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ECOSYSTEMS

Suspended Sections Within Downed Deadwood Are Drier, Have Altered Decomposer Communities, and Slower Decomposition

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ABSTRACT

The decomposition of deadwood plays a key role in forest carbon emissions. Most pieces of downed deadwood are partially suspended above the forest floor, but how this suspension affects decomposition rates is typically ignored and remains largely unexplored. Here, we combine field observations and experimental manipulations to explore how partial suspension of downed wood (that is, wood debris in contact with the ground) influences decomposer communities and patterns of decomposition in a lowland tropical forest. Experimental manipulations of wood sticks showed that small-scale suspension above the forest floor (ca. 5 cm) slowed decomposition and altered microbial community assembly, regardless of whether the suspended section was connected to a piece of downed wood. Across a 41-year chronosequence of dead trees, the average percent of wood volume suspended above the forest floor decreased during the initial 10 years post-death, but this trend reversed after 10 years, with the oldest logs being the most suspended. Among downed woody pieces sampled in situ, sections suspended above the forest floor had less moisture, fewer macrofungi, and more photosynthetic growth (for example, moss, algae, and so on) than downed sections of the same bole. Surprisingly, wood density, termite presence, and mass-specific respiration did not differ with ground contact. Combined, these data suggest that suspension within downed wood reduces moisture content, influences decomposer community assembly, and contributes to the strong variability in decomposition rates. The strong effect of partial suspension within downed wood pieces heightens concerns about the accuracy and applicability of experiments and surveys focused on down deadwood, which are the foundation of our understanding of wood decomposition and associated carbon losses.

Key words: carbon cycle; decay rate; microbial diversity; respiration activity; wood decomposition; suspended deadwood.

HIGHLIGHTS

- Decomposition is slower in suspended sections of downed woody debris

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Author Contributions EMG, JML, and ABB conceived the study and collected the data; JML performed the bioinformatics; EMG and ABB analyzed the data; ABB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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- Suspended parts of downed wood are drier and have different microbial communities
- Suspended and downed wood follow different long-term decay trends

INTRODUCTION

Deadwood contains 72 Pg of carbon (Pan and others 2011) and its decomposition is a major contributor to global carbon emissions. However, wood decomposition rates and associated carbon emissions are highly variable, and we struggle to explain this variation (Martin and others 2021; Weedon and others 2009). We know that separation from the forest floor is a major contributor to local variation in decomposition, and deadwood is typically recorded as standing or downed to account for this effect (Dunn and Bailey 2012; Onega and Eickmeier 1991; Shorohova and Kapitsa 2014; Yatskov and others 2003). Even among downed wood pieces (hereafter ''boles''), nearly half of downed wood mass is elevated above the forest floor (hereafter referred to as *suspended* sections within downed deadwood, Gora and others 2019a) due to the natural variation in wood shape and heterogeneity of forest floor topography. Boles with sections separated from the forest floor decompose approximately 40% more slowly than completely downed pieces (Přívětivý and others 2016), but we do not know if, and if so why, suspended sections of downed wood decompose more slowly than downed sections of the same log.

Suspension of downed wood likely slows decomposition because of shifts in abiotic conditions, particularly wood moisture. Decomposition exhibits a parabolic relationship with wood moisture (Chen 1999; Hicks 2000; Sha and others 2005); decomposition is fastest at moderate moisture contents, but it slows when lower moisture slows microbial activity (Brischke and others 2017; Griffin 1977; Rajala and others 2012) or when high moisture produces anaerobic conditions (Harmon and others 1986; Harmon and Chen 1991). Soil typically holds more water than air, particularly in forest ecosystems, and contact with soil allows capillary flow of water into deadwood (Gora and Lucas 2019; Shorohova and Kapitsa 2014). Suspended sections of wood should be drier because separation from the soil eliminates direct capillary flow from the soil and increases water loss by providing greater surface area for evaporative drying. However, we do not know how wood moisture differs between suspended and downed sections of boles.

Biotically, suspension within downed wood likely influences microbial communities and their capacity to perform decomposition (Gora and others 2019b; Harmon and others 1986). In addition to moisture, contact with the forest floor provides access to soil nutrients and facilitates microbial colonization via hyphal growth (fungi) or swarming (bacteria). Therefore, separation from the forest floor likely creates a habitat filter (that is, drier, and nutrient-poor conditions) and a dispersal filter (that is, limited direct colonization) influencing microbial communities and their function (Kivlin and others 2014). However, there is little information about within-bole variation in microbial communities (Lee and others 2020) and how it contributes to decomposition rates. Indeed, it is possible that all sections of downed wood have similar communities because dispersal and nutrients could flow within wood from downed sections to suspended sections (for example, hyphal growth and nutrient translocation; Gora and Lucas 2019). Experiments are needed to understand how suspension and connections to adjacent downed sections of wood influence microbially mediated decomposition.

Invertebrates, particularly wood-feeding termites, are another important biotic factor controlling wood decomposition (Cheesman and others 2018; Harmon and others 1986; Zanne and others 2022). In tropical forests, wood decomposition by termites releases about 1.9 Pg of carbon to the atmosphere every year (Cornwell and others 2009). However, termites are not present in all forests (Jones and Eggleton 2011), nor are they evenly distributed across the vertical profile of forests (Roisin and others 2006). Termites have higher densities and greater contributions to decomposition on the forest floor than within higher forest strata, contributing to slower rates of decomposition above the forest floor (Law and others 2019). Compared to microbes, termites likely disperse more easily to suspended sections because they can walk, and can therefore be an important catalyst for decomposition of suspended woody debris. However, we do not know if termite activity differs between downed and suspended sections of individual boles.

