Influences of the bark economics spectrum and positive termite feedback on bark and xylem decomposition

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Abstract. The plant economics spectrum integrates trade-offs and covariation in resource economic traits of different plant organs and their consequences for pivotal ecosystem processes, such as decomposition. However, in this concept stems are often considered as one unit ignoring the important functional differences between wood (xylem) and bark. These differences may not only affect the performance of woody plants during their lifetime, but may also have important "afterlife effects." Specifically, bark quality may strongly affect deadwood decomposition of different woody species. We hypothesized that (1) bark quality strongly influences bark decomposability to microbial decomposers, and possibly amplifies the interspecific variation in decomposition by invertebrate consumption, especially termites; and (2) bark decomposition has secondary effects on xylem mass loss by providing access to decomposers including invertebrates such as termites. We tested these hypotheses across 34 subtropical woody species representing five common plant functional types, by conducting an in situ deadwood decomposition experiment over 12-month in two sites in subtropical evergreen broadleaved forest in China. We employed visual examination and surface density measurement to quantify termite consumption to both bark and the underlying xylem, respectively. Using principal component analysis, we synthesized seven bark traits to provide the first empirical evidence for a bark economics spectrum (BES), with high BES values (i.e., bark thickness, nitrogen, phosphorus, and cellulose contents) indicating a resource acquisitive strategy and low BES values (i.e., carbon, lignin, and dry matter contents) indicating a resource conservative strategy. The BES affected interspecific variation in bark mass loss and this relationship was strongly amplified by termites. The BES also explained nearly half of the interspecific variation in termite consumption to xylem, making it an important contributor to deadwood decomposition overall. Moreover, the above across-species relationships manifested also within plant functional types, highlighting the value of using continuous variation in bark traits rather than categorical plant functional types in carbon cycle modeling. Our findings demonstrate the potent role of the BES in influencing deadwood decomposition including positive invertebrate feedback thereon in warm-climate forests, with implications for the role of bark quality in carbon cycling in other woody biomes.

Key words: bark traits; carbon turnover; deadwood decomposition; evergreen broadleaved forest; inner and outer bark; invertebrate feedback; plant functional types; termite; trait diversity.

INTRODUCTION

Ecologists have long tried to classify species, both plants and certain animal groups, based on their eco-morphological characteristics, in order to facilitate upscaling and modeling of species or ecosystem functioning. Previous categorical classifications of plant strategies in plant functional types (PFT; Sitch et al. 2003, Zakharova et al. 2019) had the disadvantage of not accounting for functional dissimilarity within a category. In contrast, a recent concept, the plant economics spectrum (PES), quantifies species' strategies based on their positions along a multivariate axis of continuous functional trait variation. At one end of the spectrum the suite of traits indicates a resource acquisitive strategy, associated with fast growth, while at the other end species are resource conservative with slow growth

(Freschet et al. 2010, Reich 2014, Diaz et al. 2016). The PES integrates corresponding previous efforts for different plant organs, which highlighted trait-based organ-specific resource economics spectra for leaves (Wright et al. 2004), wood (Chave et al. 2009) and roots (Mommer and Weemstra 2012, Bergmann et al. 2020). Here, we argue that one plant organ critical to plant and ecosystem functioning is still missing from at least the woody part of the PES, i.e., bark. Interspecific differences in bark traits can be large, even within a community (Rosell et al. 2014). Strong bark trait covariation within and across species reflect resource investment trade-offs based on the dual functionality of bark in living plants (Rosell et al. 2014). Specifically, bark with high storage and transport performance normally has less lignified tissue and ample nutrient content (Rosell et al. 2014), which fits a resource acquisitive strategy. On the other hand, thick (outer) bark with high structural carbon deposition, e.g., lignin and suberin boosting its protective function against biotic and abiotic hazards including fire (Poorter et al. 2014, Huang et al. 2020, Staver et al. 2020), fits a conservative resource strategy. Hence, according to the PES principles, we ask whether there is a consistent "bark economics spectrum" (BES) across woody species reflecting bark investment strategy.

Recent studies have extended the functional significance of trait-based resource economics spectra for the living plants to those for carbon and nutrient turnovers, based on the "afterlife" effects of the traits of different species on the decomposition rates of their dead parts, which has important implications for carbon and nutrient turnover in ecosystems. This approach has led to empirical evidence for a "PES of decomposability" across and within plant organs, at least in a subarctic flora (Freschet et al. 2012). Other studies, focusing on woody species only, found weaker or no coordination of trait-based interspecific decomposability rankings between woody stems and leaves (Pietsch et al. 2014, Zanne et al. 2015, Zuo et al. 2018). Consistent associations of trait spectra with decomposability have also been found for individual plant organs, especially leaves (Cornwell et al. 2008, Fujii et al. 2018, Guo et al. 2019), while to our knowledge no such clear pattern has been found for roots as yet (Fujii et al. 2018). Several recent studies have demonstrated how interspecific variation in deadwood decomposability at local to regional scale can be predicted to some degree from multivariate variation in stem traits (van Geffen et al. 2010, Zanne et al. 2015, Zuo et al. 2018) or from individual underlying xylem traits, such as dry matter content, lignin content, pH, vessel diameter, or nutrient content (Cornwell et al. 2009, Freschet et al. 2012, Liu et al. 2015, Hu et al. 2018). However, a prominent shortcoming of these previous studies on traits and deadwood decomposition is that they considered deadwood as a single unit, without distinguishing between xylem (underlying wood) and bark (but see Dossa et al. 2018, Chang et al. 2020, Jones et al. 2020). However, highly distinctive plant organs in

terms of chemical and structural properties have dissimilar decomposition patterns with different ecological implications (Dossa et al. 2018).

