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Title: Tree species richness increases spatial variation but not overall wood decomposition

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Abstract

Empirical evidence for the positive relationship between tree species richness and wood decomposition is weak, despite the greater numbers of decomposers in diverse stands. Tree species identity affects decomposition rates strongly by altering soil communities and micro-environments. It is therefore likely that tree species richness influences spatial variation rather than the mean rate of decomposition. We used a neighbourhood approach to test this hypothesis by quantifying decomposition rates and decomposer activities within deadwood, whilst measuring the surrounding micro-environments.

Using the BEF-China experimental platform, we placed three fine branches from seven tree species across richness gradients for one and two years. As expected, plot species richness increased the spatial variation of wood decomposition of three species but decreased the mean rate of wood decomposition of two species. Neighbourhood trees altered wood decomposition in two ways. First, increasing amounts of leaf tannins reduced termite activities and the number of fungal fruitbodies. Second, higher species richness increased tree volumes and thus cooled the understory, which reduced the occurrence and feeding intensity of ectothermic termites. Neighbourhood species richness showed positive effects on decomposer activities (i.e. termite occurrence, fruitbody number and mycelium cover) after two years, probably by weakening resource limitation of deadwood biomass and increasing the stages of decay. Neighbourhood metrics had comparable (after 1 year) and even stronger effects (after 2 years) on decomposer activities than wood traits. Our study reveals that tree species richness promotes spatial variation in wood

decomposition rates by enhancing environmental heterogeneity. Our results explain how young regenerating species-rich forests, where termites are the dominant decomposers, can maintain deadwood stocks and decomposer activities over relatively longer time spans.

Keywords: BEF-China, wood decomposition, tannins, temperature, termites, fungi

1. Introduction

Decomposition is central to ecosystem functioning, with ~ 90% of global terrestrial plant production entering the dead organic matter pool (Cebrian, 1999). One of the main drivers of decomposition is the diversity of living trees, which represents the main source of litter in forests (Cardinale et al., 2011). Tree species diversity is linked to decomposition rates because distinct litter traits among tree species attract decomposers with specific needs, leading to complementary resource use and facilitation among decomposers (Gessner et al., 2010; Austin et al., 2014). However, multi-site experiments find weak and even neutral effects of tree species richness on litter decomposition rates (Desie et al., 2023), especially for deadwood (Eichenberg et al., 2017; Joly et al., 2017; Pietsch et al., 2019).

As opposed to tree species richness, tree species identity has been shown to exert strong effects on decomposition rates (Vivanco and Austin, 2008; Desie et al., 2023), for example the 'home-field advantage' describes the rapid decomposition of litter in the vicinity of conspecifics (Purahong et al., 2019; Fanin et al., 2021). This effect is due to the plant-soil feedbacks that shape distinct soil communities and micro-environments under different tree species. For example, the dissimilarities of soil fungal communities (viz. saprotrophs, plant pathogens, and ectomycorrhizal fungi) increased significantly with woody plant phylogenetic distance in five mountain forests of eastern China (Yang et al., 2019). Moreover, more recalcitrant litters (Joly et al., 2017) and stronger shading (i.e. cooling) effects (Gottschall et al., 2019) of certain tree species could decelerate decomposition rates.

Logically, tree species richness is more likely than tree species identity to

diversify decomposition rates by creating micro-sites of distinct environmental conditions that alter the decomposing activities of soil communities. Indeed, the spatial variation of wood decomposition rates at local scales are considerable, with climate explaining only 28% of the variation in decomposition in one cross-site study (Bradford et al., 2014). In the meantime, high within-site replications and measurements of regulatory factors at the same spatial grain have been advocated to capture the spatial variation in decomposition rates (Bradford et al., 2016). We therefore set out to investigate how tree species richness causes spatial variation in wood decomposition rates, using a neighbourhood approach for each within-site replicate, i.e. measuring decomposer activities within and micro-environments around deadwood.

Termites and fungi are the major decomposers of deadwood in subtropical and tropical forests (Bradford et al., 2014; Ulyshen, 2016), meaning that rates of decomposition should be positively correlated with termite occurrence (Wu et al., 2020) and fungal fruitbody production (Raudaskoski and Salonen, 1984; Kües and Liu, 2000). Neighbourhood trees could affect termites' and fungal activities by modifying the understory environment, e.g. shedding leaves with distinct physico-chemical properties, and creating differing levels of shade depending on the size and species identity of trees (Wu et al., 2020, Wu et al., 2021b). Therefore, quantifying functional trait means, total tree volume and species richness of neighbourhood trees could better predict decomposer activities and decomposition rates.

If stand-level tree species richness increases the mean rates of wood decomposition, we should observe positive effects of neighbourhood (i.e. 3×3 tree

grid surrounding wood samples) species richness on decomposer activities which in turn promote wood decomposition. Moreover, if stand-level tree species richness increases the spatial variation of wood decomposition rates, we should observe significant effects of the environmental modifications by neighbourhood trees on decomposer activities and decomposition rates. Our experiments were based on the observation that wood traits and species identity substantially alter decomposition rate (van Geffen et al., 2010; Hu et al., 2018) and its dominant drivers (Wu et al., 2021a). By using fine branches of seven tree species as substrates, our experimental design allowed us to assess the relative contribution of neighbourhood metrics on decomposer activities and wood decomposition rates by comparing the standardised effect size with that of wood traits.

2. Material and methods

2.1 Study site and plot species richness

The study was conducted in the BEF-China experimental platform in Jiangxi Province, China (29.08°-29.11°N, 117.90°-117.93°E). The local climate is subtropical, with mean annual temperature and precipitation of 16.7°C and 1800 mm. A large-scale tree biodiversity experiment was initiated in 2009-2010 at two study sites (A and B) of approximately 20 ha each. Each plot is 25.8 m × 25.8 m in size and planted with 400 individual trees arranged on rectangular 20 × 20 grids with 1.29 m spacing between rows and columns. Plots were established adjacent to each other, forming a continuous cover across the entire site. Undesired herbs and woody species were removed from all plots annually. The composition of tree species for each richness gradient has been introduced in detail (Bruelheide et al., 2014). We selected

134 plots that spanned the study sites (Fig. S1), including 54 monocultures, 42 two-species mixtures, 21 four-species mixtures, 11 eight-species mixtures, four 16-species mixtures and two 24-species mixture plots. Given that decomposition experiments were conducted in the central grid of 6 × 6 trees, we defined plot species richness as the number of tree species within the central grid. Plot species richness ranged from 1 to 15. Number of trees per plot ranged from 108 to 400. Mean tree height (basal diameter) ranged from 0.12 m (0.27 cm) to 8.09 m (7.92 cm). Terrain slope ranged from 14.37º to 43.85 º.

2.2 Decomposition experiment

Seven tree species were chosen for the decomposition experiments: *Alniphyllum fortunei*, *Myrica rubra*, *Schima superba*, *Quercus serrata*, *Cunninghamia lanceolata*, *Platycarya strobilacea*, and *Castanopsis eyrei*. These species vary in wood density, C:N ratios, tannin content and lignin content (Table S1) and are widespread in southeast China (Wu et al., 2021b). Lignin content (%) was measured using near-infrared reflectance spectroscopy (Tsuchikawa and Kobori, 2015); tannin content (mostly condensed tannin; mg/g) by the radial diffusion method (Hagerman, 1988); C:N ratio by a CHNS-932 elemental analyzer (LECO Corporation, St. Joseph, MI, USA).