Here, we combine field observations and experiments to test how suspension influences decomposition within pieces of downed woody debris in a moist tropical forest in central Panama. We explored how patterns of wood suspension change over time and evaluated whether suspended pieces of wood tend to persist longer in this forest. We also tested the hypothesis that suspended sections of downed wood decompose more slowly because habitat and dispersal filters limit microbial activity. We evaluated four specific predictions; (1) mass loss is lower and respiration rates are slower for suspended sections than downed sections of boles; (2) moisture content is higher in downed sections of wood than suspended sections; (3) suspended sections of downed wood have distinct microbial communities, regardless of their connection to downed sections of wood; and (4) suspended sections of downed wood have fewer termites.

MATERIALS AND METHODS

Study Area

All the field work was performed in the semideciduous lowland moist tropical forest of Barro Colorado Island (BCI) in central Panama (9°10′N, 79°51′W). The mean annual temperature is 26 °C and the mean annual rainfall is 2623 mm (STRI 2023), concentrated during a wet season from May to December (Leigh and others 1990). The study site is described in greater depth elsewhere (Croat 1978; Leigh 1999).

Wood Decomposition Survey

We quantified how suspension changes during the process of decomposition by estimating mass loss from dead trees across a 41-year chronosequence of decomposing trees. From August 2021 to June 2022, we revisited 15,652 trees ≥ 10 cm in diameter at breast height (DBH) that died in a 50-ha forest dynamics plot (ForestGEO, 2021) between 1980 and 2021. Data from the 50-ha plot included taxonomic information, location in the plot to the nearest 0.1 m, DBH, and the year of recorded death for each tree. We estimated tree death date as the midpoint of the census interval during which that tree died. Death date information came from either full-plot censuses every 5 years (1980–2015) or annual monitoring of tree condition for a stratified subset of trees (2008–2021). We located each tree based on its location in the plot (*x*–*y* coordinates).

Each tree we visited was documented in one of three ways. First, if there was no deadwood that could be associated with the dead tree near the location of its death, then we recorded it as fully decomposed. Second, if the focal dead tree was indistinguishable from other pieces of deadwood (for example, three trees of similar diameter died in the same location, but only two trees remained undecomposed) or the location could not be visually surveyed (for example, dense lianas), we omitted those trees from the study. Third, if we encountered persistent and distinguishable woody debris matching the expected DBH at the correct tree coordinate, then we recorded a suite of observational data.

For each dead tree that persisted, we recorded information about volume loss, deadwood position, and suspension. Using DBH at the time of death as a reference for initial volume, we visually estimated the percent of initial volume remaining on an ordinal scale with six categories: < 5% volume remaining, 5–20%, 21–40%, 41–60%, 61–80%, 81–100%. This method is advantageous relative to other methods because it (1) facilitates the measurement of irregular trunk shapes (for example, partially hollow trees, highly fragmented trees, convoluted trunks), (2) avoids flawed measurements of wood density, which is highly variable among species and even within individual pieces of deadwood, and (3) allows the rapid sampling of thousands of trees. Moreover, previous work in this forest demonstrated that intensive measurements using cross sections or penetration measurements provided little improvement in mass estimation (Gora and others 2019a). This approach differs from more traditional decay classifications developed for northern temperate forest (see wood respiration measurements section) in that it is based on decomposition relative to a complete original tree rather than the intactness of a piece of wood with a given volume (Harmon and Sexton 1996). Tree position was recorded as one or more of standing (that is, coarse woody debris fully or partially upright, reaching at least 20 cm above the forest floor), suspended (that is, coarse woody debris primarily being supported by something other than the ground, with the only possible exception being that one end is touching the forest floor) and downed (that is, coarse woody debris in contact with the forest floor; Harmon and Sexton 1996; Figure S1). For each tree, we visually estimated the percent of remaining volume that was suspended as the percent of cross-sectional volume (that is, length weighted by the volume at a given cross section) that was not in contact with the ground to the nearest 10% from 0 to 100% (referred to as *percent suspended*).

We explored how the percent of wood volume suspended changed with the percent of volume remaining for all trees that persisted ($n = 632$) and for persisting trees of the most common species, *Trichilia tuberculata* ($n = 75$). We used a t test to evaluate if the percent of wood volume suspended was greater among *T. tuberculata* that were > 10 years old versus 5–10 years old ($n = 72$). We repeated this using only downed trees of *T. tuberculata*

(n = 26) to test if these patterns were consistent after removing standing dead trees.

Wood Respiration and Macroorganism Measurements

We compared wood condition and biotic activity between downed and suspended sections of individual boles. Boles with both downed and suspended sections were haphazardly selected during meandering walks on Barro Colorado Island. We removed four pie-shaped cross sections of wood (that is, a sector of a cylinder, 1 cm width) from every bole using a hand saw (n = 45 boles). The four subsamples corresponded to top and bottom sections of both a suspended section and a downed section of the same bole (Figure 1a) to capture the effects of suspension and within-section microclimate. We also recorded the presence of termites, visible hyphae (for example, hyphal strands, fans, rhizomorphs), and photosynthetic growth (Figure S2) on each of the four subsamples. We visually recorded the decay class of each bole on a 1–5 qualitative scale based on wood texture, shape, and intactness (Canadian Forest Innovation Committee 2008). This standard method of decay classification differed from the estimation of volume loss used in our wood decay survey. Subsamples were stored in separate, sealed plastic bags until their respiration rates were recorded.

