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RESEARCH ARTICLE

Dynamic feedbacks among tree functional traits, termite populations and deadwood turnover

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Abstract

1. Changes in the composition of plant functional traits may affect ecosystem processes through influencing trophic interactions. Bottom-up control by plant species through food availability to animals may vary with time. However, such dynamics and their consequences for deadwood turnover are poorly known for detrital food webs.
2. We introduce a dynamic conceptual model of the feedback of tree functional traits, (deadwood-feeding) termite populations and deadwood decomposition. We hypothesized that tree functional diversity (in terms of a wood resource economic spectrum [WES]) supports the sustenance of termite populations via complementary food supplied through time, as deadwood varies in traits both initially across species and because of different decomposition rates. Simultaneously, driven by this temporal dynamics of food quality, the consumption of deadwood by termites should hypothetically sustain deadwood turnover in a functionally diverse forest over time.
3. We tested our hypothesis through an 18-month termite-exclusion decomposition experiment by incubating coarse (i.e. 5 cm diameter) deadwood of 34 woody species in two subtropical forests in East China. One site still sustained a healthy population of pangolins as the keystone termite predator, whereas another had lost its pangolins due to hunting and illegal wildlife trade.
4. The results supported our hypothesis: in the first 12 months, termites amplified the positive linear relationship between % wood mass loss and initial wood quality (WES). In contrast, between 12 and 18 months, termite-mediated consumption, and associated wood mass loss, showed a humpback relation with the initial WES. This shift in termite preference of deadwood species along the WES reflects complementary food availability to termites through time.
5. *Synthesis*. Our findings imply that tree functional composition, with variation in deadwood quality through decomposition time, can help to sustain termite populations and thereby forest carbon turnover. Future studies need to test whether and how our conceptual model may apply to other detrital systems and food webs. In general, food web research would benefit from a stronger focus on temporal patterns for better understanding the interactions of basal resource functional traits and consumers on ecosystem functions.

KEYWORDS
bottom-up control, detritivore, food resource dynamics, functional trait, keystone consumer, population dynamics, resource economics spectrum, temporal pattern

1 | INTRODUCTION

Biodiversity is declining dramatically as a result of habitat alteration, unsustainable harvesting and climate change, which may affect ecosystem processes and functions (IPBES Report, 2019). Much research on terrestrial plant biodiversity has focused on how the loss or change of plant species or functional groups affects primary productivity, nutrient cycling and carbon fluxes (Handa et al., 2014; Hättenschwiler et al., 2005; Hooper & Vitousek, 1998), for example, through niche complementarity of plants or microbes. Within this biodiversity–ecosystem function debate, the emphasis has shifted from effects of taxonomic diversity or different coarse functional groups to effects of continuous variation in functional traits at the species level (Handa et al., 2014; Violle et al., 2007). However, this work has hardly addressed how variation in functional traits affects ecosystem functions and services via trophic interactions (but see Bascompte et al., 2003; Scherber et al., 2010). Those interactions are often hard to unravel, because, on the one hand, ‘top-down control’ by consumers or detritivores, and their predators, may affect nutrient flows from plant material in food webs (Srivastava et al., 2009); such trophic interactions might have a particularly strong impact on ecosystem functions if keystone consumers or predators are involved (Jones et al., 1997). On the other hand, the quality and availability of plant-based resources affect the population dynamics of consumers and their predators through ‘bottom-up control’ (Haddad et al., 2009; Scherber et al., 2010).

Variation in plant functional traits, via species' resource complementarity, may regulate the availability of basal food resources for consumers or detritivores, and consequently higher trophic levels (Thakur & Eisenhauer, 2015). However, in natural ecosystems, the resource supplied by plants might change over time, for example, as a consequence of interspecific variation in plant phenology in the consumer food web or changes in dead matter quantity and quality in the detritivore food web. Green (plant) food webs can be structured by environmental changes at different time-scales, for example, seasonal, inter-annual and decadal (McMeans et al., 2015; Voigt et al., 2003). However, no previous studies have addressed how temporal variance in food availability across plant species could lead to temporal resource complementarity to higher trophic levels in brown (detritivore) food webs. Such temporal variance in food availability could occur, for instance, in deadwood of tree species with different initial trait values that decompose at different rates. To our knowledge, no previous theoretical or empirical studies have addressed this hypothesis.

Here we test this theoretical concept in an intriguing system in warm-climate forests featuring the trophic feedback among interspecific variation in tree functional traits, the dynamic resource quality of the coarse deadwood derived from them, termites as their keystone consumers and deadwood decomposition (Figure 1). Termites are the primary invertebrate deadwood decomposer globally (Cornwell et al., 2009; Ulyshen, 2016; Wood & Sands, 1978), and have been found to contribute, for instance, about half to deadwood turnover in southern China (Liu et al., 2015). At the bottom end of the brown food web, deadwood quality, as determined by several wood traits, affects wood palatability to termites. Previous studies have shown that termites prefer to consume softer deadwood (Liu et al., 2015; Takamura, 2001). Therefore, the continuous availability of deadwood with trait composition favourable to termite consumption should help termite populations to thrive, thereby also supporting the populations of predatory vertebrates such as pangolins (Figure 1). Such availability may be affected by changes in deadwood quality of each given tree species through the decay trajectory, which may, in turn, affect the functional composition of deadwood in a forest through time. How the feedbacks in this brown food web between termites and deadwood traits affect wood decomposition rates across tree species and how these feedbacks change over time remains unknown.

Based on the theory above and our field observations in subtropical broad-leaved forests in China, our conceptual model (Figure 1) proposes that, after strong forest logging or typhoon impact, a set of functionally different woody species (ranging widely in initial wood quality) will provide a major food resource to the forest floor. Termites, being selective deadwood consumers, will first consume high-quality tree species, with low wood density, dry matter and lignin content, and high wood nutrient and cellulose content. Such a set of traits is associated with a resource-acquisitive growth strategy along a ‘wood economics spectrum’ (WES; Freschet et al., 2012; Pietsch et al., 2014; Zuo et al., 2018). Over time, after the high-quality wood has been mostly eaten (mainly by the termites), we predict that the initially medium-quality wood becomes more palatable owing to initial microbial activity and decomposition. Thus, the initially medium-quality wood (i.e. with intermediate WES values) should now be consumed preferentially by termites. This temporal pattern would imply that, in case of a broad range of initial wood qualities along the WES, that is, high functional diversity, there will be a stable provisioning of sufficient food resource for termites to maintain their population through time. In turn, the consumption of deadwood by termites should sustain deadwood turnover in a forest with high plant functional diversity (Figure 1) by the same temporal mechanism of changing wood quality over time. We put our conceptual framework to the experimental test by comparing deadwood traits and decomposition rates of 34 tree species, termite abundance and their contributions to decomposition rates in two subtropical evergreen broad-leaved forest sites in Eastern China: one with and one without Chinese pangolins *Manis pentadactyla*. This contrast was to check whether the relationships found between deadwood

