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Tree community composition modulates early-stage decomposition of standard litter through chemical and physical engineering

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ABSTRACT

Litter decomposition is an essential ecosystem process influenced by multiple factors, including substrate quality, climate, edaphic environment, and decomposer communities. However, the role of canopy species identity and diversity on leaf litter decomposition in forests remains understudied. By controlling for macroclimate, soil properties, and litter substrate in a mature common garden, we investigated whether a three-month tea bag incubation of standardized green and rooibos tea substrate is driven by canopy tree species characteristics and diversity. Our study hypothesized two primary pathways: a chemical engineering effect, where trees alter soil properties and decomposer communities through litter input, and a physical engineering effect, where tree canopy structure modulates the local microclimate. The results showed that even under uniform macroclimatic and initial soil conditions, mass loss rates varied widely for green tea (27.4%–73.2%) and rooibos tea (6.1%–34.7%), comparable as found in other research between distinct biomes. While substrate quality was the dominant factor, both engineering pathways and, to a minor extent, tree diversity modulated mass losses. For green tea, tree chemical and physical characteristics seemed equally important, while the physical environment showed an increased importance for rooibos. Incubation depth played a key role, where forest floor decomposition rates are more susceptible to temporal climate variations, and soil-layer decomposition rates are less susceptible to climate variations and more determined by tree species identity. Our findings suggest that tea bag experiments focusing solely on topsoil burial may underestimate processes in the forest floor and the mineral-organic boundary layer. This study underscores the critical role of litter substrate quality in decomposition while demonstrating that tree community composition and the associated herbaceous layer, through both chemical and physical engineering pathways, strongly modulate decomposition rates.

1. Introduction

Litter decomposition is a key process in the biogeochemistry of forest ecosystems (Berg and McClaugherty, 2014; Bradford et al., 2016). Through its impact on the nutrient and carbon cycle, it regulates the availability of essential elements and carbon dynamics in forests (Krishna and Mohan, 2017). On a global scale, studies show that litter decomposition is primarily controlled by macroclimate, litter quality, and decomposer community (Coûteaux et al., 1995). Macroclimate, which can be represented by actual evapotranspiration (Aerts, 1997), is a key factor influencing this process. Temperature, for example, plays a crucial role as microbial activity increases exponentially with it (Bradford et al., 2017). Besides, macroclimate drives plant communities, associated litter quality, and decomposer composition (Joly et al., 2023).

Litter quality, including C/N ratio and total nutrient content, varies with species identity and composition, and has been identified as a driver of decomposition rates (Prescott, 2010). In the context of climate change, shifts in local climate and associated plant community composition can occur, with implications for forest carbon fluxes (Landry et al., 2021). Tree species mixture and assisted migration of tree species are currently advocated as climate-smart forest management strategies (Paquette et al., 2018; Williams and Dumroese, 2013), which can influence local forest ecosystems. Bradford et al. (2016) suggested that

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broad-scale biogeochemical models may overemphasize the role of macroclimate for decomposition processes, while overlooking site-specific factors. This highlights the need for a better understanding of how tree species mixtures and varying proportions of non-native species influence litter decomposition processes by altering the local forest ecosystems.

Forest ecosystems are complex, and various physical, chemical, and biological factors drive decomposition processes (Krishna and Mohan, 2017). Local decomposition dynamics are influenced by site characteristics (e.g., soil properties, including texture, structure, cation-exchange capacity, organic matter content, and moisture), as well as interactions between temperature and the soil properties, which can have variable effects on the decomposition process (Angst et al., 2021; Coleman et al., 2018; Petraglia et al., 2019). These local abiotic conditions affect biota, including vegetation, soil fauna, and microbial communities (Castaño et al., 2018; Frouz, 2018; Lee et al., 2014). Feedback between vegetation, soil biota, and the edaphic environment is omnipresent. For example, tree species identity influences earthworm abundance through litter quality, affecting decomposition rates and soil properties (De Wandeler et al., 2018; Desie et al., 2021; Schelfhout et al., 2017). The decomposer community itself moreover evolves with depth and throughout the decomposition process (Tennakoon et al., 2021). Biotic and abiotic factors driving litter decomposition are intertwined and often confounded, masking the effects of tree species communities on local decomposition dynamics (Prescott and Vesterdal, 2013).

However, under comparable macroclimate, topography, and soil conditions, litter decomposition is expected to mainly depend on forest canopy composition and traits (Cornwell et al., 2008). Trees, as ecosystem engineers (Jones et al., 1994), can alter their environment chemically by modifying humus type and soil pH (Desie et al., 2021) through the quantity and quality of litter input. As physical engineers, trees affect the decomposition environment by regulating light availability and local microclimate (Joly et al., 2017; Xiao et al., 2019). Chemical and physical engineering pathways may not always be synergistic; for instance, coniferous litter proportion can have opposing effects on litter decomposition to coniferous overstory proportion, the former slowing down decomposition through low litter nitrogen content and the latter accelerating decomposition by a more humid microclimate (Xiao et al., 2019). Beyond their litter quality and quantity, tree species also affect the humus type, including the bacterial and fungal communities in the soil (Heděnec et al., 2020). In addition, they form strongly tree-species-identity-dependent mycorrhizal associations (Heděnec et al., 2023; Hofmann et al., 2023; Tanunchai et al., 2023). While assessing the drivers of litter decomposition in monospecific forest stands is complex, the effects of mixed tree communities and tree species richness on decomposition rates are even less predictable (Chapman et al., 2013). Diversity and functional properties of forest communities are crucial for studying tree effects on decomposition (Jewell et al., 2017), but positive, neutral, and negative effects of tree species richness on decomposition have all been reported in the literature (Hättenschwiler, 2005; Trogisch et al., 2016).

One way of disentangling the interacting effect of litter chemical characteristics from environmental factors on decomposition processes is the use of standardized substrates. Tea bags (Keuskamp et al., 2013) have become a widely applied method to assess an ecosystem's ability to support early-stage litter decomposition (Djukic et al., 2018). This method is suitable for examining the role of environmental drivers of decomposition and to further develop simulation models estimating the carbon balance in litter pools for different ecosystems (Didion et al., 2016). In this method, tetrahedral bags are filled with two well-known substrate types, the more palatable green tea from *Camellia sinensis* and the more recalcitrant rooibos tea from *Aspalathus linearis*. These two contrasting substrates are incubated in situ for a period of 3 months or longer to construct a decomposition curve using only one single measurement in time (Keuskamp et al., 2013). However, recent studies have highlighted limitations in the calculation of the tea bag index (TBI), particularly concerning its assumptions and interpretation as a proxy for natural litter decomposition dynamics, and have suggested that the TBI should be applied with caution and preferably alongside complementary measures (Mori, 2022a, 2022b, 2025). Therefore, a call for a deeper understanding of the index calculation is needed (Sarneel et al., 2025), and a focus on modelling relative mass loss of the tea bags is advisable (Mori, 2025) as applied in other global-scale studies (Djukic et al., 2018).

When examining factors affecting early-stage substrate decomposition, it is evident that the quality of the tea substrate will matter (Kriiska et al., 2021). Distinct decomposition pathways for different substrates, especially in carbon and nitrogen release, are influenced by microbial and fungal colonization, with moisture content playing a crucial role (Certini et al., 2023; Daebeler et al., 2022; Duddigan et al., 2020; Mori et al., 2021). Tea bags are used to compare decomposition across various land uses, climates, and soil conditions (Didion et al., 2016; Djukic et al., 2018; Petraglia et al., 2019), while local conditions, including vegetation structure and composition, should be considered (Bradford et al., 2016; Joly et al., 2017). Under forest ecosystems, palatable substrate decomposition was found to be linked to climatic factors, while low-quality substrate decomposition is influenced by soil characteristics and tree species identity (Aguilar-Cruz et al., 2020; Desie et al., 2023; Fanin et al., 2019).

