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Research Article

RESEARCH ARTICLE

Wood decomposition in aquatic and terrestrial ecosystems in the tropics: contrasting biotic and abiotic processes

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One sentence summary: Wood mass loss and fungal and bacterial communities, but not wood polymer loss, differ between stream and land habitats, suggesting functional redundancy and contrasting drivers of wood decomposition across habitats.

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ABSTRACT

Wood decomposition, a critical process in carbon and nutrient cycles, is influenced by environmental conditions, decomposer communities and substrate composition. While these factors differ between land and stream habitats, across-habitat comparisons of wood decay processes are rare, limiting our ability to evaluate the context- dependency of the drivers of decay. Here we tracked wood decomposition of three tree species placed in stream and terrestrial habitats in a lowland tropical forest in Panama. At 3 and 11 months we measured mass loss, wood nitrogen and wood polymer concentrations, and sampled wood-associated fungal and bacterial communities. After 11 months of decay we found that mass loss occurred 9% faster in streams than on land, but loss of cellulose, hemicellulose and lignin did not differ between habitats. We also observed large differences in microbial decomposer communities between habitats. Overall, we found faster mass loss of wood in water, but no differences in biotic decay processes between habitats despite distinct microbial communities in streams and on land. Our research challenges the assumption that wood decays relatively slowly in water reflecting unfavorable environmental conditions and a limited capacity of aquatic microbial communities to effectively degrade wood polymers.

Keywords: wood decay; fungal and bacterial communities; stream and terrestrial habitats; tropical forest; nitrogen

INTRODUCTION

Tropical forests hold over half of terrestrial biomass and are responsible for one-third of the net primary productivity in terrestrial ecosystems (Saugier, Roy and Mooney 2001). The decomposition rate and fate of this large pool of plant material has important effects on the global carbon (C) cycle, influencing soil C storage and the availability of energy that helps sustain both terrestrial and aquatic food webs (Harmon *et al.* 1986; Delaney *et al.* 1998; Cornwell *et al.* 2009; Tank *et al.* 2010). The factors influencing decomposition rate may be especially complex in tropical forests, where high tree diversity is associated with wide

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variation in wood chemical (Heineman, Turner and Dalling 2016) and physical (Poorter *et al.* 2010) characteristics. When coupled with heterogeneity in soil properties, this variation can result in multi-nutrient limitation, making predictions of decomposition rates difficult (Kaspari *et al.* 2008; Townsend, Asner and Cleveland 2008). In addition, environmental conditions, such as temperature and moisture (Bärlocher and Boddy 2016), and fungal and bacterial communities (Fukami *et al.* 2010; Bradford *et al.* 2014; Johnston, Boddy and Weightman 2016) interact to influence decay processes. Insights into the relative importance of these factors as drivers of decomposition can be achieved using wood decay experiments distributed across terrestrial and aquatic habitats, taking advantage of habitat-specific variation in biotic and abiotic conditions.

Wood decomposition occurs through distinct processes, including fragmentation, leaching and catabolism (Cornwell *et al.* 2009; Tank *et al.* 2010). Here we use 'decomposition' to encompass abiotic and biotic processes that influence turnover of organic matter (Tank *et al.* 2010; Bärlocher and Boddy 2016), in addition to the biological degradation of organic material (Gessner *et al.* 2010). Fragmentation is the physical breaking apart of wood by biotic or abiotic factors, including wind, invertebrates or flowing water (Harmon *et al.* 1986; Bärlocher and Boddy 2016). Leaching is the quick loss of soluble organic compounds and nutrients from plant material via water (Chapin, Matson and Vitousek 2011). While leaching and fragmentation contribute to decomposition on land and in water, they are especially important to mass loss in submerged wood (Harmon *et al.* 1986; Bärlocher and Boddy 2016). Finally, catabolism is the process by which enzymes, produced primarily by fungi and bacteria, break down wood polymers into increasingly simple organic compounds (Bärlocher and Boddy 2016), resulting in changes in the relative abundance of lignin, hemicellulose and cellulose through the course of decay (Song *et al.* 2012; Negrão, Silva Júnior and Passos 2014). Because the importance of processes influencing decomposition likely differ between habitats and can influence wood chemistry, wood in terrestrial and aquatic habitats may have distinct changes in chemistry during decay.

In addition to differences in leaching and fragmentation rates, aquatic and terrestrial habitats also likely differ in nutrient availability, which can affect microbial decay. Nutrient limitation can slow decay in wood, because the nitrogen (N) and phosphorus (P) that fungi and bacteria require to produce decay enzymes occur at low concentrations in wood (Sinsabaugh *et al.* 1993). On land, fungi that colonize wood can use hyphae to transport limiting nutrients from soil to the decomposing substrate (Boddy 1993; Gessner *et al.* 2010). In streams, flowing water prevents the creation of these hyphal connections, limiting the ability of aquatic fungi to access nutrients from sediments (Wagener, Oswood and Schimel 1998; Gessner *et al.* 2010). While fungi in streams use nutrients delivered directly to decaying substrate via flowing water, water is also more likely to wash away nutrients from the substrate, decreasing nutrient access (Wagener, Oswood and Schimel 1998). Together these observations suggest that fungi on land may overcome nutrient limitation by seeking out additional nutrient sources, while in streams, fungi are limited by substrate and stream nutrient content.

Along with nutrient availability, moisture availability also impacts decay rates. Wood on land has the potential to desiccate, making it difficult for decomposers to produce enzymes (Wagener, Oswood and Schimel 1998; Gessner *et al.* 2010; Bärlocher and Boddy 2016). However, if wood is submerged in water, reduced oxygen availability can limit the fungal production of decay enzymes (Rayner and Boddy 1988; Bilby 2003; Medeiros, Pascoal and Graca 2009). Due to less effective decay by fungi in low oxygen environments, bacteria might be expected to play a larger role in decay in low oxygen streams than on land (Rayner and Boddy 1988; O'Connell, Baldwin and Robertson 2000; Pascoal and Cassio 2004). However, even in conditions of low oxygen availability fungi still can dominate decay processes (Pascoal and Cassio 2004).

Beyond the abiotic drivers of decay, the composition of fungal communities also influences wood decay. Fungi are generally considered the primary decay agents of wood, because they produce the most diverse and effective lignocellulolytic enzymes (Sinsabaugh *et al.* 1993; Floudas *et al.* 2012; Riley *et al.* 2014). Existing studies have shown marked differences in the saprotrophic fungal communities in freshwater streams and terrestrial habitats. While all fungal groups are found in both environments, Basidiomycota dominate in terrestrial environments, and Chytridiomycota are more common in aquatic systems, while Ascomycota are found in both habitats (Shearer *et al.* 2007; Kodsueb *et al.* 2008; Jones, Hyde and Pang 2014; Duarte *et al.* 2015; Purahong *et al.* 2016). Because fungi differ in their ability to produce wood decay enzymes (Floudas *et al.* 2012), fungal community composition can influence mass loss (Fukami *et al.* 2010) and the relative breakdown of lignin, cellulose and hemicellulose (Song *et al.* 2012; Negrão, Silva Júnior and Passos 2014). For example, the capacity to breakdown lignin is predominately associated with terrestrial Basidiomycota (Floudas *et al.* 2012) and occurs in freshwater Ascomycota, but is less efficient (Bucher *et al.* 2004). As a consequence of potentially limited enzymatic activity and oxygen availability in water, wood is often assumed to decay more slowly in water than on land (Zare-Maivan and Shearer 1988b; Boonyuen, Sivichai and Jones 2014; Bärlocher and Boddy 2016).

We established an experiment to examine how decomposition rates, loss of wood structural polymers, and fungal and bacterial communities found on wood differ on land and in adjacent streams in a lowland tropical forest. Since wood characteristics, including nutrient concentrations and wood density, can impact the drivers of wood decay, we included three tree species in our experiment. We compared wood decay in streams and on land to test hypotheses about the differences in the role of fungal and bacterial community composition and nutrient availability during decomposition between the two habitats. We hypothesize that faster mass loss on land than in water, combined with greater depletion of hemicellulose, cellulose and lignin, would be consistent with greater enzyme activity and potentially higher nutrient availability on land. Alternatively, faster mass loss in streams than on land without an accompanying shift in hemicellulose, cellulose and lignin concentrations would be consistent with increased fragmentation and leaching in streams from flowing water. Finally, we analyzed fungal and bacterial communities to explore patterns of microbial community composition and diversity, and their impact on wood decay.

MATERIALS AND METHODS

We conducted a decay experiment in streams and on land using branches from three tree species: *Gliricidia sepium* (Jacq.) Kunth ex Walp (Fabaceae), *Guazuma ulmifolia* Lam. (Malvaceae) and *Tectona grandis* Lf (Lamiaceae). Throughout the paper we refer to the three species by their genus names. The branches were obtained from a plantation near Pedasí, Republic of Panama. The tree

species varied in wood polymer concentrations and had four-fold variation in N and P concentrations (Table 1). The samples were decayed in three stream plots and three adjacent terrestrial plots, and were collected after 3 and 11 months of decay.