Bark reportedly comprises up to 25% of the volume and dry mass of woody stems, as well as a substantial amount of nutrients (Franceschi et al. 2005, Jones et al. 2019), and some woody species feature periodical bark shedding during life, which results in a massive influx of organic matter into the forest litter layer (Grootemaat et al. 2017). In most cases, however, trees die with bark still attached; thus, bark and xylem start to decompose simultaneously with normally bark decomposition rate higher than that of xylem (Chang et al. 2020). Depending on the species and study, the presence of bark imposes either inhibitory or stimulatory effects on wood decay rate (Ulyshen et al. 2016, Dossa et al. 2018). Ecologists believe, on the one hand, that bark still partially maintains its defensive ability (e.g., ample defensive compounds) after tree death and thereby retards xylem decomposition (Jones et al. 2020), on the other hand, nutrient-rich bark tissue could facilitate xylem decay underlying it (Dossa et al. 2018). The inconsistency with previous findings remains poorly understood. Here we argue that interspecific variation in bark quality, as determined by multiple underlying traits, drives variation in the decomposition of the bark, and thereby possibly also the underlying xylem, not only through variation in microbial decomposition but also via the contribution of invertebrates to decomposition.

Invertebrate detritivores, especially termites and beetles, are paramount contributors to deadwood decomposition (Ulyshen 2016). In (sub)tropical regions, termites process far more volume and mass of wood than even all other invertebrate taxa combined (Ulyshen et al. 2014). Termites prefer soft, nutrient-rich, and less lignified deadwood substrates, making deadwood quality a key predictor of termite consumption (Liu et al. 2015). However, there is an important knowledge gap about the drivers of the termite contribution to bark decomposition, even though this might represent an important direct contribution to carbon losses from deadwood, as well as an important indirect one via the bark effect on xylem decomposition. While interspecific variation in bark traits of tree logs is an important driver of arthropod community assemblage in temperate forests without termites (Zuo et al. 2016), we do not know whether or how bark quality, i.e., a BES, plays a role in termite colonization and decomposition of bark on tree logs, and how the bark exerts further effects on xylem decay via termite consumption.

We propose and empirically test a new conceptual model that bridges bark quality with termite abundance and consumption, and thereby the termite contribution to bark mass loss and its secondary effects on xylem mass loss. In this framework (Fig. 1), we hypothesize (H1) that there is a "bark economics spectrum" analogous to the previously reported wood or branch economics spectrum (Baraloto et al. 2010,
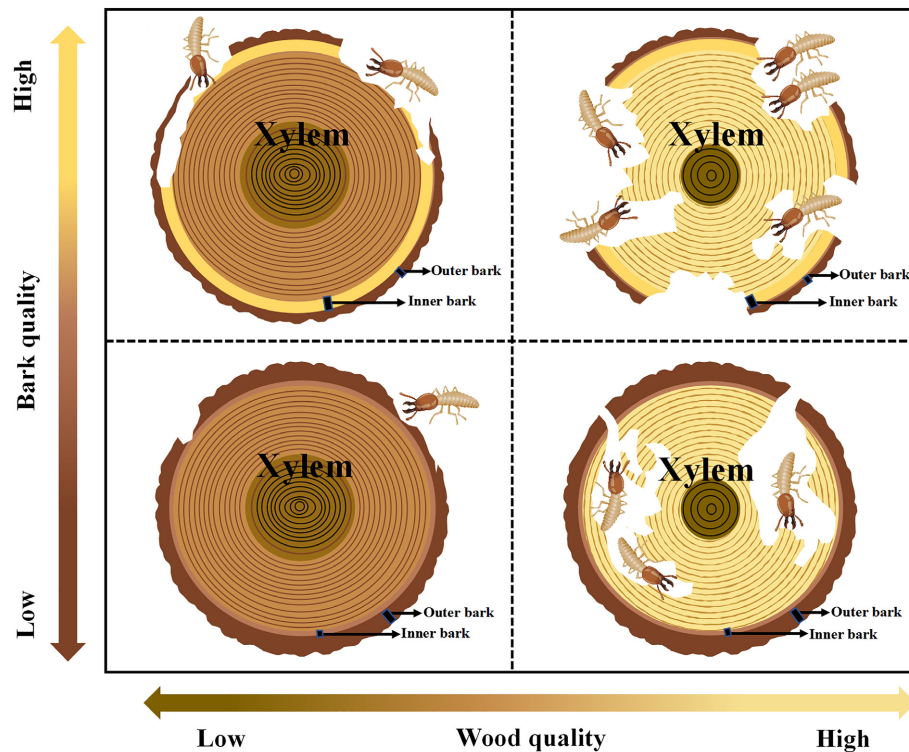
FIG. 1. Conceptual model illustrating the role of bark quality for termite colonization and consumption, and how this may predict the degree of colonization and consumption of xylem. Termite consumption of bark will be influenced by the bark economics spectrum, while termite consumption of xylem will be influenced both by access provided through bark consumption and losses and by xylem quality. Xylem represents the inner part of deadwood; the subsequent two shells represent inner and outer bark, respectively. Difference in colors (yellow to brown) indicates distinct qualities of deadwood compartments, the numbers of termite cartoons represent the severity of termite consumption on different qualities of bark and xylem, respectively.

