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Litter Traits of Native and Non-Native Tropical Trees Influence Soil Carbon Dynamics in Timber Plantations in Panama

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Abstract: Tropical reforestation initiatives are widely recognized as a key strategy for mitigating rising atmospheric CO_2 concentrations. Although rapid tree growth in young secondary forests and plantations sequesters large amounts of carbon (C) in biomass, the choice of tree species for reforestation projects is crucial, as species identity and diversity affect microbial activity and soil C cycling via plant litter inputs. The decay rate of litter is largely determined by its chemical and physical properties, and trait complementarity of diverse litter mixtures can produce non-additive effects, which facilitate or delay decomposition. Furthermore, microbial communities may preferentially decompose litter from native tree species (homefield advantage). Hence, information on how different tree species influence soil carbon dynamics could inform reforestation efforts to maximize soil C storage. We established a decomposition experiment in Panama, Central America, using mesocosms and litterbags in monoculture plantations of native species (*Dalbergia retusa* Hemsl. and *Terminalia amazonia* J.F.Gmel., Exell) or teak (*Tectona grandis* L.f.) to assess the influence of different litter types and litter mixtures on soil C dynamics. We used reciprocal litter transplant experiments to assess the homefield advantage and litter mixtures to determine facilitative or antagonistic effects on decomposition rates and soil respiration in all plantation types. Although litter properties explained some of the variation in decomposition, the microclimate and soil properties in the plantations also played an important role. Microbial biomass C and litter decomposition were lower in *Tectona* than in the native plantations. We observed non-additive effects of mixtures with *Tectona* and *Dalbergia* litter on both decomposition and soil respiration, but the effect depended on plantation type. Further, there was a homefield disadvantage for soil respiration in *Tectona* and *Terminalia* plantations. Our results suggest that tree species diversity plays an important role in the resilience of tropical soils and that plantations with native tree species could help maintain key processes involved in soil carbon sequestration.

Keywords: tropical forest; soil carbon; homefield advantage; litter decomposition; litter traits; non-additive effects; plantations; soil respiration

1. Introduction

Soil is the largest global terrestrial carbon (C) pool, containing an estimated 2344 Gt of organic C in the top three meters [1]. It is estimated that 16 to 20% of all soil organic C is in tropical evergreen forests [2]. Consequently, although tropical forests only cover c. 6% of the world's land, they are

extremely important global reservoirs of C [3]. The Bonn challenge, launched in 2011, aims to reforest 150 million hectares of degraded land by 2020; it is particularly centered around reforesting degraded landscapes in and with rural communities [4]. In Central America, much of the eroding landscape comprises land for pasture and crop agriculture, and reforestation projects are encouraging small landowners to grow timber plantations. One of the most common commercial tree species planted in the region is teak (*Tectona grandis* L.f.), an introduced species originating from South and Southeast Asia. In Panama, *Tectona* plantations represent 76% of the timber trees planted between 1992 and 2002 [5]. However, *Tectona* does not grow particularly well on the acidic clay soils typical of many areas of Panama, including around the Panama Canal Watershed [6]. This is of concern because the failure of commercial reforestation projects not only reduces the return on investments by landowners but can also have negative consequences for overall ecosystem function. More recently, reforestation projects have therefore focused on the commercial viability and ecological benefits of native tree species in tropical plantations [7–9].

The species of trees in tropical timber plantations can influence multiple ecosystem services, including belowground C storage [7,10,11]. Trees play an essential role in maintaining the soil C pool through inputs of organic C and other nutrients from decomposing leaf litter [12,13]. Tree species identity also has a strong influence on decomposition processes, because the decay rate of litter is determined by its physical and chemical traits, which determine the quality of substrate available to decomposer organisms [14,15]. Decomposers preferentially break down high-quality litter, e.g., litter with low lignin or high nutrient content, which enables the transfer of nutrients to facilitate the decomposition of low-quality litter [12,16] and as a result, the functional diversity of the litter governs the rate of decomposition [17]. Hence, different tree species produce litter of varying decomposability and interact with the rhizosphere, causing microenvironmental changes that affect microbial activity and therefore soil elemental cycling [12,18,19].

Tree diversity can also influence C cycling during decomposition through three distinct interaction mechanisms: (i) 'non-additive effects', whereby mixed species litters decompose faster than expected as a result of trait complementarity, or more slowly than expected due to inhibitory effects [20–22]; (ii) the 'homefield advantage', in which soil microbial communities have an affinity for litter from the site of origin and therefore litter decomposes faster if it is close to the parent tree; [23,24]; (iii) allelopathic chemicals released by some plant species that can hinder other plants and microbial communities [25]. However, we still know relatively little about the influence of tree species on soil C dynamics in the tropics. To date, only few studies have focused on functional properties of leaf litter in tropical forests [20,26,27] and recent work suggests that non-additive effects can occur during decomposition of litter mixtures based on functional groups of trees [17]. Given the immense biodiversity of tropical forests, the potential influence of individual species on decomposition processes and soil C dynamics remains largely uncharacterized.

Understanding the interactions between aboveground plant inputs, decomposition processes and the soil food web is an essential first step towards determining how tree species identity and diversity influence ecosystem function in reforestation projects and to assess their potential for soil C sequestration. We established an experiment in a reforestation project in Panama, Central America, to assess the influence of litter from native vs. introduced trees, and single-species litter vs. litter mixtures. We compared and contrasted soil properties in monoculture plantations of the native species Cocobolo (*Dalbergia retusa* Hemsl.) and Amarillo (*Terminalia amazonia* J.F.Gmel., Exell) and in *Tectona grandis* L.f. plantations, and measured decomposition processes and soil respiration to characterize C dynamics, using litter transplant experiments to test the following hypotheses:

1. Differences in soil microbial biomass and soil respiration among plantations and litter types will be related to soil properties and litter decomposition rates.
2. Leaf traits related to resource quality for microbial communities (such as lignin: nitrogen ratio and C content) will explain the variation in decomposition among species and litter mixtures.

3. As a result of trait complementarity, litter mixtures will have higher decay rates than expected, based on the decay rates of individual constituent species.
4. As plant inputs represent the main substrate for decomposers and as microbial communities adapt to available resources, native litter decomposes faster under the species of origin (homefield advantage), whereas the decomposition of all litter types is slower in teak plantations.

2. Materials and Methods

2.1. Study Site and Litter Mixtures

The Agua Salud Project is a large-scale experiment studying ecosystem functions and services in varying land-use types ranging from forest to timber plantations to pastoral land situated in the Panama Canal Watershed (9°13′ N, 79°47′ W, 330 m a.s.l.), in Panama, Central America [28]. The soils are classified as infertile Oxisols (Inceptic Hapludox) and Inceptisols (Oxic and Typic Dystrudepts), which are strongly weathered and well-drained, and the topsoil texture is silty clay to clay [29]. The study area has a tropical climate with a mean daytime temperature of 32 °C, mean annual rainfall of 2700 mm [30] and a distinct dry season between January and April [31].

The present study was conducted within plantations at Agua Salud, which were established on sites formerly used as pastures that had reverted to young secondary forest for five years prior to the initial clearing and planting of the monocultures in 2008. The experimental site includes plantations of the native pioneer species *Dalbergia retusa*, a nitrogen-fixing, slow-growing species [32] that is sensitive to soil fertility [29] and *Terminalia amazonia*, a fast-growing species that responds strongly to differences in soil fertility [28,29] as well as teak, *Tectona grandis*, an introduced timber species from Southeast Asia. The *Dalbergia* and *Terminalia* plantations were fertilized at planting with 57 g of a complete nitrogen-phosphorus-potassium (NPK) fertilizer (12:24:12 NPK) and organic material mixed with soil and 57 g of triple sulphate; the fertilizers were applied several centimeters from the roots [28]. The *Tectona* plantation was fertilized at planting and then twice a year for the first two years, including surface application of $CaCO_3$ once a year to raise the soil pH. The native timber species were planted in plots measuring 42 m × 36.5 m and each plot contained 225 trees; *Tectona* was planted in one large area of 1 km^2. The underlying vegetation (mostly grasses and herbaceous plants) between the trees was cut every three months, except in the *Tectona* where the vegetation was not cut during the present experiment. The distance between sites did not exceed 2 km, and the sites were chosen to ensure similar slope, elevation and bedrock.

