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RESEARCH

Tree species richness and productivity influence deadwood amount, but microclimate its decay in an early successional subtropical forest

Matteo Dadda[1] · Simon Thorn[2,3,4] · Arong Luo[5] · Xianglu Deng[6] · Xiaojuan Liu[6] · Heike Feldhaar[1]

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Abstract

Deadwood availability and turnover are fundamental for forest ecosystem functioning, affecting biodiversity and carbon storage. Identifying their drivers already at early forest successional stages is central to restoration and management, yet the effects of tree diversity on deadwood dynamics remain unclear, especially in the subtropics. We evaluated how tree species richness and identity influence accumulation and decay of deadwood in an early successional stage forest working in a large-scale tree diversity experimental platform in subtropical South-East China covering a tree species richness gradient spanning from monocultures to 24-species mixtures. Naturally occurring deadwood was assessed as volume of coarse woody debris (CWD, diameter > 7 cm) and mass of fine woody debris (FWD, diameter < 7 cm). Plots with higher tree species richness produced more FWD and showed reduced inter-plot variability in deadwood accumulation, suggesting that tree species richness is already shaping dead wood dynamics in early successional stages. Stand productivity, however, predicted deadwood accumulation more strongly than richness per se. Instead, decomposition was mainly associated with canopy closure rather than with plot-level tree species diversity or identity. These results indicate that in early successional stages tree diversity and productivity may already set the foundation for future forest structure and carbon cycling, with implications for ecosystem resilience and predictability of deadwood pools in later successional stages. From a management perspective, combining species-rich planting with targeted inclusion of productive species can accelerate the recovery of deadwood habitats for saproxylic organisms, thus yielding carbon and biodiversity co-benefits.

Keywords Decomposition · Biodiversity-ecosystem functioning (BEF) · Coarse woody debris · Fine woody debris

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✉ Matteo Dadda
matteo.dadda@uni-bayreuth.de; daddamatteo@gmail.com

✉ Heike Feldhaar
feldhaar@uni-bayreuth.de

[1] Animal Population Ecology, Bayreuth Centre of Ecology and Environmental Research (BayCEER), University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany

[2] AG Spezielle Tierökologie, Philipps Universität Marburg, Karl-von-Frisch-Straße 8, 35043 Marburg, Germany

[3] Dezernat N3 – Staatliche Vogelschutzwarte, Hessisches Landesamt für Naturschutz, Umwelt und Geologie, Europastraße 10, 35394 Gießen, Germany

[4] Biology Centre, Institute of Entomology, Czech Academy of Sciences, Branišovská 1160/31, 37005 České Budějovice, Czech Republic

[5] State Key Laboratory of Animal Biodiversity Conservation and Integrated Pest Management, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, China

[6] State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan District, Beijing 100093, China

Introduction

Tree diversity is fundamental to forest ecosystem structure and functioning. It shapes nutrient cycling and biotic interactions, influences the microclimate at a local scale, and increases biomass production and habitat heterogeneity, ultimately impacting ecosystem stability and resilience (Paquette and Messier 2011; Huang et al. 2018a). Differences in tree species functional traits—whether stemming from phylogenetic differences within communities or from adaptive divergence or convergence in response to environmental challenges (De Bello et al. 2015)—can affect tree interactions with the environment. Such interactions shape ecosystem dynamics, either promoting efficient resource use and niche partitioning (complementarity effect) or increasing the likelihood that a particularly productive species will dominate (selection effect) (Tilman 1997; Loreau and Hector 2001).

A crucial element of forest ecosystem complexity is deadwood. Deadwood contributes significantly to forest structure, biodiversity and overall functioning (Hérault et al. 2010; Seibold et al. 2015). As a carbon sink, it is estimated to account for approximately 8% of forest carbon stocks worldwide, 17% of the global carbon, and store the equivalent of 8.5% of all atmospheric carbon (Friedlingstein et al. 2019; Pan et al. 2011). Through its decomposition, deadwood facilitates nutrient cycling, enriching the soil with elements primarily derived from plant biomass or fixed from the atmosphere by bacteria (Peršoh and Borken 2017; Tláskal et al. 2021). Its presence and accumulation also support a diverse array of organisms (Lassauce et al. 2011; Stokland et al. 2012; Seibold et al. 2015). Moreover, beyond its ecological importance, deadwood has long been exploited by humans, e.g., for firewood (Pfeifer et al. 2015). Dynamics and ecological roles of deadwood differ significantly depending on size and biophysical and chemical characteristics, in turn modulated by a synergistic complex of abiotic and biotic factors (Stokland et al. 2012; Müller et al. 2015; Ulyshen 2016; Seibold et al. 2021). Coarse woody debris (CWD) typically decomposes at slow rates, even over decades, serving as a long-term carbon and nutrient reservoir (Přívětivý et al. 2018). By contrast, fine woody debris (FWD) undergoes rapid turnover and fragmentation (Müller-Using and Bartsch 2009), thus shaping diverse habitats and hosting endangered species and high fungal diversity (Heilmann-Clausen and Christensen 2004; Gedminas et al. 2007).

Although tree identity can influence deadwood dynamics through tree functional traits such as wood density and growth rate (Gottschall et al. 2019), studies on the impacts of local tree species richness have so far mostly yielded ambiguous and weak results, either noting no evident direct influence (Gottschall et al. 2019) or stressing how its impact can be altered by other factors such as environmental conditions, forest age or cultivation history (Eaton and Lawrence 2006; Cornelissen et al. 2012; Guo et al. 2021; Fernandez Barrancos et al. 2022). This is especially true in the case of early successional forest stages. Even though CWD production increases with forest age (Eaton and Lawrence 2006), demographic filtering and competition-driven mortality are strongest in young forests (Larson et al. 2015; Szmyt and Tarasiuk 2018). This makes the onset and rate of deadwood inputs in early successional forest stages (i.e., after plantings or disturbances) critical in determining later trajectories of forest structural complexity and carbon dynamics, thus also affecting ecosystem functions and diversity of deadwood related organisms during forest recovery (e.g., providing habitats and resources for colonists and modulating microhabitat conditions) (Harmon et al. 1986; Grove 2001; Eaton and Lawrence 2006; Swanson et al. 2011).