Zuo et al. 2018). This BES should strongly influence interspecific variation in bark decomposability (H2a) and drive the fraction of bark colonized and consumed by termites, thereby affecting decomposition of both bark itself and (indirectly) decomposition of the wood underneath the bark (H2b). Specifically, we predict that termite abundance on bark and the termite contribution to bark mass loss will be greater in woody species with favorable bark quality (i.e., higher values along the BES continuum). We also expect that termite consumption of xylem will be higher as bark quality increases as the larger termite-induced bark (mass) loss will promote termite and microbial access to the xylem below. However, xylem quality will also promote its own decomposition and the termite contribution to it and, to test this part, it is important to also understand the covariation between bark traits and xylem traits across tree species (Jones et al. 2019), and thereby inferring covariation between bark and xylem decomposability (cf. Chang et al. 2020). Furthermore, we hypothesize (H3) that these relationships (H2), if robust, can be found among species both across and within different woody plant functional types. If so, this would provide another

strong argument (cf. Kattge et al. 2011, Zakharova et al. 2019) for representing overall variation in (bark and wood) decomposition rates by continuous trait variation among species rather than by PFT-level mean traits in future global carbon model construction (Cornwell et al. 2009).

METHODS

Study sites

We conducted our experiment in two sites in subtropical evergreen broad-leaved forests (EBLF), Zhejiang province, East China. The first was Tiantong National Forest Park (TT, 29°52′ N, 121°39′ E), which is subject to subtropical monsoon climate, with mean annual precipitation of 1,375 mm and mean annual temperature of 16.2°C. Here, the dominant tree species was *Schima superba*. The second site was Putuo island (PT, 29°97′ N, 121°38′ E), located 6.5 km east of the mainland, which has a marine subtropical monsoon climate, mean annual precipitation and temperature are 1,358 mm and 16°C, respectively. The dominant tree species was *Quercus glauca*. In both sites, the predominant wood-

decomposing termite species were *Coptotermes formosanus*, *Odontotermes formosanus*, *Reticulitermes chinensis*, and *Reticulitermes speratus* (Yi et al. 2006), and termite abundance in PT was higher than in TT. Forest fire occurrence in this region was extremely low. Further details of the two sites were given by Guo et al. (2021).

Species sampling

We selected 34 woody species belonging to five plant functional types in PT and TT, including five coniferous trees (CT), five deciduous shrubs (DS), 10 deciduous trees (DT), five evergreen shrubs (ES), and seven evergreen trees (ET). These species, of wide-ranging phylogenetic position (Appendix S1: Fig. S1), represent the regionally common or dominant species, as well as some species typical for either of the sites. "Shrubs" were defined based on their typical height rather than growth form and included both short forest understory trees (with one dominant main stem) and multi-stemmed true shrubs. Altogether 126 healthy, undamaged individuals (three for trees, six for shrubs) were logged. We chose to start from living trees as they (1) provide a standardized starting point for decomposition across species and (2) a large proportion of trees in this typhoon-prone region enters the decomposition subsystem alive owing to disturbances, such as wind-throw, landslides, or logging. For trees, several 20 cm long, 5 ± 0.5 cm diameter segments were extracted from each crown, while we collected equal-sized shrub segments by clipping one of their main trunk(s) but avoiding top, bottom, and furcations. We also collected 2 cm thick intact disks adjacent to each end of the segment for initial xylem and bark trait measurements.

Decomposition experiment

Anticipating that intensive termite activities may result in quick physical fragmentation and decomposition of deadwood samples, we put each sample segment in a separate nylon mesh bag (25×15 cm, 4×4 mm mesh size) to make sure to retrieve most of what fell off or remained, while still providing access to termites. Each sample was weighed fresh and tagged before putting into a bag. We produced 408 samples, i.e., 34 species $\times$ 3 plots $\times$ 2 sites $\times$ 2 harvests. We established three nearly homogeneous, 20×30 m incubation plots in each site; each plot was pre-divided into several 3×4 m subplots to host each species separately. We left 20 m wide strips between plots to minimize interference between plots. Every species had two replicates within each of its respective subplots, i.e., one for each harvest.

We commenced incubation in December 2017. Termite activities were low then because of the low temperature, thus we assumed no significant termite consumption would take place soon. We randomly placed samples within subplots. The bags were tightly pinned onto the soil surface so that they would retain contact with the ground over their entire exposure times. We retrieved the samples after 6 (June 2018) and 12 months (December 2018) by putting them in separate press-seal bags after carefully removing extraneous substances. Then we swiftly transported them to a laboratory near the respective field sites for processing and measurements. We put a sample in a plastic tray and extracted termites manually and transferred them into a plastic vial to count them afterward. We set aside the cleaned sample for termite consumption measurements.