Study site

The study was conducted in an old second-growth, lowland, tropical forest at Soberania National Park, Republic of Panama. Annual rainfall averages 2200 mm per year (van Breugel *et al.* 2011), with a 4-month dry season (early January to late April; Windsor 1990). Average minimum and maximum temperatures through the year range between 23 and 32°C (Robinson, Brawn and Robinson 2000). The streams that were used in this study were Quebrada Juan Grande (N 09° 08′ 01.8″, W 79° 43′ 22.2″), Rio Frijolitos (N 09° 08′ 51.9″, W 79° 43′ 57.2″) and Rio Frijoles (N 09° 09′ 06.3″, W 79° 44′ 18.9″). Parent material surrounding the three sites consisted of Gatuncillo Formation mudstones and sandstones (Stewart and Stewart 1980), resulting in soils that are relatively low in plant available P and cations compared with soils that develop on other parent materials in the region (B. Turner, personal communication). Stream sites were selected such that branch sections would remain submerged year-round. Land sites were selected as flat, shaded areas, with open understory, without rainy season flooding, within 50 m of stream sites.

Field incubation methods

We studied wood loss, microbial communities and changes in wood chemistry on land and in streams after 3 and 11 months of decomposition. To determine the initial density and dry mass of wood, we cut a 2-cm long piece of each branch and weighed the dry mass after drying for 72 h at 60°C. Each experimental unit consisted of a single branch section (15 cm long, 2 cm diameter). We placed each unit within a separate aluminum mesh bag (2 mm mesh size) that excluded macro-invertebrates, to isolate the impact of microbial communities on wood. We set up the decay experiment in April of 2014 at three sites, which included paired stream and land plots 20–50 m apart. Three branch sections from each tree species were placed in paired stream and land plots at each site for each of the two collections (3 and 11 months) for a total of 108 samples. Bags in streams were attached to a rebar anchor to prevent the wood from flowing downstream (supplementary Fig. S1, available online). We collected the wood samples after 3 months of wet-season decay (August 2014) and 11 months of wet- and dry-season decay (April 2015). Despite the dry season, stream samples collected after 11 months were submerged in water throughout the incubation.

We placed samples in plastic bags for transport to the lab. For samples from streams we put the samples in two sealable plastic bags with stream water during transportation. We cut and dried a 2-cm long segment from each sample at 60°C for 72 h. We weighed the sample to calculate mass loss based on the mass of the initial 2-cm section of the undecomposed wood and ground the sample using a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) for nutrient analyses and acid hydrolysis. To collect wood shavings for DNA analysis, we removed the bark from the remainder of the fresh sample with a sterile razor blade and drilled into the stick in three places with a sterile drill bit. Wood samples for DNA analysis were stored at −20°C in sterile foil packets.

Wood chemical analysis

To determine N and C concentrations, 10 mg (±0.5 mg) of wood was analyzed using a CHN Analyzer (Costech, Valencia, CA, USA) at the Institute for Genomic Biology at the University of Illinois at Urbana-Champaign (UIUC). To measure P, potassium (K), magnesium (Mg) and calcium (Ca) concentrations, 30 mg (±5 mg) of ground wood tissue was ashed at 550°C for 3 h, dissolved in 10 mL of 3 M nitric acid and analyzed using an ICP-MS (iCAP Qc, Thermo Scientific, Waltham, MA, USA) in the Department of Geology at UIUC. The concentration of structural carbohydrates and insoluble lignin in the decayed wood were determined following Sluiter *et al.* (2012). Approximately 300 mg of dried tissue per sample was refluxed overnight in acetone using a Soxhlet extractor to remove non-structural carbohydrates. The samples were then dried and transferred to 100 mL glass pressure tubes, and 3 mL of 72% sulphuric acid was added to each sample. The samples were stirred every 15 min for 2 h, and then 84 mL of water was added before the samples were autoclaved (121°C) for 1 h. The samples were then vacuum-filtered through medium-frit (10–15 μm) glass filter crucibles. The retentate was assessed gravimetrically to determine the quantity of insoluble lignin. Soluble carbohydrates (derived from structural polymers) from the filtrate were separated using a System Gold 166 HPLC (Beckman Coulter, Brea, CA, USA) equipped with a 300 mm Aminex HPX-87P column (Bio-Rad, Hercules, CA, USA) at 85°C using a 0.6 mL min^{-1} flow rate with water. Carbohydrates were quantified using a RI-1530 refractive index detector (Jasco, Easton, MD, USA) along with arabinose (A3256), galactose (G0750), glucose (G8270), mannose (63 579) and xylose (X1500) standards (Sigma-Aldrich, St Louis, MO, USA).

DNA extraction and sequencing

One milliter of ground and frozen wood sample was added to the solutions in the first step of the MoBio Power Plant Pro DNA (MoBio, Carlsbad, CA, USA) extraction kit with 2 min of bead beating at 2500 r.p.m. We extracted DNA following the manufacturer's protocol with the addition of a proteinase K incubation, consisting of the addition of 4 μL of 20 mg mL^{-1} Proteinase K (New England Biolabs, Ipswitch, MA, USA), followed by incubation at 55°C for 2 h.

To examine fungal and bacterial communities associated with wood decomposition, we targeted the fungal variable regions D1 and D2 of the ribosomal large subunit using the primers LR0R-LR3 (Vilgalys and Hester 1990; Amend *et al.* 2010) and the bacterial variable V4 region of the 16S ribosomal subunit with the 515f-806r primers (Caporaso *et al.* 2012). We created our own barcoded primers (supplementary Tables S1 and S2, available online) using the barcodes suggested in Caporaso *et al.* (2012), after testing each combination *in silico* for melting temperature and hairpins (Integrated DNA technologies Oligo Analyzer 3.1). To limit barcoded primers from biasing sequence amplification (Berry *et al.* 2011), we used a two-step polymerase chain reaction (PCR) protocol in which we used non-barcoded primers for the first round of PCR and barcoded primers for a second round of PCR. Initial PCR mix was 0.2 mM dNTPs, 0.8 μM primers, 1× HF Phusion Green Buffer, 3% dimethyl sulfoxide (DMSO), 1 unit of Phusion High-Fidelity polymerase (to reduce artefactual downstream operational taxonomic units (OTUs) (Oliver *et al.* 2015) and 5 ng of 5 ng μL^{-1} of DNA (50 mL reaction). We used the following PCR protocol: (i) 98°C for 30 s, (ii) 98°C for 10 s, (iii) 54°C for 30 s, (iv) 72°C for 1 min, repeat steps (ii)–(iv) 19 times, (v) 72°C for 10

Table 1. Dry mass percentage of initial wood nutrients, cellulose, hemicellulose and lignin concentrations (mean ± standard deviation (SD)). Letters indicate significant differences among species ($P < 0.05$) from a post-hoc Tukey test. *F* values are for species effects from one-way ANOVA., $^{**}P < 0.01$, $^{***}P < 0.001$.

Nutrient	*Gliricidia sepium*	*Guazuma ulmifolia*	*Tectona grandis*	df	F
Ca (% mass)	0.73 (±0.25)	0.98 (±0.37)	0.65 (±0.14)	12	2.07
C (% mass)	45.28 (±0.65)a	46.31 (±0.58)b	48.20 (±0.58)c	11	29.75***
C:N	54.07 (±6.94)a	133.30 (±32.37)b	216.68 (±51.12)c	11	29.37***
Mg (% mass)	0.71 (±0.27)	0.37 (±0.19)	0.45 (±0.10)	12	3.79
N (% mass)	1.02 (±0.14)a	0.36 (±0.08)b	0.23 (±0.05)b	11	86.73***
P (% mass)	0.65 (±0.17)a	0.54 (±0.11)a	0.14 (±0.04)b	12	25.50***
K (% mass)	4.54 (±1.97)a	2.17 (±0.61)b	1.15 (±0.31)b	12	10.48**
Lignin (% mass)	28.04 (±2.29)	25.62 (±4.44)	31.74 (±6.11)	5	1.11
Cellulose (% mass)	50.06 (±5.91)	34.72 (±3.68)	46.94 (±3.85)	3	7.16
Hemicellulose (% mass)	19.48 (±0.89)	19.62 (±2.56)	22.52 (±1.96)	3	1.51
Density (g/cm^3)	0.52 (±0.13)a	0.51 (±0.10)a	0.60 (±0.17)b	212	10.11***

min. We did two replicate PCRs for the first round, pooled the replicates and cleaned the PCR product using Agencourt AMPure XP beads (Beckman Coulter, Brea, CA, USA). The standard Agencourt AMPure XP protocol was followed with a 1:1 ratio of DNA sample and bead solution. Secondary PCR was done using the barcoded primers on the reverse primer and the following mix: 0.2 mM dNTPs, 0.5 μM primers, 1× HF Phusion Green Buffer, 3% DMSO, 1 unit of Phusion High-Fidelity polymerase and 2.5 μL of cleaned DNA from the first PCR. The second PCR program was the same as the first except that steps (ii)–(iv) were repeated only nine times for a total of 30 PCR cycles. We then cleaned the DNA using Agencourt AMPure XP beads, used Qubit (Qubit 2.0, Life Technologies, Carlsbad, CA, USA) to quantify DNA concentration for each sample, and pooled the samples based on equal concentrations for fungal and bacterial libraries separately. We then purified the libraries once more with Agencourt AMPure XP as above. The UIUC biotechnology center then added the separate Illumina barcodes for the fungal and bacterial libraries, using the Kapa Rapid Ligation System (Kapa Biosystems, Wilmington, MA, USA), ran a two-cycle PCR, cleaned the DNA with Agencourt AMPure XP and sequenced the DNA on one reaction of Illumina MiSeq PE 300 bp using v3 chemistry.

