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Within-site drivers of leaf litter decomposition in functionally diverse tree communities

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ABSTRACT

Litter decomposition is a key process regulating carbon and nutrient cycling in forest ecosystems. However, it remains unclear how much variation in species-specific mass loss rates is structured by litter quality, substrate-matrix mismatches, and canopy characteristics under constant macroclimate and soil conditions. We quantified leaf litter decomposition across 12 tree species in a century-old common garden, combining a fully reciprocal leaf litter transplant in monocultures with parallel incubations in mixed-species stands. This design allowed us to disentangle the roles of substrate (leaf) quality, a matrix chemistry proxy based on canopy CWM leaf traits, canopy structure, and substrate-matrix interactions in shaping decomposition dynamics. After one year, relative mass loss varied strongly between species (mean 58.7% ± 19.1%), with substrate quality emerging as the dominant driver. A modest home-field advantage was observed (+1.2% mass loss conspecific), though its magnitude varied among species. Home-away differences were associated with higher ΔN/P and ΔMn in the leaf substrates relative to the matrix proxy, indicating directional, trait-specific mismatch effects rather than simple contrasts in absolute quality. Increasing canopy cover reduced mass loss, particularly for high-quality leaves, likely through reduced leaching and altered moisture conditions. Higher annual litterfall slightly enhanced decomposition of rich-quality substrates but tended to suppress decomposition of low-quality substrates. Despite these effects, variance partitioning showed that leaf substrate chemistry alone explained over 70% of the variation in mass loss, while matrix quality proxy and stand structure contributed smaller fractions. Overall, our results demonstrate that decomposition in temperate forests is primarily governed by substrate quality, with additional but moderate modulation by stoichiometric mismatch relative to litter input chemistry and stand structure. These results highlight the importance of integrating trait-based leaf litter properties with stand-level conditions when predicting carbon and nutrient cycling under changing forest composition.

1. Introduction

Leaf litter decomposition is a key forest ecosystem function, governing global nutrient cycling and soil organic matter formation (Berg and McClaugherty, 2014; Cornwell et al., 2008; Gessner et al., 2010; Handa et al., 2014). Decomposition reflects the combined action of litter breakdown and its transformation into other organic materials, thereby linking aboveground production to belowground carbon stabilization and nutrient release (Prescott and Vesterdal, 2021). In the context of climate change, shifts in temperature–moisture regimes and associated plant communities may alter decomposition dynamics and forest carbon fluxes (Cornelissen et al., 2007; Joly et al., 2023; Landry et al., 2021). These changes are directly relevant to management decisions on stand composition, including assisted migration and the diversification of forests through mixed-species stands (Paquette et al., 2018; Williams and Dumroese, 2013). However, the consequences of introducing novel species or promoting mixtures for local ecosystem functioning, particularly litter decomposition, remain insufficiently documented.

At broad spatial scales, the principal controls of litter decomposition are well established: decomposition of single-species litter is primarily

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driven by macroclimate, site characteristics, leaf litter quality, and decomposer community composition (Coûteaux et al., 1995; Prescott, 2010). These global-scale drivers act through multiple interacting physical, chemical, and biological processes (Krishna and Mohan, 2017), yet their influence becomes more complex when examined at finer spatial scales. Locally, decomposition is further shaped by site-specific soil and microclimatic conditions, including soil texture (Angst et al., 2021), temperature regimes (Bonanomi et al., 2023), soil moisture (Lee et al., 2014), interactions between climate and soil properties (Petraglia et al., 2019), and could change over time (Castillo-Figueroa, 2025). Such environmental conditions modulate the structure and functioning of soil biota and microbial communities (Castaño et al., 2018; Kemppinen et al., 2024), which feed back to influence decomposition rates. Because these interacting controls are difficult to disentangle in natural forests, common garden approaches provide a powerful framework to isolate tree species identity effects under shared macroclimatic and soil conditions (Hobbie et al., 2006).

Within a given site, tree species identity and more specifically leaf litter quality, consistently emerges as a dominant determinant of decomposition (Cassart et al., 2020; Castillo-Figueroa et al., 2025; Cornwell et al., 2008). Gymnosperms, for example, often produce relatively recalcitrant litter that decomposes slowly, promoting the build-up of thick organic layers that can acidify soils and reduce microbial functional diversity (Desie et al., 2019). These differences align with resource-use trade-offs among tree species, commonly framed through the leaf economics spectrum (de la Riva et al., 2019; Lin et al., 2019; Ma et al., 2023; Reich et al., 1997; Wright et al., 2004). Despite clear overall patterns, a considerable site-dependency on decomposition dynamics has been evidenced in literature, and different chemical traits stand out as decisive determinants of litter decomposability, particularly magnesium (Makkonen et al., 2012), calcium (Aponte et al., 2012), and manganese content (Vivanco and Austin, 2019), and the carbon-to-nitrogen ratio or carbon-to-phosphorus ratio (Prescott, 2010). Despite these general patterns, strong site-dependency indicates that stand-level conditions can modulate, amplify, or constrain trait-based expectations.

The image becomes even more complex when multiple tree species co-occur. Mixed stands can exert positive to negative effects beyond expected mass-loss rates through facilitation, complementarity, or competition (Gessner et al., 2010). At the stand level, tree-species mixing can affect decomposition processes and soil organic matter formation via changes in microclimate, increased litterfall quantities, and forest floor chemistry (Beugnon et al., 2023; Bourdin et al., 2025; Bowden et al., 2024). These effects of mixing tree species are closely linked and the need to separate these processes has been repeatedly emphasized (Fanin et al., 2016a; Freschet et al., 2012; Zhou et al., 2020).

