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Decomposition of coarse woody debris in a long-term litter manipulation experiment: a focus on nutrient availability

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Summary

1. The majority of aboveground carbon in tropical forests is stored in wood, which is returned to the atmosphere during decomposition of coarse woody debris. However, the factors controlling wood decomposition have not been experimentally manipulated over time scales comparable to the length of this process.

2. We hypothesized that wood decomposition is limited by nutrient availability and tested this hypothesis in a long-term litter addition and removal experiment in a lowland tropical forest in Panama. Specifically, we quantified decomposition using a 15 year chronosequence of decaying boles, and measured respiration rates and nutrient limitation of wood decomposer communities.

3. The long-term probability that a dead tree completely decomposed was decreased in plots where litter was removed, but did not differ between litter addition and control treatments. Similarly, respiration rates of wood decomposer communities were greater in control treatments relative to litter removal plots; litter addition treatments did not differ from either of the other treatments. Respiration rates increased in response to nutrient addition (nitrogen, phosphorus, and potassium) in the litter removal and addition treatments, but not in the controls.

4. Established decreases in concentrations of soil nutrients in litter removal plots and increased respiration rates in response to nutrient addition suggest that reduced rates of wood decomposition after litter removal were caused by decreased nutrient availability. The effects of litter manipulations differed directionally from a previous short-term decomposition study in the same plots, and reduced rates of bole decomposition in litter removal plots did not emerge until after more than 6 years of decomposition. These

differences suggest that litter-mediated effects on nutrient dynamics have complex interactions with decomposition over time.

Keywords: Tropical forest, Coarse woody debris, Respiration, Carbon cycling, Nitrogen, Phosphorus, Potassium

Introduction

Tropical forests influence global carbon dynamics more than any other terrestrial biome; they contain 25% of terrestrial biomass and account for ca. 40% of the terrestrial carbon sink (Pan *et al.* 2011; Feldpausch *et al.* 2012). The majority of aboveground carbon in tropical forests is sequestered in wood (Rice *et al.* 2004) and the process of decomposition eventually releases most of this carbon as CO_2. Indeed, actively decomposing dead woody debris accounts for as much as 20% of aboveground carbon and 15% of CO_2 emissions in tropical forests (Chambers *et al.* 2004; Rice *et al.* 2004; Palace, Keller & Silva 2008). To understand and accurately predict changes in tropical forest carbon cycling, it is therefore necessary to determine what factors control the decomposition of trees and large branches (cumulatively referred to as coarse woody debris [CWD] or individually as "boles").

Experiments investigating factors that control decomposition are generally restricted to leaf litter and fine woody debris. Substrate characteristics and microclimate are important to litter and fine woody decomposition rates (reviewed by Berg & Laskowski 2005; Fasth *et al.* 2011), and one or more nutrients typically limit litter decomposition rates in non-desert ecosystems (Hobbie & Vitousek 2000; Austin & Vivanco 2006; Kaspari *et al.* 2008). For small woody substrates (< 20 cm^3), controlled experiments indicate that decomposer species composition, community assembly history, nitrogen (N) availability, and phosphorus (P) availability all influence decomposition rates (Boddy 2001; Fukami *et al.* 2010; Bebber *et al.* 2011). For small branches in a lowland tropical forest (5 cm diameter), decomposition rates increased with P and P+N addition for some tree species but not for others, indicating that

substrate characteristics influence the effects of fertilization (Chen *et al.* 2015). Although these studies form a useful foundation for understanding wood decomposition, it remains unknown if results from short-term decomposition studies using small woody substrates are predictive of CWD decomposition.

Uncertainty regarding wood decomposition exists in part because fine woody debris is chemically different from CWD and decomposition of entire boles occurs over long time scales (Kimmey 1955; Harmon *et al.* 1986). Decomposition rates of larger boles are often slower than for smaller boles, but it remains unclear how this phenomenon is influenced by chemical composition and geometry (surface area-to-volume ratio; Oberle *et al.* 2017; reviewed in Harmon *et al.* 1986). Small woody debris is mostly composed of relatively labile sapwood, whereas a large portion of mature tree mass is recalcitrant heartwood that often contains complex compounds and lower nutrient content (Grubb & Edwards 1984; Sellin 1994; Meerts 2002; Taylor, Gartner & Morrell 2002). These types of compositional differences can have complex effects on decomposition (Carreiro *et al.* 2000) that are not well understood for woody substrates (Chen *et al.* 2015). Despite these differences, the vast majority of experimental investigations of wood decomposition focus on fine woody debris, yet most dead wood carbon is stored in coarse woody debris.

Circumstantial evidence and natural experiments provide some information about long-term wood decomposition. Wood decomposition often differs among tree species and it is faster for smaller, less dense, and low lignin woody debris in tropical forests (Chambers *et al.* 2000; van Geffen *et al.* 2010). Wood has higher carbon-to-macronutrient ratios than decomposer organisms, resulting in an initial stage of

nutrient translocation into wood during decomposition (Boddy 2001; Mooshammer *et al.* 2014). The bulk translocation of soil nutrients for wood decomposition is so substantial that CWD removal and multi-nutrient fertilization had similar positive effects on net primary productivity in a secondary tropical forest (Zimmerman *et al.* 1995). However, it is not known for how long nutrient translocation occurs and how the process of nutrient import influences decomposition rates. In a relevant study, the effects of fertilization were inconsistent through time (Chen *et al.* 2015), suggesting that nutrient limitation is only important during some stages of decomposition. Without long-term experiments spanning the duration of CWD decomposition (Cornelissen *et al.* 2012), it is impossible to determine how nutrient availability influences dead wood decomposition.

Long-term litter manipulations are useful for investigating the roles of soil nutrients during decomposition. Litter functions as a complete, stoichiometrically balanced fertilizer that releases nutrients as it decomposes over months (Sayer *et al.* 2012), and thus litter addition provides insight into the influence of bulk nutrient addition on rates of decomposition. Two features of this approach are (1) that it does not change nutrient ratios in the same way as fertilization with select elements (Sayer & Banin 2016) and (2) that it approximates future forest conditions because increased litter inputs are expected in response to increased CO_2 concentrations (Liu et al. 2009). By contrast, litter removal can provide information about the roles of soil nutrient pools during decomposition. To our knowledge, no studies to date have considered how litter inputs influence long-term wood decomposition.

We investigated long-term CWD decomposition in a litter manipulation experiment in lowland tropical forest in Panama. In this experiment, litter addition plots are relatively nutrient-rich (elevated soil nitrate and P), whereas litter removal plots are nutrient-poor (reduced soil inorganic N, soil P, litter N, and litter potassium [K]; Sayer *et al.* 2012; Sheldrake *et al.* 2017a). We hypothesized that long-term rates of wood decomposition increase with greater litter input as a result of enhanced nutrient availability (N, P, and K), whereas decomposition rates decrease with very low litter input due to nutrient limitation. We tested three predictions related to this hypothesis: 1) CWD decomposition rates are higher in litter addition treatments and lower in litter removal treatments compared to controls; 2) similarly, wood decomposer activity (respiration rates) during late-stage decomposition is greater in litter addition plots and reduced in litter removal plots; 3) respiration rates of decomposer communities exhibit a greater increase in response to nutrient addition in litter removal plots than in litter addition or control plots. We used tree survey data to establish the species and year of death for decaying boles within the plots, which allowed us to test our predictions using a 15-year chronosequence of CWD.

