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# Termites amplify the effects of wood traits on decomposition rates among multiple bamboo and dicot woody species

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## Summary

**1.** Wood decomposition is a key process in the terrestrial carbon cycle, controlling carbon storage with feedback to climate. In (sub) tropical forest, termites are major players in wood decomposition, but their role relative to that of microbial decomposers and wood traits of different tree species is poorly understood. The current literature also has strong bias towards dicot tree decomposition, while abundant woody monocots, particularly bamboos, also contribute greatly to (sub) tropical carbon cycling.

**2.** Here, we present the first experiment to disentangle effects of dead wood traits and termite activity on decomposition of 66 angiosperm species of wide-ranging phylogenetic position: 31 bamboos, eight non-bamboo Poaceae, 18 eudicots and nine magnoliids. We incubated dead stems of up to 4 size classes per species in a 'common garden' in tropical S China. We tested the hypotheses that (i) dead wood of bamboo (monocots) is less decomposable than dead wood of eudicots or magnoliids; (ii) both microbial- and termite-driven decomposition show negative relationships with initial wood density and with dry matter content.

**3.** Bamboo wood generally decomposed more slowly than dicot wood but only slightly slower at given wood density or diameter. Wood decomposition in both bamboo and dicot clades decreased with wood density or dry matter content. Termites contributed greatly to this pattern, explaining 53.4% of the variance in wood decomposition and preferentially attacking dead wood of lower initial density, which corresponded with thicker outer culm walls in the case of bamboo species. Thus, termites strongly strengthen the relationship between species' wood traits and litter decomposition as driven by microbial activity.

**4.** *Synthesis*. These previously unknown relationships among dead wood quality, diameter, termites and decomposing microbes of both woody monocots and dicots will advance our understanding of the driving mechanisms of (sub) tropical wood decomposition and its contribution to the global carbon cycle.

**Key-words:** angiosperms, bamboo, carbon cycle, coarse woody debris, decay, eudicots, functional traits, plant–soil (below-ground) interactions, termites

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## Introduction

Dead wood represents a major component of the global forest carbon pool (Dixon *et al.* 1994; Litton, Raich & Ryan 2007), estimated at 73 ± 6 Pg carbon (8% of the global forest carbon pool) globally (Pan *et al.* 2011). Its decomposition also plays a crucial role in forest nutrient cycles. While wood decomposition is affected by climate, substrate quality and decomposer organisms (i.e. bacteria, fungi, termites, beetles and other invertebrates) (Harmon *et al.* 1986; Cornwell *et al.* 2009; Cornelissen *et al.* 2012; Bradford *et al.* 2014), when local-scale variation is properly accounted for, most of the global variation in wood decomposition is driven not only by climate but also rather by biotic factors (see Cornwell *et al.* 2008 for leaf litter decomposition; Bradford *et al.* 2014). Variation in tree species traits drives decomposition rates at local to regional scales (Mackensen, Bauhus & Webber 2003; Weedon *et al.* 2009; van Geffen *et al.* 2010; Freschet *et al.* 2012; Pietsch *et al.* 2014). However, the identity and abundance of decomposer organism, especially fungi and termites, are paramount drivers of wood decomposition too (van der Wal *et al.* 2007; Cornwell *et al.* 2009; Crowther, Boddy & Jones 2011; Bradford *et al.* 2014). Soil mesofauna and macrofauna process large amounts of dead plant material via the breakdown of litter, digestion and stimulation of microbial activities, thereby accelerating litter decomposition and nutrient transformation in most ecosystems but particularly (sub) tropical ecosystems (González & Seastedt 2001; Hättenschwiler & Gasser 2005; Powers *et al.* 2009; García-Palacios *et al.* 2013). However, we know very little about the quantitative importance of interactions between tree species traits and decomposer community composition on wood decomposition rates (Cornelissen *et al.* 2012).

Arthropod taxa, especially termites and wood-boring beetles, are known to consume or excavate significant amounts of dead wood. However, their contributions to the decay process remain largely unmeasured due to methodological challenges of how to manipulate the arthropod contribution without affecting the decay process (Ulyshen & Wagner 2013). In (sub) tropical regions, termites tend to be far more important wood consumers when compared with beetles (Wood & Sands 1978). There is some preliminary evidence that termites prefer to consume relatively soft dead wood with lower density (Takamura 2001; Arango *et al.* 2006), but this evidence is based on wood sticks, excluding the likely important effects of natural stem diameter, shape and structure.

The current wood decomposition literature also has strong bias towards (mostly needle leaf) gymnosperms and (mostly broad leaf) dicot angiosperms (Cornwell *et al.* 2009), while abundant woody monocots, particularly bamboos, also contribute greatly to (sub) tropical carbon cycling. Bamboos (Poaceae, subfamily Bambusoideae; Zhang, Ma & Li 2011) are perennial clonal plants with rapid rhizomatous expansion and resource storage and mostly tree-like stature. Bamboos are predominant components of many (sub) tropical ecosystems both in the Old and the New World (Saha *et al.* 2009). Over 6.3 million km$^2$ of Asian forest potentially contains bamboo, with a band of particularly high abundance and species richness running from north-eastern India through Burma to southern China (Bystriakova *et al.* 2003).

