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RESEARCH ARTICLE

How detritivores, plant traits and time modulate coupling of leaf versus woody litter decomposition rates across species

Chao Guo[1,2] | **Bin Tuo**[1,2,3] | **Hang Ci**[1,2] | **Bi-Le Sai**[1,2] | **Yu Zhang**[1,2] | **En-Rong Yan**[1,2] | **Johannes H. C. Cornelissen**[3]

[1]Zhejiang Zhoushan Archipelago Observation and Research Station, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, and Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China

[2]Institute of Eco-Chongming (IEC), Shanghai, China

[3]Department of Ecological Science, A-Life, Faculty of Science, Vrije Universiteit (VU University), Amsterdam, The Netherlands

Correspondence
En-Rong Yan
Email: eryan@des.ecnu.edu.cn

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Abstract

1. Plant functional traits are increasingly used to understand ecological relationships and (changing) ecosystem functions. For understanding ecosystem-level biogeochemistry, we need to understand how (much) traits co-vary between different plant organs across species and its implications for litter decomposition. However, we do not know how the degree of synchronous variation in decomposition rates between organs across species could be influenced by different keystone invertebrates decomposing different senesced plant organs, especially in warm-climate forests. Here we asked whether interspecific patterns in wood and leaf decomposition rates and in the spectra of resource economics traits underpinning them, co-vary across woody species; and how (much) the keystone invertebrate decomposers of the litter of these organs enhance or lower such co-variation of decomposition rates through time.
2. We addressed these questions through an 18-month 'common-garden' decomposition experiment using leaf, twig and branch litter of 41 woody species in two distant subtropical forest sites in east China. We quantified the effects of leaf, twig and branch functional traits and their respective key invertebrates (moth larvae, termites) on the decomposition rates of those organs.
3. Interspecific variation in wood traits was partly decoupled from that in leaf traits across species, while strong coupling was found between twigs and branches. The co-variation between leaf and woody organ decomposition rates was altered dynamically through the shifting activities of the key decomposers, which created nonlinear relationships of invertebrate litter consumption as a function of species rankings along the resource economic trait spectra of leaves and branches.
4. The deviations from coupling of decomposition rates between organs were likely caused by combinations of three mechanisms: (1) (de-)coupling between organs of other traits, not commonly considered in resource economics spectra (e.g. resins) (2) leaf and wood decomposers having specific diet requirements and (3) temporal patterns of the decomposers' activity.

5. *Synthesis*. Our study highlights the importance of considering the different ways by which invertebrate detritivores drive decomposition processes through time. Under the ongoing biodiversity decline, future research would benefit from a better understanding of the role of the dynamic interactions between detritivore activities and plant functional traits on the carbon turnover in ecosystems.

KEYWORDS
coordination, decomposition trajectory, evergreen broadleaved forest, leaf economic spectrum, moth larvae, plant organs, termites, wood economics spectrum

1 | INTRODUCTION

Understanding how plant functional traits and, consequentially, litter decomposition rates vary and co-vary among different plant organs across species, is pivotal for predicting biogeochemical cycles based on vegetation species composition (Freschet et al., 2012; Pietsch et al., 2014). While such co-variation between organs is important in most biomes, it is of particular importance in terrestrial woody ecosystems (forests, savanna, shrubland) and in aquatic ecosystems that receive much leaf and wood litter input from trees (Flores et al., 2011). Combining principles of resource economics trade-offs and coordination within and between plant organs, ecologists have proposed the plant economics spectrum (PES), which dictates how different plant species may live in different environments (Freschet et al., 2010; Reich, 2014). The logic behind this is that for a species living under certain constraints (e.g. biophysical, environmental), their organs would converge towards either an acquisitive resource economy or a conservative one overall (Díaz et al., 2016; Grime, 1979; Meinzer et al., 2008; Violle et al., 2007; Wright et al., 2006).

A recent study has extended the PES to decomposability relationships across species (Freschet et al., 2012). This PES-decomposability framework does not just link economics spectra of different plant organs to their respective decomposabilities. Rather, it reflects the coordination of the decomposability rankings of different organs across species as a result of the integrated whole-plant strategy. Specifically, plant species that lean towards a resource acquisitive strategy should decompose faster for each of their vegetative organs than those leaning towards a conservative one along the spectrum (Reich, 2014). Such species should therefore promote faster carbon and nutrient cycling overall. Although the PES-decomposability relationship has been supported by evidence across wide-ranging growth forms in the Sub-Arctic (Freschet et al., 2012), the empirical support within the tree growth form has so far been weak or absent, limiting our confidence in applying the PES-decomposability framework in forest biomes across the world. This apparent lack of coordination may relate to the different functions of leaves and woody organs. While leaves photosynthesize in order to supply all organs with organic resources, the main functions of woody stems are to transport resources and to provide the skeleton to mechanically support the foliage and reproductive parts. For instance, in neotropical forests, species with thicker leaves and low-density wood, or species with short-lived leaves and durable wood (Baraloto et al., 2010), caused decoupling of economic traits within the leaf economic spectrum (LES; Wright et al., 2004) from those within the wood economics spectrum (WES). Such lack of strong trait co-variation between wood and leaves also explains why wood and leaf decomposability were partly (Zuo et al., 2018) or mostly decoupled from each other across tree species (Jackson et al., 2013; Pietsch et al., 2014). Additionally, the decomposability of different organs may partly be related to leaf and twig decomposability being more closely linked to their chemical traits and coarse wood decomposability more to wood density (WD; Jackson et al., 2013). In summary, the evidence for the PES-decomposability framework is very mixed and mostly weak when tested across tree species.

Here we add a new dimension to the PES-decomposition framework, with potential importance especially in subtropical and tropical forests. In this region the co-variation of decomposition rates of leaves and woody organs could be influenced by keystone detritivores, which contribute substantially to overall decomposition rates for both leaf litter (Wall et al., 2008) and woody litter (Seibold et al., 2021). We suggest three possible ways by which detritivore decomposers might cause deviations between the PES for living organs and the co-variation of litter decomposability among organs across tree species. First, the traits measured along the PES tend to focus strongly on C, N and P economy as well as structure (e.g. dry matter content, DMC). However, to the perception of detritivores, additional traits may be important as well, for instance cation content (e.g. calcium important for hard body parts), specific secondary defence chemistry (e.g. phenolics, resins, waxes) or epidermal/bark structure (Dix & Webster, 1995). Such traits may or may not be coordinated between organs across species and may or may not cause inconsistencies between the PES of living organs and (detritivore-mediated) decomposition rates. Second, detritivores of wood and leaf litter are different taxonomically and functionally. Termites are paramount contributors to woody organ decomposition in (sub)tropical regions (Guo et al., 2021; Liu et al., 2015; Seibold et al., 2021; Ulyshen, 2016), while Lepidoptera (moth) larvae, Diptera (fly) larvae, Millipedes and Isopods are mainly responsible for leaf litter fragmentation (Guo et al., 2020; Lin et al., 2019). These different taxa may not be consistently aligned in their food preferences. For instance, leaf litter decomposers tend to prefer leaf tissues with relatively high nutrient content (Hättenschwiler & Gasser, 2005; Lin et al., 2019), while termites have a preference for cellulose-rich tissues among the deadwood species they feed on (Guo et al., 2021; Ulyshen, 2016). On the other hand, plant species that invest more in structure-related traits, for example, lignin and DMC, are normally perceived as less palatable by both leaf and woody litter decomposers (Fujii et al., 2018; García-Palacios et al., 2013; Liu et al., 2015). Therefore, leaf and woody litter decomposition rates at local scale are determined not only by their positions on the PES (overall quality), but also by the interactions of key detritivores with specific key traits (García-Palacios et al., 2016; Hättenschwiler & Gasser, 2005). Third, another reason for inconsistency between PES and variation in decomposition rates across organs and species might be temporal mismatches. For instance, Guo et al. (2020) found that, in a subtropical forest, the interplay between current leaf litter quality (through decomposition stages) and the abundance of the main leaf consumer (Lepidoptera larvae) through the seasons substantially altered the trajectory of leaf litter decomposition rates along the green leaf quality continuum across tree species.