Termite consumption measurements

We recorded visual evidence of termite consumption (Ulyshen et al. 2013) on different components of deadwood samples at the second harvest, namely on outer bark, inner bark, and xylem, respectively. Specifically, we cleaned samples and removed termites, meanwhile recording conspicuous evidence of termite activities, such as mud galleries or gnawing marks (Appendix S1: Fig. S7). To quantify termite consumption, we placed a 100×100 mm grid paper with cell size of 5×5 mm over these areas, then recorded the percentages of grid cells that had visible symptoms of termite activity over $>50\%$ of their surface. Termite consumption on the outer bark normally hinted the inner bark would have been attacked as well. In some cases, however, termites would circumvent the outer bark and consume the inner bark directly. We therefore peeled off the outer bark to measure the area of the cavities beneath outer bark or turned bark inside out to measure termite consumption on the inner bark if the bark became detached. We also measured the xylem termite consumption based on the same symptoms to see whether bark traits indirectly influenced interspecific variation in termite consumption on the xylem surface (Fig. 1). We averaged the records of three replicates to get the mean values of inner bark, outer bark, and xylem termite consumption for each species in each site.

Traits measurements

We used the 2 cm disks to measure bark and xylem traits. We took 10 readings of bark thickness around the disk using digital Vernier calipers, and used the average in further analyses. Following, content of elements or compounds are always on a mass per mass basis. In order to obtain bark and xylem dry matter contents (XDM), a 2×2 cm bark subsample was stripped off the disk after a small chunk of xylem had been clipped off. Fresh mass of bark and xylem were measured. Dry masses were taken after samples were oven dried at 75°C for 48 h; XDM were then calculated as dry mass/fresh mass. Extra xylem and bark materials were taken from the same disk and ground to pass a 0.15-mm sieve. To determine carbon content, roughly 0.1 g of fine powder was sealed into tin foil, which was burned at 950°C in a TOC analyzer (Vario TOC, Elementar, Germany). For

nitrogen and phosphorus content we mixed 0.2 g of powder with 98% H_2SO_4 in a glass tube, and heated the tube at 370°C for 3 h to get a nutrient solution, in which we measured N and P content using an infrared spectrophotometer (Smartchem 200, Alliance, Frépillon, France). Xylem and bark lignin contents were determined by acidolysis-titration and cellulose contents by anthrone-sulfuric acid colorimetry (Poorter and Villar 1997).

Area-based bark mass loss measurement

We adopted area-based density (S) instead of volume-based bark density in order to quantify bark mass loss more accurately. Following Chang et al. (2020), we measured the mass per area at the beginning (t_0) and at the second harvest (t_2). For S_{t0} we used the 2×2 cm bark subsamples mentioned above. For S_{t2}, 3–4 rectangular bark pieces that represented the bark decomposition status were extracted from each sample. The width and length (for calculation of area) were measured using digital Vernier calipers, and their dry mass (g) was taken right after oven drying at 75°C for 48 h. Area-based bark loss percent, here referred to as minimum bark mass loss (BML_{min}), was calculated as the proportional difference in area-based mass between t_0 and t_2 using

$$BML_{min} = \frac{S_{t0} - S_{t2}}{S_{t0}}. \qquad (1)$$

In fact, without considering bark that had fallen off during decomposition, the estimation of actual bark mass loss would not reflect the loss from the branch's perspective. Hence, we also recorded the fraction of bark that disappeared from each sample using grid paper to obtain the actual bark coverage ($C_{B\%}$) and calculate the bark cover loss. Maximum bark loss (BML_{max}) was calculated as the combined mass loss per bark unit and loss of bark coverage using

$$BML_{max} = \frac{S_{t0} - (S_{t2} \times C_{B\%})}{S_{t0}}. \qquad (2)$$

Statistical analysis

Principal component analysis (PCA) was performed to quantify and visualize the axes of overall variation in bark and xylem traits respectively. The first PC axes (Bark PC1, Xylem PC1) explained high proportions of variation in their respective trait syndromes. Therefore, the species' scores along Bark PC1, and Xylem PC1, respectively, were used in subsequent analyses to represent the BES and the xylem (wood) economics spectrum (XES).

Because there were some important abiotic and biotic differences between the two sites (Guo et al. 2021), and to better test the generality of BES effects on deadwood

decomposition process within the biome, we examined the following relationships separately for both experimental stem incubation sites. Standardized major axis (SMA) analysis was employed to test the degree of linkage between XES and BES. To test the relationships of these economic spectra with termite consumption and bark mass loss as well, simple linear regression was used, as linear functions generally gave the best fits with the data. The same method was applied to examine the relationships of bark traits with termite consumption and bark mass loss across tree species. We used Pearson's correlation analysis to determine the bivariate relationships between bark traits and xylem traits. All data were checked for, and generally met homogeneity of variance and normality assumptions using Levene's test and Shapiro-Wilk test, respectively.

Statistical analyses were performed in R language version 3.5.1 (R Development Core Team 2019).

RESULTS

Bark and xylem economics spectra

The first PCA axis captured 31.4% and 50.9% of variation in bark traits (Fig. 2a) and xylem traits (Appendix S1: Fig. S2), respectively. In both PCA biplots, structural traits (C content, dry matter content, lignin content) were always orthogonal to the nutrient-related traits (N and P content) and cellulose content (Fig. 2a). The PC1s of bark (BES) and xylem (XES) were positively related overall and more strongly within deciduous shrubs, evergreen shrubs, and evergreen trees (Fig. 2b).

