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RESEARCH ARTICLE

The wood economics spectrum modulates the positive effects of termite foraging intensity on deadwood invertebrate diversity

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Abstract

1. How populations of ecosystem engineers are both driven by and drive biodiversity is poorly known, even less so in detrital subsystems. Deadwood plays a key role in maintaining biodiversity and ecosystem functions. The wood economics spectrum (WES), which represents the initial wood quality through a suite of wood traits and adheres to economic trade-offs, might affect termite populations and deadwood invertebrate community structure via afterlife effects. Termites, as ecosystem engineers, exert a significant impact on other invertebrate diversity. However, how the WES modulates the effects of termite foraging intensity on deadwood invertebrates is unclear.
2. We hypothesized that the WES had significant effects on termite foraging intensity and deadwood invertebrate abundance and richness. Moreover, the WES was hypothesized to modulate the effects of termite foraging intensity on deadwood invertebrate diversity.
3. We conducted a wood decomposition experiment to test our hypotheses in two subtropical forests of China. Logs of 22 tree species with distinct functional traits were incubated for 30 months to assess termites' foraging intensity (relative termite feeding area and the mass of soil materials imported by termites) and the associated deadwood invertebrate abundance and richness.
4. We found that, from the resource conservative (low wood quality) to the acquisitive (high wood quality) end of the WES, termite foraging intensity increased. As termite foraging activity intensified, the deadwood invertebrate abundance and richness increased correspondingly. Moreover, there were significant positive relationships between termite foraging intensity and the abundance of dominant detritivore groups (Acari, Collembola and Opisthopora). In contrast, the position along the WES had no direct effect on the abundance and richness of deadwood invertebrates besides via termite foraging intensity.

5. *Synthesis*. Our findings showed the pathway of how the WES affects deadwood invertebrate diversity. They supported the hypothesis that the WES plays a crucial role in shaping the effects of termites as ecosystem engineers on the broader invertebrate community. Future studies should focus more broadly on whether and how plant traits, via afterlife effects on ecosystem engineers, influence invertebrate community composition and structure. Such studies will promote our understanding of the importance of both plant traits and ecosystem engineer traits for ecosystem carbon and nutrient cycling and biodiversity.

KEYWORDS
coarse woody debris, decomposition, ecosystem engineers, functional traits, invertebrate abundance, taxonomic richness, termite foraging activity

1 | INTRODUCTION

The decline of biodiversity is a matter of great concern due to its long-term impacts on ecosystem functioning, such as plant production, nutrient cycling and energy flow (Handa et al., 2014; Hooper et al., 2012). Ecosystem engineers are known to be important contributors to biodiversity through physically modifying, maintaining or creating habitats and resources for other organisms (Ashton et al., 2019; Jones et al., 1994; Jouquet et al., 2016; Oberst et al., 2019; Veldhuis et al., 2017). At the same time, populations and activities of ecosystem engineers themselves can be driven by biodiversity; for instance, via plant functional diversity in terms of traits that determine food quality (Yeakel et al., 2020). How the causes and consequences of ecosystem engineer abundances and activities are jointly related to biodiversity is poorly known in general and hardly known at all in detrital subsystems.

The decomposition of dead organic matter is a critical process in the recycling of carbon and nutrients within terrestrial ecosystems (Berg & McClaugherty, 2020; Harmon et al., 1986). It serves as the primary input of nutrients for both plant and detritivore communities, thereby sustaining a rich biodiversity (Andringa et al., 2019; Fujii et al., 2023; Stokland et al., 2012; Ulyshen, 2016). The resource availability and habitat heterogeneity provided by a wide variety of deadwood are principal catalysts driving invertebrate biodiversity (Andringa et al., 2019; Fujii et al., 2020; Seibold et al., 2016; Tuo et al., 2024). Studying the relationship between deadwood and its dwelling fauna is key to providing theoretical information to guide biodiversity conservation and restoration (Seibold et al., 2023; Stokland et al., 2012). Coarse deadwood from diverse tree species significantly enhances habitat variability and nutrient acquisition, thereby serving as a crucial factor influencing the diversity and structure of detritivore communities (Fujii et al., 2023; Parajuli & Markwith, 2023; Tuo et al., 2024). Recent evidence has shown that, in general, compared to species diversity, functional identity and functional trait diversity of dead plant matter have a greater influence on the abundance and species diversity of soil organisms (De Deyn et al., 2004; Viketoft et al., 2009), especially for leaf litter (Sanchez-Galindo et al., 2021). Particularly noteworthy is the strong interspecific variation in deadwood quality based on a suite of wood resource economy traits, on the abundance and activity of deadwood-dwelling invertebrates (Zuo, Berg, et al., 2016). This suite of wood resource economy traits encapsulates major adaptive strategies and reflects trade-offs among physiological, mechanical and hydraulic functions of plant species, thus collectively referred to as the 'wood economics spectrum' (WES) (Chave et al., 2009). The WES has a significant long-term impact on deadwood decomposition rates and associated biodiversity (Stokland et al., 2012), especially termites (Guo et al., 2021; Liu et al., 2015; Tuo et al., 2021).

Termites are key examples of ecosystem engineers, which are organisms that exert significant effects on ecosystem functioning and biodiversity (Griffiths et al., 2019; Zanne et al., 2022). In tropical and subtropical forests, termites are the most effective wood consumers among all invertebrates (Liu et al., 2015; Ulyshen, 2016; Zanne et al., 2022), estimated to be responsible for about half of the deadwood turnover (Griffiths et al., 2019; Liu et al., 2015). Termites consume wood, creating extensive galleries and tunnels, which increase the size and heterogeneity of deadwood habitats, thereby enhancing other invertebrate communities (Neupane et al., 2015). Furthermore, termites are major bioturbators, which create various biogenic structures (galleries, sheeting, nests, mounds, fungus-comb chambers) to alter the physical and chemical properties of soils (Jouquet et al., 2011; Oberst et al., 2019). Consequently, termites may exert substantial impacts on the dynamics of biodiversity through their activities. However, to our knowledge, no previous empirical studies have been conducted to test the impact of termites on invertebrate diversity during deadwood decomposition.