We recorded respiration rates (ppm CO2 s^{-1}) of each subsample for a subset of boles (n = 17 boles) using a dynamic respirometry chamber (that is, cylindrical PVC chamber with a volume of 4164 cm^3) and a CO_2 meter (Vaisala CARBOCAP® Carbon Dioxide Probe GMP343). Measurements started after 3 h of wood sample collection to avoid the release of CO_2 previously trapped inside the wood sample, and we confirmed that measurements stabilized after 3 h using a subset of samples, following the methods of Chambers and colleagues (Chambers and others 2001). Respiration data were recorded and processed using MI70 Link Windows® software (Vaisala 2022). CO_2 concentrations in the chamber were recorded every 5 s during a 5-min interval. We removed the initial 45 s of the sampling periods because they tended to be more variable. Respiration rate was calculated as the slope of CO_2 concentrations (mg CO2 s^{-1}) over the remaining 255 s (Bréchet and others 2017). We repeated respiration measurements of some sections and used the average respiration rate for samples with multiple measurements. We used the dry weight of the sample to calculate respiration rate per mass ($mgCO_2\ s^{-1}\ g^{-1}$).

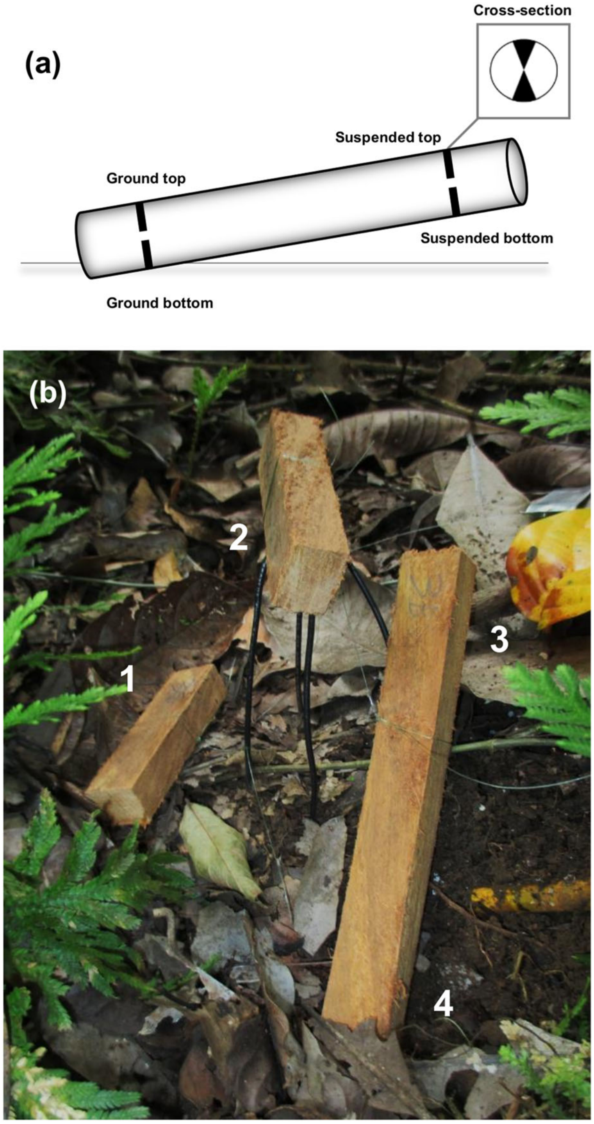

Figure 1. Field design for sampling boles and the suspension–connectivity experiment. Panel (**a**) shows the four locations where sectors were cut from downed pieces of wood with partial suspension. Specifically, black rectangular lines show the collection points where cross sections were removed, and the inset depicts a sampled cross section from an orthogonal perspective. Panel (**b**) is an image of the experimental setup for the experiment testing how suspension and connectedness interact to shape microbial communities and decomposition rates (1 = downed and separated; 2 = suspended and separated; 3 = suspended and connected; 4 = downed and connected).

After measuring respiration rates, we measured the density, moisture content, and dry weight of all wood samples (n = 45 boles with 4 subsamples each). We recorded wet weight as the mass of fresh samples on an analytical balance. Wood sample volume was estimated using the water displacement method with samples immersed at field moisture content. Differences in water absorption among samples could have influenced the volume estimates. For dry weight, we weighed the samples on the same balance after they were dried to a constant mass at 100 °C. Moisture content (%) equaled the percent of each field sample that was composed of water, calculated as the wet weight minus dry weight, divided by wet weight and multiplied by 100. We confirmed that calculating moisture content as moisture mass divided by dry mass did not influence the observed patterns of moisture content. Wood density (g/cm^3) equaled the dry weight divided by volume.

We used mixed-effect models to test how these variables differed with suspension (suspended or in contact with the ground) and position (top or bottom). We included one of moisture content, wood density, hyphal presence, termite presence, or photosynthetic growth presence as the response variable with three categorical predictors: suspension (downed or suspended), location (top or bottom), and their interaction. To account for variation among wood pieces, we included the unique identifier for each bole as a random effect. To compare respiration rates, we included mass-specific respiration rate as the response variable and added air temperature as an additional predictor with suspension, location, their pairwise interaction, and the random effect of bole. We used linear models with Gaussian errors (function *lmer*, package *lme4* in R) for moisture content, wood density, and respiration rate, whereas the three metrics of macroorganism presence were assessed using models with binomial errors and a logistic link function (function *glmer*, package *lme4* in R). We tested the effects of each term using likelihood ratio tests, and we removed nonsignificant interaction terms.