The great physical strength and durability of bamboo culms have led to myriad applications by people (McClure 1966; Longhi 1998; Lima *et al.* 2008; Disén & Clouston 2013). The structural and chemical traits underlying this durability (McClure 1966), both organic (Guo, Tao & Luo 2005; Li, Huang & Qin 2009; Sharma *et al.* 2011) and silicon based (Song *et al.* 2013; Kumar & Chandrashekar 2014), are relatively well known. In contrast, very little is known about 'afterlife' effects of these bamboo culm traits on decomposition (Cornwell *et al.* 2009). Austin & Marchesini (2012) showed that leaf and stem litters of understorey bamboo (*Chusquea culeou* E. Desv.) decomposed significantly slower than those of overstorey trees in north-west region of Patagonia, Argentina. Similarly, litter decomposition and nutrient element losses of leaf and branch/culm in bamboo plantations are slower than those in typical lowland rainforests (Shanmughavel 2004). In India and China, decomposition rates were lower in bamboo stem or twig litter than in bamboo leaf or sheath litter and grass shoot litter (Tripathi & Singh 1992; Tu *et al.* 2014). Indirect evidence for bamboo recalcitrance to decomposition comes from a study on the present annual phytolith carbon sink (amorphous silica deposited in plant tissues) in China's forests (estimated at 1.7 ± 0.4 Tg $CO_2$ year$^{-1}$), 30% of which was shown to be contributed by bamboo due to the larger phytolith-occluded carbon fraction in bamboo litter than in other major clades (Song *et al.* 2013; Li *et al.* 2014). This suggests that the litter dynamics of bamboo species are vital to evaluate the long-term terrestrial carbon sink. Laboratory assays with Kolle flasks have indicated that some bamboo species are more decomposable upon fungal attack than others (Suprapti 2010; Wei, Schmidt & Liese 2013), but these findings are hard to interpret in terms of decomposition rates of naturally senesced culms in natural environments. Also, there is no knowledge about how the decomposabilities of (monocot) bamboo stems compare with those of eudicot or magnoliid angiosperm trees across a representative set of species. This is critical for predicting consequences of large-scale land-use or climate-induced changes in (relative) bamboo abundance for carbon cycling. Thus, we hypothesized that (i) dead wood of (monocot) bamboos is generally less decomposable than dead wood of dicot trees (eudicots, magnoliids) owing to higher wood density and/or more recalcitrant chemistry, and (ii) within major clades, decomposition should be negatively related with initial wood density and with dry matter content, whether among different bamboo species or among different eudicot or magnoliid species (*cf.* Chambers *et al.* 2000; Freschet, Aerts & Cornelissen 2012; Freschet *et al.* 2012; Pietsch *et al.* 2014). To test these hypotheses, we sampled stem litters from 66 (sub) tropical species including 31 bamboos, eight herbaceous non-bamboo Poaceae species, 18 eudicot trees and nine magnoliid trees. We incubated dead stems of up to 4 size classes per species in a 'common garden' in tropical S China. As the incubation progressed, we observed that termites appeared to be major contributors to wood decomposition in our experiment. Thus, we decided to attempt to disentangle combined effects of wood traits, termite activity and stem diameter on decomposition of bamboo and other woody clades, addressing a key hypothesis emerging from the experiment: (iii) as for purely microbial decomposition, termite-driven wood decomposition should also show a negative relation with initial wood density or dry matter content. If the third hypothesis were confirmed, this would potentially indicate important positive termite feedback to trait-driven decomposition patterns at a large scale.

## Materials and methods

### STUDY SITE AND LITTER COLLECTION

Fieldwork was conducted in Xishuangbanna Tropical Botanical Garden (XTBG), Menglun, Yunnan province, China (21°55′38.03″N, 101°15′54.87″E). The climate in this area is mainly influenced by the south-west monsoons with alternating dry and wet periods; annual mean precipitation is 1463 mm, 85% of which falls during the summer monsoon season (Li *et al.* 2012). The termites with predominance of *Odontotermes yunnanensis* and *Globitermes sulphureus* are major decomposers of the native forests in this area (Yamada *et al.* 2006; Liu *et al.* 2013). The bamboo garden in XTBG hosts over 200 bamboo species widely distributed in (sub) tropical regions of China. In addition, XTBG hosts a wide representation of the basal angiosperm phylogeny in the world (Liu *et al.* 2014) as well as a wide array of eudicot trees. In total, 66 species were used in the stem litter incubation experiment including 31 bamboos, eight herbaceous non-bamboo Poaceae species, 18 eudicot trees belong to the rosid clade and nine magnoliid trees. Depending on basal diameter, up to four stem diameter classes per species were sampled including 6 ± 1 mm (58 species), 30 ± 5 mm (37 species), 70 ± 10 mm (22 species) and 150 ± 20 mm (only *Dendrocalamus sinicus*), respectively (see Fig. S1 in the Supporting Information). We collected Poaceae species including bamboo and non-bamboo grass stems by cutting dead standing wood. For most of the magnoliid and rosid species, we collected samples by clipping with a shear or saw. Only for a few species, newly senesced fallen branches or stems were collected from the ground. Based on ample observations and previous experimental experience by some of the authors, we are confident that for all species we managed to collect freshly senesced, still undecomposed dead wood samples. We generally collected from two to three individuals or branches and cut them into 20-cm segments (to go into individual litterbags) according to the diameter classes above in April and May 2012. For each sample, a small adjacent stem segments was cut simultaneously for wood trait measurement and air-dry weight correction. All samples were air-dried in the laboratory at XTBG before they were sealed into litterbags.