Methods

Study site

The study site was lowland tropical forest located on the Gigante Peninsula within the Barro Colorado Nature Monument in central Panama. Forest structure and tree composition are typical of mature lowland tropical forest in Mesoamerica (Wright *et al.* 2011) with an average annual temperature of 27˚C, mean annual rainfall of 2600 mm, and a short dry season (January-April, < 100mm monthly rainfall; (Leigh 1999).

The soils are Oxisols with moderate to low concentrations of exchangeable cations and resin-extractable phosphorus (Yavitt *et al.* 2011; Wright *et al.* 2011).

Litter Manipulation Plots

The Gigante Litter Manipulation Project (GLiMP) comprises 15 plots (45 x 45 m) in five replicate blocks of three treatments. The litter in the five "litter removal" plots has been raked and moved to the five "litter addition" plots once a month since January 2003; five unmanipulated plots were maintained as controls (estimated litterfall = 991 g m^{-2} y^{-1}; Sayer & Tanner 2010a). The experimental design is described in detail elsewhere (Sayer, Tanner & Lacey 2006). All trees with > 10 cm diameter at breast height (DBH) in the plots were measured, tagged, identified, and mapped with *c.* 0.5 m accuracy in 2000; this process has been repeated annually, with the exception of 2006 and 2008, through to the conclusion of this study (August 2016). Soil nutrient concentrations were last measured in these plots in 2010 and 2012 (Sayer *et al.* 2012; Sheldrake *et al.* 2017a).

Bole survey

In 2016, we used a chronosequence approach to compare CWD decomposition among litter treatments (van Geffen *et al.* 2010). The tree census data from the litter manipulation plots indicated the year in which a given tree died, the size of the tree at death, the species of the tree, and its location in the plot. Boles were not moved away from their original location by human activity because access to the study site is restricted. Using census information, we were able to locate remaining boles and determine if others had completely decomposed.

We returned to the original location of each dead tree and categorized these trees into two groups. The first group (n = 115) included downed and standing dead trees that we were able to unambiguously identify. Specifically, unambiguous identification relied on detecting a remnant bole with sufficient elliptical-cylindrical structure that we could determine its orientation and position relative to the original location of the tree. The second group comprised trees that had completely decomposed (n =99). Boles were only recorded with this fate if no intact sections of wood existed near their original location. We did not consider small wood fragments (typically <500 cm^3) as evidence of a remaining bole for two reasons: 1) it is nearly impossible to determine the original source of individual fragments and 2) the presence or absence of litter biases detection rates for small fragments. Consequently, small woody fragments of "completely decomposed" boles may persist in these plots, but any omissions were consistent among litter treatments. To account for species-specific differences in initial wood density, we used the published values for each species or its closest known relative (global wood density database, Chave *et al.* 2009).

We excluded dead trees from our analyses if they were unidentifiable or lacked important covariates (diameter, species, or location; n = 104), and we did not consider dead palms (n = 82). We omitted dead trees that lacked tree species identifications (n = 67) or accurate locations (n = 7). Trees that fell outside of the plots were not affected by the litter manipulation treatments and were thus removed (n = 4). We also removed trees from analyses if the tree location was obscured by a treefall (n = 7), or multiple boles were clustered and/or in an orientation that precluded a confident assignment to single point of origin (n = 19). Trees omitted from our analyses were smaller and denser

than those retained, but their cross-sectional masses did not differ (Table S1). Regardless, all criteria were applied equally to all plots, and the characteristics of excluded trees did not differ among litter treatments (Supplementary Information).

Wood Respiration

We used respiration measurements to estimate short-term decomposer community activity. We selected 28 boles in each of the three litter treatments so that bole ages (i.e., time since tree death) were relatively evenly distributed across the course of the study. To ensure accurate measurements, we only chose boles with sufficient structure (diameter, length, and shape) to support respirometry collars. We attached 10 cm tall respirometry collars (7 cm diameter PVC sections) to each bole using silicon sealant (Fig. S1) and all collars were located at least 0.3 m from a bole end.

Beginning one week after collar attachment, we began measuring respiration rates using a Viasala respirometer (Fig. S2, GMP343 CO_2 probe, Vaisala Inc.). We attached the respirometer to each collar for 5 minutes and recorded CO_2 (ppm) every 15 seconds. We removed the initial portion of each recording (ca. 15-45 seconds) because of inconsistency and we approximated respiration rates as the slope of the linear CO_2 accumulation curve during the remaining portion of the recording period (Bréchet *et al.* 2017). To control for temporal variability and estimate baseline respiration rates of wood decomposer communities, we measured respiration of each bole three times over a two-week period.

All respiration measurements were taken during the wet season (June-July 2016). Rainfall (June = 326.5 mm; July = 486.8 mm) far exceeded potential evapotranspiration (June = 48.5 mm; July = 45.4 mm) during these months, and this

typical pattern causes soil moisture (and presumably wood moisture) to be consistent among years (Steve Paton, STRI Environmental Monitoring Program, pers. com.). These measurements primarily capture microbial effects on decomposition and they are representative of the conditions underlying the majority of carbon mineralization. Specifically, decomposition occurs much more rapidly during the wet season than the dry season in this forest (Wieder & Wright 1995), and the wet season is twice as long as the dry season. However, the effects of infrequent fragmentation events and transient invertebrates are not captured by this method given its small spatial and temporal scale.

We estimated the current density of these boles using a dynamic penetrometer, as described by Larjavaara & Muller-Landau (2010). Briefly, we inserted the penetrometer vertically into each bole ca. 5 cm from the respirometry collar and measured the distance of penetration. We estimated density using the relationship between penetration and wood density previously established for CWD in this forest (Larjavaara & Muller-Landau 2010). To create a proxy for decomposition state, we then calculated bole density (%) as the percent of original density remaining (hereafter *bole density remaining*; original density estimated using the global wood density database, Chave *et al.* 2009). Although the variability of penetrometer measurements can increase with decomposition stage (Oberle *et al.* 2014), they are more accurate on a case-by-case basis than other non-destructive techniques that consider both void space and heterogeneity in wood density (Larjavaara & Muller-Landau 2010).

Sensitivity to nutrient addition

To quantify nutrient limitation of wood respiration among litter treatments, we installed a second respirometry collar on a subset of the boles (litter addition: $n = 9$:

litter control: $n = 6$; litter removal: $n = 5$). The added collars were at least 1 m apart from the original collars to reduce the likelihood of short-term nutrient translocation. We used all boles that met two criteria: 1) the trees had died > 3 years previously, and 2) they were either long enough to support two collars or separated into two large fragments. We chose boles that were > 3 years old (hereafter *old boles*) to focus on late-stage decomposition (i.e., longer than typical decomposition studies).

