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Fungal growth on a common wood substrate across a tropical elevation gradient: Temperature sensitivity, community composition, and potential for above-ground decomposition

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ABSTRACT

Fungal breakdown of plant material rich in lignin and cellulose (i.e. lignocellulose) is of central importance to terrestrial carbon (C) cycling due to the abundance of lignocellulose above and below-ground. Fungal growth on lignocellulose is particularly influential in tropical forests, as woody debris and plant litter contain between 50% and 75% lignocellulose by weight, and can account for 20% of the C stored in these ecosystems. In this study, we evaluated factors affecting fungal growth on a common wood substrate along a wet tropical elevation gradient in the Peruvian Andes. We had three objectives: 1) to determine the temperature sensitivity of fungal growth – i.e. Q_{10}, the factor by which fungal biomass increases given a 10 °C temperature increase; 2) to assess the potential for above-ground fungal colonization and growth on lignocellulose in a wet tropical forest; and 3) to characterize the community composition of fungal wood decomposers across the elevation gradient. We found that fungal growth had a Q_{10} of 3.93 (95% CI of 2.76–5.61), indicating that fungal biomass accumulation on the wood substrate nearly quadrupled with a 10 °C increase in temperature. The Q_{10} for fungal growth on wood at our site is higher than Q_{10} values reported for litter decomposition in other tropical forests. Moreover, we found that above-ground fungal growth on the wood substrate ranged between 37% and 50% of that measured in the soil, suggesting above-ground breakdown of lignocellulose represents an unexplored component of the C cycle in wet tropical forests. Fungal community composition also changed significantly along the elevation gradient, and Ascomycota were the dominant wood decomposers at all elevations. Fungal richness did not change significantly with elevation, directly contrasting with diversity patterns observed for plant and animal taxa across this gradient. Significant variation in fungal community composition across the gradient suggests that the characteristics of fungal decomposer communities are, directly or indirectly, influenced by temperature.

1. Introduction

Fungal decomposers are thought to be largely responsible for the breakdown of lignin and cellulose (i.e. lignocellulose) derived from woody plant material and plant litter (de Boer et al., 2005; Hättenschwiler et al., 2005; van der Wal et al., 2007). In temperate ecosystems, lignocellulose can comprise over 50% of plant litter dry mass (Fortunel et al., 2009; Valachovic et al., 2004) and 60–75% of wood dry mass (Kaakinen et al., 2004, 2007). As such, fungal breakdown of lignocellulose is of central importance to terrestrial C cycling, and factors that affect the colonization and growth of fungi on substrates rich in lignocellulose (e.g. temperature, moisture, soil nutrient status, microbial community composition, and physical location – that is, above versus below-ground) have the potential to affect the ecosystem C balance.

Factors influencing the fungal breakdown of lignocellulose are particularly consequential in tropical forests, as tropical forests process more C than any other biome (Schlesinger, 1997), and are an important driver of the global C cycle (Malhi et al., 2008). In addition, woody debris and plant litter that are rich in lignocellulose can account for up to 20% of the C stored in these ecosystems (Chao et al., 2008; Palace et al., 2008; Weedon et al., 2009). As future temperature increases in the tropics are predicted to be as large as 4 °C (Cramer et al., 2004), the temperature sensitivity of

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fungal growth on lignocellulose is likely to have an important influence on tropical forest responses to global warming. Moreover, due to large above-ground stocks of woody necromass, interception of litter by the canopy, as well as relatively warm, constant temperatures and high rainfall and humidity, there is the potential for considerable above-ground decomposition of lignocellulose by fungi in tropical forests (Rousk and Nadkarni, 2009). However, we do not currently know how rates of above-ground fungal colonization and growth compare to below-ground rates of these processes in tropical forests (but see Nadkarni and Matelson, 1991; Nadkarni et al., 2004).

In this study, we had three primary goals: 1) to determine the temperature sensitivity of net fungal growth on a common wood substrate across an elevation gradient in a wet tropical forest; 2) to assess the relative importance of above-ground fungal colonization and growth compared to fungal growth in the litter and soil layers; and 3) to describe the composition and richness of the fungal community on a common wood substrate across the elevation gradient.

We measured the temperature sensitivity of fungal growth on a common wood substrate by quantifying ergosterol accumulation (as a proxy for fungal biomass; de Ridder-Duine et al., 2006) on the substrate over a period of three months across a 1900 m elevation gradient on the eastern slope of the Peruvian Andes near the western edge of Amazonia. Though we chose a wood substrate, breakdown of lignocellulose in wood is also directly relevant to fungal breakdown of lignocellulose in plant litter. The temperature sensitivity of decomposition is typically defined in terms of Q_{10} – that is, the factor by which a 10 °C increase in temperature will increase some decomposition process (i.e. mass loss, C mineralization, microbial biomass accumulation, etc.). Though a handful of studies have measured Q_{10} for litter mass loss in tropical and subtropical ecosystems (e.g. Holland et al., 2000; Scowcroft et al., 2000), to the best of our knowledge the temperature sensitivity of fungal growth on woody substrates has not been studied. For measurements of Q_{10}, it is important to isolate effects of temperature from other factors that affect decomposition (i.e. moisture, vegetation type, soil type, etc.; Powers et al., 2009). The unique nature of the elevation gradient studied here allowed us to control for these factors that often confound many similar field-based studies. The very high levels of precipitation across the gradient suggest that decomposition is not limited by moisture, and the very steep topography results in well-drained soils that prevent limitations to decomposition due to low oxygen levels. Moreover, soils across the gradient all contain a thick organic (O) horizon with similar pH, and the overlying vegetation is also relatively constant (i.e. closed canopy forest with numerous tree genera conserved across sites). At one elevation along the gradient we also assessed the potential for above-ground fungal colonization and growth in the forest canopy and understory compared to fungal growth in the litter and soil layer.