Experimental Manipulations of Fine Wood Connectedness and Ground Contact

We experimentally manipulated suspension and within-block connectivity to test how contact with the forest floor influences decomposition and microbial community assembly. We performed a fully factorial manipulation of wood suspension (downed or suspended) and wood connectivity (suspended sections either connected to or separated from a downed section of the same wood piece) across 25 replicates in a randomized complete block design (Figure 1b). Each replicate used two 20 cm long wood blocks (2 × 2.5 cm width and height) of *Pachira quinata*. Before starting the experiment, we dried all wood blocks at 60 °C and recorded their mass and volume. To manipulate connectivity, one block was cut in half before the experiment, with the 10-cm-long ‘‘downed’’ treatment placed directly on the forest floor and the 10-cm-long ‘‘suspended’’ treatment suspended 5 cm above the forest floor using insulated wire (Figure 1b). The second block remained intact and was partially suspended using insulated wire so that at least 5 cm of its length was directly in contact with the soil (Figure 1b). After 16 months in the field (June 2015 to October 2016), the second block was also cut in half and all blocks were harvested. We recorded mass loss from all wood blocks, and final dry mass was recorded after drying wood at 105 °C.

To assess differences in mass loss, we constructed linear mixed-effect models with Gaussian errors. These models included mass loss (%) as a response variable, connectedness, suspension, and their pairwise interaction as categorical fixed-effect predictors, and a random grouping variable for each experimental block. We logit transformed the mass loss data before the analysis to meet model assumptions. The significance of each term was tested using single-term deletions with likelihood ratio tests based on the Chi-squared distribution.

For each of the 5 replicates, DNA was collected in the field using a battery powered drill (DCD780B 20 V MAX* Lithium Ion Compact Drill) to grind wood material from all four sides of each block at the midpoint along its length. We pooled wood from all four sides and stabilized DNA from the pooled sample using DNA/RNA Shield Stabilization Solution (Zymo Research 2022). Each wood sample was processed using bead beating at 3000 oscillations per 1 min (modified Ryobi P514 Reciprocating Saw, Andersen, South Carolina, USA). Samples were frozen at − 40 °C until DNA could be extracted.

We assessed community structure separately for bacteria and fungi using amplicon sequencing using the protocol outlined in Gora and others (2019b). We amplified the V2 region of the 16S ribosomal gene for bacteria (primers: S-D-Arch-0519-a-S-15 and S-D-Bact-0785-b-A-18; Klindworth and others 2013) and the ITS1 region for fungi (primers: ITSF-1 and ITS2; McGuire and others 2013). Barcoded amplicons were cleaned and product was standardized using SequalPrep Normalization plates (ThermoFisher, Inc, Massachusetts, USA; Harris and others 2010). Amplicons were sequenced using a MiSeq instrument with 500 V2 chemistry for paired end reads (2 × 250 bp). Illumina sequencing reads were analyzed and demultiplexed using QIIME (Caporaso and others 2010). Sequencing reads that contained errors in the barcoded region, ambiguities, homopolymers (greater than six nucleotides in length), or an average quality score below 25 were discarded. Primer sequences were trimmed, and chimeric sequences were eliminated using USEARCH (version6.1) with the ''gold'' reference database for bacteria (Edgar 2010) and the UNITE reference database for fungi (Kõljalg and others 2013). Microbial community analyses were based using operational taxonomic units (OTUs) at 97% similarity. Each OTU sequence was placed in a taxonomic category from Phyla to family via the SILVA reference database for bacteria (release119, Quast and others 2012) and the fungal UNITE reference database (version 7.1, Kõljalg and others 2013).

We successfully amplified and sequenced 20 bacterial samples and 14 fungal samples for analyses. We used negative PCR and sequencing controls, and sequences present in the negative controls were removed from all samples before analysis (316 bacterial OTUs and 21 fungal OTUs). After cleanup, the bacterial dataset contained 465,852 total reads across 28,267 OTUs, and our fungal dataset contained 174,940 total reads across 6,536 OTUs. OTUs belonging to Archaea were removed from bacterial samples prior to the analyses because their abundance was exceedingly low. Singletons were omitted, and then, to account for differences in sampling depth, we rarefied samples to 3,199 and 4,704 sequences for bacterial and fungal taxa, respectively, retaining all 20 bacterial samples and 11 fungal samples (2 connected-suspended and 3 each of connected-downed, separated-downed, and separated-suspended). Sequencing data are available online via the Figshare repository (link to be created upon acceptance).

We compared community composition, diversity (richness, Shannon diversity, and Simpson diversity), and the abundance of individual orders of bacteria among treatments. We tested for differences in composition using PERMANOVA (9999 permutations) with suspension, connectivity, and their interaction as fixed effects, and a random grouping variable for each block. We dropped nonsignificant interactions. We also tested whether compositional beta diversity differed with suspension and connectivity using permutation tests of dispersion (Anderson and others 2008). For these compositional analyses, microbial data were square-root transformed before calculating dissimilarity using Bray–Curtis distance. For all univariate response variables (that is, diversity indices and abundance of orders), we used mixed-effect models (function *lmer*, package *lme4*; Bates and others 2015) with Gaussian errors and the same predictors as the community composition analyses. We tested for significance of fixed effects using likelihood ratio tests between models with single-term deletions. The mixed-effect models were performed in the R statistical environment (R Core Team 2021), and we examined model residuals to evaluate model fit for all analyses. The permutation based-analyses were performed using PRIMER-E (Ver.7.0.13). For fungi, we only tested for compositional differences among treatments because the small sample sizes precluded robust analysis.

RESULTS

Suspension Above the Ground Influences and is Influenced by Decomposition

The most persistent trees were unusually suspended. Among all decomposing trees with material remaining in the focal 50-ha forest stand, the percent of each tree suspended tended to decrease with progressive volume loss (Figure 2a). However, two distinct temporal trends were apparent when examining patterns of suspension within the most common species. Among remaining trees of *Trichilia tuberculata,* the percent of each tree suspended tended to decrease over the first 10 years since their death, but the trees that persisted beyond 10 years remained suspended or upright despite high levels of volume loss (Figures 2b and S3). Indeed, *T. tuberculata* trees 5–10 years post-death exhibited a lower percent of their volume suspended than trees > 10 years post-death ($t = 5.0$, $P < 0.001$). We observed the same trend when only considering downed *Trichilia tuberculata* trees, but only 26 trees persisted past 10 years and this pattern was not statistically significant for this smaller sample ($t = 1.5$, $P = 0.164$).