The aim of this research is to determine the extent to which tree species communities influence early-stage litter decomposition when using standard litter and excluding confounding macroscale abiotic site conditions of climate, soil parent material, and topography as much as possible. To do so, all study plots were selected in the same common garden, located in a temperate Atlantic climate, established on Glossalbic Luvisols developed in aeolic loess as parent material, and positioned in a relatively flat plateau landscape. To clearly separate effects from the leaf litter quality itself, and from the biogeochemical decomposition environment created by the forest community, tea bags filled with well-known reference substrates were used (Keuskamp et al., 2013). This way, by controlling for the confounding factors of macroclimate, soil properties, and substrate, we were able to test the extent to which early-stage litter decomposition is driven by local tree species community characteristics and diversity. Two ecosystem-engineering pathways were identified through which tree species communities are possibly affecting litter decomposition, being i) a tree litter quality effect shaping the biogeochemical environment, e.g., the local humus and topsoil characteristics and decomposer community (De Wandeler et al., 2018; Hofmann et al., 2023; Tanunchai et al., 2023); and ii) an effect of the biophysical environment through forest canopy structure inducing a local forest microclimate (de Godoy Fernandes et al., 2021; Joly et al., 2017; Xiao et al., 2019). A simplified conceptual scheme is given in Fig. 1.

To explore the tree community-related decomposition pathways, a three-month incubation of green tea and rooibos tea was performed in the geographical arboretum of Tervuren, Belgium, a unique common garden of mature temperate and boreal forest communities mostly from the northern hemisphere, established since 1902. Teabags with green tea and rooibos tea substrates were placed in the organic layer and the topsoil under a large variety of pure and mixed tree species communities. More precisely we tested the hypotheses that (1) litter quality is the main driving factor of relative mass loss, with palatable substrate (green tea) decomposition being mainly regulated through stand structural characteristics (the physical engineering pathway of forest community), while recalcitrant substrate (rooibos tea) decomposition is mainly regulated through the topsoil characteristics (the chemical engineering pathway of forest community). (2) When excluding macroclimate variability and soil parent material, mass loss rates are mainly determined by the overstory composition of the forest community. Substrate decomposition will be negatively influenced by the share of gymnosperms and positively by increased tree diversity; (3) Above ground (forest floor) and below ground (topsoil) mass loss processes

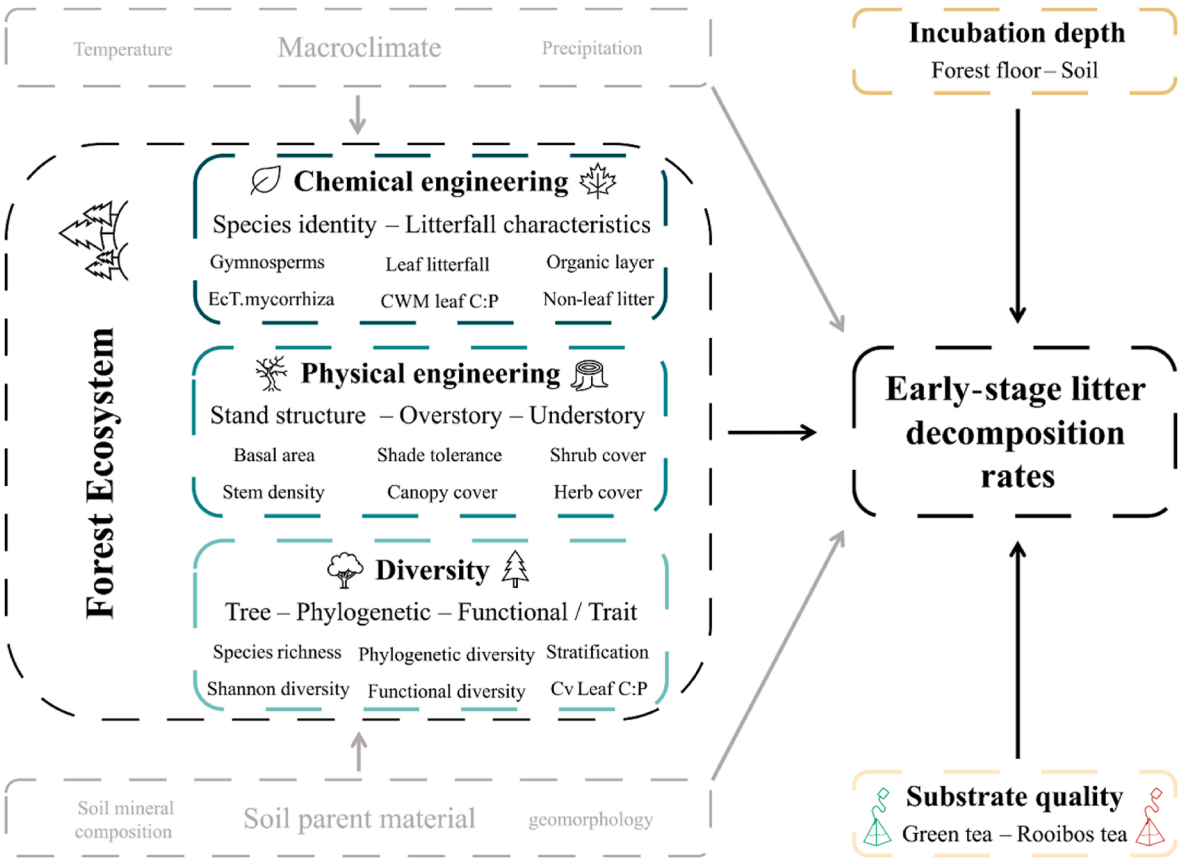

Fig. 1. Simplified decomposition scheme where the decomposition environment is modulated by the local forest ecosystem. Three groups of variables are identified, characterizing local forest ecosystems: (i) chemical engineering effect, indicating the matrix quality, (ii) physical engineering effect, inducing a local microclimate, and (iii) the complexity of the forest ecosystem, representing forest stand heterogeneity. These different forest compositions are characterized by their ability to support standardized substrate breakdown at a certain incubation depth, while excluding variability in macro-abiotic site conditions (temperature, precipitation, and soil parent material) as much as possible.

have distinct responses to the same overstory forest composition, where forest floor mass loss rates are more susceptible to the physical environment provided by the forest canopy and affected by temporal climate variations, while soil mass loss rates are less susceptible to climate variations and more determined by the steady biochemical environment co-evolved with tree species litter traits.

2. Materials and methods

2.1. Site description

This teabag experiment was performed in the Geographical Arboretum of Tervuren, Belgium, a unique common garden covering 120 ha. Unlike other arboreta, it features mixed forest communities from temperate and boreal biomes worldwide, rather than single trees or monospecific stands. Designed in 1902 by Charles Bommer as part of the Royal Donation (Huvenne et al., 2020), it has now developed into mature forest communities. The forest arboretum was designed with the intention of reflecting a number of emblematic forest types worldwide. The tree species were introduced here according to their region of origin in more or less natural proportions, sometimes with a focus on a selection of (available) tree and shrub species (Huvenne et al., 2020).