To synthesize current explanations for why decomposition patterns deviate from simple additive expectations when multiple species are involved, several hypotheses and frameworks have been proposed (Fig. 1), offering mechanistic frameworks for interpreting synergistic, antagonistic, or context-dependent outcomes. Fig. 1a (substrate-centered) represents a framework in which leaf litter decomposition is primarily determined by the chemical quality of the incubated litter substrate (Aerts, 1997; Berg and McClaugherty, 2014; Krishna and

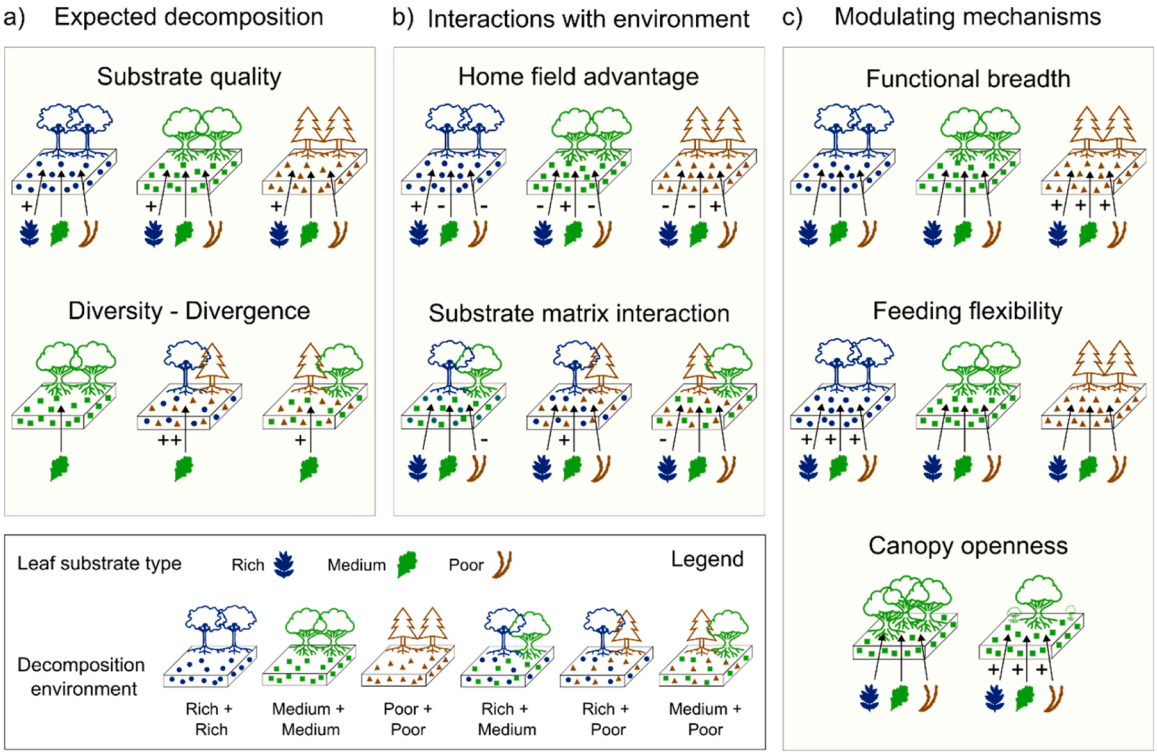

Fig. 1. Substrate-matrix interactions in tree decomposition environments. Conceptual representation of expected leaf litter mass loss when broad variation in macroclimate and soil type is minimized (e.g., in a common garden context). Arrows indicate unspecified mass loss rates; " + " denotes enhanced mass loss; "-" denotes reduced mass loss. (a) Substrate-quality model: mass loss is primarily determined by the chemical quality of the incubated leaf substrate. The diversity-divergence concept predicts higher mass loss when leaf litter diversity is high and the incubated substrate matches the average matrix quality, potentially mediated by a more diverse decomposer/fauna community. (b) Substrate-environment matching models: interactions with the local litter matrix and tree-created conditions can modify substrate-driven expectations, including home-field advantage (HFA) and substrate quality-matrix quality interactions (SMI), which may be positive, neutral, or negative across studies. (c) Mechanistic modifiers: additional processes can modulate HFA/SMI patterns, largely through differences in decomposer specialization versus generalization. Functional breadth predicts that decomposer communities from recalcitrant environments decompose a wide range of substrates at relatively similar rates, as they are used to decompose recalcitrant litter. Feeding flexibility predicts context-dependent shifts in resource use in nutrient-rich matrices (e.g., preferential use of labile substrates and potential priming), with a possible shift towards poorer substrates when preferred resources become scarce ("hungry community"). Finally, stand structure can further influence these mechanisms via canopy openness and litterfall amount.

Mohan, 2017), i.e. "substrate quality" models. In addition, when a broader range of litter types is present at the stand level, decomposition may increase through indirect effects such as a more diverse decomposer community (diversity-divergence concept) (Gessner et al., 2010; Patoine et al., 2020).

A second group of theories (Fig. 1b - substrate-environment interactions) focusses on the effects of the interaction of different tree species with their environment to explain litter decomposition patters that deviate from the simple substrate quality model. Already in the nineties, species-site matching effects were observed in decomposition experiments (Hunt et al., 1988; McClaugherty et al., 1985): in time, plant species create specific conditions (Jones et al., 1994) that could enhance the decomposition of their own litter (Vivanco and Austin, 2008). Theoretical frameworks such as the Home-Field Advantage (HFA) hypothesis (Gholz et al., 2000) propose that litter decomposes more rapidly conspecific in its own environment, aka "at home", than heterospecific, aka "away", due to local adaptation of decomposer communities (Austin et al., 2014; Ayres et al., 2009; Gholz et al., 2000) to litter input and microclimate modulated by the local tree species (Heděnec et al., 2020; Peng et al., 2022b). However, empirical support for HFA is mixed: a recent meta-analysis overall found only a modest increase (3%) in decomposition at home than away sites (Shi et al., 2025) and more detailed studies report positive (Ayres et al., 2009; Fanin et al., 2021; Veen et al., 2015), neutral (Ayres et al., 2006; Castillo-figueroa, 2024; Makkonen et al., 2012; van den Brink et al., 2023), or even negative HFA (Pugnaire et al., 2023). Furthermore, the extent of such a HFA seems to depend on leaf litter quality: with high-quality litter diminishing the HFA (Shi et al., 2025) and low quality litter inducing higher HFA (Pugnaire et al., 2023; Yuan et al., 2025).