Healthy branches (length = 20.3 ± 0.6 cm; diameter = 1.5 ± 0.3 cm) were collected from living trees around the study sites in December 2014. Bark traits are different from wood tissue (Li et al., 2021) and pose distinct effects on wood decomposition rates across tree species (Dossa et al., 2018; Tuo et al., 2021). Therefore, we removed bark to focus on wood decomposition. Meanwhile, cut

surfaces on both ends of the samples were sealed with silicone to ensure that decomposers could only enter samples radially. This is because decomposers such as termites entering cut ends might show no sign on the radial surface and therefore the level of decomposer activities would be difficult to assess (see next section for details). 35 samples per species were dried to constant weight for > 48 h at 60 °C, and dry matter content was averaged for each species. The initial dry mass of field samples was estimated by multiplying fresh mass with species-specific dry matter content. Sample volumes were calculated as the cylinder, with diameter averaged from two measurements at both ends of the sample. Wood density was calculated as initial dry mass divided by sample volume.

Each sample was enclosed in a 5 mm mesh bag. Samples of seven species were joined together as a bundle using cable ties. Six bundles were placed at the base of six trees along the diagonal in each plot's central grid of 6 × 6 trees (Fig. S2). Having placed 5628 samples (7 species × 6 bundles × 134 plots) in January 2015, we retrieved half after one year (1st, 3rd and 5th bundle per plot) and half after two years (2nd, 4th and 6th bundle per plot). After removing fungal fruitbodies and soil transported by termites, samples were dried at 60 °C until we observed no further loss of weight. Wood mass loss was calculated as the ratio of dry mass loss to the initial dry mass.

2.3 Decomposer activity

Previous studies confirmed that termites are the dominant invertebrate decomposers of deadwood in the BEF-China experimental platform (Eichenberg et al., 2017). We recorded the occurrence (0/1) of termites within samples as the first

measure of termite activities. In addition, the feeding intensity of termites was also documented to estimate the level of termite-mediated decomposition. Termite feeding was evidenced by soil sheeting and bore holes on the surface of deadwood as well as soil and complex tunnels and galleries inside deadwood (Fig. S3). To determine termite feeding intensity, one person visually inspected the surface of each sample for boreholes (Liu et al., 2015; Cheesman et al., 2018), and then rated them using six predefined area percentage classes (estimated as 0, < 5, < 10, < 25, < 50, > 50), with the respective levels (n = 0, 1, 2, 3, 4, 5) used in the analysis.

Wood-decomposing fungi exploit resources through vegetative growth, i.e. mycelium (Baldrian, 2017). Before fruiting for spore dispersal, mycelium must reach a critical biomass which serves fruitbody production (Raudaskoski and Salonen, 1984; Kües and Liu, 2000). Therefore, we used mycelium cover and fruitbody number as the indicator of fungal-mediated decomposition. Mycelium cover on the wood surface was visually inspected and rated into six levels as with termite feeding intensity. The number of fruitbodies with clear boundaries was visually counted. In cases where fruitbodies formed conglomerations (e.g. *Trametes*), we treated each basidiocarp as a separate fruitbody because it could produce and disperse its own spores.

2.4 Neighbourhood metrics

The neighbourhood trees were defined as the grid of 3 × 3 trees surrounding the bundle of wood samples (Fig. S2a). Neighbourhood species richness ranged from 0 to 6 (Fig. S4a). Death of some trees meant that there were no neighbourhood trees for some bundles and so the analyses for neighbourhood effects excluded these samples.

We calculated the abundance-weighted mean of three plant traits (measured on fresh material) at the neighbourhood level, including wood density (g/cm^3), leaf nitrogen content (mg/g) and leaf tannin content (mg/g). These traits could impact the decomposing activities of termites and fungi mechanically through wood density (Liu et al., 2015; Wu et al., 2020), nutritionally through leaf nitrogen content (Allison et al., 2009; Mullins et al., 2021) and physiologically through leaf tannin content (Scalbert, 1991; Ismayati et al., 2018). We therefore used neighbourhood mean trait values to indicate the overall palatability of fallen branches and leaf-litter. Species-level trait data was accessed from existing datasets (Eichenberg et al., 2016a, 2016b) to calculate the neighbourhood means (Fig. S5).

Individual tree volume proxies (dm^3) were calculated as $H \times \pi(BR)^2$ in which H was height and BR was basal radius at the ground level. These volume proxies were transformed to more accurate tree volume estimates by multiplying the proxies with a size-dependent correction factor estimated and applied by a previous study (Huang et al., 2018). Individual tree data (H and BR) recorded in 2014 were used to estimate total tree volumes at neighbourhood (Fig. S4b) and plot levels. To quantify the cooling effects of total tree volume, we monitored air temperature at 30-minute intervals during the first year (2014-2015) with HOBO U23 Pro V2 data loggers (Onset Computer Corporation, Bourne, MA, USA). Aluminum panels placed ca. 5 cm above the loggers protected them from direct sunlight, rain, and wind turbulence. One logger per plot was placed between the 11th and 12th row and column of trees (Fig. S2). Mean annual temperatures were calculated and analyzed for relationships with total tree volume.

205 **2.5 Statistical analysis**

206 All statistical analyses were conducted in R version 4.0.5 (R Core Team, 2021).
207 We conducted analyses at two spatial scales. At the plot scale, we fitted simple linear
208 regression models to test if plot species richness increased the mean or spatial
209 variation of wood mass loss for each of seven tree species. The spatial variation was
210 estimated as the coefficient of variation (CV = standard deviation / mean × 100%) of
211 wood mass loss, which could control for the vast difference in wood mass loss among
212 species and across plots. Furthermore, we tested if tree species richness increased total
213 tree volume (Huang et al., 2018), which in turn can reduce air temperature (de Frenne
214 et al., 2019). This analysis was also applied at the neighbourhood scale.

215 At the neighbourhood scale, we fitted linear mixed models with R package '*lme4*'
216 (Bates et al., 2015) to test if neighbourhood species richness increased wood mass
217 loss for each of the seven tree species, with plot identity as random effect. We then
218 fitted bivariate generalised linear mixed models for wood mass loss (Gaussian),
219 termite occurrence (Binomial) and fruitbody number (Poisson) to test if they were
220 significantly related to five wood traits (diameter/density/C:N ratio/tannin/lignin) and
221 five neighbourhood metrics (richness.n/volume.n/density.n/nitrogen.n/tannin.n). The
222 ten predictors were scaled (mean = 0; standard deviation = 1) so that their parameter
223 estimates were comparable. Species identity of wood samples and plot identity were
224 treated as random effects. We fitted cumulative link mixed models with R package
225 '*ordinal*' (Christensen, 2022) for termite feeding intensity and fungal mycelium cover
226 since they were ordinal data. The highest log-likelihood was reached when the
227 threshold structure was set as 'flexible', and the link function as 'cloglog' and 'logit'

for 1-year and 2-year models, respectively. We also fitted mixed models to test if environmental predictors at coarser scale (study site/air temperature/plot species richness) significantly impacted wood mass loss and decomposer activities, by treating plot identity and species identity as random effects.