In addition to measuring fungal biomass accumulation on the common wood substrate, we compared the richness and composition of the fungal communities across the elevation gradient. We hypothesized that there would be consistent changes in fungal community composition across the transect, with higher fungal biomass accumulation at lower elevation sites yielding communities distinct from those found at higher elevation sites. Likewise, we hypothesized that the taxonomic richness of the fungal communities would be negatively correlated with elevation, with the highest fungal richness at the lowest elevation. This predicted pattern would thus be similar to the diversity patterns exhibited by plant and animal communities across this transect (Patterson et al., 1998; M. Silman, unpublished data) and many other elevation gradients (e.g. Rahbek, 2005).

2. Materials and methods

2.1. Site description

Fieldwork for this study was carried out across an elevation gradient (10 km length; 1900 m vertical, from 1500 m.a.s.l. to 3400 m.a.s.l.) in a wet tropical forest on the Amazonian side of the Peruvian Andes (13° 5′ 38″ S, 71° 34′ 27″ W). Temperature and precipitation are negatively correlated with elevation across the gradient (see Results), but all sites are extremely wet (ranging between 2600 and 5000 mm precipitation y^{-1}), and precipitation exceeded potential evapotranspiration at all elevations throughout the time period examined (Table 1). Surface soils across the gradient are characterized by a thick O-horizon (15–25 cm) that is well-drained due to the steep topography (approximately 35° slopes). Although tree species composition changes across this gradient, some of the dominant tree genera are found at all elevations (e.g. *Clethra*, *Clusia*, *Hedyosmum*, *Ilex*, *Miconia*, *Myrsine*, *Nectandra*, *Ocotea*, *Persea*, *Prunus*, and *Weinmannia*). *Cyathea* spp. (tree ferns) are also abundant across the gradient. All plots are located within closed canopy forest with canopy heights averaging between 15 m and 25 m, with taller average canopy height at lower elevations.

2.2. Decomposition experiment

To determine the temperature sensitivity of net fungal growth across the elevation gradient, we first installed HOBO Pro v2 Temp/RH loggers (at 1500 m, 2020 m, 2720 m, and 3400 m), and 0.2 mm Rainfall Smart Sensors connected to HOBO Microstation data loggers (at 1500 m, 1850 m, 2720 m, 3400 m; Onset Computer Corporation, USA). Precipitation values at 2020 m were interpolated from a linear regression, and interpolated values were checked against a Peruvian national weather station located at 2000 m along the same contour in the adjacent valley. At the same sites that received temperature/RH loggers, we then placed a common wood substrate (popsicle sticks) into the top 10 cm of the soil within each of three randomly selected 2 by 2 m plots at each elevation (6 sticks per plot × 3 plots per elevation × 4 elevations = 72 total sticks). Because of the well-drained nature of

Table 1
Site conditions along the elevation gradient during the experimental time-course.

Elevation (m)	Soil %C	Soil %N	Soil pH	Month	Mean temp (°C)[a]	PPT (mm)	PET (mm)	MD (mm)
3400	40.09	2.08	4.12	July	6.7	63.4	40.5	−22.9
				August	6.5	108.8	39.6	−69.2
				September	7.0	99.6	42.4	−57.2
				October	8.0	203.8	47.3	−156.5
2720	44.84	2.32	4.20	July	10.2	68.0	45.9	−22.1
				August	10.2	132.6	45.8	−86.8
				September	11.0	152.8	50.0	−102.8
				October	11.5	239.8	52.3	−187.5
2020	46.57	2.16	4.10	July	13.9	97.0	51.9	−45.1
				August	14.2	120.7	53.8	−66.9
				September	15.2	189.2	59.6	−129.6
				October	15.5	390.7	60.9	−329.8
1500	45.03	2.14	4.25	July	16.2	115.3	56.2	−59.1
				August	17.1	117.6	61.5	−56.1
				September	18.9	219.0	73.9	−145.1
				October	18.1	486.4	68.4	−418.0

All soil measurements were made on samples from the O-horizon. PPT, precipitation; PET, potential evapotranspiration; MD, moisture deficit.
[a] Temperature data are mean monthly data from the forest understory at each site.

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the soils, we are confident that fungal colonization and growth were not limited by anoxic soil conditions, despite the high levels of precipitation.

At the 2720 m study site, we measured the potential for above-ground fungal colonization and growth on lignocellulose by tethering additional popsicle sticks to nylon line fixed in both the understory (1–2 m above-ground), and the canopy (12–15 m above-ground). Tethered popsicle sticks were free-hanging in the air (6 sticks per plot × 3 plots × 2 above-ground locations = 36 above-ground sticks).