Termite foraging activity can create cavities in the wood, leading to a reduction in wood volume, thereby providing access for other animals (Neupane et al., 2015). As observed in studies by other ecosystem engineers, beetles facilitate habitat and resource availability for other arthropods. For instance, long-horn beetles and other beetles create holes in wood (Novais et al., 2021; Tuo et al., 2024; Ulyshen & Wagner, 2013) or bark beetles (Scolytinae) puncture holes in the bark and engrave inner bark and outer wood with their galleries (Zuo, Cornelissen, et al., 2016), which can enhance heterogeneity in habitat, microclimate and resource availability to wide-ranging arthropods. It is noteworthy that certain termite species, such as the dominant species *Odontotermes formosanus* (Isoptera: Termitidae) in our subtropical study region in SE China, exhibit a behaviour of importing soil into wood (Bagine, 1984) to increase environmental humidity, while others use a range of materials to construct sheeting and nests (Chen et al., 1998), thereby enhancing habitat quality and biodiversity. Through these activities, termites import substantial amounts of inorganic and organic particles, primarily consisting of clay-rich soil, deadwood debris, and termite faeces, which modify the habitat and support various forest floor invertebrates (Chen et al., 1998; Ulyshen & Wagner, 2013). As mentioned above, deadwood identity may affect termite activity (Guo et al., 2021; Liu et al., 2015), which in turn affects biodiversity during decomposition. However, the mechanisms by which the WES drives deadwood invertebrate diversity via the modulating effects of termite foraging intensity remain unclear.

Based on our field observation and literature research, we propose the following pathways as alternative hypotheses (Figure 1): (i) the WES regulates termite foraging intensity, which in turn affects the diversity of other deadwood-inhabiting invertebrates during deadwood decomposition. (ii) The WES may also directly affect the abundance and diversity of other deadwood-dwelling invertebrates without the interference of termites (Seibold et al., 2023; Zuo, Berg,

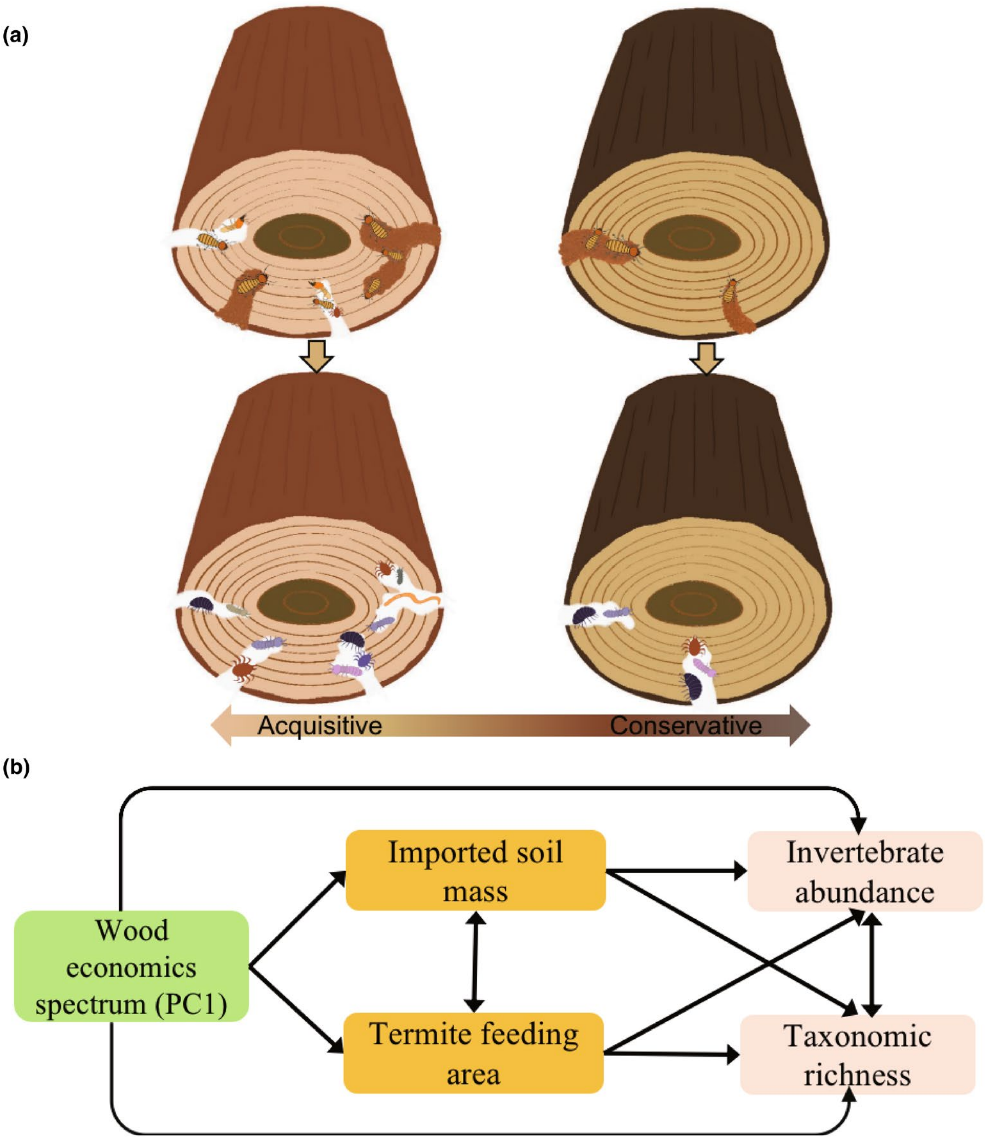

FIGURE 1 Conceptual framework elucidating the influence of the wood economics spectrum on termite foraging activity and deadwood invertebrate community. (a) Termite activity has the ability to alter deadwood structure and traits by creating tunnels and carrying soil materials into deadwood (top cartoons), thereby facilitating the presence and diversity of other deadwood invertebrates (bottom cartoons). Variations in colours (ranging from yellow to brown) indicate different functional qualities of deadwood. The numerical representation of termite cartoons corresponds to the intensity of termite foraging activity on specific qualities of deadwood. (b) A priori conceptual structural equation modelling (SEM) depicting that the wood economics spectrum may affect deadwood invertebrate abundance and richness both directly and indirectly via termite foraging intensity.

et al., 2016). We put our conceptual framework to the experimental test by comparing wood traits, termite foraging intensity parameters, and invertebrate diversity in deadwood of the same 22 tree species in two subtropical evergreen broad-leaved forest sites in Eastern China. In each of these two forest sites, we carried out an identical, simultaneous 30-month in situ incubation experiment of coarse deadwood. Since the experimental exclusion of termites cannot be done without also excluding other invertebrates from the wood, we employed an alternative approach to disentangle the direct and termite-mediated effects of the WES on the abundance and diversity of other deadwood-dwelling invertebrates. This approach involved a methodological framework that combined bivariate relationship analysis and structural equation modelling (SEM, Figure 1). Specifically, we analysed bivariate relationships between tree species' WES positions and termite activity variables, as well as between termite activity indicators and broader invertebrate abundance and richness, to test the direct effects of the WES on termite activity and the subsequent impact of termite activity on broader invertebrate communities. Additionally, SEM was used to examine whether the WES modulates the positive effects of termite foraging intensity on other invertebrate communities.

