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Microbial Composition and Wood Decomposition Rates Vary with Microclimate From the Ground to the Canopy in a Tropical Forest

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ABSTRACT

Wood decomposition is a key component of carbon cycling. However, our understanding of decomposition is limited by the absence of information regarding wood separated from the forest floor, which represents approximately half of total woody debris. We hypothesized that turnover in microbial (bacterial and fungal) community structure from the ground to the canopy causes decreasing rates of decomposition. To test this hypothesis, we used standardized wood sticks and metabarcoding to provide the first replicated assessment of decomposition and decomposer microbial community structure along a vertical gradient within a tropical forest. Community composition and functional groups of fungi and bacteria covaried strongly from ground to canopy, and both microbial groups exhibited distinct community types at different levels within the forest. Mass loss from wood sticks was strongly associated with both microclimate conditions and microbial community composition. However, unlike the continuous turnover of microbial communities, wood decomposition exhibited a binary pattern such that differences in decomposition were driven by soil contact and associated with increased moisture content. These findings are contrary to dominant models of decomposition that primarily consider environmental effects at larger scales and thus take an important first step in challenging the contemporary, ground-based understanding of decomposition. Contrasting patterns in the relative abundance of bacterial and fungal saprotrophs observed in this study suggest that additional work is needed to delineate the roles of invertebrate, fungal, and bacterial decomposers in higher levels of the forest.

Key words: microbiome; fungi; bacteria; environmental conditions; dead wood; community assembly; saproxylic communities.

HIGHLIGHTS

- Turnover of fungal and bacterial communities covaries from the ground to the canopy.
- Decomposition and microbial communities are strongly associated with microclimate.
- Soil contact and wood moisture content determined rates of wood decomposition.

INTRODUCTION

The validity of carbon cycling models depends on accurate quantification of decomposition rates across multiple spatial scales (Adair and others 2008; Bradford and others 2014). Dead wood is particularly important to these models as it constitutes 73 ± 6 Pg C globally and contributes 10–20% of CO_2 emissions from tropical forests—the largest global terrestrial carbon sink (Brown 1997; Pan and others 2011; Palace and others 2012). Dominant models of wood decomposition indicate that abiotic factors control decomposition globally, whereas biotic effects on decomposition (wood traits and decomposer organisms) are mediated at regional and local scales (Parton and others 2007; Adair and others 2008; Cornwell and others 2009; Bradford and others 2014; Zanne and others 2015; Oberle and others 2018). However, evidence for these patterns comes almost entirely from measurements of ground-level decomposition. This ground-level approach is somewhat flawed because, in many forests, the majority of dead wood is situated above the forest floor where it loses as much as 40% of its mass before falling to the ground (either as suspended, elevated, or standing dead wood; Ovington and Madgwick 1959; Swift and others 1976; Christensen 1977; Palace and others 2012; Gora and others 2019). Given the limited information regarding the decomposition of dead wood separated from the forest floor, the local factors that regulate wood decomposition remain poorly understood.

Abiotic factors differ dramatically along vertical gradients from the ground to the canopy within tropical forests, and these differences determine the distribution of microbial decomposers (Parker 1995; Kivlin and others 2014; Freedman and Zak 2015; Figure S1). Specifically, conditions shift from wet and dark on the forest floor to arid and highly insolated in the canopy (Juniper 1991; Beattie and Lindow 1995; Parker 1995). These extremes likely affect the composition of microbial decomposer communities, as decomposer colonization is at least partly determined by environmental filtering (Kivlin and others 2014; Freedman and Zak 2015). But multiple factors affect the distributions of microbes: the disinfecting effects of sunlight are highest in the canopy (Parker 1995) and propagule pressure (for example, fungal spore density) decreases with height due to dispersal limitation (Gilbert and Reynolds 2005; Nemergut and others 2013; Albright and Martiny 2017). Consequently, the role of environmental filtering likely increases with height, and competition filtering (which typically exhibits a tradeoff with habitat filtering; Tilman 1988; Webb and others 2002) is likely more important to community assembly on the forest floor where conditions are not as harsh. These abiotic and biotic processes combine to determine the structure and function of saproxylic (that is, dead wood inhabiting) communities.

Decomposition rates fundamentally are driven by microbial communities (Fukami and others 2010; Fukami 2015), especially assemblages of saproxylic fungi (Boddy and others 1989; de Boer and others 2005; van der Wal and others 2015), and invertebrates (for example, termites; Law and others 2019). Prokaryotes also influence wood decomposition both directly and via interactions with fungi (Wilhelm and others 2018; Johnston and others 2016). Vertical patterns of saproxylic microbial composition remain poorly described, particularly in tropical forests; however, both decomposition rates and microbial diversity tend to decrease above the forest floor. Small branches decompose more slowly when suspended in the understory versus when on the forest floor (Fasth and others 2011), and even ''downed'' logs that are partially elevated decompose ca. 40% slower than those with more soil contact (Prívetivý and others 2016). Field surveys suggest that saprotrophic fungi decrease in diversity with increasing height (Stone and others 1996; Unterseher and Tal 2006; reviewed by Lodge and Cantrell 1995). Bacterial diversity also tends to decline with height (Andrews and others 1980; Beattie and Lindow 1995; Griffin and Carson 2015), but research on bacterial communities in forests remains sparse (Lambais and others 2006; Kembel and others 2014); to our knowledge there is no information regarding the vertical distribution of saproxylic prokaryotes. Moreover, interactions among decomposition rates, microbial community structure, and abiotic conditions along vertical gradients within forests remain unexplored. Here, we provide the first quantitative assessment of such interactions.