Furthermore, the HFA theory is more challenging to apply for mixed species stands with highly contrasting tree species, as it is unlikely that decomposer communities can develop enhanced efficiency in decomposing high and low quality litter at the same time (Gießelmann et al., 2011; Wardle et al., 2006). The Substrate Quality-Matrix Quality Interaction (SMI) hypothesis (Freschet et al., 2012) extends the HFA theory to mixed tree species environments, by considering the interaction between the incubated leaf litter of a certain species (the 'substrate') and the leaf litter present in the surrounding forest floor (the 'matrix') (Perez et al., 2013), where it is expected that similar quality of the leaf litter substrate and the leaf litter in decomposition environment will promote decomposition rates, while dissimilarity will decrease observed decomposition rates (Freschet et al., 2012).

Several other concepts (Fig. 1c – modulating mechanisms) focus on potential mechanisms that may further modulate the dynamics proposed on the HFA and SMI (Fig. 1b). A first is functional breadth (Osburn et al., 2022), stating that decomposer communities from recalcitrant environments may have a broader ability to decompose litter than decomposer communities associated with nutrient rich environments (Fanin et al., 2016a; Keiser et al., 2014). However, opposite effects were also observed, where decomposers may favor the most advantageous food source first (Briones, 2014; Fontaine et al., 2003; Heitkötter et al., 2017), conceptualized in the term "feeding flexibility" (Briones, 2018; Briones et al., 2020). Additionally, the tree canopy can promote or inhibit decomposition also indirectly, as canopy openness influences both the forest microclimate as the amount of litterfall (Kim et al., 2014; Lin et al., 2024; Schnabel et al., 2025; Wang et al., 2021a; Xiao et al., 2019; Zhang et al., 2024). Decomposition rates seem favored by moderate temperatures and good moisture availability (Bourdin et al., 2025), and several authors highlight that not just the quality of the litter input but the quantity could also strongly influence the decomposition dynamics and nutrient cycling (Pisani et al., 2016). Species-diverse stands produce more leaf litter, which was linked to a positive effect on the decomposition rates (Beugnon et al., 2023). Higher litter inputs may also contribute to increased soil organic matter formation (Bowden et al., 2024), which may enhance microhabitat conditions for edaphic organisms involved in decomposition processes (Carayugan et al., 2023; Castillo-avila et al., 2025; Castillo-figueroa and Posada, 2025). Together with previous hypothesis, this could suggest that the decomposer community may shift resource preferences once litter substrate becomes scarce, i.e. a "hungry" community. They also highlight a high degree of functional plasticity within the decomposer community, whereby decomposition rates adjust according to the availability of litter resources for soil fauna and microbes (Briones, 2014). Hättenschwiler and Gasser (2005) observed a litter-quality dependent effect, where macro decomposers seemed more influential for rich litter species than for poor litter species (Yang et al., 2022), an effect that may be influenced by evolutionary traits (Peng et al., 2025) or growth strategy (Augusto et al., 2025).

To explore these different concepts, litterbags are widely used in leaf litter decomposition experiments (Krishna and Mohan, 2017). However, many litterbag studies focus on only a limited number of tree species (Aponte et al., 2012; Lin et al., 2024; Midgley et al., 2015; Pearse et al., 2014; Zhang et al., 2008 and 2024), or relatively young forest stands (Martin-Guay et al., 2022), which restricts the generalizability of their findings to more diverse and mature systems. In addition, stands with different tree species compositions are often located on different sites (Canessa et al., 2021; Shi et al., 2025; Veen et al., 2015), making it difficult to disentangle the effects of tree species identity from confounding factors such as soil properties, macroclimate, and other environmental variables (Castillo-Figueroa et al., 2025; Esquivel et al., 2020). Because these interacting mechanisms are difficult to separate in natural forests, common garden experiments offer a powerful framework to isolate the effects of tree species under shared environmental conditions. Such designs allow researchers to directly assess how tree species identity shapes litter decomposition and forest floor dynamics (Hobbie et al., 2006).

In this study, we performed a reciprocal litterbag transplant experiment in the geographical arboretum of Tervuren (Belgium), a unique common garden of mature forest communities, from all over the northern hemisphere, established in 1902. Our objective was to quantify location-dependent variation in the decomposition of species-specific leaf litter and to identify the processes responsible for such variation. Specifically, we tested whether decomposition differs systematically between 'home' and 'away' environments, how this is influenced by overstorey canopy characteristics, and how decomposition patterns change in species-diverse stands. We hypothesize that H1: leaf substrate decomposes faster at home than away (HFA); H2: increasing dissimilarity between substrate chemistry and a proxy for the matrix quality reduces mass loss (SMI); and H3: canopy characteristics and matrix quality modulate decomposition suggested by the functional breadth concept in recalcitrant environments and feeding flexibility in nutrient-rich environments.

2. M &M

2.1. Study area

The litterbag transplant experiment was conducted at the Geographic Arboretum of Tervuren (50° 48' 38" N, 4° 30' 25" E, Tervuren, Belgium). Unlike conventional arboreta, which typically feature isolated trees or monospecific stands, this site, originally founded in 1902, hosts forest communities representing temperate and boreal biomes worldwide (Huvenne et al., 2020), grouped according to the provenance of the trees (Fig. 2).