Recovery of deadwood amount and diversity after forest disturbances still represents a significant gap in our knowledge of deadwood dynamics (Kissing and Powers 2010; Pfeifer et al. 2015; Falconí-López et al. 2024), in particular in tropical and subtropical regions, which harbour some of the largest and most biodiverse forests worldwide (Seibold et al. 2015; Artaxo et al. 2022) and where deadwood production and decay dynamics are accelerated by high temperatures and precipitation (Chambers et al. 2000). Understanding how drivers such as tree species richness and identity shape the patterns of deadwood production and decay already in young forests, i.e. 10–30 years old in the subtropics (Bruelheide et al. 2011; He et al. 2022), would therefore improve our knowledge of deadwood dynamics at later stages and their potential role in promoting the re-establishment of complex forest communities in recovering ecosystems.

Here we used a unique experiment (Bruelheide et al. 2014) to address the lack of knowledge on the mechanisms shaping deadwood dynamics in early successional forest stages. We investigated the role of tree species richness and tree identity (the latter through stand productivity, generally positively related to dead wood production and driven by tree functional traits rather than directly by tree species richness) (Liira and Kohv 2010) on the patterns of deadwood abundance and decay in two sites of plots ranging from monocultures to 24-species mixtures in a young subtropical broad-leaved forest in Jiangxi, Southeast China. To our knowledge, research on deadwood, particularly with regard to tree species richness, remains scarce in this area (Yan et al. 2007). Despite being only 15 years old at the time of our sampling, the stumps of our experiment had already reached heights > 10 m and closed canopies (Fig. 4a, in the appendix), which, consistently with other studies (Perles-Garcia

et al. 2021; Fernandez Barrancos et al. 2022), made them suitable study systems for early forest stage dynamics in the subtropics. Within the biodiversity-ecosystem functioning (BEF) framework, we asked whether tree species richness affects deadwood production and decay; whether these effects are mediated by stand productivity, forest structure or environmental conditions; and whether phylogenetic relatedness among tree species further influence deadwood production.

More specifically, we hypothesised that the total amount of deadwood would increase with tree species richness and with stand productivity (Liang et al. 2016; Fichtner et al. 2018), as the presence of highly productive species within a mixture may result in disproportionate contributions to more deadwood formation through selection effects (Liu et al. 2018). Additionally, as tree traits could be related to phylogenetic diversity within the community (De Bello et al. 2015), phylogenetic clustering may locally amplify deadwood production, even at low richness levels, via competition-driven mortality within closely related trees. At the same time, the variance of deadwood amount among forest plots should decrease along the tree species richness gradient. In low-diversity stands, tree identity and selection effects by some trait combinations may dominate, while at higher tree species richness levels selection effects and phylogenetic clustering effects should be stabilised by complementarity. In contrast to its generation, the decay of deadwood should primarily be driven by environmental parameters (Pietsch et al. 2019), even though modulated by wood traits (Cornwell et al. 2009).

Materials and methods

Study area

This study was conducted at the BEF-China platform (Bruelheide et al. 2014), in Xingangshan, Dexing, Jiangxi province, south-eastern China (29°08′–29°11′ N, 117°90′–117°93′ E), within the cooperative research unit MultiTroph (Klein et al. 2026) (Fig. 4b, in the appendix). The climate of the area is subtropical seasonal monsoon, with hot and humid summers and dry and cool winters; the mean annual temperature is 16.7 °C, and the mean annual precipitation is 1821 mm (Yang et al. 2013). BEF-China is a large-scale tree biodiversity experiment established in two 20 ha sites (A and B), where trees were planted in 2009 and 2010, respectively. 566 plots of 25.8 × 25.8 m^2 were established continuously covering the whole surface of the two sites. In each plot 400 trees were planted in 20 × 20 grids, at a distance of 1.29 m from each other. Tree species were chosen and assembled from a pool of 40 native broadleaved evergreen and deciduous tree species, and each plot was randomly assigned in terms of species composition, tree richness levels and planting positions (Fig. 5, Table 3, in the appendix). Mixture compositions were randomly allocated following a "broken-stick" design, to equally represent all species at all richness levels by splitting overlapping species pools (3 per site) into non-overlapping species compositions of lower richness. Understorey vegetation and wild trees are removed every year to maintain the designed tree composition, but dead trees which did not survive were replanted only during the first years of the platform establishment until spring 2013. More information on the experimental design of the BEF-China platform is provided by Bruelheide et al. (2014).

Out of the 566 plots of the platform, we used 300 plots, covering a tree species richness gradient ranging from 1 to 24 species (1, 2, 4, 8, 16 and 24 species, represented by 69, 85, 56, 39, 31 and 4 plots, respectively). We also had to exclude 16 plots (one with a 4-species mixture, three with 2-species mixtures, and 12 monocultures) beforehand due to failed design establishment. Thus, we ultimately conducted our survey and analyses on 284 plots (144 in site A and 140 in site B). Moreover, due to the much lower number of plots belonging to the 24-species mixtures compared to the other richness levels (only n = 4, with other tree species richness levels being represented by at least 31 to 85 plots each), we merged them with 16-species plots into a single category for the statistical analyses to prevent overfitting of models.

Deadwood sampling

We sampled the naturally occurring deadwood in July–August 2023 (site A) and April–May 2024 (site B), classifying as coarse woody debris (CWD) each piece of deadwood with a diameter > 7 cm and as fine woody debris (FWD) everything smaller than this diameter. In each plot, we assessed the volume and decay stage of CWD and the mass of FWD. All pieces of CWD present in each plot were assessed individually, measuring length and circumference, and distinguishing 5 type categories (t1 = fallen whole tree, t2 = standing whole tree, t3 = standing broken tree—at least 1.3 m high –, t4 = stumps—below 1.3 m high –, t5 = downed trunks, branches and logs) (Fig.1) as well as 4 decay stages (1 = freshly dead, 2 = beginning of decomposition, 3 = advanced decomposition, 4 = completely rotten/mouldered) according to Albrecht (1991). In the case of standing or fallen trees (t1, t2 and t3 pieces) the circumference was measured at breast height (130 cm), while for stumps and logs at mid length. As for FWD, in each plot we collected all the naturally occurring debris in one randomly chosen 5 × 5 m area and measured its fresh weight in the field (Fig. 1).