2.2. Experimental Design

We established a mesocosm experiment with five replicate blocks in each of the three plantation types. Each block consisted of two sets of eight mesocosms (16 per block) to allow destructive sampling after three and six months. The mesocosms were made of PVC pipe (20 cm inner diameter and 15 cm height), which were sunk into the ground to 5 cm depth, so that the height above the soil was 10 cm. The mesocosms were installed at least one month prior to the start of the experiment to allow the surrounding soil to recover from the initial disturbance, any existing litter was removed from the mesocosms prior to the application of litter treatments and the area around the mesocosms was maintained free of herbaceous plants and grasses.

Litter for the experiment was collected by hand, choosing freshly fallen leaves in each monoculture plot and air-drying them at 30 °C. Each single-species litter was cut to yield pieces of *c.* 4 cm^2. Each mesocosm received 6 g of litter at the start of the experiment. Two mesocosms per block were randomly assigned to one of seven litter treatments, comprising single-species *Dalbergia* (DAL), *Terminalia* (TERM) and *Tectona* (TEC) litter, as well as all possible two-species combinations and a three-species mixture (Figure 1). Henceforth, we use genus to refer to trees and plantations and the abbreviations DAL, TERM and TEC to refer to litter types. We used equal mass of each species in the litter mixtures. Subsamples of each litter type were ground for nutrient analysis (see below).

To simulate natural litterfall, we then added 1 g of litter, taken from the same initial samples per litter type and mixture, every month over 6 months so that each mesocosm had received a total of 12 g of air-dried litter by the end of the study, which was equivalent to the mean litter standing crop of all three monocultures (n = 15). To control for differences in soil properties and rhizosphere respiration among plantations, the remaining mesocosms were left as bare soil controls (CT) with no litter inputs. All mesocosms were covered with 1 cm^2 wire mesh to exclude natural litterfall. Hence, the experiment comprised three plantation types, each with five replicate blocks containing two sets of mesocosms assigned to eight treatments (Figure 1), making a total of 240 mesocosms.

To calculate litter decomposition after three and six months, we made litterbags using 1.4 mm fiberglass mesh. Each bag was 8 cm × 8 cm and contained 3 g of air-dried material of one of the seven litter treatments, which was equivalent to half the surface area and half the amount of litter in the mesocosms. We placed two bags per litter type in each replicate block on the soil surface within 1 m of the corresponding mesocosms, making a total of 210 bags. We collected one bag per litter type and block after three months and again after six months. The remaining litter from each bag was rinsed under running water for two minutes to remove as much soil as possible without losing material; the rinsed litter was then oven-dried at 40 °C for 48 h before being weighed to calculate percentage mass loss after three and six months. We calculated percentage mass loss by subtracting the remaining litter after three or six months from the weight of the litter at the start of the experiment.

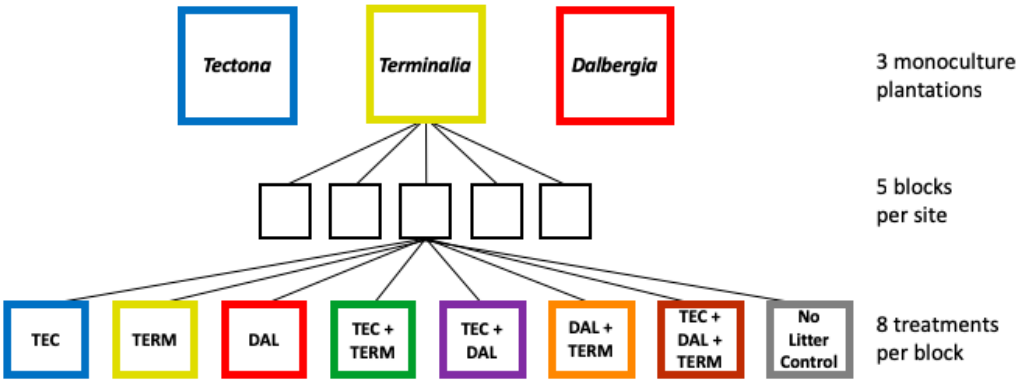

Figure 1. Schematic diagram showing the design of a litter mesocosm experiment in tropical timber plantations in Panama, Central America; the top row of boxes represents three monoculture plantations; in each plantation there are five replicate blocks (centre row), and in each block there are mesocosms with one of eight treatments (bottom row) including single-species litter and all two-and three-species mixtures, as well as a bare soil control without litter, where TEC is *Tectona grandis*, TERM is *Terminalia amazonia* and DAL is *Dalbergia retusa* litter.

2.3. Field Measurements and Sampling

Soil respiration was measured monthly in situ over the mesocosms using an infrared gas analyzer (Li-8100; LI-COR Biosciences, Lincoln, NE, USA) with a 20 cm diameter survey chamber. At the same time, soil temperature was measured using a Fisherbrand® Traceable Thermometer (Fisherbrand, Hampton, FL, USA) and moisture was measured using a SM150T soil moisture sensor (Delta-T Devices, Cambridge, UK).

We measured nutrient release during litter decomposition in April 2017, four months after the start of the experiment. We placed pairs of anion and cation exchange resin membranes (PRS Probes®, WesternAG, SK, Canada) beneath the litter for each litter treatment in three replicate blocks per plantation (n = 3 per litter treatment and plantation). After one month (exposure time 27–29 days), we collected the probes and stored them at 5 °C before cleaning them thoroughly with pressurized deionized water according to manufacturer instructions. The cleaned probes were then sent to the manufacturer for analysis of available nitrate-N, ammonium-N, phosphorus, potassium, calcium and magnesium.

To characterize initial soil total C and N, phosphorus (P) and potassium (K) concentrations and soil pH, we collected five soil cores from each block in December 2016. The soil samples were mixed to form one composite sample per block, air-dried at 30 °C, and then stored in polyethylene resealable bags until chemical analysis. After three and six months, we collected two soil cores inside one mesocosm per treatment and block; the two samples were pooled to yield five replicate samples per treatment and monoculture. Samples for analysis of soil microbial biomass C and N were refrigerated for seven days. The remaining material was air-dried at 40°C. All soil sampling was carried out to a depth of 10 cm using a 3-cm-diameter punch corer.

2.4. Laboratory Analyses

2.4.1. Soil and Litter Nutrients

Total C and N were analyzed on ground air-dried soil and litter samples (Mixer Mill 400, Retsch®, Haan, Germany) by high temperature combustion gas chromatography (Vario El III C/N analyser; Elementar, Stockport, UK) at Lancaster University using 30 mg of soil and 15 mg of litter. Air-dried, ground soil and litter samples were sent to SAC Consulting (Aberdeen, Scotland, UK) for analysis of soil extractable phosphorus (P) and potassium (K) and litter P, K, calcium (Ca) and magnesium (Mg) concentrations.

2.4.2. Soil Microbial Biomass by Fumigation-Extraction

To determine microbial biomass C and N, we used the modified fumigation-extraction method [33,34] with paired 6 g subsamples of fresh soil. Briefly, one subsample per pair was fumigated with ethanol-free amylene-stabilized chloroform for 24 h. Both the fumigated and non-fumigated subsamples were then extracted with 40 mL 0.5 M K_2SO_4 and then centrifuged and filtered through pre-washed Whatman 42® (GE Healthcare, Chicago, IL, USA) filter paper or equivalent. The extracts were then diluted nine times with deionized water before being analyzed for total organic C and total N on a TOC-L combustion analyzer coupled with a TNM-L unit (Shimadzu Corp, Kyoto, Japan). Microbial biomass C and N were calculated from the difference between non-fumigated and fumigated samples.