Sequence screening

We used the program mothur (v.1.35.1; Schloss *et al.* 2009) to screen and assign sequences to OTUs. For bacteria, we trimmed sequences based on quality score (qwindowaverage = 30), paired the trimmed sequences and assigned the sequences to samples via the sample barcodes. For fungi, we only used the forward read for analysis since the ∼600 bp amplicon prevented successful pairing. Because the sample barcode was on the reverse read and we used the forward read for analysis, we first merged the pairs of reads end to end. Then we identified the sequences based on the sample barcode. We then quality-screened the sequences from the forward end and trimmed the sequences based on the quality score (qwindowaverage = 20). We then trimmed any sequences that were longer than 250 base pairs to ensure that the sequences did not include the reverse read. We used a less stringent quality score for fungal sequences because sequence quality declined early, a problem not encountered with bacteria, because there was enough overlapping sequence to have well-supported pairing. We proceeded with the same analysis protocol for fungi and bacteria. We aligned bacterial sequences using the SILVA database (16S, release 123, Quast *et al.* 2013) and fungal sequences using the Ribosomal Database Project (RDP) database (Fungal 28S, release 11.4, Cole *et al.* 2014). We then trimmed sequences to similar aligned lengths, used the precluster command (following Huse *et al.* 2010) to reduce sequences likely caused by sequencing error, and screened for and removed putative chimeras using UCHIME (Edgar *et al.* 2011). We classified sequences to taxonomic identities using the naïve Bayesian autoclassifier (Wang *et al.* 2007) using the RDP training sets for bacteria (v.14) and fungal large subunit (v.11) as implemented in mothur. We clustered OTUs at 97% similarity using the cluster.split command in mothur (split by Class), using the average neighbor algorithm (Schloss *et al.* 2009). We removed all OTUs with fewer than 10 sequences globally (Brown *et al.* 2015) and removed all taxonomic information that had less than 50% bootstrap support (fungi: Table S15, bacteria: Table S16, supplementary data available online). For bacteria, some of the sequences were unclassified beyond kingdom level. We therefore used representative sequences for each OTU and checked them in GenBank (BLASTn nr/nt with exclusion of environmental sequences) and recorded the phylogenetic information and the match quality scores. We used the following sequence screening procedure. All sequences that matched less than 70% identity score of the sequence in GenBank were deleted. We recorded the name to the family level if the sequence had a 100% identity score, order was retained for identity score 99–95%. Class was retained for identity score 95–90%. Phylum was retained for identity score 90–85%. For identity scores below 85% only kingdom was retained. Then we subsampled the number of sequences for bacteria to 3000 sequences per sample and 2250 sequences per sample for fungi. The sequence and OTU screening resulted in 789 000 bacterial sequences in 13 937 bacterial OTUs, and 596 160 fungal sequences in 3509 fungal OTUs. We deposited raw sequences in the National Center for Biotechnology Information Sequence Read Archive under the BioProject ID PRJNA493292.

Microbial analyses

For fungal and bacterial community analysis, we created OTU-by-sample matrices using sequence abundance data and Bray-Curtis dissimilarity matrices using the vegdist command in the vegan package version 2.5–1 in R (Oksanen *et al.* 2018). We calculated Shannon diversity index (H) using the vegan package in R.

Calculations and statistical tests

To calculate % mass loss, pre-decay and decayed dry mass were calculated as the dry mass (g) per length (cm) and entered in the following equation:

$$Mass\ loss\ \% = \left(\frac{pre\text{–}decay\ dry\ mass - decayed\ dry\ mass}{pre\text{–}decay\ dry\ mass}\right) * 100$$

We calculated gravimetric water content per dry mass using the following equation:

$$Moisture\ \% = \left(\frac{wet\ mass - dry\ mass}{dry\ mass}\right) * 100$$

Hemicellulose was calculated by adding arabinose, galactose, mannose and xylose. In order to calculate the % change in concentration (i.e. % dry mass) of N, C, hemicellulose, cellulose and insoluble lignin, we used the following equation:

$$Change\ in\ concentration\ \% = \left(\frac{decayed\ \%\ mass - pre\text{–}decay\ \%\ mass}{pre\text{–}decay\ \%\ mass}\right) * 100$$

We analyzed differences across tree species in pre-decay concentrations of nutrients and wood polymers using an analysis of variance (ANOVA). To examine the differences between pre-decay and 3 months of decay, we used *t*-tests. To examine differences in mass loss and differences in concentration of N, C, hemicellulose, cellulose and insoluble lignin between 3 and 11 months of decay, we used linear mixed effects models implemented in the lme4 package in R (Bates *et al.* 2015). We coded site as a random effect and habitat, tree species and decay duration as fixed effects. We then conducted Tukey's Honest Significant Difference test to further examine differences between groups using the lsmeans package (Lenth 2016). For moisture analysis, we used a *t*-test to compare the moisture of samples between habitats for each decay duration separately.

We used permutational multivariate ANOVA (PERMANOVA) analyses (Anderson 2001) to test for differences in microbial community composition across substrate type, habitat, decay duration and tree species, using the adonis command in the vegan package version 2.5–1 in R (Oksanen *et al.* 2018). We used the strata command to constrain permutations within site. To analyze treatment effects on bacterial and fungal Shannon diversity, we used a linear mixed effects model with habitat, tree species and decay duration as fixed effects, and site as a random effect. To determine which fungal phyla, class, order and family, and bacterial phyla and class, were significantly impacted by decay duration and habitat, we used generalized linear models with family = 'negative.binomial' using the manyglm command in the mvabund package version 3.12.3 in R (Wang *et al.* 2012). We first tested for significant differences in read number across each of the habitat and census combinations for each taxonomic group. We then fit models testing for habitat, census and habitat × census interactions. Finally, to explore the relationships between fungal and bacterial community composition, mass loss, and change in N and polymer concentration, we used constrained canonical correspondence analysis separately for each habitat and decay duration using the cca command in vegan package version 2.5–1 in R (Oksanen *et al.* 2018). Relationships between mass loss and changes in N and polymer concentrations and fungal and bacterial diversity were explored, separately for each habitat and decay duration, using Kendall rank correlation coefficient. To visualize differences in community composition across habitat, decay duration and tree species, we calculated non-metric multidimensional scaling (NMDS) axes using the vegan package in R.

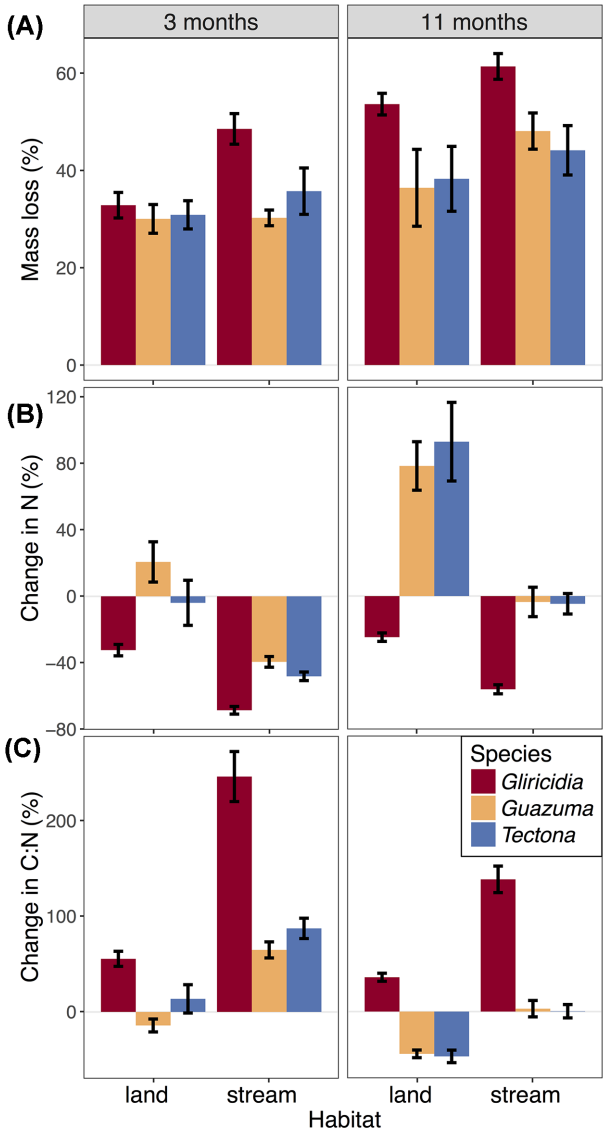

Figure 1. Percent mass loss (**A**), and % change in concentration of N (% dry mass) (**B**) and C:N (**C**) across species, habitats and decay duration (mean ± standard error).