2 | METHODS

2.1 | Study area

We selected two sites for our wood decomposition experiment in the subtropical evergreen broad-leaved forests located in Zhejiang province, eastern China: (1) Putuo island (PT, 29°97′ N, 121°38′ E) and (2) Tiantong National Park (TT, 29°52′ N, 121°39′ E). The climate of both sites belongs to the subtropical monsoon. Site PT is located in the Zhoushan archipelago. The mean annual temperature is 16.9°C and the precipitation averages 1358 mm. The soil type is sandy clay laterite with pH ranging from 4.7 to 4.8. Site TT, located in Ningbo city, experiences a mean annual temperature of 16°C and an average annual precipitation of 1375 mm. Soils are mainly red and yellow earths with pH ranging from 4.4 to 5.1. Evergreen broad-leaved trees (*Cyclobalanopsis glauca* (Thunb.) Oerst. or *Schima superba* Gardn. et Champ.) predominate in both incubation sites. Termites are the dominant macrodetritivores as they are the pioneer invertebrates in the process of decomposition. The dominant termite species are *Odontotermes formosanus* Shiraki 1909 and *Reticulitermes periflaviceps* Ping & Xu, 1993, which are the predominant wood consumers and soil importers in our ecosystem (Guo et al., 2024; Tuo et al., 2021). Termites, as ecosystem engineers, along with their foraging activity, carry a large amount of soil material and other new resources into wood and create habitat in the form of a wide variety of different sizes of pores and tunnels (Figure 1a; Figure S1). All fieldwork was conducted with the authorization of the Zhejiang Zhoushan Island Ecosystem Observation and Research Station and the Zhejiang Tiantong Forest Ecosystem National Observation and Research Station.

2.2 | Tree species sampling and wood decomposition experiment

22 common tree species in the study sites were sampled (with three overlapping species extracted from and incubated in both sites) for our decomposition experiment. The species set included eight evergreen trees (one overlapping species), 11 deciduous trees (one overlapping species) and three conifer trees (one overlapping species) (full species lists see Table S1). For each species, we selected four healthy trees, of which the trunk was approximately 20 ± 3 cm in diameter and with the height at least 15 m. From each individual tree, we chain-sawed eight logs, each 70 cm long without major side branches from the main trunk. Additionally, we sawed out a 5 cm thick disk adjacent to each end of a given log to measure initial wood trait analyses.

In November 2017, we established three replicate plots with similar slope, altitude, soil type and forest structure in each site to incubate our 600 logs ((22 species + three overlapping species) × three plots × two sites × four harvests). The size of each plot was about 20 m × 30 m. Each plot was divided into several 3 m × 4 m subplots to host each species separately. We left 20 m wide strips between the three plots as buffer zones to minimize any possible interference between plots. Every species had four replicate logs for four harvests within each of its respective subplots. The wood decomposition experiment was started in winter because low temperatures were expected to suppress termite activity and wood consumption.

2.3 | Log harvest and invertebrate sampling, identification and counting

In July 2019, half of each 70 cm length log had been harvested and the remaining 35 cm log had been carefully laid back in its original position in the field. We did the second harvest after 30 months in July 2020. One hundred and forty-seven logs ((22 species+ three overlapping species) × three plots × two sites (minus three logs of *Alniphyllum fortunei* (Hemsl.) Makino decomposed completely in the PT site)) of 35 cm length were quickly and carefully placed into plastic zip-lock bags in the field and taken into the laboratory at Tiantong and Putuo Ecological Station, respectively, where the samples were stored at 15°C until subsequent processing. First, we put the wood sample in a deep plastic tray and collected visible larger, active invertebrates by hand to prevent their escape before processing. Then, we sawed the log into two halves and sawed off a 2.5 cm thick disk from each end of each half log. This way, we collected two disks from the middle and end positions. We used one middle disk and one end disk to measure termite foraging intensity, and the other half was used for measuring mass loss and wood traits (not included in this study). The remaining logs (25 cm long) were used to analyse the composition and diversity of the other wood-inhabiting invertebrate community. It is worth noting that we did not measure the intensity of termite activity after 18 months of decomposition (July 2019) because unclear signs of termite activity were found; thus, it was not included in the analysis.

We collected both macro- and mesoinvertebrates from the logs. To collect the macroinvertebrates (body width >2 mm) in logs, first we placed the residual wood sample in a deep plastic tray and separated the bark from the wood using chisels or manually. After the bark had been peeled off and fragmented into small pieces, we extracted the invertebrates living in the bark. The wood remaining after peeling off the bark was split into small pieces by an axe, after which we collected the macroinvertebrates by hand. The soft xylem with holes from termite consumption was carefully cut away with chisels until all soft wood was removed to make sure that all invertebrates were collected and then transferred into the 30 mL sealed plastic bottles with 70% ethanol for subsequent identification and counting. If the wood under the bark was intact and did not show any signs of xylophagy, we did not break it for invertebrate searching. The fragmented and soft xylem that we cut away was collected to extract the mesoinvertebrates by using a modified Tullgren funnel at 35°C for 24 h and collected in 50 mL sealed plastic bottles with 70% ethanol solution. All the samples were processed within 20 days after collection from the field, that is when the invertebrates were generally still alive inside the logs. No formal ethical approval was required for this study, as it focused on insects, which are not subject to ethical approval regulations in China.