2.4.3. Litter Fiber and Lignin

To determine the fiber and lignin content of the litter, we used the acid detergent extraction described by Van Soest et al. (1991) [35]. The method has two steps; the first acid detergent fiber (ADF) step extracts all the fiber from the litter and the second acid detergent lignin (ADL) step extracts the lignin from the extracted fiber. Briefly, 1 g of each dried and ground litter sample was placed in a crucible with 1 g of acetanilide. The litter and acetanilide mixtures were boiled with 100 mL of acid detergent solution for one hour in a FOSS fibertec™ 8000 fiber analysis system (FOSS, Hilleroed, Denmark). The samples were then washed with warm distilled water until acid-free and were rinsed with reagent-grade acetone. The samples were dried overnight at 105 °C before being weighed, and the total extracted fiber content (ADF) was calculated by subtracting the weight of the processed sample from the original sample weight (corrected with blanks). After weighing, the samples were soaked in 25 mL H_2SO_4 (72%) for three hours; the crucibles were rinsed with hot distilled water using the FOSS fibertec™ 8000 fiber analysis system (FOSS, Hilleroed, Denmark) and dried at 105 °C overnight before being placed in a furnace at 525 °C for three hours. The samples were finally left to cool to room temperature in a desiccator before weighing. The lignin content (ADL) was calculated by subtracting the weight of the sample at the final stage from the weight of total extracted fiber (ADF) with correction with blanks.

2.5. Data Analyses

To compare decomposition across litter treatments and sites, we calculated the decay rate k (1) for each litter treatment and block according to Olson (1963) [36]:

$$\ln\left(\frac{X}{X_0}\right) = kt \quad (1)$$

where t is time in years, X_0 is the original weight and X is the weight after decomposition.

To assess the influence of litter treatments on soil respiration across sites, we calculated the log response ratios of soil respiration (2) [22] for each litter treatment, replicate block and month using the following equation:

$$\text{Response ratio, } RR_X = \ln(R_X/R_{CT}) \quad (2)$$

where R_x is the value of soil respiration in a given treatment and R_{CT} is the value of soil respiration in the corresponding control.

Homefield Advantage and Non-Additive Effects of Species Mixtures

We calculated the homefield advantage (HFA) for litter decomposition and mean soil respiration of the single-species litters after three and six months using the Equations (3)–(6) described by Ayres et al. (2009) [23] where values >0 indicate that the litter decomposes faster in its home plantation, values <0 indicate that the litter decomposes slower in its home plantation, and zero indicates no HFA.

$$Home\ Decomposition\ (HDD) = (D_{aA} - D_{bA}) + (D_{aA} - D_{cA}) \quad (3)$$

$$Away\ Decomposition\ (ADD) = (D_{aB} - D_{bB}) + (D_{aC} - D_{cC}) \quad (4)$$

$$H = \frac{(HDDa + HDDb + HDDc)}{(N-1)} \quad (5)$$

$$HFA = HDD - ADD - H \quad (6)$$

where D is the measure of decomposition (decay or respiration rate), $_a$, $_b$, and $_c$ are the single-species litters, $_A$, $_B$, and $_C$ are the plantations, N is the number of species, and H is the mean HFA for all the species used in the experiment.

To calculate if there were any facilitative or antagonistic effects during decomposition of litter mixtures, we compared the observed rates of mass loss and soil respiration of two- or three-species mixtures to the expected rates calculated from the means of the component species.

2.6. Statistical Analyses

All statistical analyses were conducted in R version 3.4.2 [37], using the vegan package [38] for multivariate analyses and the lme4 package for mixed effects models [39].

First, we used Principal Component Analysis (PCA) to visualize differences among plantations based on initial soil properties (total C, Total N, C:N ratio, P, K and pH). We then used linear models to assess if there were differences in individual soil properties among the plantations (lm function). We also used PCAs assess differences in nutrient release from different litter treatments and among plantations; values of individual nutrients were fitted as vectors to aid interpretation.

We tested the effects of plantation type and litter treatment on litter mass loss, soil temperature, soil moisture, mean soil respiration and the response ratios of soil respiration using linear mixed effects models with plantation, litter treatment and their interaction as fixed effects and time and block as random effects (lmer function). The significance of individual terms was tested with nested models using AIC and p-values to compare models as terms were dropped sequentially. The final model was tested against the appropriate null model and the model fit was assessed using diagnostic plots [36]. The effects of plantation and litter type on microbial biomass and nutrient supply from the resin probes were assessed using linear models (lm function) [40].

Finally, we tested the HFA for litter mass loss or soil respiration by performing a t-test on HFA scores (n = 5) to assess if they differed significantly from zero.

Results are reported as significant at $p < 0.05$ but as our replication is low ($n = 5$), we also present marginally significant trends at $p < 0.1$.

3. Results

3.1. Site and Litter Characteristics

Principal component analysis of the soil properties showed a separation of the *Dalbergia* plantations from the *Tectona* and *Terminalia* plantations (Figure 2); the separation was explained by soil total C and N on the first PCA axis and by soil P on the second axis. The first PCA axis explained 41% of the variation and soil C and N had the highest loading; the second axis explained 33% of the variation and soil P had the highest loading. Accordingly, the *Dalbergia* plantation had a significantly lower soil C:N ratio ($F_{2,12} = 21.42$, $p < 0.001$) and lower soil extractable K ($F_{2,12} = 4.35$, $p = 0.038$) compared to the other two plantations, whereas total soil N was marginally lower in the *Tectona* plantation ($p = 0.09$; Table 1).

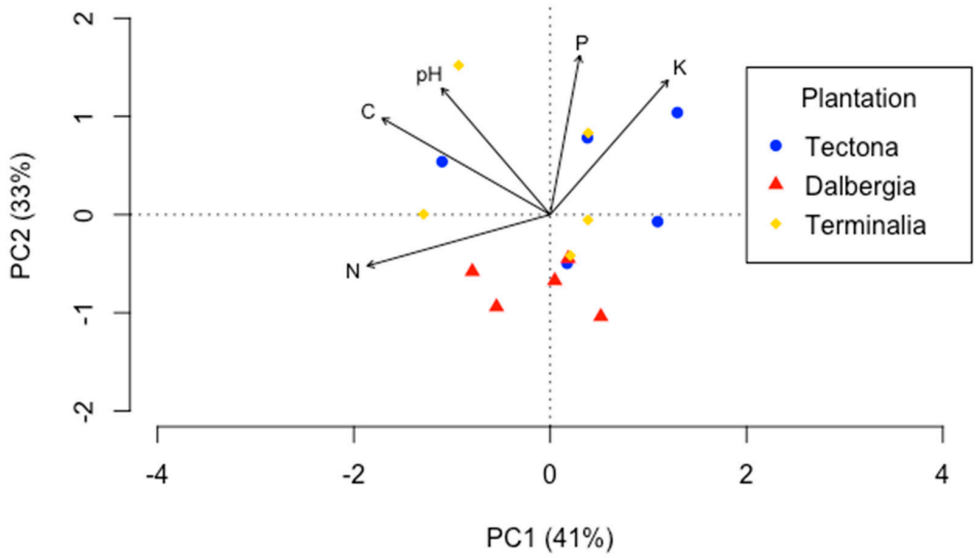

Figure 2. Principal component analysis of soil properties (C, N, P, K and pH) measured in each of five blocks in three monoculture plantations: *Tectona grandis* (blue circles), *Dalbergia retusa* (red triangles) and *Terminalia amazonia* (yellow diamonds) at the start of a mesocosm experiment in Panama, Central America.

Table 1. Initial soil properties in three monoculture plantations used in a litter decomposition experiment in Panama, Central America, showing total soil carbon (C), total soil nitrogen (N) and carbon to nitrogen (C:N) ratios, extractable phosphorus (P), and potassium (K) concentrations, and soil pH. Means ± standard errors are shown for $n = 5$ composite soil samples; different lower-case superscript letters indicate significant differences among plantations at $p < 0.05$ and different upper-case superscript letters indicate trends at $p < 0.1$.