BES effects on bark mass loss and on xylem termite consumption

In both sites, termite consumption on outer and inner bark was largely explained by BES, the percentages explained ranging from 55% to 59% in both sites (Appendix S1: Fig. S4a–d). Termite consumption on bark had significant overall effects on BML_{min} and BML_{max} across species (Appendix S1: Fig. S4e–h), with explained variance ranging between 47% and 64%. These two relationships broadly existed within different plant functional types (Appendix S1: Fig. S4). Across species, BES generally explained between 53% and 63% of variation in BML (Fig. 3). Within plant functional types, BES of conifer trees, evergreen shrubs and evergreen trees was positively related to BML_{min} in site TT (Fig. 3a), and apart from deciduous shrubs and deciduous trees, this positive relationship was found within the other three plant functional types in site PT (Fig. 3b). Regarding the relationship between BML_{max} and BES, in site TT all plant functional types but conifer trees displayed positive relationships (Fig. 3c), and similar relationships were only shown within conifer trees, evergreen shrubs and evergreen trees in site PT (Fig. 3d).
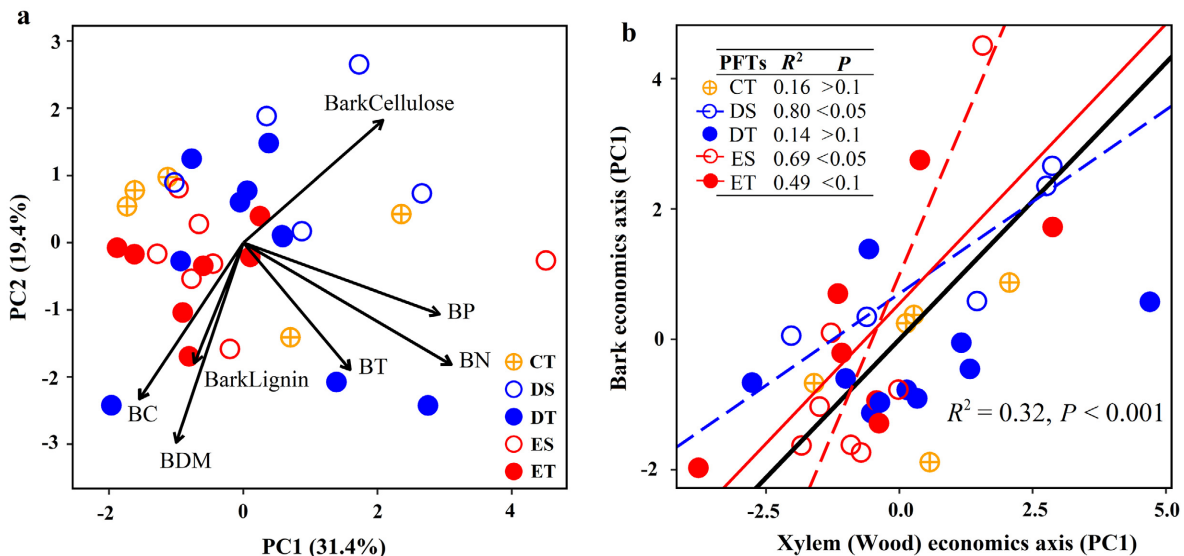
FIG. 2.　(a) Principal component analysis (PCA) ordination of seven deadwood bark traits: BD, bark density; BDM, bark dry matter content; BC, bark carbon content; BP, bark phosphorus content; BN, bark nitrogen content; BT, bark thickness; BarkCellulose, bark cellulose content; BarkLignin, bark lignin content. The species are categorized according to plant functional types (PFTs, different colors): coniferous tree (CT), deciduous shrub (DS), deciduous tree (DT), evergreen shrub (ES), evergreen tree (ET). The percentage of the trait variation explained by each PC axis is given in parentheses. (b) Relationship between XES and BES with regard to plant functional types. The solid black line represents the combined regressional relationship across all species. Inset: significance between BES and WES within plant functional types. Points represent different species.

Moreover, larger numbers of termites congregated on deadwood species at the acquisitive end of BES than on conservative species at the first harvest (Appendix S1: Fig. S5).

The BES was also strongly correlated with xylem termite consumption on deciduous trees in site TT, while neither within the other four plant functional types nor across species was there a significant relationship (Fig. 4 a). In fact, the majority of species did not show any xylem termite consumption by the second harvest in site TT. In site PT, there was a significant positive relationship between BES and xylem termite consumption overall, and within plant functional types it was also found in evergreen shrubs (Fig. 4b).

The XES effect on xylem termite consumption only manifested across species in site PT (Appendix S1: Fig. S6b) and the effect was stronger when the BES effect on xylem termite consumption increased (Fig. 4b). Within plant functional types the same positive relation was also found for evergreen shrubs and evergreen trees. In the site TT there was no overall relationship of XES with xylem termite consumption (Appendix S1: Fig. S6a), while within plant functional types, conifer trees and evergreen trees did show positive relationships.

DISCUSSION

Here we have demonstrated that (1) besides traits of wood, i.e., xylem, bark traits play an important role in explaining, and probably partly driving, variation in deadwood decomposition rates among subtropical tree species and (2) that the associated keystone invertebrate detritivores are pivotal to this relationship. To our knowledge this is the first empirical study to reveal a bark economics spectrum across woody plants, supporting H1. In support of H2a, this BES could explain most of the variation in bark mass loss in two independent subtropical forests. We also found a strong bark trait "after-life" effect on termite consumption across species (supporting H2b), which was also tightly connected to bark mass loss. Moreover, the relative amount of termite consumption of xylem could partly be explained by the afterlife effects of the BES on bark palatability and hence bark mass loss, implying xylem decomposition was influenced by the bark decomposition process. Together these findings provide strong support for our conceptual model (Fig. 1), which attributes a key role to interspecific bark trait variation in termite-mediated deadwood turnover.