The study area experiences a temperate warm climate (Cfb) with an average annual temperature of 10.9 °C and approximately 780 mm of precipitation (KMI, 2020). The region is characterized by tertiary sand layers covered by niveo-eolic loess sediments intersected by dry valleys (Baeyens, 1959). According to the WRB classification, the soils are identified as Retisols on the plateaux and Cambisols in the valleys (Dondeyne et al., 2014).

2.2. Plot selection and characterization

A total of 120 study plots were selected (Fig. 2) across various tree species communities to encompass a broad range of tree species traits related to physical and chemical ecosystem engineering (Table S1). The criteria for selecting a study plot included i) stands over 40 years old, ii) visually healthy conditions, iii) absence of disturbances or planned management actions, and iv) location on Retisol soil type (IUSS Working Group WRB, 2022) with minimal or no slope, to minimize confounding factors.

Each study plot, with an 18 m radius, was subjected to a forest inventory between late April and early May 2022. All tree species within the 1,018 m^2 plot were identified, and their diameter at breast height was measured. The abundance of species in the shrub layer within a 5 m radius was estimated using the Braun–Blanquet scale. Three 2 m^2 subplots were randomly located within a 5 m radius to estimate herb layer abundance and identify herb layer species, also using the Braun–-Blanquet scale. Braun–Blanquet scale values were translated to cover percentages using the method of Tichý et al. (2020) and averaged to obtain one herb cover percentage per plot. Canopy cover was estimated using a spherical densiometer, applied from the plot center towards the four cardinal directions and averaged to optimize mirror coverage (Baudry et al., 2014).

Litterfall was monitored in all plots using litter traps, with buckets attached to the soil at 5 m from the center point. In monocultures, three

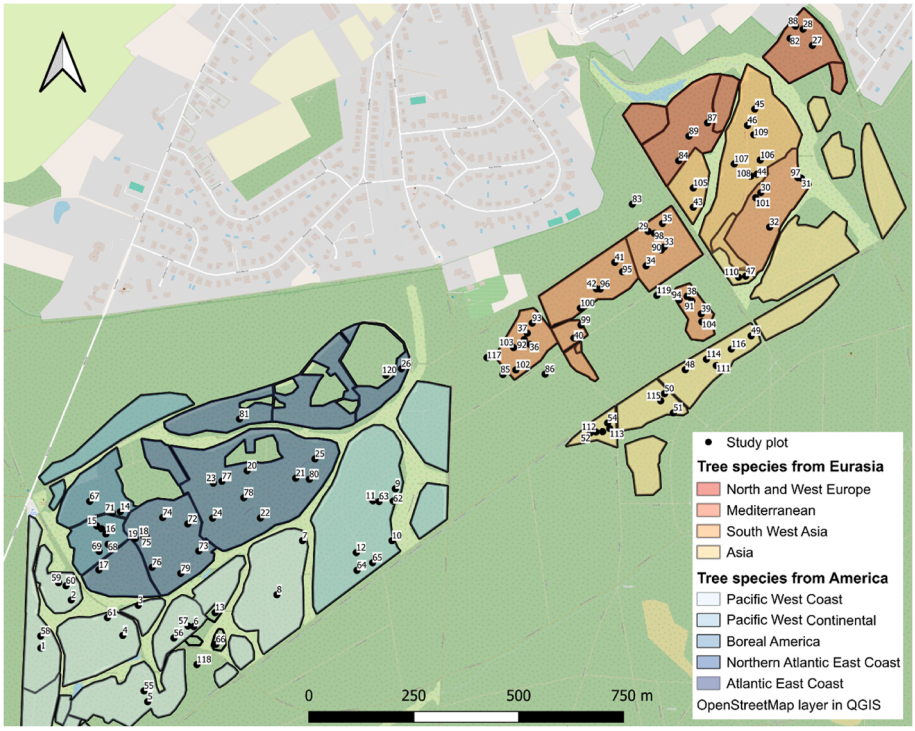

Fig. 2. Illustration of the study area in the arboretum of Tervuren, Belgium, with references to the geographical regions indicated in colour groups and selected study plots with a black dot. The underlying map is obtained through the OpenStreetMap plugin in QGIS3.34.

buckets with a 33 cm diameter were placed at 0°, 120°, and 240°, while in mixed stands, four buckets with a 30.5 cm diameter were placed in the four cardinal directions. Due to delivery issues, two different diameters were used. Collections were performed year-round, with monthly to bi-weekly retrievals. Samples were dried at 30 °C for 48 h to prevent molding, then stored in a climate room at 25 °C until sorting. Leaves and needles of 109 tree species were identified, and the litter was sorted and weighed. Other materials collected, such as seeds, branches, mosses, insects, and other particles, were also sorted and weighed.

In each circular study plot, four composite samples from the ectorganic layer (O_L, O_F, and O_H), further called "forest floor", were randomly selected in each quadrant. These samples were pooled to account for local heterogeneities in the organic layer, classified based on the European humus forms reference base (Zanella et al., 2014). Forest floors were sampled in early autumn 2022, just before leaf senescence, using a 25 cm × 25 cm wooden frame. Prior to the forest floor collection, the present herb layer was collected for the same area. The 120 samples were dried at 65 °C for 72 h to stop decomposition. The organic layer samples were sorted and weighed according to the RENECOFOR protocol (Ulrich et al., 2009), e.g., excluding big branches and seeds.

2.3. Decomposition experiment

2.3.1. Preparation and incubation

The standard protocol for manipulating tea bags, as described by Box 1 in Keuskamp et al. (2013), was followed. Two types of substrate were used: Green Tea "Sencha", Lipton reference EAN: 87 22700 05552 5, with a measured average weight of 1.83 ± 0.07 g, and Rooibos Tea, Lipton reference EAN: 87 22700 18843 8, with a measured average weight of 1.98 ± 0.04 g. Tea bags were dried at 70 °C for 48 h, original labels were removed, tea bags were weighed on a precision balance (resolution 0.0001 g), and engraved plastic tags were attached with nylon string. Besides, 20 green tea (0.1252 ± 0.0022 g) and 20 rooibos tea (0.1317 ± 0.0037 g) bags were emptied and measured to correct initial and incubated tea bags' weights, assuming that the placed empty bags would not decompose significantly during the incubation period.

Considering the protocol of Fanin et al. (2019), two incubation depths were selected: the forest floor and the mineral soil. If a clear organic layer was present, tea bags were placed between the humified layer O_h, and recognisable organic litter layers, O_l or O_f. If no organic layer was present, tea bags were placed directly on the mineral topsoil. In the mineral soil, tea bags were placed at a depth of 3 cm in the Ah horizon, considered the "active" soil layer. Each plot included three replicates, resulting in 12 tea bags per plot (2 tea types × 2 depths × 3 replicates). A total of 1,440 tea bags were installed over a one-week period (10–17 March 2022) and incubated for three months.

2.3.2. Retrieval and post-treatment

After the incubation period, tea bags were retrieved, and disturbances or lost bags were noted. A total of 1,342 tea bags were recovered. The tea bags were dried again at 70 °C for 48 h, and dirt and roots were removed. The bags were classified into eight categories based on their condition (Table S2) following Fanin et al. (2019). Plastic labels and nylon string were detached, and dry weights of the tea bags were measured. Relative mass loss was calculated by dividing the net tea mass loss by the initial tea weight. Bags were classified depending on the retrieval state (Table S2). To determine whether bags with small holes (Classes 2–4) could be included in further analyses, damage-to-intact ratios were calculated (Fanin et al., 2019). Bags with small holes showed an average increase in relative mass loss of 0.4% (Class 2) and 4% (Class 3) compared to the corresponding intact bags. Therefore, Classes 2 and 3 were included in further analyses. Bags where small roots had entered (Class 6) only had a minor increase in relative mass loss (0.2%) after careful root removal. Heavily damaged bags (129), displaced bags (129), and non-retrieved bags (98) were excluded from further analyses.