After concluding our baseline wood respiration measurements, we performed a one-time fertilization of each bole to test for sensitivity to nutrient addition. Specifically, one collar per bole received 50 mL of nutrient solution (hereafter *NPK addition*) and the other collar received 50 mL of distilled water (*H_2O addition*). The nutrient solution contained total amounts of N, P, and K commonly used in other fertilization experiments (described by Kaspari *et al.* 2008). Specifically, we fertilized the collars with the equivalent of 125 kg N ha^{-1} (as NH_4Cl), 60 kg P ha^{-1} (as KH_2PO_4), and 75 kg K ha^{-1} (as KH_2PO_4). Respiration rates were measured 3, 11, and 18 days after treatment application.

Differences in chemical composition and the historic interactions with biotic or abiotic factors (e.g., insects, pathogens, and soil contact) are important to bole decomposition, yet they were unknown in this study. By pairing NPK and water treatments, our intent was to control for chemical composition and bole history. We assessed the magnitude of the respiration response to NPK and water addition by calculating the percentage change in respiration rates from average pre-treatment respiration of each collar.

Core collection and elemental analysis

We also compared the elemental composition of each fertilized bole prior to NPK and H_2O addition. We collected a small core (2 cm diameter, 2 cm depth) from the top of each bole and 5 cm from each respirometry collar. Wood cores were oven-dried (60˚C) and ground with a Wiley-Mill before chemical analysis. Total carbon and nitrogen were determined by elemental analysis (Thermo Flash EA1112, CE, Elantech, Lakewood, NJ, USA), while concentrations of mineral elements (P, K, Na, Zn, Ca, Mn, Mg, Al, B, Cu, Fe) were determined by nitric acid digestion at 180°C under pressure in PTFE vessels, with detection by inductively-coupled plasma optical-emission spectrometry (ICP-OES) on an Optima 7300 DV (Perkin Elmer, Inc, Shelton, CT). Analytical quality was confirmed in both procedures using the NIST peach leaves standard. All elemental analyses were performed in the Soils Laboratory at the Smithsonian Tropical Research Institute.

Statistical methods

Analyses were performed in the R statistical environment (R Core Team 2016) using the lme4 and lmertest packages for logistic regression and linear mixed effects models (Bates *et al.* 2014; Kuznetsova, Brockhoff & Bojesen 2016) and the vegan package for multivariate analyses *(*Oksanen *et al.* 2007*)*. The significance of each term in the models was determined by comparing nested models with likelihood ratio tests. We sequentially dropped terms according to AICs and likelihood ratio p-values until a minimum adequate model was identified (Pinheiro & Bates 2000; Bolker *et al.* 2009). Finally, we examined residuals to confirm appropriate model fit.

We compared the likelihood of complete decomposition of boles among litter manipulation treatments using the initial bole survey data. We used a generalized linear

mixed effect model (*glmer* function; logistic regression) with a binary response variable: either the bole was present in 2016 or had completely decomposed. We approximated bole "size" at the time of death as the product of basal area and density (*cross-sectional mass*) because basal area and initial density were correlated and would violate the assumption of independence (R = -0.36, t = 5.57, df = 212, $p < 0.001$). We included litter treatment, bole age, and cross-sectional mass as fixed effects and plot as a random effect. The random effect 'plot' did not affect the fit of the model, likely because the tested phenomenon occurs at a smaller scale than a plot, and therefore we removed this term to identify the minimum adequate model. The grouping effect 'plot' was removed from all other linear models after being similarly tested. The interactions between cross-sectional mass and the other predictors were sequentially dropped because they did not affect the fit of the model. To further investigate the interaction between litter manipulations and bole age, we performed pairwise comparisons among litter treatments with the same three main effects as above and the interaction effect between bole age and litter treatment (*glm* function). We log-transformed cross-sectional mass to improve the model fit. Finally, we used the Bonferroni correction to account for multiple comparisons using the same data.

Although tree species characteristics (e.g., chemical composition and wood density) influence decomposition, we could not directly account for tree species in our linear models because species were not evenly distributed across litter treatments (71 of 74 species were present in ≤1 replicate set of plots). Alternatively, we considered the species composition of dead trees among litter treatments using perMANOVA (Bray-Curtis distance) and pseudo-F values. The perMANOVA included litter treatment and

bole status (completely decomposed or remaining in 2016) as fixed effects and plot as a random effect. We also performed blocked indicator species analysis (PC-ORD v6.08) for bole status to identify tree species with particularly labile or recalcitrant wood and to statistically control for the effects of litter treatment (Dufrene & Legendre 1997). Apart from these multivariate tests, we accounted for species effects using species-specific density in the logistic regression and elemental composition in models for the NPK and H_2O manipulation experiment.

We used a linear mixed effects model (*lmer* function) to compare respiration rates among litter treatments. For boles that supported two respiration collars, we used the means of measurements that occurred on the same day. As respiration rates are influenced by wood decay status and decomposition rates differed among treatments (see results), we used bole density remaining (defined above) instead of bole age as a proxy for decomposition status. The initial model therefore included litter manipulation treatment and bole density remaining as fixed effects and the unique bole identifier nested within plot as random effects. We tested for differences among litter treatments using a post-hoc Tukey HSD test.

We used this same model to compare the elemental concentrations of boles used in the NPK limitation experiment. We also considered interspecific differences in chemical composition by exploring differences in elemental composition among fertilized boles with a Principal Components Analysis using standardized variables (Table 2). We fit each input variable as a vector to the ordination (*envfit* function) to visually display which elements best explained the separation of boles along the first two ordination axes.

Finally, we compared the change from baseline respiration rates among litter treatments after NPK and H_2O addition using a repeated measures mixed-effect model. Litter manipulation and NPK/H_2O treatment were included as fixed effects, and both plot and unique bole identifier were random effects. For repeated measures covariance, bole identifier was the subject and the days post-treatment was the repeated measure. We included the scores from the first two PCA axes as covariates to account for differences in elemental composition. The bole identifier term standardized our nutrient addition comparisons within a single bole and thereby accounted for the effects of bole history and chemical composition when comparing NPK and H_2O treatments (analogous to the structure of a paired t-test). To further explore the interaction effect between litter manipulations and nutrient addition, we made pairwise comparisons between nutrient additions within each litter addition treatment.

Results

Bole decomposition

The likelihood that boles decomposed completely was affected by the initial size of the bole, bole age, and the litter treatment. In all cases, the likelihood of decomposition increased with lesser initial cross sectional mass ($\chi^2_1 > 28.46$, $p < 0.001$, $\alpha = 0.0167$) and greater bole age ($\chi^2_1 \geq 28.87$, $p < 0.001$, $\alpha = 0.0167$; Fig. 1). However, the likelihood of a bole completely decomposing during the 15-year study was not consistent among the three litter manipulation treatments (treatment x bole age interaction: $\chi^2_2 = 6.67$, $p = 0.036$; Fig. 1). Specifically, the pattern of bole decomposition with increased bole age differed between the control and litter removal treatments (pairwise treatment x bole age interaction: $\chi^2_1 = 5.86$, $p = 0.015$, $\alpha = 0.0167$).