Then an electron optical type microscope (DVM6, Leica Germany) at a magnification of 35–500× was used for mesoinvertebrate identification and counting. All extracted Acari were grouped into Mesostigmata, Oribatida and Prostigmata (also including any Astigmata) following Yin (1992). All Collembola and adults of other dominant groups were identified to family level following Yin (1992, 2000). Juveniles and some rare taxa were only identified to the order level due to the difficulty of identification. Taxonomic richness was quantified as the number of all other taxa (including ants) present per log. Abundance was calculated as the total number of invertebrate individuals per log, excluding ants due to their high spatial aggregation as social insects (Vincent et al., 2018), but a separate analysis of termite-ant relationships was conducted because ants are the most abundant omnivores and are important for ecosystem functions.

2.4 | Initial wood traits measurement

After we cut all trees into logs, we took the adjacent wood disks to the lab for analyses of initial wood traits. We measured the wood density (WD), nutrient concentration (N, P concentration), wood dry mass content (WDMC), cellulose and lignin content. These traits are considered to be important resource economic and structural traits and may significantly affect the feeding preferences of deadwood invertebrates (Guo et al., 2021; Ulyshen, 2016).

For measurement of initial wood traits (without bark) considered relevant to the WES and to deadwood invertebrate preference, each 5 cm disk was stored in a zip-lock plastic bag immediately after collection in the field and kept cool until processing. Within 12 h, after the bark had been removed, a subsample was cut from each disk to obtain fresh mass and initial volume using Archimedes' principle of water displacement. Then wood subsamples that had been measured for fresh mass and volume were dried at 75°C for 72 h to determine dry mass. Initial wood density ($g·cm^{-3}$) was calculated as dry mass per (fresh) volume. Initial wood dry matter content was calculated as dry mass/fresh mass. Initial dry subsamples were ground in a laboratory mill and passed through a 0.15 mm sieve. Thereafter, 0.2 g subsamples were digested using concentrated H_2SO_4 to determine N and P concentrations ($mg·g^{-1}$) on an infrared spectrophotometer (Smartchem 200, Alliance, France). Cellulose content was determined by anthrone-sulfuric acid colorimetry (Kumar & Turner, 2015). Briefly, 0.3 g milled wood samples (same samples as for N, P concentration) were washed with 80% ethanol, then precipitated to obtain coarse cell wall material. Starch was removed, and the resulting cell wall material was dried. Subsequently, 5 mg of cell wall material was hydrolyzed with sulfuric acid, and the supernatant was collected by centrifugation. The hydrolysate was mixed with a special anthrone reagent, heated in a water bath for 10 min and then cooled. Cellulose content was measured spectrophotometrically. For lignin measurement, the ground samples were put through an acid detergent solution (20 g cetyl trimethyl ammonium bromide and 1 L sulfuric acid with a concentration of 49.04 g/L). Following this treatment, the samples were washed with 72% sulfuric acid to extract acid detergent lignin and acid-insoluble ash. Finally, the samples were combusted in a muffle furnace, and the lignin content was determined by calculating the difference in weight before and after ashing (Gessner, 2005).

2.5 | Measurement of termite feeding area and imported soil mass

After the harvested disks had been cleaned thoroughly and dried, we first measured the thickness of the disk (for the subsequent calculation of disk volume); then digital images of the top and bottom surfaces of each disk were taken. The image resolution was enhanced (e.g. backgrounds made whiter and brighter, Figure S2a) and areas of the remaining wood surface after termite consumption were delineated (e.g. coloured white, Figure S2b) using Adobe Photoshop CC19.0. Thereafter, Image J 1.53c was used to measure the surface area of intact wood. During this process, each wood sample had two disks and was measured four times. The average of the percentage of termite feeding area and intact wood area of the four measurements was used as termite feeding extent due to the relatively short length of the wood samples. The damage could still be discerned rather clearly in the 30-month samples, but soon after that, it became too difficult to estimate the damage accurately.

We conducted experimental burns to measure the termite imported soil mass as an additional proxy of termite foraging intensity. The measured soil mass cannot represent the activity of all termites, but represents the activity of *Odontotermes* and partly *Reticulitermes* (the dominant species in the study area). According to Ulyshen and Wagner (2013), completely burning the wood away to leave only the mineral soil behind as ash is a more accurate method than washing to isolate soil from decomposed wood and collect the soil for quantifying the termite foraging intensity. The fire experiment was performed in the Fire Laboratory located at Hangzhou Normal University, Zhejiang province. From September 2020 to January 2021, we conducted a complete combustion of all the wood disks of all 22 species. All burns were conducted under a fume hood on a solid fire-resistant plate. Before the fire experiment started, the fume hood was turned on and ventilated at a constant speed. Prior to each burn, the laboratory door was closed, and the fume hood was turned on, and the experiment started when the room temperature was 21 ± 4°C. For each burn, we placed the wood disk on a stainless-steel plate and then put the plate on an electronic heating plate. We set the temperature of the electronic heating plate at 300°C. After about 30 min of preheating, we ignited the wood with a butane gas torch. After ignition, we let the wood burn and smoulder naturally until completely burnt. For wood with low flammability that cannot completely burn by itself after ignition, we used a butane gas torch to burn the remaining mass completely.

Based on our observations, only minimal amounts of soil appeared to be evaporated as evidenced by smoke during the burning process. The tree species in our experiment were dicotyledons and conifers, which are known to contain less than 0.1% silicon in wood (Cooke & Leishman, 2011). So, we considered that minerals from the wood itself were a negligible fraction of the ash content and that virtually all the ash represented soil particles imported by termites. As the diameter of the deadwood varied, the absolute soil mass could not be compared meaningfully between different deadwood samples, so we used the soil mass per unit volume (soil mass per volume, $g{\cdot}cm^{-3}$) of deadwood as the amount of soil imported by termites.

2.6 | Statistical analysis

All statistical analyses were conducted in the statistical software R version 4.2.0 (R Core Team, 2020).