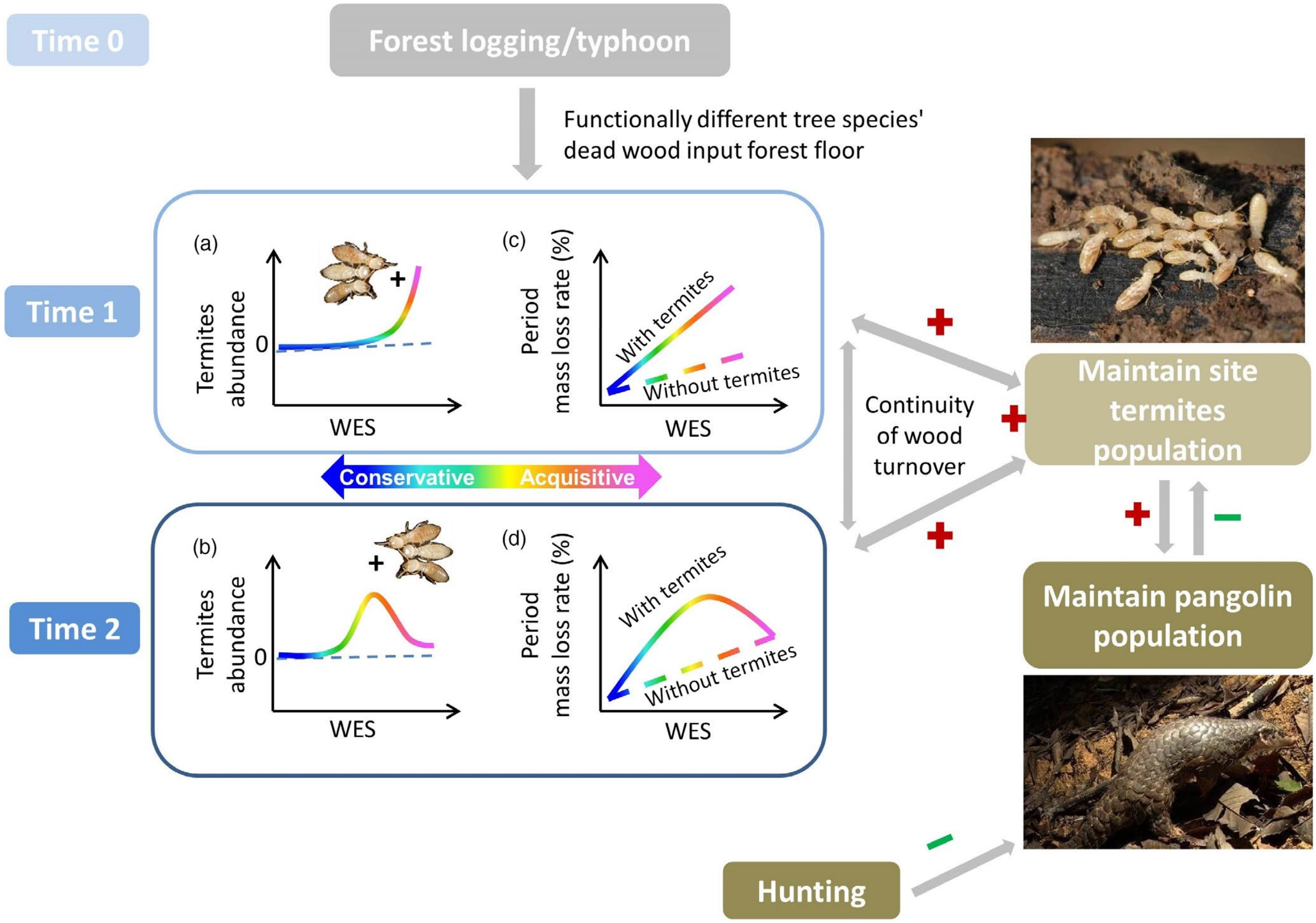

FIGURE 1 Conceptual model hypothesizing the feedbacks between tree functional traits, their palatability to termites and dead wood (carbon) turnover. Coarse wood litters of a wide range of functionally different tree species in terms of their position along the wood economics spectrum (WES) enter the forest floor as dead wood owing to logging or typhoon impact (Time 0). Until time 1, during the initial period of decay, the termites prefer tree species with high dead wood quality (i.e. high WES values), on which they reach high abundance and through consumption accelerate carbon turnover. After the high-quality wood has mostly been used up (Time 2), the initially medium-quality wood has decayed somewhat and become more palatable, resulting in higher termite abundance and consumption and relatively high decomposition rate. Thus, for a given amount of coarse deadwood on the forest floor, a wide range in tree functional traits should result in a temporally stable availability of dead wood of suitable quality to maintain termite populations. If so, such 'bottom-up' control could help termite-feeding pangolins, which, in turn, could exert 'top-down' control over termites, but these interactions are not an explicit focus of this study

quality, termites and decomposition would be robust to top-down control by this termite-specialized predator. In each of these two forest sites, we carried out an identical 18-month coarse deadwood decomposition experiment with 34 woody species, with and without termite exclusion.

2 | MATERIALS AND METHODS

2.1 | Study systems

We conducted this study in two sites in Zhejiang Province, East China: (a) Tiantong National Forest Park (TT) (29°52′N, 121°39′E), which has a subtropical monsoon climate. The dominant vegetation is subtropical evergreen broad-leaved forest. (b) Putuo island (PT) (29°97′N, 121°38′E), in the Zhoushan archipelago at 6.5 km from the mainland, has a marine subtropical monsoon climate. The island supports evergreen broad-leaved forests dominated by *Cyclobalanopsis glauca* and mixed evergreen–deciduous broad-leaved forests. On the mainland, Chinese pangolins *Manis pentadactyla* are critically endangered (IUCN, 2016) and no pangolin evidence was observed TT during the two study years. In contrast, in PT the Chinese pangolin population is thriving because of conservation efforts and the island isolation from the mainland. In both sites, termites (mainly *Coptotermes formosanus*, *Odontotermes formosanus*, *Reticulitermes chinensis*, *Reticulitermes speratus*) are the predominant macroinvertebrates (Figure S5) and the major invertebrate deadwood decomposers (Yi et al., 2006), as they are in many other warm-climate Asian forests (see e.g. Griffiths et al., 2019). All of these termite species belong to pangolins' preferred food (Wu et al., 1999, 2005). Table 1 has further data for abiotic and biotic features of both sites (see also Yan et al., 2006).