Decomposition was similar between control and litter removal plots in the short-term, but the long-term probability of complete decomposition in control plots was substantially higher than in removal plots (Fig. 1). The probability of complete decomposition was marginally significantly greater in the litter addition treatment than in the litter removal treatment (pairwise comparison: $\chi^2_1 = 5.42$, $p = 0.02$, $\alpha = 0.0167$), whereas bole decomposition was similar in the litter addition and control treatments (pairwise comparison: $\chi^2_1 = 0.016$, $p = 0.899$, $\alpha = 0.0167$).

Tree species effects

Neither tree species nor species-related characteristics influenced differences in the probability of decomposition among litter treatments. Both predictors in the best-fit model, bole age ($\chi^2_2 = 1.94$, $p = 0.38$) and initial cross-sectional mass ($\chi^2_2 = 4.07$, $p = 0.13$), did not differ among litter treatments. Moreover, tree species composition was similar among litter treatments (pseudo-$F_{2,23} = 0.54$, $p = 0.99$, Fig. S3). By contrast, the composition of tree species that had completely decomposed during the 15-year study differed from the tree species that remained in 2016 (pseudo-$F_{1,23} = 2.24$, $p = 0.001$). Indicator species analysis revealed that *Tetragastris panamensis* (IV = 38.5, $p = 0.021$), *Lonchocarpus heptaphyllus* (IV = 30.8, $p = 0.048$), and *Zanthoxylum acuminatum* (IV = 30.8, $p = 0.058$) had a large proportion of boles remaining and thus were identified as species with potentially recalcitrant wood. Only *Cordia bicolor* (IV = 42.9, $p = 0.017$) was indicative of completely decomposed boles and therefore was identified as a species with particularly labile wood.

Wood respiration and NPK addition

Respiration rates from decomposing wood differed among litter treatments (χ^2_2 = 8.63, p = 0.013; Fig. 2). Specifically, wood respiration rates in control plots were approximately 60% greater than those in litter removal plots (Tukey HSD: z = 2.83, p = 0.013). Wood respiration rates in litter addition plots were intermediate and did not differ significantly from either control or litter removal plots (Tukey HSD: z < 2.06, p > 0.10). Respiration rates were unaffected by bole density remaining (χ^2_1 = 0.39, p = 0.53, α = 0.0167).

Changes in respiration rates in response to NPK and H_2O additions differed among litter treatments (Fig. 3; litter treatment x NPK/H_2O addition interaction: χ^2_2 = 10.61, p = 0.005, α = 0.0167). NPK addition increased wood respiration rates more than H_2O addition in the litter removal (χ^2_1 = 7.13, p = 0.008, α = 0.0167) and litter addition plots (χ^2_1 = 12.85, p < 0.001, α = 0.0167). By contrast, the NPK addition did not change wood respiration rates more than H_2O in the control plots (χ^2_1 = 1.06, p = 0.304, α = 0.0167). Regardless of treatment, scores from PCA axes 1 and 2, representing bole chemical properties, were not related to changes in respiration (χ^2_1 < 0.671, p > 0.413). Respiration rates of NPK and H_2O treatments were consistent between 3 and 18 days post-treatment (X^2_1 < 1.75, p > 0.417) and bole density remaining did not differ among treatments (X^2_2 = 2.75, p > 0.254).

Wood chemistry

The first two PCA axes from the ordination of bole chemical properties explained nearly 50% of the variation in the elemental composition of old boles (Fig. 4). Boles from litter addition and removal treatments separated along PCA axis 2, but there was no clear separation between either litter treatment and the controls. PCA axis 2

loadings (loading > 0.3) indicated that concentrations of Ca, K, Mg and Na were higher in litter addition boles, whereas B, C, N, and Zn were all greater in the litter removal boles (Table 2). PCA axis 1 (31% of variation) explained nearly twice as much variation in elemental composition as PCA axis 2 (17% of variation), but axis 1 was not clearly related to differences among litter treatments.

Despite apparent differences in ordination space, concentrations of individual elements in old boles were generally similar regardless of treatment (Table 1). Neither N concentrations nor ratios of C:N and C:P differed among treatments ($\chi^2_2 > 4.58$, $p > 0.1$). Na concentrations were lower in litter removal plots relative to litter addition plots ($\chi^2_2 = 8.23$, $p = 0.016$, Tukey: $t = 2.78$, $p = 0.015$), but Na concentration in the litter manipulations did not differ from controls (Tukey: $t < 1.53$, $p > 0.27$). Similarly, there was a trend towards lower K in the litter removal plots relative to the other treatments ($\chi^2_2 = 5.15$, $p = 0.08$) and K concentrations were weakly related to bole density remaining ($\chi^2_2 = 2.83$, $p = 0.09$). C and Cu concentrations exhibited interaction effects between bole density remaining and litter treatments ($\chi^2_2 > 8.19$, $p < 0.017$). However, these interaction effects were largely due to a single high-leverage outlier, and thus it is unlikely that they indicate a biologically relevant response. Concentrations of all other elements (P, Zn, Ca, Mn, Mg, Al, B, Fe) were similar among treatments ($\chi^2 < 4.06$, $p > 0.13$). Calcium and K concentrations were correlated with bole density remaining ($\chi^2_1 > 5.7$, $p < 0.02$), but bole density remaining was unrelated to nutrient concentrations for Al, B, Fe, Mg, Mn, N, P, and Zn ($\chi^2_1 < 2.07$, $p > 0.15$).

Discussion

403 The controls of CWD decomposition, particularly exogenous factors such as
404 nutrient availability, remain poorly understood. Here we provide experimental evidence
405 that litter is important to CWD decomposition and that the effects of litter manipulation
406 on wood decomposition are mediated by nutrient availability. These differences in
407 decomposition outcomes were only apparent after 6 years (Fig. 1), and the directional
408 differences in these outcomes among litter treatments were counter to a previous, co-
409 located experiment using small substrates over a short time frame.

410 Greater availability of macronutrients is generally expected to increase
411 decomposition rates, but relevant data for CWD are lacking (Harmon *et al.* 1986; Chen
412 *et al.* 2015). A previous short-term study (70 days) in the GLiMP plots concluded that
413 increased nutrient availability explained faster rates of birch stick decomposition in the
414 litter addition treatments relative to removal and control treatments (Sayer, Tanner &
415 Lacey 2006). By contrast, respiration rates (Fig. 2) and long-term CWD decomposition
416 (Fig. 1) did not differ between the litter addition and control treatments in our study. In
417 terms of nutrients, decomposer respiration rates in the litter addition plots were
418 relatively nutrient limited (Fig. 3) despite greater soil inorganic N and resin-P measured
419 previously. It is likely that differences between our study and the earlier study from
420 these same plots (Sayer, Tanner & Lacey 2006) were caused by substrate effects
421 (decomposition of birch sticks versus CWD) and a difference between the short and
422 long-term effects of litter manipulations, as suggested by the interaction effect between
423 litter treatment and bole age (Fig. 1). The moderate increases in soil nutrients did not
424 influence long-term decomposition, and the contrasting results demonstrate that short-

term and small-scale experiments (such as Sayer, Tanner & Lacey 2006) are not necessarily predictive of the long-term outcomes for CWD.