We hypothesized that differences in microbial community structure from the ground to the canopy of tropical forests cause decreasing rates of wood decomposition. To test this hypothesis, we quantified differences in microclimate, decomposition rates, and parameters of microbial community structure (that is, richness, diversity, composition, functional guilds) along a vertical gradient within a tropical forest. We assessed microbial communities during the wet season because dry season drought severely limits decomposition (Swift and others 1979; Wieder and Wright 1995). Specifically, we used metabarcoding to assess the community

structure of fungi and prokaryotes on standardized wood sticks at five vertical positions on emergent tropical trees: forest floor, understory, subcanopy, canopy, and emergent (Parker 1995; Tables S1, S2). We evaluated three specific predictions. First, we expected that microbial composition shifts from primarily decomposers on the forest floor to primarily plant pathogens and photosynthetic taxa in higher levels of the forest. Second, we predicted that the vertical shift in microbial community composition is associated with harsher microclimate conditions, reduced alpha and beta diversity, and greater phylogenetic clustering. Finally, we expected that decomposition rates along the vertical gradient are strongly correlated with differences in microclimate parameters (for example, water content, temperature, and light intensity) and fungal community composition, but show little association with bacterial communities.

MATERIALS AND METHODS

Study Site

All field work was performed in the seasonally moist lowland tropical forest on Barro Colorado Island (BCI) in central Panama (09.210°N, 79.745°W). The mean annual temperature is 26 °C, and mean annual rainfall is ca. 2600 mm, concentrated during a long-wet season (mid-May to December). The soils are Oxisols with moderate to low concentrations of exchangeable cations and resin-extractable phosphorus (Wright and others 2011; Yavitt and others 2011). The study site is described in greater depth elsewhere (Croat 1978; Leigh 1999).

Experimental Substrates

Using a traditional litter bag technique (4 mm nylon mesh; Bocock and Gilbert 1957), we quantified decomposition as mass lost from standardized wood sticks (11.5 × 1.0 × 0.15 cm). We used a locally novel substrate (Betula sp.) to avoid the potentially biased effects of coevolved specialists (Cheesman and others 2018). The medium-sized mesh limited access of invertebrates while facilitating microbial colonization, and the substrates were otherwise unattractive to many invertebrates because they were too small for internal feeding galleries. This approach limited confounding factors (for example, wood traits, invertebrate colonization) to facilitate direct comparisons of primarily microbial decomposition along a vertical gradient.

We selected large diameter trees that were locally emergent to facilitate climbing and litter bag placement (N = 10; 9 Pseudobombax septenatum and 1 Cavanillesia platanifolia; Table S2). Using insulated wire, we attached litter bags directly to each emergent tree at four vertical positions based on the surrounding vegetation, as typically used to define tropical forest structure: understory, subcanopy, canopy, and emergent (Parker 1995; Tables S1, S2). The final litter bag, the forest floor treatment, was placed within the leaf litter adjacent to each focal tree. All comparisons and analyses in this study use these vertical positions rather than absolute tree height.

In both 2015 and 2016, we harvested one wood stick from each vertical position after it had decomposed for the duration of either the wet season (start date-end date: May–November 2015, June–November 2016) or the dry season (December–May 2015, December–June 2016; Table S1). Before placement in the field, the wood sticks were sterilized with ethanol, oven dried at 60 °C to a constant mass, and weighed to the nearest 1.0 mg on an electronic balance. After the focal wet or dry season, samples were collected and cleaned to remove attached soil, then weighed to the nearest 1.0 mg to determine wet mass. We then dried the samples at 60 °C to a constant weight to determine dry mass. Decomposition was estimated as the percent of initial mass lost. Moisture content (%) equaled the difference between final wet mass and final dry mass, divided by final wet mass. We note that unsafe tree climbing conditions and the destructive behaviors of arboreal mammals caused minor imbalances in sample sizes (see Table S2).

Microbial Community Sampling

We collected and stabilized microbial DNA from wood sticks at the conclusion of the wet season in 2015 (that is, after 7 months in the field). We focused our microbial sampling on the wet season because decomposition in this forest primarily occurs during the wet season (Swift and others 1979; Wieder and Wright 1995). Microbial samples were taken from a duplicate set of wood sticks at the same time that we harvested wood sticks for mass loss and moisture content in 2015. One sample was not recovered from the field and therefore not included in our microbial analyses. We stabilized DNA in the field to minimize community turnover during transport from field sites to the laboratory. Wood sticks were retrieved via climbing and then placed on a stainless-steel sampling platform. Before processing each sample, the platform and sampling tools (drill bits and forceps) were sterilized with ethanol, remnant DNA was oxidized with

hydrogen peroxide (3% aqueous H_2O_2 for 1 min), and the surface was dried with sterile gauze. We then used a 2 mm bit and a battery powered drill (DCD780C2 20V, DeWalt) to grind each stick into a fine powder, providing a comprehensive sample of the microbial community. DNA from this wood powder was immediately stabilized using Xpedition Soil/Fecal DNA MiniPrep extraction kits (Zymo Research, Inc), and the microbial cells were pulverized in the field via bead beating (1 min at 3100 oscillations per minute; modified Ryobi P514 Reciprocating Saw, Andersen, South Carolina, USA). All samples were then returned to the laboratory and frozen at $-40\,°C$ until extraction was performed according to manufacturer's protocols.