RESULTS

Mass loss and moisture across habitats and collections

Mass loss differed between habitats and among tree species (Table 2, Fig. 1A). We found that mass loss was faster in streams than on land ($\chi^2 = 11.6$, df = 84, $P < 0.001$, Table 2, Fig. 1A), both after 3 months of decay (stream: mean (± SD) 38% ± 12.7; land: 31% ± 8.2) and after 11 months (stream: 51% ± 13.0; land: 43% ± 17.7). For moisture, after 3 months of decay, during the rainy

Table 2. Explaining mass loss, % change in concentration of N, C, C:N, cellulose (Cell.), hemicellulose (Hem.) and lignin, and fungal and bacterial diversity (Div.) using linear mixed effects models with duration, habitat and species as fixed effects and site as a random effect. Fungal and bacterial community (Com.) results are from PERMANOVA analysis. For complete model details see supplementary Appendix S1 and Tables S4–S14, available online. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

								Fungi		Bacteria	
	Mass loss df = 84 χ^2	N df = 85 χ^2	C:N df = 85 χ^2	C df = 85 χ^2	Cell. df = 53 χ^2	Hem. df = 53 χ^2	Lignin df = 55 χ^2	Com. df = 82 F	Div. df = 80 χ^2	Com. df = 82 F	Div. df = 80 χ^2
Duration (D)	29.2***	62.3***	88.0***	34.8***	2	14.4***	3.5	6.5***	23.9***	7.9***	23.7***
Habitat (H)	11.6***	116.1***	196.1***	0.8	1.4	2	3.3	5.7***	13.6***	6.6***	0
Species (S)	25.9***	92.2***	258.3***	238.6***	14.4***	28.3***	4.7	1.2	3.5	1.7**	10.3**
D × H	0.1	4.9*	13.6***	0.8	1.2	0.5	0.2	3.7***	1.3	3.5***	0
D × S	2.6	21.1***	3	0.6	0.6	3.1	4.1	1.3	7.4*	1.3	4.3
H × S	2	9.7**	39.2***	1.5	0.1	0.7	0.2	1.2	5.3	1.8**	10.5**
D × H × S	3	5	4.5	0.8	4.1	2.5	6	1.1	3.5	1.4	0.9

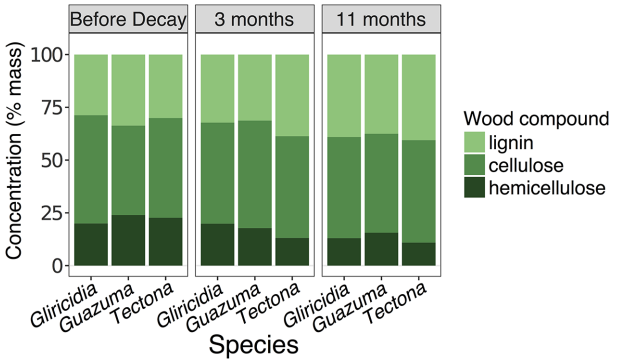

Figure 2. Cellulose, hemicellulose and lignin mean % dry mass across species and decay duration.

season, we found that our samples had a similar mean moisture content on land (194% of dry mass) and in streams (210%) ($t = -1.15$, df = 47, $P = 0.26$). However, after 11 months of decay, during the dry season, the wood samples decomposed on land (26%) were drier than samples in streams (202%) ($t = -13.21$, df = 22, $P < 0.001$).

Wood nutrient and polymer chemistry change through decay

The concentrations of lignin, cellulose and hemicellulose did not differ between habitats at any time in the experiment (Table 2). Nevertheless, lignin, cellulose and hemicellulose concentrations changed through decomposition. In the first 3 months of decay, lignin concentration increased ($t = 6.71$, df = 36, $P < 0.001$, Fig. 2), hemicellulose concentrations declined ($t = -3.40$, df = 34, $P = 0.002$, Fig. 2) and cellulose concentrations did not change ($t = 1.46$, df = 34, $P = 0.154$, Fig. 2). Between 3 and 11 months of decay, lignin and cellulose concentrations did not change, while hemicellulose concentration declined (Table 2, Fig. 2). In contrast to wood polymers, in the first 3 months, N concentration declined in all tree species in streams, but only in the relatively N-rich species, *Gliricidia* on land (Table 2, Fig. 1B), consistent with higher leaching rates in streams than on land. Through the rest of the experiment, N concentration was also higher on land than in streams for all tree species (Table 2, Fig. 1B). In contrast to the first 3 months, between 3 and 11 months of decay, the N concentrations increased for *Tectona* and *Guazuma*, but not *Gliricidia* (Table 2, Fig. 1B). The C:N ratio generally followed the inverse trend of N (Table 2, Fig. 1C). Together, the contrasting dynamics of wood polymers, N and mass loss suggest that differences in physical processes (leaching and fragmentation) likely contributed to mass loss differences between habitat types.

Species-specific wood characteristics impact mass loss

Tree species varied in their pre-decay nutrient composition and in their rates of decay. We found that the pre-decayed wood of the three tree species varied in N, C:N, K, P, C and density (but not Ca and Mg) (Table 1). *Gliricidia* had higher N and K than *Tectona* or *Guazuma*, while *Tectona* had a higher C concentration, C:N ratio and wood density, and lower P concentration than the other two species. In contrast, no differences were found in cellulose, hemicellulose and lignin concentrations based on the limited sample size of pre-decayed wood (Table 1). During decay, tree species differed in their mass loss and the change in cellulose, hemicellulose and N concentrations (Table 2, Fig. 2; supplementary Table S3, available online). *Gliricidia*, the species with the highest wood nutrient concentration, decayed faster (48.4% ± 13.1%) than *Guazuma* (35.6% ± 13.7%) and *Tectona* (37.0% ± 14.5%) (Table 2, Fig. 1A). While the habitat × species interaction was not significant, *Gliricidia* was the only species that decayed faster in water than on land (*Gliricidia*: $\chi^2 = 41.42$, df = 27, $P < 0.004$; *Guazuma*: $\chi^2 = 1.74$, df = 25, $P = 0.20$; *Tectona*: $\chi^2 = 1.33$, df = 28, $P = 0.25$). The hemicellulose concentration in *Tectona* decreased faster than in *Gliricidia* or *Guazuma* (Table 2, Fig. 2). As hemicellulose was removed during decay, cellulose concentration in the remaining wood increased in *Guazuma* relative to pre-decay wood, while cellulose concentration in *Gliricidia* and *Tectona* decreased in concentration or did not change (Table 2, Fig. 2). Between 3 and 11 months of decay, lignin concentration did not differ among tree species (Table 2, Fig. 2).

Fungal and bacterial communities differ between habitats, decay duration and tree species

As expected, we found differences in fungal and bacterial community composition and diversity across habitats and decay duration (Table 2, Fig. 3A–D), yet differences in community composition among tree species were only observed for bacteria (Table 2, Fig. 3E and F). A higher percentage of bacterial OTUs were shared across habitats and decay durations than fungal OTUs (Fig. 3A–D).

Basidiomycota accounted for the major compositional difference between habitats in fungi (Fig. 4A). Between 3 and 11 months of decay, Basidiomycota percentage of total reads significantly increased on land (3 months: 19%, 11 months: 57%) but not in streams (3 months: 8%, 11 months: 19%, ANOVA: habitat × census, $F = 11.47$, $P = 0.002$, supplementary Table S17,

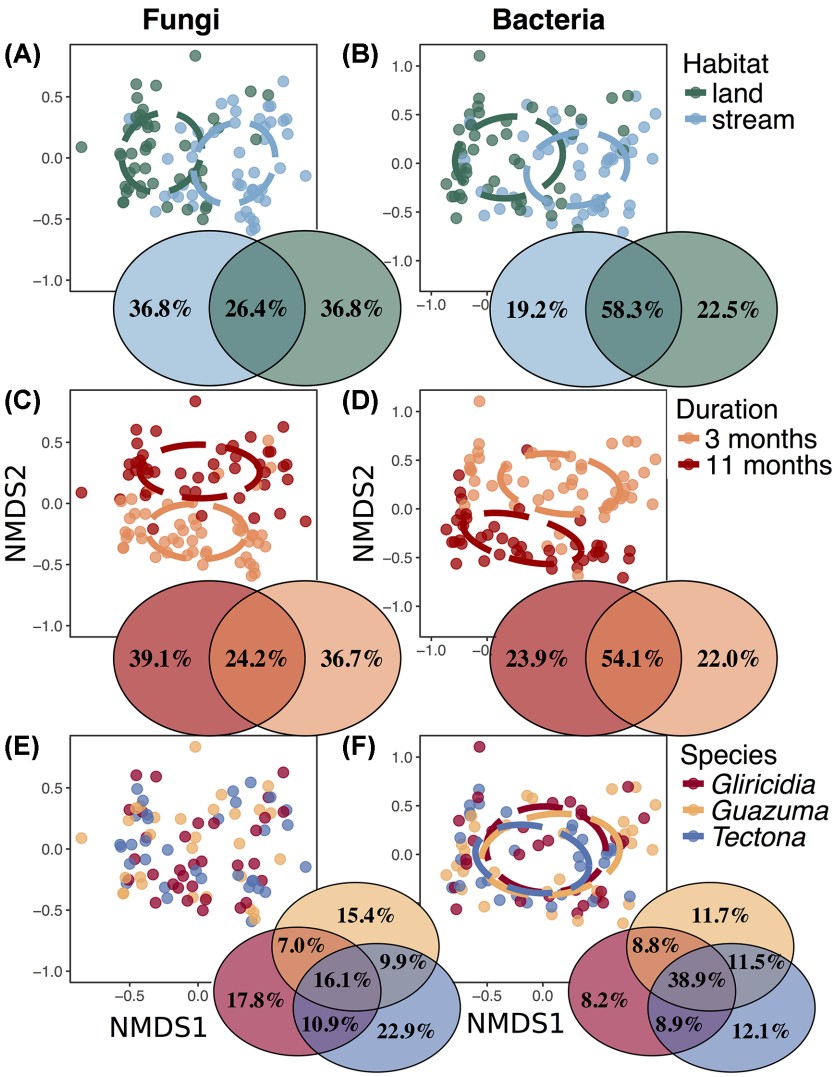

Figure 3. NMDS axes of variation for fungal (**A**, **C**, **E**; stress = 0.19) and bacterial (**B**, **D**, **F**; stress = 0.13) community composition distinguishing between habitat type (A, B), decay duration (C, D) and species (E, F). Circles indicate significant differences between groups using a PERMANOVA analysis. Venn diagrams have the % of OTUs unique to each group and shared.