Finally, we fitted piecewise structural equation models with R package '*piecewiseSEM*' (Lefcheck, 2016) to test the potential paths from five wood traits and five neighbourhood metrics, via termite occurrence and fruitbody number, to wood mass loss. Previous studies have confirmed that termite feeding could alter fungal activities (Wu et al., 2020; Bradford et al., 2021), and we thus tested if termite occurrence significantly impacted fruitbody number. Instead of assuming an *a priori* full path model, we first ran a backward stepwise selection to remove variables of little importance. R package '*lmerTest*' (Kuznetsova et al., 2017) and '*StatisticalModels*' (Newbold, 2021) were used for variable selection of gaussian and non-gaussian mixed models, respectively. The remaining variables for each response were the input for *piecewiseSEM* analyses. Apart from the causal paths, we added the correlative path between neighbourhood species richness and total tree volume (Kunz et al., 2019). We used Shipley's d-separation test to evaluate model fit through Fisher's C statistic and χ^2-based *p*-value (Shipley, 2013). We refined the initial model by dropping non-significant paths or including missing paths that were significant, until the decrease in AICc (i.e. ΔAICc) was less than 2 units. See Table S2 for model selection and see Table S3-S4 for model summaries.

3. Results

We successfully retrieved complete samples from 134 plots after one year, and

from 126 plots after two years. Mean wood mass loss across the seven species was 46.6% ± 23.8% after one year, and 71.7% ± 25.0% after two years.

3.1 Does plot species richness increase the mean or spatial variation of wood mass loss?

Based on simple linear regressions (Fig. 1), we found negative effects of plot species richness on mean wood mass loss of two species (*A. fortunei* and *Q. serrata*), and positive effects on the coefficient of variation (CV%) of three species (*A. fortunei*, *Q. serrata* and *S. superba*). Results for the other species were insignificant ($p \geq 0.1$). Mixed models pooling all seven species (Table 1 and Table S5) showed that plot species richness had insignificant effects on wood mass loss and decomposer activities.

3.2 Does neighbourhood species richness drive wood mass loss via decomposer activities?

Bivariate linear mixed models at the sample-level (Fig. 2) showed that neighbourhood species richness had negative relationships with wood mass loss of three species (*A. fortunei*, *C. eyrei* and *S. superba*). Results for the other species were insignificant ($p \geq 0.1$). Similar results were found after pooling seven tree species (Fig. 3), namely that neighbourhood species richness significantly ($p \leq 0.05$) and marginally significantly ($0.05 < p < 0.1$) decreased wood mass loss after one year and two years, respectively.

Unexpectedly, neighbourhood species richness did not increase decomposer activities after one year but after two years (Fig. 3 and Fig. S6). Bivariate models showed that after one year of decomposition, there were significant negative effects of

neighbourhood species richness on fruitbody number but not on other metrics of decomposer activities. After two years of decomposition, we found positive effects of neighbourhood species richness on termite occurrence ($p = 0.010$) and fungal mycelium cover ($p = 0.069$) and found no significant effects on other metrics of decomposer activities. By incorporating all causal paths, *piecewiseSEM* models further showed that neighbourhood species richness had direct positive effects on fruitbody number after two years, which was neutralized by the indirect negative effects through increasing termite occurrence and the negative interactions between termites and fungi (Fig. 4b).

Bivariate linear mixed models (Table 2) showed that termites predominantly drove wood mass loss. After one year of decomposition, both termite occurrence and termite feeding intensity significantly increased wood mass loss, while fungal effects were insignificant. After two years of decomposition, termite feeding intensity increased wood mass loss significantly whereas termite occurrence had no significant effects. In contrast, both fungal fruitbody number and mycelium cover showed significant negative relationships with wood mass loss.

3.3 How do neighbourhood metrics alter decomposer activities and wood mass loss?

Besides species richness, three neighbourhood metrics showed impacts on decomposer activities and wood mass loss, including total tree volume ('Volume.n'), mean leaf tannin content ('Tannin.n') and mean wood density ('Density.n'). Although wood traits exerted stronger effects on wood mass loss, neighbourhood metrics exerted comparable and even stronger effects on decomposer activities (Fig. 3 and

297 Fig. S6).

298 Bivariate mixed models showed that Volume.n negatively affected termite
299 occurrence after one year ($p = 0.054$) but positively affected fruitbody number after
300 two years ($p < 0.001$; Fig. 3). The *piecewiseSEM* analyses showed that Volume.n
301 indirectly decelerated wood mass loss after one year by decreasing termite occurrence
302 (Fig. 4a). Similarly, Volume.n showed an indirect negative relationship with wood
303 mass loss after two years, which was mediated by the increase of fruitbody number
304 and its negative correlation with wood mass loss (Fig. 4b). Further analyses revealed
305 that neighbourhood species richness increased Volume.n, which in turn decreased air
306 temperature (Fig. 5 and Table S6). Mixed models at the sample-level (Table 1 and
307 Table S5) showed that temperature increased termite occurrence after one year ($p =$
308 0.006), and increased termite feeding intensity ($p = 0.063$) and wood mass loss after
309 two years ($p = 0.002$). In contrast, temperature showed negative relationships with
310 fungal mycelium cover after two years ($p = 0.003$).

311 Bivariate mixed models (Fig. 3) showed that Tannin.n had negative effects on
312 wood mass loss ($p = 0.070$), termite feeding intensity ($p = 0.066$; Fig. S6) and
313 fruitbody number ($p < 0.001$) after one year, and had significantly negative effects on
314 termite occurrence and fruitbody number after two years. The *piecewiseSEM* analyses
315 did not report direct or indirect effects of Tannin.n on wood mass loss but confirmed
316 that Tannin.n negatively impacted fruitbody number after one year (Fig. 4a), and
317 termite occurrence and fruitbody number after two years (Fig. 4b).

318 Bivariate mixed models (Fig. 3) showed that Density.n had significant negative
319 relationships with wood mass loss after two years. Density.n also had significant

positive relationships with fruitbody number at both time-steps, which was supported by the *piecewiseSEM* analyses (Fig. 4). Accordingly, we found that deadwood density decreased wood mass loss at both time-steps (Fig. 3). Meanwhile, deadwood density showed significant positive relationships with fruitbody number and mycelium cover at both time-steps, except that fruitbody number after two years decreased with higher deadwood density (Fig. 3f). Although we did not find significant relationships between Density.n and termite activitiy, we found significant negative effects of deadwood density on termite feeding intensity (Fig. S6a).

4. Discussion

4.1 Tree species richness decreases wood decomposition rate

Theoretically, increasing tree species richness should strengthen complementary resource use and facilitation among different decomposers, thus increase decomposition rate (Gessner et al., 2010). On the contrary, we observed negative effects of tree species richness on wood mass loss of four tree species at the plot scale and at the neighbourhood scale. Greater wood volume production and crown complementarity in the species-rich neighbourhood (Kunz et al., 2019) exert stronger cooling effects on the understory microclimate (de Frenne et al., 2019). Termites are ectothermic and their wood consumption rates generally scale with temperature (Gautam and Henderson, 2011; Griffiths et al., 2021). Accordingly, we found negative effects of total tree volume and positive effects of mean air temperature on termite activities, meaning that the 'Richness-Volume-Temperature' pathway could be an important mechanism reducing wood decomposition rates in young regenerating forests. Furthermore, increasing tree volume reduced maximum temperature but

343 increased minimum temperature (Fig. S9), which in turn reduced termite feeding
344 activity (Table S7). While reduction in maximum temperature could depress termite
345 activities due to their ectothermic and metabolic-driven nature, we posit that
346 increasing minimum temperature might release the overwintering termites
347 (*Reticulitermes* for most specimens discovered), which would have dwelled in and fed
348 on branch samples at low temperature (Hu and Song, 2014). Our study therefore
349 suggests that in young regenerating species-rich forests, where termites are dominant
350 decomposers, deadwood accumulation is greater (Liu et al., 2018) not only because of
351 biomass production (Huang et al., 2018), but also because of slower wood
352 decomposition.