Results from the litter removal plots provide direct and indirect evidence that reduced soil nutrients decreased long-term rates of CWD decomposition. The importance of soil nutrients during CWD decomposition was clearly established by previous work (Swift 1977; Zimmerman *et al.* 1995), and experiments at our study site demonstrated that P and K limit decomposition of more labile substrates (Kaspari *et al.* 2008). Without litter inputs, long-term decomposition rates decreased, soil P concentrations were reduced (as were soil Ca, Mg, and inorganic N; Sheldrake *et al.* 2017a), and there was a trend towards decreased K concentrations in old boles in the litter removal plots. Moreover, experimental NPK addition provided direct evidence that the activity of wood decomposers in the litter removal plots is limited by N, P, and/or K availability (Fig. 3). Finally, there was a greater proportion of standing dead trees (*snags*) in the litter removal plots than in controls or litter addition plots (Table S2), suggesting that decreased decomposition rates increased snag residence time. This potentially explains the interaction between litter treatment and bole age – snags decompose more slowly than downed boles (Harmon *et al.* 1986; Song *et al.* 2017) and the accumulation of snags should have a positive feedback effect that further reduces long-term CWD decomposition rates. Cumulatively, these results suggest that reduced nutrient availability decreased wood decomposition rates, and thus soil nutrient availability is important to long-term CWD decomposition.

Apart from N, P, and K, it is likely that other nutrients influence wood decomposition. In the same forest used for our study, fertilization with a combination

448 of other nutrients (B, Ca, Cu, Fe, Mg, Mn, Mo, S, and Zn) increased leaf litter
449 decomposition more than N, P, and/or K (Kaspari *et al.* 2008). The soil concentrations
450 of two of these nutrients, Mg and Ca, were lower in the litter removal plots, but the
451 relative concentrations of Mn, Al, and Zn were unchanged (Sayer *et al.* 2012; Sheldrake
452 *et al.* 2017a) and the others were not quantified. The PCA indicated that the elemental
453 composition of boles differed between litter manipulations (Fig. 4), but high variation in
454 the concentrations of individual nutrients likely obscured biologically relevant
455 differences among litter treatments (mean coefficient of variation ± SD: 108 ± 74).

456 Only sodium (Na) concentrations in boles differed among litter treatments
457 (addition > removal, Table 1). This is potentially important because Na influences
458 decomposition (Kaspari *et al.* 2009) and catalyzes the use of N and P by soil
459 invertebrates (Kaspari *et al.* 2017) and potentially other saproxylic eukaryotes. A
460 detailed investigation of how Na influences CWD decomposition was beyond the scope
461 of this study, but our results suggest it is worthy of future exploration.

462 It is also likely that changes in microbial community structure decreased CWD
463 decomposition rates in the litter removal plots. Although total soil microbial biomass
464 did not differ among litter treatments (Sayer *et al.* 2012), communities of arbuscular
465 mycorrhizal fungi were significantly altered in the litter removals (Sheldrake *et al.*
466 2017a) and similar substrate addition experiments changed bacterial communities as
467 well (Nottingham *et al.* 2009). Reduced nutrient availability in the litter removal plots
468 potentially limited fungal growth (Swift 1977; Kaye & Hart 1997; Sheldrake *et al.* 2017a)
469 and it is possible that the lack of litter substrate for decomposition decreased the
470 biomass of fungal saprotrophs. Without sufficient nutrients or substrate, the resulting

fungal community is potentially optimized for other strategies (e.g., scavenging for soil nutrients and symbiosis with plants, Zimmerman *et al.* 1995; Sheldrake *et al.* 2017a; Sheldrake *et al.* 2017b) leading to reduced wood decomposition.

Tree species effects likely caused substantial variability within the patterns observed in our study. Although bole species composition was similar among litter treatments (Fig. S3), most species had low replication and thus the statistical power of this comparison was limited. We identified three relatively recalcitrant tree species and one relatively labile species. The separation of these species suggests that shade-tolerant species (e.g., *Tetragastris panamensis* and *Lonchocarpus heptaphyllus*) are likely to have recalcitrant wood, whereas certain pioneer species have particularly labile wood (*Cordia bicolor*; Ruger *et al.* 2009). However, these results were potentially influenced by unbalanced sample sizes. Wood density and concentrations of nutrients, lignin, and other compounds differ among species and profoundly affect decomposition (reviewed by Harmon *et al.* 1986). Consequently, we used proxy variables (wood density and chemical composition) to consider the role of tree species. Given these considerations, our results demonstrate that the influence of litter manipulation was strong enough to emerge despite unstructured variation in tree species composition between treatment blocks.

Temporal differences in bole selection, year-to-year decomposition dynamics, and environmental effects potentially influenced the patterns observed in our study. Boles omitted from this study tended to be smaller and denser than boles that were retained (Table S1), and respiration measurements required structurally stable boles that are likely more recalcitrant than average. However, both of these differences were

494 consistent among litter treatments and unlikely to affect the observed differences in
495 decomposition. Given that our study was performed across a chronosequence, we only
496 captured outcomes of long-term decomposition, which we related to single time-point
497 measurements of respiration and relative differences in nutrient limitation. Thus
498 possible year-to-year differences in decomposition within and among litter treatments
499 were not considered. Moisture and temperature are important controls of
500 decomposition, but previous measurements indicated that neither soil moisture content
501 nor temperature differed among litter treatments (Sayer & Tanner 2010b). Given the
502 unusually large sample size (n = 214) and multiple lines of evidence, it is unlikely that
503 these caveats affected our finding of nutrient limitation of decomposition in the litter
504 removal plots. However, these sources of error could have obscured other biologically
505 significant responses, such as our unsupported prediction that increased nutrient
506 availability in the litter addition plots would increase decomposition and respiration
507 rates.

508 In general, studies of wood decomposition aim to understand how carbon and
509 other nutrients return to the atmosphere and biosphere. Short-term studies of small
510 substrates provide a great foundation for understanding how endogenous (e.g., size,
511 chemical composition, density) and exogenous (e.g., nutrient availability, climate,
512 organismal effects, and their complex interactions) factors control wood decomposition
513 (reviewed by Harmon *et al.* 1986; Cornwall *et al.* 2009). However, CWD comprises the
514 majority of all wood mass and, to date, studies of factors that control long-term
515 decomposition of entire boles are limited to the effects of substrate characteristics
516 (species, size, density, and chemistry; Lang & Knight 1979; Brias, Paré, & Lierman 2006;

van Geffen *et al.* 2010) and climate (Chambers *et al.* 2000, Přívětivý *et al.* 2016). Conspicuously missing from the literature are experimental manipulations of exogenous factors, such as nutrient availability, that influence CWD decomposition.