Considering these three points, we propose and empirically test a conceptual model (with some roots in Pietsch et al., 2014) with different scenarios by which keystone detritivores and trait-based economics spectra of leaves, twigs and branches may together determine the degree of co-variation of decomposition trajectories among these organs. In this model (Figure 1), we hypothesize that, if any relationships between keystone detritivores intensity and economics spectra are positive and linear (panel A and all white boxes to the right), we could expect the following scenarios to happen: (a) if the WES is decoupled from the LES (a-1) and so is the wood detritivore feeding preference from the leaf detritivore feeding preference (a-2), then we will not find any relationship between the decomposition rates of leaves and woody organs (a-3). (b) If the WES and LES are significantly correlated (b-1) and so are the feeding preferences of woody organs and leaf decomposers (b-2), then the decomposition rates of these plant organs will be correlated (b-3). (Note: there can theoretically be no case where LES and WES are not correlated, but leaf detritivore intensity and wood detritivores intensity (feeding preference) are positively correlated in scenario A, because the detritivore activity rankings are prescribed as a linear function of the respective economics spectra for each organ. For the same reason, there is no theoretical case in scenario A where LES and WES are linearly correlated while leaf detritivore intensity (feeding preference) and wood detritivores

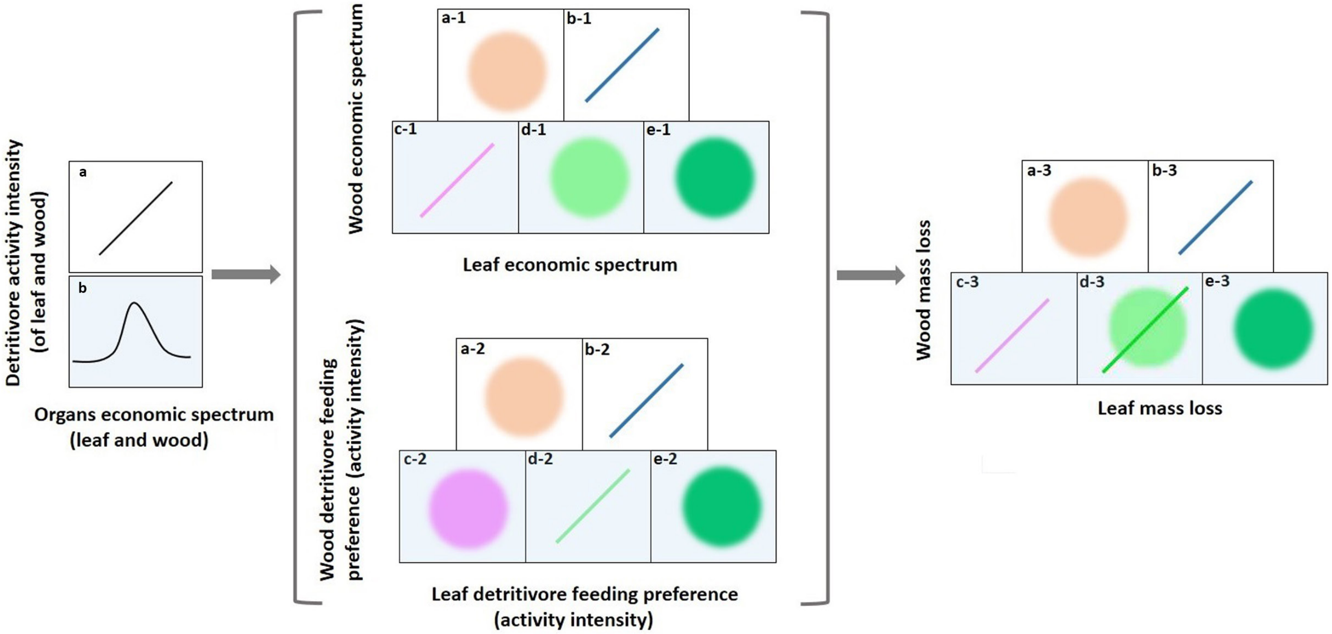


FIGURE 1 Conceptual model showing different hypothetical scenarios by which the litter species preferences of key detritivores and the degree of coordination of economic spectra between organs may lead to coupling or decoupling of mass loss rankings of leaf versus woody litter across tree species. Coupling is indicated by lines, decoupling is indicated by filled circles. Panel a and all white boxes show scenarios in which detritivore decomposer activity is positively correlated with tree species rankings along respective organ economic spectra. Here, letters a (beige circles) represents the lack of any co-variation between leaves and woody organs for any of the response variables and letters b (blue lines) represents strong linear co-variation of leaves and woody organs for all response variables. Panel b and all blue-shaded boxes show possible scenarios in which detritivore decomposer activity in leaf and/or wood litter does not have a positive relationship with their respective economic spectra. Here, c (purple lines and circle) represents strong organ co-variation for trait economic spectra but not for invertebrate preferences, still leading to strong co-variation of decomposition rates of leaves versus woody organs; and d (light green circle and lines) represents no organ co-variation for trait economic spectra but strong co-variation of invertebrate preferences (e.g. because of effects of traits that are outside the economics spectra); both co-variation or decoupled variation of decomposition rates of leaves versus woody organs are possible. Finally, e (dark green circles) represents neither organ co-variation for trait economic spectra nor for invertebrate preferences, thus leading to no co-variation of decomposition rates of leaves versus woody organs. Further details including explanation of letter-number codes, and the hypothesized mechanisms involved, are in the main text.

intensity (feeding preference) are not correlated). Panel B (and all blue shaded boxes to the right) represents scenarios by which the trajectories of keystone detritivores' feeding intensity follows a nonlinear curve with the WES or LES because of one of the three mechanisms introduced above, that is, (1) coupling or decoupling between organs of other traits, of importance to detritivores, that are not part of the economics spectra as commonly interpreted, (2) leaf and wood detritivores having specific diet requirements in terms of biochemical traits and (3) temporal patterns of the detritivores' activity. In these scenarios, we expect that, (c) if the LES and WES are positively coupled (c1), while the feeding preference of leaf decomposers do not match those of woody litter decomposers (c-2), we can still find (weaker) positive correlation between leaf and wood mass losses across species (c-3). Another case (d) is that there is no correlation between WES and LES (d1), but the feeding preferences of leaf and wood consumers are correlated, for instance because of coupling of other traits than those in the economics spectra (d2); thereby the mass losses of leaf and woody litter may either co-vary or not across tree species (d3). In addition, panel B includes a case (e), that has neither correlation between WES and LES, nor between the feeding preferences of leaf and wood consumers (e2); thereby the mass losses of leaf and woody litter may not be correlated across tree species (e3).