353 Other mechanisms which are not covered in this study could contribute to the
354 negative effects of tree species richness on termite activities and wood decomposition.
355 First, the top-down control of decomposers by predators directly affects
356 decomposition rates (Gessner et al., 2010). Ants are widespread and efficient
357 predators of termites (Tuma et al., 2020). Previous studies in the BEF-China
358 experimental platform found that leaf-litter ant species richness increased with plot
359 tree species richness (Skarbek et al., 2020). Predatory ant species richness increased
360 with canopy density, lowering termite abundance (Wu et al., 2021b). Second, the
361 amount of surrounding deadwood could also play a role. We found that termite
362 occurrence (Fig. 3) and feeding intensity (Fig. S6) increased with wood diameter,
363 indicating that larger pieces of wood attract more termites than smaller pieces.
364 Termites would therefore be less likely to discover small pieces of deadwood when
365 more large-sized wood was being shed from neighbouring trees. Meanwhile, we

found that termites disliked deadwood of high density, C:N ratio and lignin content (Fig. 3 and Fig. S6). The amount and palatability of deadwood will therefore also affect decomposition rates.

4.2 Tree species richness increases the spatial variation of decomposition

Multiple studies have documented significant effects of tree species identity on decomposition rates (Vivanco and Austin, 2008; Gottschall et al., 2019; Peng et al., 2022; Desie et al., 2023). Our study has aligned tree species identity effects at the fine-scale with the spatial variation caused by tree species richness at the stand-level, which is often overlooked when only focusing on the relationship between tree species richness and the mean rate of wood decomposition (Eichenberg et al., 2017; Joly et al., 2017; Pietsch et al., 2019). In accordance with our hypothesis, three of seven tree species showed higher spatial variation of wood decomposition rates with increasing tree species richness at the plot scale. This indicates that environmental variation at the neighbourhood scale significantly alters decomposer activities and thus wood decomposition rates. To more accurately predict fine-scale wood decomposition rate in forests, the spatial variation in properties of neighbourhood trees, e.g. canopy gap and shading (Griffiths et al., 2021), should be fully considered.

In addition to the shading effects of neighbourhood trees, plant functional traits such as leaf tannin content and wood density could also impact decomposer activities and wood decomposition rates. First, tannins are detrimental for microbes because they inhibit extracellular enzymes, depriving the microbes of substrates for growth, and directly affecting metabolism (Scalbert, 1991). As expected, we found that leaf tannin content reduced fruitbody production, and even decreased termite activities,

probably by inactivating gut microbes and digestive enzymes (Ismayati et al., 2018). Although fruitbody production was not positively related with wood decomposition rates, tannins might influence fungal-mediated wood decomposition via unmeasured pathways, such as decelerating enzyme activities and biomass accumulation (Rubenstein et al., 2017). Second, wood density is one of the key traits that mechanically hinders termites from efficient consumption (Liu et al., 2015; Cosme Jr et al., 2018). Accordingly, we observed negative effects of deadwood density on termite feeding intensity. Therefore, neighbourhood trees with higher mean wood density could repel termites and thus indirectly lower wood decomposition rates (Fig. 3a, 3d) . Unexpectedly, mean leaf nitrogen content was unrelated with decomposer activities or wood decomposition rates, even though deadwood C:N ratios negatively affected termite activities and fruitbody production. Considering the high (> 50%) and species-specific resorption rate of limiting nutrients (e.g. N) from senesced leaves, nutrient traits of fresh leaves might not accurately represent those of litters (Vergutz et al., 2012). Therefore, future studies should consider measuring nutrient traits of senesced leaves to better predict decomposer activities and wood decomposition at the neighbourhood scale.

4.3 Tree species richness maintains decomposer activities over time

In addition to the richness-decomposition relationship, our study also stresses the critical role of tree species richness for maintaining wood decomposers and their activities over the course of the decomposition process, as we found that neighbourhood species richness increased termite occurrence, fruitbody number and mycelium cover after two years. Note that although two years appear short to study

412 wood decomposition, branch samples in our study already reached ~72% mass loss
413 after two years. First, deadwood serves as the food resources and habitats for various
414 wood-dwelling organisms (Thorn et al., 2020), meaning that the size and biomass of
415 deadwood stocks are critical for preserving the longevity and diversity of saproxylic
416 communities not limited to decomposers (Sandström et al., 2019; Uhl et al., 2022).
417 We found that wood diameter was positively associated with termite activities at all
418 time-steps (Fig. 3) and fungal mycelium growth (i.e. the vegetative state) after one
419 year (Fig. S6b). Furthermore, fungal activities were negatively correlated with wood
420 decomposition rates (Table 2 and Fig. 4b). Given that fungi are one of the major wood
421 decomposer groups in forest ecosystems, it is unlikely that increasing fungal activities
422 would decrease wood decomposition rate. Instead, with termites being the dominant
423 decomposers, faster decomposition rates due to termite activity lower the remaining
424 wood biomass. This may reduce fungal activities through resource limitation. This
425 was further supported by the finding that neighbourhood tree volume positively
426 impacted fungal fruitbody number (Fig. 3f). These findings altogether indicate that
427 tree species richness could attract and strengthen decomposer activities through
428 increasing wood production (Kunz et al., 2019) and decreasing wood decomposition
429 rates. Second, diversifying decomposition rates could contribute to the spatial and
430 temporal ‘source-sink’ dynamics of decomposer communities among deadwood of
431 different decay stages (Benbow et al., 2019). Comparatively speaking, termites are
432 early colonists (Ulyshen, 2016), whereas fungal diversity often peaks in advanced
433 stages of decomposition (Kubartová et al., 2015). As expected, we observed that
434 termite feeding marks were common for samples after one year of decomposition

(Fig. S7), whereas fungal marks were scarce until the second year (Fig. S8). Considering that saproxylic taxa colonize and utilize deadwood at different decay stages (Stokland and Siitonen, 2012; Yang et al., 2021), increasing the spatial variation of wood decomposition rates by increasing tree species richness could contribute to the conservation of saproxylic species diversity.

Finally, increasing tree species richness could enhance environmental heterogeneity, and thus mitigate interspecific competition among decomposers via niche partitioning. Consistent with previous studies (Ulyshen et al., 2016; Bradford et al., 2021), we found that termite feeding suppressed fungal activities, especially fruitbody production. This pattern could be due to the resource limitation caused by termite feeding and also due to the anti-fungal substances released by termites (Bulmer et al., 2012; Martin and Bulmer, 2018). We observed that fungi performed better in the absence of termites. First, fungal activities tended to increase with deadwood density and neighbourhood mean wood density. The only exception was that fruitbody production after two years of decomposition was higher for lower density deadwood. Given that the economic spectrum of wood traits shows a hump-shaped relationship with termite foraging populations in deadwood at later stages of decay (Guo et al., 2021), the predictive power of initial wood traits on decomposer activities weakens as decomposition proceeds. Fungal fruiting processes might be sensitive to such changes. Second, termites and fungi seemed to prefer different temperatures, which is consistent with empirical studies (Jonsson and Stokland, 2012; Zanne et al., 2022). We found that air temperature increased termite activities whilst suppressing fungal mycelium cover, and neighbourhood tree volume suppressed

458 termite occurrence whilst enhancing fungal fruitbody production. Altogether, these
459 findings suggest that fungi could avoid intense competition by occupying undesired
460 niches of termites.