The Effects of Within-Bole Ground Contact on Wood Characteristics and Macroorganisms

Suspension within a single piece of downed wood affected moisture content, but had little influence on instantaneous wood density and respiration. Moisture content varied within trunks that were partially suspended. Downed wood sections had 5.4% higher moisture content than suspended

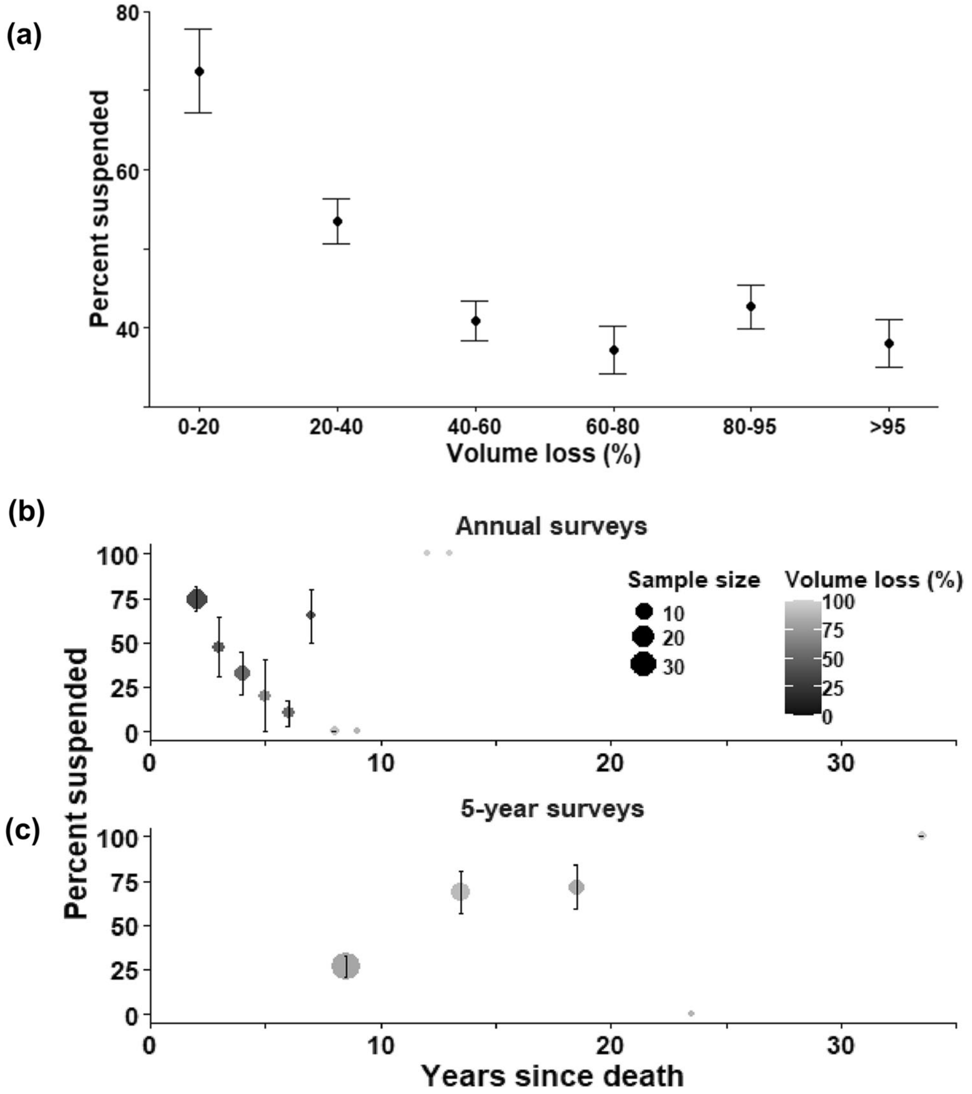

Figure 2. Wood suspension tended to be lower for more decomposed trees across all remaining dead trees in the BCI 50 ha plot (632 remaining trees; panel **a**). Within the most common species, *Trichilia tuberculata*, suspension tended to decrease over time as wood decomposed (panel **b** and **c**), but suspension increased beyond 10-year postmortem. Points represent average values of suspension within bins of mass loss (panel a) or within intervals of years since death plotted at the median value of years since death for that interval for either a 1-year census interval (43 trees; panel b), or a 5-year census interval (61 trees; panel c). Error bars are 95% confidence intervals. The color and size of dots depict the average mass loss and sample size, respectively, in panels **b** and **c**.

sections (downed mean ± SE: 104.9% ± 8.7%; suspended mean ± SE: 97.1% ± 11.7%), but moisture did not differ between the bottom and top sections ($X^2 = 0.7$, $P = 0.397$; Figure S4). Neither wood density nor respiration varied with suspension (density: $X^2 < 0.1$, $P = 0.881$; respiration: $X^2 = 0.4$, $P = 0.523$), location (that is, top or bottom of each section; density: $X^2 = 0.2$, $P = 0.671$; respiration: $X^2 = 0.1$, $P = 0.736$) or their interaction (density: $X^2 = 0.3$, $P = 0.565$; respiration: $X^2 < 0.1$, $P = 0.6309$; Figure S5).