Community structure was assessed separately for prokaryotes (archaea and bacteria) and fungi using DNA barcoding. With the DNA stabilized above, we amplified the V2 region of the bacterial/archaeal 16S ribosomal gene (primers: S-D-Arch-0519-a-S-15 and S-D-Bact-0785-b-A-18; Klindworth and others 2013) and the fungal ITS1 region (primers: ITSF-1 and ITS2; McGuire and others 2013). The S-D-Arch-0519-a-S-15 and ITS-F1 primers were modified to include a 16 bp M13 sequence (GTAAAACGACGGCCAG) at the 5′ end to allow for the attachment of a unique 12 bp barcode in a subsequent PCR reaction. 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).

Bioinformatics

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 (version 6.1) with the ''gold'' reference database for prokaryotes (Edgar 2010) and the UNITE reference database for fungi (Kõljalg and others 2013). All sequences were clustered into de novo operational taxonomic units (OTUs) at 97% similarity. Bacterial and archaeal taxonomic classification was assigned via the SILVA reference database (release 119, Quast and others 2012) using the pyNAST alignment algorithm. Fungal taxonomic classification was assigned using the UNITE reference database (version 7.1, Kõljalg and others 2013). We constructed a phylogenetic tree for bacteria using the ClustalW method in QIIME, but the ITS1 region lacks sufficient information to construct a tree for fungi. All samples were successfully sequenced and retained in all analyses. After cleanup, the prokaryotic dataset contained 1,976,655 total reads across 72,798 OTUs (only 16 of these OTUs were assigned to Archaea), and our fungal dataset contained 446,138 total reads across 15,534 OTUs. We were able to assign 74.2 and 77.2% of our bacterial and fungal OTUs, respectively, to at least the phylum level. We used negative PCR and sequencing controls, and sequences present in the negative controls were removed from all samples before analysis. Singletons were omitted, and then, to account for differences in sampling depth, we rarefied samples to 2635 sequences and 764 sequences for bacterial and fungal taxa, respectively (Figure S2). When possible, we assigned putative functional guilds to fungal OTUs using FunGuild (Nguyen and others 2016) and inferred bacterial function from relevant literature (Bugg and others 2011; Chen and others 2012; Rosenberg and others 2014; Bhatnagar and others 2018; Wilhelm and others 2018). Sequencing data are available online via the Figshare repository (https://doi.org/10.6084/m9.figshare.7272641).

Microclimate

We measured temperature (°C) and light intensity (lumens) at 10-min intervals during a 24-h cycle at each location using environmental data loggers during 2015 (HOBO H08-004-0 with TMCx-HD thermometer, Onset Computer Corporation, Massachusetts, USA). During each 24-h cycle, microclimate was simultaneously recorded at all five relative vertical positions in a single tree; thus, each tree represents an independent sample of an independent day. This was repeated on haphazardly selected days after typical weather patterns had developed during both the wet and dry seasons (that is, one total day of sampling per location per season; Paton 2016).

Respiration Measurements

We also measured respiration when wood sticks were harvested at the end of the 2016 wet season to compare microbial activity (*wood respiration*) among vertical positions. Wood sticks were placed in a cylindrical PVC respirometry chamber (20 cm length, 7 cm diameter) with an attached respirometer (GMP343 CO_2 probe, Vaisala Inc, Helsinki, Finland). We recorded CO_2 (ppm) every

5 s over a 5-min period and calculated the CO_2 flux per gram of the remaining wood substrate. The chamber was returned to local atmospheric CO_2 concentrations (ca. 390 ppm) between each sample so that all measurements were taken across a similar range of CO_2 concentrations. The initial portion of each recording (ca. 15–45 s) was discarded to allow the rate to stabilize. Respiration rates were approximated as the slope of the linear portion of the resulting CO_2 accumulation curve (Bréchet and others 2017).

Linear Models

Most analyses were performed in the R statistical environment (R Core Team 2017). For mixed effect models, we performed nested model reduction based on AIC values and P values from likelihood ratio tests. If all random effects were removed because they did not contribute to the model, we compared model fit using F-statistics instead. In all cases, we examined residuals to confirm appropriate model fits. We used the Bonferroni correction to correct for multiplicity, and we report alpha when less than 0.05.

We compared mass loss among vertical positions using data from both seasons of 2015 and 2016. We accounted for differences in season length by comparing the proportion of mass lost from wood sticks as an annual rate (percent mass loss per year). We included season (wet or dry), relative vertical position, and their interaction as fixed effects. We also included year (2015 or 2016) and the unique tree identifier (hereafter *tree ID*) as random grouping effects. There was an interaction between relative vertical position and season, indicating that differences among vertical positions were not consistent between seasons. Consequently, we compared mass loss among vertical positions separately for the wet season and the dry season. We compared dry season light intensity, OTU richness, Shannon-Weiner diversity, phylogenetic dispersion, and the relative abundance of taxonomic orders of microbial taxa (the number of sequences per taxonomic order divided by the total sequences per rarefied sample for orders with $> 1.5\%$ relative abundance) using mixed effect models of similar construction. Relative vertical position was a fixed effect, and tree ID was a random effect in these analyses.