### LITTER DECOMPOSITION EXPERIMENT

To compare species and samples for 'decomposability', we adopted the 'common garden' approach with simultaneous incubation of all stem litter samples, in litterbags, in an outdoor, semi-natural 'litter bed' *sensu* Cornelissen (1996). The sizes of the litterbags, with 3 × 3 mm mesh size (to allow mesofauna including termites to move in and out freely), were 30 × 6, 30 × 9, 30 × 9 and 50 × 25 cm to accommodate the four different stem diameter classes (see above), respectively. The 6 or 9 litterbags were filled for each species–diameter combination to obtain three replicates for each harvest (2 or 3). The mean ± standard deviation of filled air-dried weight in a litterbag was 3.22 ± 1.20, 76.66 ± 26.21, 290.66 ± 96.63 and 504.85 ± 31.81 g for the four diameter classes (see above), respectively. The incubation site in XTBG, with a size of 7 × 7 m, was divided into three blocks (2 × 7 m each) with 0.5 m distance between adjacent blocks. We placed two or three litterbags (one replicates each harvest) for a species–diameter combination in each block. The bare brick-red loamy soil, cleared of weeds, was covered with a thoroughly mixed litter matrix containing surface leaf litter (with predominance of *Camellia oleifera*, *Mangifera indica*, *Litchi chinensis*, *Hevea brasiliensis*, *Artocarpus heterophyllus* and mixed bamboo spp.) collected from several woody stands in XTBG. Then, the litterbags were laid on the first layer of mixed litter matrix and covered by the second layer of similar mixed litter matrix to prevent sun exposure and buffer against desiccation. The litter decomposition experiment lasted 1 year from 4 June 2012 to 4 June 2013. Litterbags were harvested three times, that is after 1, 3 and 12 litter incubation months. However, there were only first and final harvests for species with big and very big diameter classes (70 ± 10, 150 ± 20 mm) due to insufficient sampled segments. We cleaned decomposed stem litters carefully in the laboratory and removed mud and sand brought in by termites by cutting and brushing repeatedly. While doing this, we visually scored the intensity of damage to the stem segment inflicted by termites, distinguishing three classes based on the easy-to-recognize biting marks (see photos in Fig. S2): (0) no visible damage (and usually neither biting damage to the mesh nor mud brought in); (1) light biting damage to the stem segment; and (2) strong biting damage to the stem segment (usually coinciding with much import of mud and/or strong biting damage to the mesh). Litter samples were then oven-dried at 65 °C for 48 h to obtain their dry mass.

### STEM LITTER TRAIT MEASUREMENTS

Initial (i.e. undecomposed) stem litter samples were immersed into plastic water sinks for 8 days to be fully saturated and to ensure homogeneous filling of air spaces (Freschet *et al.* 2012). Initial litter volume was measured using Archimedes' principle of water displacement (details in Williamson & Wiemann 2010). The saturated samples were then gently blotted dry with filter paper and weighed to obtain saturated mass, subsequently oven-dried at 65 °C for 72 h to obtain dry mass. Saturated stem dry matter content (SDMC, g $g^{-1}$) was calculated as dry mass divided by saturated weight and initial wood density (g $cm^{-3}$) as litter dry mass divided by litter volume.

### DATA ANALYSIS

All the statistical analyses were conducted in R software v3.0.2 (R Core Team 2013). The $k$ value (g $g^{-1}$ $year^{-1}$) is the decomposition constant in the standard litter decay model $Y_t = Y_0\, e^{-kt}$ (Olson 1963), where $Y$ is the fraction of remaining litter mass for a species after incubation period $t$ (year). The $k$ values were obtained using the 'nls' function based on two or three harvest data with three replicate observed values each (i.e. one per block). To be able to assign a 'mean' value for termite damage to each $k$ value per species–diameter combination on a semi-continuous scale (see Figs 2 and 3), based on the 6–9 decomposed samples and three initial samples, we used linear rank regression model with independent and response variables being incubation duration and termite damage classes (0: no damage, 0.5:

light damage and 1: heavy damage), respectively, using the 'rfit' function in the RFIT package (Kloke & McKean 2012). Then, the slope parameter in the regression was used as a proxy for termite damage level during wood decomposition. Ordinary linear square (OLS) regressions were performed to test whether the significant relationships exist between initial wood density and *k* values or between SDMC and *k* values across species or across clades including magnoliids, monocots (bamboos) and rosids. For bamboo samples, the OLS regressions were also used to test whether significant relationships exist between wood density and wall thickness or between litter mass loss and wall thickness. Two-way ANOVAS were used to examine the main effects of clades and stem diameter classes and their interaction on *k* values, termite damage, wood density and SDMC. As there were no significant interactive effects for those traits, one-way ANOVA was then carried out to test the effects of clade or stem diameter class on *k* values, termite damage, wood density and SDMC, followed by multiple contrasts using Tukey's honestly significant difference (HSD) test. A linear mixed effects model with random effects was carried out to uncover the effects of sequential nesting factors including stem diameter classes, species, litter incubation times, termite damage classes on fraction of woody stem litter mass loss using likelihood ratio test. This procedure was conducted using the 'lmer' and 'VarCorr' functions in the LME4 package (Bates *et al.* 2014) and using the 'rand' function in the LMERTEST package (Kuznetsova, Brockhoff & Christensen 2014) to test the statistical significance of random effects in the model. The *k* values and termite damage were $\log_{10}$-transformed to satisfy the assumption of ANOVA.

## Results

The linear mixed model showed that termite damage, species, incubation time and stem diameter class each had significant influences on fraction of stem litter decomposition, explaining 53.4%, 17.1%, 9.6% and 5.4% of total variation, respectively (Table 1). Two-way ANOVAS showed that clade and stem diameter class significantly influenced *k* values in stem litter decomposition, termite damage, initial wood density and SDMC in an additive way (Table 2). There was no preference for termites towards a specific phylogenetic group (Table 2, Fig. 1b). The *k* value was lower in bamboos than in magnoliids and rosids (Fig. 1a), which corresponded to the pattern of initial wood density or SDMC (Fig. 1c,d). The termites also showed no significant preference towards any specific stem diameter class (Fig. 1f). The overall *k* value was lower in the big diameter class than in the small diameter class (6 ± 1 mm); there was no significant difference in *k* value between middle and big diameter classes due to a larger variation of the former (Fig. 1e). Although initial wood density and SDMC were greater in the middle diameter class than in the small diameter class, consistent with termite damage, there was no detectable difference in *k* value between small and middle stem classes due to the large variation of the latter (Fig. 1. right panel). The *k* value (both termite-mediated and microbial wood decomposition) decreased significantly both with initial wood density and with SDMC (Fig. 2), but initial wood density explained a much larger fraction of the variation in litter decomposition than SDMC ($R^2$ = 0.53 vs. 0.38). When only samples without termite damage were considered (presumably reflecting virtually only microbial decomposition), similar negative relationships of the *k* value with initial wood density and with SDMC, respectively, were observed (Fig. S3). However, the overall negative relationship between initial wood density or SDMC and decomposition rate was partly due to termite consumption (Figs 2, S4 and S5, Table 1). When the sampled species were categorized into magnoliids, bamboos and rosids, the negative relationships between initial wood density (Fig. 3) or SDMC (data not shown) and decomposition rate still existed. At a given initial wood density, bamboos had only slightly lower *k* values than dicots (Fig. 3). As for the overall relationship of wood density and *k*, within each clade, the termites had a strong preference for stem litter of lower density (Figs 2 and S4). With increasing bamboo culm wall thickness, wood density decreased while the fraction of litter mass loss increased (Fig. 4). This suggests that termites preferred a low wood density over thin culm wall.

**Table 1.** Effects of stem diameter class, species, harvest time and termite damage class on fraction of stem litter mass loss using likelihood ratio test on random effects in a linear mixed effects model, with sequential nesting factors. Species, harvest time and termite damage, respectively, are nested in the variable in the row above

| Variables | $\chi^2$ | d.f. | $P$ | Explained variance (%) |
|---|---|---|---|---|
| Diameter class | 5.28 | 1 | 0.022 | 5.4 |
| Species | 18.13 | 1 | <0.001 | 17.1 |
| Harvest time | 2.85 | 1 | 0.091 | 9.6 |
| Termite damage | 207.26 | 1 | <0.001 | 53.4 |

## Discussion

This is the first study to experimentally disentangle the relative effects of plant clades (bamboo vs. dicot), wood traits, termite activity and wood diameter on decomposition rates in tropical woody plants. We found that termite activity could explain half of the total variation in decomposition rate,

**Table 2.** Two-way anovas of *k* values in litter decomposition, termite damage, stem wood density and saturated stem dry matter content (SDMC) as related to clades (magnoliid basal angiosperms, monocots and eudicot rosids comprising 9, 39 and 18 species, respectively) and stem diameter classes (58, 37, 22 and one samples denotes branches, middle stems, big stem and very stem, respectively)

| | Clade (CL) | | Stem diameter class (SDC) | | CL*SDC | |
|---|---|---|---|---|---|---|
| | $F$ | $P$ | $F$ | $P$ | $F$ | $P$ |
| *k* values | **23.11** | **<0.001** | **10.28** | **<0.001** | 1.84 | 0.126 |
| Termite damage | 0.11 | 0.896 | **4.42** | **0.006** | 1.74 | 0.146 |
| Initial wood density | **5.88** | **0.004** | **8.07** | **<0.001** | 0.93 | 0.447 |
| SDMC | **3.64** | **0.030** | **4.38** | **0.006** | 0.25 | 0.910 |

Values in bold denote $P < 0.05$.