TABLE 1 Comparison of the biotic and soil characteristics of the two sites where the wood samples were incubated

Variables	Putuo (PT)	Tiantong (TT)
Forest type	Evergreen broad-leaved forest	Evergreen broad-leaved forest
Mean annual temperature	16°C	16.2°C
Mean annual precipitation	1,358 mm	1,375 mm
Dominant species	*Quercus glauca*	*Schima superba*
Range of the community wood economic spectrum (PC1)	−2.06 to 3.44	−2.94 to 2.53
Range of WES of deadwood samples added	−3.99 to 4.65	−3.99 to 4.65
CWM of wood economic spectrum (PC1)	−0.02 ± 0.03	−0.035 ± 0.04
Community-weighted variance of WES (PC1)	2.51	1.60
Annual production (t/ha) of leaf litter	19.34 ± 6.55 ns	19.51 ± 4.21 ns
Annual production (t/ha) of wood litter	4.83 ± 1.02 ns	0.66 ± 0.63 ns
Soil type	Sandy clay laterite	Red and yellow
Soil pH	4.78 ± 0.03 ns	4.09 ± 0.06
Soil available K (mg/kg)	14.76 ± 0.75 ns	16.65 ± 1.63
Soil available P (g/kg)	5.19 ± 0.53*	2.33 ± 0.19
Soil organic matter (g/kg)	6.70 ± 0.58**	20.43 ± 0.50
Soil N (g/kg)	1.06 ± 0.05*	3.44 ± 0.25
Termite density (ind/m^2) in August 2018	153.23 ± 20.92*	67.18 ± 11.86
Termite density (ind/m^2) in August 2019	395.22 ± 38.95**	184.20 ± 23.21
Pangolin burrow density (ha^{-1}) in wood sample incubation plots in November 2019	133 ± 30***	0
Pangolin burrow density (ha^{-1}) in control plots in November 2019	33 ± 8***	0

Note: Asterisk indicated there was significant difference between TT and PT.

Abbreviation: ns, no significant difference.

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

2.2 | Tree species sampling and wood decomposition experiment

From October to November 2017, we selected 32 important and representative woody species in TT and PT, and 2 island endemic woody species in PT (*Pittosporum tobira*, *Eurya emarginata*). The species set included 7 evergreen trees and 11 evergreen shrubs, 7 deciduous trees and 4 deciduous shrubs, 4 conifer trees and 1 monocot tree (bamboo; full species names see Table S1). Here 'shrubs' included both short stature, single-stem understorey trees and multi-stemmed shrubs from exposed habitats. In total, 147 individual healthy adult trees/shrubs were selected, that is, 19 species × 3 individuals for trees and 15 species × 6 individuals for shrubs. The larger number of shrub individuals, with their shorter stature, were needed to obtain sufficient 5 cm diameter segments for three replications (see below). We chain-sawed those trees/shrubs and collected wood samples as 20-cm long stem sections of 5 ± 0.5 cm diameter so as to control for size effects on decomposition. Adjacent to each end, a 2-cm thick disk was sawn out for analyses of initial wood traits. Here we used the healthy living trees standardizing the initial, undegraded phase for all samples, thereby avoiding complications of prior pathogen attack having altered wood quality and providing a direct link to the functional traits of living trees (Cornelissen et al., 2012). Moreover, in the forests studied typhoon-induced wind-throw as well as logging is very common, so a large fraction of the trees is still alive when downed. We therefore consider these wood samples as representative of deadwood going into the decomposition process.

We used 25 cm × 15 cm litter bags differing in mesh size to assess the termite contribution to litter decomposition: (a) termite exclusion treatment, enclosed stainless steel litter bags with 0.05-mm mesh and (b) termite access treatment, nylon litter bags with 4-mm mesh. In a survey during the experimental period, we found that the strongly dominant group of macro-invertebrates was Isoptera-termites in both sites (Figure S5). Hymenoptera had intermediate abundance in the PT site, and the remaining fauna taxa, for example, Coleoptera, Araneae, Isopoda, Geophilomorpha, Lumbricida, Lepidoptera larva and Coleoptera, contributed less than 5% to macro-invertebrate abundance. Therefore, based on our observations, very few macroinvertebrates other than termites entered the 4-mm mesh bags. Acarina, Collembola and Diptera larva were the dominant meso-invertebrates in the two sites, while Tubificida, Corrodentia, Hemiptera larva, Pseudoscorpionida, Thysanoptera and Symphyla contributed <5% (Figure S5). Although our mesh did possibly not exclude all of the smaller mesofauna, we expect their contribution to wood decomposition to be negligible, also because these taxa mostly do not feed on the wood itself but on substrates such as frass and fungi. Each fresh wood sample was weighed immediately after cutting (see below for measurement of water content), and sealed into a litter bag. In total, 1,224 litter-bag samples were produced, that is, 34 tree species × 2 treatments × 3 replications (plots) × 2 incubation sites × 3 harvest times.

In December 2017, we established three 20 m × 30 m replicate plots in PT and TT, respectively. Plots within each site had broadly similar slope, altitude, soil type, litter substrate and forest structure and composition and plots within a site were 10 m apart to minimize interference between them. We started litter-bag incubation in December 2017, when termite activity and wood consumption were low because of low temperatures. The litter bags of each species were pinned onto the forest floor in their respective subplots within each of the three replicate plots randomly, and each species' replicate had three litter bags per treatment in each subplot, that is, one for each harvest. The distances between subplots were approximately 2 m. Litter bags were harvested after 6 months (July 2018), 12 months (December 2018) and 18 months (July 2019).

After collection of the experimental deadwood samples from the plots, we transported them to the laboratory where we carefully removed extraneous materials and soil from the deadwood remains within a few days. Each wood sample was put in a large tray with tall enough edges for the termites not to crawl out. We cut the sample into small pieces and cleaned mud and sand (brought in by termites) with a brush carefully. We then collected the termites from the tray and counted them. All pieces of the wood sample were then oven-dried at 75°C to constant mass and weighed (dry mass).

2.3 | Wood trait measurements

For measurement of initial wood traits considered relevant to the WES and to decomposition, each 2-cm subsample was stored in a sealed plastic bag immediately after collection in the field, and kept cool until processing. Within 12 hr, after the bark had been removed, a subsample was cut from each disk to obtain fresh mass initial volume using Archimedes' principle of water displacement (Williamson & Wiemann, 2010).