All popsicle sticks were installed in the field on the 26th and 27th of July 2007, and sticks were collected from the field between the 23rd and 26th of October 2007. Immediately following collection, sticks were dried by placing into plastic zip-lock bags filled with silica gel (28–200 mesh, Fisher Scientific, Denver, CO, USA). Dried sticks were then brought back to the laboratory and analyzed for net fungal biomass accumulation and fungal community composition on the wood substrate (described below). In each plot, soil organic C and N content and soil pH were measured from samples of soil collected from the O-horizon in 2004 (Table 1). Soil organic C and N (%) were measured on a CE Elantech Model NC2100 elemental analyzer (ThermoQuest Italia, Milan, Italy) with combustion at 900 °C. Soil pH was measured after shaking a soil/water (1:1 w/v) suspension for 30 min.

We quantified net fungal growth on each popsicle stick over the 3-month period by measuring ergosterol accumulation with a non-alkaline extraction protocol (de Ridder-Duine et al., 2006). Previous work has demonstrated that ergosterol is a good proxy for live fungal biomass when fungi are actively growing (i.e. substrate is not limiting), and edaphic conditions are relatively stable (Helfrich et al., 2008; Högberg, 2006; Montgomery et al., 2000; Zhao et al., 2005). When fungal biomass declines rapidly – e.g. due to chloroform fumigation or severe substrate limitation – ergosterol correlates poorly with other measures of live fungal biomass like chloroform-labile biomass C, substrate induced respiration, live fungal hyphal length, and fungal-specific PLFA markers like 18:2ω6,9 (Helfrich et al., 2008; Högberg, 2006; Mille-Lindblom et al., 2004; Scheu and Parkinson, 1994; Zhao et al., 2005). Because our sticks were in the field for only three months, we are confident that substrate supplies were not limiting to the relatively slow-growing fungi that specialize on the breakdown of lignocellulose. The ergosterol values we obtained should therefore be a reliable proxy for live fungal biomass accumulation on the common wood substrate.

To prepare samples for ergosterol analysis, dried sticks were cut into 1–2 mm^2 pieces with scissors and ground as finely as possible with a mortar and pestle. We then placed ~0.5 g of the ground stick (recorded to the nearest 0.1 mg), 2 g large glass beads (Sigma G1152, St. Louis, MO, USA), and 2 g small glass beads (Sigma G1277) into plastic 20 mL scintillation vials, and added 6 mL methanol per vial. Vials were then vortexed for 10 s, and shaken for 60 min at 320 rev min^{-1} on a shaker table. Following shaking, a 1.5 mL aliquot of the methanol/wood suspension was centrifuged (14 000 rpm, 10 min), and the supernatant was filtered with a 0.2 μm PTFE syringe filter (Grace Discovery #2394, Deerfield, IL, USA). To measure ergosterol concentrations in the supernatant, 20 μL was injected into a Hewlett–Packard 1090 HPLC equipped with a diode array detector (DAD). Ergosterol was isolated and identified with a 15 min isocratic separation in 100% methanol over an Apex ODS 5 μm reverse phase C-18 column (250 mm × 4.6 mm o.d., Jones Chromatography, U.K.), protected with a guard column of the same material (7.5 mm × 4.6 mm). Detection was at 282 nm, and spectra for ergosterol peaks were acquired from 200 to 525 nm and checked for spectral purity. Ergosterol from the experimental samples was quantified by comparison with a purified ergosterol external standard (Sigma 45480) of known concentration dissolved in methanol.

To determine fungal community composition on sticks placed across the gradient, we randomly selected one stick that had been placed in each sub-plot for molecular analysis (3 sub-plots per elevation for a total of 12 sticks). Half of each stick was cut into 1–2 mm^2 pieces with sterile scissors and DNA was extracted from a 0.25 g sub-sample of each stick using the MOBIO PowerSoil DNA extraction kit (MOBIO Laboratories, Carlsbad, CA). Clone libraries were constructed by amplifying the DNA samples with the fungal-specific primer pair EF4 and fung5 (Smit et al., 1999). This primer pair amplifies the fungal 18S rRNA gene yielding a PCR product that is approximately 550 bp in length. PCR reactions were performed using the Platinum PCR Supermix (Invitrogen, Carlsbad, CA). Primers were added to a final concentration of 0.2 μM, and 2 μL of DNA template was used in each reaction. PCR amplification was performed with an initial denaturation at 94 °C for 3 min followed by 35 cycles of 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 30 s with a final extension at 72 °C for 10 min. Each sample was amplified in triplicate and the amplicons were pooled by sample and run on a 1.2% agarose gel. The bands were purified with the Qiaquick gel extraction kit (Qiagen, Carlsbad, CA). PCR amplicons were cloned into the TOPO TA cloning vector and transformed into TOP10 chemically competent cells following the manufacturer's instructions. Following overnight incubation at 37 °C, colonies were picked and M13 colony PCR was performed using identical PCR conditions to those described above. PCR products were sent to Agencourt Bioscience (Beverly, MA) for single pass sequencing ($n = 32$ clones sequenced per sample).

