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Disentangling drivers of litter decomposition in a multi-continent network of tree diversity experiments

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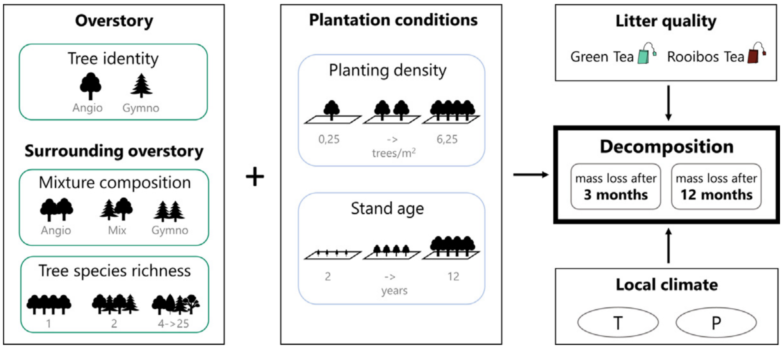
HIGHLIGHTS

- Tree species identity and composition affected decomposition of low-quality litter.
- Young gymnosperm overstories promoted decomposition.
- Tree species identity effects on decomposition depended on the age of the stand.
- Tree species richness explained <1 % variation in mass loss across continents.
- Planting density did not impact decomposition dynamics.

GRAPHICAL ABSTRACT



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ABSTRACT

Litter decomposition is a key ecosystem function in forests and varies in response to a range of climatic, edaphic, and local stand characteristics. Disentangling the relative contribution of these factors is challenging, especially along large environmental gradients. In particular, knowledge of the effect of management options, such as tree planting density and species composition, on litter decomposition would be highly valuable in forestry. In this study, we made use of 15 tree diversity experiments spread over eight countries and three continents within the global TreeDivNet network. We evaluated the effects of overstory composition (tree identity, species/mixture composition and species richness), plantation conditions (density and age), and climate (temperature and precipitation) on mass loss (after 3 months and 1 year) of two standardized litters: high-quality green tea and low-quality rooibos tea. Across continents, we found that early-stage decomposition of the low-quality rooibos tea was influenced locally by overstory tree identity. Mass loss of rooibos litter was higher under young gymnosperm overstories compared to angiosperm overstories, but this trend reversed with age of the experiment. Tree species richness did not influence decomposition and explained almost no variation in our multi-continent dataset. Hence, in the young plantations of our study, overstory composition effects on decomposition were mainly driven by tree species identity on decomposer communities and forest microclimates. After 12 months of incubation, mass loss of the high-quality green tea litter was mainly influenced by temperature whereas the low-quality rooibos tea litter decomposition showed stronger relationships with overstory composition and stand age. Our findings highlight that decomposition dynamics are not only affected by climate but also by management options, via litter quality of the identity of planted trees but also by overstory composition and structure.

1. Introduction

Leaf litter decomposition is a central function in forest ecosystems that significantly affects global terrestrial carbon and nutrient cycling (Hättenschwiler, 2005; Gessner et al., 2010; Handa et al., 2014; Bradford et al., 2016). Litter decomposition rate mainly depends on the net effect of litter quality, (micro)climatic conditions, soil properties and the composition of the decomposer community (Coûteaux et al., 1995). Accordingly, the decomposition process is very sensitive to a changing climate while simultaneously forming an important feedback to the global carbon budget, resulting in potential mitigation or amplification of climate change (Aerts, 1997; Davidson and Janssens, 2006; García-Palacios et al., 2016). Several studies have already targeted the impact of macroclimate on litter decomposition dynamics across large spatial scales (Djukic et al., 2018) and along gradients of global change drivers such as atmospheric nitrogen (N) deposition (Kwon et al., 2021). However, the impact on litter decomposition of forest silvicultural management decisions such as overstory tree species composition and planting density, relative to litter quality and climate, has rarely been explored on a multi-continental scale (Joly et al., 2017).

Anthropogenic influences on tree composition and diversity in forest ecosystems include direct effects of silvicultural management decisions (planting and thinning) as well as indirect effects of environmental changes. Although it is obvious that the surrounding tree community considerably affects decomposition, its specific role in decomposition processes at broader scales is still poorly understood (Scherer-Lorenzen et al., 2007; Prescott and Vesterdal, 2013). Furthermore, our knowledge of the impact of silvicultural management decisions such as planting density or thinning regimes on decomposition remains incomplete (Lado-monserrat et al., 2015; Bueis et al., 2018). A better understanding of tree community and silvicultural management decisions on forest nutrient and carbon cycles would allow us to design mixed forest plantations that are not only more resilient to climate change (Messier et al., 2022) but also better at mitigating climate change (Silva Pedro et al., 2015).

Multiple factors related to overstory tree composition influence litter decomposition (Joly et al., 2017). First and foremost, tree identity strongly affects decomposition by influencing litterfall mass (Prescott, 2002), litter quality (Cornwell et al., 2008; Vivanco and Austin, 2008; Zuo et al., 2018; Hoeber et al., 2020), microclimate (Gottschall et al., 2019), and even soil properties (Reich et al., 2005; Desie et al., 2019) and decomposer communities (Hobbie et al., 2006; Zhang et al., 2020; Peng et al., 2022). Given the large biogeographic area encompassed by this study, we define species identity according to the two major lineages of trees, i.e. angiosperm species or gymnosperm species, assuming that they impact microclimate, water availability and nutrient cycling in different ways (Augusto et al., 2015) and harbor different decomposer communities which dominate different stages of decomposition (Zhang et al., 2020). Typically, gymnosperm species have higher LAI and rainwater interception resulting in drier soil surfaces (Aranda et al., 2012) and tend to acidify soils due to their low litter quality more than angiosperm species (Finzi et al., 1998; De Schrijver et al., 2012).