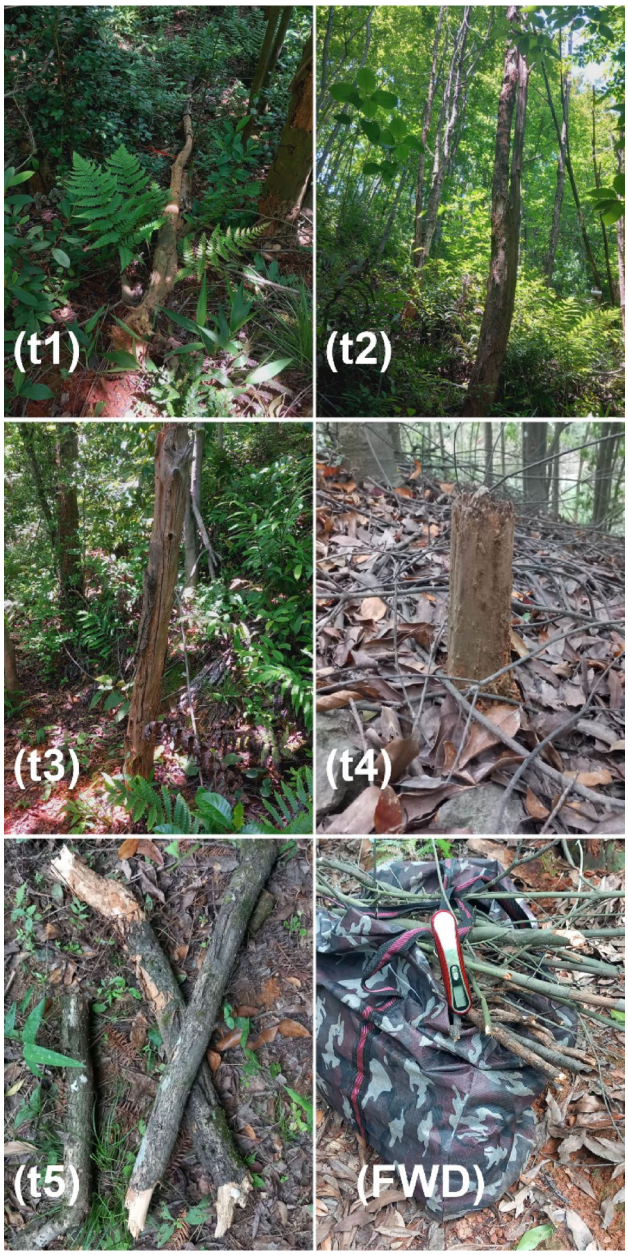


Fig. 1 Pictures of different types of deadwood sampled. t1 = fallen tree; t2 = standing whole tree; t3 = standing broken tree; t4 = stump; t5 = log; FWD = fine woody debris, here shown with the bag and the scale we used to measure it

Due to the fact that the BEF-China platform was established in areas previously used for tree plantations of the conifer *Cunninghamia lanceolata* (Yang et al. 2013), most of the occurring stumps belonged to this species rather than to the trees planted within the BEF-China experiment. For an assessment of deadwood accumulation in dependence of tree species richness, we therefore excluded them from the CWD analyses. Since the former plantations were all logged shortly before planting of the BEF-China platform at site A and site B, the stumps of *C. lanceolata* were all generated almost at the same time. We therefore used them as a baseline for an analysis of the dynamics of deadwood decay. To be as conservative as possible in avoiding legacy effects from other potential remnant trees, we first excluded all stumps with a diameter larger than 30 cm, as, based on our observations in the field, it is unlikely that they derived from trees planted within the BEF-China platform or the previous conifer plantation (trunks of the planted tree species have not reached this diameter yet, and likewise the stumps of *C. lanceolata* of the former plantation were smaller when cut). Based on our observations, we then created two datasets for the stumps, with pieces higher than 40 cm being considered as CWD deriving from trees planted within the BEF-China platform, while those below 40 cm in height considered to belong to the previous conifer plantation. This is because the conifers seemed to be cut below this threshold (mostly approximately 25–40 cm above ground, personal observation), while trees falling due to natural causes likely tended to break at higher heights. We are aware that both datasets may include a low number of misclassified stumps, but given the size of the datasets, we assume that this should only have a very minor impact on the statistical results.

Tested potential drivers of deadwood generation and decay

We tested several biotic and abiotic variables as possible predictors of deadwood production and/or decay along the tree species richness gradient.

Stand productivity was included because related to tree identity. Schnabel et al. (2021) calculated stand productivity as the aboveground wood production per plot per year (m^3/ha/year); it was derived from yearly measurements of the stand basal area and height in the core 12 × 12 grid of each plot (6 × 6 in case of monocultures) from 2010–2011 (in Site A and Site B, respectively) to 2019, eventually scaled to 1 hectare and reduced to a single value per plot.

Wood density was included as a property directly related to tree identity, and influencing how fast trees of different tree species break and decompose. For each plot it was calculated as the community-weighted mean of the dry mass of a fixed volume of the different tree species by Huang et al. (2018b).

Mean pairwise phylogenetic distance (MPD), chosen for its independence of tree species richness (Vellend et al. 2011) and obtained from a node age-calibrated phylogenetic tree of the community of each plot (Faith 1992) by Huang et al. (2018b), was tested as we assumed that more closely related tree species with similar traits may be subject to stronger competitive interactions, even though potentially mitigated by the fixed grid layout of BEF-China experiment, due to similar ecological niche occupation (Guo et

al. 2021). To correct for the possible leverage caused by the monocultures, where MPD is zero—a common issue in experimental communities—we introduced a small offset (3.25, the 1% of the smallest MPD value we had) before a log transformation.

Canopy cover was assessed as it influences microclimatic conditions in the plots (Thom et al. 2020) and also deadwood production, as greater lateral crown expansion may intensify interspecific competition and thus induce breakage of branches (Pretzsch 2014). We computed canopy cover for each plot using elevation-normalised drone-based LiDAR data (Liu et al. 2024a). The drone-based LiDAR data was acquired during the leaf-on season of September 2023 using a Hesai Pandar 40P laser scanner (LiAir 220N system, GreenValley International). Canopy cover was approximately the inverse of the gap fraction and estimated as the proportion of the ground of the plot covered by forest canopy (above 2 m from the forest floor) (Atkins et al. 2023).