The BES across woody plants

Four traits (Bark cellulose, nitrogen, phosphorus content, thickness) reflecting acquisitive strategy were largely aligned with the BES (PC1), traits (Bark lignin and carbon content, BDM) reflecting conservative strategy have relatively lower loadings on the BES (Appendix S1: Table S1), with increasing values running from a resource acquisitive to a resource conservative strategy. On closer inspection of the correlations among pairs of bark traits, bark thickness was also included in our bark spectrum. Indeed, this trait reflects the bark resource
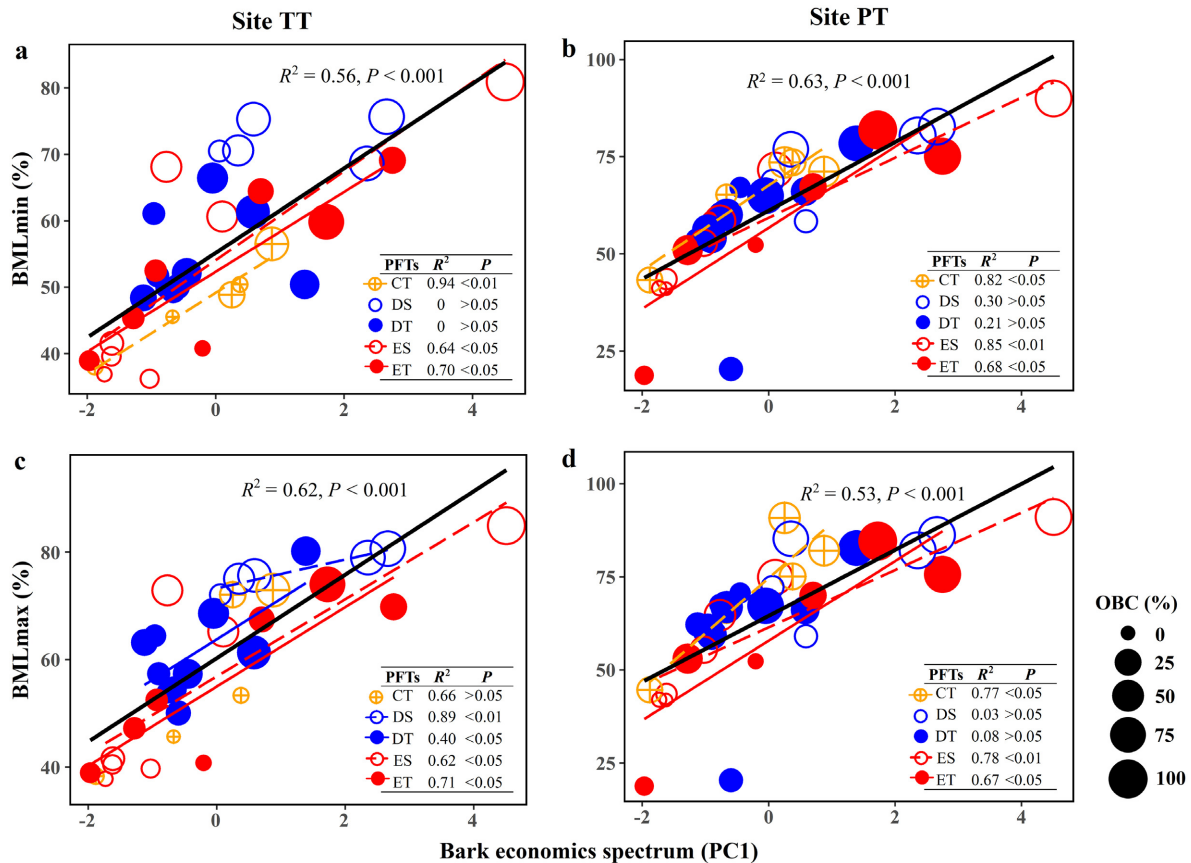
FIG. 3. Linear regressions between BES and BML (BMLmin, minimum bark mass loss; BMLmax, maximum bark mass loss) with regard to plant functional types (see Fig. 2 for abbreviations) in sites TT and PT, respectively. The solid black line represents the combined regression fit across all woody species. Insets: significance of the relationships between BES and BMLmax or BMLmin within plant functional types. The size of the points denotes the degree of termite consumption to the outer bark (OBC). Points represent mean values per species.

investment trade-offs (Pausas and Poorter 2014, Poorter et al. 2014) and, accordingly, could be linked to bark decomposability (Chang et al. 2020). Contrary to what Jones et al. (2019) have found in tropical forests in Panama, bark thickness was positively related to N content. Lignin is associated with promoting tissue physical structure (high BDM) and protection, i.e., resource conservation, leading to recalcitrant dead bark (cf. Cornwell et al. 2009). Bark cellulose content ranged from $16.4\% \pm 0.70\%$ across species, with on average 26.3% for *Manglietia insignis* being the highest and 9.76% for *Alniphyllum fortunei* being the lowest. It was positively correlated with N content (Fig. 2a; Appendix S1: Fig. S3), which may result from a high proportion of living cells in inner bark tissue, especially in the active phloem, requiring much cellulose in cell walls.