The study area has a temperate oceanic climate (Cfb) with a mean annual temperature of 10.9°C and an average annual precipitation of approximately 780 mm (RMI, 2020). During the one-year litterbag incubation period, precipitation was above average, totaling around 1100 mm (RMI, 2025). The region is characterized by undulating plateaus formed by tertiary sand layers overlain by niveo-eolic loess sediments and dissected by dry valleys (Baeyens, 1959). According to the World Reference Base (WRB) classification, soils are predominantly

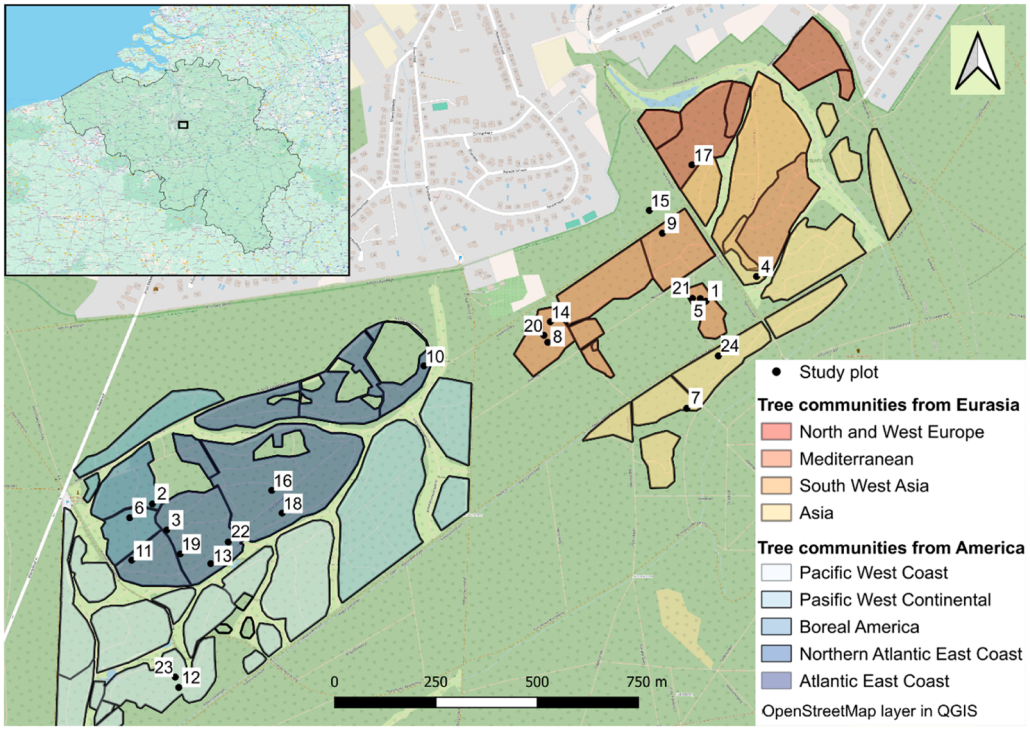

Fig. 2. The selected study plots (Annex 2) with monoculture (1−12) and mixtures (13−24) indicated with a black dot in the arboretum of Tervuren, Belgium (50° 48' 38" N, 4° 30' 25" E). References to the geographical regions are indicated in color groups. The underlying map is obtained through the OpenStreetMap plugin in QGIS3.34.

Retisols on plateaus and Cambisols in valleys (IUSS Working Group, 2022) based on the Belgian soil classification (Digital Flanders Agency, 2017).

2.2. Leaf litter and study plot selection

The study was structured around two complementary experimental components: a reciprocal leaf litter transplant among monoculture stands and a parallel incubation experiment comparing decomposition in monocultures versus mixed species stands. These two approaches allowed us to examine both substrate-driven (H1 & H2; Fig. 1a&b) and forest stand induced micro-environment (H3; Fig. 1c) mechanisms interacting with leaf litter decomposition, while the common garden setup ensures controlled macroclimatic and edaphic conditions.

In the first component, a reciprocal transplant was established across twelve monoculture stands selected to represent two gradients in leaf litter characteristics (Fig. 3, Annex 1). The first gradient captured differences in intrinsic leaf quality, estimated from published trait information (Kattge et al., 2020) together with field-based observations of leaf turnover rates derived from annual litterfall and forest floor mass. The second gradient reflected differences in local microclimatic conditions associated with canopy structure, quantified using the shade tolerance index of Niinemets and Valladares (2006), which ranges from zero (shade intolerant species) to five (highly shade tolerant species). Crossing these two gradients yielded four functional leaf substrate groups, each represented by three tree species, resulting in twelve selected leaf substrate types for the transplant experiment. Corresponding monoculture stands were identified for each of the twelve species to ensure that "home" sites matched the canopy origin of the leaves. All monoculture stands satisfied strict site selection criteria: they were at least 40 years old, undisturbed, free of planned management interventions, located on Retisols (IUSS Working Group, 2022), and situated on minimal slopes to reduce potential confounding influences (Annex 2).

The second component of the design aimed to assess how forest stand composition affects decomposition by incubating a subset of eight of the original twelve leaf substrates in mixed-species stands. As the previously selected species did not naturally co-occur in mixtures, mixed stands were instead chosen to represent a broader ecological gradient structured by both tree-species composition and community-weighted leaf quality (Annex 1 & 2). Stands were categorized according to three composition types; gymnosperm - gymnosperm, gymnosperm -

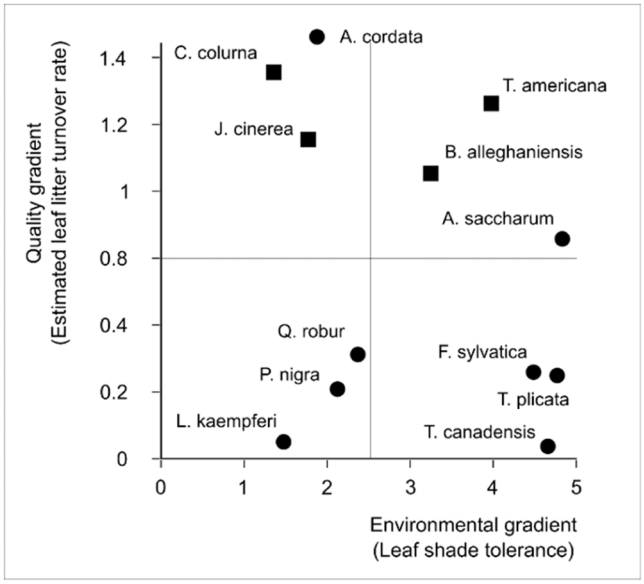

Fig. 3. Twelve selected tree species and leaf litters, based to represent poor and rich leaf litters (proxy by estimated leaf litter turnover rates) on the y-axis and an environmental gradient (proxy by leaf shade tolerance). The substrate species with square icons were excluded in the mixture incubation (Annex 1).

angiosperm, and angiosperm - angiosperm, and within each category, sites were further differentiated by leaf quality. Two stands per category were selected, yielding twelve mixed-species plots. Four leaf substrates (*Corylus colurna*, *Juglans cinerea*, *Tilia americana*, and *Betula alleghaniensis*) were omitted to match the ecological gradient.