Second, the species composition of the tree community can influence decomposition through complementary nutrient use (Tilman et al., 2014; Lin et al., 2021) and rhizosphere processes (Binkley and Giardina, 1998; Wardle et al., 2004). To date, evidence for the influence of tree species diversity on decomposition remains ambiguous, with studies reporting inconsistent (Naeem et al., 1994; Wardle and Nicholson, 1996), mere additive (Scherer-Lorenzen et al., 2007), synergistic (Handa et al., 2014;

Maxwell et al., 2020; Strukelj et al., 2021), and antagonistic effects (Blair et al., 1990; Wardle et al., 1997; Seidelmann et al., 2016; Joly et al., 2017). These context-dependent results are probably a consequence of the multitude of pathways through which tree species identity, composition, and diversity could affect decomposition (Jewell et al., 2017), which are simultaneously affected by stand characteristics, management, and climate (Lin et al., 2021). For example, planting density, another important management decision besides tree species selection, could change decomposition by affecting the forest microclimate, soil nutrient-availability, and the total quantity of litter that is produced (Bueis et al., 2018). Furthermore, the driving factors of decomposition can change with a) litter type (Bradford et al., 2016) as high-quality litter is more controlled by abiotic (edaphic and climatic) factors whereas low-quality litter with more structurally complex C substrates is more affected by biotic (overstory) factors (Fanin et al., 2020); b) the age of the stand: as the opening of the forest canopy due to stem exclusion at late successional stages can reduce humidity and thus slow down litter decomposition (Trogisch et al., 2016); and c) the decomposition process itself (Berg and McClaugherty, 2020) where there is a shift in control from biotic to abiotic factors with ongoing litter decay (García-Palacios et al., 2016). Hence, it remains a challenge to control for multiple factors of influence in observational studies, particularly due to confounding factors like tree composition and climate affecting decomposition. Consequently, the relative contribution of these factors and their context-dependencies are even less studied.

The combination of different tree diversity experiments across biomes (TreeDivNet, Verheyen et al., 2016; Djukic et al., 2018; Paquette et al., 2018) provides a unique opportunity to investigate effects of tree species identity, composition and diversity on litter decomposition, and their relative importance to climate related variables. This coordinated multi-site experiment across different continents (Fraser et al., 2013) has made use of the standardized Tea Bag method (Keuskamp et al., 2013) to evaluate decomposition processes without having litter quality confounded with biome and local environment, or with diversity in litter composition (of the litterbag), or with overstory diversity effects (Lin et al., 2021). We incubated standardized litter bags for three and 12 months under 29 focal tree species, encompassing both high-quality angiosperm litter and low-quality gymnosperm litter, occurring in 90 different compositions (monocultures and different combinations of angiosperm and gymnosperm species) with tree species richness ranging from one to 24 species (most experiments have a species richness gradient between one and four species) grown on 15 different experimental sites (Fig. S1). We used green tea and rooibos tea which are representative for fast (high-quality) and slow (low-quality) decomposing leaf litter (Didion et al., 2016). Our main objective was to evaluate how the multiple factors related to the overstory composition (tree identity, species/mixture composition, and species richness), plantation conditions (age and planting density) and local climate (temperature and precipitation) affect mass loss of high and low-quality litter at two different stages of decay (after 3 and 12 months) (Fig. 1). We hypothesized the following:

1) Overstory tree species composition impacts decomposition directly via litter quality with angiosperm and/or more diverse communities promoting faster decomposition rates in comparison to the recalcitrant gymnosperm overstories. Moreover there is an indirect effect of overstory tree species composition via the type of micro-environment found on the forest floor: dense and evergreen canopies of gymnosperms reduce water availability at the forest floor through higher rainwater interception and evaporation, despite dense canopies better preserving a humid forest microclimate, thus impeding decomposition.
2) The effect of overstory composition on decomposition becomes stronger with time (i.e., the age of the stand) as differences among microbial communities and microclimate have had more time to accumulate.
3) Planting density impacts decomposition through changes in the microclimate, with higher densities leading to less favorable conditions for decomposition due to higher rainwater interception.

2. Materials and methods

2.1. Study sites

The experiment was carried out at 15 sites belonging to the global Tree Diversity Network (TreeDivNet network, http://www.treedivnet.ugent.be/) (Verheyen et al., 2016; Paquette et al., 2018) (Table 1, Fig. S1), designed to test tree diversity effects on ecosystem functions worldwide. The studied sites are distributed over boreal, temperate, Mediterranean, and subtropical biomes. Planting densities of the experiments range between 0.25 and 6.25 trees.m^{-2}. At the time of the litterbag experiment (2016), the forests were still rather young with tree age ranging between 1 and 12 years. Local climate data for the year 2016 (extracted from TerraClimate (Abatzoglou et al., 2018)) varied from 6.9 °C to 19.4 °C for mean annual temperature (MAT) (12.5 °C to 24.1 °C for the summer of 2016) and mean annual precipitation (MAP) 591 mm to 1903 mm (28 mm to 615 mm for summer) (Table 1).

2.2. Decomposition experiment

We used two varieties of Lipton tea bags as our standard litter: fast decomposing green tea and slowly decomposing rooibos tea (Keuskamp

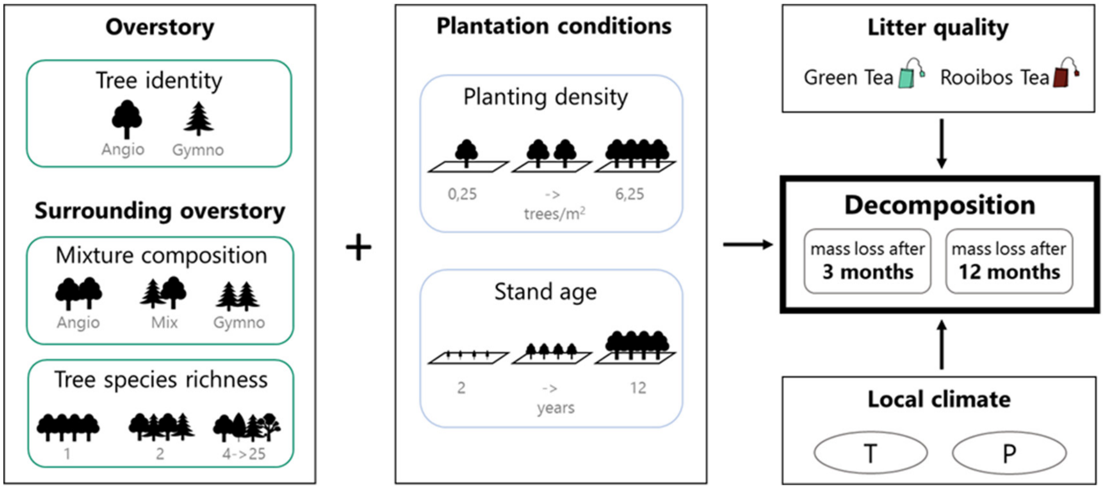

Fig. 1. Conceptual model showing the possible factors affecting litter decomposition in the tree diversity experiments. Angio = angiosperms, Gymno = gymnosperms, Mix = mixture of angiosperm and gymnosperm species; T = temperature; P = precipitation.