Visually observable organisms differed significantly with suspension and top or bottom position (Figure 3). Across all samples, 40% had hyphae, 58% had termite galleries, and 9% had photosynthetic growth. Visible hyphae were 16% more common in suspended sections than downed sections of the boles ($X^2 = 6.0$, $P = 0.014$) and 24% more common in the bottom portions of both downed and suspended sections ($X^2 = 14.3$, $P < 0.001$). Termite galleries were 5% more common on the bottom sides of boles than their tops ($X^2 = 7.3$, $P = 0.007$), but did not differ with

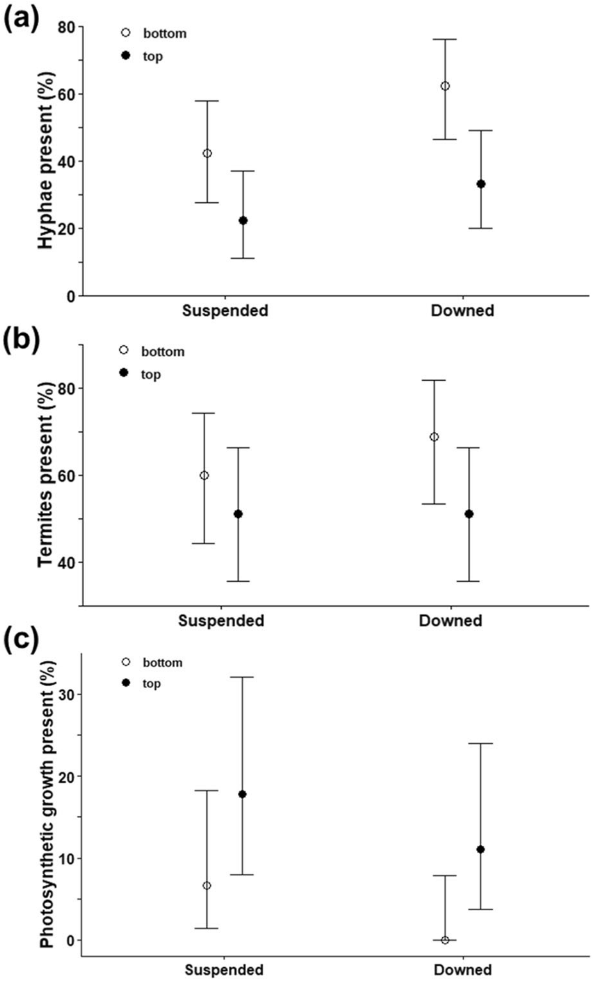

Figure 3. Differences in the presence of visible organisms between downed and suspended sections of boles and the top and bottom sides of each section. Points represent the proportion of samples with visible hyphae (downed sections: $X^2 = 6.0$, $P = 0.014$; bottom sides of boles: $X^2 = 14.3$, $P < 0.001$; panel a), evidence of termite activity (bottom sides of boles: $X^2 = 7.3$, $P = 0.007$; panel b), or photosynthetic growth (suspended sections: $X^2 = 9.8$, $P = 0.002$; top sides of boles: $X^2 = 20.2$, $P < 0.001$; panel c), and error bars represent 95% confidence intervals based on the binomial distribution.

suspension ($X^2 = 0.8$, $P = 0.357$). By contrast, photosynthetic growth was 7% more common in suspended sections ($X^2 = 9.8$, $P = 0.002$) and 11% more common on the top sides of boles ($X^2 = 20.2$, $P < 0.001$) than in downed or bottom sections, respectively. None of these biotic groupings exhibited significant interactions.

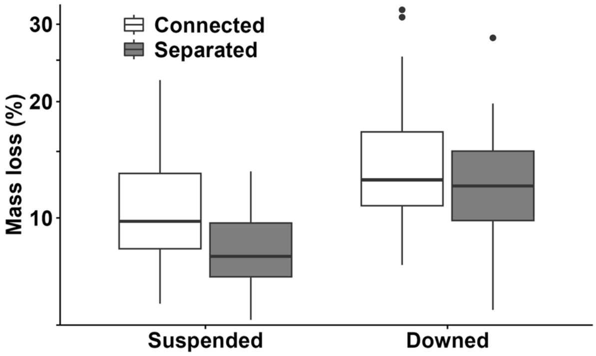

Figure 4. Boxplots of mass loss (% of initial mass) from wood blocks after one year in the field with factorial manipulations of connectivity and suspension. Median values are depicted by horizontal lines and mean values are reported here: suspended-connected mean ± SE: 10.6% ± 1.2%; suspended-separated mean ± SE: 8.2% ± 0.5%; downed-connected mean ± SE: 15.4% ± 1.6%, and downed-separated mean ± SE: 12.8% ± 1.1%.

Suspension of Fine Wood Influences Decomposition and Microbial Communities More Than Connections to the Ground

Suspension substantially decreased mass loss from small wood blocks, whereas connectedness was relatively less important. Mean mass loss across all samples was 11.8% (SE = 0.6%) after 16 months in the field. Suspended wood blocks had 5% less mass lost, on average, than downed wood blocks (suspended mean ± SE: 9.4% ± 0.7%, downed mean ± SE: 14.1% ± 1.0; $X^2 = 22.3$, $P < 0.001$), indicating that ground contact increased mass loss by 50%. Separated wood blocks had 2% less mass loss than connected blocks, on average, but this effect was much weaker and only marginally significant ($X^2 = 4.2$, $P = 0.041$; Figure 4). There was no interaction between suspension and connectedness ($X^2 < 0.1$, $P = 0.929$).