We also included in our models slope, northness and eastness, obtained by Scholten et al. (2017) with a digital elevation model (DEM) on a cell size of 5×5 m interpolated from elevation measurements with a differential global positioning system (DGPS) using the Kriging algorithm (Behrens et al. 2010). Slope was included to capture slope-dependent directional exposure, while northness and eastness (cosine- and sine- transformed radian values of aspect, describing the compass direction faced by the plots) accounted for aspect-driven microclimatic variation independent of steepness.

Statistical analyses

All statistical analyses were performed using R software (v. 4.2.2) and, unless otherwise stated, its R base tools and packages (R Core Team 2022). All the plots were created with ggplot2 package (Wickham 2016). Possible multicollinearities among predictors were checked with *performance* package (Lüdecke et al. 2021). All models were run with glmmTMB package (McGillycuddy et al. 2025), then checked with Type II ANOVA post-hoc tests (car package) (Fox et al. 2001) and diagnostics from DHARMa package (Hartig 2016). To approximate normality, we used a log2 transformation of tree species richness (matching the power-of-two structure of the experimental design) and a log10 transformation of MPD (better compressing its wide range of values than a normal log transformation), while no transformations were required for other variables. All models were run using Gaussian distribution with an identity link function, and model choices were supported by DHARMa diagnostics (all $p > 0.1$ for uniformity, dispersion, and outliers).

The volume of CWD along the tree species richness gradient was assessed with a generalised linear mixed-effects model, including tree species richness, stand productivity, mean phylogenetic distance, wood density, canopy cover, slope, northness and eastness as fixed factors, and site as a random effect to account for potential minor impacts of differences among the sites.

For FWD, sites represented a direct proxy for the season (since site A was sampled in summer during the dry season while site B was sampled in spring during the rainy season), with potentially important consequences on the fresh weight measured in the field. We therefore assessed it with a GLM, again with tree species richness, stand productivity, mean phylogenetic distance, wood density, canopy cover, slope, northness and eastness as fixed factors, but including also site as a fixed factor.

Next, we assessed the variability of CWD volume and FWD biomass separately across tree species richness levels in a custom function built with dplyr and tidyr packages (Wickham et al. 2014a, b). Given the substantial variation in mean deadwood amounts across richness levels (Table 4, in the appendix), the coefficient of variation (CV%), calculated from raw plot-level observations, was preferred over absolute variance, to account for differences in the scale of deadwood amounts across richness levels. To make variability estimates comparable across richness levels with unequal sample sizes, we standardised the effective sample size by repeatedly drawing fixed-size resamples (bootstrap samples drawn with replacement, i.e. with possible repeats of observations) within each richness group. For each comparison, the resample size k was set to 90% of the smallest available sample size in the relevant grouping structure. We then generated 1,000 resamples of size k and calculated CV% for each one. The resulting distribution of CV values was summarised using the median and the 2.5th and 97.5th percentiles. For the site-level analyses, k was defined separately within each site, so that comparisons among tree species richness levels within a site were made at equal effective sample size.

Lastly, we tested for differences in plot-level deadwood decomposition. We calculated the mean decay stage of the stumps of former plantation trees per plot by weighting the decay stage of each wood piece by its volume. Then, as, unlike in the case of CWD, the use of site as a random effect was not acceptable based on DHARMa diagnostics, we used again a GLM (Gaussian distribution with log link) including tree species richness, canopy cover, site, slope, northness and eastness, site and volume of CWD as covariates. Specifically, CWD was included in order to evaluate whether plots producing more deadwood also showed accelerated processes leading to its turnover and decay.

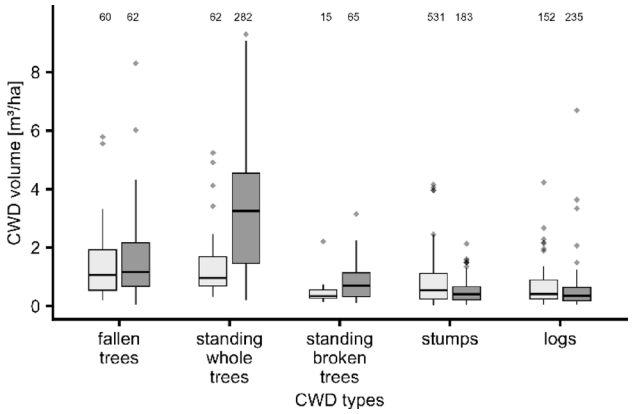


Fig. 2 Amount of CWD we measured by type. For each CWD type the mean volume of the plots (converted to hectare) is shown for site **A** (light grey, on the left) and site **B** (dark grey, on the right). The total number of CWD pieces found per category is given above each boxplot