461 **4.4 Conclusions**

462 Using a neighbourhood approach, we found evidence for the positive effects of
463 tree species richness on the patchiness but not the overall mean of wood
464 decomposition. Diverse stands in young forests or those undergoing regeneration will
465 experience cooler understory and thus lower rates of decomposition, due to the faster
466 volume growth and the suppression of termite feeding activity. Furthermore, different
467 tree species composition and functional traits at the neighbourhood scale strengthens
468 environmental heterogeneity and thus the spatial variation of decomposer activities
469 and wood decomposition rates. Altogether, our findings suggest that: 1) young
470 regenerating species-rich forests could maintain higher deadwood stocks by
471 decreasing wood decomposition rates, where termites are dominant decomposers; 2)
472 decomposition will be patchier in species-rich forests, which can be predicted by
473 crown shading and plant functional traits at the neighbourhood scale. Meanwhile, our
474 study suggests that tree species richness could contribute to the persistence of
475 decomposers by weakening resource limitation, and increasing the heterogeneity of
476 stages of wood decay. While two years seem to be enough for branch samples to be
477 highly decomposed in our study, future studies might consider monitoring
478 decomposer communities for longer temporal span (e.g. 3-5 years for coarse woody
479 debris) to verify if tree species richness drives the long-term maintenance of
480 decomposer activities.

Two open questions remain unresolved in our study. First, some species showed significant responses to tree species richness while others did not. While the small sample size (n = 3) per species per plot might not be enough to detect patterns, wood traits and quality might also alter the species richness effect. For example, species with higher lignin content would suffer from stronger negative effects by neighbourhood tree species richness (Table S8; marginally significant interaction between lignin content and richness). Future studies could select more species of varying traits to better understand the interaction effects between wood traits and neighbourhood species richness. Second, neighbourhood effects of tree communities might change with topography, for instance, the variation associated with sloping terrain. We found that terrain slope strengthened the effects of five neighbourhood metrics on fungal fruitbody number but not wood mass loss and the other proxies of decomposer activities (Table S9-S13). More studies would be needed to resolve the intricate effects of neighbourhood trees on decomposition given the complex terrain in many forest ecosystems.

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761

762 **Table 1.** Generalised linear mixed models of wood mass loss and decomposer
763 activities. Fixed terms included study site, air temperature and plot species richness.
764 Significant effects ($p \leq 0.05$) are printed in bold.

Response	Predictor	Estimate	SE	*t*(*z*)-value	*p*-value
	1-year-decomposition				
Wood mass loss	Intercept	0.464	0.077	6.058	<0.001
	Site [B]	0.011	0.007	1.451	0.149
	Air temperature	0.006	0.004	1.603	0.111
	Plot species richness	-0.001	0.001	-0.844	0.400
Termite occurrence	Intercept	-5.219	0.581	-8.983	<0.001
	Site [B]	**2.360**	**0.557**	**4.238**	**<0.001**
	Air temperature	**0.736**	**0.266**	**2.763**	**0.006**
	Plot species richness	0.076	0.094	0.809	0.418
Fruitbody number	Intercept	-10.739	1.161	-9.253	<0.001
	Site [B]	-0.597	1.184	-0.504	0.614
	Air temperature	-0.110	0.583	-0.189	0.850
	Plot species richness	0.115	0.198	0.580	0.562
	2-year-decomposition				
Wood mass loss	Intercept	0.707	0.074	9.533	<0.001
	Site [B]	**0.038**	**0.012**	**3.188**	**0.002**
	Air temperature	**0.018**	**0.006**	**3.089**	**0.002**
	Plot species richness	-0.003	0.002	-1.377	0.171
Termite occurrence	Intercept	-3.351	0.363	-9.233	<0.001
	Site [B]	**0.877**	**0.384**	**2.283**	**0.022**
	Air temperature	-0.115	0.182	-0.631	0.528
	Plot species richness	0.004	0.072	0.051	0.959
Fruitbody number	Intercept	-0.581	0.420	-1.384	0.166
	Site [B]	0.453	0.325	1.395	0.163
	Air temperature	-0.088	0.156	-0.565	0.572
	Plot species richness	0.025	0.060	0.419	0.675

765

766 **Table 2.** Bivariate linear mixed models of wood mass loss. Four indicators of

767 decomposer activities were treated as the fixed effect separately. Significant effects (p

768 ≤ 0.05) are printed in bold.

Predictor	Estimate	SE	*t*-value	*p*-value
1-year-decomposition				
(Intercept)	0.463	0.076	6.083	<0.001
Termite occurrence	**0.026**	**0.009**	**2.756**	**0.006**
(Intercept)	0.378	0.063	5.993	<0.001
Termite feeding intensity	**0.048**	**0.002**	**25.146**	**<0.001**
(Intercept)	0.466	0.076	6.101	<0.001
Fruitbody number	-0.001	0.001	-1.183	0.237
(Intercept)	0.467	0.076	6.109	<0.001
Mycelium cover	-0.009	0.011	-0.885	0.376
2-year-decomposition				
(Intercept)	0.719	0.074	9.747	<0.001
Termite occurrence	-0.017	0.012	-1.496	0.135
(Intercept)	0.452	0.049	9.254	<0.001
Termite feeding intensity	**0.075**	**0.002**	**43.323**	**<0.001**
(Intercept)	0.720	0.074	9.773	<0.001
Fruitbody number	**-0.001**	**0.000**	**-5.852**	**<0.001**
(Intercept)	0.736	0.072	10.180	<0.001
Mycelium cover	**-0.039**	**0.003**	**-12.640**	**<0.001**

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Fig. 1 Plot tree species richness effects on wood mass loss of seven species. The response variable of the left and right panel is the mean rate and the spatial variation of wood mass loss, respectively. The upper (or lower) panels refer to 1-year (or 2-year) decomposition. Significant ($p \leq 0.05$) relationships are printed as solid lines with the 95% confidence interval; marginally significant ($0.05 < p < 0.1$) relationships are printed as solid lines; insignificant ($p \geq 0.1$) relationships are printed as dashed lines.