We apply this conceptual model to subtropical forest through a ‘common garden’ field experiment in which leaves, twigs and coarse branches of 41 diverse woody species were simultaneously assessed for decomposition rates and detritivore abundances over 18 months in two forest sites. Based on previous findings of strong temporal patterns of decomposer consumption activity of two separate plant organs from this experiment (Guo et al., 2020, 2021) albeit without any reference to organ co-variation and without reference to twigs as the organ connecting branches and leaves both physically and functionally, we expect that one of the scenarios under B in Figure 1 should prevail. To our knowledge, this is the first study in terms of theory and empirical testing of linkages between the trait co-variation in the PES, feeding behaviour of different detritivores and co-variation patterns in the decomposition rates among tree organs across species.

2 | MATERIALS AND METHODS

The twig component of this experimental work, including the huge twig-related dataset for traits, termite consumption and decomposition across 41 species in two sites, is entirely new and critical to testing our conceptual model and hypotheses. The work and datasets for leaf and branch traits and decomposition rates overlap strongly (but not completely; see our new data subsets on leaf and branch decomposition below) with those used in two previous studies on single tree organs to test different hypotheses unrelated to organ co-variation of traits and decomposition (Guo et al., 2020, 2021); for these organs we provide brief methods here with reference to these two studies for further details.

2.1 | Study sites

We conducted the in situ decomposition experiment Funlog in two subtropical evergreen broad-leaf forest sites in Zhejiang Province, E-China (details in Suppl. Table S1; Guo et al., 2020, 2021), both with subtropical monsoon climate: (i) Tiantong National Forest Park (TT; 29°52′N, 121°39′E) on the mainland, with *Schima superba* as the predominant tree species; (ii) Putuo island (PT; 29°97′N, 121°38′E), in the Zhoushan archipelago, with *Quercus glauca* being predominant. Based on previous observations (Guo et al., 2020), the moth *Arippara indicator* Walker is a key leaf litter detritivore in the PT forest litter layer. While 3–4 generations inhabit the litter layer from May to November (Leraut, 2013), larval abundance and consumption activity peak from August through November (details in Appendix S1: Figure S1). In both sites, termites are the main detritivores of deadwood including branches in the litter layer (details in Appendix S1: Figure S2; Guo et al., 2021).

2.2 | Tree species and sampling

In October–November 2017, we collected leaf, twig and branch samples from 41 common woody species in TT and PT, 8 evergreen trees, 12 evergreen shrubs (including short understory trees), 11 deciduous trees, 5 deciduous shrubs and 5 conifer trees (see Guo et al., 2021, details in Appendix S1: Table S2). In total, 195 individual healthy adult trees/shrubs were selected, that is, 27 species ×3 tree individuals and 19 species ×6 shrub individuals. The rationale for selecting living trees was (1) to standardize the initial, undegraded phase for all samples (Cornelissen et al., 2012); (2) to mimic typhoon-induced windthrow and logging as predominant agents of deadwood formation on the forest floor. We chain-sawed 20 cm long branch sections of approx. 5 cm diameter; cut twig samples into 10 cm long sections of approx. 2 cm diameter (to standardize diameter as a possible covariate of decomposition rate). Adjacent to each end of a branch we cut off a 2 cm thick disk for initial branch trait analyses, while for twigs and leaves we randomly selected subsamples from each individual per species for initial trait measurement. All leaf litter and twig samples were stored air-dried until further use. Due to space/time constraints, branch samples were weighed at field moisture before sealing them into litter bags (see below).

2.3 | Litter decomposition experiment

Similar sub-experiments were set up simultaneously at both sites. Leaf, twig and branch subsamples from each individual per species were weighed air-dried and oven-dried (75 °C) for the calculation of initial dry mass of the litter-bag samples via water content. For the leaf litter incubation, details are in Guo et al. (2020), but here we added a harvest after 18 months, which yielded a large new dataset compared with that study. Briefly, 10 g of pre-weighed air-dried leaves were sealed into 1-mm mesh nylon litter bags, with broadly similar packing density among species. For the twig incubation, we sealed two pre-weighed twig sections per sample into 10×20cm nylon litter bags with 4-mm mesh. For branch incubation (details in Guo et al., 2021, but here we added an additional 12 woody species to the decomposition dataset), we used 4-mm mesh nylon litter bags. These different mesh sizes were based on achieving the best compromise in terms of allowing free access to the main detritivores (allowing ranking of the 'natural' contribution of invertebrates to decomposition for each organ) while preventing litter particles from falling out throughout the decomposition trajectory for each of the tree organs – the latter was especially important for leaf litter of small-leaved conifers and fragile-leaved deciduous species. Based on field surveys before the experiment, the main leaf litter detritivores were moth larvae (Guo et al., 2020), which could enter the 1-mm mesh easily. Termites, which are estimated to be responsible for >90% of the invertebrate contribution to decomposition, were found to have body diameters between 1.21mm and 2.67mm (authors' measurements), leading to the choice of 4-mm mesh. The only other possible significant contributor to leaf and woody litter decomposition in our study sites, large millipeds, have body diameters around 7mm, so these had to be excluded from the experiment altogether to prevent litter-particle losses from the litter bags. In total, 2484 litter-bag samples were used, based on 46 tree species (including 5 repeated species)×3 organs ×3 replications (plots)×2 incubation sites ×3 harvest times.

The litter-bag samples were distributed over three replicate forest plots in each sites, in January 2018 (details in Guo et al., 2020, 2021). 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 organ one for each harvest. Harvests were after 6 (Jul. 2018), 12 (Jan. 2019) and 18months (Jul. 2019).

We carefully cleaned the collected leaf samples with a brush. Each twig and branch sample was put in a large tray with steep, tall edges to retain the termites. We cut the sample into small pieces and removed soil (brought in by termites) with a brush carefully. All samples were then oven-dried at 75 °C to constant mass and weighed (dry mass).

2.4 | Plant organ trait measurements

Details of leaf trait measurements relevant to the LES, including leaf thickness, leaf chemistry, specific leaf area and leaf dry matter content, were reported by Guo et al. (2020).

For initial wood traits considered relevant to the WES and to decomposition, each 2 cm subsample of branch or 10 cm long twig was stored cool in a sealed plastic bag between collection in the field and processing. Within 12h, after bark removal, a subsample was cut from each disk of branch and twig to obtain fresh mass and determine initial volume (Williamson & Wiemann, 2010). All wood subsamples were dried at 75 °C for 72h. Initial WD was calculated as dry mass per volume.

For chemical trait measurements of leaf and woody litter, initial leaf, twig and branch subsamples were ground to powder. Thereafter, 0.2 g sub-samples were digested using concentrated H_2SO_4 to determine N and P concentrations on an infrared spectrophotometer (Smartchem 200, Alliance, France). For branches, lignin content was determined by acidolysis-titration, and cellulose content was determined by anthrone-sulfuric acid colorimetry.