The sequences were combined together and aligned against an internal database containing fungal guide sequences downloaded from the Silva ssu RNA database (http://silva.mpi-bremen.de/). Sequences were aligned using MUSCLE (Edgar, 2004) and we constructed a neighbor-joining tree containing all fungal sequences from the constructed libraries in MEGA (Tamura et al., 2007) using *Arabidopsis thaliana* as an out-group. Taxonomic classification was determined by comparing each sequence to the fungal sequences from the Silva database using the BLAST algorithm (Altschul et al., 1997). Five to ten% of the sequences were removed from the database as they were low quality or poor matches (E values $> 10^{-6}$) to sequences in the fungal database. We used the weighted UniFrac algorithm (Lozupone et al., 2006) to quantitatively compare the communities on each stick. UniFrac provides an overall estimate of the phylogenetic distance between each pair of communities by examining the fraction of the total branch length within a single phylogenetic tree that is unique to either of the two communities (as opposed to being shared by both). Pairwise UniFrac distances between the fungal communities on the sticks were visualized using a non-metric multi-dimensional scaling procedure with the strength of the differences between communities at different elevations tested using the ANOSIM procedure as implemented in PRIMER (Clarke, 1993). The number of phylotypes per stick, an estimate of taxonomic richness, was estimated using FastGroup (Yu et al., 2006) with a phylotype defined as those sequences that are 97% similar.

2.3. Data analyses

We determined the mean temperature for the duration of the experimental period at each elevation by calculating a weighted average based on mean monthly temperatures, and the number of days in a given month that the sticks were in the field. We then used Eq. (1) (as in Lloyd and Taylor, 1994) to describe the relationship between ergosterol accumulation on the sticks and

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variation in mean weighted temperature across the elevation gradient (7.1–17.9 °C):

$$\ln(E_T) = B + kT \quad (1)$$

where E_T is ergosterol accumulation at any given temperature (in μg ergosterol g^{-1} dry weight wood), T is temperature in °C, and B and k are constants. To determine the parameter k, which is the temperature sensitivity of ergosterol accumulation across the elevation gradient, we analyzed natural log-transformed ergosterol accumulation as a function of temperature, using a simple linear regression model. We then compared the simple regression model to multiple regression models that always included temperature, but were additionally allowed to include moisture stress (defined below as F_W), soil C:N ratio, and soil pH across the gradient. We ultimately chose k from the model that best fit the data based on a stepwise forward and backward elimination procedure and AIC scores. We then used Eq. (2) to calculate Q_{10}, the average increase in ergosterol accumulation for a 10 °C increase in temperature, since Q_{10} values are easier to interpret than k:

$$Q_{10} = e^{10k} \quad (2)$$

To account for possible effects of variation in moisture stress across the gradient on fungal biomass accumulation, we used Eq. (3) (as in Adair et al., 2008):

$$F_W(\mathrm{PPT}_i, \mathrm{PET}_i) = \frac{1.0}{1.0 + 30 \times \exp(-8.5 \times \mathrm{PPT}_i/\mathrm{PET}_i)} \quad (3)$$

where $F_W(\mathrm{PPT}_i, \mathrm{PET}_i)$ is the monthly effect of water stress, and PPT_i and PET_i are monthly precipitation (in mm) and monthly potential evapotranspiration (in mm), respectively. Values for PET_i were calculated using equations from Thornthwaite (1948). The weighted mean water stress was calculated based on monthly F_W values weighted by the number of days the sticks were in the field in a given month. Additionally, we calculated the moisture deficit (MD) at each elevation for each month that the sticks were in the field according to Eq. (4):

$$\mathrm{MD}_i = \mathrm{PET}_i - \mathrm{PPT}_i \quad (4)$$

where PET_i and PPT_i are defined as above.

We were unable to correlate ergosterol values with mass loss of the common wood substrate for the following reasons: 1) we could not obtain accurate (nearest 0.1 mg) initial mass measurements of the individual popsicle sticks in the field; and 2) popsicle stick blanks that had not been deployed in the field varied in mass, making it problematic to obtain a meaningful average initial weight that was relevant to all sticks that were deployed in the field.

To compare rates of above-ground fungal growth in understory and tree canopy locations with below-ground fungal growth, we analyzed untransformed ergosterol values as a function of height above-ground, using a linear mixed-effects model with height as a categorical fixed-factor and sub-plot as a random effect. We then compared above-ground fungal growth to below-ground fungal growth using *a priori* contrasts.

For all analyses, outliers were identified as those points in the initial dataset with absolute standardized residuals outside of the 95% confidence interval of a standard normal distribution. Quantile–quantile plots were used to assess the normality of residuals, and data were examined for homogeneity of variance with fitted versus residual plots. Pearson's correlation coefficients (r) were used to describe correlations between environmental variables like elevation, temperature, precipitation, soil C:N ratio and soil pH across the gradient ($n = 4$ for Pearson's correlations). Statistical analyses were performed with R ver. 2.10.1 (R Corporation, Vienna, Austria).