Table 1
Basic characteristics of the experimental sites and number of tea bags used in this study.

No.	Country	Name of experiment	Site	Location		Climate			Local weather during experiment				SR gradient[e]	Tree planting year	Tree density (tree m^{-2})	No. bags 3 M[f]	No. bags 12 M
				Latitude	Longitude	Biome	MAT[a]	MAP[b]	MPT[c] 3 M	MPT 12 M	CPP[d] 3 M	CPP 12 M					
A	Belgium	FORBIO	Gedinne	49.99	4.98	Temperate	10.40	670	15.45	10.81	322.20	897.30	1, 2, 4	2010	0.44	62	52
B	Belgium	FORBIO	Hechtel-Eksel	51.16	5.31	Temperate	8.60	1030	16.99	11.43	278.20	631.80	1, 2, 4	2012	0.44	69	69
C	Belgium	FORBIO	Zedelgem	51.15	3.12	Temperate	10.10	708	16.73	11.90	265.00	688.30	1, 2, 4	2009	0.44	71	71
D	Canada	IDENT	Auclair	48.23	−69.10	Boreal	2.30	1015	12.52	4.88	615.90	1400.90	1, 2, 6	2010	6.25	126	NA[g]
E	Canada	IDENT	Montreal	45.86	−73.93	Temperate	6.20	976	20.78	8.64	236.90	1166.40	1, 2, 4	2009	4.00	120	120
F	China	BEF-China	Xingangshan	29.12	117.91	Warm-temperate, humid	17.10	1777	24.10	19.41	534.60	1903.30	1, 8, 24	2009	0.60	94	101
G	Germany	BIOTREE	Kaltenborn	50.78	10.22	Temperate	7.80	650	15.83	10.22	266.00	885.90	1, 2, 4	2004	0.25/0.44	48	47
H	Germany	ECOLINK- Salix	Rostock	54.06	12.08	Temperate	8.50	590	17.92	10.17	194.20	810.20	1, 2	2014	1.56	36	NA[g]
I	Germany	Kreinitz	Zeithain	51.23	13.15	Temperate	8.40	575	18.04	11.24	212.60	607.30	1, 3, 6	2005	1.25	68	72
J	Germany	MyDiv	Bad Lauchstädt	51.39	11.88	Temperate	9.00	492	19.32	11.17	164.70	538.40	1, 2, 4	2015	1.00	72	71
K	France	ORPHEE	Pierroton	44.74	−0.80	Temperate	12.75	876	17.55	14.63	136.00	705.30	1, 2, 3	2008	0.25	141	141
L	Italy	IDENT	Macomer	40.24	8.70	Mediterranean	13.80	866	22.33	15.74	28.80	867.00	1, 2, 6	2014	4.00	108	108
M	Sweden	ECOLINK- Salix	Uppsala	60.44	18.08	Temperate	5.60	470	13.79	7.93	241.80	591.30	1,2	2014	1.56	26	31
N	UK	Climate-match	Kent	53.40	−0.30	Temperate	9.30	763	15.88	11.41	116.40	681.2	1, 4	2011	0.25	62	NA[g]
O	USA	IDENT	Cloquet	46.68	−92.52	Temperate	2.60	717	16.48	6.99	545.90	1113.50	1, 2, 6	2010	6.25	123	118

[a] MAT = mean annual temperature in °C from Djukic et al. (2018).

[b] MAP = mean annual precipitation in mm from Djukic et al. (2018).

[c] MPT = Mean Period Temperature in °C with Period referring to the experimental incubation period.

[d] CPP = Cumulative Period Precipitation in mm; 3 M = 3 months of incubation; 12 M = 12 months of incubation.

[e] SR gradient = species richness gradient.

[f] No. of bags = number of installed tea bags.

[g] NA = 12 M not included in the experiment.

et al., 2013). Before field installation, the bags were dried at 70 °C for 48 h, and the initial mass was recorded. During the summer of 2016, tea bags of each tea type were installed in the topsoil (0–5 cm below the surface) underneath different focal tree species (comprising a total of 29 different tree species) in plots with different tree species compositions along a gradient of different species richness (including 1, 2, 3, 4, 6, 8, and 24 species, depending on the site). In total, 2227 bags were incubated and recovered after 3 months (1226 bags) and after 12 months (1001 bags) of incubation (Fig. 1, Table 1). In mixtures, tea bags were placed under specific focal trees at the base of the stem. The list of tree species is provided in Table S1 (Supporting information). Total weight of the tea bags was recorded by weighing the filled tea bags with the string and label, and an averaged weight for the empty bags with string and label (0.248 g) was subtracted from this value to estimate the amount of tea before incubation. After the incubation period, tea bags were carefully collected, dried at 70 °C for 48 h, and the remaining weight of the tea was recorded, assuming that the bag itself did not lose any mass. For a more detailed description of the method, please refer to Djukic et al. (2018) where more information on the methodology is provided.