2.5 | Moth larvae and termite activity measurements

Upon harvesting of the leaf litter bags, macrofauna (*Arippara indicator* larvae) were collected and counted, and moth larvae faeces extracted, oven-dried at 75 °C and weighed for dry mass (details in Guo et al., 2020). The feeding intensity of larvae was defined by larval abundance and divided into six classes: (0), (1), (2), (3), (4) indicated 0, 1, 2 3, 4 larvae, respectively; (5) ≥ 5 larvae.

We visually scored the termites' feeding intensity of branches and twigs after cleaning the litter-bag samples. We (see Guo et al., 2021 for details) adjusted the method that classifies termite feeding intensity based on the bite marks (Liu et al., 2015). Briefly, we measured the percentage surface area loss due to termite activity using a visual grid method. After removing soil brought in by termites, we estimated the depth of termite damage in five random spots along the sample surface. The area loss and foraging depth were used to estimate the percentage of sample volume of twig or branch consumed by termites, distinguishing five classes: (1) 1–10% (2) 11–20%, (3) 21–30%, (4) 31–40% and (5) > 41% volume loss.

2.6 | Calculation of plant organ decomposition rate

Litter mass loss % was calculated as $\left[\left(M_i - M_f\right) / M_i\right] \times 100\%$, where M_i and M_f are the initial and final litter dry mass.

2.7 | Statistical analysis

All statistical analyses were performed in *R* language version 3.5.1. To test our main hypothesis, we quantified the degree of co-variation of trait variation across leaves, twigs and branches. We performed a principal component analysis (PCA; R package 'vegan', 'rda' function) to quantify the main axes of trait variation in of leaves, twigs and branches by using (1) the full set of (partly different) traits for the respective organs across species (as some traits representing organ-specific characteristics could not be measured on other tree organs; for details see Figure S3) and (2) a subset of analogous traits (organ N, P and C concentration, DMC; for details see Figure S3). Because the first axis score was high in both cases, we used the PC1 scores for the respective tree species to represent their position along the specific organs' economics spectrum positions in the subsequent analyses (Figure S3). Then, for each of the possible pairwise combinations of leaves, twigs and branches (full organs' trait set and analogous organs' trait subset), the strength of the relationships between the scores of the PC1 was assessed using Pearson's correlation analysis. We also calculated the Pearson's coefficients among all trait pairs between organs (see Figure S4).

Pearson's correlation analysis was also used to test whether the % mass loss of leaves, twigs and branches across species co-varied across harvest times (Jackson et al., 2013), that is, whether each of the three plant parts of all species decomposed with a similar decay curve (1:1 line in Figure 3; Table S3). Linear regression was used to find the best-fit relationship between organs' mass loss % and the economics spectrum (PC1 scores) of the specific organs separately for the different harvest times (see Figure 4; Table S4).

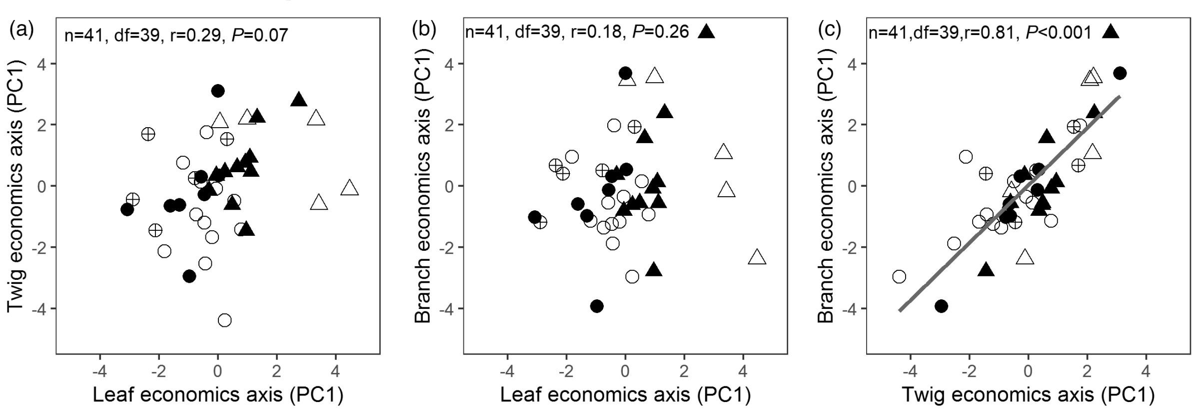
To evaluate the relationship between detritivore intensity and mass loss % of three plant organs in each of the two sites at each harvest time, linear regression was used (see Figure 5; Table S5). Also, to evaluate the relationship between detritivore intensity and the economics spectrum (PC1) of the three plant organs in each of the two sites at each harvest time, linear and nonlinear regressions were used to find the best-fit relationship (see Figure S5; Table S6). We used the R package 'ggplot2' for data visualization. For mass loss data, we used Levene's test to examine the homogeneity of variance and the Shapiro–Wilk test for normality.

3 | RESULTS

3.1 | The relationships among leaf, twig and branch economics spectra

The first PCA axis (PC1) accounted for 47.9%, 41.8% and 55.9% of trait variation in leaves (Figure S3a), twigs (Figure S3b) and branches (Figure S3c), respectively. The PC1 axes of woody organs and leaves were not related to each other (Twig: $p = 0.07$, Figure 2a; Branch: $p = 0.26$, Figure 2b), but there was significant relationship between PC1 axes for twigs and branches ($r = 0.81$, $p < 0.001$, Figure 2c). When considering the analogous set of traits (C, N and P content, DMC), the PC1 accounted for 36.5%, 45.3% and 50.1% of trait variation for leaves (Figure S3d), twigs (Figure S3e) and branches (Figure S3f), respectively. Wood and leaf traits were clearly

Different traits of organs



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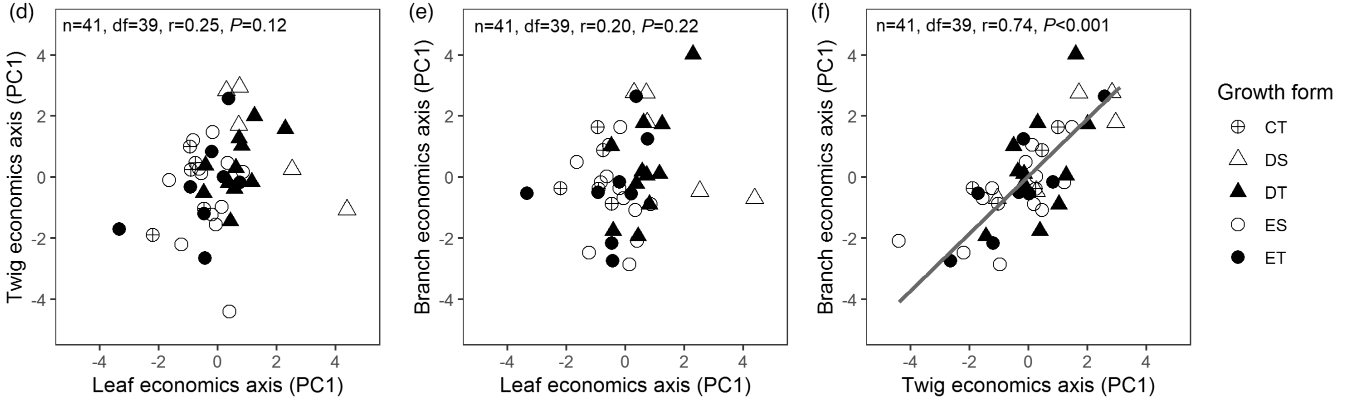

FIGURE 2 Correlations between organ-specific economics spectra for leaves, twigs and branches, as indicated by principal component analysis first axis score. In the top panels (a, b, c), the economic spectrum is constructed with the full set of (partly different) traits for each organ (with specific leaf area, leaf thickness and wood density as organ-specific traits), while the bottom panels (d, e, f) show the economic spectra constructed with the analogous traits (C, N, P, dry matter content) for each organ. (a, d) leaves versus twigs, (b, e) leaves versus branches, (c, f) twigs versus branches. Different symbols represent different functional groups and each point indicates one species.