2.4. Data analyses

2.4.1. Relative mass loss

Since the tea bags were not all incubated for the same duration (average = 93.2 days, standard deviation (SD) = 1.888), the observed

relative mass losses were linearly standardized (Djukic et al., 2018) to the median incubation time (93 days) prior to further mass loss data analyses. A boxplot was constructed to illustrate the observed substrate mass losses. Due to non-normality in the data, a non-parametric test (Kruskal–Wallis and Wilcox pairwise comparison) was used to test for significant differences between substrate type and incubation depth. To verify minimal confounding from study sites, the Kruskal–Wallis test was also performed on the observed average mass losses and several abiotic site conditions. The test indicated no significant differences for soil type ($p = 0.5$) and geology layer ($p = 0.6$) concerning the measured average mass losses after the incubation period.

2.4.2. Tea bag indices

Analysis of the tea bag-derived indices needs to be interpreted carefully, as several assumptions of the TBI methodology have been reported to be incorrect (Mori, 2022a, 2022b, 2025). Therefore, the indices calculated below will only be used as an indicator of the environment for comparison purposes and not as a true decay constant.

The decomposition constant k and stabilization factor S were calculated following the protocol of Keuskamp et al. (2013), where S is determined as Eq. 1:

$$S = 1 - \frac{a_g}{H_g} \quad (1)$$

where a_g is the decomposable fraction ($1 - \frac{\text{Final weight of green tea}}{\text{Initial weight of green tea}}$) and H_g the hydrolysable fraction (0.842) of green tea. H_g is the sum of water-soluble components in green tea (Keuskamp et al., 2013, Table 1). The decomposition constant k is calculated as Eq. 2:

$$k = \frac{\ln\left(\frac{a_r}{W_t - (1-a_r)}\right)}{t} \quad (2)$$

where a_r is the predicted labile fraction $a_r = H_r \times (1 - S)$, with H_r being the hydrolysable fraction (0.552) of rooibos tea. W_t is the final weight of the rooibos tea divided by the initial weight, and t is the incubation time.

2.4.3. Tree species traits and diversity indices

Tree class (gymnosperm/angiosperm) and shade tolerance (on a 1 to 5 scale) were obtained from Niinemets and Valladares (2006). The tree class was used to represent the chemical influence on the forest environment, while shade tolerance contributed to the structure of the tree canopy (physical engineering). Forest matrix quality was represented by the leaf total carbon-to-phosphorus (C/P) ratios, as carbon or nitrogen traits were too correlated with tree class. C/P ratios were retrieved from the TRY database (Kattge et al., 2020). For tree species missing in this database, genus-averaged values were used for further analyses. Expected tree root mycorrhizal colonization was determined using the FungalRoot database from GBIF (Soudzilovskaia et al., 2020). The coefficient of variation (CV) was calculated for tree diameters (stratification) and community-weighted chemical litter composition (leaf C/P). The community-weighted mean of leaf litter C/P ratio was calculated using the "functcomp" function in the FD package (Laliberté and Legendre, 2010).

Tree species richness per study plot was determined by counting the number of unique species, while the Shannon diversity index accounted for species abundance and evenness. Phylogenetic diversity was assessed using RStudio by employing a multi-step approach. First, the "taxize" package (Chamberlain and Szöcs, 2013) was used to verify scientific names against the National Center for Biotechnology Information (NCBI) database. Subsequently, a phylogenetic tree encompassing all 116 tree species (Fig. S1) was constructed using the "V.PhyloMaker2" package, based on the vascular plant phylogeny proposed by Smith and Brown (2018). Finally, abundance-weighted phylogenetic diversity was calculated using the "pd" function from the "picante" package. Functional diversity was estimated with the "FD" package in R (Laliberté and Legendre, 2010), incorporating tree class, mycorrhizal association, shade tolerance, and leaf C/P ratio as key functional traits characterizing tree species identity.

2.4.4. Statistics

Data processing and linear mixed modelling were conducted in R (version 4.6.3) using various statistical and visualization packages. A principal component analysis (PCA) analysis (R packages: corrr,

Table 1
LMM parameter estimation testing the effect of chemical engineering, physical engineering, and tree diversity characteristics on the observed relative mass loss of (a) green tea and (b) rooibos tea after three months of incubation. Plot was included as a random variable, and model conditional R^2 were given.

	(a) Green tea $R_m^2 = 0.18$, $R_c^2 = 0.4$				(b) Rooibos tea $R_m^2 = 0.32$, $R_c^2 = 0.39$			
Fixed effect	Estimate	Standard error	*t*-value	*p*-value	Estimate	Standard error	*t*-value	*p*-value
Intercept	0.544	0.005	116.15	**< 0.001**	0.186	0.003	69.41	**< 0.001**
Gymnosperm percentage	−0.006	0.008	−0.76	0.45	−0.010	0.004	−2.52	**0.01**
Ectomycorrhizal association	0.007	0.005	1.40	0.16	−0.004	0.003	−1.64	0.11
Yearly leaf litterfall	0.019	0.006	3.32	**0.001**	0.003	0.003	1.23	0.22
CWM leaf C/P ratio	0.003	0.006	0.52	0.60	0.003	0.003	0.84	0.40
Yearly non-leaf litterfall	0.012	0.005	2.57	**0.01**	0.005	0.002	2.31	**0.02**
Organic layer weight	−0.009	0.005	−1.76	0.08	−0.002	0.003	−0.85	0.40
Basal area	−0.001	0.006	−0.16	0.87	−0.001	0.003	−0.24	0.81
Leaf shade tolerance	−0.004	0.004	−0.94	0.35	−0.003	0.002	−1.37	0.17
Stem density	0.009	0.004	2.12	**0.04**	0.004	0.002	1.63	0.11
Canopy cover percentage	−0.004	0.006	−0.68	0.50	−0.006	0.003	−2.06	**0.04**
Shrub cover percentage	−0.001	0.004	−0.33	0.74	0.003	0.002	1.59	0.11
Herb cover percentage	0.021	0.006	3.85	**< 0.001**	0.014	0.003	5.02	**< 0.001**
Tree species richness	−0.002	0.009	−0.20	0.84	−0.006	0.005	−1.36	0.18
Shannon diversity	−0.002	0.008	−0.19	0.85	0.006	0.004	1.50	0.14
Phylogenetic diversity	0.010	0.007	1.42	0.16	0.007	0.004	1.85	0.07
Functional diversity	0.002	0.007	0.23	0.82	−0.004	0.004	−1.06	0.29
Coefficient of variance leaf C/P	−0.006	0.006	−0.98	0.33	−0.003	0.003	−0.96	0.34
Diameter stratification	−0.008	0.005	−1.70	0.09	−0.004	0.002	−1.62	0.11
Incubation depth (soil)	0.012	0.005	2.55	**0.01**	0.032	0.003	9.90	**<0.001**

Note: CWM refers to "community weighted mean".

ggcorrplot, factoextra, factoMineR, corrplot, and GGally) and correlation matrix (Fig. S2) were employed to explore relationships among explanatory variables and identify highly correlated variables to minimize the variance inflation factor (VIF) in subsequent modelling steps. Prior to analysis, all explanatory data were standardized, and missing values (NA) were excluded.