Soil Property/Plantation	*Tectona*	*Dalbergia*	*Terminalia*
Total C (%)	4.58 ± 0.20	4.38 ± 0.08	4.90 ± 0.23
Total N (%)	0.41 ± 0.02 ^{A}	0.45 ± 0.01 ^{B}	0.44 ± 0.02 ^{B}
C:N ratio	11.29 ± 0.13 ^{a}	9.69 ±0.07 ^{b}	11.07 ± 0.32 ^{a}
P (mg kg^{-1})	3.35 ± 0.30	3.09 ± 0.17	3.75 ± 0.34
K (mg kg^{-1})	759 ± 72 ^{a}	501 ± 58 ^{b}	651 ± 55 ^{a}
pH	5.064 ± 0.08	4.93 ± 0.08	5.032 ± 0.06

Of the three single-species litters, DAL had the highest N concentrations, the lowest C:N ratio, P concentrations and lignin to N (L:N) ratio compared to the other litter types. TEC litter had the

highest fiber and lignin content but a similar L:N ratio to the TERM litter. TERM litter had the highest C:N ratio and nearly double the Ca content of the TEC and DAL litter (Table 2).

Table 2. Litter properties of the three species used in a decomposition study in Panama, Central America; where TEC is *Tectona grandis* litter, DAL is *Dalbergia retusa* litter and TERM is *Terminalia amazonia* litter. The values shown are from one composite sample (n = 1) per litter type for total carbon (C), nitrogen (N), phosphorus (P), potassium (K), C:N ratio, fibre, lignin (L), L:N ratio, calcium (Ca), and magnesium (Mg).

Litter Nutrients\Litter Type	TEC	DAL	TERM
Total C %	49.31	46.91	47.28
Total N %	1.48	2.24	1.03
C:N ratio	33.2	20.9	46
P %	0.0894	0.0399	0.0568
K %	0.468	0.479	0.673
Fibre %	29.9	22.8	24.5
Lignin (L) %	13.6	8.1	10.2
L:N	10.18	3.86	10.29
Ca %	1.23	1.35	2.16
Mg %	0.36	0.322	0.215

3.2. General Patterns for Individual Species

Overall, soil respiration was lowest in the *Tectona* plantation and highest in the *Terminalia* plantation, which can be at least partly explained by consistently higher soil water content in the *Terminalia* plantation (χ^2 = 253.75, $p < 0.001$; Figure S1). However, soil temperature in the *Terminalia* plantation was significantly lower than that in the *Tectona* and *Dalbergia* plantations (χ^2 = 182.07, $p < 0.001$, Figure S2) from February until April. The model that best explained soil respiration included plantation, litter treatment and their interaction (χ^2 = 68.309, $p < 0.001$), as respiration rates from mesocosms with TEC litter were slightly higher in the *Terminalia* plantation, but lower in the *Tectona* plantation when compared to the other litter types (Figure 3). There was no significant effect of plantation or litter treatment when the response ratios of soil respiration were analyzed, indicating that the surface litter contributed relatively little to total belowground respiration.

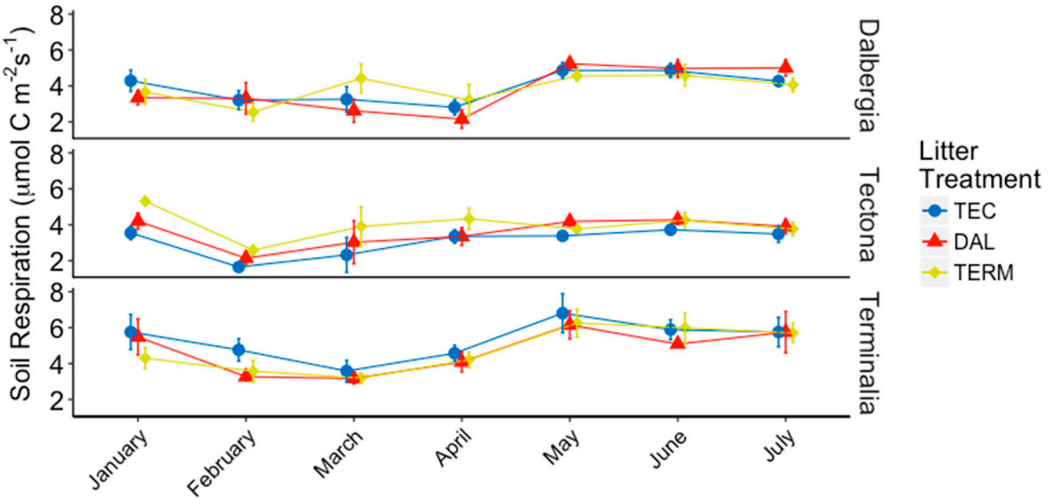

Figure 3. Soil respiration in a litter decomposition experiment in monoculture plantations of *Tectona grandis*, *Dalbergia retusa* and *Terminalia amazonia* in Panama, Central America, where TEC (blue circles) is *Tectona grandis* litter, DAL (red triangles) is *Dalbergia retusa* litter and TERM (yellow diamonds) is *Terminalia amazonia* litter. The measurements were taken over the mesocosm (n = 5 per plantation) every month during 7 months from May until July 2017.

After six months, DAL litter had the highest decay rate regardless of plantation and the TERM litter tended to have a lower decay rate, but all single-species litters decayed more slowly in the *Terminalia* plantation (Figure 4). Litter treatment ($F_{2,32} = 5.75$, $p = 0.007$) and plantation ($F_{2,32} = 10.48$, $p < 0.001$) both had a significant effect on litter decay rates.

The PCA of the nutrients released from the decomposing litter using resin probes showed no separation of the different litter treatments or the plantations, indicating similar dynamics of nutrient release across litter treatments and sites. The only nutrient that differed significantly among sites or litter treatments was N; total N release was highest in the *Tectona* plantation ($F_{2,18} = 8.20$, $p = 0.003$) whereas nitrate concentrations were below the detection limit for all the litters in the *Terminalia* plantation, which may indicate immobilization of N. The DAL litter showed the highest release of nitrate in the *Tectona* plantation ($F_{2,8} = 12.75$, $p = 0.002$).

Microbial biomass C was lowest in the *Tectona* plantation, regardless of litter treatment, but microbial biomass N was significantly higher in *Tectona* than in *Terminalia* and *Dalbergia* plantations, which had similar microbial biomass C (Figure 5); and *Terminalia* had significantly lower microbial biomass N. Litter treatment had no significant effect on microbial biomass C or N after six months of decomposition and the models that best explained microbial biomass C and N included plantation only (microbial C: $\chi^2 = 710.57$, $p < 0.001$; microbial N: $\chi^2 = 444.12$, $p < 0.001$).

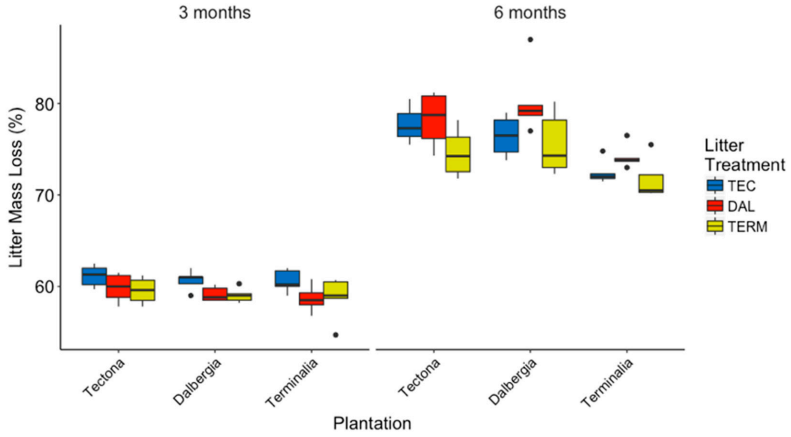

Figure 4. Litter mass loss after three months (April 2017) and six months (July 2017) in a litter decomposition experiment in monoculture plantations of *Tectona grandis*, *Dalbergia retusa* and *Terminalia amazonia* in Panama, Central America. Mass loss was measured for each litter type in all plantations, where TEC is *Tectona grandis*, DAL is *Dalbergia retusa* and TERM is *Terminalia amazonia* litter ($n = 5$).