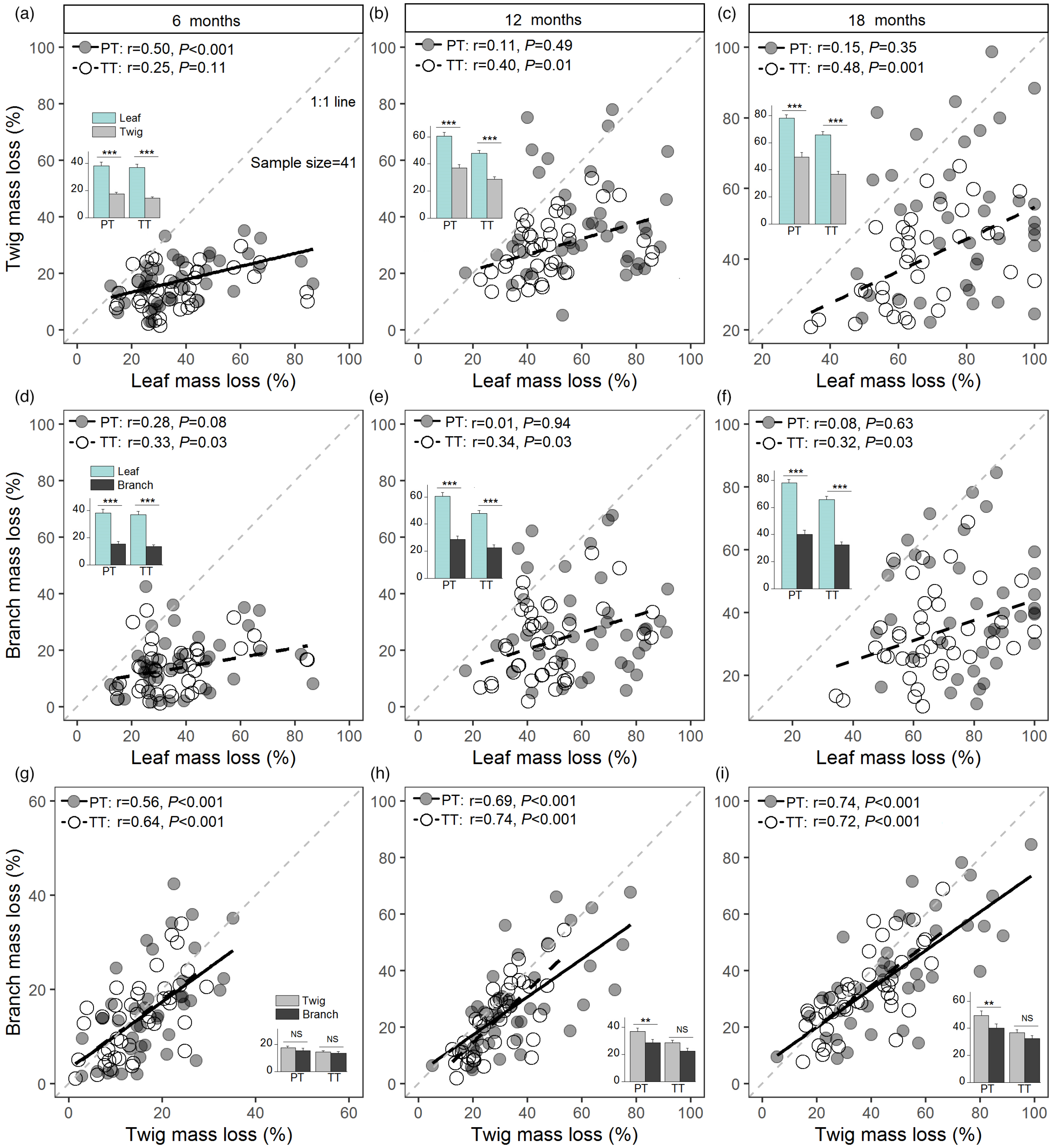

FIGURE 3 Comparison of mass loss % between leaves and woody organs at three harvest times in the PT and TT sites. (a, b, c) Relationships of leaf mass loss and twig mass loss, (d, e, f) relationships of leaf mass loss and branch mass loss and (g, h, i) relationships of twig mass loss and branch mass loss. Each circle represents a species. Solid line indicate there has a significant correlation trend in PT site and dashed line indicate there has a significant correlation trend in TT site ($p < 0.05$). And the light grey dashed line is 1:1 line. The inserted bar diagrams represent the mean mass loss values for each organ across species. Asterisks indicate significant differences between organs in each site (**$p < 0.01$; ***$p < 0.001$; NS, not significant).

decoupled in general (Twig: $p = 0.12$, Figure 2d; Branch: $p = 0.22$, Figure 2e), but leaf N content was positively correlated with twig P and branch N content (Figure S4); However, within woody organs there was again significant correlation between the PC axes of twigs and branches ($r = 0.74$, $p < 0.001$, Figure 2f), mainly due to C, N and P content (Figure S4).