available online). Within the Basidiomycota, the class Agaricomycetes (which accounted for 99% of Basidiomycota reads) and the order Agaricales generally followed the same trend as the phylum Basidiomycota. In contrast to the increase in Basidiomycota reads, Ascomycota decreased from 3 to 11 months of decay on land (3 months 76%, 11 months 43%) but not in streams (3 months: 76%, 11 months: 78%, Fig. 4A, supplementary Table S17, available online). Within the Ascomycota, there were more variable responses to habitat and decay duration than in Basidiomycota (supplementary Table S17, available online). Eurotiomycetes and Chaetothyriales (Eurotiomycetes) had more sequences on land than in streams. Jahnulales (Dothideomycetes) had higher sequence count in streams than land, and Pezizomycetes had higher sequence count after 3 months of decay than 11 months (supplementary Table S17, available online). Only one class, Sordariomycetes, followed the general trend of Ascomycota (low abundance on land after 11 months of decay) (supplementary Table S17, available online). The third abundant phylum, Chytridiomycota, was found in greater sequence abundance in water after 3 months of decay than any other habitat or decay duration (Fig. 4A, supplementary Table S17, available online). Within the Chytridiomycota, Chytridiomycetes and Monoblepharidomycetes at the class level and Chytridiales at the order level had higher sequence abundance after 3 months of decay than 11 months (supplementary Table S17, available online).

For bacteria, seven dominant phyla significantly differed between habitats and decay durations. Bacteroidetes and Firmicutes had greater sequence abundance after 3 months of decay than 11 months (Fig. 4B, supplementary Table S18, available online). In contrast, Acidobacteria, Actinobacteria and Chloroflexi had greater sequence abundance after 11 months of decay. Spirochaetes and Proteobacteria were the only dominant phyla that differed significantly between habitats. Spirochaetes were less abundant on land than in water, while Proteobacteria were found at lowest abundance in streams after 3 months of decay (Fig. 4B, supplementary Table S18, available online). Other bacteria differed in abundance between habitats and decay duration, but had very low sequence count (<2500 sequences total: Ignavibacteriae, Chlamydiae, Armatimonadetes, Chlorobi and Parcubacteria) (supplementary Table S18, available online).

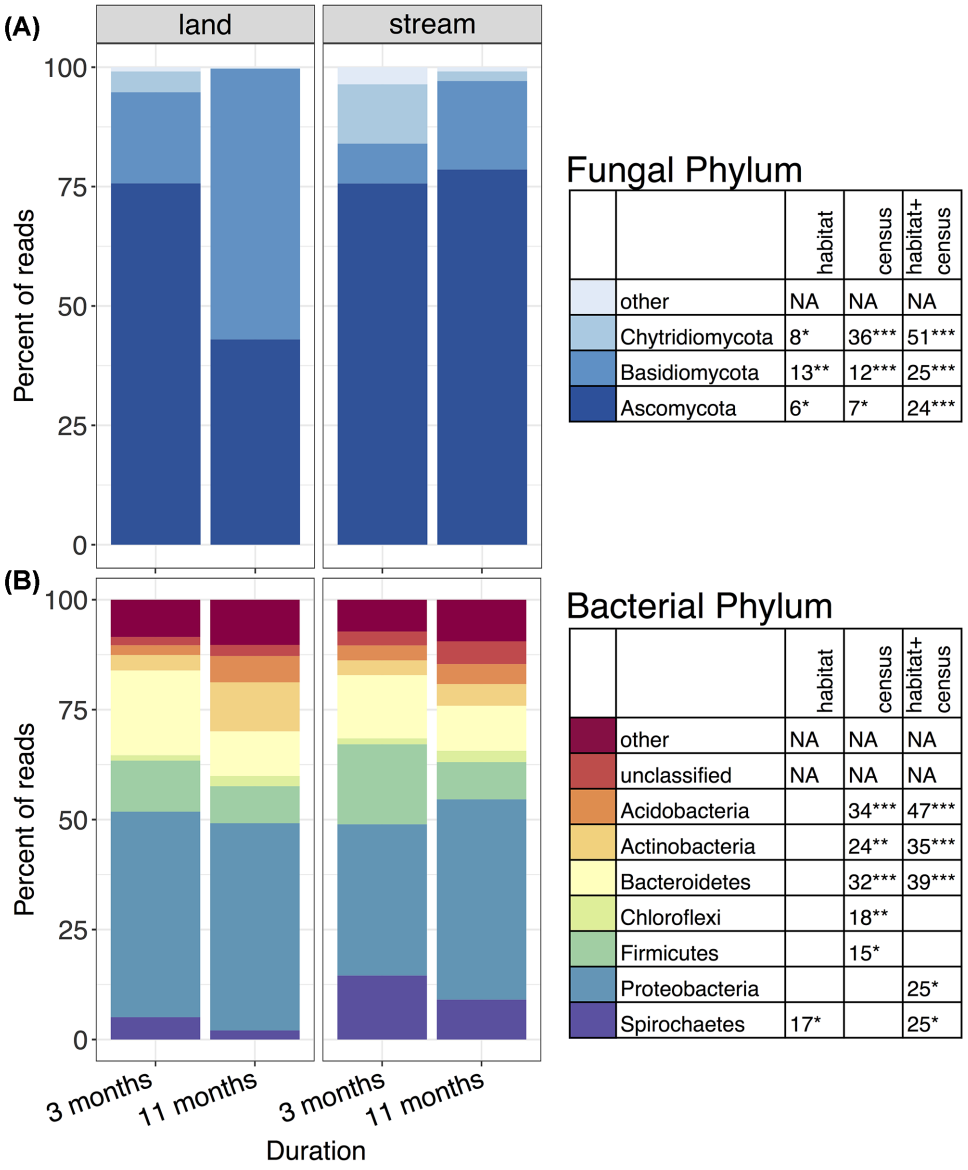

Figure 4. Mean % of reads from each fungal (**A**) and bacterial (**B**) phyla across habitat and decay duration. 'Other' are sequences that do not belong to the three most abundant phyla for fungi or phyla that have <2500 sequences total for bacteria.

We observed contrasting patterns of diversity for fungi and bacteria across habitat, decay duration and tree species. For fungi, the per-sample diversity was significantly higher in streams than on land (Shannon diversity index: land: 2.25, stream: 2.65, Table 2), while the total number of OTUs at each habitat were nearly the same in both habitats (land 2217 OTUs, water: 2218 OTUs, supplementary Fig. S2, available online). In contrast, the differences in bacterial diversity across habitats depended on tree species. Bacterial diversity in *Gliricidia* was higher in streams than on land, *Guazuma* had the opposite trend and *Tectona* did not differ between habitats (Table 2). Overall, the total number of bacterial OTUs in land and water were also similar (land: 10 011, water: 9612). Additionally, fungal per-sample diversity declined between 3 and 11 months of decay for *Gliricidia* and *Tectona*, but not *Guazuma* (3 months: 2.70, 11 months: 2.17, Table 2), while bacterial diversity increased during the experiment (3 months: 5.41, 11 months: 5.98, Table 2). Tree species did not significantly influence fungal community composition or diversity (Table 2, Fig. 3E). In contrast, bacterial per-sample diversity was significantly higher on *Tectona* than *Guazuma* wood (Table 2).

Fungal and bacterial communities correlate with mass loss and changes in wood chemistry

Through comparing multiple analyses restricted to a single habitat and decay duration, we examined how associations between decomposer communities and decay rate differ between habitats and through time. Fungal and bacterial community composition was associated with mass loss, but only for land samples after 11 months of decay (canonical correspondence analysis: fungi, $F = 1.7$, $P = 0.004$; bacteria, $F = 1.5$, $P = 0.003$). Additionally, bacterial community composition and diversity were associated with the % change in hemicellulose concentration on land after 3 months of decay (canonical correspondence analysis, $F = 1.2$, $P = 0.04$; diversity correlation test, tau $= -0.483$, T $= 31$, $P =$

0.009). Neither fungal nor bacterial community composition or diversity were associated with differences in N, lignin or cellulose concentrations.

DISCUSSION

We used a wood decay experiment to explore how nutrient availability and microbial communities impact decay processes on land and in streams. Our results support a greater role for physical fragmentation and leaching in accelerating mass loss in streams compared with land. We found that wood decay depended on tree species in both streams and land habitats, suggesting that wood composition is equally important to decay in both habitats. As expected, our data indicated that the fungal and bacterial communities that colonized dead wood differed between land and stream habitats. However, more surprisingly, we saw little evidence that their combined ability to decay wood differed between habitats. In the sections below we first compare the differences in mass loss and change in nutrients and wood polymers across habitats and tree species. Then we discuss the differences in microbial composition and diversity between the stream and land habitats.