Suspension strongly influenced bacterial colonization of fine wood sections, regardless of whether the suspended section was connected to downed wood. After 1 year in the field, bacterial composition differed between suspended and downed wood sections (Pseudo-$F_{1,19} = 1.9$, $P = 0.002$) and among blocks (Pseudo-$F_{1,19} = 1.3$, $P = 0.001$), whereas connectedness had no effect on bacterial community composition (Pseudo-$F_{1,19} = 1.0$, $P = 0.574$). Bacterial community dispersion did not differ with suspension (Pseudo-$F_{1,18} = 1.1$, $P = 0.443$) or connectedness (Pseudo-$F_{1,18} = 0.2$, $P = 0.8291$; Figure 5a). Of the ten most

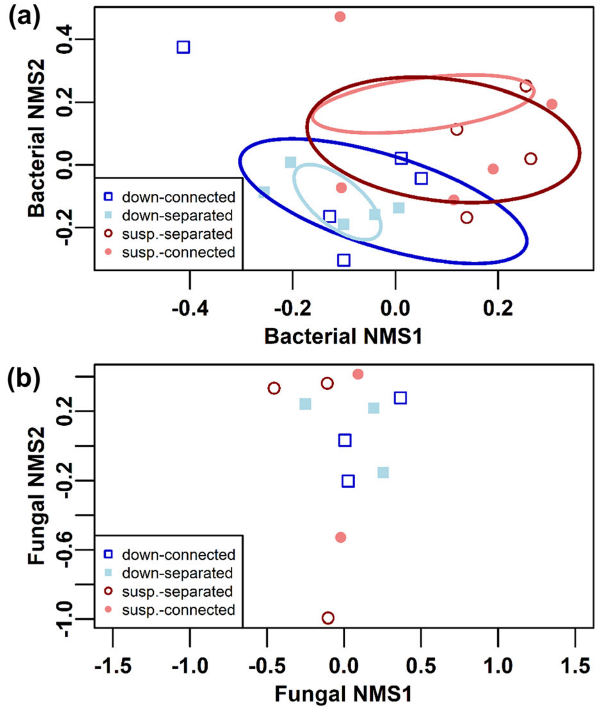

Figure 5. Nonmetric multidimensional scaling ordinations of the community composition of bacteria (panel a; stress = 0.12) and fungi (panel b; stress = 0.08) in wood blocks with factorial manipulations of suspension (suspended or downed) and connectedness (connected or separated). Circles represent 95% confidence intervals for the location of the centroid from each group. Ordinations were based on Bray–Curtis distance of bacterial and fungal OTUs.

common orders of bacteria, Rhizobiales, Actinomycetales, and Saprospirales had higher relative abundance in the suspended sections than the downed sections, but did not vary with connectedness. None of the seven remaining orders differed among treatments (Table S1). Richness, Shannon diversity, and Simpson's diversity (Table 1) did not differ with suspension ($X^2 = 213{,}624$, $P = 0.081$; $X^2 = 0.5$, $P = 0.104$; $X^2 < 0.1$, $P = 0.184$ for richness, Shannon diversity, and Simpson's diversity, respectively), connectedness ($X^2 = 361$, $P = 0.940$; $X^2 < 0.1$, $P = 0.760$; $X^2 < 0.1$, $P = 0.502$) or their interaction ($X^2 = 68{,}094$, $P = 0.310$; $X^2 = 0.2$, $P = 0.0313$; $X^2 < 0.1$, $P = 0.339$).

Fungi exhibited similar trends, but we lacked the data needed for robust statistical analyses. Neither fungal composition nor dispersion varied significantly with suspension (composition: Pseudo-$F_{1,10} = 1.4$, $P = 0.256$; dispersion: Pseudo-$F_{1,9} = 3.4$, $P = 0.085$) or connectedness (composition: Pseudo-$F_{1,10} = 1.0$, $P = 0.513$; dispersion: Pseudo-$F_{1,9} = 1.6$, $P = 0.320$; Figure 5b). We did not perform statistical tests on fungal order-level abundance or metrics of diversity because of their low sample size.

DISCUSSION

A substantial proportion of downed wood mass is suspended above the ground (estimated as 23–52% of downed wood in this tropical forest; Gora and others 2019a), yet almost all studies of woody decomposition focus on fully downed pieces. Here, we show that suspended sections of downed wood pieces have slower decomposition with accompanying changes in the decomposer community, challenging our current understanding of carbon emissions from deadwood. These effects occurred over small vertical distances (< 10 cm) and persisted regardless of connections to downed sections of the same bole. These findings emphasize that small-scale vertical variation within downed wood pieces can play a major role in regulating wood decomposition rates and likely contributes to the extreme heterogeneity in wood decomposition rates (Dai and others 2021; Harmon and others 1986).

The strong effects of suspension within downed wood heighten concerns about how we study and understand wood decomposition. Most deadwood mass is contained in large, irregularly shaped pieces that decompose over long time periods. Because these pieces are logistically challenging to study, the mechanisms controlling wood decomposition are typically tested using small, homogenous wood pieces in direct contact with the soil. The results presented here, prior work showing vertical turnover in wood saprotrophs (Gora and others 2019b; Law and others 2019), and the need for longer-term studies that capture decay patterns (Oberle and others 2019) collectively indicate that this common approach fails to capture realistic processes of wood decay. This is particularly concerning for up-scaling to carbon fluxes and taxa-specific contributions to decomposition using short-term, ground-focused experiments (for example, Seibold and others 2021; Zanne and others 2022). At best, these studies are imprecise. However, it is possible that they include fundamental, yet unquantified, biases regarding decomposition rates, carbon fluxes, and the contributions of key decomposers. It is critical to consider how well a given experiment captures realistic processes of decay, including small-scale vertical suspension.