To test the first hypothesis, a linear mixed model (LMM) was constructed using the lme4 package of Bates et al. (2015), complemented by lmerTest and MuMIn (Barton, 2024) for model evaluation, incorporating 18 explanatory variables representing the tree diversity, physical and chemical engineering characteristics. Additionally, incubation depth (forest floor vs. soil) and substrate quality (green tea vs. rooibos) were included as fixed factors. Given the hierarchical study design, where three replicates were placed within each plot, plot identity was included as a random effect.

To test hypothesis two and further investigate mass loss patterns while accounting for substrate-specific effects, two additional LMMs were developed separately for green tea and rooibos tea. Similarly, the effect of incubation depth was examined by constructing separate models for the forest floor and soil layer. The proportion of variance explained by fixed and random effects was assessed by comparing marginal and conditional R^2 values using the r.squaredGLMM function in the MuMIn package (Barton, 2024).

Variance partitioning analysis was performed using the partR2 package (Stoffel and Schielzeth, 2021) to quantify the contribution of different explanatory variables or variable groups to the model. Explanatory variables were categorized into three predefined groups for interpretability, as depicted in Fig. 1. Additionally, the analysis accounted for other effects, including incubation depth ("depth"), substrate type ("tea"), grouping effects ("Grouping"), plot variability, and unexplained variance ("residuals"). Part R^2 is often different from the model R^2, since it represents the unique variance explained by a particular predictor after removing the variance explained by the other predictors (Stoffel and Schielzeth, 2021). We indicated this difference as the "grouping effect".

To test the third hypothesis, five LMMs were constructed to assess the decomposition dynamics for each substrate type (green and rooibos tea) at a specific incubation depth (forest floor and soil). Average mass loss was also modelled to represent decomposition potential at the forest stand level. The explanatory variables remained consistent with those used in previous models.

3. Results

3.1. Relative mass loss variability

In total, 1,084 tea bags (75.28% of the incubated number) were considered suitable for further analysis. An overall mass loss (mean ± SD) of 38.03% ± 18.28% was observed, with significant differences between substrate types. Palatable green tea exhibited a relative mass loss of 55.19% ± 6.57%, whereas recalcitrant rooibos tea showed a substantially lower mass loss of 20.42% ± 4.53%. Burying the bags significantly increased the overall mass loss (Kruskal-Wallis test, $p < 0.001$), though the magnitude of this effect varied by substrate type. Specifically, relative mass loss for rooibos tea increased significantly from 18.44% ± 4.53%–21.93% ± 3.9% when buried, while green tea exhibited only a non-significant increase from 54.44% ± 7.68%–55.77% ± 5.49% (Fig. 3a).

To further explore these patterns, a simple LMM was constructed (Table S3a). This model explained 90.94% of the observed variability in relative mass loss, with the random effect "plot" accounting for an additional 2.08%. Only incubation depth and substrate type were significantly associated with mass loss. Therefore, a more complex model was developed (Table S4), by incorporating fixed variables related to local forest composition, including physical, chemical, and diversity indices (Fig. 1). This extended LMM demonstrated significantly improved explanatory power compared to the initial simple model ($p < 0.001$, analysis of variance (ANOVA) test), accounting for 91.98% of the observed variance in relative mass loss. Among the explanatory variables, substrate type contributed the largest proportion of variance (90.13%), followed by additional fixed effects (1.85%), while the random effect "plot" accounted for 1.03%. Variance partitioning of the grouped variables is visually represented in Fig. 3b.

3.2. Effects of tree canopy composition, substrate quality, and incubation depth on relative mass loss

Given that substrate accounted for most of the variability in mass loss, separate models were constructed for green tea and rooibos tea (Table 1). Mass loss of green tea was primarily positively associated with local herbaceous cover ($p < 0.001$) and yearly leaf litterfall amounts ($p = 0.001$). Additionally, green tea was influenced by several forest stand characteristics, including stem density ($p = 0.04$), non-leaf litterfall ($p = 0.01$), and the quantity of the organic layer ($p = 0.08$). Similarly, rooibos tea mass loss was strongly related to local herbaceous cover ($p < 0.001$), but negatively associated with the proportion of gymnosperms in the canopy ($p = 0.01$) and canopy cover ($p = 0.04$), while positively related with non-leaf litterfall amount ($p = 0.02$). Furthermore, the model suggested a near-significant effect of phylogenetic diversity, while incubation depth had a significant positive effect on rooibos tea decomposition ($p < 0.001$).

Besides substrate type, incubation depth significantly influenced the observed mass losses. Therefore, two separate models were developed to characterize mass loss in the forest floor (Table S5a) and in the soil layer (Table S5b). In both models, rooibos tea exhibited significantly lower

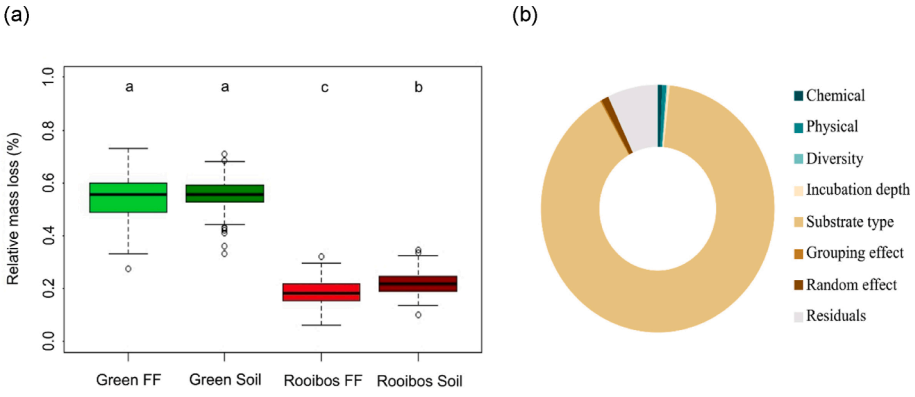

Fig. 3. (a) Boxplots of relative mass loss divided by tea type and depth of incubation. FF indicates "forest floor" and soil indicates the mineral topsoil ±3 cm in the Ah horizon. Different lower-case letters indicate significant differences between groups. **(b)** Variance partitioning (Stoffel and Schielzeth, 2021) of the modelled relative mass loss, where forest explanatory variables are grouped into three categories: chemical engineering, physical engineering, and forest stand heterogeneity (diversity). Besides the effects of incubation depth, substrate type (green vs. rooibos tea), grouping (the grouping effect represents the variance explained by analyzing sets of variables independently, rather than considering all variables simultaneously in a single mixed model), random effect "plot", and non-explained variability or "residuals" are given as well.

mass losses than green tea ($p < 0.001$). Mass loss in the forest floor followed a pattern similar to green tea, with strong positive relationships to herbaceous cover and, to a lesser extent, litterfall characteristics and stem density. In contrast, mass loss in the soil layer was more strongly influenced by overstory characteristics, including the proportion of gymnosperms ($p < 0.001$), the leaf C/P ratio, and the phylogenetic diversity of the forest stand.

The variance partitioning results of the previous LMMs are presented in Fig. 4. Substrate quality remained the dominant explanatory factor (A and B), accounting for a greater proportion of variance in the soil layer (92.49%) compared to the forest floor (87.97%). Notably, the proportion of variance in decomposition explained by microclimatic variables (0.9% in the forest floor and 0.32% in the soil layer) is modest, especially when compared to the dominant effect of substrate type (~90%). Focusing on the substrate type itself (Fig. 4c and d), it was noticed that palatable substrate (green tea) mass loss variability was much more explained by the random variable "plot" (22.14%), matrix quality (7.47%), and tree diversity (1.87%) than that of the recalcitrant substrate. The recalcitrant substrate, on the other hand, was more dependent on the incubation depth (11.6%) and microclimate (11.9%). Despite these identified explanatory factors, a substantial portion of the variance remained unexplained, with residuals accounting for approximately 60% (Fig. 4c and d).