Using litter manipulations, we provide evidence that soil nutrients are partially responsible for maintaining long-term rates of CWD decomposition, but moderate increases in soil nutrient availability do not meaningfully affect decomposition or wood respiration. Moreover, our results suggest that short-term studies potentially miss biologically important effects. To improve our understanding of decomposition and carbon cycling, further experimental manipulations of CWD decomposition are necessary, particularly investigations into the roles of exogenous nutrient availability, decomposer organisms, and their interactions (Fukami *et al.* 2010). We suggest that long-term CWD experiments be paired with more traditional manipulations of small substrates to test the connection between short-term and long-term decomposition.

Authors contributions:

E.M. Gora designed the study, collected the data, analyzed the data, and wrote the manuscript. E.V.J. Tanner established the experiment, contributed to the study design, and shaped the conceptual framework of the manuscript. E.J. Sayer assisted with statistical analyses and writing the manuscript. B.L. Turner performed elemental analyses, provided conceptual input, and assisted in writing the manuscript.

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Data accessibility:

All data from this manuscript are available in the Dryad Digital Repository: 10.5061/dryad.kh657 (Gora et al. 2017).

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Figure captions:

Figure 1. The log odds of complete decomposition (with 95% confidence interval) for boles in different litter manipulation treatments considering both their age and initial cross-sectional mass (litter removal: triangles and dashed line; litter control: squares and solid line; litter addition: circles and dotted line) across a 15 year chronosequence of tree death in lowland tropical forest in Panama. Greater log odds correspond with greater likelihood of complete decomposition, whereas lesser log odds indicates reduced likelihood of decomposition.

Figure 2. Average wood respiration rates (CO_2 efflux ± 95% confidence interval) of decomposing boles in litter addition, litter removal and control treatments (n= 28 for each litter treatment).

Figure 3. Change in wood respiration (%) for older boles (> 3 years old) in response to both NPK and water addition. Changes in respiration presented here are averages from three different measurement periods over 18 days. The treatments were divided among litter addition (circles and dotted line), litter removal (triangles and dashed line), and litter control treatments (squares and solid line).

Figure 4. PCA ordination of the elemental concentrations of boles from the NPK limitation experiment. Each point represents the average elemental concentrations of a bole and boles are grouped by litter manipulation treatment. Vectors indicate the direction and magnitude of correlations ($R^2 > 0.3$) among elemental concentrations of each bole (Table 2). Note that Mn, Fe, and Al overlap in the positive direction along the X axis. Ellipses are the 95% confidence interval wherein the centroid for boles of each litter treatment is located (addition = dashed, removal = dotted, control = solid).

741 **Table 1.** Elemental concentrations (±SE) of old boles distributed among the three litter
742 manipulation treatments prior to NPK addition. Superscript letters denote differences
743 among treatments. Sample sizes (N) indicate the number of total samples, but two
744 separate samples were taken from each individual bole.

Elements	Control (N = 12)	Litter Addition (N = 18)	Litter Removal (N = 10)
Al (mg/g)	6.01 (4.28)	1.19 (0.49)	4.71 (2.46)
B (mg/g)	0.01 (<0.01)	<0.01 (<0.01)	0.01 (<0.01)
C%	42.10 (1.39)	43.16 (0.58)	46.42 (1.26)
Ca (mg/g)	6.50 (0.94)	13.01 (2.52)	6.56 (1.38)
Cu (mg/g)	0.01 (<0.01)	0.01 (<0.01)	0.02 (0.01)
Fe (mg/g)	4.97 (3.46)	1.01 (0.41)	4.20 (2.22)
K (mg/g)	0.67 (0.12)	0.63 (0.09)	0.39 (0.06)
Mg (mg/g)	0.28 (0.09)	0.39 (0.11)	0.31 (0.08)
N%	0.74 (0.10)	0.69 (0.07)	1.04 (0.13)
Na (mg/g)	0.08^{ab} (0.02)	0.12^{a} (0.01)	0.05^{b} (0.01)
P (mg/g)	0.07 (0.02)	0.07 (0.02)	0.07 (0.02)

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748 **Table 2.** The PCA loadings for axes 1 and 2 reported along with the results of vector
749 fitting for each variable (R-squared). These values are from older boles used in the NPK
750 limitation experiment before they were treated with aqueous NPK.

Variable	PC1 loadings	PC2 loadings	R^2
Al	0.95	-0.04	0.81
B	0.61	-0.35	0.44
C	-0.58	-0.47	0.50
C:N	-0.39	0.59	0.44
Ca	0.33	0.53	0.35
Cu	0.32	0.00	0.09
Fe	0.95	-0.06	0.81
K	0.42	0.54	0.42
Mg	0.56	0.49	0.50
Mn	0.96	0.00	0.81
N	0.23	-0.75	0.54
Na	0.02	0.77	0.53
P	0.58	0.14	0.31
Zn	0.71	-0.48	0.64
Bole density remaining	0.26	-0.02	0.06

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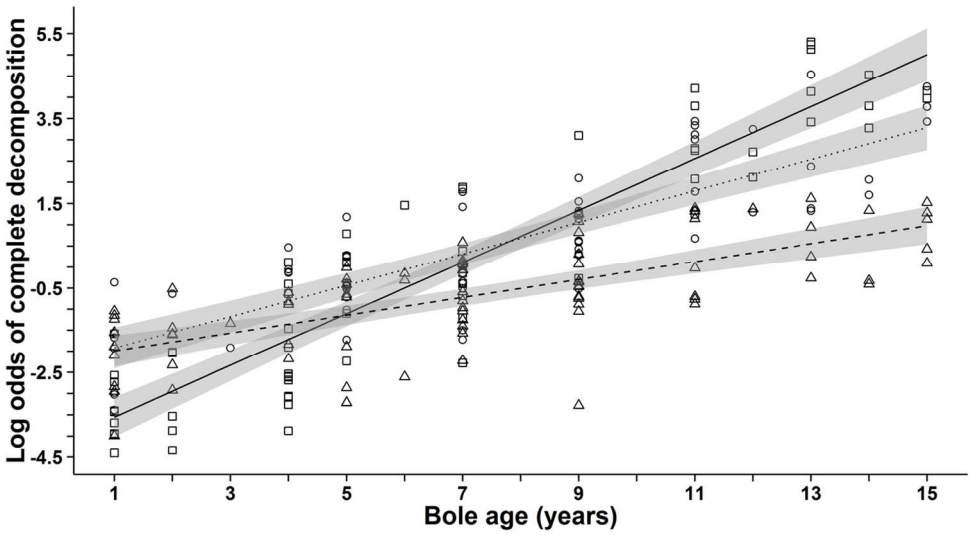
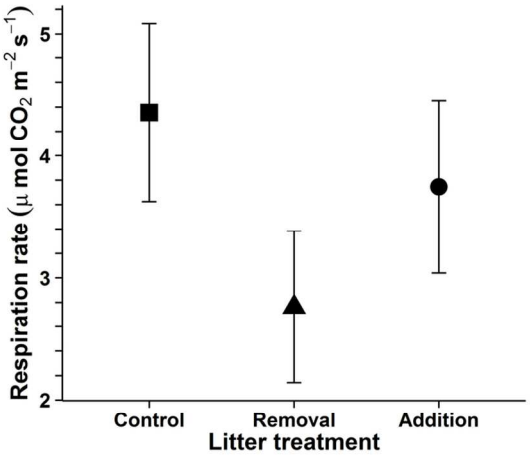