All wood subsamples were dried at 75°C for 72 hr to determine dry mass. Initial wood density (g/cm^3) was calculated as dry mass per volume. Initial water content, that is, (fresh mass − dry mass)/fresh mass, was used to calculate the initial dry mass of the litterbag samples. Initial wood subsamples were ground in a laboratory mill and passed through a 0.15-mm sieve. Thereafter, 0.2 g of subsamples was digested using concentrated H_2SO_4 to determine N and P concentrations on an infrared spectrophotometer (Smartchem 200, Alliance, France). Lignin content was determined by acidolysis-titration method, and cellulose content was determined by anthrone–sulphuric acid colorimetry (Poorter & Villar, 1997). Bark traits and their possible influence on decomposition (cf. Kahl et al., 2017) or their promotion of termite consumption (cf. Ulyshen et al., 2016) were measured in a companion study but were not a focus in this study.

2.4 | Termite and pangolin abundance measurements

To quantify the termite abundance in situ, we sampled the termites in the experimental plots of PT and TT in July 2018 and July 2019 through the adopting and adjusting transects method (Jones & Eggleton, 2000). Since the area of our plots was 30 m × 20 m, we took our entire plot as belt transect, in which we surveyed ten 30 m × 2 m sections along a diagonal. In each section, we counted the number of termites with an area meter (with 10 cm × 10 cm grid), based on counts of 1 cm × 1 cm grid cells across the diagonal. We scaled these data up to the plot and also examined all deadwood and leaf litter for termites to obtain total termite abundance of each plot. See above for termite counts in the harvested deadwood samples.

We determined the density of pangolins in PT by counting their mounds in each incubation plot, simultaneously, in three nearby plots of the same area but without wood samples.

2.5 | Calculation of wood mass loss rate

Wood litter mass loss rate % was calculated according to Equation 1:

$$\text{(Period) Mass loss } \% = \left[\left(M_\mathrm{i} - M_\mathrm{f}\right)/M_\mathrm{i}\right] \times 100\%, \tag{1}$$

where M_i and M_f are initial and final wood dry mass; when calculating the period-specific mass loss (i.e. mass loss over an interval between two adjacent harvests), M_i is the final wood dry mass of the previous stage and M_f is the final wood dry mass for this period.

2.6 | Statistical analysis

All statistical analyses were performed in *R* language version 3.5.1. To quantify the main axes of wood trait variation across species, a principal component analysis (PCA) was performed (R package 'VEGAN', 'rda' function). The first axis (PC1), accounting for 55.9% of variance in litter quality, was strongly related to the contents of wood nutrients (nitrogen and phosphorus), cellulose and lignin, and wood density. We used the PC1 scores for the respective tree species to represent their position along the WES positions in the subsequent analyses. The second axis (PC2) was related to wood water content, accounting for 17.1% of variance (Figure S1).

We also used PCA to quantify the community-level tree functional trait variability for forest plots in TT and PT. The PC1 of PT and TT accounted for 50.3% and 40.9% of trait variance, respectively, and were strongly related to leaf resource economic traits (specific leaf area, nitrogen, phosphorus and mean leaf area) and wood density. We used the community abundance-weighted mean (CWM) of WES, specific leaf area and wood density to compare differences of community functional identity between PT and TT sites using Student's *t* tests. To derive CWM of WES and the community-weighted trait variance of WES in each site, we multiplied the PC1 scores of each species with its relative abundance for a given community.

To test the effect of different factors on wood mass loss, we first constructed linear mixed effects models to examine the effects of termite treatment (access or exclusion), WES, and harvest time on both period and cumulative wood mass loss for each site. For period wood mass loss, we constructed a model including termite treatment (access or exclusion), WES, harvest time and their interactions as fixed factors, and the incubation plot as a random factor, while the linear mixed effect model was constructed with Equation 2. For cumulative wood mass loss, the model was similar to that of the period wood mass loss model, but we removed harvest time as a factor and its related interaction factors; see Equation 3.

$$y_{\text{period}} \sim T + W + H + (T \times W) + (T \times H) + (T \times W \times H) + (1 \mid \text{plot}) + \varepsilon, \tag{2}$$

$$y_{\text{cumulative}} \sim T + W + (T \times W) + (1 \mid \text{plot}) + \varepsilon, \tag{3}$$

where y_{period} and $y_{\text{cumulative}}$ are period and cumulative wood mass loss for each site, respectively; T, W and H are termite treatment, WES and harvest time, respectively, for the period-specific and cumulative wood mass loss in a specific site. The error term is defined by ε.

The R package 'LME4' was applied for linear mixed effect model construction. Prior to analysis, the wood mass loss data were logit-transformed (Griffiths et al., 2019; Warton & Hui, 2011). The performance of the models was assessed based on the marginal and conditional R squares, which indicate the variance explained by the fixed effects (R^2_m; marginal) and the whole model (R^2_c; conditional), respectively. The explanatory power of each independent variable for period and cumulative wood mass loss was calculated with variance decomposition in the model as suggested by Nakagawa and Schielzeth (2013). In this calculation, the variance proportion of the specific fixed variable was the ratio of the variance of that variable to the total variance (i.e. R^2_c) of the response variable (i.e. the wood mass loss of the period and cumulative).

Second, linear regression and/or nonlinear regression were used to test the relationships between (cumulative) mass loss % (for termite access and exclusion treatments) and the WES scores separately for the different incubation periods. Also, linear and nonlinear regressions were used to test the relationship between (period-specific or cumulative) mass loss % and termite abundance (in the deadwood samples) at each harvest time. Again, linear and nonlinear regressions were used to test the relationship between termite abundance (in the deadwood samples) and WES scores at each harvest time in each of the two sites.

In the first two regression analyses, we used the R package 'GGPLOT2' for data visualization, and in the stat smooth function of the ggplot2, we selected the linear model for each of the period 6–12 months in both sites, period 12–18 months in the TT site, and cumulative mass loss at 18 months in both sites. Comparably, we used the binomial model for the period 12–18 months in the PT site. We used the Student's t test to test the differences in cumulative mass loss % of termite access and exclusion treatment, termite abundance and the contribution of termites to wood mass loss between the sites. For the relationship between termite abundance (in the deadwood samples) and WES, the *glm* (generalized linear mixed models) method was selected, with binomial (for 6 months) and Gaussian (for 12 and 18 months). For mass loss data, we used Levene's test to examine the homogeneity of variance and Shapiro–Wilk test for normality.