2.3. Litterbag experiment

To quantify substrate litter mass loss, we employed litterbags (10 × 10 cm) constructed from polyester monofilament mesh. Each bag contained approximately 2 g of oven-dried leaf litter, to represent the average annual leaf litterfall per square meter. Leaf litter was collected continuously over one year, with monthly to bi-weekly retrievals using litter traps, pooled by incubation site (plot), and sorted by species. The leaf litter traps consisted of three buckets (33 cm diameter) in monocultures placed at 0°, 120°, and 240°C and in mixture stands four buckets (30.5 cm diameter) at the four cardinal directions at 5 m from the plot center. To standardize initial conditions and halt microbial activity, all material was oven-dried at 40°C for 48 h. Only intact leaves without visible damage were selected for bag filling. Litterbags were filled with monospecific leaf litter substrates from 12 tree species.

2.4. Litterbag deployment

Substrate bags were placed both conspecifically and heterospecifically beneath the canopies of 12 monospecific-dominated plots (Annex 1a), with two replicates per plot, resulting in 288 litterbags (12 substrates × 12 plots × 2 replicates). Replicates were randomly placed in close proximity within each study plot. Additionally, eight of the 12 substrate types were deployed in 12 mixed-species plots (Annex 1b) representing a range of canopy compositions, combining variation in leaf quality (palatable vs. recalcitrant) and taxonomic groups (angiosperms vs. gymnosperms). This yielded an additional 192 litterbags, for a total of 480 deployed bags.

All litterbags were deployed on 14–15 September 2023 for an incubation period of approximately 1 year, in the fresh litter layer (Ol) if available and secured to the forest floor using chicken wire and pickets to prevent displacement. Each bag was individually labeled for identification. The mesh design incorporated two sizes, 2 mm on top and 0.5 mm at the bottom, to allow access by meso- and macrofauna while minimizing gravitational particle loss (Patoine et al., 2020; Zhang et al., 2024).

2.5. Incubation and retrieval

After one year of incubation, leaf substrate bags were retrieved on 10 September 2024, cleaned with brushes and tweezers to remove extraneous material, and oven-dried at 60 °C for ≥ 48 h to halt decomposition. For accurate weight determination, bags were opened, and soil particles, macrofauna feces, fauna, and foreign material were removed using tweezers and a 1 mm sieve. The remaining residue mass was weighed on a precision balance (±0.01 g). Relative mass loss was calculated as:

$$\text{Relative mass loss} = \frac{Mass_{initial} - Mass_{final}}{Mass_{initial}} \quad (1)$$

Wild boar activity disturbed 28 bags, which were excluded from analysis. Additionally, some *Tsuga canadensis* needles fell into litterbags in plots 11, 19, 21, and 22 (Annex 2). These needles were removed from the substrate bags, weighed, and their average weight per plot was subtracted from the bags containing *Tsuga canadensis* substrate to avoid bias and approximate actual relative mass losses as closely as possible.

2.6. Study plot and leaf litter characterization

Each study plot (18 m radius ~ 1018 m^2) was inventoried for stand characteristics, including tree species identity, diameter at 1.3 m height, basal area calculation, stem density, canopy cover, shrub and herb cover, annual litterfall, and forest floor properties. Litterfall was monitored year-round using litter traps (López et al., 2026). Canopy cover was quantified using a spherical densiometer, with measurements taken in all four cardinal directions and averaged (Baudry et al., 2014). Forest floor dry weight was assessed from four composite samples (25 × 25 cm), one from each quadrant of the inner 5 m radius. Herb cover was also estimated within the inner 5 m radius of the plot center using the Braun-Blanquet scale in three 2 m^2 subplots, translated into cover percentages (Tichý et al. 2020).

Leaf chemical composition was analyzed on freshly collected leaves in late summer by the IBED Biogeochemical lab of the university of Amsterdam, Netherlands. Oven-dried and ground samples were digested using HNO_3 and HCl, followed by microwave-assisted destruction, diluted in ultrapure water, and analyzed using inductive coupled plasma optical emission spectrometry (ICP-OES). Carbon and nitrogen contents were determined using a Thermo Fisher Scientific Flash 2000 elemental analyzer. As shown in Annex 3, the incubated leaf substrates span a broad gradient in calcium concentrations (Ca ranging from 5.14 to 18.64 g/kg) and carbon-to-nitrogen ratios (C/N ranging from 14.07 to 39.49 g/g).

The forest floor (matrix) chemical composition was approached by calculating the community weighted mean of the leaf chemical composition in the annual leaf litterfall produced by the local forest canopy. To visualize the distribution of the incubation plots, a 3D scatterplot was produced (Annex 4) using the scatterplot3d function (Ligges and Mächler, 2003). Leaf functional diversity was calculated by using the FD package in R (Laliberté et al. 2014) including shade tolerance, leaf Ca, leaf C/N and Leaf Mn concentrations as the tree leaf's functional fingerprint.