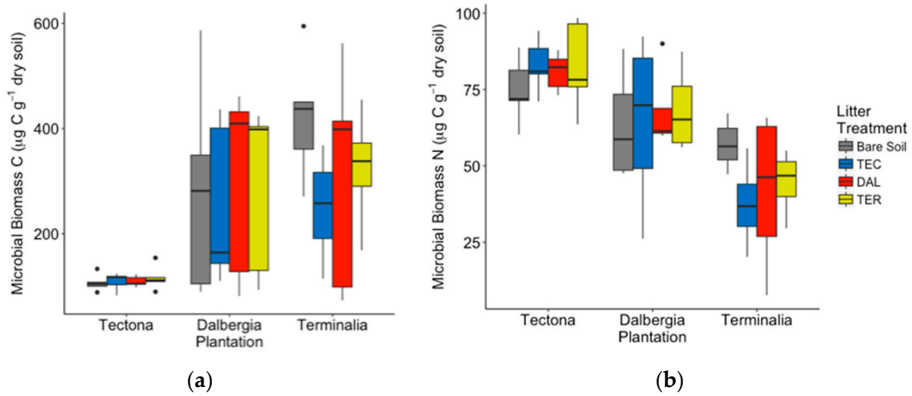

Figure 5. Soil microbial biomass carbon (C) (**a**) and nitrogen (N) (**b**) after six months (July 2017) in a litter decomposition experiment in monoculture plantations of *Tectona grandis*, *Dalbergia retusa* and *Terminalia amazonia* in Panama, Central America. Mass loss was measured for each litter type in all plantations, where TEC is *Tectona grandis*, DAL is *Dalbergia retusa* and TERM is *Terminalia amazonia* litter ($n = 5$).

3.3. Homefield Advantage

There was no evidence of a homefield advantage for decomposition after three or six months, as the HFA did not differ significantly from zero for any of the litter types. However, there was evidence of a homefield disadvantage for soil respiration (Figure 6), where respiration in mesocosms with TEC litter was significantly lower in its home plantation after both three ($t_4 = -3.19$, $p = 0.033$) and six months ($t_4 = -2.93$, $p = 0.043$).

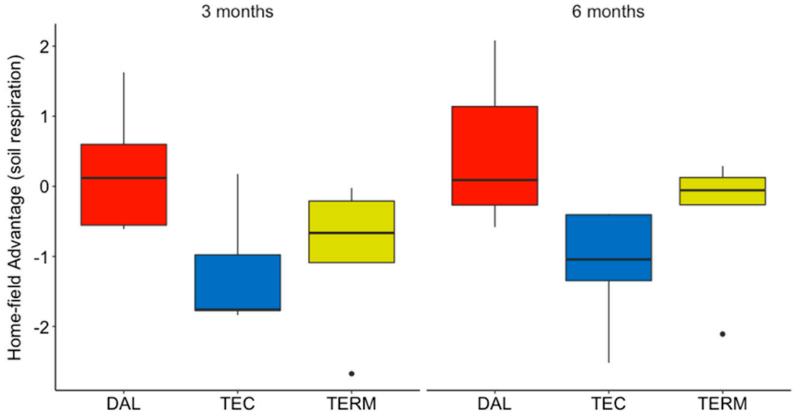

Figure 6. Homefield advantage of mean soil respiration during three and six months of a litter decomposition experiment in monoculture plantations of *Tectona grandis*, *Dalbergia retusa* and *Terminalia amazonia* in Panama, Central America. The homefield advantage was calculated for each litter type, where TEC is *Tectona grandis*, DAL is *Dalbergia retusa* and TERM is *Terminalia amazonia* litter within each plantation ($n = 5$).

3.4. Non-Additive Effects of Species Mixtures

There were no significant non-additive effects for decomposition or soil respiration for mixed TEC + TERM, DAL + TERM or TEC + DAL + TERM litters. However, after three months of decomposition, the observed mass loss of the TEC + DAL mixed litter was lower than expected in all the plantations ($F_{1, 45} = 11.24$, $p = 0.002$). After six months, the decay rate was lower for the mixed species TEC+DAL litterbags in the *Dalbergia* plantation only (Figure 7).

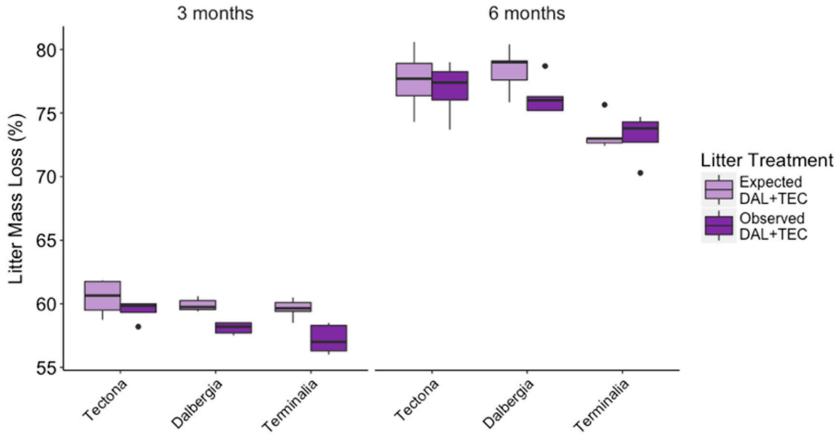

Figure 7. Non-additive effects of mixed litter from *Tectona grandis* (TEC) and *Dalbergia retusa* (DAL), showing the expected mass loss, calculated as the mean mass loss of the single-species litters, and the observed mass loss after three and six months of decomposition in monoculture plantations of *Tectona grandis*, *Dalbergia retusa* and *Terminalia amazonia* as part of a litter decomposition experiment in Panama, Central America. Boxes show the interquartile range (IQR) with median lines for $n = 5$, and dots show outliers.

Although decomposition of the TEC + DAL litter mixture was lower than expected, observed respiration from the TEC + DAL mesocosms was slightly but consistently higher than expected rates, albeit only in the *Tectona* plantation. Hence, the model that best explained non-additive effects of TEC + DAL litter mixtures on soil respiration included plantation and litter type as well as their interaction ($\chi^2 = 62.10$, $p < 0.001$, Figure 8).

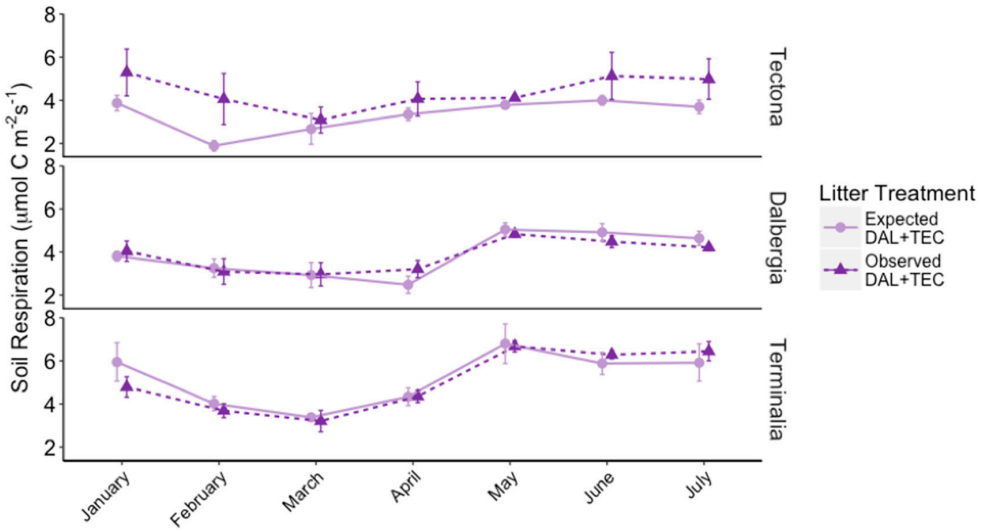

Figure 8. Non-additive effects of mixed litter from *Tectona grandis* (TEC) and *Dalbergia retusa* (DAL), showing expected soil respiration calculated as the mean respiration of the single-species litter treatments, and the observed respiration during seven months of decomposition in monoculture plantations of *Tectona grandis, Dalbergia retusa* and *Terminalia amazonia* as part of a litter decomposition experiment in Panama, Central America, showing means and standard errors for $n = 5$.