3. Results

3.1. Temperature sensitivity of fungal growth in the soil

After three months in the field, there was visible and extensive fungal growth on the common wood substrate (authors personal observation), and ergosterol accumulation increased considerably with mean temperature across the elevation gradient according to a simple linear regression analysis ($R^2 = 0.53$, $F_{1,66} = 75.3$, $p < 0.0001$; Fig. 1). Ergosterol was below the detection limit on popsicle stick blanks that were not deployed in the field. However, mean temperature and cumulative precipitation were strongly correlated along the elevation gradient for the duration of the experimental period (Pearson's $r = 0.99$), with both temperature and precipitation decreasing as elevation increased (Pearson's $r = -0.99$ and -0.99, respectively; Table 1). Increasing elevation was also correlated with small decreases in soil C:N ratios and soil pH (Pearson's $r = -0.85$ and -0.49, respectively; Table 1). For this reason, it is possible that changes in water stress, soil C:N ratio, and soil pH also influenced the rate of ergosterol accumulation across the elevation gradient.

We first used an equation for moisture stress (F_W) based on precipitation (PPT) and potential evapotranspiration (PET) values to determine whether changes in both temperature and moisture stress along the gradient affected fungal growth. Because PPT was greater than PET at all elevations at all time points (Table 1), F_W was always equal to 1, indicating moisture stress likely did not affect growth of fungal biomass. As discussed in the Methods, we are confident that the high levels of soil moisture did not cause anoxic conditions that limited fungal growth, due to the steep topography resulting in very well-drained soils at our site. As such, we concluded that temperature changes across the gradient, not changes in moisture stress, had the largest effect on fungal growth.

Soil C:N ratios and soil pH also varied somewhat across the gradient (Table 1), and we used a multiple regression model and stepwise elimination procedure based on AIC scores to determine whether multiple environmental factors might explain variation in

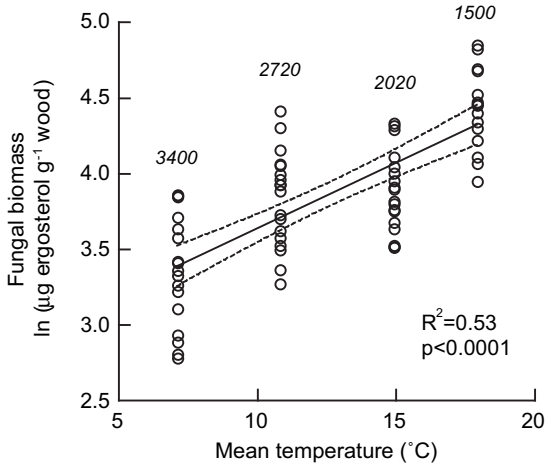

Fig. 1. Correlation between ergosterol accumulation on a common wood substrate, and mean temperature over the course of the experimental period. Wood sticks were placed in the field at four sites along a 1900 m elevation gradient in Peru from late July to late October 2007; numbers in italics refer to the elevation in meters at each site along the gradient. $n = 18$ sticks per elevation (6 sticks in each of 3 randomly selected plots per elevation). Dashed lines represent the 95% confidence interval of the regression line. Here we have plotted the effect of temperature alone on ergosterol accumulation; however, the temperature sensitivity of ergosterol accumulation (i.e. k) was obtained from a multiple regression analysis that included both temperature and soil C:N ratio as independent variables (see Results).

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ergosterol accumulation on the substrate. Based on this analysis, we found that ergosterol accumulation was best modeled as a function of both temperature and soil C:N ratios ($R^2 = 0.60$, $F_{2,65} = 49.0$, $p < 0.0001$). Temperature was positively correlated with ergosterol accumulation (slope [k] $= 0.137 \pm 0.018$, $R^2 = 0.53$, $F_{1,65} = 86.9$, $p < 0.0001$), and soil C:N ratios were negatively correlated with ergosterol accumulation (slope $= -0.231 \pm 0.069$, $R^2 = 0.068$, $F_{1,65} = 11.1$, $p < 0.01$), with changes in temperature explaining considerably more variation in net fungal growth than soil C:N ratios. Using the slope associated with temperature (i.e. k) from the best-fit multiple regression model, we calculated a Q_{10} of 3.93 for fungal growth on a woody substrate in wet tropical forest (95% confidence interval of $Q_{10} = 2.76–5.61$).

3.2. Above-ground decomposition

To quantify the potential for fungal breakdown of lignocellulose above-ground in a wet tropical forest, we measured ergosterol accumulation on a common wood substrate placed in the ground, and suspended in the air in both the understory and the canopy at the 2720 m site. We found that the vertical location of the sticks strongly influenced the net accumulation of ergosterol per gram wood over the 3-month period ($F_{2,49} = 26.9$, $p < 0.0001$; Fig. 2). Sticks hung in the forest understory averaged 50.1% of the fungal growth obtained for sticks placed in the ground, and sticks hung in tree canopies averaged 37.4% of the fungal growth obtained for sticks placed in the ground (Fig. 2). Despite having lower fungal biomass than sticks placed in the soil, sticks placed above-ground still accumulated a substantial amount of fungal biomass. These data indicate that although fungal colonization and growth on the wood substrate was fastest in the soil, a considerable amount of lignocellulose breakdown could take place above-ground in wet tropical forests.