2.7. Statistical analysis

The relative mass loss after one year in situ incubation of all litter bags was linked to the individual leaf substrate types using generalized linear mixed models (GLMMs) implemented in the glmmTMB package (Brooks et al., 2017), specifying a beta distribution with a logit link to account for the bounded nature of the response variable (0−1) as the observed minimum and maximum relative mass loss rates fell within this boundary (18.4% and 97.5% respectively). *Plot* was included as a random effect to reflect the hierarchical structure of the experimental design. Model outcomes are given in Annex 5. Significance groupings for differences among substrate types (Fig. 4) were generated using emmeans (Lenth and Piaskowski, 2025) with Tukey adjustment, combined with the cld function from the multcomp package. Marginal and conditional R^2 values were calculated using the r.squaredGLMM function in the MuMIn package (Barton, 2024).

2.8. Home-field advantage calculation

In addition to interspecific differences in relative mass loss rates, we quantified location-dependent variation in the decomposition of species-specific leaf litter (intraspecific effects). For these statistical analyses, mass loss values were aggregated by first averaging replicate litterbags within each plot and substrate combination, and subsequently calculating HFA. To evaluate the first hypothesis concerning the Home-Field Advantage (HFA), substrate mass loss was analyzed using a well-established HFA index and by modeling the difference in mass loss between home and away incubation sites in the monoculture stands.

We calculated the Additional Decomposition at Home (ADHi) index to determine whether a substrate decomposed faster (positive values) or slower (negative values) at its home site compared to the eleven away sites (Annex 8). The ADHi index was calculated following the method described in the overview by Ma et al. (2023), which corrects for decomposition differences among substrates and incubation site effects:

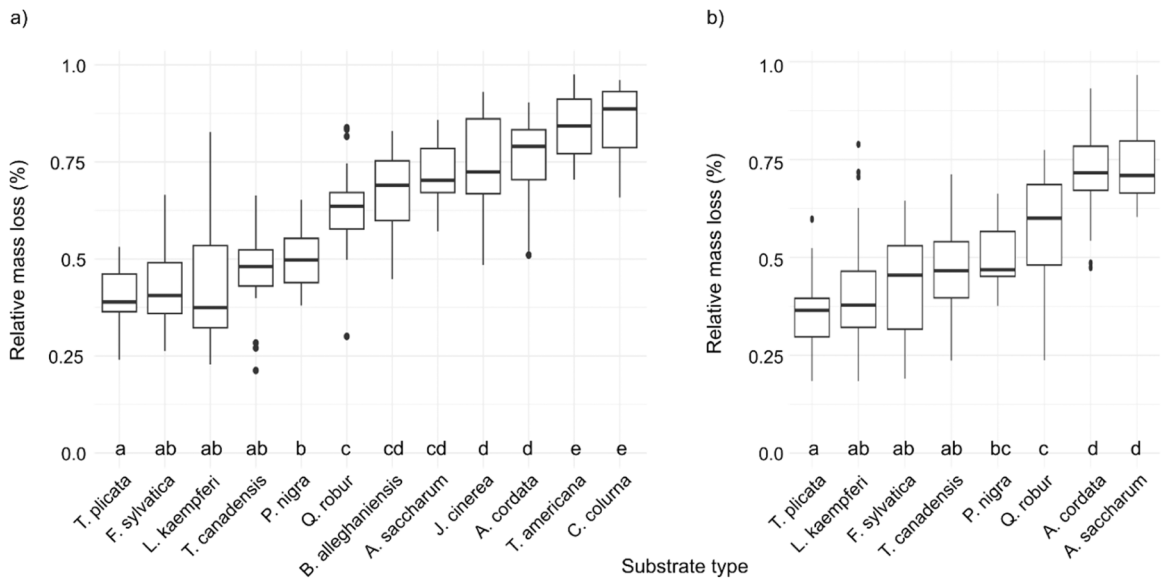

Fig. 4. a) Observed relative mass losses per incubated litter substrate type in monoculture stands, presented in increasing mean leaf substrate mass loss. Letters indicate significant differences between substrate type mass loss (emmeans test of the glmm model: Relative mass loss ~ Substrate type + (1|Plot) with beta family logit). For the monocultures relative mass loss was strongly explained by leaf substrate type ($R^2m = 0.89$, $R^2c = 0.96$). b) same boxplot but for the 8 incubated leaf substrates in the mixed stands ($R^2m = 0.8$, $R^2c = 0.875$).

$$ADH_i = \frac{HDD_i - ADD_i - H}{N - 2} \quad (2)$$

Where:

HDD (Home Decomposition Difference) is the sum of pairwise differences between the mass loss of leaf litter *a* at its home site *A* and the mass loss of the other leaf substrates (*b,…,l*) at the same site. Here, RML denotes the observed relative mass loss, lower-case letters indicate substrate types, and upper-case letters represent incubation sites. HDD is calculated for each incubation site $i = A,…,L$:

$$HDD_i = (RML_{aA} - RML_{bA}) + (RML_{aA} - RML_{cA}) + \ldots + \quad (RML_{aA} - RML_{lA}) \quad (3)$$

H is the mean of all HDD values across sites:

$$H = \frac{HDD_A + HDD_B + \ldots + HDD_L}{L - 1} \quad (4)$$

ADD (Away Decomposition Difference) is the sum of differences between the mass loss of substrate *a* at away sites (*B,…,L*) and the mass loss of the locally native substrates (*b,…,l*) at those sites. These values capture incubation-environment effects for all substrates, calculated for each substrate $i = a…,l$:

$$ADD_i = (RML_{aB} - RML_{bB}) + (RML_{aC} - RML_{cC}) + \ldots + \quad (RML_{aL} - RML_{lL}) \quad (5)$$

To complement the ADHi index and to allow extension of the analysis beyond fully reciprocal designs, we additionally calculated pairwise differences in relative mass loss (Δ mass loss) between home and away incubation environments. For each substrate, Δ mass loss was defined as the difference between its mass loss at the home site and its mass loss at each individual away site. This resulted in multiple Δ values per substrate, each capturing a substrate-specific performance shift across a particular incubation environment. Here again, mass loss values were aggregated by first averaging replicate litterbags within each plot and substrate combination, and subsequently calculating Δ values using these plot-level means, in order to avoid pseudo-replication arising from multiple non-independent pairwise comparisons.