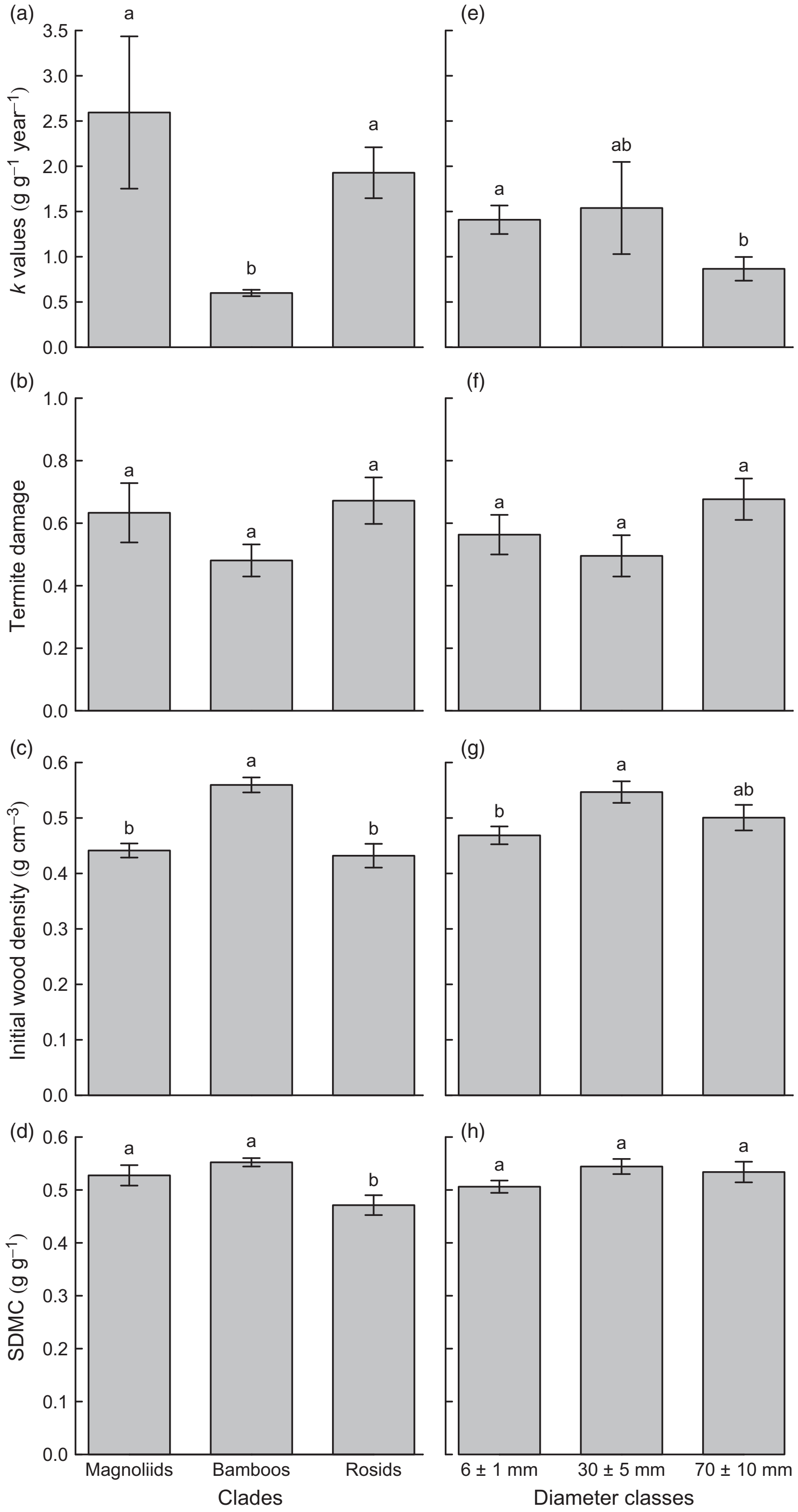

**Fig. 1.** Bar plots (means ± SE) of *k* values in litter decomposition, termite damage extent, wood density, and saturated stem dry matter content (SDMC) among clades (left panel), and among diameter classes (right panel). The termite damage mean was derived via the logistic regression procedure using the glm function with the binomial ('probit') family based on three classes (no damage, light damage and strong damage) per sample, where a value of 0 represents no damage. Same lowercase denotes no significant difference in response variables among clades or among stem diameter classes.