3.3. Fungal community composition and richness

In addition to differences in fungal biomass accumulation across the elevation gradient, the composition of the fungal community on the common wood substrate changed substantially with elevation (Fig. 3). This pattern was confirmed by ANOSIM results

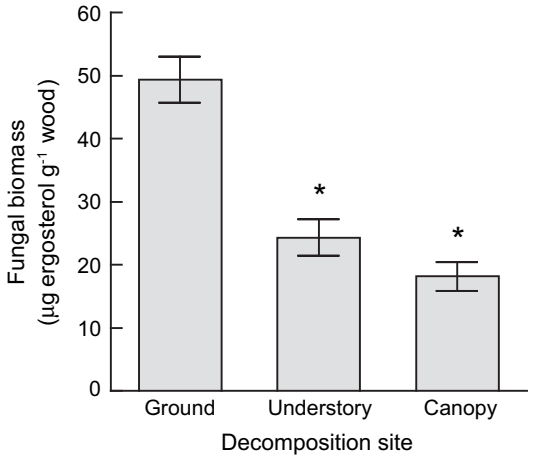

Fig. 2. Ergosterol accumulation on a common wood substrate placed in the top 10 cm of the soil O-horizon (ground), the forest understory (1–2 m above-ground), and the forest canopy (12–15 m above-ground). For this element of the study only one elevation (2720 m) was used. Asterisks indicate means are significantly different from ergosterol accumulation on sticks placed in the ground ($p < 0.0001$, *a priori* contrasts). For statistical analysis, response variables were natural log-transformed, but untransformed data are graphed.

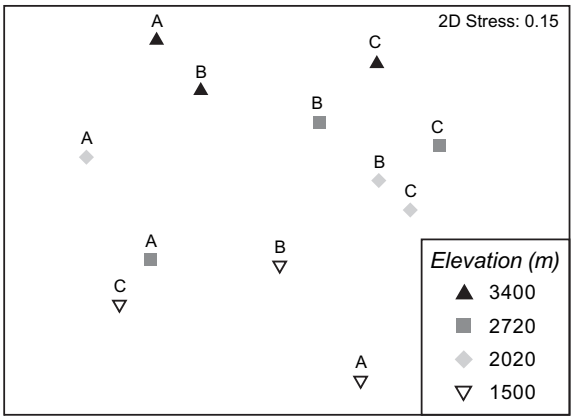

Fig. 3. Non-metric multi-dimensional scaling (NMDS) plot of fungal community structure at each elevation across the gradient. DNA sequences of the fungal community were obtained from 12 randomly selected sticks, one stick from each of the 3 plots at each elevation. Letters (A–C) identify unique plots within an elevation. The axes on NMDS plots are unitless.

showing a significant effect of elevation on fungal community composition (Global $R = 0.51$, $p = 0.02$). In particular, the communities on sticks placed at 3400 m were clearly distinct from fungal communities on sticks placed at 1500 m (Fig. 3). Ascomycota represented between 58.5% and 100% of the fungal phylotypes on all but one stick (Table 2), and at all elevations, fungi in this phylum were the dominant wood decomposers in terms of relative phylotype abundance. However, there was variation in the types of ascomycetes colonizing the sticks across the gradient (Table 2). Leotiomycetes represented $51 \pm 11\%$ of the total number of fungal phylotypes at 3400 m, and only $11.1 \pm 9.5\%$ of the phylotypes at 1500 m. Similarly, Dothideomycetes accounted for $12.3 \pm 4.3\%$ of the fungal phylotypes at 3400 m, and $2.1 \pm 1.1\%$ of the phylotypes at 1500 m. Also within the Ascomycota, Chaetothyriomycetes and Sordariomycetes showed the opposite trend, and were relatively more abundant at 1500 m ($18 \pm 11\%$ and $55 \pm 12\%$, respectively) than at 3400 m ($1.1 \pm 1.1\%$ and $10.8 \pm 3.8\%$, respectively). We found one Zygomycota phylotype at relatively high abundance (25.8%) at 3400 m, but Zygomycota represented $< 3.5\%$ of the sequences on all the other sticks that were sampled (Table 2). Across all the sticks for which we obtained fungal sequences, there was no correlation between elevation and fungal phylotype richness ($R^2 = 0.14$, $F_{1,10} = 1.58$, $p = 0.24$; Table 2).

4. Discussion

4.1. Q_{10} in tropical ecosystems

Using four sites located across a 1900 m elevation gradient in a wet tropical forest, we calculated a Q_{10} value of 3.93 for net fungal growth on a common wood substrate by measuring ergosterol accumulation, which is a robust proxy for live fungal biomass accumulation under our experimental conditions. Our results are relevant to the fungal breakdown of lignocellulose from wood as well as from plant leaf and root litter, as these are the plant materials that are rich in lignocellulose. However, because we evaluated the temperature sensitivity of fungal growth on wood sticks specifically, our determination of Q_{10} is particularly relevant to the decomposition of coarse and fine woody debris in the wet tropics. Coarse and fine woody debris comprise significant components of the C cycle in Amazonian forests, accounting for up to 15% of the above-ground vegetative biomass, and 14–19% of the above-ground C flux (Chao et al., 2008; Palace et al., 2008; Weedon

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Table 2
Summary description of fungal community structure across the elevation gradient.