3.3. Effects of tree canopy composition and incubation depth on decomposition rates

In addition to directly analyzing the relative mass loss of substrate types, *k* and *S* were calculated as proposed by Keuskamp et al. (2013). *k* significantly increased from 8.03 ± 2.66 to 10.24 ± 2.98 $mg \cdot g^{-1} \cdot day^{-1}$ when the tea bags were buried in the soil (Fig. 5a). *S*, on the other hand (Fig. 5b), did not significantly decrease when buried in the soil, changing from 0.353 ± 0.092 to 0.336 ± 0.065 $g \cdot g^{-1}$.

Across all study plots, a wide range of *k* from 2.86 to 21.76 $mg \cdot g^{-1} \cdot day^{-1}$ and *S* from 0.13 to 0.68 $g \cdot g^{-1}$ were observed. Angiosperm-dominated forest communities exhibited the highest observed decomposition rates, particularly in the soil layer (11.43 ± 3.27 $mg \cdot g^{-1} \cdot day^{-1}$). Overall, decomposition rates are higher in the soil layer compared to the forest floor, while stabilization was more pronounced in the forest floor.

Similar to the previous modelling of relative mass losses, the two tea bag indices, *k* and *S*, were related to the local forest composition through linear mixed modelling. *k* seems only significantly related to the incubation depth and, to a lesser extent, negatively associated with ectomycorrhiza colonization (Table S6a). *S*, which reflects the inhibiting effect of the forest environment on decomposition, was primarily influenced by annual leaf litterfall characteristics and cover percentage of the local herb layer, in addition to the important role of incubation depth (Table S6b).

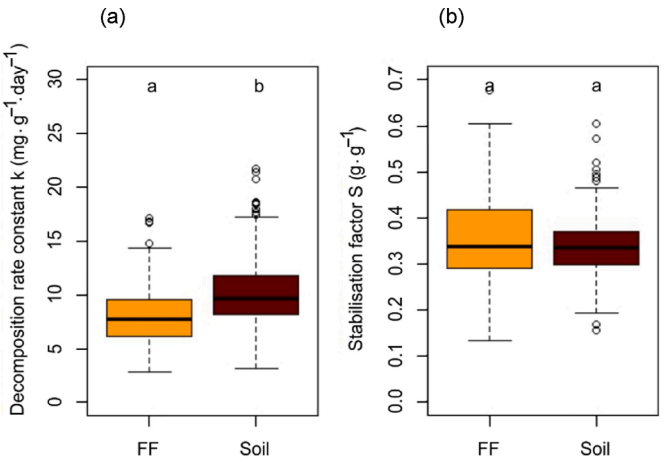

Fig. 5. Boxplots of calculated **(a)** TBI-k and **(b)** TBI-S. Different lowercase letters indicate a significant difference between the forest floor and the soil layer.

3.4. Disentangling drivers of early-stage substrate decomposition

Given that both substrate type and incubation depth significantly influence the decomposition processes, five separate models were constructed to represent the mass loss rate of each substrate type at a specific incubation depth (Table 2). Additionally, average mass loss was modelled to represent overall forest stand decomposition abilities.

At first view, nine out of the 16 selected explanatory variables significantly influenced one or more models (Table 2). Local herb coverage positively impacted observed mass losses. Contrary, the gymnosperm shared in the tree canopy composition negatively affected mass loss. Differences in explanatory variables were apparent between the forest floor and the soil layer. Notably, all model R^2 values were relatively low, whereas including the effect of the random variable "plot" increased the explained variance, or conditional R^2, to about 40%–50%. The model explaining the average mass loss reached the highest $R_m{}^2$ (0.308).

In the forest floor, green tea mass loss was mainly influenced by herb cover and litter inputs, whereas in the soil, significant effects of local forest composition were observed (e.g., negative effects of gymnosperm percentage and positive effects of increasing phylogenetic diversity). For the recalcitrant rooibos tea substrate, this shift was even more pronounced. On the forest floor, only herb and canopy cover significantly influence mass loss, whereas this changes completely in the soil layer to negative influences of gymnosperm percentages and expected ectomycorrhizal associations. On average, independently of incubation depth and substrate type, mass loss seems to be positively influenced by herb

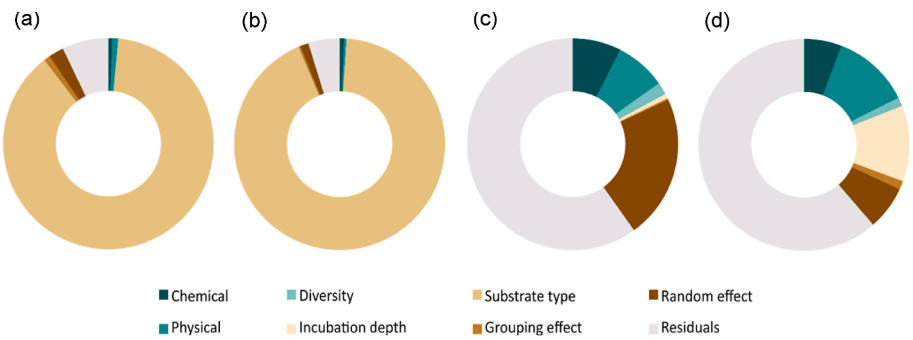

Fig. 4. Variance partitioning of four LMMs (Tables 1 and S5) with response variable: **(a)** forest floor relative mass loss, **(b)** soil layer relative mass loss, **(c)** green tea mass loss, and **(d)** rooibos tea mass loss. Explanatory variables are grouped into three categories, e.g., chemical, physical, and diversity. Besides the effects of incubation depth, substrate type, grouping effect, plot variability, and non-explained variability or "residuals" are given.

Table 2
Estimated effect on the response variable of the modelled variables. Parameter estimates of the five LMMs are given in Table S7–S9. Explanatory variables are divided into 3 categories of variables describing, from top to bottom: chemical effects, physical effects, and diversity indices. Blue tones indicate positive relations and red tones indicate negative ones. Added "+" or "−" to represent significance in the LMMs. Dots indicate near-significant relationships ($p < 0.1$).

	Green tea		Rooibos tea		Avg.
Explanatory var.	FF	Soil	FF	Soil	
Gymnosperm (%)		− −		− − −	
Ectomycorrhiza (%)				− −	
Yearly leaf litterfall	++	.			++
CWM leaf C/P ratio				.	
Yearly non-leaf litterfall	+		.		+
Organic layer weight					−
Basal area					
Leaf shade tolerance					
Stem density	.		.		
Canopy cover (%)			−		
Shrub cover (%)				.	
Herb cover (%)	+++	+	+++	.	+++
Tree species richness					
Shannon diversity					
Phylogenetic diversity		++			
Functional diversity					
CV leaf C/P					
Diameter stratification		.			−
R_m^2	0.182	0.248	0.306	0.281	0.308
R_c^2	0.475	0.56	0.437	0.412	0.589

cover and increased yearly litterfall, while being limited by thick organic layers and more stratified forest stands.