consistent with previous estimates for tropical forests (Cornwell *et al.* 2009) and the Southern Guinea Savanna of Nigeria (Collins 1981). Thus, termites drive a large carbon flux from dead wood to the atmosphere thereby regulating the global carbon cycle (Dixon *et al.* 1994; Pan *et al.* 2011), and they may be the main driver in the tropical forest, relegating the

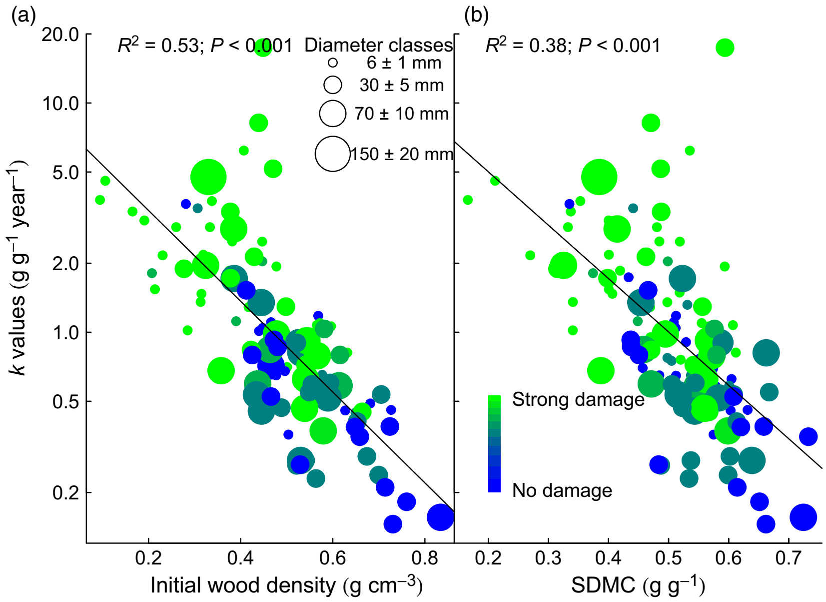

**Fig. 2.** Relationships between $k$ values representing stem litter decomposition and wood traits including initial wood density (a) and saturated stem litter dry matter content (SDMC) (b). The solid lines denote a significant relationship between wood density or SDMC and $k$ values at $P < 0.05$, and the colour gradient from blue to green colour for scatter points denotes termite-induced litter damage levels.

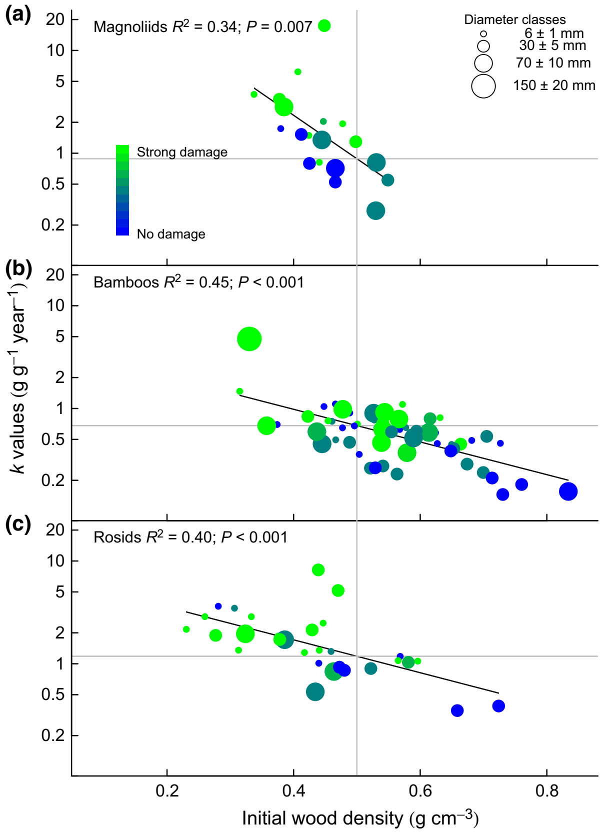

**Fig. 3.** Scatter plots between wood density and $k$ values in litter decomposition for each of magnoliids (a), bamboos (b) and rosids (c), in which the solid lines denote significant relationships between wood density and $k$ values at $P < 0.05$, and the colour gradient from blue to green colour for scatter points denotes termite-induced damage levels.

free-living micro-organisms. Although it has been suggested that termites preferentially consume wood decayed by fungi rather than undecomposed wood possibly because of an increase of its nutrient values (Waller *et al.* 1987), the interactions between termites and fungi on wood decomposition are more complex (Kirker, Wagner & Diehl 2012). This study reinforces the view that both arthropod-mediated and microbial decomposition have a significant influence on the carbon cycle of (sub) tropical terrestrial ecosystems (Powers *et al.* 2009; Bradford *et al.* 2014; Handa *et al.* 2014). What is new and important about our findings is that they quantify how the arthropod contribution to decomposition depends on variation in the same traits that have previously been linked to microbial decomposition *per se*.