To visualize the overall variation in wood functional traits and quantify the main axes of wood trait variation across species, a principal component analysis (PCA) was conducted using the R package 'vegan' (function *prcomp*). The first PCA axis (PC1) accounted for 48.2% of the variance in wood quality (Figure S3); thus, we used species' PC1 scores to represent their WES position in the subsequent analyses. Tree species with higher scores in PC1 tend to have higher cellulose, N and P contents and lower lignin content, wood density and wood dry matter content. This pattern indicates that species with higher PC1 scores take acquisitive strategy characterized by high wood quality. Conversely, species with lower PC1 scores exhibit the conservative strategies. To test our first hypothesis that the WES significantly correlates with foraging intensity of termites, and thereby overall deadwood invertebrate abundance and richness, we first performed linear regressions with species' PC1 scores separately as predictor variables and the imported soil mass and termite feeding area as response variables. We then used linear regression (*lm* function) to fit bivariate relationships between imported soil mass or termite feeding area and deadwood invertebrate abundance or richness (averaging across every log of a species). Deadwood invertebrate abundance (the number of individuals) data were log-10 transformed and imported soil mass data and termite feeding area data were arcsine-transformed before analysis to better achieve normality and linearity. Moreover, we used linear regression to test the relationship between termite feeding intensity (imported soil mass, termite feeding area) and major detritivore abundance. Further, to understand the termite-ant interactions across deadwoods, we separately employed Generalized Linear Models (GLM, function *glm* in package '$_{\text{LME}}$4') with the binomial function 'logit' to investigate the impact of termite activity intensity on the presence or absence of ants and the Poisson distribution 'log' on ant abundance.

Finally, to quantify whether the WES modulates the positive effects of termite foraging intensity on other invertebrate abundance and richness (versus alternative hypothesis 2: the WES determining invertebrate abundance and richness directly), we employed structural equation modelling (SEM, *sem* function in package 'lavaan', Rosseel, 2012) in which we included WES, imported soil mass, and termite feeding area to assess their impact on invertebrate abundance and richness. Mardia's multivariate normality test confirmed the multivariate normality of our data. The a priori full SEMs contained all possible correlations among these variables, but encountered difficulties in passing the chi-square test (see Figure S4). Then, we simplified the initial model by eliminating nonsignificant pathways to attain the final model with a good fitting degree (chi-square test with $p > 0.05$) and the lowest Akaike information criterion (AIC) value. We assessed the fit of the models using the goodness-of-fit index (GFI), comparative fit index (CFI) and standardized root mean square residual (SRMR). The standardized coefficients were used to compare direct effects across paths. The standardized direct and indirect effects from all the given exogenous variables were added to calculate their total effects on deadwood invertebrate abundance and richness.

3 | RESULTS

The intensity of termite foraging was significantly influenced by the species identity of deadwood, as determined by the WES (PC1). A clear pattern emerged, that is from the resource-conservative to acquisitive ends of deadwood positions, the imported soil mass and termite feeding area increased (Figure 2). This finding indicates that termites preferably consume species with high wood quality during early stages of decomposition, specifically within the 30-month periods examined across both experimental sites in this study (Figure 2). On the other hand, the WES did not have a significant direct impact on other deadwood invertebrate abundance (i.e. excluding termites and ants) and taxonomic richness (Figure S5). Moreover, in line with our first hypothesis, the overall abundance of deadwood invertebrates increased significantly with increasing termite foraging intensity in both incubation sites (Figure 3a,c,e,g). Interestingly, while

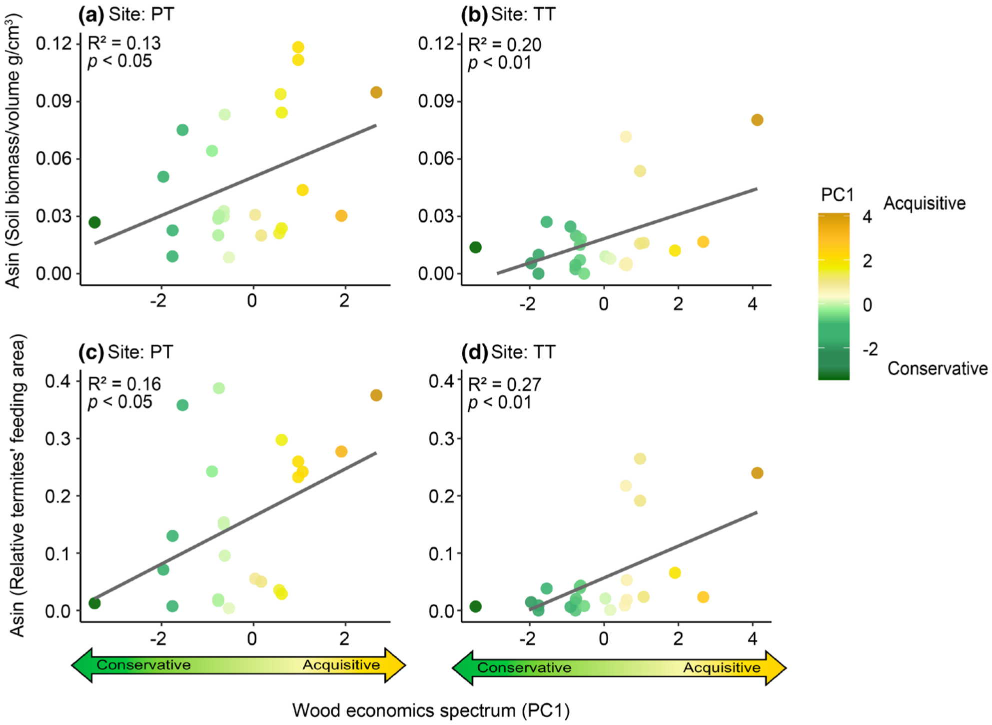

FIGURE 2 Relationships between the WES (species scores of the PC1 axis) and termite foraging intensity. (a, b) Relationships between the WES and arcsine transformed imported soil mass in sites PT and TT, respectively. (c, d) Relationships between the WES and relative termite feeding area in sites PT and TT, respectively. PT, Putuo island; TT, Tiantong National Park; WES, wood economics spectrum.