3 | RESULTS

3.1 | Overall termite impact on wood decomposition

Comparisons of the termite exclusion and access treatments strongly support the view that termites play an important role in coarse wood mass loss (Figure 2), not only in tropical (see Section 1) but also in subtropical forests. Specifically, after 18 months of incubation of the wood samples, the termite access treatment resulted in an average cumulative mass loss of 26.6% (range: 1.5%–84.6%) at PT and 21.1% (range: 1.18%–68.8%) at TT across species. In contrast, mass loss without termite consumption was on average 14.7% (range: 1.1%–60.7%) at PT and 12.7% (range: 1.0%–45.7%) at TT (Figure S2a,b). The difference between termite exclusion and access treatments was generally high during the first 12 months and then decreased at 18 months in both sites (Figure 2, Figure S2a,b).

The linear mixed effect model showed that WES, termite treatment, harvest time and their interaction significantly affected period and cumulative mass loss in both sites (Table 2). In PT, the joint explanatory power of WES, termite treatment, harvest time and their interaction for period and cumulative mass loss was 42% and 43% (i.e. R^2_m), respectively. Termite treatment, WES and their interaction explained 8%, 2% and 20% of the total variance (i.e. R^2_c) in period mass loss, respectively. Harvest time alone had no significant effect on period mass loss, but with WES and termite treatment jointly explained 11% of the total variance (i.e. R^2_c) of period mass loss. Termite treatment, WES and their interaction explained 13%, 10% and 11% of the total variance (i.e. R^2_c) of cumulative mass loss, respectively.

In TT, the joint explanatory power of WES, termite treatment, harvest time and their interactions for period and cumulative mass loss was 46% and 37% (i.e. R^2_m), respectively (Table 2). Termite treatment, WES and harvest time explained 2%, 20% and 3% of the total variance (i.e. R^2_c) of period mass loss, respectively. The interaction between WES and harvest time explained 16% of the total variance (i.e. R^2_c) of period mass loss. Termite treatment, WES and their interaction explained 5%, 25% and 2% of the total variance (i.e. R^2_c) of cumulative mass loss, respectively (Table 2).

3.2 | Relationships between wood quality, termite activity and decomposition over time

Multiple traits, notably wood N, P, cellulose and lignin content and wood density, together explained 55.9% of all variance explained by PC1, interpreted here as the WES (see Methods and Figure S1). Wood litter of more resource-acquisitive strategy species (i.e. high WES values), generally decomposed faster than that of conservative strategy species; in the treatment without termite access (Figure S1, Figure 2), there were significant positive linear relationships between WES score and mass loss in the periods 0–6 and 12–18 months (but non-significant ones at 6–12 months), and cumulatively over 18 months, in both sites.

Our termite access treatment revealed that termites not only significantly accelerated wood mass loss rate overall but also there was a clear time pattern within this acceleration (Figure 3), as hypothesized (Figure 1). In the first year (periods 0–6, 6–12 months), decomposition rates scaled positively and linearly with WES in both sites (Figure 2a–d), indicating that termites preferentially consumed

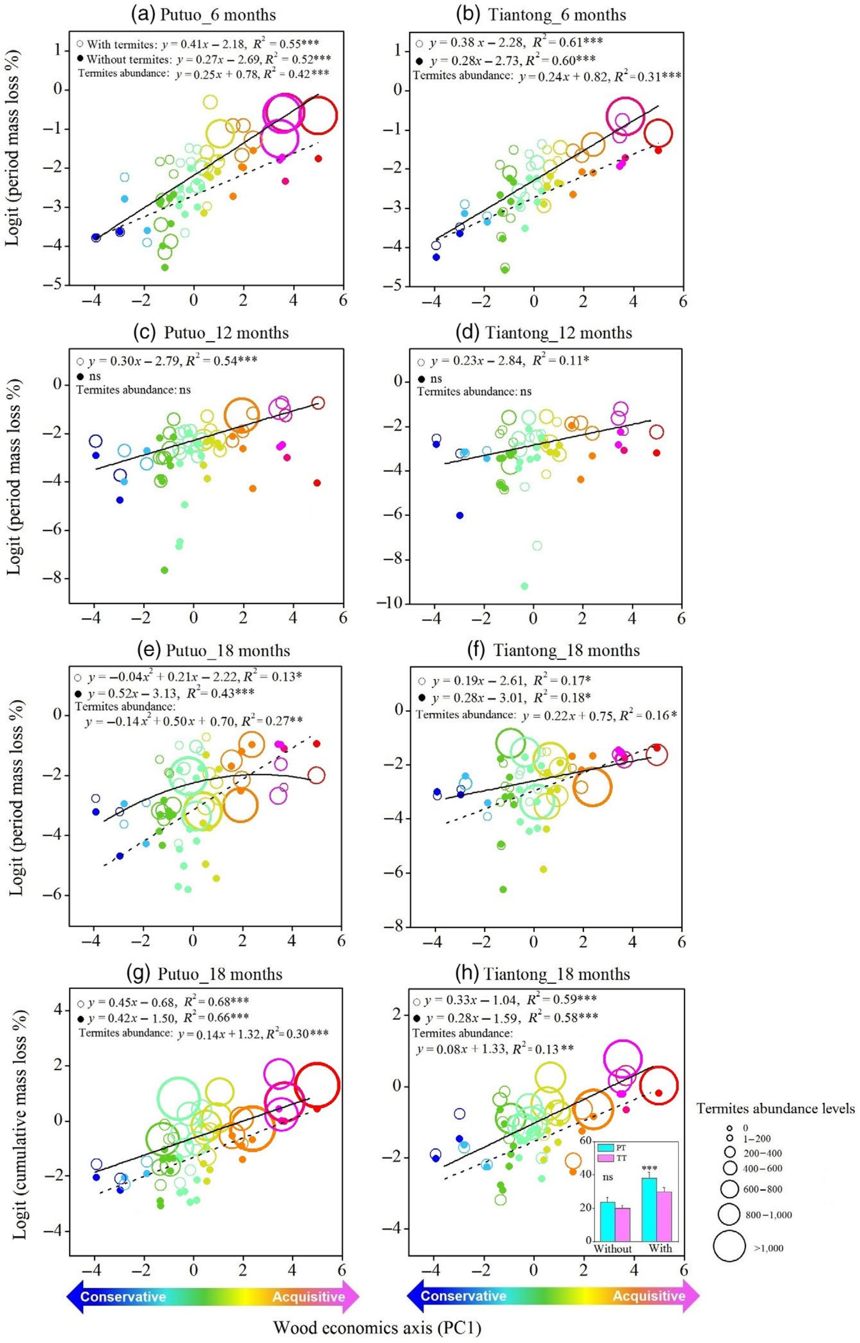

FIGURE 2 Relationships between the wood economics spectrum (PC1 values) and (logit-transformed) wood mass loss % with termite access (open circles, solid line) and without termite access (filled circles, dotted line) in site of Putuo and Tiantong at each harvest time (period mass loss) and cumulatively over the entire 18 months. The size (diameter) of the circles denotes termite abundance (in the deadwood samples), and the colour gradient from blue to red for the circles denotes the conservative end to the acquisitive end of the WES. Regression equations are also given for the relationships between termite abundance and mass loss in the dead wood samples across species. The comparison of overall final cumulative mass loss between Putuo and Tiantong with and without termite access is shown in the inserted bar diagrams. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; ns, not significant. In panels g and h, the diameters of the circles representing termite abundance values are based on the sum of the termite abundances in the three harvests

the species of resource-acquisitive strategy (high nutrient content, less lignin and less dense structure). Thereby, the termites' consumption amplified the initial WES effect on decomposability, that is, it increased its positive linear regression slope.