Parameter estimates of the five LMMs are given in Table S7–S9, with explained variances illustrated by Fig. S3. When focusing on the three categorical groups of this research, it is clear that on the forest floor, the biophysical characteristics are the main drivers of mass loss. Shifting to the soil layer, the biochemical variables become the main drivers. Diversity of the tree canopy does not seem to consistently influence mass loss rates, except for palatable green tea in the soil layer.

Besides gymnosperm percentages, herb layer cover turns out to be an important predictor of green tea and rooibos tea mass loss. Fig. S4 provides an overview of the dominant species present in the herb layer and overall herb biomass per plot. Most of the forest stands are dominated by brambles (*Rubus fruticosus*) in varying densities.

4. Discussion

The impact of tree species identity and diversity on litter decomposition remains understudied and is often overlooked in global decomposition research (Giweta, 2020). By controlling for macroclimate, soil properties, and substrate in a mature common garden, we tested whether early-stage litter decomposition is driven by tree species characteristics and diversity.

We identified two key pathways through which tree communities can influence early-stage mass loss of standardized substrate: (1) a chemical engineering effect, where litter quality alters topsoil characteristics and decomposer communities (De Wandeler et al., 2018; Hofmann et al., 2023; Tanunchai et al., 2023); (2) a physical engineering effect, where canopy structure modulates microclimate (de Godoy Fernandes et al., 2021; Joly et al., 2017; Xiao et al., 2019). Although climate variables were not directly measured, we targeted forest structures that induce local microclimatic variation.

4.1. Relative mass loss variability

It is well established that litter decomposition is largely influenced by litter quality, climate, and associated decomposer community (Coûteaux et al., 1995). Our study, however, excluded macroclimate and soil variation by having all plots in one site. Litter quality was standardized using two well-known substrate types, palatable green tea and recalcitrant rooibos tea. After three months of decomposition across 120 study plots, substrate quality significantly affected mass loss, with an average weight reduction of 55.01% ± 5.79% for green tea and 20.2% ± 4.57% for rooibos tea. These values align with previous studies reporting green tea mass losses of 62%–65% and rooibos tea losses of 20%–25.8% (Desie et al., 2023; Djukic et al., 2018; Fanin et al., 2019). The differences in mass loss stem from distinct biochemical compositions of the tea materials (Keuskamp et al., 2013), particularly variations in carbohydrates, lipids, and lignin content (Certini et al., 2023).

Compared to other studies, green tea exhibited relatively lower mass loss, while rooibos tea decomposition remained consistent. This may be attributed to the relatively dry conditions during the incubation period. Meteorological data from a nearby station confirmed minimal precipitation (2.2 mm vs. a normal of 59.3 mm) and higher-than-average maximum temperatures (13.7 °C vs. 10.9 °C) in March 2022 (Koninklijk Meteorologisch Instituut, 2022), the first month of the three-month incubation period. These conditions likely slowed decomposition compared to studies in wetter environments (Petraglia et al., 2019). Soil characteristics, including texture, can also influence decomposition rates (Blume-Werry et al., 2021; Fanin et al., 2019), with finer-textured soils supporting higher microbial activity (Xia et al., 2020), whereas the soil of our study area featured a well-developed loamy soil, likely supporting a diverse decomposer community. Tea bags were incubated at a 3-cm depth within the Ah horizon, making them more susceptible to fluctuating moisture conditions. This differs from previous studies using depths of 5 cm (Djukic et al., 2018) or 8 cm (Fanin et al., 2019; Keuskamp et al., 2013). Unlike Fanin et al. (2019), our results showed a stronger effect of incubation depth on recalcitrant rather than palatable substrate.

The initial model of relative mass loss (Table S3a) identified significant effects of substrate quality and incubation depth but not for gymnosperm percentage, basal area, or species richness, despite their broad ranges (0%–100%, 14.3–102.5 $m^2 \cdot ha^{-1}$, and 1–9 species, respectively). When analyzing substrate quality separately, gymnosperm percentage became significant and negatively affected rooibos tea mass loss, consistent with Desie et al. (2023), who also found no significant effects of planting density and species richness on mass loss. Other studies, however, reported significant effects of basal area and planting density (de Godoy Fernandes et al., 2021; Trogisch et al., 2016), though their findings may reflect indirect relationships with factors such as forest characteristics, tree age, soil variation, or water availability.

Determining the influence of tree species richness on decomposition remains challenging due to non-additive mixture effects on both litter quality (Hättenschwiler, 2005; Jewell et al., 2015; Trogisch et al., 2016) and local microclimate (Zhang et al., 2024). In our common garden experiment, species richness alone proved insufficient to properly predict ecosystem functioning, as quite contrasting functional diversity levels could be observed at similar richness levels. Trait-based diversity indices often provide better explanatory power than species richness alone (Fujii et al., 2017; Meier and Bowman, 2008). To improve our models, we incorporated additional diversity metrics, including Shannon diversity, functional diversity, and phylogenetic diversity (Fig. S1), where phylogenetic diversity emerged as a particularly promising variable.

4.2. Effects of tree canopy composition, substrate quality, and incubation depth on relative mass loss

Referring to the first hypothesis, our results confirm that substrate quality is the primary driver of observed mass loss rates, as variance partitioning (Fig. 3b) showed that substrate type accounted for 90% of the observed variance in mass losses. Palatable green tea mass loss is not primarily regulated by the biophysical environment, nor is recalcitrant rooibos tea decomposition mainly driven by the biochemical environment (Fig. 4c and d). These two models captured approximately 40% of the variance. Notably, for green tea, 20% of the variability was attributed to the random effect of plot, suggesting that an important explanatory variable remains unidentified. We can only partially accept hypothesis one, as green tea mass loss is not primarily driven by forest physical characteristics, nor by rooibos tea chemically. Both physical and chemical engineering pathways drive early-stage litter mass losses, but their influence varies depending on substrate type.

Our second hypothesis stated that mass loss rates are mainly determined by the overstory composition of the forest community and that mass loss will be negatively influenced by the share of gymnosperms and positively by increased tree diversity. This can only be partially accepted as the gymnosperm percentage in the canopy indeed showed a significant effect on rooibos tea mass loss, but not on green tea. The effect of phylogenetic diversity also reached near significance, suggesting an indirect influence on the observed mass losses. For both green tea and rooibos tea, herb layer coverage emerged as a key factor, positively influencing mass loss rates (Table 1). Wang et al. (2021) reported a strong mediating effect of herbaceous litter on decomposition, yet herb layer coverage and species identity are often overlooked in decomposition studies, despite their potential significance. Often but not always, herb layer species show higher litter decomposition rates than leaf litter of woody species (Rawlik et al., 2021). The understory vegetation contributes to the decomposition environment not only by supplying palatable litter but also by modifying the forest floor microclimate (He et al., 2020). Exploring the underlying mechanisms of the herb layer would be an interesting topic to verify which herb litter input modifies the decomposition environment; however, it is not feasible to deeply explore the herb layer in this study due to the lack of sufficient quantitative and qualitative data.

When analyzing the drivers of mass loss separately in the forest floor (Table S5a) and soil layer (Table S5b), distinct mechanisms were observed. Besides the dominant role of substrate type, microclimatic conditions are known to play a crucial role in decomposition (de Godoy Fernandes et al., 2021; Joly et al., 2017; Xiao et al., 2019), which also became apparent in our results when focusing on mass loss in the forest floor. In contrast, mass loss in the soil layer is related mostly to chemically engineered characteristics and composition of the canopy (e.g., share of gymnosperm, carbon-to-phosphorus ratios, and phylogenetic diversity) besides the predominant effect of substrate type.