2.3. Data analysis

Decomposition was modeled as a function of various drivers using linear mixed models including site and plot as random intercepts (plot nested in site) using the package lme4 (Bates et al., 2015). Fixed effects were: the identity of the focal tree (i.e., the tree under which the litterbag was installed); whether it was an angiosperm or gymnosperm; mixture composition of the plot in which the litterbag was installed (pure angiosperms, pure gymnosperms, or mixture of angiosperms and gymnosperms); tree species richness of the plot; planting age of the experiment; planting density; mean period temperature (MPT) and cumulative period precipitation (CPP) during the experimental period. As not all tea bags were incubated for exactly three months (mean = 103 days, SD = 21) or twelve months (mean = 364 days, SD = 26), we included length of the incubation period in the statistical analysis to account for this variation. All models were executed on centered variables. The different levels of the fixed effects (e.g., tree identity varying within plot and site vs climate and plantation conditions only varying between sites) were accounted for by the hierarchical structures of the linear mixed effects models (Zuur et al., 2009). The response variables of the mixed models were litter mass loss per litter type (green and rooibos). Because the impact of tree identity (here defined as the difference between angiosperm and gymnosperm overstories) can change over time due to differences in early growing rates (Zhang et al., 2022), the interaction between focal tree identity and planting age was included in the models. Likewise, the interaction between MPT and CPP was included in all models. Type I anova tests were executed on all models (Table 2). Alternative models including aridity indices or excluding BEF-China (with the outlying species richness level 24) are provided in the appendix (Table S4). The normality and homogeneity of residuals of models were checked by plotting the fitted values versus the standardized residuals, and by graphically evaluating the histograms of the standardized residuals. The partial effects of these regressions were plotted separately for each variable (Figs. 3–5) accounting for the other variables in the models using the effects package (Fox et al., 2022).

Variance partitioning analysis was executed using the partR2 package (Stoffel,M.A., Nakagawa, S., Schielzeth, H, 2021). Variables were grouped to reduce complexity: temperature (T) and precipitation (P) are ‘climate’; identity of the target tree and type of mixture of the surrounding trees are ‘tree composition’, and age and density are ‘plantation conditions’. We determined both the unique effects of single predictors and the effects shared by each pair of predictors. The proportion of variance explained by the fixed effects and the random effects was calculated by comparing the marginal and conditional R^2 of the mixed model (sensu Nakagawa and Schielzeth, 2013) calculated using r.squaredGLMM using the MuMln package (Barton, 2022). All statistical analyses were performed using R version 4.0.5 (R Core Team, 2018).

3. Results

3.1. Litter quality and climate effects on mass loss over time

Across experimental sites and biomes, green tea decomposed significantly faster (65 % ± 9 % after 3 months and 72 % ± 10 % after 12 months, mean ± SE) compared to rooibos tea (20 % ± 12 % after 3 months and

Table 2

ANOVA output of linear mixed models testing the effect of tree species composition, planting, and climate related variables on mass loss of green and rooibos tea after 3 months and 12 months, respectively. The interaction between age and focal tree identity (angiosperm or gymnosperm) and between mean period temperature (MPT) and cumulative period precipitation (CPP) were included in all models. Site and plot were included as random factors with plot nested in site. Models were executed on centered variables.

Fixed effect	Mass loss of green tea after 3 months						Mass loss of rooibos tea after 3 months					
	Sum Sq	Mean Sq	Num DF	Den DF	F value	*P*	Sum Sq	Mean Sq	Num DF	Den DF	F value	*P*
Incubation period length	0.024	0.024	1	503.29	7.83	0.005	0.003	0.003	1	487.30	0.97	0.32
Focal tree identity	0.002	0.002	1	174.13	0.93	0.33	0.019	0.019	1	78.21	4.87	0.03
Age	0.000	0.000	1	9.30	0.02	0.88	0.008	0.008	1	9.30	2.05	0.18
Tree composition	0.000	0.000	2	187.72	0.10	0.89	0.004	0.002	2	94.07	0.60	0.54
Species richness	0.001	0.001	1	84.57	0.43	0.50	0.001	0.001	1	45.32	0.27	0.59
Planting density	0.000	0.000	1	8.93	0.10	0.75	0.001	0.001	1	9.04	0.25	0.62
MPT	0.000	0.000	1	9.12	0.14	0.71	0.001	0.001	1	9.23	0.45	0.51
CPP	0.000	0.000	1	9.14	0.20	0.65	0.001	0.001	1	9.20	0.30	0.59
Focal tree identity: age	0.020	0.020	1	205.25	6.50	0.01	0.079	0.079	1	126.59	19.63	<0.001
MPT: CPP	0.001	0.001	1	9.01	0.46	0.51	0.002	0.002	1	9.10	0.66	0.43

Fixed effect	Mass loss green tea after 12 months						Mass loss rooibos tea after 12 months					
	Sum Sq	Mean Sq	Num DF	Den DF	F value	*P*	Sum Sq	Mean Sq	Num DF	Den DF	F value	*P*
Incubation period	0.037	0.037	1	213.86	7.12	0.008	0.170	0.170	1	139.54	26.85	<0.001
Focal tree identity	0.000	0.000	1	155.04	0.05	0.81	0.008	0.008	1	130.22	1.42	0.23
Age	0.003	0.003	1	6.50	0.66	0.44	0.024	0.024	1	6.05	3.81	0.09
Tree composition	0.011	0.005	2	168.62	1.06	0.34	0.045	0.022	2	146.08	3.61	0.02
Species richness	0.017	0.017	1	40.57	3.27	0.07	0.002	0.002	1	108.45	0.34	0.55
Planting density	0.001	0.001	1	6.26	0.29	0.60	0.009	0.009	1	5.78	1.54	0.26
MPT	0.061	0.061	1	6.08	11.71	0.01	0.002	0.002	1	5.68	0.31	0.59
CPP	0.013	0.013	1	6.31	2.56	0.15	0.000	0.000	1	6.02	0.14	0.71
Focal tree identity: age	0.000	0.000	1	163.90	0.02	0.87	0.008	0.008	1	134.38	1.38	0.24
MPT: CPP	0.007	0.007	1	6.83	1.48	0.26	0.006	0.006	1	6.76	1.00	0.35

35 % ± 12 % after 12 months, mean ± SE) (Fig. S3-S5). The increase in mass loss rate between 3 and 12 months was higher for rooibos tea, as indicated by the significant interaction effect between time and litter type (Fig. S2, Table S2). Sites were located over a large climatic gradient, with mean temperature during the experiment ranging from 4.8 °C at Auclair, Canada, to 19.4 °C at Xingangshan, China, and mean annual precipitation from 591 mm at Bad Lauchstädt, Germany, to 1903 mm at Xingangshan, China (Table 1). Highest mass loss was found in Xingangshan and lowest in Montreal, Rostock and Auclair (Figs. S3 and S4). Generally, mass loss increased from boreal < Mediterranean < temperate < warm temperate humid biomes (Fig. S5). Mass loss was, however, not significantly influenced by MPT or CPP, irrespective of tea type (Table 2).