Multivariate Microbial Community Analyses

We compared microbial community composition and beta diversity using Primer (version 7.0.13).

Microbial community data were square root transformed before calculating Bray–Curtis dissimilarity. We used these community distance matrices to generate ordinations (non-metric multidimensional scaling or NMS) for both bacteria and fungi. We fit vectors to these ordinations to test for associations between microbial community composition and environmental variables, decomposition rates, putative functional guilds (fungi), and major taxonomic orders (bacteria). Details of these associations are reported in the supplemental material (Figures S3, S4, Tables S3, S4). We then performed PERMANOVA with the community distance matrices to compare these factors among relative vertical positions and individual trees (Anderson and others 2008). We included vertical position as a fixed effect and tree ID as a random effect (9999 permutations). We also compared beta diversity among relative vertical positions using PERMDISP tests (that is, an assessment of multivariate homoscedasticity; Anderson and others 2008). PERMDISP tests calculate within vertical position dissimilarity in community composition and then compare the magnitude of dissimilarity among relative vertical positions (9999 permutations). We determined if bacterial and fungal communities covary by examining the correlation between the community dissimilarity matrices using a permutation-based Mantel test (Legendre and Legendre 1998).

Multivariate Environmental Analyses

We used PCA and PERMANOVA to compare environmental conditions among trees and vertical positions using Primer (version 7.0.13) and R (package *vegan*). The environmental parameters used for PCA were maximum light intensity, average light intensity, maximum temperature, minimum temperature, average temperature, and wood moisture content. Wood moisture content was recorded at the end of each season, and all other environmental parameters were determined from 1 day of sampling at each location in each season. We chose these variables because they are associated with microorganism life history and/or patterns of decomposition (Beattie and Lindow 1995; Boddy 2001; Bell and others 2009; Griffin and Carson 2015). Environmental data were rescaled before analyses (*scale* in R), and we used Euclidean distance to perform PERMANOVA comparing environmental conditions among positions, trees, and seasons (9999 permutations; Anderson and others 2008). We included vertical

position as fixed effect and tree ID as a random effect.

Phylogenetic Dispersion

We compared phylogenetic dispersion, estimated as mean pairwise distance among individuals (Webb and others 2002), among bacterial communities to evaluate the potential roles of competitive and environmental filters (package *picante*; Horner-Devine and Bohannan 2006). Functional dissimilarity within a community is associated with strong competitive interactions (Weiher and Keddy 1995), and these interactions can cause increased phylogenetic dispersion (Webb and others 2002; Philippot and others 2010; but see Kraft and others 2015). By contrast, strong environmental filtering limits the functional diversity of a community, and this can cause phylogenetic clustering (Webb and others 2002). However, these phylogenetic patterns can be misleading (Kraft and others 2015) and thus are included here as one potential explanation for patterns in the data.

RESULTS

### Microbial Community Composition and Function Along the Vertical Gradient

Fungal and bacterial communities exhibited compositional turnover from the ground to the emergent layer of this forest (pseudo-$F_{4,35} > 2.82$,

$P < 0.001$; Figures 1, 2, and S3, S4, Tables S3, S4). Community composition of both fungi and bacteria differed among all vertical positions (18 pairwise comparisons: $t > 1.3$, $P < 0.046$) with two exceptions; canopy-level fungi were similar to fungi at both the subcanopy and emergent positions ($t < 1.3$, $P > 0.073$). Moreover, the magnitude of dissimilarity increased with distance between vertical positions (Figures 1, 2 and S3, S4). These differences persisted despite spatial autocorrelation wherein bacterial and fungal communities were similar among positions in individual trees (pseudo-$F_{9,35} > 1.13$, $P < 0.004$).