4. Discussion

4.1. Differences in Decomposition and Soil Respiration among Plantation Types

Plantation type had a strong influence on rates of decomposition and soil respiration in this study, which can be partly attributed to the distinct microclimate at the soil surface among plantations as a result of differences in canopy cover during the dry season. In particular, the *Terminalia* is an evergreen tree that forms a closed canopy [28], which maintained a lower soil temperature (Figure S1) and higher levels of soil moisture (Figure S2) during the dry season as opposed to *Dalbergia* and *Tectona*, which are deciduous [29]. In addition, litter cover buffers temperature and moisture fluctuations on the forest floor [41] and the litter standing crop was greater in the *Terminalia* plantation than in the *Tectona* or *Dalbergia* plantations. Hence, the microclimate of the forest floor is likely to have influenced litter decay rates, but there were also important differences in soil properties among plantations.

Although there was no clear relationship between soil respiration and litter decomposition, we nonetheless found some evidence to support our hypothesis that litter decomposition influenced soil respiration and microbial biomass via specific plant traits. Although the *Tectona* and *Terminalia* plantations had similar soil nutrient content and pH, soil microbial biomass C was significantly lower in *Tectona* compared to the other plantations, whereas the *Terminalia* plantations had the highest microbial biomass C and soil respiration rates. *Tectona* trees are known to have allelopathic properties, releasing chemical compounds that restrict the growth of other plants, which could explain the lower microbial biomass [42–44] and soil respiration in the *Tectona* plantation (Figure 3). Furthermore, as extraradical mycorrhizal mycelium can comprise up to one third of the microbial biomass and *Tectona* is not native to Panama, it is possible that its symbiotic mycorrhizal fungi might not be present [45]. Hence, the allelopathic properties of the *Tectona* may have restricted native soil microbes, which would

explain the lower microbial biomass (Figure 5) [42,45]; this possibility merits further study to inform plantation management to sustain soil function in future.

Litter decomposition was slowest in the *Terminalia* plantation (Figure 4), regardless of litter type; this is surprising, because high microbial biomass C and soil respiration rates (Figure 3) could suggest greater microbial activity. However, given that we found no relationship between litter decomposition and soil respiration, it is likely that the high respiration rates in the *Terminalia* plantations were largely due to root-rhizosphere respiration [46–50], rather than decomposer activity. The rapid growth of *Terminalia* [28] would explain higher rates of root-rhizosphere respiration, but it is nonetheless intriguing that the mass loss at six months was lowest in the *Terminalia* plantation for all litter types, because the microclimate was more favorable to decomposition during the dry season. It is possible that the lower decomposition rates in the *Terminalia* plantations were a result of low N-availability: although total soil N was comparable to *Dalbergia* plantations (Table 1), the nitrate concentrations in the resin probes were below detection limits in all the mesocosms in the *Terminalia* plots, which is indicative of N-immobilization during decomposition. As nitrate is an important nutrient for litter decomposition [51] it is conceivable that low availability of nitrate in the *Terminalia* plantations slowed litter decomposition processes.

4.2. Leaf Properties Explained some Variation in Litter Decomposition

Litter quality is often defined in terms of the nutrient and structural carbon content of the leaves [17] and, as hypothesized, these litter traits influenced the decomposition rates in our study, although the effects often interacted with seasonality and soil nutrient availability. In the present study, DAL litter had the lowest L:N ratio, which is related to rapid decomposition [52] and we therefore expected the most rapid mass loss in DAL litter. However, the greatest mass loss during the first three months of the experiment was observed in TEC litter (Figure 4). It is possible that the rapid initial mass loss of TEC litter is a methodological artefact: *Tectona* leaves are large and had to be cut for use in the litterbags and mesocosms, whereas the leaves of the other two species were much smaller and did not receive the same amount of damage from chopping. Cutting leaves is a method used to simulate herbivory and can affect leaf functional traits [53]. By contrast, the lower rates of decomposition of the TERM litter is likely explained by its high C:N ratio (Table 2) and greater leaf toughness of mature *Terminalia* leaves compared to mature *Dalbergia* leaves measured in the Agua Salud project [15,54].

Dalbergia is an N-fixing species, and previous work has demonstrated high rates of N fixation by *Dalbergia* at the study site [31]; accordingly, the DAL litter had the highest N concentrations and the highest decay rate after six months of decomposition regardless of the plantation (Figure 4). The slower decomposition rates at three months could be explained by dry season conditions and the limited access of invertebrates to litter in the mesocosms and litterbag as comminution by invertebrates can be important to start the decomposition process by damaging intact leaves and making more complex carbon compounds available [54–56]. Another study carried out as part of the Agua Salud project [54] found that the *Dalbergia* leaves had the lowest herbivory rates of all the species planted in the experiment and it is therefore conceivable that reduced comminution of DAL litter by invertebrates could have slowed initial decomposition. The stoichiometric needs of microbial decomposers may also have played a role in the initial stages of decomposition because soil P in the *Dalbergia* plantations was slightly lower than in the other two plantations (Table 1), which could be explained by the high P requirements for N fixation in *Dalbergia* [31]. High concentrations of N in the *Dalbergia* soil and litter (Table 1; Table 2) coupled with low availability of soil P could have resulted in P-limitation of decomposition [57]. This is supported by the results of the resin probes, showing lower release of P from the DAL litter, which could indicate immobilization of P in the N-rich DAL litter.

4.3. Limited Evidence for Non-Additive Effects and Homefield Advantage during Decomposition

Given the relatively minor differences in litter nutrient and fiber content (Table 2), the lack of strong HFA and non-additive effects is perhaps not surprising. We found no facilitative or antagonistic

effects for the DAL + TERM, the TEC + TERM, or the three-species mixtures, which is likely due to the high decay rates of all three litter types [58,59]. Nonetheless, the antagonistic effects on mass loss of the DAL+TEC litter mixture in the *Dalbergia* plantations are likely explained by the high resistance to herbivory of the *Dalbergia* leaves and the release of allelopathic compounds from TEC leaves [44]. This could also explain why the antagonistic effect was strongest in the early stages of decay. However, it is noteworthy that the TEC + DAL litter mixture had a facilitative effect on soil respiration in the *Tectona* plantation, which could indicate that leachates from the high-quality DAL litter stimulated microbial activity in the underlying soil. This mismatch between decay processes in the litter and microbial activity in the underlying mineral soil could arise because belowground C dynamics are more affected by the litter leachate than the litter itself [26,60]. It is also possible that litter leachates interacted with rhizosphere processes, which would explain the significant interactive effect of plantation and litter type on soil respiration (Figure 2).

We expected the two native species litters to have a greater homefield advantage than the TEC litter because the microbial decomposer communities would be better adapted to litter from native trees species [23]. Although this hypothesis was not fully supported, we nonetheless measured a negative HFA (home-field disadvantage) for the TEC litter, which could be explained by the lower microbial biomass in the *Tectona* plantation resulting from changes in soil properties or, potentially, allelopathic compounds in the *Tectona* leaves [25]; the latter possibility merits further study because it may help explain the strong negative impact of *Tectona* plantations on soils.

The lack of a clear HFA during decomposition could indicate that soil microbial communities in the tropics are adapted to high plant diversity. It is possible that relatively minor shifts in community composition enable decomposition of different litter types, which would facilitate the recovery of soils after land-use change. However, there is currently a dearth of information on interactions between plant traits and soil microbial communities during decomposition, especially in the tropics. It is also possible that we did not observe a strong HFA during decomposition because the litter types retained some of their initial microbial communities after washing and drying. We did not sterilize the litter to avoid affecting key litter traits, which could have allowed 'home' microbial decomposers to persist. However, given that the litter decomposed in situ for up to 6 months, we would nonetheless expect site-specific microbial communities to have a substantial influence. It should also be noted that there was a trend towards a positive HFA for both decomposition and soil respiration for the DAL litter (Figures 7 and 8), although the result was not statistically significant. This suggests that there may be a specialization of microbial and/or invertebrate communities in the *Dalbergia* plantations, especially as the soil properties from the *Dalbergia* plantation differed from the other two plantations (Figure 2) and arthropods are essential to litter decomposition and have been known to specialize to specific litter [17,59].