These pairwise differences therefore represent environment-specific contrasts, rather than a comparison between home conditions and a single aggregated "away" value. For summary purposes and comparison with ADHi, mean Δ mass loss per substrate was calculated by averaging these pairwise differences across all monoculture away sites (N - 1), and plot-level performance was derived by averaging Δ values across all substrates incubated within a given environment.

Importantly, Δ mass loss differs conceptually from ADHi. While ADHi is based on a fully reciprocal design and corrects for both substrate and site effects, Δ mass loss captures direct pairwise contrasts between home and away environments and can therefore be applied more flexible to both non-fully reciprocal designs and multi-species stands. As a result, the two metrics are not expected to yield identical values, but instead provide complementary perspectives on decomposition patterns.

To assess whether mean Δ values deviated significantly from zero (i.e. indicating a home-field advantage or disadvantage), we fitted a linear mixed model (lmer(Δmass ~ 0 + Substrate + (1|Plot), dataset)) for monoculture stands, with post hoc comparisons using emmeans (Fig. 5).

2.9. Substrate-matrix interaction (SMI) analysis

To test the second hypothesis, we examined how differences in chemical quality between the incubated leaf substrate and the surrounding FF matrix of each incubation plot influenced decomposition dynamics, expressed as pairwise differences between average mass loss at home and each average at individual away site. The surrounding FF matrix chemistry was approached though the CWM leaf chemistry of the annual litterfall composition per study plot. Because direct chemical measurements of the FF matrix were not measured, we performed a sensitivity analysis using FF dry mass as a rough structural proxy for the organic layer development and accumulated leaf litter inputs. This proxy does not represent matrix chemistry, but tried to assess whether relationships based on annual litterfall derived CWM chemistry are robust to an alternative descriptor of the receiving decomposition environment. This approach allowed us to explore the potential mechanisms underlying observed species-site matching in decomposition.

Based on ecological relevance and literature, the following indicators of chemical quality were included: C/N ratio, N/P ratio, and concentrations of calcium (Ca), magnesium (Mg), and manganese (Mn) (See Annex 13). Note that Mg was ultimately not considered due to its high correlation with Ca. Three linear mixed-effects models (LMMs) were

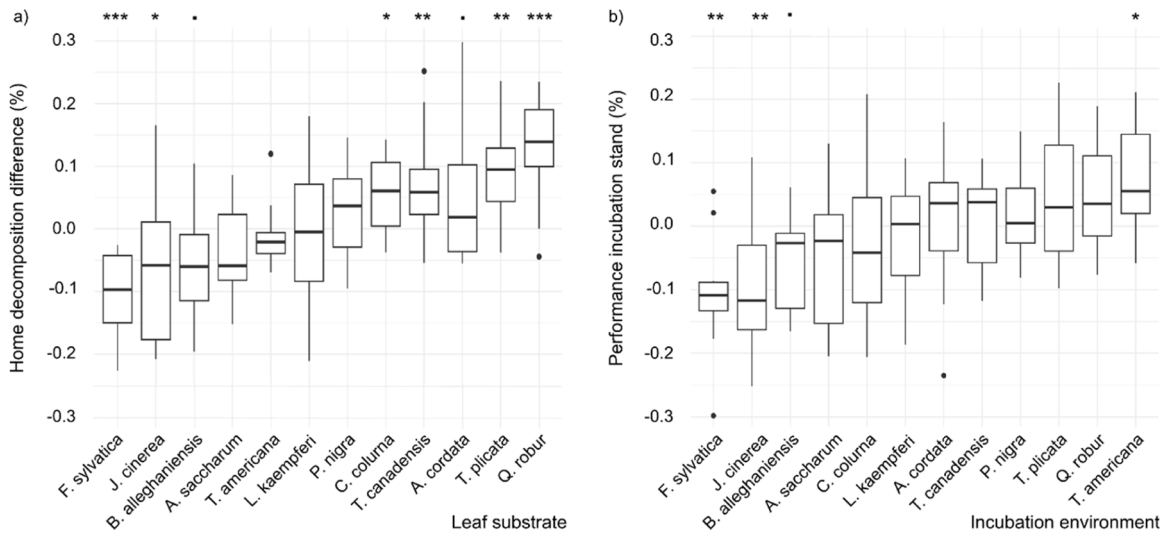

Fig. 5. Left: Home decomposition difference with leaf substrate ordered by increasing mean decomposition difference. Right: The effect of the monoculture incubation plots on all incubated leaf substrates, ordered by increasing mean plot performance. Significance was calculated through an LMM with random variable plot (left - $R^2m = 0.345$, $R^2c = 0.532$) and substrate (right - $R^2m = 0.215$, $R^2c = 0.536$). Home decomposition differences that are significantly different from zero are indicated on top with: p-values < 0.1 (.); p < 0.05 (*), < 0.01 (**) and < 0.001(***).

fitted using substrate type and plot as random variables, to account for the hierarchical structure and focus on the continuous predictors:

$$lmer(\Delta mass \sim \Delta C.N + \Delta N.P + \Delta Mn + \Delta Ca + (1|Substrate) + (1|Plot), \quad dataset) \tag{6}$$

The first model focused on monoculture stands, the second on mixed stands (Table 1), and the third on all observed mass loss differences (Annex 9). To visualize the effects of Δ quality (leaf substrate – community-weighted mean matrix quality) on mass loss variability, a principal component analysis (PCA; prcomp) was conducted (Annex 10), with a color gradient representing Δ mass loss using the factoextra package (Kassambara and Mundt, 2020).

2.10. Modulating effect of the environment

A GLMM was used to relate relative mass loss of the different leaf substrate types across all incubation plots (monoculture and mixture) to variables describing leaf litter quality, matrix quality, and forest stand structure (Annex 12). Given the hierarchical and crossed structure of the data (multiple substrate bags per plot, and substrate types distributed across plots), generalized linear mixed models (GLMMs) were fitted using glmmTMB (Brooks et al., 2017) with a beta distribution and logit link, appropriate for the bounded response variable (0−1).