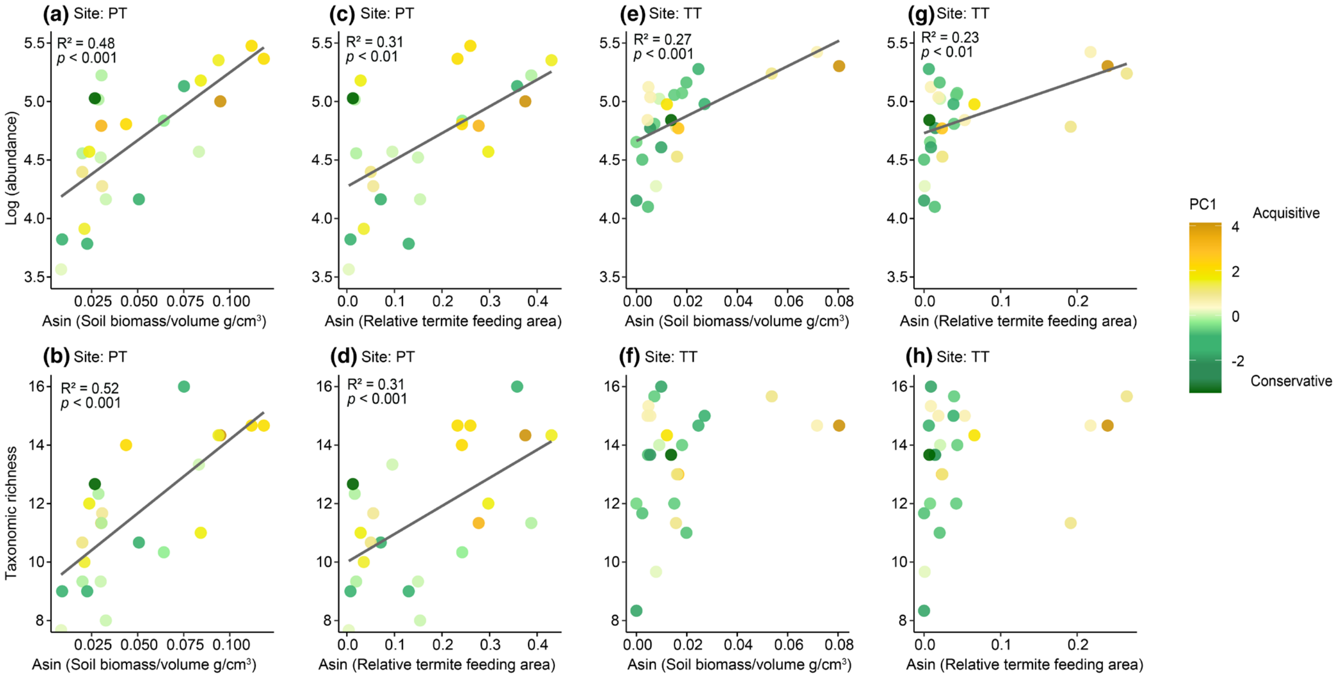

FIGURE 3 Relationships between arcsine transformed imported soil materials content (soil mass per volume) or relative termite feeding area and the abundance or taxonomic richness of deadwood invertebrates, respectively, in sites PT (a–d) and TT (e–h). Regression lines were added only when the relationships were significant ($p < 0.05$). PT, Putuo island; TT, Tiantong National Park.

deadwood invertebrate taxonomic richness increased with termite foraging intensity in site PT (Figure 3b,d), this relationship was not observed in site TT (Figure 3f,h).

There was a significant positive correlation between termite foraging intensity and the abundance of the most abundant mesodetritivores (Acari—mites and Collembola—springtails) in both sites

(Figure S6). Among the macrodetritivores, we found positive relationships between termite foraging intensity and the abundance of Opisthopora (earthworms and allies), while there were no significant relationships with Isopoda (woodlice) abundance (Figure S7). In addition, termite feeding intensity did not significantly influence the presence or absence of ants but significantly and positively influenced the abundance of ants in both sites, except for a marginal negative effect of termite feeding area on ant abundance in the TT site (Table S2).

Finally, we tested the support for our two alternative hypotheses (indirect termite-mediated versus direct effect of WES on deadwood invertebrate abundance and richness) using structural equation modelling (SEM). The best-fitting models accounted for 57% and 40% of the variation in deadwood invertebrate abundance and 60% and 10% of the variation in deadwood invertebrate taxonomic richness in sites PT and TT, respectively (Figure 4). In site PT, the model showed that imported soil mass significantly promoted deadwood invertebrate abundance ($r=0.56$, $p<0.001$) and richness ($r=0.59$, $p<0.001$) directly, while termite feeding area marginally directly affected deadwood invertebrate abundance ($r=0.30$, $p=0.096$) and richness ($r=0.28$, $p=0.05$). Moreover, the WES affected invertebrate abundance indirectly just via termite feeding area ($r=0.25$, $p=0.02$), while it affected invertebrate richness indirectly via imported soil mass ($r=0.24$, $p=0.05$) and termite feeding area ($r=0.12$, $p=0.08$) (Figure 4a; Table S3). In TT, the WES also did not affect invertebrate abundance and richness directly but instead affected them indirectly via imported soil mass ($r=0.38$, $p=0.05$) (Figure 4b; Table S3). The patterns in TT were less clear than in PT;that is in TT, termite foraging intensity did not affect the taxonomic richness of deadwood invertebrates (although there was a positive trend for soil material content), and the WES could not indirectly affect deadwood invertebrate abundance through the path of termite feeding area (Figure 4; Table S3).