3.2. Tree identity, composition, and diversity effects

Mass loss of rooibos tea after 3 months of incubation was significantly higher under gymnosperm compared to angiosperm overstories (Fig. 2). The functional group of the focal tree under which tea bags were placed did not influence mass loss after 12 months of incubation (Figs. 2 and S2). After 12 months of incubation, tree composition significantly affected mass loss of rooibos tea with gymnosperm overstories resulting in lower mass loss compared to mixed overstories (Fig. 2). This is after accounting for tree identity, where gymnosperm focal trees promote mass loss (although not significant $P = 0.23$) (Fig. 2, Table 2). Species richness did not significantly impact mass loss, irrespective of substrate type or stage of decay (Fig. 2). The marginally significant increase of green tea mass loss with species richness after 12 months is based on the highest species richness level of BEF-China (Table S4).

3.3. Plantation conditions effects

Planting density did not impact mass loss. Mass loss of rooibos tea after 12 months decreased marginally significantly ($P = 0.09$) with the age of the experiment whereas decomposition of green tea was not affected by age or planting density (Fig. 3). We did, however, find a significant interaction effect of age and focal tree species identity on mass loss after 3 months incubation ($P = 0.01$ for green tea and $P < 0.001$ for rooibos tea): for gymnosperm focal trees we observed more negative relationships between mass loss and stand age (Fig. 4).

3.4. Variance partitioning

Litter type explained most of the variation (80 %) in mass loss after three months in our study with minimal contributions of climate (temperature and precipitation combined, 0.9 %) and plantation conditions (age and density combined, 0.1 %). Overstory composition (identity or composition of the mixture) did not explain any variation (~0 %). After 12 months of incubation, the proportion of variation explained by climate variables increased (to 2 %). When analyzed for tea type separately, random effects (site and plot) explained most of the variation in green tea mass loss (58 %) after 3 months, with very limited variance explained by climate (1 %), plantation conditions (0.4 %), overstory species composition (identity and composition combined, 0.1 %) and species richness (0.1 %). Variance in rooibos mass loss after 3 months was explained by climate (3 %), plantation conditions (3 %) and species composition (0.3 %), whereas species richness explained almost no variation (~0 %). After 12 months of incubation, climate explained more of the variance in green tea mass loss (23 %). For rooibos tea, mass loss after 12 months was increasingly explained by species composition and by

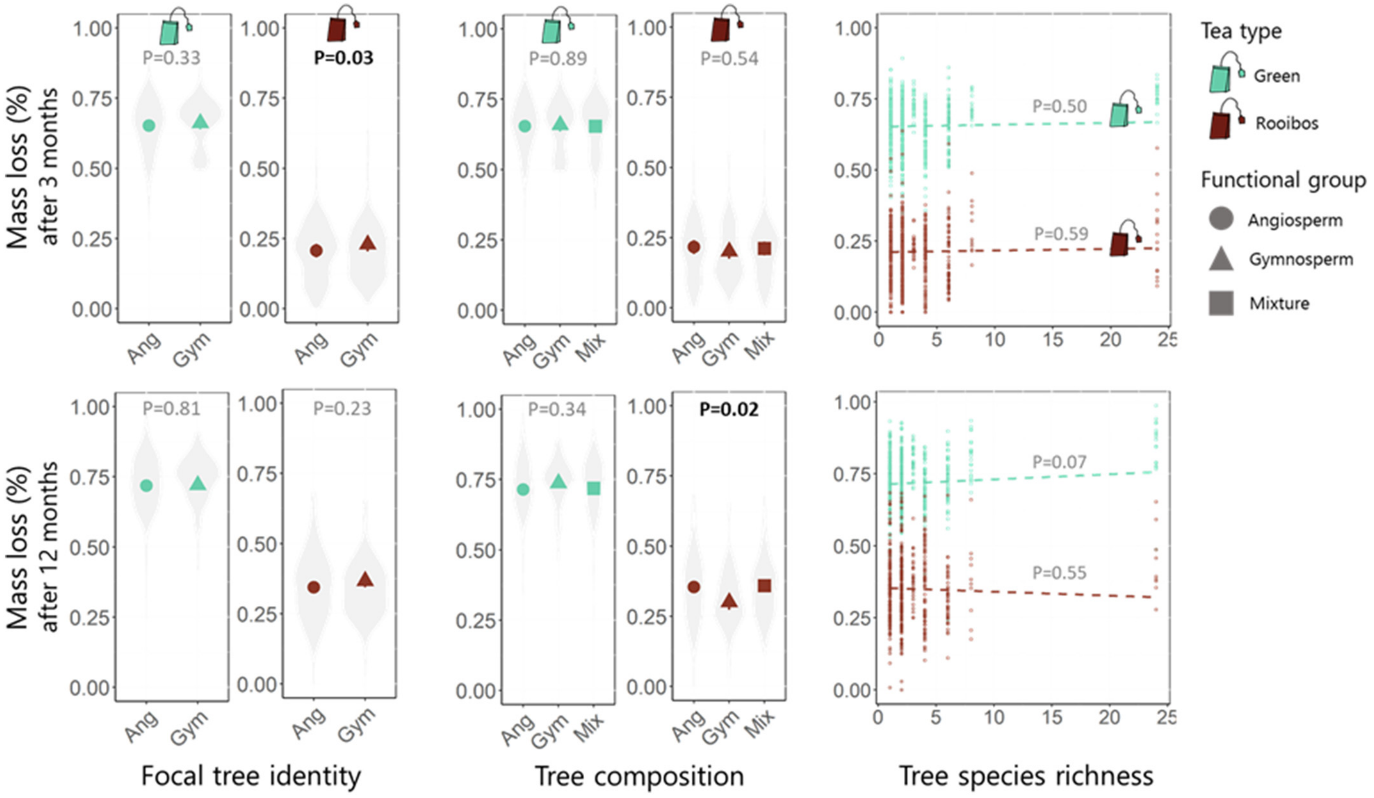

Fig. 2. Mass loss (%) as a function of focal tree identity (left), surrounding tree functional composition (middle) and tree species richness (right) for the two litter types. Relations were tested using linear mixed models (Table 2) accounting for other overstory related variables, climate, plantation conditions, plot and site. Significant relations are indicated by a full line whereas non-significant (NS) relations are indicated by a dotted line. The shaded parts indicate the standard error interval. Observations are indicated for litter types, green tea (green) and rooibos tea (red) and per incubation periods, 3 month (top) and 12 months (bottom).