The significant role of the BES in regulating termite consumption and bark mass loss

We revealed strong evidence of an after-life effect of bark economics traits on bark decomposition across species, and termite consumption bolstered this relationship. Specifically, we found larger numbers of termites congregated on deadwood species at the acquisitive end of the BES than on more conservative species at the first harvest (Appendix S1: Fig. S5), i.e., initial termite colonization scaled with bark quality. Subsequently, as predicted termite consumption was prominently related to initial bark quality at second harvest in both sites. Termite consumption was negatively related with structure-related deadwood bark traits (BDM and C content), while termites preferentially consumed bark with higher cellulose and nutrient (N and P) contents (Appendix S1: Table S2). Surprisingly, bark termite consumption was not related to bark lignin content (Appendix S1: Table S2), perhaps because some plant species invest in other chemicals than lignin (e.g., suberin) for protection (Franceschi et al. 2005). Overall, bark mass loss and termite consumption had the same relations with initial bark traits as mentioned above, while we also found bark thickness positively related with overall bark mass loss (Appendix S1: Table S2). This may be because of the positive relationship between bark thickness and
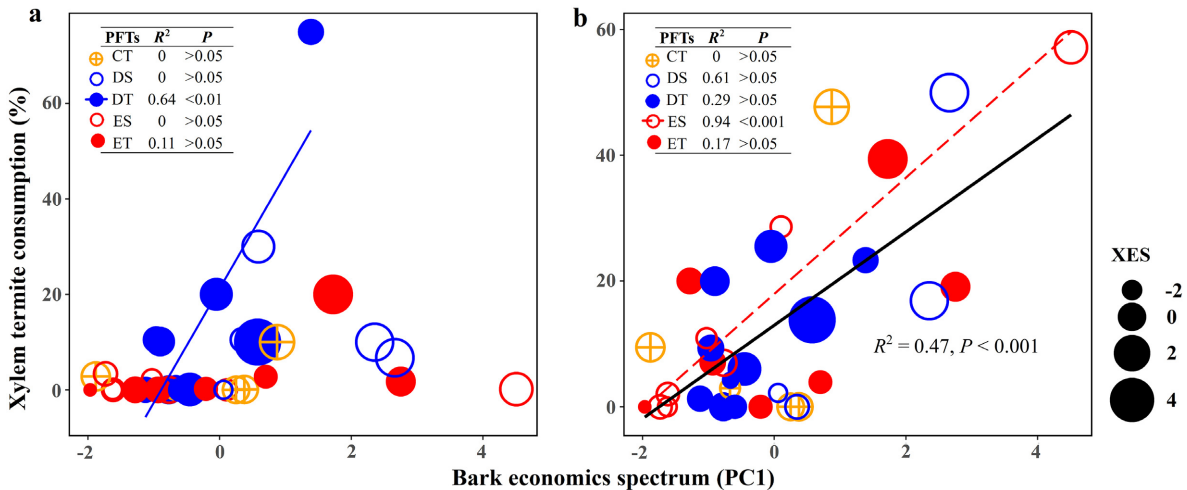
Fig. 4. The linear regression of BES against Xylem termite consumption, with regard to plant functional types (see Fig. 2 for abbreviations) in (a) Tiantong and (b) Putuo, respectively. The solid black line represents the combined regression fit across all woody species. Inset: significance of the relationships between BES and xylem termite consumption within plant functional types. The size of points denotes the XES value of each species. Points represent mean values per species.

nutrient content in our study, especially nitrogen (Appendix S1: Fig. S3), which normally promotes dead matter decomposition (Wardle et al. 1998). Generally, bark mass loss was primarily explained by the BES and the BES effect was likely to be influenced consistently by termite consumption (Fig. 3).

While we found strong bark-trait–decomposability relationships, we need to dig deeper to reveal their underlying mechanisms in future. For instance, bark is generally made up of two layers, i.e., tough outer bark is mainly responsible for plant protection (Rosell 2016), whereas inner bark composed of living cells is the major path for photosynthate transport and is closely related to tissue growth (Ryan and Asao 2014). The functional and structural differences between these two layers may result in their different palatability for decomposers, hence disproportionate mass losses in these two layers, with outer bark being more recalcitrant to decomposition than inner bark (Chang et al. 2020). Moreover, without follow-up studies, we cannot extrapolate our findings for 5 cm diameter stems to very coarse stems (e.g., ≥20 cm diameter) with any confidence at this stage, even though we would expect the (PCA) trait ordination of tree species to be somewhat robust to stem diameter in spite of absolute value differences.

Interaction among the BES, the XES, and termite consumption to xylem decomposition

One of the PES's arguments is that plant decomposability is coordinated across vegetative organs as the result of covariation of the functional traits among organs across species (Freschet et al. 2012). However, the covariation between xylem and bark traits is still largely unexplored (but see Jones et al. 2019, Chang et al.

2020) and so is the question whether the BES will affect the decomposition of xylem underlying bark. We first revealed strong covariation for four individual resource economics traits between bark and xylem across species, except for P and cellulose content (Appendix S1: Fig. S3), which suggest some parallels of resource use strategy adopted between bark and xylem. Indeed, as we predicted, BES and XES were significantly correlated with each other, albeit with substantial scatter around the trend-line (Fig. 2b), resulting in corresponding covariation in decomposability between bark and xylem across species; in other words, highly decomposable bark is likely to occur on trees with fast-decomposing xylem.