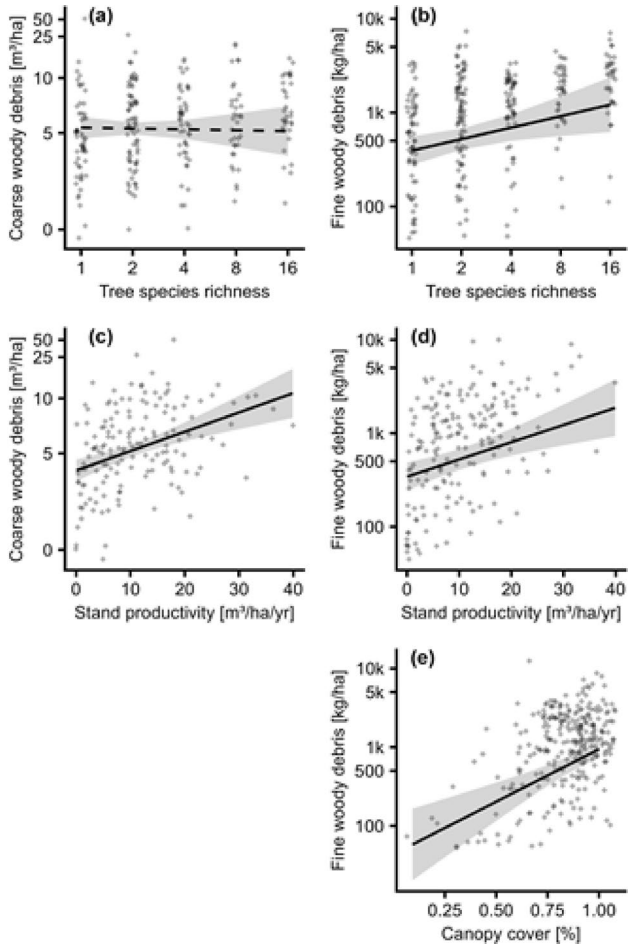


Fig. 3 Predicted values of coarse woody debris volume (in the plots where present) and FWD biomass, in relation with tree species richness (**a**, **b**), stand productivity (**c**, **d**) and canopy cover (the only other variable found significant) (**e**). Lines show model predictions (mean), and shaded ribbons indicate 95% confidence intervals (mean ± 95% CI)

Table 1 ANOVA (type II Wald chi-square tests) of models run on FWD biomass and CWD volume and FWD biomass

Predictors		CWD Volume (m^3/ha)		FWD Biomass (kg/ha)	
		Chi^2	*p*-value	Chi^2	*p*-value
Site				10.022	**0.001**
Forest structure					
Tree sp. richness	1	0.046	0.831	6.119	**0.013**
Stand productivity	1	20.906	**<0.001**	15.181	**<0.001**
Canopy cover	1	0.500	0.479	23.199	**<0.001**
MPD	1	2.533	0.112	2.385	0.123
Tree traits					
Wood density	1	0.181	0.670	1.901	0.168
Topography					
Slope	1	1.860	0.173	0.141	0.708
Northness	1	2.436	0.119	0.583	0.445
Eastness	1	2.470	0.116	0.531	0.466

The *p*-values of the significant variables are in bold. The summaries of the same models are in Table 4, in the appendix

Results

Deadwood survey

Our deadwood survey ultimately included 1647 pieces of CWD (820 in Site A and 827 in Site B) (Fig. 2), with a total volume of 44.14 m^3 (mean 0.18 ± 0.28 m^3 per plot, range from 0 to 2.88 m^3), in addition to 4397 stumps remaining from the previous *C. lanceolata* plantations (2717 in Site A and 1680 in Site B; mean volume 0.06 ± 0.05 m^3—15.4 pieces—per plot, range from 0 to 0.33 m^3), and 1114.5 kg of FWD (632.07 kg in Site A and 482.43 kg in Site B) (mean 3.92 ± 3.72 kg/25m^2, range from 0.12 to 27.96 kg/25m^2). This means that on average 2.69 ± 4.19 m^3/ha of CWD, 0.90 ± 0.75 m^3/ha of stumps from the former conifer plantations, and 1569.72 ± 1487.50 kg/ha of FWD were present per plot.

Drivers of CWD and FWD presence and amount

Tree species richness did not have any significant influence on the volume of CWD but it was significantly positively associated with the biomass of FWD (est. = 0.155, $p = 0.013$) (Fig. 3a, b; Table 1; Table 5 in the appendix). Stand productivity had a significant positive effect on CWD volume (est. = 0.226, $p < 0.001$) as well as on FWD biomass (est. = 0.155, $p < 0.001$) (Fig. 3c, d; Tables 1, 5).

Mean phylogenetic distance (MPD) of tree species within plots, as well as the wood density of the stand communities, had no significant impacts on either CWD or FWD (Tables 1, 5).

We detected a highly significant positive association between canopy cover and the biomass of fine woody debris (est. = 0.221, $p < 0.001$), suggesting higher FWD

accumulation in plots covered by denser canopies (Fig. 3e; Tables 1, 5). Site appeared to be highly significant in the case of FWD, with higher biomass in site B (est. = 0.312, $p = 0.001$), but, as a random effect, did not explain any of the residual variance of the model on CWD volume. As for the topography, none of the variables (slope, northness, eastness) had significant effects on either CWD or FWD (Tables 1, 5).

The pattern of the coefficient of variation of deadwood amount along the tree species richness gradient (Table 2), in line with our hypotheses, appeared to be overall decreasing with the increase of the tree species richness. For CWD, CV% dropped from an average of 164.2 in monocultures to 98.2 in plots containing 16 or more tree species, whereas for FWD it decreased less, from 141.5 to 60.5. Looking at the two sites separately, site B showed higher initial CWD variability than site A (179.8 vs. 122.4) and a steeper decline, while FWD was more uniform across sites. The uncertainty around CV estimates, expressed as 95% confidence intervals, broadly followed the same pattern, with narrower intervals at higher tree species richness levels. This tendency was more consistent for FWD than for CWD, for which confidence intervals remained comparatively wider, particularly at low richness levels (Fig. 3).

Deadwood decay measured on stumps

The decay stage of the stumps of the former *C. lanceolata* plantations (Table 6, in the appendix), which had been generated in all plots within a short period of time shortly before trees of the BEF-China platform were planted, was not associated with tree species richness (est. = 0.002, $p = 0.852$). Instead, we observed a significant positive effect of canopy cover (est. = 0.029, $p = 0.026$) and site (est. = −0.164, $p < 0.001$), while no relations emerged between the stumps decay stage and CWD presence, slope, northness and eastness of the plots.

Discussion

Our results showed that in early successional stages of forest growth, the production of CWD and FWD was mostly related to stand productivity, while tree species richness had a significant influence on the production of FWD but not that of CWD. We also found that the impact of tree identity (selection effect) was more pronounced at low tree species richness, where the coefficient of variation in amounts of generated deadwood differed more strongly among plots, than at higher tree species richness levels. In contrast, the decomposition of deadwood was more dependent on abiotic and environmental factors.