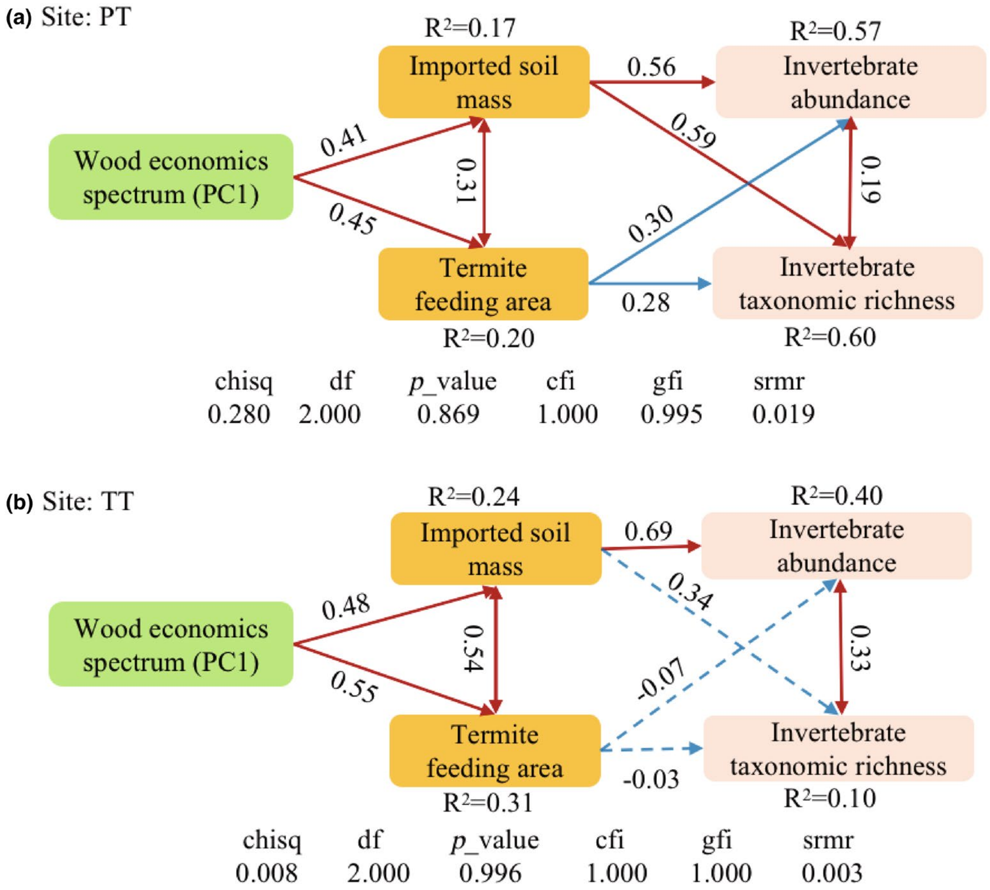

FIGURE 4 The final best-fitting structural equation models showing the pathways through which the wood economics spectrum, imported soil mass and termite feeding area affect abundance and taxonomic richness of deadwood invertebrates. Numbers along the arrows are standardized path coefficients. The explained variance (R^2) which total variation in an endogenous (dependent) variable explained by any exogenous (independent) variables is shown in each panel. One-sided arrows represent regression path or direct effect, while double-sided arrows represent estimated covariance between two predictors. Red solid lines indicate highly significant paths ($p<0.05$), blue solid lines indicate marginal significant paths ($0.05 \leq p<0.1$), and blue dashed lines are for non-significant paths ($p \geq 0.1$). Model-fit statistics are provided. CFI, comparative fit index; chisq, chi-square value; df, degree of freedom; GFI, goodness of fit index; p, chi-square test p value; SRMR, standardized root mean square residual.

4 | DISCUSSION

We found powerful support for our first hypothesis that termite foraging intensity can promote overall deadwood invertebrate abundance and taxonomic richness, and that the WES modulates these relationships in the early stage of coarse deadwood decomposition. In contrast, there was no significant support for our second, alternative hypothesis of the WES directly affecting invertebrate communities without termites as mediators. Indeed, our study has demonstrated that especially the soil materials imported by termites, but to some degree also the termite-consuming area, significantly enhanced the abundance and richness of other deadwood-dwelling invertebrates. This finding supports our expectation, based on incidental field observations, that termites consume deadwood, thereby creating galleries and pores of different shapes and sizes, which in turn facilitate other invertebrates (like earthworms) access into the deadwood (Ulyshen, 2016). It is also possible that the imported soils help maintain the moisture of deadwood habitats (Neupane et al., 2015) or enhance nutrient availability by importing clay particles loaded with base cations (Jouquet et al., 2022), which can be beneficial for the survival and activity of various invertebrates. In our study, these possible mechanisms (and the chewing and internal processing by termites; see below) cannot be separated from the habitat provisioning mechanism, but unravelling these alternative mechanisms would be an important topic of in-depth study. Whichever the exact mechanism, both the imported soil mass and feeding area caused by termite activities appeared to promote the abundance of the major macrodetritivores (Opisthopora), mesodetritivores (Acari and Collembola) and ants in this subtropical forest ecosystem. Below, we will discuss the details and associated caveats of our results critically, to be able to evaluate the importance and broader implications of our findings.

4.1 | The wood economics spectrum affected termite foraging intensity and thereby deadwood invertebrate communities

Consistent with our hypothesis, we found that the WES significantly influenced termite foraging intensity. From resource-conservative to acquisitive ends along the WES gradient in both study sites, there was a noticeable increase in termite foraging intensity (Figure 2), indicating that termites prefer consuming deadwood species with traits belonging to a resource-acquisitive growth strategy in the early decomposition stage. These results are consistent with previous studies on finer deadwood decomposition in tropical and subtropical forests (Guo et al., 2021; Liu et al., 2015). Termites showed a strong feeding preference for wood with higher nutrient and cellulose content but lower density and lignin content (Liu et al., 2015; Wu et al., 2021). This is because deadwood with such characteristics is more susceptible to termite consumption, making it easier to digest and providing more nutritional value (Guo et al., 2021).

Previous studies have shown that tree species functional traits significantly affect deadwood invertebrate communities in a temperate forest (Andringa et al., 2019; Zuo, Berg, et al., 2016). However, in our study, we did not observe a significant direct effect of the WES on broader overall invertebrate abundance and richness (Figure 4; Figure S4). This discrepancy may be attributed to the active involvement of termites in the decomposition process, as they dynamically alter the relative rankings of species along the WES over time (Guo et al., 2021). Consequently, the influence of the WES on invertebrate communities is superseded by the intensity of termite activity. Alternatively, the WES may exert direct effects on detritivores (see above), while the addition of other fauna at higher trophic levels may mitigate these direct effects (Li et al., 2023; Scherber et al., 2010). These findings emphasize the complex interactions between plant traits, termite foraging behaviour, and the subsequent effects on broader invertebrate communities. They suggest that the indirect effects mediated by termite activity are crucial in understanding the relationship between the WES and invertebrate biodiversity. Additionally, these interactions may create a positive feedback loop that enhances deadwood decomposition and nutrient cycling (Guo et al., 2021).