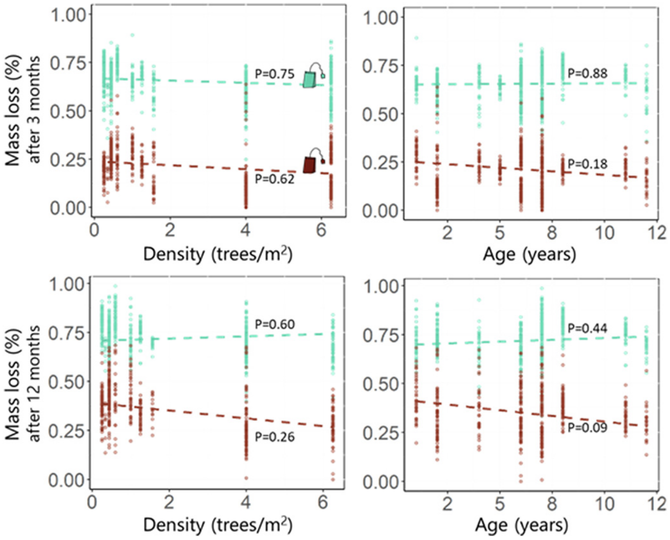

Fig. 3. Mass loss (%) as a function of planting density (left) and age since the plantation (right) for two litter types after 3 months (top) and 12 months (bottom) of incubation. Relationship were tested using linear mixed models (Table 2) accounting for overstory effects, local climate, and random effects. There were no significant relationships ($\alpha < 0.05$) between the variables shown in these figures. Observations are given for litter types: green tea (green) and rooibos tea (red).

incubation period length and its interaction with plantation conditions (14 %) (Fig. 5).

4. Discussion

The impact of forest silvicultural management practices, such as the selection of a certain species composition and planting density, on biogeochemical processes and their potential co-benefits for carbon sequestration is still not well understood. Our study of the mass loss of two standardized litter types in planted juvenile forests across biomes aimed to examine the effects of overstory composition (tree identity, mixture composition and diversity), plantation conditions (density and age) relative to climate (temperature and precipitation) on the litter decomposition process over time.

4.1. Litter quality and climate effects on mass loss over time

As generally acknowledged (Coûteaux et al., 1995; Aerts, 1997), litter decomposition is largely influenced by litter quality and climate. We observed two times faster decomposition of high-quality green tea compared to low-quality rooibos tea along the investigated gradients of tree diversity located in three continents (Fig. S3). The higher water-soluble fraction and nutrient content in green tea compared to rooibos result in faster mass loss due to leaching and decomposer activity during early stages of decomposition (Berg and McClaugherty, 2008; Ristok et al., 2017; Fanin et al., 2020). Hence, our results (80 % of variance explained by tea type in our study; Fig. 5) further illustrates the importance of litter quality for decomposition at a multi-continental scale (Djukic et al., 2018; Kwon et al., 2021). After litter quality, climate was the most important driver of mass loss in our study, explaining 0.9 % of variation after 3-months and 2 % after 12-months (Fig. 5). Accordingly, biome significantly affected decomposition dynamics with mass loss increasing from boreal < Mediterranean < temperate < warm, temperature humid biomes (Fig. S5, Table S3), as already illustrated by Djukic et al. (2018), corresponding to the anticipated increase in mass loss with temperature (Bradford et al., 2016), as long as moisture does not become limiting (Petraglia et al., 2019). It is important to note that the impact of temperature on mass loss depends greatly on soil moisture conditions (Petraglia et al., 2019), but we did not consider this factor specifically in our study. Moreover, differences in microclimate (e.g., through shading and interception) and local differences in the environment (e.g., micro-relief, litter traits on the forest floor) all play an important role in decomposition (Joly et al., 2017), yet they are often neglected when evaluating broader climatic gradients.

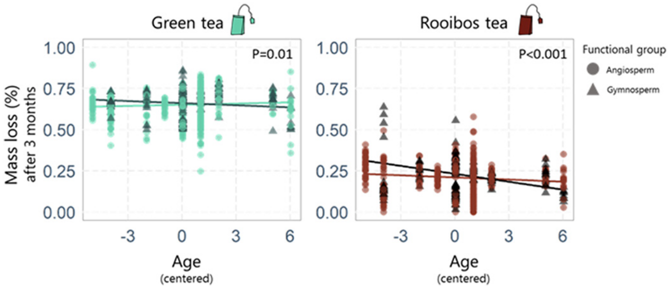

Fig. 4. Mass loss (%) as a function of age (centered variable) for green tea (left) and rooibos tea (right) for overstory functional group (pale circles: angiosperms and dark triangles: gymnosperms). Relationships were tested using linear mixed models (Table 2) accounting for overstory, climate and random effects. The significance level of the interaction is indicated in top left corners.