5. Conclusions

The decomposition of litter and associated microbial activity are influenced by a multitude of different factors, including microclimate, litter traits, and soil properties. Our study demonstrates that phenomena such as non-additive effects and the home-field advantage of decomposition may be much more complex in tropical forests compared to temperate regions because the soils and microbial decomposer communities are adapted to very high species diversity, which could mitigate facilitative or antagonistic effects of different litter types and mixtures, even in monoculture plantations. It is nonetheless striking that some of the largest differences were found in the *Tectona* plantations and for TEC litter, which indicates that microbial processes are being modified by this non-native species. It is further noteworthy that although the different litter types had a variable influence on soil respiration rates, there was no clear link between decomposition rates and soil microbial activity stimulated by litter leachates. Further research should focus on identifying how different tree species influence soil microbial community composition via litter leachates and whether non-additive effects and the

home-field advantage of litter decomposition can be better detected with greater differences in litter traits and tree functional types.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/3/209/s1, Figure S1: Soil temperature in monoculture plantations of *Tectona grandis*, *Dalbergia retusa* and *Terminalia amazonia* during a litter decomposition experiment of the Agua Salud project in Panama, Figure S2: Soil moisture in monoculture plantations of *Tectona grandis*, *Dalbergia retusa* and *Terminalia amazonia* during a litter decomposition experiment of the Agua Salud project in Panama.

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References

1. Stockmann, U.; Adams, M.A.; Crawford, J.W.; Field, D.J.; Henakaarchchi, N.; Jenkins, M.; Minasny, B.; McBratney, A.B.; De Courcelles, V.D.R.; Singh, K.; et al. The knowns, known unknowns and unknowns of sequestration of soil organic carbon. *Agric. Ecosyst. Environ.* **2013**, *164*, 80–99. [CrossRef]
2. Dixon, R.K.; Brown, S.; Houghton, R.A.; Solomon, A.M.; Trexier, M.C.; Wisniewski, J. Carbon pools and flux of global forest ecosystems. *Science* **1994**, *263*, 185–190. [CrossRef] [PubMed]
3. Mayaux, P.; Holmgren, P.; Achard, F.; Eva, H.; Stibig, H.; Branthomme, A. Tropical forest cover change in the 1990s and options for future monitoring. *Philos. Trans. R. Soc. B-Biol. Sci.* **2005**, *360*, 373–384. [CrossRef] [PubMed]
4. IUCN The Bonn Challenge. Available online: http://www.bonnchallenge.org/content/challenge (accessed on 7 January 2019).
5. Food and Agricultural Organization. Global Forest Resources Assessment 2000: Main Report Food and Agricultural Organisation of the United Nations, National Forestry Action Plans and Forest Resources Assessment, FAO. Available online: http://www.fao.org/forestry/site/fra2000report (accessed on 7 January 2019).
6. Stefanski, S.F.; Shi, X.; Hall, J.S.; Hernandez, A.; Fenichel, E.P. Teak-cattle production tradeoffs for Panama Canal Watershed small scale producers. *For. Policy Econ.* **2015**, *56*, 48–56. [CrossRef]
7. Potvin, C.; Mancilla, L.; Buchmann, N.; Monteza, J.; Moore, T.; Murphy, M.; Oelmann, Y.; Scherer-Lorenzen, M.; Turner, B.L.; Wilcke, W.; et al. An ecosystem approach to biodiversity effects: Carbon pools in a tropical tree plantation. *For. Ecol. Manag.* **2011**, *261*, 1614–1624. [CrossRef]
8. Hall, J.S.; Ashton, M.S.; Garen, E.J.; Jose, S. The ecology and ecosystem services of native trees: Implications for reforestation and land restoration in Mesoamerica. *For. Ecol. Manag.* **2011**, *261*, 1553–1557. [CrossRef]
9. Schwendenmann, L.; Pendall, E.; Potvin, C. Surface soil organic carbon pools, mineralization and CO_2 efflux rates under different land-use types in Central Panama. In *Stability of Tropical Rainforest Margins. Environmental Science and Engineering (Environmental Science)*; Tscharntke, T., Leuschner, C., Zeller, M., Guhardja, E., Bidin, A., Eds.; Springer: Berlin/Heidelberg, Germany, 2007.
10. Kraenzel, M.; Castillo, A.; Moore, T.; Potvin, C. Carbon storage of harvest-age teak (*Tectona grandis*) plantations, Panama. *For. Ecol. Manag.* **2003**, *173*, 213–225. [CrossRef]
11. Ruiz-Jaen, M.C.; Potvin, C. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *New Phytol.* **2011**, *189*, 978–987. [CrossRef] [PubMed]

12. Hättenschwiler, S.; Tiunov, A.; Scheu, S. Biodiversity and litter decomposition in terrestrial ecosystems. *Annu. Rev. Ecol. Evol.* **2005**, *36*, 191–218. [CrossRef]
13. Swift, R.S. Sequestration of carbon by soil. *Soil Sci.* **2001**, *166*, 858–871. [CrossRef]
14. Berg, B.; Berg, M.P.; Bottner, P.; Box, E.; Breymeyer, A.; Ca de Anta, R.; Couteaux, M.; Escudero, A.; Gallardo, A.; Kratzet, W.; et al. Litter mass loss rates in pine forest of Europe and Eastern United States: Some relationships with climate and litter quality. *Biogeochemistry* **1993**, *20*, 127–159. [CrossRef]
15. Pérez-Harguindeguy, N.; Díaz, S.; Cornelissen, J.H.C.; Vendramini, F.; Cabido, M.; Castellanos, A. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant Soil* **2000**, *218*, 21–30. [CrossRef]
16. Talbot, J.M.; Treseder, K.K. Interactions among lignin, cellulose, and nitrogen drive litter chemistry-decay relationships. *Ecology* **2012**, *93*, 345–354. [CrossRef] [PubMed]
17. Laird-Hopkins, B.C.; Bréchet, L.M.; Trujillo, B.C.; Sayer, E.J. Tree functional diversity affects litter decomposition and arthropod community composition in a tropical forest. *Biotropica* **2017**, *49*, 903–911. [CrossRef]
18. Fornara, D.A.; Tilman, D.; Hobbie, S.E. Linkages between plant functional composition, fine root processes and potential soil N mineralization rates. *J. Ecol.* **2009**, *97*, 48–56. [CrossRef]
19. Hobbie, S.E. Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* **1992**, *7*, 336–339. [CrossRef]
20. Hättenschwiler, S.; Jørgensen, H.B. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. *J. Ecol.* **2010**, *98*, 754–763. [CrossRef]
21. Sayer, E.J. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biol. Rev. Camb. Philos. Soc.* **2006**, *81*, 1–31. [CrossRef] [PubMed]
22. Xu, S.; Liu, L.L.; Sayer, E.J. Variability of above-ground litter inputs alters soil physicochemical and biological processes: A meta-analysis of litterfall-manipulation experiments. *Biogeosciences* **2013**, *10*, 7423–7433. [CrossRef]
23. Ayres, E.; Steltzer, H.; Berg, S.; Wall, D.H. Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. *J. Ecol.* **2009**, *97*, 901–912. [CrossRef]
24. Freschet, G.T.; Aerts, R.; Cornelissen, J.H.C. Multiple mechanisms for trait effects on litter decomposition: Moving beyond home-field advantage with a new hypothesis. *J. Ecol.* **2012**, *100*, 619–630. [CrossRef]
25. Cummings, J.A.; Parker, I.M.; Gilbert, G.S. Allelopathy: A tool for weed management in forest restoration. *Plant Ecol.* **2013**, *213*, 1975–1989. [CrossRef]
26. Fanin, N.; Hättenschwiler, S.; Barantal, S.; Schimann, H.; Fromin, N. Does variability in litter quality determine soil microbial respiration in an Amazonian rainforest? *Soil Biol. Biochem.* **2011**, *43*, 1014–1022. [CrossRef]
27. Liang, J.; Lu, Z.; Yu, Z.; Wang, J.; Wang, X. Effects of leaf litter extraction fluid from dominant forest tree species on functional characteristics of soil microbial communities. *J. For. Res.* **2016**, *27*, 81–90. [CrossRef]
28. Mayoral, C.; van Breugel, M.; Cerezo, A.; Hall, J.S. Survival and growth of five Neotropical timber species in monocultures and mixtures. *For. Ecol. Manag.* **2017**, *403*, 1–11. [CrossRef]
29. Turner, B.L.; Engelbrecht, B.M.J. Soil organic phosphorus in lowland tropical rain forests. *Biogeochemistry* **2011**, *103*, 297–315. [CrossRef]
30. Ogden, F.L.; Crouch, T.D.; Stallard, R.F.; Hall, J.S. Effect of land cover and use on dry season river runoff, runoff efficiency, and peak storm runoff in the seasonal tropics of Central Panama. *Water Resour. Res.* **2013**, *49*, 8443–8462. [CrossRef]
31. Batterman, S.A.; Hall, J.S.; Turner, B.L.; Hedin, L.O.; LaHaela Walter, J.K.; Sheldon, P.; van Breugel, M. Phosphatase activity and nitrogen fixation reflect species differences, not nutrient trading or nutrient balance, across tropical rainforest trees. *Ecol. Lett.* **2018**, *21*, 1486–1495. [CrossRef] [PubMed]
32. Sayer, E.J.; Tanner, E.V.J. A new approach to trenching experiments for measuring root–rhizosphere respiration in a lowland tropical forest. *Soil Biol. Biochem.* **2010**, *42*, 347–352. [CrossRef]
33. Jones, D.L.; Willett, B.M.J. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. *Soil Biol. Biochem.* **2006**, *38*, 991–999. [CrossRef]
34. Vance, E.D.; Brookes, P.C.; Jenkinson, D.S. An extraction method for measuring soil microbial biomass C. *Soil Biol. Biochem.* **1987**, *19*, 703–707. [CrossRef]
35. Van Soest, P.J.; Robertson, J.B.; Lewis, B.A. Methods for Dietary Fiber, Neutral Detergent Fiber, and Nonstarch Polysaccharides in Relation to Animal Nutrition. *JDS* **1991**, *74*, 3583–3597. [CrossRef]