Deadwood amount: influence of tree species richness and tree identity

Our analyses revealed that deadwood production increased with tree species richness only with respect to fine woody debris, therefore only partially aligning with biodiversity-ecosystem functioning (BEF) theory, according to which higher biodiversity promotes increased biomass production and consequently greater resource accumulation (Fichtner et al. 2018; Liu et al. 2018). However, biodiversity–ecosystem functioning research also revealed that not only species richness per se but also other facets of tree diversity, such as tree identity, have to be considered to understand the underlying mechanisms (Gottschall et al. 2019). In fact, the decreasing coefficient of variation in the generation of deadwood with higher levels of tree species richness could be explained by tree identity and selection effects (Lehman and Tilman 2000). As we hypothesised, at low tree species richness variance of deadwood production was high, likely driven by stochastic dominance of species with divergent traits (e.g., growth speed, wood density) (Cornwell et al. 2009; Woodall et al. 2015), while in more diverse plots this variation may have been mitigated by stabilising effects of functional complementarity (Loreau and Hector 2001) and

Table 2 Coefficients of variation (CV% median and 95% percentile intervals) of deadwood amount along the tree species richness gradient, estimated via repeated subsampling to a fixed sample size

		1 sp.	2 sp.	4 sp.	8 sp.	16 sp.
CWD	Site A	122.4 (70.3–183.5)	117.0 (77.4–182.8)	96.5 (57.4–153.4)	94.5 (59.3–131.4)	95.0 (64.3–132.9)
	Site B	179.8 (102.4–305.8)	160.6 (94.1–262.2)	109.0 (74–159.8)	117.8 (79.4–169.6)	83.9 (57.4–124.3)
	Tot	164.2 (109.9–346.5)	149.1 (105–221.4)	127.6 (94.4–173.2)	146.7 (108.3–193)	98.2 (76.6–126)
FWD	Site A	125.2 (54.9–205.8)	93.2 (58.8–139.8)	52.7 (35.2–75)	57.8 (36.1–85)	60.9 (39.9–87.2)
	Site B	113–0 (75.1–161.9)	86.0 (59.1–124.3)	64.6 (36.9–95.4)	51.5 (32.9–73.5)	45.8 (27.2–68.6)
	Tot	141.5 (76.1–209.5)	94.4 (68.1–133.2)	60.3 (45.2–78.2)	54.8 (40.5–70.6)	60.5 (45.9–75.6)

Results are shown for FWD and CWD, for all plots combined and per site

by the increased likelihood of having one or a few very productive species in each plot at a particular tree species richness level (Lehman and Tilman 2000).

Stand productivity ultimately appeared to be a stronger predictor of deadwood accumulation than tree species richness itself, being more significantly associated with FWD biomass and also having a significant positive effect on the volume of CWD. These results are in line with several studies (Paquette and Messier 2011; Gottschall et al. 2019) arguing that the presence of particularly productive species can drive ecosystem functions, even in less diverse communities. From a broader perspective, the lower deadwood amount variability in high-richness plots aligns with the biodiversity-stability hypothesis (Liang et al. 2016), implying that diverse forests may better buffer carbon cycling against environmental fluctuations.

As for the possible role of phylogenetic distance on deadwood production, no significant associations emerged either with CWD or FWD. Our hypothesis here is that the fixed grid disposition of the trees at the BEF-China platform helped avoid competition at the earliest stages, thus shifting it to the current stage among adult trees in more closely related communities. This is in line with Guo et al. (2021) who argue that competitive exclusion in closely related assemblages can result in higher deadwood production due to stress and resource competition. Moreover, as phylogenetic signals can be scale-dependent (Cavender-Bares et al. 2009; Hao et al. 2018), such grid disposition may have partially obscured fine-scale competitive interactions, limiting the competition, and ultimately making it unlikely for MPD to outweigh the effects of stand productivity, reinforcing the importance of stand productivity and corroborating the idea that complementarity can override or at least outweigh competition (Liang et al. 2016). Similar patterns, where phylogenetic or functional diversity provide little additional explanatory power beyond stand structure, have already been reported in larger-scale forest datasets and at coarser spatial resolutions, where productivity is primarily driven by initial stand conditions and environmental factors (Zhai et al. 2024; Liu et al. 2024b).

We also found a positive association between FWD biomass, but not CWD volume, with canopy cover as well as with site. Because FWD was weighed fresh, site effect should be interpreted cautiously. As site A and site B were sampled in different seasons, differences in rain regime and moisture content likely affected FWD fresh-weight estimates. The higher FWD biomass in site B therefore may reflect a combination of wetter sampling conditions and residual site-specific differences rather than a pure spatial site effect. This highlights the high sensitivity of FWD biomass measurements to microclimatic and seasonal conditions, aligning also with the positive effect of canopy cover and therefore of more humid conditions, but the relevance of other significant drivers, even though possibly slightly tarnished, remains. Importantly, the overall higher association of stand parameters with FWD than with CWD is in line with the early developmental stage of the BEF-China forest, where most mortality still occurs via branch and crown losses rather than whole-stem breakage (Grove 2001; Fernandez Barrancos et al. 2022; Falconí-López et al. 2024). As the forest matures, CWD will become then more abundant and prominent (Read and Lawrence 2003; Eaton and Lawrence 2006). Support for this interpretation and its implications for later forest stages comes from studies conducted in a nearby mid-successional to mature subtropical forest. In the nearby Gutianshan National Natural Reserve, Liu et al. (2018) showed that carbon stored in CWD increased with stand age and that tree species richness had consistent positive effects on CWD across a chronosequence with plot age ranging from 25 to almost 120 years.

Furthermore, in subtropical biomes deadwood accumulation-decomposition dynamics may differ from temperate forests (Song et al. 2017), showing a faster turnover due to the relatively high temperatures and abundant precipitation (Wall et al. 2008; Seibold et al. 2021). This should reduce the residence time of deadwood and its capacity to act as a long-term carbon reservoir compared to temperate zones. Such implications for carbon cycling make these dynamics critical also when modelling forest responses to climate change, as even small shifts in microclimatic conditions could alter the balance between carbon storage and release. After all, despite the importance of dead wood dynamics in determining the carbon balance of tropical forests, decay rate variation remains one of the major sources of uncertainty in models of the global carbon cycle (Weedon et al. 2009; Hérault et al. 2010).