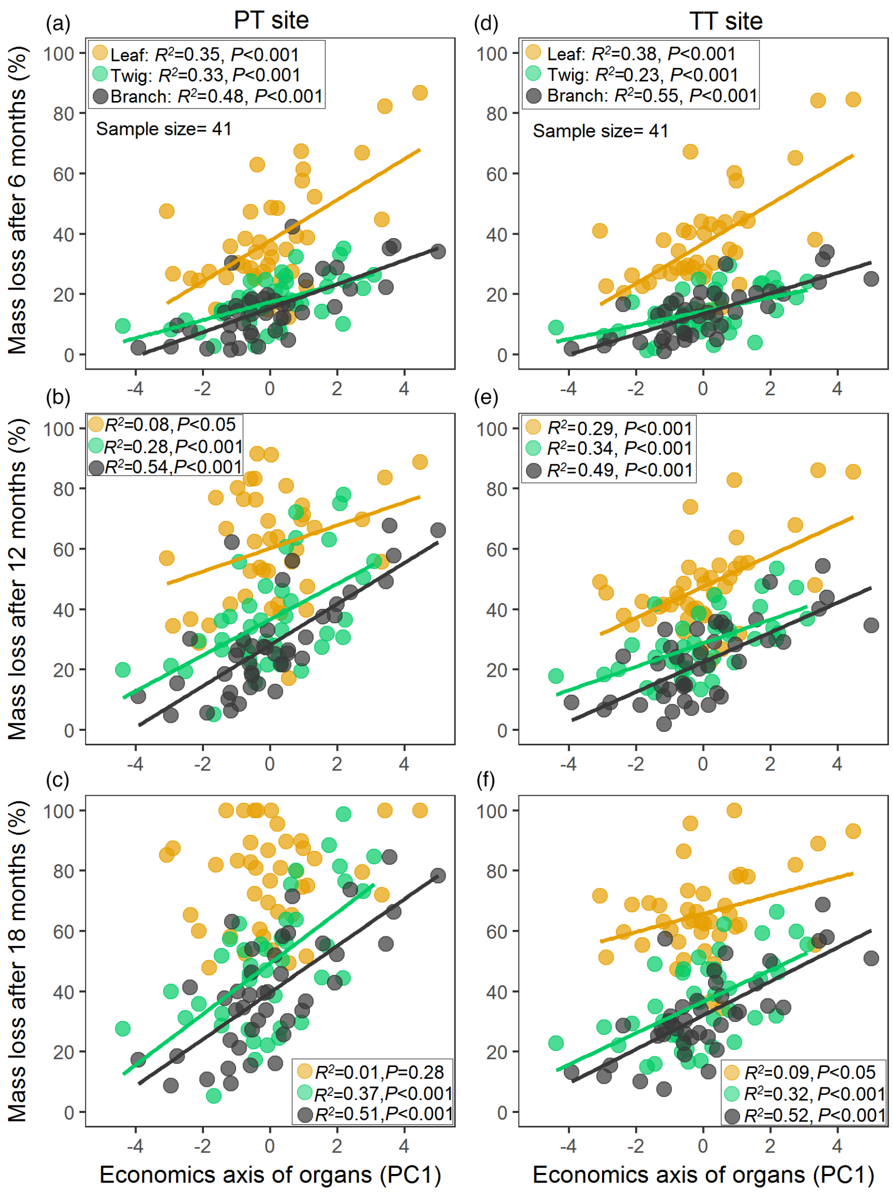

FIGURE 4 Relationships between economics axis of different organs (include leaf PC1, twig PC1 and branch PC1) and organs mass loss of harvest times at PT (a, b, c) and TT (d, e, f) sites.

3.2 | The decomposability of woody organs and leaves

After 18 months of decomposition, leaf litter lost on average 58.76 ± 2.84% of its mass in PT and 50.20 ± 2.38% in TT, twig mass loss was 34.52 ± 2.43% in PT and 26.65 ± 1.66% in TT and branch mass loss was 28.24 ± 2.88% in PT and 23.08 ± 1.72% in TT. Thus, when selecting the mass loss at the same harvest time for comparison, the order of decomposability was leaves > twigs > branches, while mass loss was generally faster in PT than in TT (Figure 3). There was a positive correlation between leaf and twig mass loss across species ($r = 0.50$, $p = 0.0008$, Figure 3a; Table S3b) in PT after 6 months, but the correlation disappeared after 12 and 18 months ($p = 0.49$, Figure 3b; $p = 0.35$, Figure 3c; Table S3b). Conversely, the correlation between leaf and twig mass losses in TT vanished for the first 6 months: ($p = 0.11$, Figure 3a; Table S3b) but emerged after 12 ($r = 0.40$, $p = 0.009$, Figure 3b) and 18 months ($r = 0.48$, $p = 0.001$, Figure 3c; Table S3b). Leaf and branch mass losses were not correlated in PT, and only a marginally significant trend was found in TT (Figure 3d–f; Table S3b). Within woody organs, twig and branch mass losses were correlated in both sites at different harvests time (Figure 3g–i; Table S3b). Mass loss rates did not differ between twigs and branches across three incubation periods in TT and for the first 6 months in PT but were significantly higher in twigs than in branches for 12 ($t = -8.09$, $p < 0.001$, Figure 3h; Table S3a) and 18 months in PT ($t = -9.57$, $p < 0.001$, Figure 3i; Table S3a).

3.3 | Relationships among organ-specific economics spectra, detritivore intensity and decomposition rate over time

The LES was positively correlated with leaf mass loss, and its coefficient declined over incubation time in both PT (6 months: $R^2 = 0.35$,

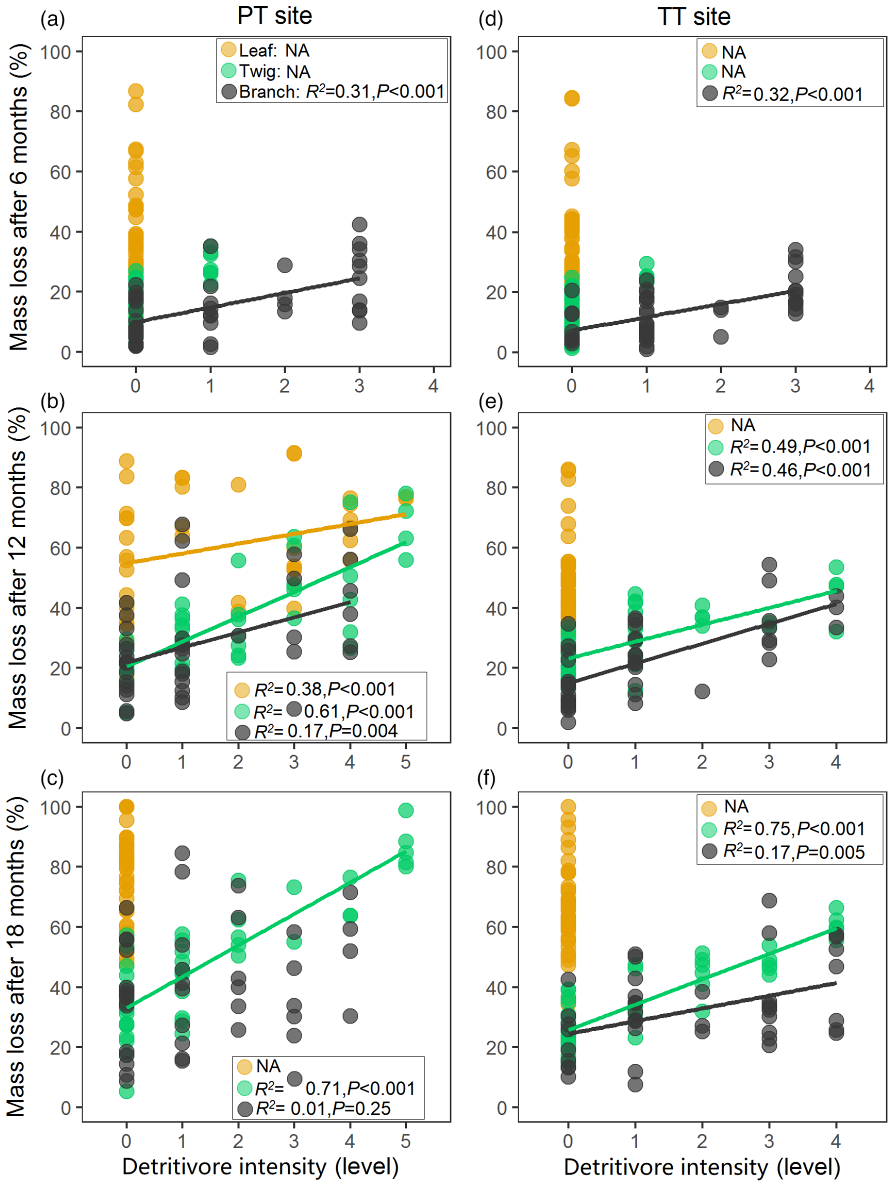

FIGURE 5 Relationships between detritivore intensity and organ mass loss at successive harvest times at PT and TT sites. There were no moth larvae in TT. The yellow dots indicate the relationship between leaf mass loss and the intensity of moth larvae in the leaf litter bags; the green dots indicate the relationship between twig mass loss and the intensity of termites in the twigs, while the black dots indicate the relationship between branch mass loss and the intensity of termites in the branch.