Fragmentation and leaching likely contribute to faster mass loss in streams than on land

In this experiment, we inferred the contribution of fragmentation and leaching to decay by measuring wood mass loss and the concentrations of N and wood structural polymers. We interpret mass loss and N loss without an associated shift in the relative proportions of lignin, cellulose and hemicellulose as indications of substrate fragmentation and leaching (Ibrahima, Joffre and Gillon 1995). Indeed, we found faster mass loss and N loss in streams than on land, without differences in hemicellulose, lignin and cellulose concentrations between the two habitats, suggesting that fragmentation and leaching contribute to faster wood mass loss in streams than on land.

High rates of mass loss from physical processes in the stream environment may explain why decomposition proceeded faster in water than on land, contrary to many previous studies (Harmon *et al.* 1986; Bilby 2003; but see Boonyuen, Sivichai and Jones 2014). Although fragmentation can cause mass loss on land (Bond-Lamberty and Gower 2008), flowing water breaks apart partially decayed wood faster in streams than on land (Harmon *et al.* 1986; Wagener, Oswood and Schimel 1998; Langhans *et al.* 2008; Boonyuen, Sivichai and Jones 2014; but see Baldy *et al.* 2002). Additionally, fragmentation is likely to be more important for small diameter wood than large diameter wood (Mattson, Swank and Waide 1987). The small (2 cm diameter) branch size used in our study potentially accounts for the increased importance of fragmentation in our experiment compared with other studies.

Decomposer community differences could also contribute to the observation of greater wood mass loss in streams compared with on land. Previous studies have found that terrestrial fungi have more efficient decay capabilities than aquatic fungi (Bucher *et al.* 2004; Boonyuen, Sivichai and Jones 2014). However, because we observed no differences in polymer concentrations between habitats, we found no evidence to suggest that microbial communities performed decay faster in streams than on land. In addition to microbial communities, invertebrate communities likely influence wood mass loss via their effects on fragmentation and catabolism (Ulyshen, Müller and Seibold 2016). To isolate the contribution of fungi and bacteria to wood decay, we attempted to exclude termites and other invertebrates. Our exclosures successfully excluded termites, but worked less well for other invertebrates. On land only 1 of 49 samples had visible invertebrates, but in streams 14 of 49 samples had visible invertebrates. Therefore our exclosures may have prevented some mass loss that would otherwise have occurred.

Nutrient availability and tree species influence wood decay in streams and on land

We examined the effects of nutrient availability and substrate characteristics on decay by comparing mass loss and the change in lignin, cellulose and hemicellulose among tree species and habitats. We hypothesized that decomposition would be more nutrient-limited in streams than on land. In streams, fungi cannot use their hyphae to move nutrients from sediment to substrate, or substrate to substrate, while wood in flowing water is presumably more susceptible to nutrient losses from leaching (Wagener, Oswood and Schimel 1998; Gessner *et al.* 2010). Consistent with leaching, N concentration decreased faster in streams than on land in our experiment. Interestingly, despite initial N loss, N concentration increased between 3 and 11 months of decay across all tree species and habitats, likely due to either preferential loss of C or microbial N storage in the decaying wood (Melillo *et al.* 1984). Additionally, we found that *Gliricidia*, the tree species with the highest N and K concentrations, had the fastest mass loss, which supports previous studies that have shown high wood N concentrations can increase wood mass loss (Melillo *et al.* 1984; Sinsabaugh *et al.* 1993; Weedon *et al.* 2009; Zanne *et al.* 2015). Thus, while we found faster mass loss in the tree species with the highest wood N, increasing N concentration through decomposition was not consistent with greater N limitation in streams than on land.

In addition to nutrients, species-specific wood characteristics can also impact wood decay. We found that cellulose and hemicellulose loss differed among tree species and were consistent across habitats. While we found no significant differences between wood structural polymers before decay, our ability to detect these differences was constrained by small sample sizes. Nonetheless, there are likely to be unmeasured tree species characteristics that influence the loss of specific wood polymers.

Microbial diversity differences between habitats and decay duration

In our experiment, we found that fungal per-sample diversity was higher in wood incubated in water, while the number of fungal OTUs unique to streams was similar to the number of OTUs unique to land. Although this result is surprising because the described global diversity of terrestrial fungi is 25 times higher than aquatic fungi (Bärlocher and Boddy 2016), previous studies have also found higher fungal diversity in dead wood in freshwater habitats compared with on land (Aprile, Delitti and Bianchini 1999; Cai, Ji and Hyde 2006). Cai, Ji and Hyde (2006) found that, on bamboo, fungi were more diverse in streams than on land in a temperate forest. They attributed this difference in diversity to a greater importance of wood as a source of organic matter in streams because leaves break apart more quickly in streams than on land, resulting

in stronger selection for wood substrate utilization in aquatic fungi. Our results also indicate contrasting controls on fungal and bacterial diversity. While fungal diversity decreased during decay, bacterial diversity increased slightly from the first to the second census, consistent with previous studies indicating that bacterial diversity increases through the decay process (Sun *et al.* 2014; Hoppe *et al.* 2015). In contrast to fungal diversity, bacterial diversity did not differ between habitats, suggesting different assembly processes operate in these groups. Further studies are needed to determine whether this is a common finding.

Microbial community composition differences between habitats, decay duration and tree species

We found differences in fungal community composition between land and streams consistent with previous observations that different fungal phyla dominate communities in freshwater and terrestrial habitats. Basidiomycota have been found primarily on land, while Ascomycota can be found on land and in water (Shearer *et al.* 2007; Kodsueb *et al.* 2008; Jones, Hyde and Pang 2014; Duarte *et al.* 2015; Purahong *et al.* 2016). Supporting these studies, we found more Basidiomycota sequences on land than in streams. Furthermore, on land, Basidiomycota abundances increased between 3 and 11 months of decay. This finding is consistent with previous work showing that, while Ascomycota species dominate in early stages of decay and degrade cellulose and hemicellulose, Basidiomycota abundances increase at intermediate and later stages when lignin degradation occurs (Gessner *et al.* 2010; Purahong *et al.* 2016; but see Kodsueb *et al.* 2008; Fukasawa, Osono and Takeda 2017). We also found that Chytridiomycota were in higher abundance in water than on land, which is consistent with previous studies (Shearer *et al.* 2007). In contrast to Basidiomycota and Chytridiomycota, Ascomycota classes and orders have diverse responses to habitat and decay duration (i.e. Jahnulales (Shearer *et al.* 2009); Chaetothyriales (Liu *et al.* 2015)).

We found that bacterial community composition differed at the phylum level across habitat type and census, including many groups that are commonly found in decaying wood (Actinobacteria: Sun *et al.* 2014; Hoppe *et al.* 2015; Rinta-Kanto *et al.* 2016, Acidobacteria: Sun *et al.* 2014; Rinta-Kanto *et al.* 2016, Bacteroidetes: Valášková *et al.* 2009; Hervé *et al.* 2014; Sun *et al.* 2014, Firmicutes: Zhang *et al.* 2008; Kielak *et al.* 2016, and Chloroflexi: Zhang *et al.* 2008). Other studies have found that decay stage impacts bacterial community composition at the phylum level (Sun *et al.* 2014; Kielak *et al.* 2016; Purahong *et al.* 2016; Rinta-Kanto *et al.* 2016). Consistent with previous studies, we found Actinobacteria, which include lignin degraders (Brown and Chang 2014), and Acidobacteria, which include degraders of cellulose and hemicellulose (Ward *et al.* 2009), in higher abundance later in decay (Actinobacteria: Rinta-Kanto *et al.* 2016, Acidobacteria: Sun *et al.* 2014; but see Rinta-Kanto *et al.* 2016).

Bacterial communities differed among tree species, while fungal communities did not. Consistent with our experiment, previous studies from terrestrial habitats have also shown that bacteria differ across tree species (Kulhánková *et al.* 2006; Prewitt *et al.* 2014; but see Sun *et al.* 2014). The apparent lack of tree species preference in fungi is in contrast to many studies using both culture-based (Lumley, Gignac and Currah 2001) and non-culture methods (Kulhánková *et al.* 2006; Rajala *et al.* 2010; Hoppe *et al.* 2016; Purahong *et al.* 2017), most of which are from the temperate region. It is possible that substrate preferences among wood decay fungi are stronger in temperate than tropical regions (Lodge 1997), are contingent on substrate size (Hammond 1992; Lodge 1997) or depend on tree species abundance (Hammond 1992; Ferrer and Gilbert 2003).

Fungal and bacterial community composition effects on wood decay

Because fungi in Basidiomycota have more diverse wood decay enzymes that are capable of efficiently breaking down lignin (Floudas *et al.* 2012; Riley *et al.* 2014) and are more common on land than in streams (Bärlocher and Boddy 2016), we predicted faster mass and lignin loss on land than in streams. While we found the expected patterns in fungal community composition, we found no difference in the loss of hemicellulose, cellulose and lignin between habitats despite 9% difference in mass loss by the end of the experiment. These results suggest a high degree of functional overlap between terrestrial and aquatic fungi. Indeed, laboratory studies show that freshwater fungi can decay a variety of substrates, including cellulose, hemicellulose and lignin (Zare-Maivan and Shearer 1988a; Bucher *et al.* 2004).