Stump decay

The role of microclimate was clearly confirmed by our analyses of the decay of stumps. Tree species richness had no influence on their decay, which appeared to depend primarily on the local environmental conditions instead, specifically on a more closed canopy cover, used as a reliable proxy for a more humid microclimate (Newell et al. 2026; Schnabel et al. 2025). The fact that our analysis was based on legacy *Cunninghamia lanceolata* stumps, despite providing a relatively uniform substrate advantageous for comparing decay among plots, also means that effect sizes should be interpreted with some caution when extrapolating to deadwood

produced by the current broadleaved tree community. At the same time, we would expect tree species richness to primarily influence deadwood decay indirectly, through effects of tree identity, decomposer communities, microclimate and stand structure (Gottschall et al. 2019). Therefore, our main inference that local microclimatic conditions override indirect tree species richness effects on deadwood decay should remain robust but the magnitude of decay responses may differ for broadleaved deadwood, and in general across different forest types.

Our results are in line with other studies, such as Kou et al. (2020) and Pietsch et al. (2019), showing that CWD decomposition is predominantly climate-driven rather than diversity-dependent. To our knowledge, though, within BEF-China only one study (Wu et al. 2021) has so far extensively tested the effects of tree diversity on wood decomposition (in 2015/2016, six to seven years after trees were planted). In that study, the authors used fine woody debris of seven different tree species and estimated the respective contribution of insects and fungi to the decomposition process. Their results were ambiguous, with positive effects of tree species diversity on the mass-loss rate of FWD of the conifer *Cunninghamia lanceolata* but negative effects on that of the broad-leaved *Schima superba* after one year. Moreover, increased fungal hyphal growth on FWD in plots with higher tree species diversity was registered after two years. This suggests that tree species richness may have at least indirect effects on deadwood decomposition, in this case by affecting decomposer activity (fungi, insects), even though these are strongly mediated by tree identity (Van Geffen et al. 2010).

Conclusion

In our study we found that in this early successional forest the effects of tree species richness on deadwood are limited and overridden by stand productivity when it comes to deadwood production and by environment in relation to decomposition. However, a positive, even though secondary, association between tree species richness and fine woody debris biomass already started emerging. Future work should therefore assess how interactions between tree diversity and deadwood dynamics shift with forest age and disturbance regimes. From a management perspective, our results matter for carbon balance as well as for biodiversity conservation. The productivity-driven dynamics emerging from our study, where stand productivity significantly predicts CWD volume, suggest that, when managing and restoring forests, prioritising the planting of high tree diversity and the inclusion of high-productivity species in mixtures can enhance early deadwood pools and rapidly build habitats for deadwood related organisms. At the same time, stabilisation effects in high tree species richness mixtures may reduce variability in deadwood pools, yielding more predictable resources amid rapid subtropical turnover.

Appendix

See Figs. 4, 5 and Tables 3, 4, 5, 6.

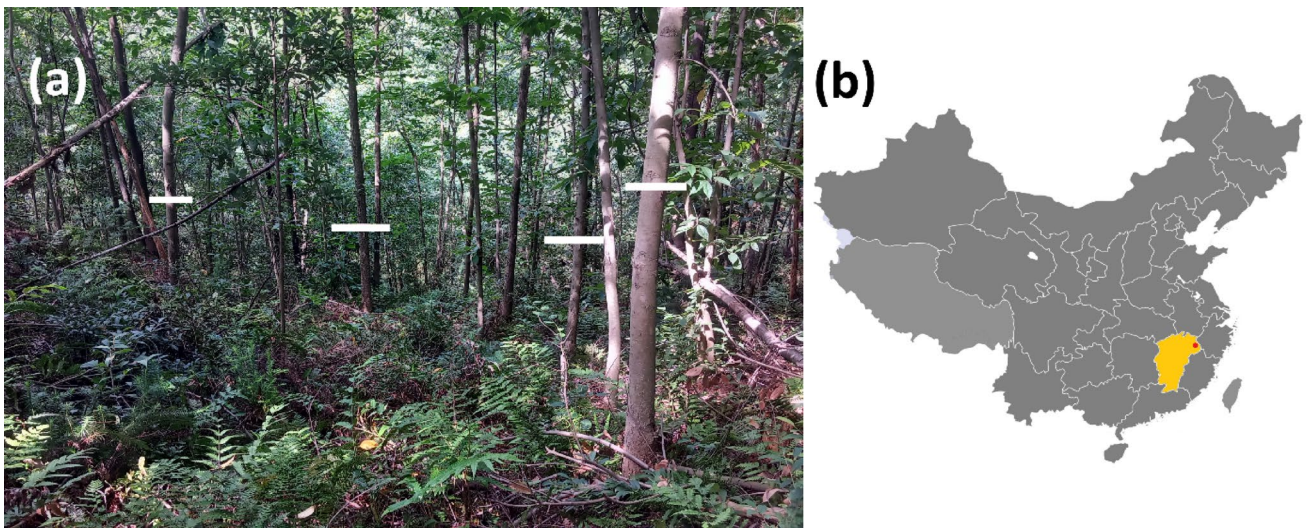


Fig. 4 Picture of a BEF-China platform plot at the time of our sampling showing the already high growth of the forest (for comparison, the white horizontal lines represent the breast height) (**A**), and location of the platform (marked with a red dot) within China and Jiangxi province (in yellow) (**B**)

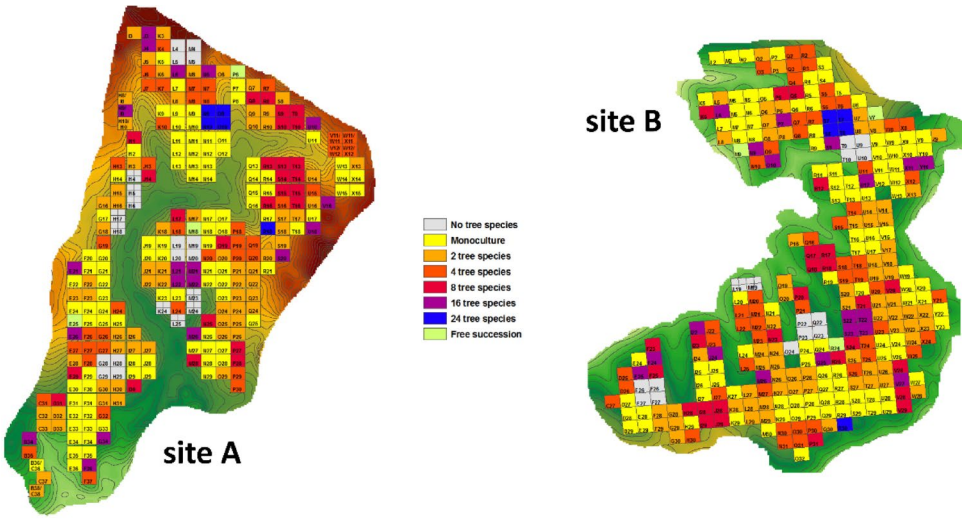


Fig. 5 Maps of sites **A** and **B** of the BEF-China platform showing the distribution of the tree species richness level across the whole platform