In contrast, partly owing to termite activity, the wood of the acquisitive species had been considerably depleted after 12 months. In the subsequent period of 12–18 months, the initially medium-quality species were consumed more by the termites, which modulated the tree species' decomposition trajectory on the WES. Now, in contrast to the positive linear relation in the treatment without termite access, there was a humpback relationship between WES and period mass loss in the treatment with termite access, at least in the more termite-rich PT site (Figure 2e, Table 1). Termite abundance showed a corresponding humpback pattern with mass loss (equation in Figure 2e). In the less termite-rich site, TT, such a humpback relation was not apparent, but here the positive relationship between WES and mass loss was less steep in the latter (Figure 2d,f) than in the initial period (Figure 2b). This pattern also suggests negative termite feedback on the positive relation between WES and mass loss. These changing patterns of WES over period-specific mass loss were confirmed by a significant interaction among WES, harvest time and termite presence/absence on period mass loss in PT and TT, respectively (Table 2). Together, as hypothesized (Figure 1), these deviating relationships over time caused overall convergence of cumulative

TABLE 2 Results of the linear mixed-effects models for period-specific wood mass loss and cumulative wood mass loss. The plots within each site were treated as a random factor

	Factors	Estimate	*SE*	*df*	*t* value	*P*	$R^2_{\text{fixed effect}}$
PT site							
Period wood mass loss							
$R^2_m = 0.419$	Termite treatment	8.26	2.54	562	3.26	<0.001	0.08
$R^2_c = 0.420$	WES	3.07	1.91	562	2.17	<0.001	0.02
	Harvest time	0.03	0.14	562	0.20	>0.05	0.00
	Termite treatment × WES	4.53	1.25	562	3.61	<0.001	0.20
	Termite treatment × Harvest time	0.23	0.20	562	1.20	>0.05	0.01
	WES × Harvest time	0.03	0.07	562	0.41	>0.05	0.00
	Termite treatment × WES × Harvest time	0.26	0.10	562	2.67	<0.01	0.11
Cumulative wood mass loss							
$R^2_m = 0.426$	Termite treatment	12.24	1.17	596	10.44	<0.001	0.13
$R^2_c = 0.427$	WES	2.69	0.41	596	6.51	<0.001	0.10
	Termite treatment × WES	3.87	0.57	596	6.75	<0.001	0.11
TT site							
Period wood mass loss							
$R^2_m = 0.459$	Termite treatment	3.70	1.87	574	1.98	<0.05	0.02
$R^2_c = 0.460$	WES	3.35	0.67	574	5.91	<0.001	0.20
	Harvest time	0.47	0.09	574	5.23	<0.001	0.03
	Termite treatment × WES	0.99	0.91	574	1.08	>0.05	0.00
	Termite treatment × Harvest time	0.07	0.15	574	0.50	>0.05	0.00
	WES × Harvest time	0.22	0.04	574	4.92	<0.001	0.16
	Termite treatment × WES × Harvest time	3.67	1.07	574	2.09	<0.05	0.05
Cumulative wood mass loss							
$R^2_m = 0.372$	Termite treatment	6.52	0.79	594	8.27	<0.001	0.05
$R^2_c = 0.373$	WES	3.30	0.23	594	14.06	<0.001	0.25
	Termite treatment × WES	1.44	0.39	592	3.73	<0.001	0.02

Notes: R^2_m, marginal; R^2_c, conditional. The explanation power of the plot was calculated by $R^2_{\text{random effect}}$ ($=R^2_c - R^2_m$). $R^2_{\text{fixed effect}}$ is the explanation power of each fixed factor in R^2_c, and R^2_m is the total explanation power of the fixed effect for period wood mass loss and cumulative wood mass loss, respectively.

mass loss along the WES between the termite treatments in both sites (Figure 2g,h), as indicated by a lack of interaction of WES × termite access treatment on cumulative mass loss over 18 months (Table 2).

Termite abundance patterns in the wood samples were consistent with the above changing patterns of period-specific wood mass loss (Figure 3) and the termite contribution to decomposition (Figure S3) along the WES through time. At 6 months, there was a significant, exponential increase from the conservative end to the acquisitive end of the WES in both the sites (Figure 3a,b). At 12 months, the termite abundance peak occurred at slightly higher than medium initial wood quality (Figure 3c,d). By 18 months in PT, the termite abundance peak had moved further towards the conservative end of the WES (Figure 3e), that is, to the centre of the range, matching the humpback for mass loss (Figure 2e). In TT, both the height and the width of the peak (i.e. the range) increased at 12–18 months (Figure 3f). On the whole, the peaks of termite abundance and the termite contribution to mass loss shifted from high to medium initial wood quality during the decomposition process, broadly matching that of mass loss itself.

4 | DISCUSSION

To our knowledge, this is the first study to experimentally unravel the dynamics of feedbacks among interspecific variation in plant functional traits, animal populations and the turnover of dead plant matter. Our conceptual model and findings have added a new dimension to the ‘afterlife effects’ of plant functional traits by pinpointing the effects of variation in deadwood quality among tree species through a ‘brown’ food chain, with important consequences for both forest carbon turnover and animal populations.