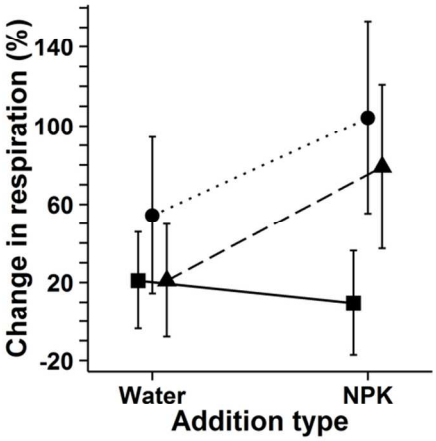
The log odds of complete decomposition (with 95% confidence interval) for boles in different litter manipulation treatments considering both their age and initial cross-sectional mass (litter removal: triangles and dashed line; litter control: squares and solid line; litter addition: circles and dotted line) across a 15 year chronosequence of tree death in lowland tropical forest in Panama. Greater log odds correspond with greater likelihood of complete decomposition, whereas lesser log odds indicates reduced likelihood of decomposition.

124x69mm (300 x 300 DPI)



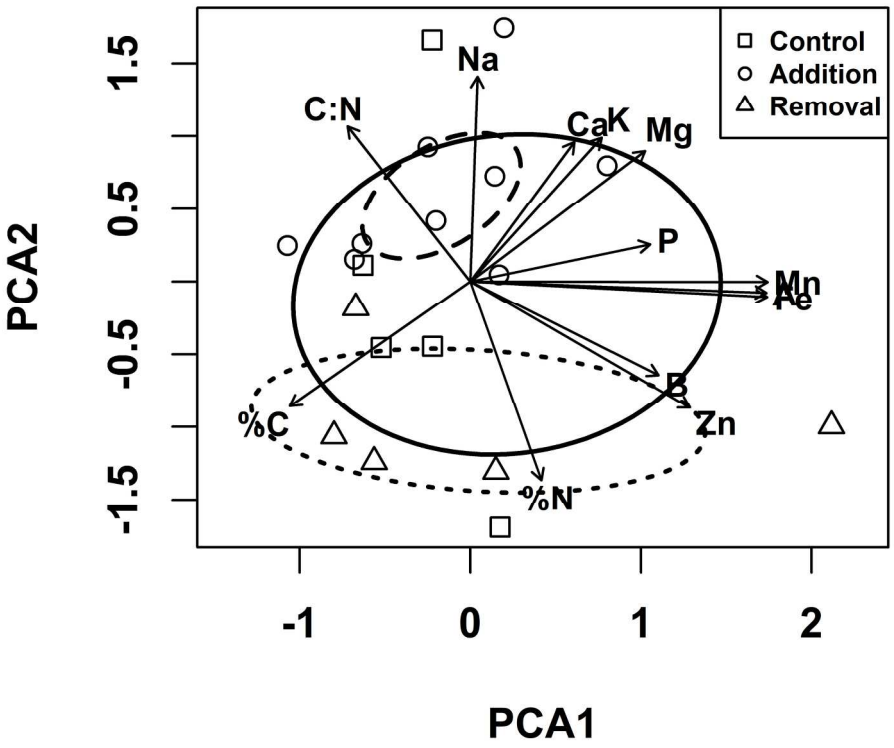
Average wood respiration rates (CO2 efflux ± 95% confidence interval) of decomposing boles in litter addition, litter removal and control treatments (n= 28 for each litter treatment).

115x63mm (300 x 300 DPI)



Change in wood respiration (%) for older boles (> 3 years old) in response to both NPK and water addition. Changes in respiration presented here are averages from three different measurement periods over 18 days. The treatments were divided among litter addition (circles and dotted line), litter removal (triangles and dashed line), and litter control treatments (squares and solid line).

96x52mm (300 x 300 DPI)



PCA ordination of the elemental concentrations of boles from the NPK limitation experiment. Each point represents the average elemental concentrations of a bole and boles are grouped by litter manipulation treatment. Vectors indicate the direction and magnitude of correlations (R2 > 0.3) among elemental concentrations of each bole (Table 2). Note that Mn, Fe, and Al overlap in the positive direction along the X axis. Ellipses are the 95% confidence interval wherein the centroid for boles of each litter treatment is located (addition = dashed, removal = dotted, control = solid).

101x101mm (600 x 600 DPI)

Supplementary Appendix

Table S1. The original diameter at breast height (DBH, mm), density (g cm^{-3}), and cross-sectional mass (g m^{-2}, ± standard error) of boles retained in our study compared with boles that were excluded. We compared these values using a mixed effect linear model with treatment as a fixed effect and plot as a random grouping factor. Lowercase letters denote similar values of DBH (a or b) and density (x or y), as determined with a post-hoc Tukey test. Many excluded boles were removed because the lacked species identification and therefore could not be assigned densities. Consequently, the sample size "N (with density)" is only for the number of excluded boles with known density (and thus known cross-sectional mass) within each treatment. Similarly, the other sample size of excluded boles [N (with DBH)] specifies the number of boles within each treatment with known diameter-at-breast height.

Litter treatment	Boles retained					Boles excluded			
	N	DBH (mm)	Density (g cm^3)	Cross-sectional mass (g m^2)	N (with DBH)	N (with density)	DBH (mm)	Density (g cm^3)	Cross-sectional mass (g m^2)
Control	67	769^a (50)	0.536^x (0.019)	460 (30)	23	1	464^b (47)	0.675^y (N/A)	242 (N/A)
Addition	62	893^a (55)	0.489^x (0.020)	346 (18)	35	12	519^b (44)	0.628^y (0.043)	494 (83)
Removal	85	764^a (42)	0.552^x (0.018)	407 (27)	42	14	534^b (55)	0.637^y (0.042)	421 (78)

Supplementary Information.

Trees omitted from this study had smaller DBH ($\chi^2_1 = 37.08$, $p < 0.001$) and were denser ($\chi^2_1 = 11.30$, $p < 0.001$) than those retained in the dataset. However, DBH and density did not differ among litter treatments (DBH: $\chi^2_2 = 2.36$, $p = 0.31$; Density: $\chi^2_2 = 3.38$, $p = 0.185$). Cross-sectional masses of boles did not differ ($\chi^2_1 = 2.64$, $p = 0.104$) between groups or among litter treatments ($\chi^2_2 = 2.74$, $p = 0.25$). Furthermore, there were no interactions between the characteristics of boles in the litter treatments and whether they were retained or omitted (DBH: $\chi^2_2 = 3.32$, $p = 0.19$; Density: $\chi^2_2 = 0.69$, p

= 0.71; cross-sectional mass: $\chi^2_2 = 3.26$, $p = 0.20$), indicating that the effects of these omissions were similar across litter treatments.

Table S2. The distribution of boles in each litter treatment among different classifications including standing, downed, suspended, and completely decomposed boles. Classifications with two components indicate that two separate sections of the tree were concurrently classified as different types of CWD.