Table 3 List of tree species used at the BEF-China experiment, with the site where the species were planted and the species pool used for different extinction scenarios

Tree species	Site and pool	Tree species	Site and pool
Acer davidii	A2,A3	*Koelreuteria bipinnata*	A1,A2
Ailanthus altissima	B1,B2	*Liquidambar formosana*	A1,A3
Alniphyllum fortunei	B1,B2	*Lithocarpus glaber*	A1,A2,B2,B3
Betula luminifera	B1,B3	*Machilus grijsii*	B1,B3
Castanea henryi	A1,A3	*Machilus leptophylla*	B1,B2
Castanopsis carlesii	A2,A3	*Machilus thunbergii*	B1,B2
Castanopsis eyrei	A1,A2,B2,B3	*Manglietia fordiana*	B1,B3
Castanopsis fargesii	B1,B2	*Melia azedarach*	A2,A3
Castanopsis sclerophylla	A1,A3,B2,B3	*Meliosma flexuosa*	B1,B3
Celtis biondii	B1,B2	*Nyssa sinensis*	A1,A2
Choerospondias axillaris	A1,A3	*Phoebe bournei*	B1,B2
Cinnamomum camphora	A2,A3,B2,B3	*Quercus acutissima*	A2,A3
Cyclobalanopsis glauca	A1,A3,B2,B3	*Quercus fabri*	A1,A2
Cyclobalanopsis myrsinifolia	A1,A2	*Quercus phillyreoides*	B1,B3
Daphniphyllum oldhamii	A2,A3,B2,B3	*Quercus serrata*	A1,A3
Diospyros japonica	A2,A3,B2,B3	*Rhus chinensis*	A1,A3
Elaeocarpus chinensis	B1,B3	*Sapindus saponaria*	A1,A2
Elaeocarpus glabripetalus	B1,B2	*Schima superba*	A1,A2,B2,B3
Elaeocarpus japonicus	B1,B3	*Triadica cochinchinensis*	A2,A3
Idesia polycarpa	B1,B3	*Triadica sebifera*	A1,A3

Data from Bruelheide et al. (2013a, b); tree species composition of each plot is also available in the same datasets

Table 4 Mean amounts of CWD volume (m^3/ha) and FWD biomass (kg/ha) per tree species richness level

		Site A	Site B	Tot
1 sp	cwd	1.35±1.76	3.31±8.49	2.20±5.77
	fwd	1374±2214	767±928	1093±1755
2 sp	cwd	2.52±2.66	2.81±5.00	2.66±3.93
	fwd	1704±1716	1194±1069	1452±1448
4 sp	cwd	1.10±1.13	3.61±3.41	2.30±2.78
	fwd	1303±707	1502±982	1406±859
8 sp	cwd	1.28±1.07	5.37±5.92	3.27±4.62
	fwd	2039±1208	1845±970	1945±1088
16 sp	cwd	1.98±1.97	4.87±3.52	3.38±3.15
	fwd	3103±1983	2203±1111	2640±1636

Due to the high variation of such amounts across the tree diversity levels, we then analysed them with CV% instead of absolute variance

Table 5 Summaries of the models run on CWD and volume and FWD biomass, with estimates and standard errors

Predictors	CWD Volume (m^3/ha)			FWD Biomass (kg/ha)		
	Est	SE	*p*-value	Est	SE	*p*-value
Site				0.312	0.099	**0.001**
Forest structure						
Tree sp. richness	−0.017	0.053	0.831	0.155	0.062	**0.013**
Stand productivity	0.226	0.005	**<0.001**	0.155	0.039	**<0.001**
Canopy cover	−0.039	0.056	0.479	0.221	0.046	**<0.001**
MPD	0.107	0.067	0.112	−0.082	0.053	0.122
Tree traits						
Wood density	−0.023	0.054	0.670	0.055	0.040	0.168
Topography						
Slope	0.066	0.048	0.173	0.013	0.035	0.708
Northness	−0.070	0.045	0.119	0.028	0.036	0.445
Eastness	0.070	0.044	0.116	−0.025	0.034	0.466
Residuals	131			157		

The *p*-values of the significant variables are in bold

Table 6 Summary, with estimate and standard error, and Anova (type II Wald chi square test), of the model on stump decay

Predictors	df	Chi^2	Est	SE	*p*-value
Site	1	49.214	−0.164	0.023	**<0.001**
Forest					
Tree sp. richness	1	0.035	0.002	0.009	0.852
Canopy cover	1	4.980	0.029	0.013	**0.026**
CWD volume	1	0.321	−0.009	0.015	0.571
Topography					
Slope	1	3.659	−0.017	0.009	0.056
Northness	1	0.667	−0.007	0.009	0.414
Eastness	1	0.785	−0.008	0.009	0.376

The *p*-values of the significant variables are in bold

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Author contributions MD: conceptualisation, methodology, investigation, data curation, formal analysis, visualisation, writing—original draft, review & editing. ST: conceptualisation, funding acquisition, supervision, writing—review & editing. AL: conceptualisation, supervision, writing—review & editing. XD: investigation, writing—review & editing. XL: resources, investigation, writing—review & editing. HF: conceptualisation, methodology, funding acquisition, supervision, writing—review & editing.

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Data availability The data supporting this study are available online on Zenodo (https://doi.org/10.5281/zenodo.17312268) and on the BEF-China data portal (https://data.bef-china.de/bef-china).

Declarations

Conflict of interest The authors declare no competing interests.

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