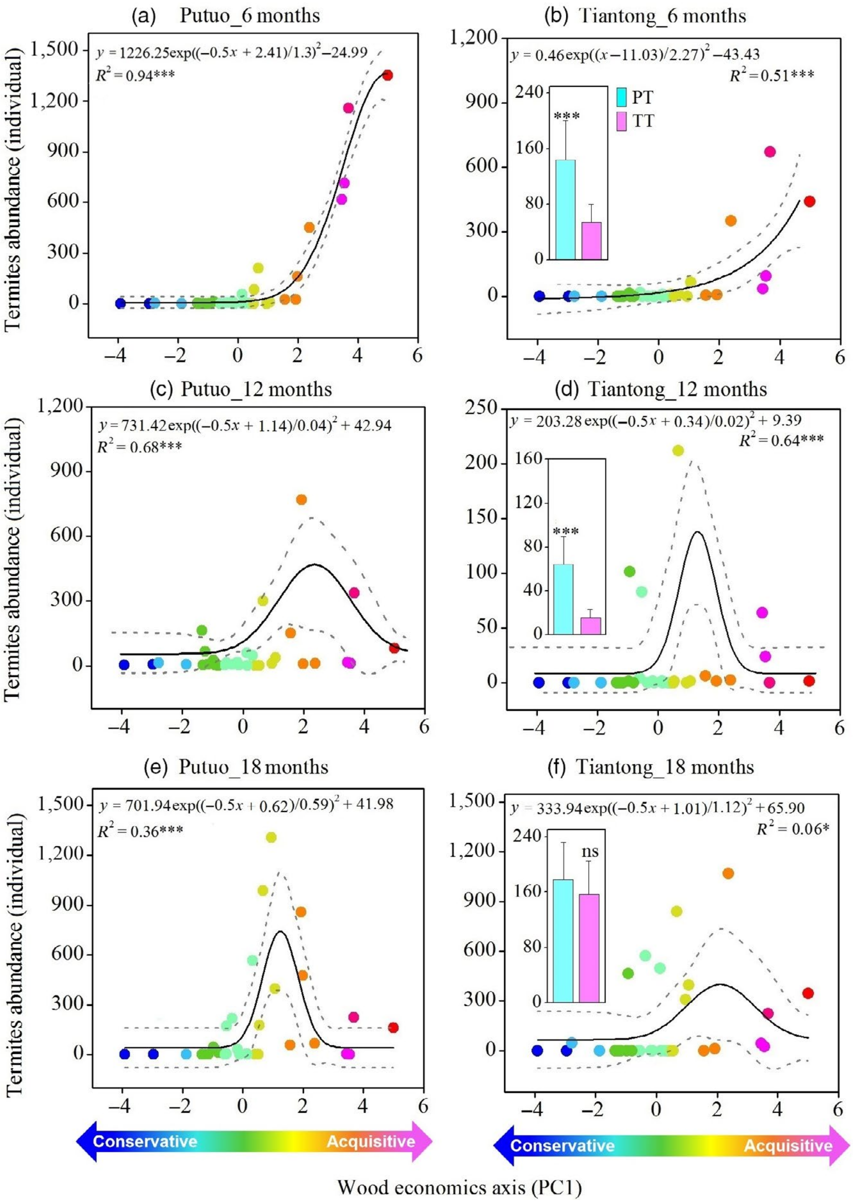

FIGURE 3 Relationships between the WES values (PC1) and termite abundance in the two respective sites across harvest times. The best-fit regression lines with confidence intervals (between dotted lines) are given where significant. The colour gradient from blue to red colour for the circles denotes the conservative end to the acquisitive end of the WES. The comparison of overall termite abundance between Putuo and Tiantong with and without termite access is shown in the inserted bar diagrams. *$p < 0.05$; ***$p < 0.001$; ns, not significant

While, without the involvement of invertebrate decomposers, wood decomposition rates were predicted by initial values along the wood economics spectrum (WES); when termites participated in the decomposition process, they actively altered the species' ranking in terms of the WES through time and moved in abundance and activity from initially high WES species to initially medium WES species. These findings have an interesting parallel with a recent study that found a modulating effect of invertebrate consumption on leaf mass loss rankings along an axis of initial litter quality, that is, the leaf economics spectrum, over time (Guo et al., 2019). However, in that study, the modulation was due to a single outbreak by detritivorous moth larvae, while in this study the decomposing invertebrates (i.e. termites) were present in considerable abundance through time in the studied forests, but changed their relative abundance and contribution to decomposition among tree species as decomposition progressed. Below, we discuss our findings on the dynamic feedbacks among interspecific variation in plant functional traits, termite populations and deadwood turnover in forest ecosystems. We also discuss next research steps to examine the role of plant trait variation for regulating trophic interactions and the turnover of dead plant matter.

4.1 | 'Afterlife effects' of plant functional traits on deadwood turnover and animal populations through time

We found that in the without-termites treatment, deadwood mass loss could be predicted by the WES, which means that without major involvement of invertebrate decomposers, microbial decomposition rates increased from the resource conservative side to the acquisitive side of wood functional trait composition. Previous studies generally found that microbial decomposition per se was related to single chemical traits, such as (positively) to high cellulose content or high N content (Maillard et al., 2019; Zak et al., 2011) or (negatively) to lignin content (Austin & Ballare, 2010), but could also be captured by a suite of biochemical traits belonging to the plant (resource) economic spectrum (Freschet et al., 2012; Zuo et al., 2018). However, in our study, the period mass loss rates at 12 months in both sites had non-significant correlations with WES (Figure 2c,d). The most likely explanation for this is that after a first rapid decomposition stage (via leaching or microbial decomposition) of high-quality deadwood, the nutrients and labile carbohydrates of high-quality deadwood had been reduced while low-quality deadwood was still more recalcitrant, thereby reducing the overall range of wood qualities. In addition, in winter the low temperature leads to the weakening of microbial activity (e.g. fungi), which likely contributed to the lack of an obvious tendency of mass loss rate for woody species on the WES during the period of 6–12 months.

Consistent with our hypothesis, we found that tree functional traits belonging to a wood resource economic spectrum supported the sustenance of termite populations via complementary food supplied through time, as deadwood varied in traits both initially between species and because of different mass loss rates. Although we did not capture variation in deadwood traits throughout the decomposition period, the differences in structural and chemical traits of fresh deadwood we analysed should also have similar consequences on palatability to termites across deadwood species (Zuo et al., 2020). As Oberle et al. (2019) demonstrated, relative to soft wood, denser wood lost mass slowly at first but quickly with advancing decay, thus indicating the significant temporal effects of key traits (e.g. wood density and vessel diameter) on deadwood decay rates across functional diverse species. In addition, the initial wood chemical composition of different species should have consequences for the deadwood turnover through time as experienced by termites. Indeed, species located at the acquisitive side on the WES in our study, that is, with high initial wood nutrient and cellulose contents, were preferentially consumed by termites in the first half year and possibly some months after that. However, once the acquisitive side species had been depleted after 1 year of decomposition, initially medium-quality species that were positioned in the middle of the WES had become more palatable. This could explain why the consumption by termites reached its maximum for initially medium quality. Therefore, the WES maintained the termite population through the temporal complementarity of food resources. In turn, the contribution of termite consumption on deadwood carbon turnover showed a strong time pattern. To be specific, the termites amplified the WES decomposability for acquisitive species (with high initial quality), increasing the slope of wood mass loss on WES with 1 year of decomposition while there was a humpback relationship between termite abundance and WES at 18 months in PT (the site richest in termites). This means that termite consumption accelerated the mass loss of medium-quality (i.e. mid-WES) species and altered the species' decomposability trajectory on the WES.