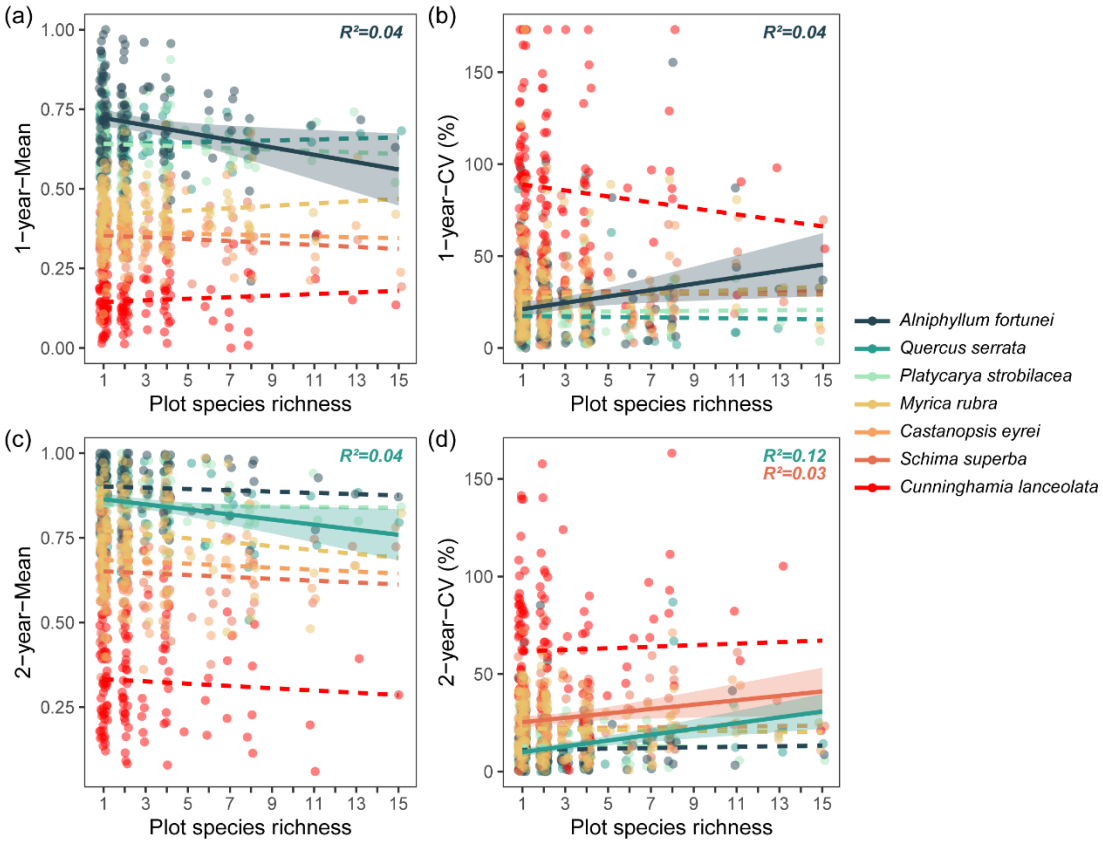
Fig. 2 Neighbourhood tree species richness effects on sample-level wood mass loss of seven species. The predictor variable of the left and right panel includes and excludes zero values, respectively. The upper (or lower) panels refer to 1-year (or 2-year) decomposition. Significant ($p \leq 0.05$) relationships are printed as solid lines with 95% confidence intervals; marginally significant ($0.05 < p < 0.1$) relationships are printed as solid lines; insignificant ($p \geq 0.1$) relationships are printed as dashed lines.

Fig. 3 Bivariate generalised linear mixed model results of wood mass loss and decomposer activities. The response variable of the left, middle and right panels is wood mass loss, termite occurrence and fruitbody number, respectively. The upper (or lower) panels refer to 1-year (or 2-year) decomposition. The mean (dot) and 95% confidence intervals (bars) of the standardised parameter estimates for each of five wood traits and five neighbourhood metrics were reported separately. Note that positive effects are printed in black while negative effects in red. Significance is indicated as: +, $0.05 < p < 0.1$; *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

Fig. 4 The piecewise structural equation model results after 1-year (a) and 2-year decomposition (b). The causal relationship is denoted as the single-arrow line while

the correlative relationship as the double-arrow line. Wood traits (in the brown box) and neighbourhood metrics (in the green box) are distinguished by colour. The path coefficients and model fits (in the grey box) are reported, as well as the marginal (and conditional) R^2. Note that all significant paths are solid lines ($p \leq 0.05$) except for the dashed paths ($0.05 < p < 0.1$). Path colour indicates the direction of relationship, with positive in black and negative in red. The paths related to neighbourhood tree species richness are printed thicker for readers' convenience.

Fig. 5 The linear relationship among tree species richness, total tree volume and mean air temperature. The upper panel tests the linear relationship at the plot scale while the lower panel at the neighbourhood scale. Total tree volume is log(1+V) transformed before analysis. Note that plot species richness effect on plot tree volume is marginally significant ($0.05 < p < 0.1$) while the other linear relationships are significant ($p \leq 0.05$). The piecewise structural equation models are used to summarise the relationship between three variables at the plot scale (c) and at the neighbourhood scale (f).


(a)
R²=0.04
1−year−Mean
1.00
0.75
0.50
0.25
0.00
1 3 5 7 9 11 13 15
Plot species richness
(b)
R²=0.04
1−year−CV (%)
150
100
50
0
1 3 5 7 9 11 13 15
Plot species richness
(c)
R²=0.04
2−year−Mean
1.00
0.75
0.50
0.25
1 3 5 7 9 11 13 15
Plot species richness
(d)
R²=0.12
R²=0.03
2−year−CV (%)
150
100
50
0
1 3 5 7 9 11 13 15
Plot species richness
Alniphyllum fortunei
Quercus serrata
Platycarya strobilacea
Myrica rubra
Castanopsis eyrei
Schima superba
Cunninghamia lanceolata

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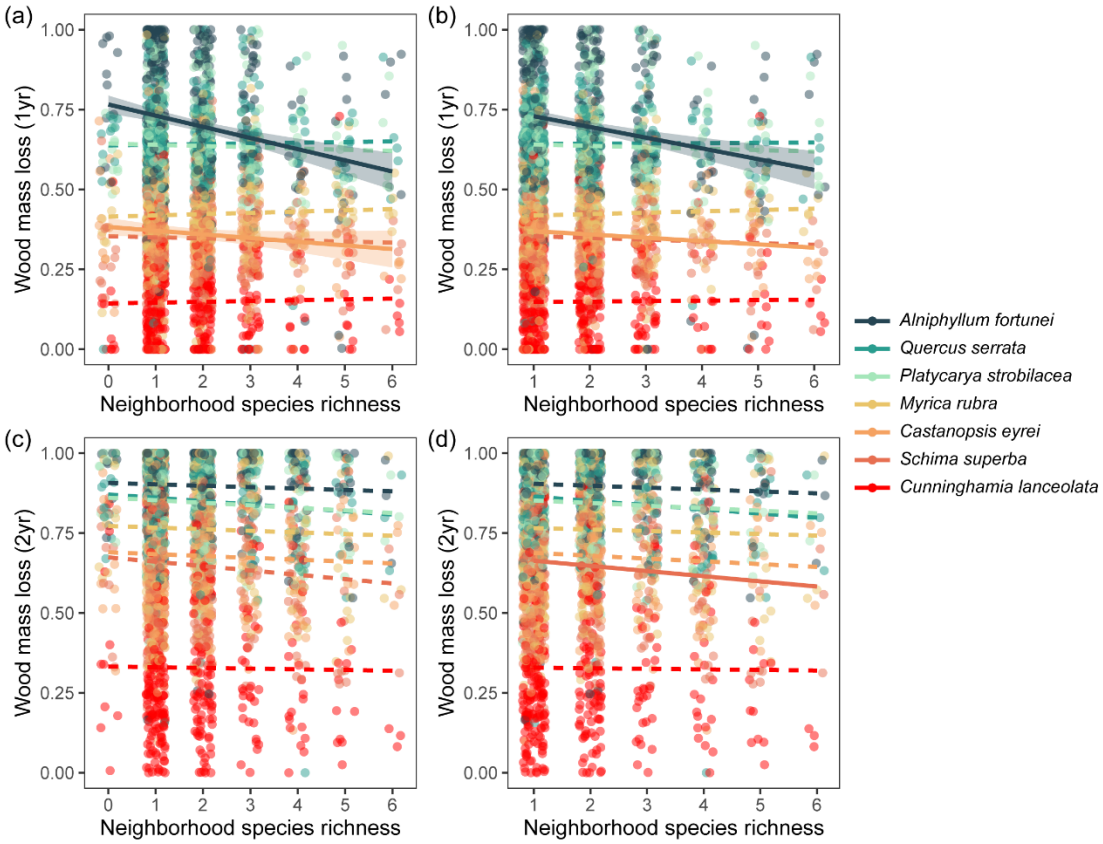
810 **Fig. 1**