4.3. Effects of tree canopy composition and incubation depth on decomposition rates

Complementary to analyzing variability in observed mass losses, decomposition and stabilization indices were calculated following Keuskamp et al. (2013). This aims to bridge the gap between empirical measurements (Desie et al., 2023; Djukic et al., 2018; Mori et al., 2021) and standardized indices (Blanco et al., 2023; Elumeeva et al., 2018; Fujii et al., 2017; Sarneel et al., 2024). Interestingly, this study revealed that mature forest stands in the same study area with varying tree species composition resulted in a broad range of decomposition rates (2.86–21.76 $mg \cdot g^{-1} \cdot day^{-1}$). Environmental conditions affecting decomposition, represented by S, also covered a considerable range of values (0.13–0.68 $g \cdot g^{-1}$). Order of magnitudes are comparable to experiments covering a large spatial extent (Sarneel et al., 2024), different vegetation biomes (Blanco et al., 2023), and elevation gradients (Petraglia et al., 2019). This suggests that local forest community composition can be as important as large macroclimatic and soil variations. Of course, our field study does not reach the extreme decomposition values observed in (wet) tropical systems (Sarneel et al., 2024) but reveals major differences in decomposition rates, purely induced by tree community composition. This contradicts, to some extent, with findings of Certini et al. (2023), who did not find much effect on the decomposition process of standardized substrate when incubated under only three types of monospecific stands.

When decomposition rates are relatively low and stabilization is high, caution is needed for interpreting the TBI indices (Mori et al., 2022). Keuskamp et al. (2013) indicated that in the case of extremely low k values, it is not certain that green tea has reached its limit value (actual decomposed fraction), resulting in an overestimation of S. Due to the absence of time-series data, we could not verify whether the green tea decomposition reached an asymptote, as assumed in the TBI method. Therefore, TBI-based estimates of k and S should be interpreted with caution (Sarneel et al., 2025). Especially as it is assumed that green tea and rooibos tea have the same stabilization for calculating the decomposition rate, which is not necessarily true (Mori, 2025).

4.4. Disentangling drivers of early-stage substrate decomposition

We accept hypothesis 3, as we found that above-ground (forest floor) and below-ground (soil) incubation have distinct responses to the same overstory forest composition.

In the forest floor, mass loss rates appear to be primarily regulated through the physical engineering pathway (Table 2), with key variables including herb cover, canopy cover, and stem density. In contrast, mass loss in the soil layer is largely influenced by the identity and composition of the local tree community, particularly the proportion of gymnosperms, the share of trees with ectomycorrhizal associations, and the phylogenetic diversity of the tree canopy. The significant role of mycorrhizal associations in shaping soil microbiota, as indicated by Heděnec et al. (2023), underscores the importance of tree species identity in the decomposition process.

The influence of gymnosperm percentage on mass loss rates has been reported in several studies (Desie et al., 2023), though the underlying mechanisms remain debated. This effect may be related to matrix quality (Fanin et al., 2019), canopy-induced temperature buffering (Zhang et al., 2022), hydrological response through litter layer interception (Xia et al., 2019), and associated soil moisture (Petraglia et al., 2019). The predominance of physical drivers in decomposition suggests a high susceptibility to climate variations and potential climate change impacts on decomposition processes (de la Casa et al., 2024). Similarly, herb cover plays a dual role by often contributing palatable litter with higher decomposition rates than woody species (Rawlik et al., 2021) and by regulating the forest floor microenvironment (He et al., 2020). Additionally, aboveground and belowground responses to decomposition drivers may diverge even under the same local conditions (Wardle et al., 2016).

4.5. Limitations and further research

It is worth mentioning that the tea bag analysis method does not directly account for the degradation of lignin, as highlighted by Mori et al. (2023). Besides, Keuskamp et al. (2013) formulated two indices, decomposition rate "k" and stabilization factor "S", in order to have integrative estimators, characterizing and comparing carbon decomposition dynamics between ecosystems. Using those indices, however, assumes among others that the stabilization is equal for rooibos and green tea, which under certain circumstances is not always true (Mori et al., 2022). While separating those two parameters can provide valuable insights into the decomposition process, an in-depth ecological interpretation of the decomposition indices would require further

investigations, including chemical analysis of the tea litter (Sarneel et al., 2025).

Depending on the experimental period, other results can be obtained as decomposition and stabilization are seasonally influenced through temperature and humidity conditions (Mori et al., 2023). Temperature, humidity, and vegetation type also interact with observed decomposition rates and stabilization factor (Petraglia et al., 2019). Therefore, the tea bag method can serve as a comparison between ecosystems, but it may not always be suited for catching realistic year-round decomposition conditions in the field. Besides, Joly et al. (2023) found that standardized litter could overrate the effect of microclimate and did not accurately predict local decomposition of plot-specific litter.

Trying to further unravel early-stage litter decomposition of standardized substrate surely could be a topic of further research, as Fig. 4 shows that about 50% of the variance is still not explained. However, Fanin et al. (2019) also observed 35%–55% of residuals while macroclimate variability, soil types, and geology parameters were included. We noticed sometimes a relatively large residual mass loss variability just within the same plot, although it was rather doubtful to statistically check this due to the use of a maximum of 3 replicates. An experiment linking intraplot variability to capture microenvironmental conditions such as microrelief, small canopy openings, forest floor intactness, and bag placement could potentially be of added value. Besides, further research could focus on a combined litter bag experiment with tea bags to compare and analyze what exactly is decomposing through carbon fractioning analysis, for example.

The observed influence of herbaceous cover on decomposition, represented through tea bag mass loss, suggests an important ecological role, potentially via microclimatic buffering (He et al., 2020) or litter interactions (Rawlik et al., 2021). Future studies should explore the herb layer composition, functional traits, interactions with canopy structure, and the effect on litter decomposition in more depth.

5. Conclusions

Our study demonstrates that by controlling for the confounding factors of macroclimate, soil properties, and substrate in a mature geographical arboretum, we are able to test the hypothesis that early-stage litter mass loss in forests is modulated by both physical and chemical engineering pathways of forest communities, as well as their tree species diversity. Although substrate quality is by far the most important driver of decomposition, within-substrate variability is significantly affected by both pathways and, to a lesser extent, by tree diversity. For green tea, chemical and physical seemed equally important, while the physical pathway showed an increased importance for rooibos. Simplifying the modelling of litter decomposition to gymnosperm percentage, basal area, and species richness underestimated the local forest composition's impact on this process. We observed a wide range of mass loss rates, like those observed in studies across macroclimates, biome types, and soil conditions. The interaction between substrate type and incubation depth plays a crucial role in observed mass losses and associated explanatory variables. Aboveground mass loss rates are more susceptible to the physical environment of temporal climate variations, while soil mass loss rates are less susceptible to climate variations and more determined by the humus form and soil process domain, co-evolved with the chemical engineering pathway of tree species litter traits. We also highlighted the limitations of tea bag experiments that focus solely on soil decomposition for forests. Our findings underscore the importance of litter substrate quality for mass loss rates, which is further modulated by chemical and physical engineering effects of the forest composition. This research contributes to a deeper understanding of the complex factors influencing litter decomposition in forest ecosystems and provides some key forest ecosystem variables that should be included in further studies.

CRediT authorship contribution statement

Joachim López: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Karen Vancampenhout:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Bart Muys:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Quentin Ponette:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

In the final stage of this manuscript, the first author used Microsoft 365 Copilot licensed through KU Leuven in order to improve coherence and grammar, as the author is a non-native English speaker. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2025.100387.

Data availability

Data are available upon reasonable request.

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