Microbial diversity and taxonomic richness decreased above the forest floor, but these effects were less pronounced than the differences in composition. Bacterial OTU richness decreased monotonically with increasing height (dAIC = 42.6, $X_4^2 = 50.55$, $P < 0.001$), and fungal beta diversity was greater on the forest floor than in the subcanopy or above (pseudo-$F_{4,44} = 3.38$, $P = 0.043$; $t > 3.07$, $P < 0.014$; Table S5). This outcome partially supports our prediction that alpha and beta diversity decrease along this vertical gradient. However, there were no other differences in OTU richness, beta diversity, or Shannon–Weiner diversity (dAIC < 0.5, $X_4^2 < 8.5$, $P > 0.074$; Table S5). By contrast, the most abundant orders of bacteria and fungi changed categorically with forest height (Tables S6, S7) and the dominant taxa at
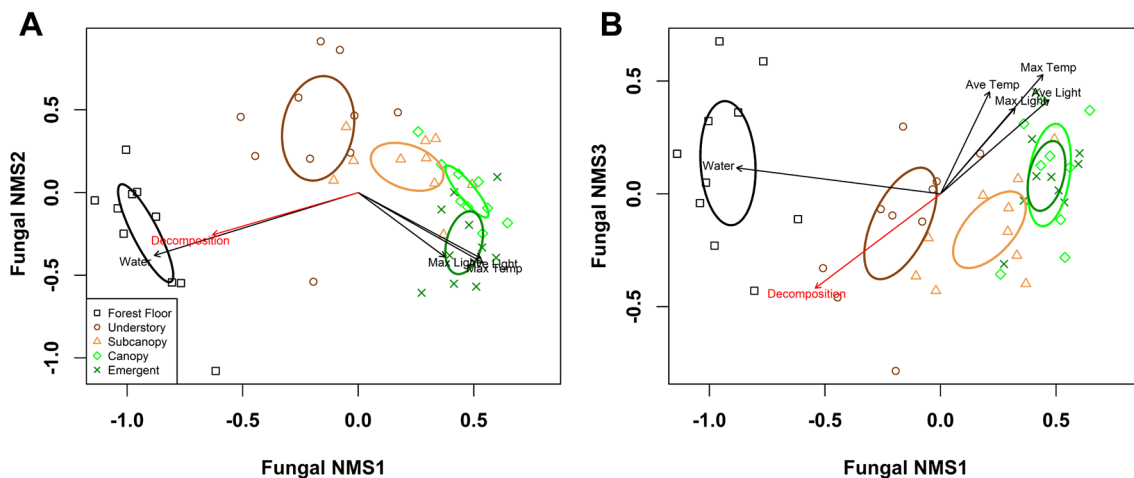
Figure 1. Ordination of fungal community structure along the vertical forest gradient (stress = 0.12). **A** Shows ordination axes 1 and 2, whereas **B** depicts ordination axes 1 and 3. Circles represent 95% confidence intervals for the location of the centroid from each group. Vectors indicate significant associations between points in the ordination and decomposition rates and environmental conditions at each position. The length of each vector is proportional to the strength of the correlation. The vectors for maximum temperature, maximum light intensity, and average light intensity are obscured by overlap in **A**.
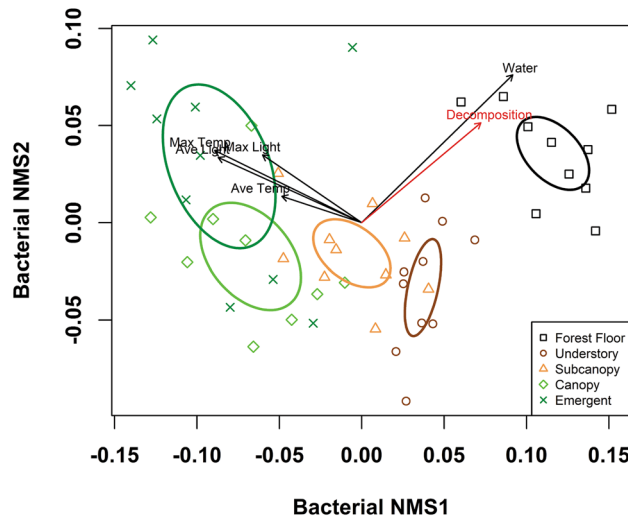
Figure 2. Ordination of bacterial community composition along the vertical forest gradient (stress = 0.11). Vertical positions are color coded, and ellipses are the 95% confidence intervals wherein the centroid for communities from each vertical position is located. Vectors represent significant associations between points in the ordination, and decomposition rates and environmental conditions at each position. The length of each vector is proportional to the strength of the correlation. Vectors for maximum temperature, maximum light intensity, and average light intensity are obscured by overlap.

each vertical position were associated with different putative and inferred functions (Table S3, S8).

Three broad and functionally based microbial subcommunites were readily identifiable: the first occurs on the forest floor, the second in the understory and subcanopy, and the third in the canopy and emergent positions (see Supplementary Tables and Figures for details). The forest floor fungal community was dominated by Agaricales and soil/litter saprotrophs, whereas a distinct community of wood saprotrophs (Pleosporales and Polyporales) defined fungal communities in the understory and subcanopy (Tables S3, S8). Endophytes and pathogens were the prominent fungal functional guilds in the canopy and emergent positions. Ground-level bacterial communities included an abundance of antagonistic competitors, such as pathogens (Xanthomonadales) and predators (Myxococcales; Figure S4), and very few decomposers. By contrast, the understory and subcanopy bacterial communities were dominated by decomposers that were uncommon on the ground (Actinomycetales and Sphingomonadales, Table S7). The canopy and emergent communities were similarly dominated by these bacterial decomposers, but also included many photosynthetic (Chlorophyta) and nitrogen fixing (Nostocales) bacteria. Overall, these patterns suggest that fine woody debris functions as a substrate for competitive and saprotrophic interactions in the litter, mild saprotrophic activities in middle layers

of the forest, and as physical support for photosynthetic and nitrogen fixing taxa in the upper canopy.

Vertical patterns of community composition were strongly correlated between bacteria and fungi (Mantel test: $R = 0.71$, $P < 0.001$), and vector fitting suggested that these communities responded similarly to environmental conditions (Figures 1, 2; Tables S3, S4). Community turnover from the ground to the emergent layer of the forest was associated with decreasing water content, increasing light intensity, and increasing temperature (Figures 1, 2). In particular, decomposition and water content exhibited nearly identical relationships with bacterial and fungal communities. These results suggest that fungal saprotrophs are most abundant in wet conditions near the ground where decomposition is fastest, whereas bacterial saprotrophs on drier substrates at higher positions are associated with slower decomposition.

Archaea

We were unable to quantitatively assess Archaea because they were exceedingly rare. In total, we isolated only 41 archaeal sequences distributed among Nitrososphaerales (25 sequences) and the candidate orders WCHD3-30 (2 sequences) and YLA114 (14 sequences). Archaea were concentrated on wood sticks on the forest floor (80% of sequences) and, to a lesser degree, the understory

(10%). Only 4 sequences were isolated from higher vertical positions, and zero archaeal sequences were found at the emergent level of the forest.