36. Olson, J.S. Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. *Ecology* **1963**, *44*, 322–331. [CrossRef]
37. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2017. Available online: https://www.R-project.org/ (accessed on 12 December 2018).
38. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; Mcglinn, D.; Wagner, H. Vegan: Community Ecology Package. R Package Version 2.3-2, 2015. Available online: https://CRAN.R-project.org/package=vegan.Retrievedfromhttps://github.com/vegandevs/vegan (accessed on 12 December 2018).
39. Bates, D.M.; Mächler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed- Effects Models using lme4. *J. Stat. Softw.* **2014**, *67*, 1–48.
40. Crawley, M.J. *The R Book*; John Wiley & Sons: Chichester, UK, 2007.
41. Sayer, E.J.; Tanner, E.V.J.; Lacey, A.L. Effects of litter manipulation on early-stage decomposition and meso-arthropod abundance in a tropical moist forest. *For. Ecol. Manag.* **2006**, *229*, 285–293. [CrossRef]
42. Hawkes, C.V.; Belnap, J.; D'Antonio, C.; Firestone, M.K. Arbuscular mycorrhizal assemblages in native plant roots change in the presence of invasive exotic grasses. *Plant Soil* **2006**, *281*, 369–380. [CrossRef]
43. Jung, S.C.; Martinez-Medina, A.; Lopez-Raez, J.A.; Pozo, M.J. Mycorrhiza-Induced Resistance and Priming of Plant Defenses. *J. Chem. Ecol.* **2012**, *38*, 651–664. [CrossRef] [PubMed]
44. Leela, P.; Arumugam, K. Allelopathic influence of teak (*Tectona Grandis* L.) leaves on growth responses of green gram (*Vigna Radiata* (L.) Wilczek) and Chilli (*Capisum Frutescens* L.). *Int. J. Curr. Biotechnol.* **2014**, *2*, 55–58.
45. Ajeesh, R.; Santhoshkumar, A.V.; Gopal, S.; Binu, N.K. Screening of selected native arbuscular mycorrhizal fungi at different levels for their symbiotic efficiency with *tectona grandis* seedlings. *J. Trop. For. Sci.* **2017**, *29*, 395–403.
46. Högberg, M.N.; Högberg, P. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytol.* **2002**, *154*, 791–795. [CrossRef]
47. Binkley, D.; Stape, J.L.; Takahashi, E.N.; Ryan, M.G. Tree-girdling to separate root and heterotrophic respiration in two Eucalyptus stands in Brazil. *Oecologia* **2006**, *148*, 447–454. [CrossRef] [PubMed]
48. King, J.; Pregitzer, K.; Zak, D.; Sober, J.; Isebrands, J.; Dickson, R.; Hendrey, G.; Karnosky, D. Fine-root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO_2 and tropospheric O_3. *Oecologia* **2001**, *128*, 237–250. [CrossRef] [PubMed]
49. Trumbore, E.; Davidson, A.; Camargo, D.; Nepstad, C. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochem. *Cycles* **1995**, *9*, 515–528. [CrossRef]
50. Yi, Z.; Fu, S.; Yi, W.; Zhou, G.; Mo, J.; Zhang, D.; Ding, M.; Wang, X.; Zhou, L. Partitioning soil respiration of subtropical forests with different successional stages in south China. *For. Ecol. Manag.* **2007**, *243*, 178–186. [CrossRef]
51. Ferreira, V.; Gulis, V.; Graça, M.A.S. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* **2006**, *149*, 718–729. [CrossRef] [PubMed]
52. Bréchet, L.; Le Dantec, V.; Ponton, S.; Goret, J.Y.; Sayer, E.; Bonal, D.; Freycon, V.; Roy, J.; Epron, D. Short- and Long-term Influence of Litter Quality and Quantity on Simulated Heterotrophic Soil Respiration in a Lowland Tropical Forest. *Ecosystems* **2017**, *20*, 1190–1204. [CrossRef]
53. Hjältén, J. Simulating Herbivory: Problems and Possibilities. In *Insects and Ecosystem Function*; Weisser, W.W., Siemann, E., Eds.; Springer: Berlin/Heidelberg, Germany, 2008; pp. 243–255. [CrossRef]
54. Paul, G.S.; Montagnini, F.; Berlyn, G.P.; Craven, D.J.; van Breugel, M.; Hall, J.S. Foliar herbivory and leaf traits of five native tree species in a young plantation of Central Panama. *New For.* **2012**, *43*, 69–87. [CrossRef]
55. Hättenschwiler, S.; Coq, S.; Barantal, S.; Handa, I.T. Leaf traits and decomposition in tropical rainforest: Revisiting some commonly held views towards a new hypothesis. *New Phytol.* **2010**, *189*, 950–965. [CrossRef]
56. Wardle, D.A.; Bonner, K.I.; Barker, G.M. Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Funct. Ecol.* **2002**, *16*, 585–595. [CrossRef]
57. Hobbie, S.; Vitousek, P.M. Nutrient limitation of decomposition in Hawaiian forests. *Ecology* **2000**, *81*, 1867–1877. [CrossRef]
58. Gartner, T.B.; Cardon, Z.G. Decomposition Dynamics in Mixed-Species Leaf Litter. *Oikos* **2012**, *104*, 230–246. [CrossRef]

59. Hättenschwiler, S.; Gasser, P. Soil animals alter plant litter diversity effects on decomposition. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 1519–1524. [CrossRef] [PubMed]
60. Joly, F.X.; Fromin, N.; Kiikkilä, O.; Hättenschwiler, S. Diversity of leaf litter leachates from temperate forest trees and its consequences for soil microbial activity. *Biogeochemistry* **2016**, *129*, 373–388. [CrossRef]

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