On land but not in streams, fungal and bacterial community composition correlated with mass loss, suggesting that fungal and bacterial identity is more important on land than in streams. Many potential mechanisms could explain this result. Most freshwater fungi degrade cellulose and hemicellulose (Zare-Maivan and Shearer 1988a; Bucher *et al.* 2004; Bärlocher and Boddy 2016), potentially leading to high functional redundancy in freshwater fungi. Additionally, because leaf litter in streams quickly breaks apart and flowing water prevents fungi from accessing soil C and nutrients, wood is a more important and stable source of C (Tank and Winterbourn 1996) and nutrients (Cai, Ji and Hyde 2006) in streams than on land. Therefore, freshwater fungi and bacteria may prioritize growth and rapid colonization of wood substrates, whereas the diversity of stable C sources (e.g. leaves, soil and wood) on land may select for specialization on specific C sources and the allocation of resources to defending substrates (Gessner *et al.* 2010). This may lead to greater differentiation in fungal decay efficiencies on land than in streams. Alternatively, higher fragmentation rates in streams may reduce the portion of mass loss explainable by microbial community composition, therefore reducing the detectability of significant influences of microbial community composition. Lastly, on land, differences in the degree to which fungal taxa access soil nutrient resources, or have hyphal connections to other substrates, could translate to greater variation in decay efficiency by fungi on land than in streams (Gessner *et al.* 2010).

In summary, we show that abiotic and biotic factors drive different decay dynamics in streams and on land. While we found expected patterns of microbial community composition, we unexpectedly found that wood decays faster on land than in streams. By showing similar loss of wood structural polymers across habitats, our paper challenges the current paradigm that wood decays slowly in freshwater habitats because most freshwater fungi cannot efficiently degrade lignin and oxygen limitation slows the efficient enzymatic decay of wood (Zare-Maivan and Shearer 1988b; Bucher *et al.* 2004; Boonyuen, Sivichai and Jones 2014; Bärlocher and Boddy 2016). We instead conclude that increased mass loss by physical processes likely caused the differences in wood mass loss between habitats. More comparative studies on wood decay in terrestrial and aquatic habitats are necessary to generalize the patterns of mass loss and microbial decay observed here, and will be essential for modeling C and nutrient cycling at the ecosystem scale.

SUPPLEMENTARY DATA

Supplementary data are available at *FEMSEC Journal* online.

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Conflicts of interest. None declared.

REFERENCES

Amend AS, Seifert KA, Samson R *et al.* Indoor fungal composition is geographically patterned and more diverse in temperate zones than in the tropics. *Proc Natl Acad Sci USA* 2010;**107**:13748–53.

Anderson MJ. A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 2001;**26:** 32–46.

Aprile FM, Delitti WBC, Bianchini I, Jr. Aspectos cinéticos da degradação de laminados de madeiras em ambientes aquático e terrestre. *Rev Bras Biol* 1999;**59**:485–92.

Baldy V, Chauvet E, Charcosset JY *et al.* Microbial dynamics associated with leaves decomposing in the mainstem and floodplain pond of a large river. *Aquat Microb Ecol* 2002;**28**:25–36.

Bärlocher F, Boddy L. Aquatic fungal ecology - How does it differ from terrestrial? *Fungal Ecol* 2016;**19**:5–13.

Bates D, Machler M, Bolker B *et al.* Fitting linear mixed-effects models using lme4. *J Stat Soft* 2015;**67**:1–48.

Berry D, Ben Mahfoudh K, Wagner M *et al.* Barcoded primers used in multiplex amplicon pyrosequencing bias amplification. *Appl Environ Microb* 2011;**77**:7846–9.

Bilby R. Decomposition and nutrient dynamics of wood in streams and rivers. In: Gregory S, Boyer K, Gurnell A (eds). *The Ecology and Management of Wood in World Rivers*, American Fisheries Society, Bethesda, Maryland, USA, 2003:135–47.

Boddy L. Saprotrophic cord-forming fungi: warfare strategies and other ecological aspects. *Mycol Res* 1993;**97**:641–55.

Bond-Lamberty B, Gower ST. Decomposition and fragmentation of coarse woody debris: Re-visiting a boreal black spruce chronosequence. *Ecosystems* 2008;**11**:831–40.

Boonyuen N, Sivichai S, Jones EBG. Decomposition of wood in tropical habitats. In: Jones EBG, Hyde KD, Pang K-L (eds). *Freshwater Fungi and Fungi Like Organisms*, De Gruyter, Berlin/Boston, 2014:465–79.

Bradford MA, Warren RJ, II, Baldrian P *et al.* Climate fails to predict wood decomposition at regional scales. *Nat Clim Change* 2014;**4**:625–30.

Brown ME, Chang MC. Exploring bacterial lignin degradation. *Curr Opin Chem Biol* 2014;**19**:1–7.

Brown SP, Veach AM, Rigdon-Huss AR *et al.* Scraping the bottom of the barrel: are rare high throughput sequences artifacts? *Fungal Ecol* 2015;**13**:221–5.

Bucher VVC, Pointing SB, Hyde KD *et al.* Production of wood decay enzymes, loss of mass, and lignin solubilization in wood by diverse tropical freshwater fungi. *Microb Ecol* 2004;**48**:331–7.

Cai L, Ji K-F, Hyde KD. Variation between freshwater and terrestrial fungal communities on decaying bamboo culms. *Antonie Van Leeuwenhoek* 2006;**89**:293–301.

Caporaso JG, Lauber CL, Walters WA *et al.* Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. *ISME J* 2012;**6**:1621–4.

Chapin FS, III, Matson PA, Vitousek P. *Principles of Terrestrial Ecosystem Ecology*, 2nd edn. Springer Science & Business Media, New York, 2011.

Cole JR, Wang Q, Fish JA *et al.* Ribosomal Database Project: data and tools for high throughput rRNA analysis. *Nucleic Acids Res* 2014;**42**:D633–42.

Cornwell WK, Cornelissen JHC, Allison SD *et al.* Plant traits and wood fates across the globe: rotted, burned, or consumed? *Glob Chang Biol* 2009;**15**:2431–49.

Delaney M, Brown S, Lugo AE *et al.* The quantity and turnover of dead wood in permanent forest plots in six life zones of venezuela. *Biotropica* 1998;**30**:2–11.

Duarte S, Barlocher F, Trabulo J *et al.* Stream-dwelling fungal decomposer communities along a gradient of eutrophication unraveled by 454 pyrosequencing. *Fungal Divers* 2015;**70**:127–48.

Edgar RC, Haas BJ, Clemente JC *et al.* UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* 2011;**27**:2194–200.

Ferrer A, Gilbert GS. Effect of tree host species on fungal community composition in a tropical rain forest in Panama. *Divers Distrib* 2003;**9**:455–68.

Floudas D, Binder M, Riley R *et al.* The paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science* 2012;**336**:1715–9.

Fukami T, Dickie IA, Paula Wilkie J *et al.* Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. *Ecol Lett* 2010;**13**:675–84.

Fukasawa Y, Osono T, Takeda H. Dynamics of physicochemical properties and occurrence of fungal fruit bodies during decomposition of coarse woody debris of *Fagus crenata*. *J For Res* 2017;**14**:20–9.

Gessner MO, Swan CM, Dang CK *et al.* Diversity meets decomposition. *Trends Ecol Evol* 2010;**25**:372–80.

Hammond P. Species inventory. In: Groombridge B (ed). *Global Biodiversity: Status of Earth's Living Resources*. Dordrecht: Springer, Dordrecht, 1992, 17–39.

Harmon ME, Franklin JF, Swanson FJ *et al. Ecology of Coarse Woody Debris in Temperate Ecosystems*. Vol. **15**. Elsevier, London, 1986:133–302.

Heineman KD, Turner BL, Dalling JW. Variation in wood nutrients along a tropical soil fertility gradient. *New Phytol* 2016;**211**:440–54.

Hervé V, Le Roux X, Uroz S *et al.* Diversity and structure of bacterial communities associated with *Phanerochaete chrysosporium* during wood decay. *Environ Microbiol* 2014;**16**:2238–52.

Hoppe B, Krüger D, Kahl T *et al.* A pyrosequencing insight into sprawling bacterial diversity and community dynamics in decaying deadwood logs of *Fagus sylvatica* and *Picea abies*. *Sci Rep* 2015;**5**:133–9.

Hoppe B, Purahong W, Wubet T *et al*. Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. *Fungal Divers* 2016;**77**:367–79.

Huse SM, Welch DM, Morrison HG *et al*. Ironing out the wrinkles in the rare biosphere through improved OTU clustering. *Environ Microbiol* 2010;**12**:1889–98.

Ibrahima A, Joffre R, Gillon D. Changes in litter during the initial leaching phase: An experiment on the leaf litter of Mediterranean species. *Soil Biol Biochem* 1995;**27**:931–9.

Johnston SR, Boddy L, Weightman AJ. Bacteria in decomposing wood and their interactions with wood-decay fungi. *FEMS Microbiol Ecol* 2016;**92**:w179.

Jones EBG, Hyde KD, Pang K-L. Introduction. In: Jones EBG, Hyde KD, Pang K-L (eds). *Freshwater Fungi and Fungi Like Organisms*. De Gruyter, Berlin/Boston, 2014, 1–22.

Kaspari M, Garcia MN, Harms KE *et al*. Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecol Lett* 2008;**11**:35–43.