(a)
(b)
(c)
(d)
Wood mass loss (1yr)
Wood mass loss (2yr)
Neighborhood species richness
1.00
0.75
0.50
0.25
0.00
0 1 2 3 4 5 6
1 2 3 4 5 6
Alniphyllum fortunei
Quercus serrata
Platycarya strobilacea
Myrica rubra
Castanopsis eyrei
Schima superba
Cunninghamia lanceolata

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812 **Fig. 2**

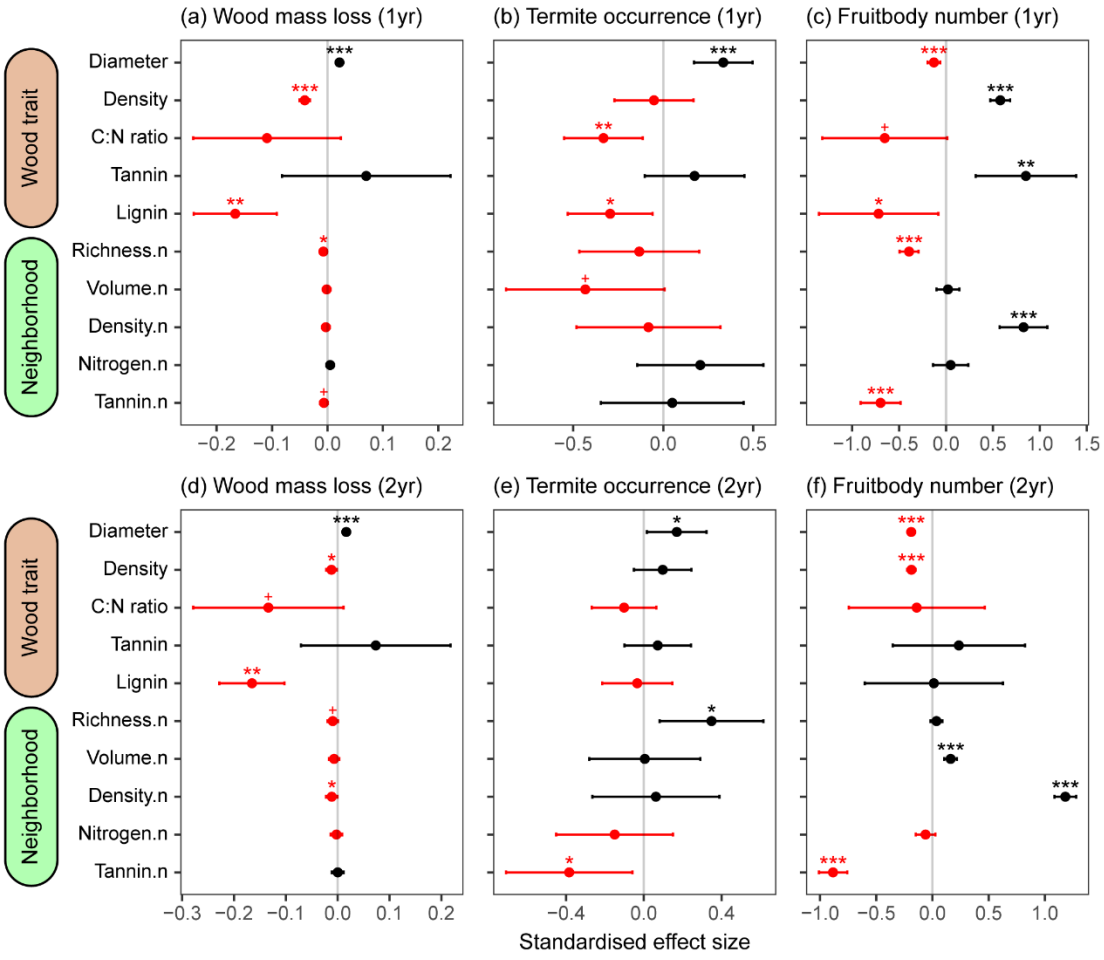
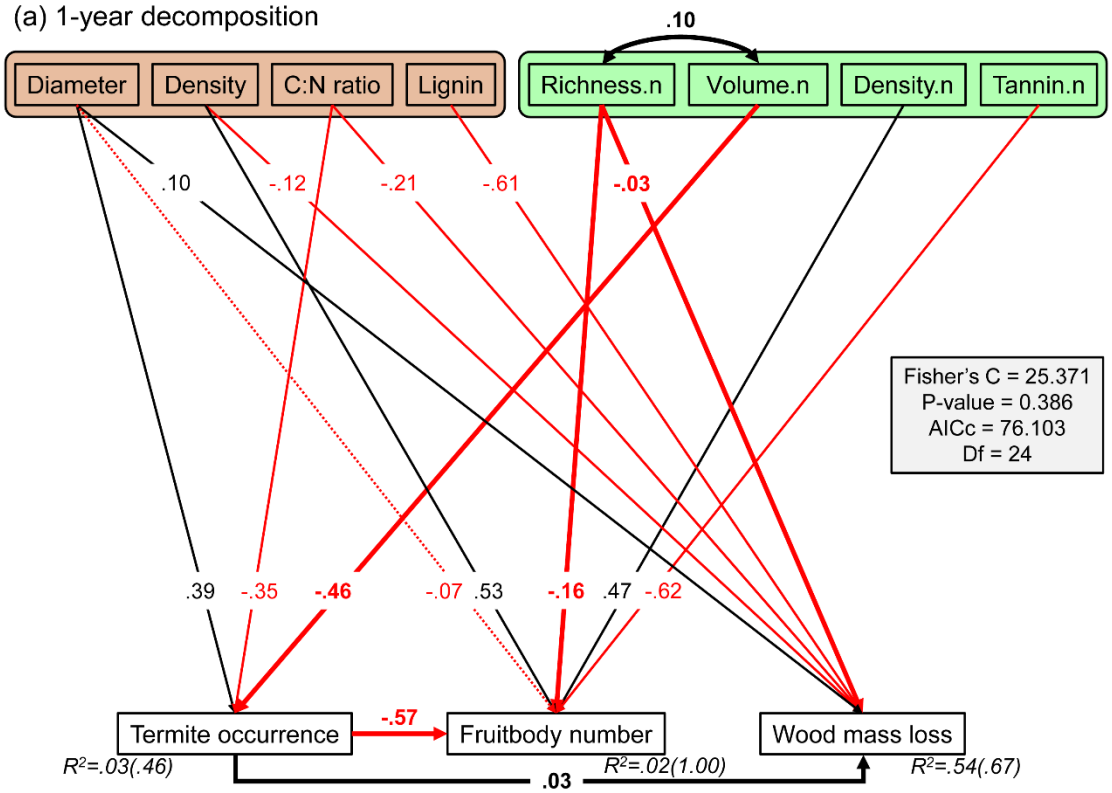

(a) Wood mass loss (1yr)
(b) Termite occurrence (1yr)
(c) Fruitbody number (1yr)
(d) Wood mass loss (2yr)
(e) Termite occurrence (2yr)
(f) Fruitbody number (2yr)
Wood trait
Neighborhood
Diameter
Density
C:N ratio
Tannin
Lignin
Richness.n
Volume.n
Density.n
Nitrogen.n
Tannin.n
Standardised effect size