Elevation (m)	Ergosterol (μg g^{-1} wood)	Sub-plot	Ascomycota					Basidiomycota		Zygomycota	Fungal richness (# phylotypes)
			Leotiomycete	Dothideomycete	Chaetothyriomycete	Sordariomycete	Other	Agaricales	Aphyllophorales		
3400	47.47	A	51.6	6.5	0.0	12.9	3.2	0.0	0.0	25.8	12
	82.51	B	71.0	9.7	0.0	16.1	3.2	0.0	0.0	0.0	11
	25.16	C	31.0	20.7	3.4	3.4	0.0	17.2	24.1	0.0	14
2720	29.05	A	6.5	12.9	0.0	74.2	6.5	0.0	0.0	0.0	10
	58.41	B	29.0	9.7	0.0	35.5	0.0	22.6	0.0	3.2	12
	34.08	C	45.2	6.5	0.0	12.9	0.0	35.5	0.0	0.0	10
2020	43.13	A	28.1	9.4	3.1	50.0	9.4	0.0	0.0	0.0	13
	34.11	B	53.1	6.3	0.0	6.3	6.3	28.1	0.0	0.0	9
	61.20	C	0.0	6.3	0.0	6.3	0.0	87.5	0.0	0.0	5
1500	128.4	A	30.0	0.0	10.0	36.7	6.7	16.7	0.0	0.0	11
	68.23	B	0.0	3.1	3.1	78.1	0.0	15.6	0.0	0.0	10
	124.9	C	3.3	3.3	40.0	50.0	0.0	0.0	0.0	3.3	11

Values represent the relative abundance of each fungal group as a percent of the total number of sequences identified at a given location. Fungal richness (i.e. the total number of phylotypes on a given stick) was calculated by defining a phylotype as a group of sequences with 97% sequence similarity. Fungal communities were analyzed on a subset of 12 sticks using a sequence-based approach (1 stick randomly selected from each sub-plot at each elevation).

et al., 2009). To the best of our knowledge, this is the first study to determine the temperature sensitivity of fungal growth on a common wood substrate (i.e. lignocellulose) in a wet tropical forest using ergosterol accumulation in the field. The accumulation of ligninolytic live fungal biomass on a wood substrate is likely correlated with the disappearance of that substrate (i.e. mass loss), as well as evolution of $C-CO_2$ from that substrate, though our measurements do not allow us to quantitatively link these processes.

The apparent temperature sensitivity of decomposition in the field can also be influenced by soil moisture deficit (Davidson et al., 1998; Davidson and Janssens, 2006; Ise and Moorcroft, 2006), soil nutrient status (Scowcroft et al., 2000), substrate availability (Holland et al., 2000), and substrate quality (Fierer et al., 2006, 2005). Collectively, these potentially confounding factors typically make it difficult to measure Q_{10} accurately in the field. For example, inhibition of decomposer growth due to substrate limitation would result in an apparently lower Q_{10} value. By measuring ergosterol accumulation over a relatively short period of time (to avoid substrate limitation), and by employing a common wood substrate across a unique tropical elevation gradient (where soil pH, soil nutrient status, and the effects of soil moisture were held nearly constant), we were able to isolate the effects of temperature on a key component of decomposition in a field setting.

The Q_{10} of 3.93 that we calculated for fungal growth is higher than other values of Q_{10} obtained for litter mass loss and soil respiration from other tropical and sub-tropical sites. For example, Scowcroft et al. (2000) reciprocally transplanted plant litter across three elevation gradients in Hawaii, and used a 36-month time-course to obtain Q_{10} values for mass loss that did not differ significantly from 2 in most cases. Another study used a laboratory incubation approach to compare the temperature sensitivity of heterotrophic respiration among soils from multiple land-use types (e.g. forest, pasture, etc.) sampled from multiple tropical and sub-tropical regions (Brazil, Costa Rica, Hawaii, and south Texas) (Holland et al., 2000). These authors found that although Q_{10} varied substantially with land-use type and region, the average Q_{10} was 2.37, and most Q_{10} values fell between 1 and 3. It is worth noting that differences in Q_{10} between our study and others could be related to the fact that we coupled a field-based approach with a relatively short experimental time-course that helped to eliminate effects of substrate limitation on fungal growth. It is also possible that Q_{10} values for fungal growth are influenced by different biochemical reactions than those that determine Q_{10} for heterotrophic respiration. That is, there may be distinct temperature sensitivities associated with fungal biomass accumulation and respiration.

4.2. Potential for above-ground fungal colonization and growth

Fungal growth on wood suspended in the forest canopy was 37–50% of fungal growth on the wood placed in the soil (Fig. 2). This ratio of above-ground to below-ground net fungal biomass accumulation is similar to that reported by Nadkarni and Matelson (1991) where below-ground leaf litter mass loss was 2 times faster than mass loss of litter fixed to branches in a tropical Costa Rican cloud forest. Because we analyzed sticks that were free-hanging in the air, and not attached to branches or embedded in epiphyte mats that retain fungal spores and moisture more efficiently, our results are most pertinent to above-ground colonization and subsequent decomposition of standing dead woody debris. We hypothesize that above-ground fungal growth could be even higher at our site within the understory and canopy microsites (i.e. epiphyte mats) that intercept the majority of above-ground litter. The free-hanging above-ground sticks we analyzed were likely drier than the microsites in which above-ground decomposition of leaf litter occurs, and initial fungal colonization was likely slower, making the above-ground fungal biomass values reported here a conservative proxy for above-ground leaf litter decomposition at our site.