Kielak AM, Scheublin TR, Mendes LW *et al*. Bacterial community succession in pine-wood decomposition. *Front Microbiol* 2016;**7**:2011.

Kodsueb R, McKenzie E, Lumyong S *et al*. Fungal succession on woody litter of *Magnolia liliifera* (Magnoliaceae). *Fungal Divers* 2008;**30**:55–72.

Kulhánková A, Béguiristain T, Moukoumi J *et al*. Spatial and temporal diversity of wood decomposer communities in different forest stands, determined by ITS rDNA targeted TGGE. *Ann For Sci* 2006;**63**:547–56.

Langhans SD, Tiegs SD, Gessner MO *et al*. Leaf-decomposition heterogeneity across a riverine floodplain mosaic. *Aquat Sci* 2008;**70**:337–46.

Lenth RV. Least-squares means: the R package lsmeans. *J Stat Soft* 2016;**69**:1–33.

Liu X-Y, Udayanga D, Luo Z-L *et al*. Backbone tree for Chaetothyriales with four new species of *Minimelanolocus* from aquatic habitats. *Fungal Biol* 2015;**119**:1046–62.

Lodge DJ. Factors related to diversity of decomposer fungi in tropical forests. *Biodivers Conserv* 1997;**6**:681–8.

Lumley TC, Gignac LD, Currah RS. Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixedwood region of Alberta. *Can J Bot* 2001;**79**:76–92.

Mattson KG, Swank WT, Waide JB. Decomposition of woody debris in a regenerating, clear-cut forest in the southern Appalachians. *Can J For Res* 1987;**17**:712–21.

Medeiros AO, Pascoal C, Graca MAS. Diversity and activity of aquatic fungi under low oxygen conditions. *Freshw Biol* 2009;**54**:142–9.

Melillo JM, Naiman RJ, Aber JD *et al*. Factors controlling mass-loss and nitrogen dynamics of plant litter decaying in northern streams. *B Mar Sci* 1984;**35**:341–56.

Negrão DR, Silva Júnior TAFD, Passos JRDS *et al*. Biodegradation of *Eucalyptus urograndis* wood by fungi. *Int Biodeter Biodegr* 2014;**89**:95–102.

O'Connell M, Baldwin DS, Robertson AI *et al*. Release and bioavailability of dissolved organic matter from floodplain litter: influence of origin and oxygen levels. *Freshwater Biol* 2000;**45**:333–42.

Oksanen J, Blanchet FG, Friendly M *et al*. *vegan: Community Ecology Package*. 2018. https://cran.r-project.org/web/packages/vegan/index.html, last accessed date was April 5, 2018.

Oliver AK, Brown SP, Callaham MA, Jr *et al*. Polymerase matters: non-proofreading enzymes inflate fungal community richness estimates by up to 15%. *Fungal Ecol* 2015;**15**:86–9.

Pascoal C, Cássio F. Contribution of fungi and bacteria to leaf litter decomposition in a polluted river. *Appl Environ Microb* 2004;**70**:5266–73.

Poorter L, McDonald I, Alarcón A *et al*. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol* 2010;**185**:481–92.

Prewitt L, Kang Y, Kakumanu ML *et al*. Fungal and bacterial community succession differs for three wood types during decay in a forest soil. *Microb Ecol* 2014;**68**:212–21.

Purahong W, Wubet T, Lentendu G *et al*. Life in leaf litter: novel insights into community dynamics of bacteria and fungi during litter decomposition. *Mol Ecol* 2016;**25**:4059–74.

Purahong W, Pietsch KA, Lentendu G *et al*. Characterization of unexplored deadwood mycobiome in highly diverse subtropical forests using culture-independent molecular technique. *Front Microbiol* 2017;**8**:109–17.

Quast C, Pruesse E, Yilmaz P *et al*. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res* 2013;**41**:D590–6.

Rajala T, Peltoniemi M, Pennanen T *et al*. Relationship between wood-inhabiting fungi determined by molecular analysis (denaturing gradient gel electrophoresis) and quality of decaying logs. *Can J For Res* 2010;**40**:2384–97.

Rayner ADM, Boddy L. *Fungal Decomposition of Wood: It's Biology and Ecology*, Chichester. John Wiley and Sons, 1988.

Riley R, Salamov AA, Brown DW *et al*. Extensive sampling of Basidiomycete genomes demonstrates inadequacy of the white-rot/brown-rot paradigm for wood decay fungi. *Proc Natl Acad Sci USA* 2014;**111**:9923–8.

Rinta-Kanto JM, Sinkko H, Rajala T *et al*. Natural decay process affects the abundance and community structure of Bacteria and Archaea in *Picea abieslogs*. *FEMS Microbiol Ecol* 2016;**92**:fiw087.

Robinson WD, Brawn JD, Robinson SK. Forest bird community structure in central Panama: Influence of spatial scale and biogeography. *Ecol Monogr* 2000;**70**:209–35.

Saugier B, Roy J, Mooney HA. Estimations of global terrestrial productivity. In: Roy J, Saugier B, Mooney HA (eds). *Terrestrial Global Productivity*. Academic Press, San Diego, Calif., 2001, 543–57.

Schloss PD, Westcott SL, Ryabin T *et al*. Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Appl Environ Microb* 2009;**75**:7537–41.

Shearer CA, Descals E, Kohlmeyer B *et al*. Fungal biodiversity in aquatic habitats. *Biodivers Conserv* 2007;**16**:49–67.

Shearer CA, Raja HA, Miller AN *et al*. The molecular phylogeny of freshwater Dothideomycetes. *Stud Mycol* 2009;**64**:145–53-S4.

Sinsabaugh RL, Antibus RK, Linkins AE *et al*. Wood decomposition: Nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. *Ecology* 1993;**74**:1586–93.

Sluiter A, Hames B, Ruiz R *et al*. Determination of structural carbohydrates and lignin in biomass. *Technical Report*, National Renewable Energy Laboratory, Golden, Colorado, USA, 2012;TP–510-42618.

Stewart RH, Stewart JL. *Geologic map of the Panama Canal and vicinity, Republic of Panama*, United States Geological Survey 1980: No. 1232. https://pubs.er.usgs.gov/publication/i1232, accessed on April 17, 2018

Song Z, Vail A, Sadowsky MJ *et al*. Competition between two wood-degrading fungi with distinct influences on residues. *FEMS Microbiol Ecol* 2012;**79**:109–17.

Sun H, Terhonen E, Kasanen R *et al*. Diversity and community structure of primary wood-inhabiting bacteria in boreal forest. *Geomicrobiol J* 2014;**31**:315–24.

Tank JL, Winterbourn MJ. Microbial activity and invertebrate colonisation of wood in a New Zealand forest stream. *New Zeal J Mar Fresh* 1996;**30**:271–80.

Tank JL, Rosi-Marshall EJ, Griffiths NA *et al*. A review of allochthonous organic matter dynamics and metabolism in streams. *J N Am Benthol Soc* 2010;**29**:118–46.

Townsend AR, Asner GP, Cleveland CC. The biogeochemical heterogeneity of tropical forests. *Trends Ecol Evol* 2008;**23**:424–31.

Ulyshen MD, Müller J, Seibold S. Bark coverage and insects influence wood decomposition: Direct and indirect effects. *Appl Soil Ecol* 2016;**105**:25–30.

Valášková V, de Boer W, Klein Gunnewiek PJA *et al*. Phylogenetic composition and properties of bacteria coexisting with the fungus *Hypholoma fasciculare* in decaying wood. *ISME J* 2009;**3**:1218–21.

van Breugel M, Hall JS, Craven DJ *et al*. Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. *For Ecol Manage* 2011;**261**:1580–9.

Vilgalys R, Hester M. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *J Bacteriol* 1990;**172**:4238–46.

Wagener SM, Oswood MW, Schimel JP. Rivers and soils: parallels in carbon and nutrient processing. *Bioscience* 1998;**48**:104–8.

Wang Q, Garrity GM, Tiedje JM *et al*. Naive Bayesian Classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Appl Environ Microbiol* 2007;**73**:5261–7.

Wang Y, Naumann U, Wright S *et al*. mvabund: an R package for model-based analysis of multivariate data. *Methods Ecol Evol* 2012;**3**:471–4.

Ward NL, Challacombe JF, Janssen PH *et al*. Three genomes from the phylum *Acidobacteria* provide insight into the lifestyles of these microorganisms in soils. *Appl Environ Microbiol* 2009;**75**:2046–56.

Weedon JT, Cornwell WK, Cornelissen JHC *et al*. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? *Ecol Lett* 2009;**12**:45–56.

Windsor DM. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panamá, *Smithsonian Contributions to the Earth Sciences* 1990;**29**:1–145.

Zanne AE, Oberle B, Dunham KM *et al*. A deteriorating state of affairs: How endogenous and exogenous factors determine plant decay rates. *J Ecol* 2015;**103**:1421–31.

Zare-Maivan H, Shearer CA. Extracellular enzyme production and cell wall degradation by freshwater lignicolous fungi. *Mycologia* 1988a;**80**:365.

Zare-Maivan H, Shearer CA. Wood decay activity and cellulase production by freshwater lignicolous fungi. *Int Biodeterior* 1988b;**24**:459–74.

Zhang D, Hui D, Luo Y *et al*. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J Plant Ecol* 2008;**1**:85–93.