Plant species traits predominantly determine microbial-driven litter decomposition rates (Cornwell *et al.* 2008; Weedon *et al.* 2009; Pietsch *et al.* 2014) via controlling litter substrate quality indicative of the species' different positions along leaf, wood or plant resource economic spectra (Wright *et al.* 2004; Chave *et al.* 2009; Freschet, Aerts & Cornelissen 2012; Reich 2014). As we expected, both microbial- and termite-mediated decomposition showed a negative correlation with initial wood density or dry matter content independently of specific phylogenetic group and independently of wood diameter considered (Figs 3 and S6). Interestingly, termites even preferentially consumed a thicker tissue layer of the outer wall of bamboo culms as they also had lower wood density. This positive termite feedback will amplify the negative relationship of species traits (i.e. wood density or SDMC) and microbial-driven decomposition rates found in either our findings (Fig. S3) or previous studies (Freschet *et al.* 2012; Pietsch *et al.* 2014). This viewpoint is consistent with a previous study by Smith & Bradford (2003), who found that larger

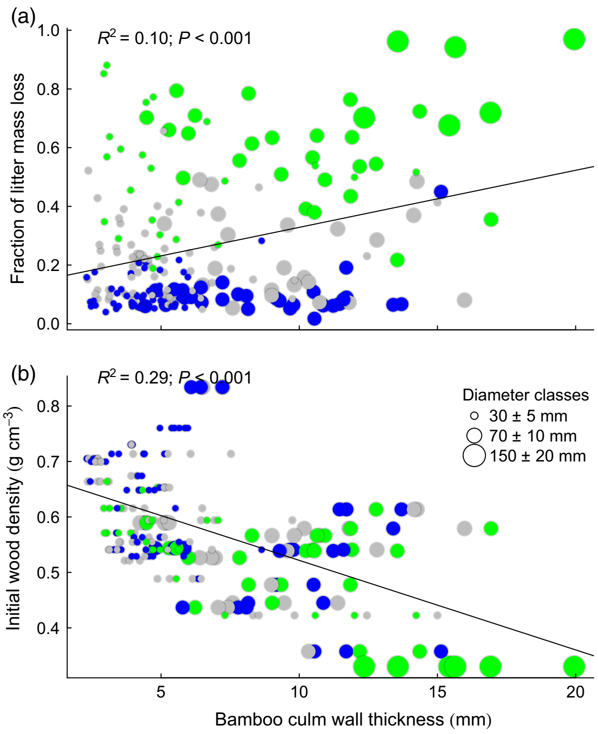

**Fig. 4.** Scatter plots between fraction of litter mass loss (a) or initial wood density (b) and culm wall thickness (with different diameter classes) across 26 bamboo species except for bamboo branch species. The solid lines denote significant relationships at $P < 0.05$. Points with blue, grey and green colours denote no termite damage, slight damage and strong damage, respectively.

bodied soil fauna could generate much more pronounced differences in the rate of decomposition of lower vs. higher quality litters than microflora alone. However, their (grassland) context and (non-trait-based) approach were different from those in our study. By way of caveat, although we used a strict ‘common garden’ incubation experiment, the termite component in our study was still essentially observational. To unambiguously quantify the potential extent to which termites might amplify the trait–decomposition relationship would probably require a rigid manipulative design. For instance, steel mesh of different mesh sizes could vary the accessibility of the litter to termites and might quantify the termite contribution to litter mass loss more directly as long as abiotic conditions remain rather similar. Also, even though the 3 × 3 mm mesh was meant to provide access to mesofauna including termites, frequently observed termite biting damage to the mesh may possibly have accelerated decomposition through further improvement of mesofauna or macrofauna accessibility to the litter during the period of interlitterbag harvests, even though the damaged litterbags used for longer incubation time were replaced with new ones upon first and second litterbags harvests (to reduce woody litter falling out). In addition, cutting the stems into 20 cm lengths for incubation may have caused a further possible experimental artefact by facilitating access to especially the inside of the hollow bamboo culms. However, without such an artefact, bamboo recalcitrance would be expected to come out even more strongly than in our study. Further study with stems of given diameter cut in different lengths could account for this and reveal how such accessibility effects might interact with those of wood density and culm wall thickness.

As an important functional trait of trees, wood density links to the morphological and physiological properties of plants (Chave *et al.* 2006; Swenson & Enquist 2007), with lower wood density generally being associated with faster growth (Poorter *et al.* 2010). Combining this with our findings, lower density wood is both produced at faster rate and decomposed at faster rate by microbes and termites alike when compared to higher density wood. In other words, trees with lower density wood accelerate the carbon cycle. This raises two important questions for in-depth research: (i) to what extent do production rates and decomposition rates as dependent on wood density match; and (ii) what is the quantitative contribution of termites to these major aspects of the forest carbon balance?