4.2. Tree identity, composition, and diversity effects

In our study, we found significant overstory tree identity effects on mass loss of low-quality litter during early stages of decomposition (after 3 months of incubation - conducted in the growing season): rooibos tea decomposed faster under gymnosperm compared to angiosperm overstories (Table 2, Fig. 2). Most studies report opposite trends: for instance, Chomel et al. (2015) observed slower decomposition of cellulose in a spruce plantation than in a poplar plantation; Joly et al. (2017) reported a negative correlation between litter decomposition and the relative basal area of evergreen trees; and recent findings of Fanin et al. (2020) showed that rooibos tea decomposed slower under coniferous species than under broadleaved species. These studies were executed in mature forest stands, whereas our study was carried out in young plantations (maximum 12 years old) where microbial and invertebrate communities had less time to adapt to the prevailing tree species (and its litter input) and also microclimatic conditions still change considerably in the first years after planting (Zhang et al., 2022). The higher mass loss of low-quality litter after three months of incubation, when placed under young gymnosperm canopies in our study could be related to higher shading provided by gymnosperm species due to their dense canopies. This could have improved moisture retention (Petraglia et al., 2019) or provided a more buffered temperature regime (Zhang et al., 2022), both of which promote mass loss. This mechanistic explanation is thus in contrast to our expectation that denser canopies may reduce soil moisture due to higher rainfall interception than in the more open canopies of the angiosperm species (cf Hypothesis 1). These identity effects became subtler with progressing decomposition. We assume that this reflects the decreasing impact of climate on decomposition processes as the proportion of lignin increases with time (Berg and McClaugherty, 2020), explaining the lack of effects after 12 months of incubation. Additionally, we cannot exclude the effect of differences in the decomposer communities between angiosperm and gymnosperm overstories, which could affect decomposition differentially through decomposition stages.

We did not find a significant effect of tree species richness on the decomposition of standardized substrates (Table 2, Fig. 3). This is in line with other studies that identified a predominant role of identity over diversity in belowground ecosystem functioning (Schwarz et al., 2015; Dawud et al., 2016, 2017; Joly et al., 2017; Zhou et al., 2020). We did, however, find a significant effect of tree composition on mass loss of low-quality rooibos tea after 12 months: more diverse neighborhoods (e.g., mixtures

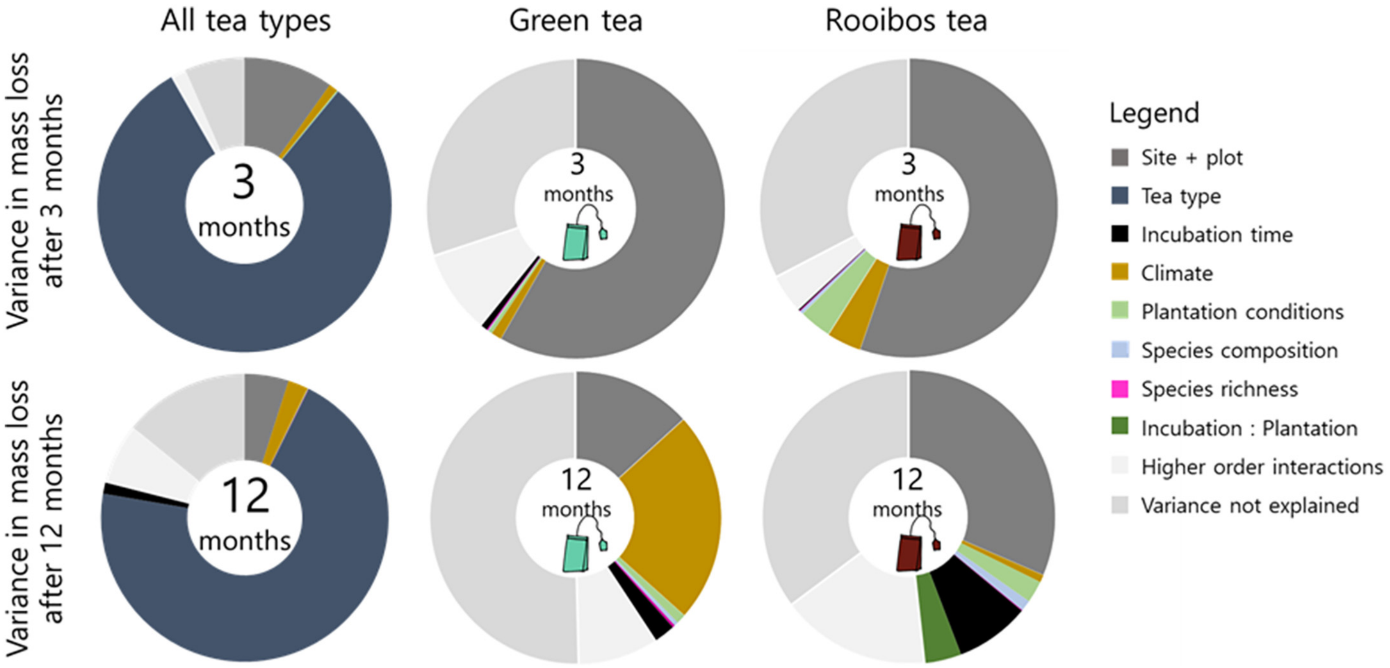

Fig. 5. Percentage of variation explained by site, litter type, climate (MAT + MAP), tree composition (Focal tree identity + mixture composition), species richness (SR), plantation conditions (age + density), and the shared effects between incubation period, climate, and plantation conditions for the total mass loss (left), green tea mass loss (middle) and rooibos tea mass loss (right) for incubation periods (top: 3 months, bottom: 12 months).

of angiosperm and gymnosperm species) promote the decomposition of low-quality litter after accounting for the positive impact of the focal species being a gymnosperm, which is in line with our hypothesis 1. Taken together, these results suggest that tree species diversity and specifically mixtures of angiosperms and gymnosperms can have positive effects on the decomposition of low-quality litter, as mentioned in previous research (Gartner and Cardon, 2004; Handa et al., 2014; Joly et al., 2017): (1) the presence of tree species with high-quality litter (which are more likely to be present in mixtures) promotes the breakdown of low quality litter via nutrient transfer, improved water retention or other positive interactions with recalcitrant litter (Porre et al., 2020), and (2) more diverse substrates support a larger decomposer community, which is more likely to process low-quality litter (Vogel et al., 2013). A probable mechanism is that specific decomposers break down specific litter components, such as lignin or phenolics (Ristok et al., 2017), and the diversity of these different decomposer groups increases the overall decomposition process through niche partitioning. This implies that, beyond the overarching importance of focal tree identity, the surrounding environment and its diversity and composition could also affect decomposition (Hättenschwiler, 2005). Such diversity effects are often context dependent and cannot be generalized across continents and over different species compositions (Scherer-Lorenzen et al., 2007); this may explain the subtle differences found in our study, which could become more pronounced with time (Li et al., 2019; Xu et al., 2020).