Phylogenetic Dispersion

Phylogenetic dispersion differed among bacterial communities. Bacterial communities on the forest floor were phylogenetically overdispersed relative to all other positions, but their phylogenetic dispersion did not differ from random (dAIC = 19.2, $X_4^2 = 27.2$, $P < 0.001$; $z > 4.1$, $P < 0.001$; Figure 3). By contrast, phylogenetic dispersion was similar among all communities above the forest floor ($z < 0.88$, $P > 0.91$) and exhibited phylogenetic clustering that can result from strong environmental filtering (Figure 3).

Microclimate

As is typical for lowland wet forests, local microclimatic conditions became drier, hotter, and brighter with increasing height above the ground (pseudo-$F_{4,36} = 11.41$, $P < 0.001$; Figure 4). Wet season conditions separated into two groups with the canopy and above differing from the subcanopy and below (pseudo-$t > 2.59$, $P < 0.014$). The forest floor conditions also differed from the subcanopy (pseudo-$t = 2.09$, $P = 0.028$). However, microclimatic parameters were similar between the emergent and canopy positions, and understory conditions were similar to both the forest floor and the subcanopy (pseudo-$t < 1.5$, $P > 0.145$; Table S9). The PCA results indicate that differences
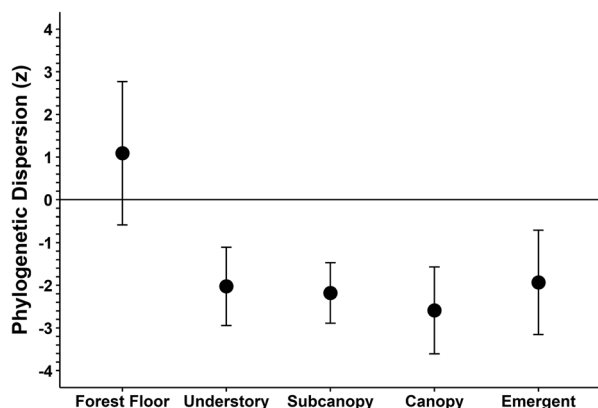

Figure 3. Phylogenetic structure of bacterial communities along the vertical forest gradient. The points represent the mean z value ($\pm$ 95% CI) for each vertical position as calculated using the mean pairwise distance measure of phylogenetic dispersion. Points that are significantly below zero are phylogenetically clustered, whereas values above zero are phylogenetically evenly distributed.

were caused by greater moisture content at lower levels of the forest, and more light and higher temperatures at higher levels of the forest (Figure 4). Differences in microclimate also exhibited distinct seasonal patterns (season × vertical position interaction: pseudo-$F_{4,56} = 5.32$, $P < 0.001$). By contrast with the wet season, differences in dry season microclimatic conditions were driven by the forest floor (pseudo-$F_{4,16} = 7.44$, $P = 0.003$; Figure S5); ground-level conditions differed from all higher levels (pseudo-$t > 3.2$, $P < 0.011$), but these higher levels of the forest did not differ from each other (pseudo-$t < 2.50$, $P > 0.06$). Additionally, environmental conditions did not differ among individual trees (pseudo-$F = 1.32$, $P = 0.199$).
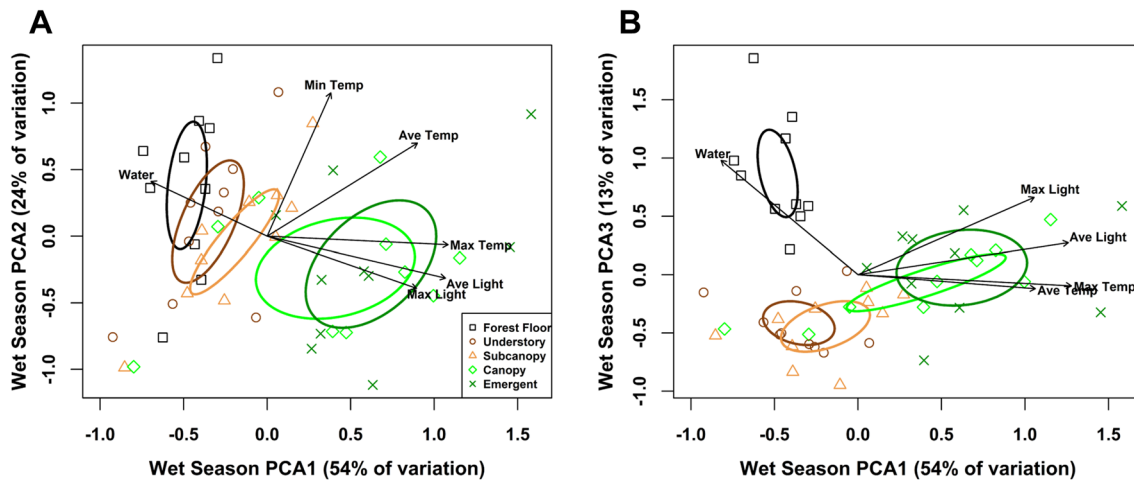
Decomposition