We found that dead wood of bamboos was (at given diameter) less decomposable than wood of basal angiosperm or eudicot trees, which supported our hypothesis. This is partly due to bamboos generally having higher wood density (more grams of dry matter per volume excluding internal hollows) and (given the much stronger relative reduction in $k$ than the relative increase in wood density compared to dicot clades) probably partly because of the more recalcitrant quality of a gram of dry matter (Song *et al.* 2013; Kumar & Chandrashekar 2014) or the denser arrangement of cellulose microfibrils (Suzuki & Itoh 2001). The structural strength and hardness of woody monocots are due, particularly, to numerous heavily lignified tracheids and fibres associated with the vascular bundles (Aloni 1987; Cornwell *et al.* 2009). These traits may be related to woody monocots such as bamboo or palm not having secondary growth owing to the lack of vascular cambium. Generally, plant stem architecture evolves towards either building stronger and harder structures in woody monocots (e.g. bamboos) or building thicker trunks by secondary growth in most woody basal angiosperms and eudicots. Thus, termites’ consumption and/or microbial decomposition of the denser wood of bamboo are reduced. This suggests that the current literature, which has strong bias towards dicot (especially eudicot) tree decomposition, overestimates the rate of wood turnover in (sub) tropical regions, especially in areas where bamboos are common such as tropical bamboo plantation, bamboo forest or bamboo savanna (Tripathi & Singh 1992; Tu *et al.* 2014). In addition, bamboos, mostly strongly rhizomatous clonal plants, are generally favoured by disturbance. This suggests that carbon cycles might slow down with increasing bamboo dominance in forests (Gagnon & Platt 2008) and gregarious flowering and death of woody bamboos could lead to slower carbon and nutrient fluxes and major ecosystem change in bamboo-dominated regions (Austin & Marchesini 2012).

Furthermore, we found that wood structure (density, dry matter content) predicts decomposition rates of bamboo and dicot trees in similar ways, even though the relationship was stronger in bamboos. Although bamboos are a peculiar growth form, phylogenetically affiliated to otherwise herbaceous grasses, their trait 'afterlife' effects on the carbon cycle are comparable to those of dicots. While, within dicot trees, lower decomposition rates were found in leaf litters of basal angiosperms due to higher leaf toughness as compared to eudicots (Cornwell *et al.* 2014; Liu *et al.* 2014), we did not detect a difference in wood decomposition between magnoliids and rosids, which also were very similar in wood density. However, the variation in decomposition rate of basal angiosperms was based on only nine magnoliid species constrains general conclusions about evolutionary implications. Future research on wood decomposition of major clades comparing basal angiosperms, eudicots and monocots other than bamboos (e.g. Araceae and Pandanaceae) should be considered at a finer taxonomic resolution and with more species.

In conclusion, our study fills the knowledge gap on the impact of bamboos, on the carbon cycle, both as abundant woody plants in warm climate zones and as important branch of the tree of life (Cornelissen & Cornwell 2014; Liu *et al.* 2014). The decay rate is lower in wood of bamboos than that in wood of dicots due to higher tissue density and probably also more recalcitrant wood chemistry. Functional traits (density, dry matter content) control the decay rate of bamboo wood as they do in dicot wood. Termites account for large contributions to the variance of wood decomposition, as they preferentially attack dead wood with lower density. This amplifies the negative relationship of plant species traits and microbial-driven litter decomposition. Our findings on the relative effects of plant traits, termites and diameter on decomposition of woody stems of bamboo and dicots advance our understanding of the driving mechanisms of (sub) tropical wood decomposition and its contribution to the global carbon cycle.

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## Data accessibility

Uploaded as online supporting information ('JEcol-2014-0832.data.xls').

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Fig. S1.** Phylogenetic position of species sampled and representation in each of four stem diameter classes including 6 ± 1 mm, 30 ± 5 mm, 70 ± 10 mm, and 150 ± 20 mm.

**Fig. S2.** The damage classes of termites on decomposed wood litter.

**Fig. S3.** The relationship between *k* values (based on only samples without termite damage, which stand for microbial driven wood decomposition) representing stem litter decomposition and wood traits including initial wood density (g cm$^{-3}$, a) and SDMC (saturated stem litter dry matter content, g g$^{-1}$) (b).

**Fig. S4.** The relationship between termite damage and wood density (a) or stem dry matter cotent (SDMC) (b).

**Fig. S5.** The relationships between *k* values in wood decomposition and termite damage for different diameter classes including 6 ± 1 mm (a), 30 ± 5 mm (b), and 70 ± 10 mm (c).

**Fig. S6.** The relationships between *k* values in wood decomposition and initial wood density for different diameter classes including 6 ± 1 mm (a), 30 ± 5 mm (b), and 70 ± 10 mm (c).

**Appendix S1.** The six supplementary figures on plant species sampled in this study, termite damages classes and the relationships between wood traits, damage level and *k* values in wood decompositon (detailed descripitions seen in Figs S1, S2, S3, S4, S5 and S6).