Overall, suspension within downed boles appeared to produce substantial variation in decay

Table 1. Total Number of Taxa (Richness) and the Mean Diversity Metrics of Bacterial Taxa in Wood Blocks with Factorial Manipulations of Suspension (Suspended or Downed) and Connectedness (Connected or Separated)

Diversity metrics	Suspended		Downed	
	Connected	Separated	Connected	Separated
Richness	1226.6 (72.4)	1101.4 (188.3)	1316.6 (80.8)	1424.8 (43.6)
Shannon	6.45 (0.1)	6.20 (0.3)	6.57 (< 0.1)	6.70 (< 0.1)
Simpson	1 (< 0.1)	1 (< 0.1)	1 (< 0.1)	1 (< 0.1)

All values are from rarefied samples. Numbers in parentheses indicate the standard error of the diversity metrics.

rates. Trees tended to come into greater contact with the ground as they decomposed, as might be expected for trees losing structural integrity, but dead trees that persisted the longest were unusually suspended (Figure 2c). These divergent trends within the same species likely contribute to the difficulty of accurately measuring wood decomposition rates and related carbon emissions. It is possible that considering suspension as a continuum, as done in this study, will better represent patterns of decomposition than binary categorizations, such as ''downed'' and ''standing.''

The divergent communities in suspended sections of downed wood likely contributed to their slower decomposition. Saprotrophic macroorganisms (termites and fungal structures) tended to be more abundant in the downed or bottom sections of wood, whereas photosynthetic growth was more common on the upper sections. Moreover, amplicon sequencing showed that bacterial community structure was driven by separation from the soil surface, and fungal communities trended in the same direction, albeit with fewer data. Combined with the similar levels of total activity approximated with respiration rates, this suggests that the faster decomposition of downed sections was caused by differences in saproxylic community composition. Overall, these patterns contribute to a growing body of evidence that local biotic effects play a major role in regulating decomposition rates (Fukami and others 2010; Bradford and others 2014; Zanne and others 2015).

The effect of suspension on community composition likely arose, in part, via habitat filtering and dispersal limitation. Suspended sections of downed wood were comparatively dry, likely limiting both the establishment and activity of decomposers relative to downed sections of the same log. Dispersal filters could also contribute to these patterns, as shown for fungal colonization of deadwood in the canopy (Gora and others 2019b). Our study cannot explicitly differentiate the contributions of habitat and dispersal filtering, but our experiment indicates that connectivity does not overcome potential dispersal limitation, suggesting a stronger role of habitat filtering. We had relatively poor data for fungi in this experiment, but we expect them to exhibit the same strong patterns as bacteria for three reasons: (1) bacterial communities are strongly predictive of fungal composition in deadwood (Gora and others 2019b), (2) visible hyphae were less common in suspended sections of downed woody debris in situ (Figure 3a), and (3) bacteria are important contributors to wood decomposition (Clausen 1966; Greaves 1971; Johnston and others 2016; Bhatnagar and others 2018; Embacher and others 2023; Mieszkin and others 2021) that also depend on connectivity to colonize wood (for example, ''swarming'' bacteria or assisted dispersal; Greaves 1971; Shi and Zusman 1993; Johnston and others 2016). Experimental manipulations of environmental conditions and dispersal would reveal the relative importance of dispersal and habitat filtering to regulating the decomposition of downed woody debris.

Although most factors in this study varied with the percent of the tree that was suspended, neither respiration nor wood density exhibited this trend. Respiration is expected to be higher in boles experiencing higher decomposition rates (Chambers and others 2001), but not all respiration is associated with decomposition (for example, environmental stress can decrease microbial efficiency; Schimel and others 2007) because deadwood is a common habitat across the tree of life (Błoszyk and others 2021; Bunnell and Houde 2010; Chećko and others 2015; Jonsell and others 1998). Microbial and invertebrate decomposers coexist with saproxylic organisms that do not perform decomposition (for example, predatory bacteria, mites, and nematodes), and it is possible that organisms other than decomposers are contributing to the respiration rates recorded in this study. Correspondingly, our observations of macrofauna indicate that macro-saprotrophs were more common on the ground, but other taxa (such as photosynthetic growth) were more abundant on the upper sections of wood. Beyond this ecological explanation, this pattern could arise for various other reasons. Decay rates and associated respiration rates decrease as wood decomposes, and therefore, respiration rates will slow more rapidly in sections of wood that decompose faster, potentially confounding comparisons of overall decay using instantaneous measures of respiration. Additionally, it is possible that decomposition rates did not differ between the suspended and downed sections of these suspended logs, which could occur for many reasons; for example, the population of remaining logs with suspended sections could be a recalcitrant, biased subset of the broader community that decomposes more slowly than expected and exhibits no differences in mean decay. It is also possible that these patterns were influenced by measurement imprecision and the small sample size, especially for wood density because the immersion approach to measuring volume did not account for void space or prior water content. Additional work is needed to explore these possibilities and separate the role of specific saproxylic taxa in regulating the process of decomposition across variation in suspension.

The results of this study highlight multiple directions for future research. We describe strong and multifaceted effects of within-bole suspension in a single tropical site, but comparable studies in other ecosystems are needed to evaluate the broader importance of suspension to decomposition and decomposers. Relevant information is particularly scarce in the tropics (Chagnon and others 2022). Our study also provides experimental evidence that suspension influences decomposer community assembly, but this process requires further investigation in situ, tests over longer timeframes, and greater attention to termites (Hättenschwiler and others 2005). Lastly, we struggled to quantify differences in historic decomposition within boles in situ, and a more careful evaluation of volume loss, fragmentation, and elemental composition will provide a clearer picture of how suspension influences the geochemical processes of decomposition. Addressing these next steps will bring us closer to a mechanistic, predictive framework for understanding decomposition-related carbon emissions, which is critical to understanding the future carbon budget as forest composition and dynamics change.

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DATA AVAILABILITY

Barrera-Bello, Ángela; Gora, Evan; Lucas, Jane (2023), Suspended sections within downed deadwood are drier, have altered decomposer communities, and slower decomposition, Dryad, Dataset. https://doi.org/10.5061/dryad.bzkh189g2

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