Combined with the results from other studies (Chao et al., 2008; Nadkarni and Matelson, 1991; Nadkarni et al., 2004; Palace et al., 2008), our results suggest that above-ground decomposition could contribute significantly to ecosystem C fluxes in wet tropical ecosystems, due to: 1) large stocks of dead wood above-ground; and 2) abundant epiphyte communities and the large quantity of litter intercepted by the canopy. However, the ultimate amount of C mineralized above-ground likely depends on several ecosystem-specific factors. First, the amount of material (i.e. wood and leaf litter) left to decompose in the understory and the canopy is critical, and is poorly constrained (but see Nadkarni and Matelson, 1991; Nadkarni et al., 2004). In addition, because available moisture and temperature strongly influence below-ground decomposition rates (Swift et al., 1979), these variables are likely also important controls on above-ground decomposition. Material decomposing above-ground should experience higher temperatures, and is probably more susceptible to drying compared to forest-floor soil. All three of these variables (i.e. above-ground necromass accumulation rate, canopy temperature, and canopy moisture) likely vary across sites.

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Further work focusing on these three critical factors across multiple sites is required to better constrain the amount of C that evolves from plant material decomposing above-ground in wet tropical systems.

4.3. Changes in fungal community structure with elevation

Comparing fungal communities at 1500 m with those at 3400 m, we found that the community composition on the wood sticks changed significantly at the level of taxonomic resolution afforded by our molecular analyses (Fig. 3). Fungal community composition at the two intermediate elevations was not significantly different from each other, though the lack of significant distinction between fungal communities at these two sites was strongly influenced by sub-plot A at 2720 m (Fig. 3). One possible explanation for differences in fungal community composition across the elevation gradient is that different wood-decomposing fungal communities can be associated with different tree species (Kulhánková et al., 2006). While vegetation type did not change across the elevation gradient (i.e. all sites were dominated by closed canopy forest), tree species composition and richness do undergo large changes with increasing elevation (M. Silman, unpublished data). Changes in tree species composition with elevation could therefore be correlated with changes in the composition of fungal wood decomposers. Another possible explanation for changes in fungal communities with elevation is that sticks were collected in different stages of decomposition, and it is possible that succession of fungal communities occurred even over the relatively short decomposition period of three months.

Despite changes in fungal community composition across the gradient, the fungal classes we identified from our tropical site were the same classes of wood-decomposing fungi found in northern European temperate forests (Allmér et al., 2006; Kulhánková et al., 2006). However, there were differences between temperate and tropical wood-decomposing fungi at the order level of taxonomic resolution, particularly among the Basidiomycota (Allmér et al., 2006). Because differences in microbial community composition can account for up to 20% of the observed variation in litter C mineralization rates (Strickland et al., 2009), it is possible that the changes in fungal community composition observed here could contribute to differences in ergosterol accumulation across the gradient, and the observed temperature sensitivity of fungal growth. However, without more detailed experimentation, we cannot link the fungal community composition to the observed differences in ergosterol accumulation.

We found no effect of elevation on fungal community richness (Table 2). This lack of correlation between fungal richness and elevation is in marked contrast to the monotonic decreasing or hump-shaped relationships frequently observed between species richness and elevation for plants and animals (Rahbek, 2005; M. Silman, unpublished data). One possible explanation for the lack of correlation we observed is that, compared to plants and animals, microbial communities are structured more by edaphic conditions than by the changes in temperature we observed (Fierer and Jackson, 2006; Strickland et al., 2009). Because edaphic conditions like soil pH and soil nutrient status did not change markedly across the elevation gradient at our study site, there may not have been a relevant, strong abiotic filter limiting fungal richness at higher elevations. In addition, we also know that the spatial scale of sampling is a strong determinant of observed species richness patterns (Rahbek, 2005), and it is unclear how the spatial scale of sampling influences patterns of richness for very small organisms like bacteria and fungi. Combined with results from our study, the collective data indicate more work is necessary to elucidate which factors structure microbial communities in the field, and whether there are inherent differences between 'macro'-bial and microbial diversity patterns across elevation gradients.

5. Summary

To our knowledge, this study is the first to measure the temperature sensitivity of net fungal growth on wood in a wet tropical forest using an elevation gradient approach that is free from the confounding effects of differences in substrate quantity and quality, soil moisture, and soil pH. Using a common wood substrate we calculated a Q_{10} of 3.93, which is higher than Q_{10} values reported for other components of decomposition in tropical ecosystems like mass loss and C mineralization. In addition, we showed that above-ground fungal growth on woody debris may be substantial at our field site, and likely represents a largely unexplored component of the C cycle in wet tropical forests. We also found significant variation in fungal community composition across the elevation gradient, but fungal richness did not change significantly with elevation, contrasting markedly with patterns observed for plant and animal taxa across this elevation gradient and others. However, this study was not designed to ascertain whether changes in the fungal community were directly responsible for the observed differences in net fungal biomass accumulation.

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