Figure 4a; 12 months: R^2 = 0.08, Figure 4b; 18 months: p = 0.28, Figure 4d) and TT (6 months: R^2 = 0.38, Figure 4d; 12 months: R^2 = 0.29, Figure 4e; 18 months: p = 0.04, Figure 4f). The correlation between the twig economics spectrum (TES; PC1 score for twigs) and twig mass loss remained significant across three harvests in both sites with increasing explanatory power of the TES over time (PT site: 6 months, R^2 = 0.33, Figure 4a; 12 months, R^2 = 0.28, Figure 4b; 18 months, R^2 = 0.37, Figure 4d; and TT site: 6 months R^2 = 0.23, Figure 4d; 12 months, R^2 = 0.34, Figure 4e; 18 months, R^2 = 0.32, Figure 4f; Table S4). The branch economics spectrum (BES; PC1 axis score for branches) correlated with branch mass loss in both sites, and the predictive power of the BES was approximately 52% throughout (Figure 4; Table S4).

The moth larvae foraging effect on leaf mass loss was not observed at the first and third harvests in PT (Figure 5a,c; Table S5) and all three harvests in TT (Figure 5d–f; Table S5), but only at the second harvest in PT (R^2 = 0.38, Figure 5b; Table S5). The termite feeding effect on twigs was not significant at the first harvest in either site, but significant during the 12- and 18-month periods in both sites (Figure 5; Table S5). There was a significant termite feeding effect on branches at the first two harvests in PT (6 months, R^2 = 0.31, Figure 5a; 12 months, R^2 = 0.17, Figure 5b; Table S5) and across the three harvests in TT (6 months, R^2 = 0.32, Figure 5d; 12 months, R^2 = 0.46, Figure 5e; 18 months, R^2 = 0.17, Figure 5f; Table S5).

There was a unimodal relationship between the initial LES and larval intensity at the second harvest in PT (R^2 = 0.15, Appendix S1: Figure S5b; Table S6), while the termite feeding effect on twigs showed positive correlations with the initial TES at the second and third harvests in both sites (Figure S5; Table S6). In addition, termite feeding intensity had a positive linear relationship with the BES in the first year of incubation (6 and 12 months) in both sites (Figure S5a–e; Table S6), while a hump-back relationship between termite feeding intensity and the initial BES manifested at the third harvest in both sites (PT: R^2 = 0.12, Figure S5c; TT: R^2 = 0.10, Figure S5f; Table S6).

4 | DISCUSSION

We present the first explicit study of the combined effects of plant traits and detritivores on the degree of coupling of leaf and woody organ decomposition rates across tree species. We demonstrate that functional traits of the leaf, twig and branch economics spectra are good predictors of interspecific variation in mass loss of these respective organs. This supports previous findings that plant functional traits can predict the decomposition of plant organs through their afterlife effects with substantial co-variation patterns between organs (Freschet et al., 2012; Zuo et al., 2018). This co-variation is an extension of the 'strategy theory' in which, under different regimes of environmental stress and disturbance, plants show a coordinated response across organs (Freschet et al., 2010; Grime, 1974; Westoby, 1998). However, our findings only partially support this theory. Specifically, our study demonstrates that woody organ traits and leaf traits are hardly or not correlated across species in subtropical monsoon forests, consistent with the results of 668 tree species in the tropical rain forest (Baraloto et al., 2010). In contrast, within woody organs (twigs versus branches) traits show strong co-variation across tree species, supporting previous findings in temperate forests (Zuo et al., 2018). Remarkably, we found some coupling of leaf and woody litter decomposition rates in spite of the mostly uncoupled economics spectra of leaves versus twigs or branches. Below we put these findings in the context of our conceptual framework and previous literature, emphasizing the non-negligible roles of dominant detritivores of leaf and woody litters in modulating the degree of co-variation between their decomposition rates.

4.1 | Hypotheses revisited: Decoupled leaf and wood economics spectra but some coupling of decomposition rates

Previous studies have found that the decomposition rates of leaves and woody organs are decoupled from the perspective of organ traits only, due to leaf litter decomposition largely being driven by chemistry traits, while wood decomposition is influenced strongly by structural traits (Jackson et al., 2013; Zanne et al., 2015). However, these studies ignored the effect of the role of specific decomposers on this relationship. Among the four alternative hypotheses in Figure 1, the most intuitively plausible ones are the (white) 'A' scenarios, that is, either (a) no co-variation of economics spectra, neither of consumption ranking along these spectra nor of decomposition rates between leaves and woody organs across woody species or (b) strong (or partial) linear coupling of economics spectra, of consumption ranking and of decomposition rates. Instead, our findings are somewhat consistent with one of the (light blue) 'B' scenarios in Figure 1 (d1, d2/3, d4): no co-variation of resource economics spectra, (partial) co-variation of detritivore consumption ranking and (partial) co-variation of decomposition rates between leaves and woody organs. Interestingly, the co-variation of decomposition rates between leaves and woody organs depended on the combination of incubation site and duration of decomposition (Figure 3). The moth larvae played a big role in leaf litter decomposition, and its temporal pattern, but only in PT (for further details see Guo et al., 2020), while the termite intensity in woody litter, especially in twigs, was higher in PT than in TT, while both detritivore taxa had strong temporal activity patterns in the litter (Figure 5). These differences together point to an important role for detritivores in the degree of coupling of decomposition rates between leaves and woody organs.