Interestingly, the temporal variation trajectory of termite abundance (or deadwood carbon turnover) on the WES was closely related to wood quality variation in decomposition. For example, the increase in nutrient content may at least partly be attributed to deadwood becoming increasingly infiltrated and degraded by fungi (Stokland et al., 2012); these fungi import nutrients from the surroundings as the decomposition process goes on (authors' unpublished data). Moreover, there is an evidence that termites preferentially consume wood decayed by fungi rather than undecomposed wood possibly again because of an increase in nutrient content (Waller et al., 1987). Based on preliminary evidence that termites prefer to consume softer and lower density dead wood (Liu et al., 2015; Takamura, 2001), it should be expected that species higher in lignin (like the species with intermediate WES values in our study) should become more palatable to termites during lignin degradation over time, especially with nutrient content increasing concurrently. In contrast to the trajectory for the PT site, there was a positive linear relationship between wood mass loss and WES at 18 months in TT, and a weaker time pattern of variation along the WES. What is worth discussing here is that the termites' abundance in a site also strongly affects the relationship of woody species' decomposition rates along the WES. If termite activity is less intense in an incubation site, more time may be needed to change the shape of the trajectory of species' decomposition rates along the WES.

Although differing in some details, the above patterns were broadly robust to ecological and floristic dissimilarities between the two geographically distant forest sites (Table 1, Table S1, Figures S4 and S5). Specifically, one (PT) had a stronger disturbance regime, a less content of soil organic matter, a slightly more resource-acquisitive tree species composition (CWM and range of WES values), and a dense termite population and a top-down control by a dense population of pangolins. In contrast, another site (TT) had less frequent and severe typhoon disturbance, more soil organic matter, slightly more resource conservative tree species composition, less dense termite population and no pangolins.

4.2 | Implications for the role of WES in modulating dynamic feedbacks between termite population and deadwood decomposition

Our main findings, revealing the dynamic relationships of initial deadwood quality of different woody species with termite abundances and their contribution to decomposition, have potential implications for the role of forest tree functional traits in regulating both forest carbon turnover and animal populations (Figure 1, right side). Our findings are consistent with our prediction that, all else being equal in terms of abiotic conditions and regional animal species pool available, functionally more diverse warm-climate forests, that is, with wide-ranging initial deadwood qualities, are more likely to provide stable food supply to termites and thus allowing larger termite populations to establish. This should be the case especially in forests with occasional major disturbances such as in the typhoon-prone forests of both sites in our study, as such disturbance events simultaneously bring down a large fraction of the trees of different initial wood qualities depending on forest composition. This could potentially have knock-on effect on populations of top predators such as termite-feeding pangolins

(Figure 1). Our study was not designed to test the latter predictions explicitly, but our findings merit new studies to do so, as they could advance our understanding of the ecological needs of both deadwood detritivores and thereby the conservation of their predators. To add more real-world complexity, such studies might also involve ants. Some ants are also known to have termites as a staple food (Buczkowski & Bennett, 2007), but whether or how they compete for termites with vertebrate termite feeders such as pangolins, or are themselves eaten and thereby controlled top-down by these vertebrates, and thereby indirectly affect wood decomposition, are intriguing questions for further investigation.

It is noted that, we only recorded termite abundances on the experimentally added deadwood of different species but did not identify termite species composition during their decay (only dominant species overall, see Methods). Future studies should pay much effort to investigate how termite species composition associates with deadwood decomposition rates across species in terms of the WES through time. By so doing, our conceptual model would benefit from the mechanistic interactions of basal resource functional traits and consumers on ecosystem functions. Another issue for future research is to extend our approach and experiment, based on coarse deadwood of the relatively small diameter class, that is, 5 cm as a standard to compare across species, to logs of larger diameter classes. Such logs should generally have a higher proportion of (more recalcitrant) heartwood relatively to sapwood and also thicker bark, both of which could affect the species ranking of palatability to termites as compared to that for the 5 cm diameter class.

Moreover, new experiments and field observations are needed to test and enrich our conceptual model about dynamic feedbacks between plant functional trait variation, animal populations and decomposition with further empirical evidence, beyond the specific food chain studied here. Terrestrial decomposition is integrated in multiple food chains in the food web. Thus, to better understand the generality of the positive deadwood turnover feedback studied here, we need to identify the interactions between other wood (or leaf, root) decomposing invertebrates or predators of other detritivores and plant functional trait composition. Although termites are the dominant species in warm-climate wood decomposition, other invertebrates such as beetles tend to control the animal contribution to decomposition in temperate ecosystems; either directly through feeding or by facilitating other decomposers such as fungi or similar-sized animals to invade the deadwood by tunnelling, feeding, nesting or intended microbe cultivation (Ulyshen, 2016; Zuo et al., 2014). In our experiment, we found a wide variety of deadwood beetles and millipedes; although their abundance is far less than that of termites, how (much) they affect wood decomposition, directly or by affecting other decomposers such as fungi and termites, needs in-depth study. Importantly, we need to study how these different decomposers, through time (e.g. decay stages, seasons), interact with each other and with the trait variation of their basal resource via their decomposing function. Multiple harvests and tracking animal population dynamics (Schwarzmüller et al., 2015) in such experiments can provide further insights into time effects of decomposers, and their suppression by predators, as influenced by resource availability.

To conclude, we have shown clear positive and dynamic feedbacks between interspecific variation in tree functional traits, termite populations and deadwood turnover. Our findings also suggest that high wood functional diversity may help to provision sufficient food resource in terms of deadwood quantity and quality for termites to maintain their population through time, with possible implications for the sustenance of pangolin populations. In-depth research is needed to extend our findings to the consequences of forest composition in terms of function traits for animal populations and their direct or indirect contributions to carbon turnover.

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AUTHORS' CONTRIBUTIONS

E.-R.Y., J.H.C.C. and C.G. designed and conceptualized the experiment; C.G., B.T. and H.C. collected the data; C.G. analysed the data and wrote the manuscript; J.H.C.C. and E.-R.Y. revised and improved the manuscript. All authors contributed substantially to revisions.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.wpzgmsbm6 (Guo et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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