4.3. Plantation conditions effects on mass loss

We did not find any effect of planting density on mass loss, irrespective of tea type, during early stages of forest development, leading to the rejection of hypothesis 3. This suggests that the density at which young trees were planted did not affect nutrient availability or the forest microclimate to the extent that it affected decomposition. In other studies of mature forests, variables such as canopy density and packing had some explanatory power for decomposition (Jucker et al., 2015; Trogisch et al., 2016), similarly we expect density effects in our experiments may strengthen as the experiments age. Furthermore, we found that mass loss of low-quality litter after 12 months marginally decreases with stand age ($P = 0.09$), whereas we found no effect of stand age on green tea decomposition. We did, however, find a significant interaction effect between age and tree identity during decomposition after 3 months for both rooibos and green tea: the impact of stand age on litter decomposition was more negative under gymnosperm overstories. Hence, we reject hypothesis 2, that tree species identity effects become more pronounced with the age of the stand, as we observed a reversal of the impact tree identity. The possible beneficial microclimate effect of young gymnosperm stands promoting decomposition (by providing a more buffered temperature regime (Zhang et al., 2022) or higher soil moisture due to shading (Petraglia et al., 2019)) compared to angiosperm stands is likely to disappear with stand age. In addition, the soil biochemical composition is likely to change over time under gymnosperm species, negatively affecting acidity status, nutrient availability, and microbial communities (Coûteaux et al., 1995). This illustrates that plantation age can alter identity effects and that caution is needed when generalizing our findings to mature stands where belowground functioning, canopy closure and microclimate may be very different (Trogisch et al., 2016; Joly et al., 2017; Zhang et al., 2022). In addition, the interaction effect between tree identity and stand age was not observed for the 12-month incubation period (Table 2). This suggests that earlier stages of litter decomposition may be better suited to understanding the relative importance of overstory-related decomposition drivers compared to mid-stages of decomposition; as decomposition progresses (and thus relative higher lignin content and less mass remains) overstory effects become subtler. This corresponds with García-Palacios et al. (2016) who also illustrated a shift in control from biotic (overstory) to abiotic (edaphic and climatic) factors with ongoing litter decay.

4.4. Limitations and scope for further research

This study was carried out in young plantations (maximum 12 years old) across boreal, temperate, Mediterranean, and subtropical biomes. As a consequence, some tree community effects on decomposition processes may emerge in the future as ecosystem functioning may become more strongly controlled by biotic factors during later stand development

(Jucker et al., 2020; Xu et al., 2020). For example, decomposer community (Eisenhauer et al., 2012) and soil chemistry (Dhiedt et al., 2022), microclimatic conditions (Mayer et al., 2017), and litter production (in absolute quantities) change over time, and such differences can vary among biomes. Moreover, no information on edaphic properties could be included in our research, despite its explanatory importance for context-dependent effects on litter decomposition (Fanin et al., 2020; Desie et al., 2021). Previous research has indicated that the local environment (including edaphic properties, microrelief and microclimate (Seidelmann et al., 2016; Joly et al., 2017)), the quantity and quality of the litter (Briones, 2014), the composition of the local soil community (Hättenschwiler, 2005; Briones, 2014), as well as the interactions between litter quality and decomposing environment (Veen et al., 2019) all affect decomposition. Such interactions are very complex, and future large-scale studies should take into account the ambient soil conditions, litter quality, and microclimate (Makkonen et al., 2012). Nevertheless, our study using standardized litters across a multi-continent set of tree diversity experiments provides a first indication of the relative importance of the surrounding tree community and its diversity, relative to macroclimate.

5. Conclusions

Our findings highlight the important role of local conditions shaped by the forest overstory composition and stand structure as determinants of litter decomposition dynamics in young plantations. Overstory diversity had no clear effect on mass loss, irrespective of tree type, whereas tree species identity (and composition) affected decomposition of low-quality litter directly via overstory litter quality and quantity and indirectly via changes in the micro-environment. Moreover, these direct and indirect effects of tree species composition on litter loss were dependent on the age of the stand. In these young stands, both planting density and overstory composition had little effect on litter decomposition compared to litter quality and macroclimate, suggesting limited consequences of management decisions related to planting density or species choice at early stages of stand development. To further disentangle these effects, it will be important for future studies to include a direct quantification of the micro-environmental conditions at the site of decomposition. Further, we suggest not only relying on standard substrates for such studies, which can only test the role of the environmental and edaphic controls of decomposition, but combining them with the decomposition of plot-specific litters that would capture the influence of tree diversity and species composition through their effects on litter quality and quantity.

CRediT authorship contribution statement

ID designed the experiment; AP, AS, BY, BM, CB, CM, CN, CAN, HB, HF, HJ, JR, KV, LM, LW, MSL, MW, NB, NE, OF, PBR, QP, StS, ST, SS collected data; ED, ID, JZ assembled the data from the sites; ED, JZ, KVM analyzed the data; ED and JZ wrote the first draft of the manuscript; BM, KV, ID and KVM provided thorough feedback on the manuscript, all coauthors commented on the advanced manuscript.

Data availability

Data will be made available on request.

Declaration of competing interest

All authors reports equipment, drugs, or supplies was provided by UNILEVER Lipton Tea Bags. Juan Zuo reports financial support was provided by Belspo. Nico Eisenhauer and Olga Ferlian reports financial support was provided by German Research Foundation FZT 118, 202548816. Helge Bruelheide, Bo Yang, Stefan Trogisch, Heike Feldhaar, Steffen Seitz reports financial support was provided by German Research Foundation FZT 118, 202548816. Martin Weih reports financial support was provided by Swedisch Energy Agency (36654-1, 36654-2, 36654-3 project DiPTiCC 16-CE32-0003. Michael Scherer-Lorenzen reports administrative support was provided by Federal Forestry Office Thüringer Wald.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.159717.

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