4.2 | The effects of termite foraging intensity on deadwood invertebrate abundance and taxonomic richness

Termites, as ecosystems engineers, hold a prominent position among the major macrodetritivores, significantly influencing ecosystem dynamics beyond mere decomposition in tropical and subtropical forests (Griffiths et al., 2019; Zanne et al., 2022). Their activities include the construction of biostructures, such as mounds, galleries and sheetings (Ashton et al., 2019; Oberst et al., 2019), significantly shaping the distribution of essential natural resources, including water and nutrients, in the landscape, ultimately impacting the diversity of soil microbes, plants and invertebrates (Jouquet et al., 2011; Neupane et al., 2015). The significance of termites on ecosystem functioning and biodiversity preservation has been consistently highlighted in previous studies (Ashton et al., 2019; Guo et al., 2021; Oberst et al., 2019; Veldhuis et al., 2017). In our study, we found a positive correlation between termite foraging intensity and the other invertebrate diversity. Furthermore, the abundances of major mesodetritivores (Acari and Collembola), macrodetritivores (especially Opisthopora) and ants exhibited a positive relationship with termite foraging intensity. These findings confirm the significant role of termite foraging activities in maintaining soil biodiversity (LeClare et al., 2020) and thereby enhancing rates of deadwood turnover (Ulyshen, 2016). Termites accelerate the breakdown of compact deadwood structures, which are initially inaccessible to many invertebrates (like earthworms).

Fungal decay contributes to wood softening and nutrient enrichment, facilitating the colonization of other invertebrates, and in this way fungi may interact with the termites' effect on invertebrate communities. Besides such interactions related to the decay process itself, possibly modulated by tree species' wood traits, which would be an important topic for future research, termite activities play further critical roles in ecosystem functioning and biodiversity in our study area (Guo et al., 2021; Ulyshen, 2016). Termite foraging activity involves chewing wood into particles (which are then excreted as faeces to make their nests) or creating spaces (new habitat), which increase resource palatability and habitat complexity, thereby enabling other organisms to access and consume the wood, and eventually promoting further decay (Enagbonma & Babalola, 2022; Jouquet et al., 2011; Wu et al., 2023). Termite consumption creates internal cavities that provide habitat for higher trophic level invertebrates, that is predators. Additionally, since termites serve as a food resource for ants, termite foraging activity (or population) can lead to an increase in ant populations through bottom-up effects (Tuma et al., 2020). However, a marginally negative effect of termite feeding area on ant population in the site of TT suggests that an alternative top-down control by predatory ants may also exist (Table S2); the mechanism behind such pattern needs to be examined further in the andfuture.

We noted that the effects of termite foraging activity on deadwood invertebrate diversity were taxon-dependent and differed between the experimental sites. This variation might be partly attributed to the differences in plant community composition, termite abundance, and environmental conditions between the two sites (Hedenec et al., 2023). In our studied sites, the PT site had higher soil phosphorus content, a more neutral soil pH (Guo et al., 2021), and higher soil invertebrate functional diversity and complexity of soil food webs (unpublished data) compared to the TT site. With the favourable environmental conditions and the abundant food resources, more abundant termites were supported by PT than by TT (Guo et al., 2024). As such, termite foraging intensity (Figure 2) and the deadwood decomposition rate (Guo et al., 2021, 2024) were notably higher in site PT than in TT. Consequently, the direct and indirect positive effects of termite foraging activity on the diversity of invertebrate communities were pronounced in PT than in TT.

5 | CONCLUSIONS

Wood identity (WES) and termite foraging intensity have been recognized as factors influencing deadwood invertebrate diversity in previous studies (Enagbonma & Babalola, 2022; Jouquet et al., 2011; Zuo, Berg, et al., 2016). In our study, we linked the critical role of the WES with that of ecosystem engineers, which involve several complex mechanisms. Both the bivariate relationships between the WES and termite foraging indicators and the SEM results indicate that the WES indirectly affects overall deadwood invertebrate abundance and richness by modulating termite foraging activity. Our findings therefore contribute to a nuanced understanding of the complex interactions among wood identity, termite activity and deadwood invertebrate communities. To gain a deeper understanding of these interactions, further research should investigate the specific mechanisms through which termite activity modifies the influence of the WES on the composition and structure. Additionally, exploring how the wood economic spectrum and ecosystem engineers such as termites drive the functional diversity of deadwood invertebrates will contribute to a more comprehensive understanding of the biodiversity dynamics during deadwood decomposition and its implications for ecosystem-level processes such as carbon and nutrient cycling. By unravelling these intricate ecological relationships, we can enhance our ability to manage and conserve forest ecosystems effectively.

AUTHOR CONTRIBUTIONS

En-Rong Yan, Hang Ci, Chao Guo and Johannes H.C. Cornelissen designed and conceptualized the experiment; Hang Ci, Chao Guo, Bi-Le Sai, Bin Tuo, Wei-Wei Zhao, Han-Tang Qin and Tian Zhang carried out the field and lab work; Hang Ci analysed data and wrote the manuscript; Johannes H.C. Cornelissen and En-Rong Yan revised and improved the manuscript. All authors critically reviewed the drafts and provided final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at Dryad Digital Repository: https://doi.org/10.5061/dryad.bg79cnpmr (Ci et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Species lists in the deadwood decomposition experiment at TT and PT sites.

Table S2: The effects of imported soil mass and termite feeding area on the occurrence (presence/absence) and abundance of ants at PT and TT sites.

Table S3: The direct, indirect and total standardized effects on the abundance and richness of deadwood invertebrates based on the structural equation models (SEMs).

Figure S1: Images of holes, tunnels and soil materials caused by termite activity. Photos credited by the Hang Ci.

Figure S2: Termite damage visible on the disks (A) was marked in white (B) and quantified using computer imaging software to estimate the percentage of deadwood area consumed.

Figure S3: Graphical output from the principal component analysis of wood traits of 20 cm diameter logs of 22 different woody species.

Figure S4: The a priori full structural equation models illustrate the pathways through which the wood economics spectrum, imported soil mass and termite feeding area affect the abundance and taxonomic richness of deadwood invertebrates.

Figure S5: Relationships between the wood economics spectrum (species scores of the first principal component analysis (PCA) axis) and deadwood invertebrate abundance (a, b) and taxonomic richness (c, d) respectively at PT and TT sites.

Figure S6: Relationships between arcsine transformed imported soil mass or termite feeding area and major mesodecomposers abundance respectively.

Figure S7: Relationships between arcsine transformed imported soil mass or termite feeding area and major macrodecomposers abundance respectively.

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