Fig. 3


(a) 1-year decomposition
.10
Diameter
Density
C:N ratio
Lignin
Richness.n
Volume.n
Density.n
Tannin.n
.10
-.12
-.21
-.61
-.03
Fisher's C = 25.371
P-value = 0.386
AICc = 76.103
Df = 24
.39
-.35
-.46
-.07
.53
-.16
.47
-.62
Termite occurrence
-.57
Fruitbody number
Wood mass loss
R²=.03(.46)
R²=.02(1.00)
R²=.54(.67)
.03

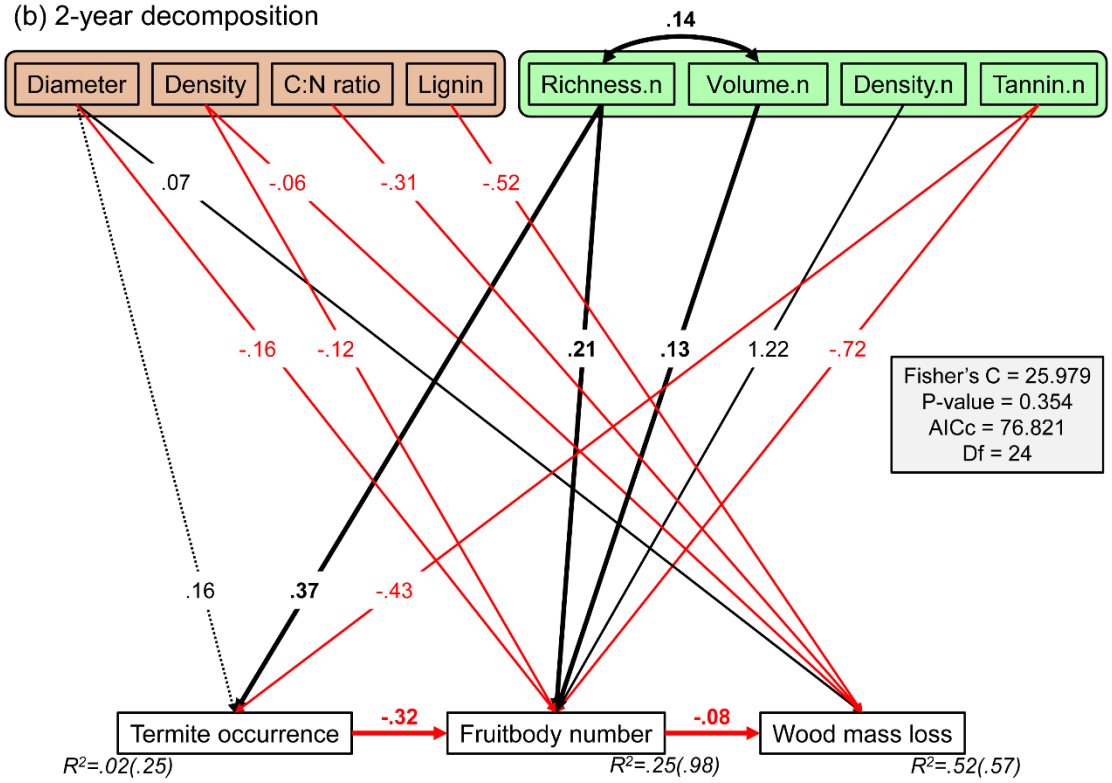

(b) 2-year decomposition
.14
Diameter
Density
C:N ratio
Lignin
Richness.n
Volume.n
Density.n
Tannin.n
.07
-.06
-.31
-.52
-.16
-.12
.21
.13
1.22
-.72
Fisher's C = 25.979
P-value = 0.354
AICc = 76.821
Df = 24
.16
.37
-.43
Termite occurrence
-.32
Fruitbody number
-.08
Wood mass loss
R²=.02(.25)
R²=.25(.98)
R²=.52(.57)

Fig. 4

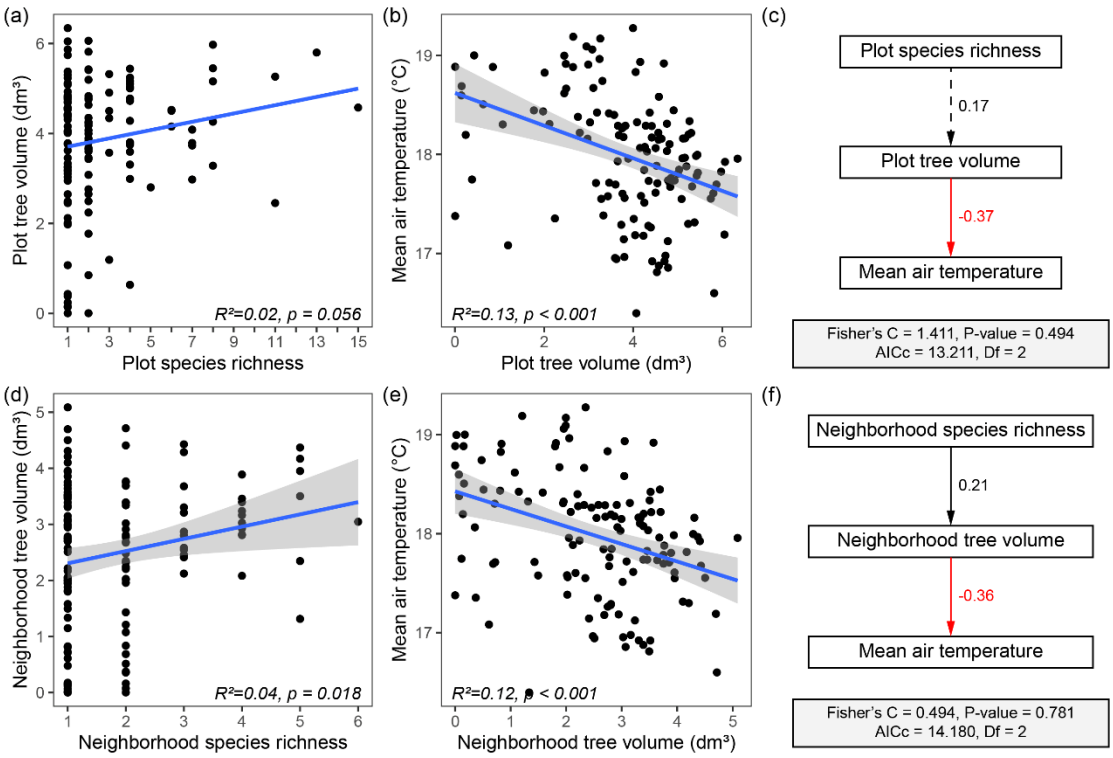

(a)
Plot tree volume (dm³)
Plot species richness
R²=0.02, p = 0.056
(b)
Mean air temperature (°C)
Plot tree volume (dm³)
R²=0.13, p < 0.001
(c)
Plot species richness
0.17
Plot tree volume
-0.37
Mean air temperature
Fisher's C = 1.411, P-value = 0.494
AICc = 13.211, Df = 2
(d)
Neighborhood tree volume (dm³)
Neighborhood species richness
R²=0.04, p = 0.018
(e)
Mean air temperature (°C)
Neighborhood tree volume (dm³)
R²=0.12, p < 0.001
(f)
Neighborhood species richness
0.21
Neighborhood tree volume
-0.36
Mean air temperature
Fisher's C = 0.494, P-value = 0.781
AICc = 14.180, Df = 2

Fig. 5