As predicted, termites consumed more xylem if bark quality was high. Specifically, we found BES explained 47% of variation in termite consumption to wood in site PT, so the XES effect on xylem decomposition was likely to be influenced by BES (Fig. 4). In contrast, XES only explained 31% of variation in xylem consumption due to termites (Appendix S1: Fig. S6b). This result implies there is a strong potential afterlife effect of BES on xylem decomposition besides XES itself, which corroborates previous research on the importance of the effect of bark during deadwood decomposition (Zuo et al. 2016, Dossa et al. 2018, Jones et al. 2020).

Even though our experiment provides strong evidence of the effect of bark quality on xylem decomposition, the nature of the bark effect and how long it lasts might depend on the bark quality. The questions arise whether bark with contrasting qualities would also impose other biotic or abiotic effects on xylem decomposition, e.g., by modulating xylem moisture or microbial access (Dossa et al. 2018); and how the invertebrates (termites) will modulate the relationship between such effect and xylem decomposition. In addition, the weight of BES and XES

effects on deadwood decomposition may shift in different decay stages (Dossa et al. 2018). Specifically, at the early decomposition stage, termites chiefly attack bark, and the species with different BES values interact with termites distinctly, leading to various degrees of termite consumption and bark mass losses. Later, after the high-quality bark has mostly been consumed, termites move down to the xylem, stay longer and cause more decomposition if the xylem is palatable; this is when the xylem quality becomes the dominant control on deadwood decomposition. Furthermore, because we cut stems to 20 cm long segments, there is a possibility that for some species with unpalatable bark, termites might have bypassed the bark and directly consumed the xylem underlying it via the cut surfaces. Actually, based on our field observation and termite consumption measurement, most of the termite consumption took place on bark first. In some cases, however, termites indeed circumvent the outer bark and enter from the cut ends, thus resulting in depletion of inner bark and termite consumption on xylem. One way to avoid this in future studies would be to seal the ends, with precautions to avoid other artefacts.

The positive relationship between bark termite consumption and bark mass loss across species (Fig. 3) indicates that the termite contribution to deadwood decomposition rates was mediated by deadwood quality. It seemed that xylem termite consumption in PT being higher than in TT (Fig. 4) was a result of more abundant termites in PT (Guo et al. 2021), which implies besides deadwood quality, the environmental variables (e.g., microclimate, soil properties, and decomposers pool) in two sites may affect termite communities and their contributions to deadwood decomposition across species. However, unlike studies conducted in plantation forests, where the compositions of deadwood substrate and decomposers are simple, the research into how the environment influences termite-mediated deadwood decomposition of a wide range of woody species is still scarce in diverse forests, given that it is often cumbersome to control and examine these convoluted variables. Therefore, further research is needed to enhance our understanding of how abiotic and biotic factors such as diverse invertebrate decomposers interactively affect deadwood decomposition dynamics.

Are the overall relationships among BES, termites, and bark mass loss also seen within plant functional types?

Based on the assumption of strong functional similarity among species belonging to the same growth form and/or leaf habit, plant functional types have been widely applied in vegetation modeling. However, this discrete classification may blur the variations in functional traits among species within plant functional types (see *Introduction*), thus issues emerge when modelers try to simulate and predict ecosystem functions, such as energy and chemical element flows (Kattge et al. 2011, Van

Bodegom et al. 2012). In support of H3, we demonstrated that species within plant functional types had broadly similar relationships of bark quality with termite consumption and bark mass loss across a number of plant functional types (Fig. 3, Appendix S1: Fig. S4). As a continuous index of species bark economics, BES captured much of these variations both across all species as well as within most plant functional types. This means it is not useful to assign a PFT with a single mean BES value to represent its bark mass loss and bark quality driven termite consumption during decomposition. Therefore, future bark ecology and bark trait-decomposability studies should focus on continuous bark trait variation at species-level rather than just at the PFT level.

Conclusion

We applied a functional-trait-based approach to extend the "plant-traits–decomposability" relationship previously shown for various plant organs across species to the last "missing" organ: bark. Our BES has helped to advance the understanding of the driving forces of bark mass loss and species-specific bark effects on deadwood decomposition. The BES could predict the termite inflicted bark consumption and bark mass loss across species and also within most plant functional types. Additionally, the BES also propelled termite consumption on xylem. The consequences of biodiversity change, e.g., through changes in nutrient cycling and carbon flux, has received recent attention (Handa et al. 2014). Our work has added a new dimension to this research field by showing the ecological significance of bark functional diversity to decomposition and how it mediates invertebrate (termite) activity in a subtropical region. Given the tremendous bark trait diversity observed at various spatial scales (Rosell et al. 2017) and the non-negligible control of the bark resource investment effect on deadwood decomposition as well as on fire-associated carbon emission (Staver et al. 2020), more bark ecology studies are needed in different biomes and ecosystems. Such studies will help to better understand the biogeochemical consequences of shifts in bark functional diversity and the potential role of bark traits in building more accurate versions of global carbon cycling models in response to climate changes.

out the data analysis; J. H. C. Cornelissen, C. Guo, and B. Tuo conceived the conceptual model. B. Tuo drafted the manuscript with input from all coauthors on one or more drafts.

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