposition bag and overstory plot levels allowed us to address different potential mechanisms of tree species richness on decomposition. Given that decomposition is a dynamic process, we recommend including temporal and spatial approaches to evaluate if diversity effects are present at specific stages of decomposition or if diversity influences are not reflected in mean decomposition rates but in their variance across space. Using a wide array of 27 root traits, we found strong interspecific variation in structural traits associated with C quality to decomposers, as well as chemical micronutrient traits that predict root decomposition. These traits can provide not only a basis for further studies on root decomposition as new species are assessed, but also contribute to understanding the link between specific plant ecological strategies and ecosystem functions. Finally, intrinsic soil chemical and physical characteristics that could influence soil decomposer communities may also strongly modulate root decomposition in tropical forests, suggesting the importance of integrating multi-site studies to determine the consistency of the results, e.g. the relationship between tree diversity and belowground-processes, under varied environmental conditions.

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