CWD classification	Control (N)	Addition (N)	Removal (N)
Down	23	14	19
Completely decomposed	31	35	33
Snag	10	11	27
Snag/suspended	1	0	3
Snag/down	2	0	1
Suspended	0	2	2
Totals	67	62	85

Figure S1. Research assistant R. Kneale uses silicon sealant to attach a respirometry collar to a bole.

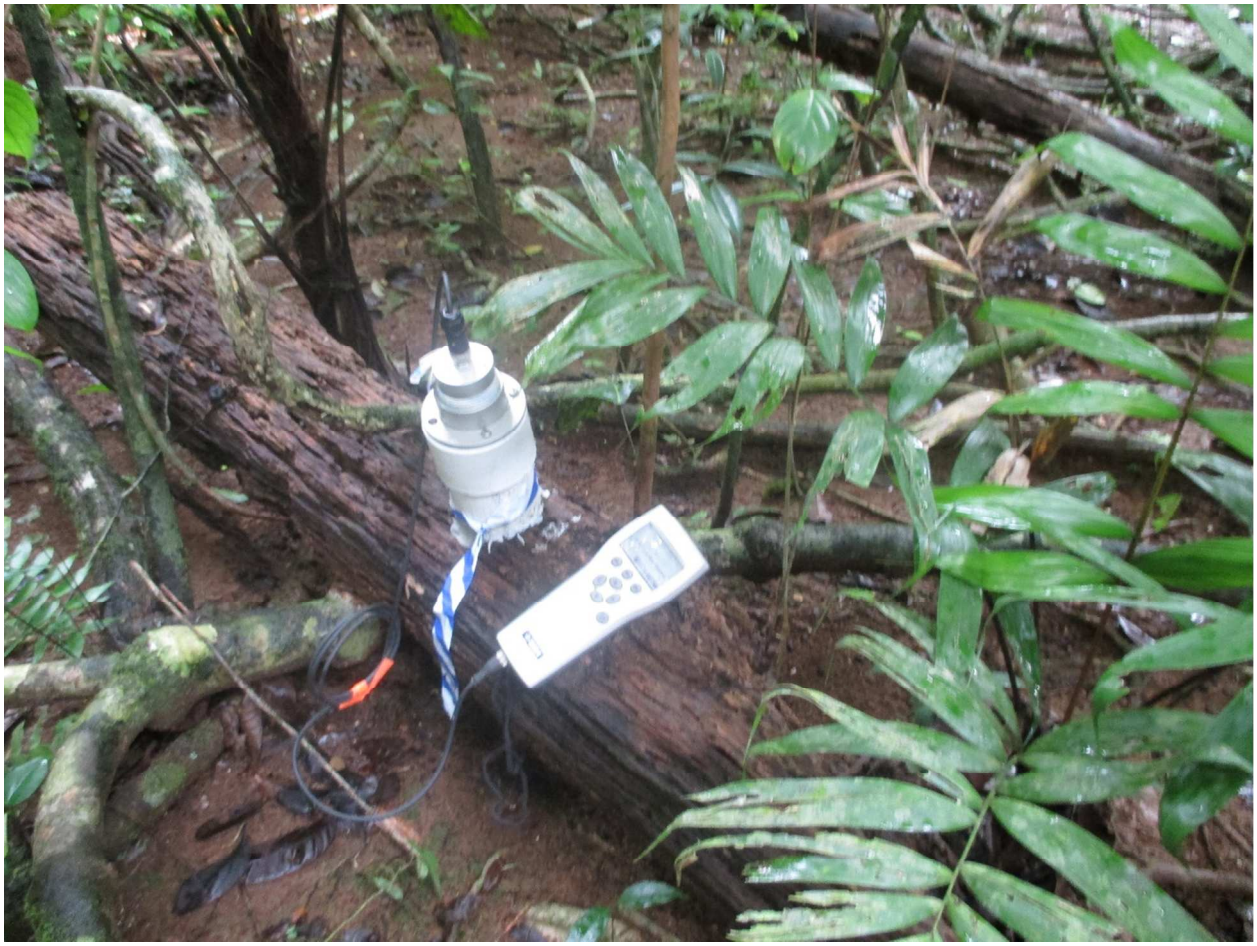


Figure S2. Viasala CO_2 probe and data logger record respiration rate of a bole located in a litter removal treatment.

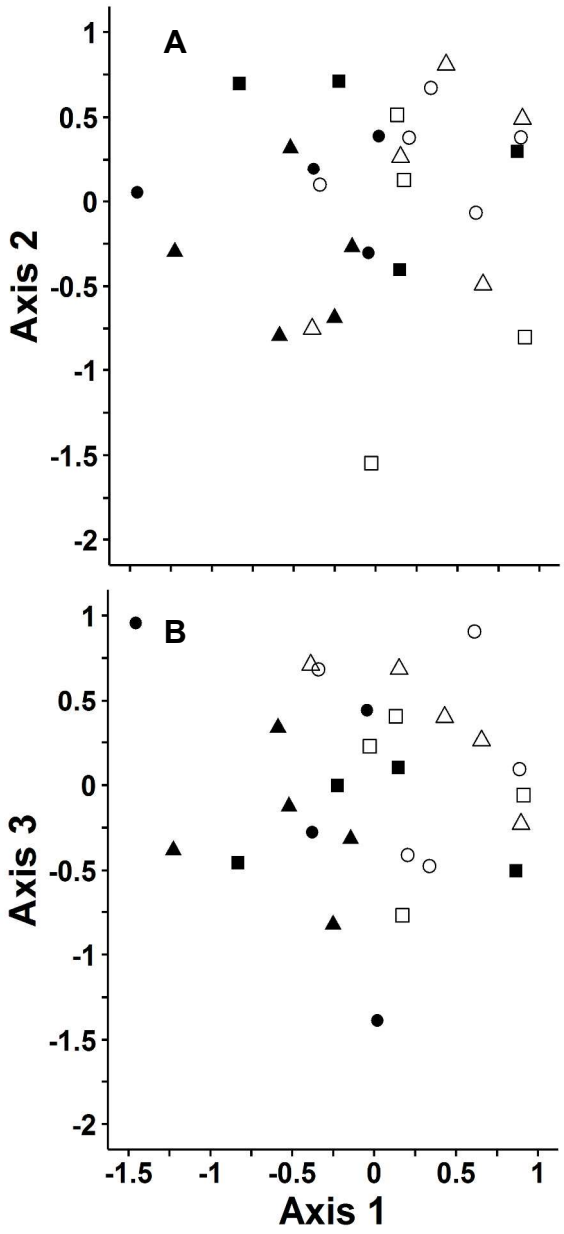


Figure S3. Nonmetric multidimensional scaling plot of tree species composition of completely decomposed trees (hollow points; n = 14) and dead trees that are still identifiable in 2016 (filled points; n = 13). Each point represents either the decomposed or remaining boles of a single plot. Panel A depicts NMS axes 1 and 2, whereas panel B depicts NMS axes 1 and 3. Circles represent litter addition treatment plots (n = 9), triangles represent litter removal plots (n = 10), and squares represent control plots (n = 8).