More specifically, we found evidence for all three detritivore-related mechanisms (see Introduction) operating at the same time, that is, (1) other traits than those measured for the economics spectra being at play (e.g. secondary chemistry traits inhibiting decomposition: polyphenols and tannins in Hegnauer & Hegnauer, 1964; stilbenes in Hart, 1981; terpenes, phenolic resins, flavonols and tropolones in Dix & Webster, 1995; pH increasing decomposability in Cornelissen et al., 2006; Fortunel et al., 2009); (2) specific food requirements of leaf versus wood detritivores (Lin et al., 2019; Strickland et al., 2009; Ulyshen, 2016) and (3) effects of temporal detritivore activity patterns (Guo et al., 2020). As for mechanism (1), our findings only partly corroborate those of the global analysis by Pietsch et al. (2014), who also reported moderate coupling of leaf and wood decomposition rates (as corrected for the contributions of environmental drivers) in spite of a general lack of coupling of resource economics traits. They explained this pattern by fundamental divergences between high-level taxa, especially gymnosperms (e.g. Berg & McClaugherty, 2008) versus angiosperms, pointing to a possible role for resins and recalcitrant chemical forms of lignin in the generally low decomposability of both leaves and wood of gymnosperms (Chave et al., 2009; Cornwell et al., 2008; Jackson et al., 2013; Pietsch et al., 2014; Weedon et al., 2009). In our Funlog common-garden experiment we found a comparable pattern in a termite exclusion sub-experiment (Guo et al., 2021), in which four Pinaceae gymnosperms had comparatively low decomposability of both leaf litter and woody litter compared with that of the (dicot) angiosperms (Appendix S1: Figure S6), in spite of a lack of clear separation of these taxa along the resource economics spectra for leaves and woody organs (Figure 2). However, this pattern only emerged in the absence of termites in the branch litter, presumably because of differences in microbial decomposition (Hättenschwiler & Gasser, 2005; Schwarze et al., 2000). Preferential consumption of gymnosperm branches by termites led to similar average branch decomposition rates between gymnosperms and angiosperms (Appendix S1: Figure S6). In contrast, the lepidopteran moth larvae were hardly found in litter bags with gymnosperm leaf litter (data not shown here), that is, they presumably contributed to the general pattern of low decomposability of gymnosperms leaves (due to their recalcitrant secondary chemistry, see above). These findings suggest that moth larvae are deterred by resins in gymnosperm leaves, while termites are not deterred by resins in gymnosperm wood. This negative modulation of the coupling of decomposition rates across major taxonomic divergences is also an example of mechanism (2) being at play, that is, leaf and wood detritivores having diverging trait preferences across species.

4.2 | The interactions of detritivores, time and organ-specific trait spectra on the co-variation of decomposition rates between organs

We also found evidence for combined effects of mechanisms 2 (food specificity of different detritivores) and 3 (temporal patterns of detritivores) on the degree of co-variation between organs. On the one hand, consistent with previous studies (Freschet et al., 2012; Jackson et al., 2013; Zuo et al., 2018), both chemical and structural traits in the LES, TES and BES largely controlled leaf, twig and branch decomposability, respectively. These patterns were very similar for twigs and branches across time in both sites (Figure 4), explaining the strong linear coupling between twig and branch mass loss rates throughout (Jackson et al., 2013; Zuo et al., 2018). However, this coupling would probably have been even stronger in the absence of termites, as the trajectories of termite consumption in relation to economics spectra differed between twigs and branches. Indeed, initially (after 6 months) the termite activity levels were still low in twigs and apparently independent of species ranking along the TES, while already then there was a linear relationship between the BES and termite activity level (Figure 5a,d), which must have amplified the linear positive mass loss pattern across the BES (Figure S5a,d). Subsequently (12, 18 months), the termite patterns also differed between twigs and branches but in a different manner. For twigs there was a consistent positive linear relationship between termite activity and mass loss (Figure 5b–f) and between the TES position and detritivore activity through time in both sites (Figure S5b–f). In contrast, termites initially followed the BES, while gradually (after 12 and 18 months respectively), they changed their preference towards species that had intermediate scores along the BES, resulting in a humpback relation of detritivore consumption level against BES (Figure S5b–f). Guo et al. (2021) interpreted this as the resources of the most palatable species (high BES scores) already having been depleted after the initial decomposition phase, while the intermediate species by then had been decomposed sufficiently to have become palatable to the termites; whereas the species with the lowest BES scores were still unpalatable. These deviations between the roles of termite activity in twigs versus branches through time must have made the coordination of mass losses of twigs versus branches less tight than would have been expected without termite interference.

In addition, we found a general positive trend of co-variation between leaf litter and twig decomposition rates, which is probably due to the fact that both leaf and branch decomposition are closely related to chemical traits (Jackson et al., 2013). However, the strength of co-variation of leaf and twig decomposition rates depended on the duration of decomposition and incubation site, as in a temperate study (Zuo et al., 2018). The leaf and twig mass losses in TT, in the absence of moth larvae, were significantly coordinated across species from 12 months and were the strongest by the end of the decomposition period (Figure 3a–c), suggesting indirectly that detritivores reduced the co-variation among plant organ carbon turnover patterns (Guo et al., 2020, 2021). Correspondingly, in PT, despite co-variation being significant after 6 months, the degree of co-variation kept reducing subsequently until it was no longer detectable. The pattern of co-variation for leaves versus branches was broadly similar to that for leaves and twigs, but the trend never reached the level of statistical significance (Figure 3d–f). We can largely explain these findings from the temporal pattern of consumption by the lepidopteran moth larvae in the PT site (Figure 5; Figure S5). Here, leaf litter of the initially more palatable species was consumed during the first 6 months; subsequently the species in middle-low positions along the LES continuum had likely become more palatable, while the palatable species had mostly been decomposed already (Guo et al., 2020). This led to a hump-back relationship of moth larval consumption against the LES (Figure S5) and the falling apart of co-variation between mass losses of leaves and twigs (or branches). We have to add a small caveat based on the different mesh sizes we used for leaf litter and woody litter. While we believe that our litter bags enabled a 'natural' ranking of invertebrate contributions to decomposition rates across tree species for each of the tree organs, with the possible exception of large millipedes to all organs (see Methods), we cannot exclude possible effects of small differences in microclimate inside 1 mm versus 4-mm mesh litter bags for these rankings. This issue is unlikely to have affected our main findings for the degree of coupling of decomposition rates between leaves, twigs and branches, demonstrating how such coupling can be strongly modulated by detritivore decomposers, and specifically by the interactive effects of litter traits, different detritivores and time.

In conclusion, we have shown that interactions between plant traits, key detritivores and time, are important for our understanding and predictive power of the co-variation of leaf, twig and coarse wood decomposition rates; and thereby of ecosystem-level carbon turnover based on woody species composition. Global quantification of these interactions are an important research challenge both for terrestrial woody ecosystems (e.g. forests, shrubland, savanna) and for stream and lake ecosystems that receive large amounts of litter input from neighbouring woody plants.

When combining decomposition of different organs, we should focus not only on the broad pattern that leaves decompose faster than twigs and twigs faster than branches of the same species (this study, Freschet et al., 2013). It is also important to understand how interspecific variation in mass losses of leaves, twigs and branches are or are not coordinated across species though the decomposition trajectory, as a result of the interplay of plant trait spectra and detritivore activity. This is part of a much broader research agenda, that is, interactions between animals and plants, whether in 'green' or 'brown' food webs, should be studied through time, as the temporal patterns of such interactions may contribute importantly to key ecosystem processes and functions.

AUTHOR CONTRIBUTIONS

En-Rong Yan, Johannes H. C. Cornelissen and Chao Guo designed and conceptualized the experiment; Chao Guo, Bin Tuo, Hang Ci, Bi-Le Sai and Yu Zhang collected the data; Chao Guo analysed data and wrote the manuscript; Chao Guo, Johannes H. C. Cornelissen and En-Rong Yan revised and improved the manuscript. All authors contributed substantially to revisions.

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CONFLICT OF INTEREST

The authors declare no competing interests.

PEER REVIEW

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DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.qjq2bvqkj (Guo et al., 2022).

ORCID

En-Rong Yan https://orcid.org/0000-0002-8064-3334

Johannes H. C. Cornelissen https://orcid.org/0000-0002-2346-1585

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SUPPORTING INFORMATION

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

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