Mass loss from wood tended to be greater during the wet season, but did not differ seasonally in the upper reaches of the canopy, causing an interaction effect between vertical position and season (dAIC = 7.35 $X_4^2 = 15.4$, $P = 0.004$; Figure 5). During the wet season, wood decomposed fastest on the forest floor (dAIC = 30.9, $X_4^2 = 38.9$, $P < 0.001$, $\alpha = 0.025$; $z > 4.4$, $P < 0.002$), but there were no other differences among vertical positions ($z < 1.8$, $P > 0.38$). During the dry season, mass loss on the forest floor was greater than in the understory, subcanopy, and canopy (dAIC = 16.3, $X_4^2 = 24.4$, $P < 0.001$, $\alpha = 0.025$; $t > 3.8$, $P < 0.002$), and wood decomposed similarly at all levels above the forest floor ($t < 1.7$, $P > 0.46$). However, the dry season diverged from the wet season in that mass loss was similar for the litter and emergent levels ($t = 2.5$, $P = 0.09$). This idiosyncratic result likely reflects photodegradation in the emergent portions of trees; dry season light intensity was significantly higher in the emergent category than all other levels of the forest (dAIC = 27.8, $X_4^2 = 35.8$, $P < 0.001$, $\alpha = 0.025$; Figure S6).

Wood Respiration

We estimated wood respiration as a proxy for microbial activity by measuring CO_2 efflux from wood sticks at the conclusion of the 2016 wet season. Wood respiration differed among vertical positions (dAIC = 12.1, $X_3^2 = 18.1$, $P < 0.001$; Figure S7) as respiration rates were greater on the forest floor than in the understory, subcanopy, and canopy ($z > 2.84$, $P < 0.024$). However, wood respiration was similar among all levels above the forest floor ($z < 1.66$, $P > 0.35$). We lacked sufficient emergent-level samples to include this position in analyses of respiration.

Figure 4. Principle components analysis of wet season microclimate with sampling locations color coded by relative vertical position. **A** Depicts PCA axes 1 and 2, whereas **B** shows PCA axes 1 and 3. Ellipses depict the location of the centroid for each vertical position with 95% confidence, and the vectors indicate the strength of the correlations between each environmental variable and the axes.
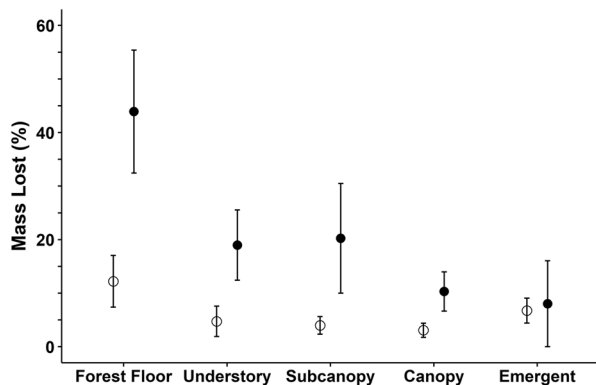
Figure 5. Total mass loss from wood sticks at the end of the wet (filled points) and dry (hollow points) seasons. Points represent average mass loss (95% CI) for both 2015 and 2016.

DISCUSSION

The majority of dead wood begins decomposing above the forest floor (Ovington and Madgwick 1959; Christensen 1977; Gora and others 2019), yet the processes underlying the decomposition of dead wood separated from the forest floor are largely unstudied. Here, we provide evidence that rates of wood decomposition are strongly associated with microclimate and microbial community structure along a vertical forest gradient. The strong associations between the microbial communities and environmental conditions suggest that microclimate was largely responsible for the vertical differences in saprotrophic communities and, thereby, decomposition. Finally, microbial community structure differed dramatically from the ground to the crown of each tree, representing a previously unquantified dimension of microbial diversity.

The dramatic compositional and functional differentiation along this short vertical gradient was similar to or greater than that observed along environmental gradients of pH, elevation, and temperature in other settings (Bryant and others 2008; Meier and others 2010; Rousk and others 2010). These differences are particularly notable because communities within an individual tree arise from a common pool of species. Moreover, the range of phylogenetic dispersion observed over just 30 m of height within this forest was greater than that observed along 1.2 km in elevation in temperate soils (Bryant and others 2008), and was similar to a 2.2 km elevation gradient in a subtropical aquatic system (Wang and others 2012). These phylogenetic patterns could arise from non-environmental processes (for example, facilitation; Kraft and others 2015), but the concomitant vertical changes in abiotic conditions suggest that the turnover in community composition was caused by a vertical shift from primarily competitive interactions to environmental filtering. Given the strong correlation between bacterial and fungal community composition (Mantel $R = 0.74$), it is likely that fungal community assembly follows the same general patterns. However, further work is needed to determine whether fungal and bacterial covariance is caused by their interactions, or by their similar responses to abiotic conditions.

Despite their strong covariance, bacterial and fungal communities exhibited some contrasting vertical patterns. Similar to soil pH gradients and

some elevation patterns (Bryant and others 2008; Meier and others 2010; Rousk and others 2010), differences among bacterial communities along the vertical forest gradient were greater than among their fungal counterparts. Decomposition is the primary function of most saproxylic communities, and the results of this study suggest that bacterial and fungal decomposers were partially vertically segregated. Fungal decomposers were abundant where decomposition was fastest (forest floor and understory) and they are known to outcompete saprotrophic bacteria (de Boer and others 2005), but they were less common in the subcanopy and above. By contrast, saprotrophic and ligninolytic bacteria (Sphingomonadales and Actinomycetales) were the dominant taxa at all positions above the forest floor (Table S7, Bugg and others 2011; Chen and others 2012). In particular, *Sphingomonas* was most abundant genus in our study and it consists of unusual oligotrophs capable of decomposing recalcitrant aromatic compounds, such as lignin (Masai and others 1999) and industrial waste products (for example, *S. wittichii*, Yabuuchi and others 2001; Wilhelm and others 2018). The contrasting shifts in the abundances of bacterial and fungal decomposers suggest that bacterial saprotrophs are an important component of canopy-level decomposition where they are largely unstudied.

In contrast with the continuous vertical turnover of microbial communities, mass loss from wood sticks exhibited a binary pattern, suggesting that soil contact is the primary factor determining rates of wood decomposition. This finding highlights a major gap in our understanding of decomposition; approximately 50% of wood necromass is separated from the forest floor (Gora and others 2019), yet information describing wood decomposition comes almost exclusively from ground-level studies (that is, decomposing wood in contact with the soil; Weedon and others 2009; van Geffen and others 2010; Bradford and others 2014; Zanne and others 2015). Soil contact influences decomposition by facilitating dispersal (Boddy and others 2009), providing access to exogenous nutrients (Boddy and Watkinson 1995; Zimmerman and others 1995), and altering water content (Boddy 2001). Although each of these factors is likely influential, the parallel patterns of wood mass loss and water content suggest that water availability is particularly important to vertical differences in decomposition (Figures 1, 2). This finding challenges the dominant models of local decomposition processes and suggests that vertical differences in microclimate are major determinants of wood decomposi-

tion rates (Adair and others 2008; Bradford and others 2014). These local, vertical processes must be incorporated into relevant models to improve our understanding of wood decomposition and forest carbon cycling (Fissore and others 2016).

Seasonal patterns of decomposition and microclimate also highlight a potential role for photodegradation in tropical rainforests. Decomposition rates in the desert-like conditions (Parker 1995) of the emergent stratum were aseasonal, and respiration results indicated that microbial activity was negligible in the canopy. During the dry season, it is likely that abiotic factors regulating emergent-level decomposition caused mass loss at similar rates to biotic processes on the forest floor. Photodegradation likely caused this abiotic decomposition—light intensity increases with canopy height (Figures 4, S1) and is greater in the dry season when leaves are abscised and clouds are less common (Croat 1978; Paton 2016). Photodegradation is an important mechanism of litter decomposition in arid ecosystems (Austin and Vivanco 2006), and it is expected to influence wood decomposition (Cornwell and others 2009). However, this is the first indication of wood photodegradation in tropical forests, highlighting the need for experimental tests of the role that sunlight plays in the decomposition of natural wood substrates.

Caveats, Conclusions, and Future Directions

Conducting this study with standardized and sterilized wood substrates facilitated comparisons of community assembly among vertical positions, but this approach has some limitations. By using sterile substrates, we did not capture the priority effects of endophytic and epiphytic microbial communities that colonize wood prior to decomposition in nature (Boddy 2001; Cline and others 2018). Substrate standardization and uniformity allowed us to exclude many confounding variables that are otherwise important in nature, including differences in wood traits (Zanne and others 2015) and the effects of bark. Bark changes wood microclimate, and many invertebrate taxa that consume wood and serve as vectors for decomposer microbes (for example, beetles) will only colonize wood with intact bark (Dossa and others 2016). Lastly, we used small substrates to enable sampling of the complete saproxylic microbiome. However, larger wood substrates decompose differently and support different taxa (for example, termites) than smaller substrates (Harmon and others 1986; Ulyshen

2016). Additionally, although microbial communities and environmental conditions did not differ conspicuously between the *C. platanifolia* and *P. septenatum* trees in our study, interspecific differences in chemistry and environmental profiles among tree species likely influence decomposition rates and decomposer community assembly (Weedon and others 2009; van Geffen and others 2010). Consequently, further work is needed to understand how interactions with invertebrates and phyllosphere microbes shape aboveground microbial community assembly and decomposition rates among diverse wood substrates (Leopold and others 2017).

Of these omitted factors, invertebrates are particularly important to wood decomposition. Termites alone are responsible for up to half of wood decomposition in tropical forests, and therefore, they have a substantial impact on global carbon cycling (Collins 1981; Cornwell and others 2009). In a recent study, Law and others (2019) demonstrated that termites prefer ground-level substrates, ignoring wood blocks suspended in the understory and canopy of adjacent living trees. Consequently, termite activity is likely important to vertical differences in decomposition and, despite the absence of empirical evidence, they could have contributed to the patterns observed in our study. Given the parallel trade-offs between saprotrophic fungi and bacteria, factorial manipulations of bacteria, fungi, and invertebrates are needed to reveal the relative roles of these taxa along vertical forest gradients.

The results of this study provide an important first step in understanding the mechanisms regulating decomposition rates of dead wood separated from the forest floor. Filling this knowledge gap is particularly important given the expectation that changing disturbance regimes (for example, drought, lightning; Phillips and others 2009; Greenwood and others 2017) will create more standing dead trees and shift the physical distribution of woody debris to higher vertical positions. Moreover, the results suggest that microclimate regulates rates of decomposition locally; thus, climatic effects on local microclimate (for example, via precipitation) will potentially change future rates of wood decomposition. Understanding the importance of these and related factors will help us understand the processes underlying wood decomposition and their links to carbon cycling.

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