Variance partitioning of fixed effects was assessed using the glmm.hp function (Lai et al., 2023) and visualized in a doughnut chart. The three main categories of fixed predictors were represented by a green gradient (leaf substrate quality), a blue gradient (delta quality), and a red gradient (forest stand characteristics).

Beyond the overall model, we assumed that environmental conditions would interact with substrate quality to influence mass loss outcomes, and that the strength and direction of these interactions would differ with leaf substrate quality. Local forest environmental conditions, including litterfall amounts, matrix quality, stand structure, and leaf diversity characteristics, can modulate decomposition by altering decomposer community activity and substrate preferences (Annex 15–18).

To capture these modulating effects, observed mass losses were assigned to two substrate-quality classes ("high" and "low"), based on negative or positive scores along the first PCA axis of leaf substrate quality (Annex 14). Significant interactions were identified through the GLMMs, and effect slopes were examined using the emtrends function in the emmeans package (Lenth and Piaskowski, 2025), which tests whether slopes differ from zero within each substrate-quality class.

All analyses were conducted in R version 4.5.0 (R Core team, 2025).

3. Results

3.1. Remaining residual mass largely depends on the leaf substrate type

After one year of incubation on the forest floor, leaf litter substrates showed an average mass loss of 58.7% ± 19.1% of their initial dry weight. This substantial reduction reflects the combined influence of decomposition and associated transformation processes under field conditions.

Relative mass loss differed markedly among substrate types. Based on initial dry mass and remaining residue after one year, the average

Table 1
Linear mixed model relating difference in mass losses ("away" – "home") with the difference in chemical "quality" between the incubated substrate and the local forest floor (substrate – matrix) of the monoculture (left) and mixture (right) incubation plots with random variables "leaf substrate type" and "plot". The model for all plots together is give in Annex 10.

	LMM mono $R^2m = 0.431$, $R^2c = 0.546$					LMM mix $R^2m = 0.335$, $R^2c = 0.482$				
	Estim.	Std. Error	t value	p-value		Estim.	Std. Error	t value	p-value	
(Intercept)	−0.012	0.013	−0.93	0.38		−0.045	0.019	−2.35	0.05	*
Delta C/N	0.004	0.012	0.37	0.72		0.032	0.017	1.93	0.11	
Delta N/P	0.063	0.010	6.19	< 0.001	***	0.080	0.016	5.12	0.01	**
Delta Mn	0.035	0.010	3.31	< 0.01	**	0.052	0.015	3.52	0.01	**
Delta Ca	0.020	0.012	1.64	0.12		0.037	0.018	1.98	0.09	.

relative mass loss for the four predefined groups (Fig. 3) was:

1. Rich leaf – shade intolerant (76.9%): *Corylus colurna, Juglans cinerea, Alnus cordata*
2. Poor leaf – shade intolerant (51.4%): *Larix kaempferi, Pinus nigra, Quercus robur*
3. Rich leaf – shade tolerant (74.2%): *Tilia americana, Acer saccharum, Betula alleghaniensis*
4. Poor leaf – shade tolerant (42.6%): *Tsuga canadensis, Thuja plicata, Fagus sylvatica*

Significant differences were detected between the two quality groups (rich vs. poor leaf substrate; $p < 0.001$) using emmeans applied to the GLMM. However, within each quality class, shade tolerance did not significantly influence mass loss (group 1 & 3 - $p = 0.86$; group 2 & 4 - $p = 0.46$).

Fig. 4 presents the relative mass loss by substrate type in monoculture stands (a) and mixed stands (b), illustrating substantial within-substrate variability. A model including substrate identity as the only fixed effect (with plot as a random effect) explained 87.5% of the observed variation in mass loss, underscoring the dominant influence of species identity and intrinsic litter traits in decomposition dynamics. Comprehensive GLMM outputs for the full dataset are provided in Annex 5. Leaf calcium content was positively influencing observed leaf substrate mass losses (Annex 7)

Eight leaf substrate types were incubated both in monoculture and mixed stands, but no significant differences in leaf substrate mass loss were detected between the stand types (emmeans: $p = 0.4$), nor significant interactions between leaf substrate type and stand type.

3.2. Home-field advantage effects

Across all substrates incubated in monoculture stands, leaf substrate decomposed on average 1.2% faster under its native canopy "home' than under other canopies "away" (Annex 8), indicating a modest overall HFA effect. However, this effect largely depended on the tree species, with calculated HFA index ranging from −11% (*Tilia americana*) to + 7.5% (*Corylus colurna*) or indicating almost no overall effect −0.2% (*Acer saccharum*).

Fig. 5 gives a detailed overview of mass loss differences under home and away incubation conditions, illustrating both substrate-specific responses (panel a) and incubation-site environmental effects (panel b). The boxplots of Fig. 5 tend to suggest that species characterized by lower N/P ratios tended to show positive HFA values, whereas species with higher N/P ratios generally showed negative values (Annex 9). This effect was also significant ($p = 0.01$) in a glmm linking substrate quality to home decomposition differences. For instance, *Juglans cinerea* (−6.2%) and *Fagus sylvatica* (−10.2%) exhibited negative home decomposition difference responses, decomposing more rapidly away from their native canopy. Both species also displayed negative incubation-site effects (−9.3% and −10.6%, respectively), suggesting that their forest environments were generally less conducive to decomposition for all incubated substrates.

In contrast, *Corylus colurna* (+5.3%), *Quercus robur* (+12.8%), *Thuja plicata* (+9.4%), and *Tsuga canadensis* (+7.3%) showed positive HFA values, indicating enhanced decomposition of their own litter under their native canopy, though without significant effects of these sites on other incubated substrates. Additionally, *Tilia americana* (+5.5%) emerged as a decomposition-enhancing environment, significantly increasing mass loss for multiple substrate types under its canopy (+7.5%). Whether an incubation site exerted positive or negative effects on other substrates appeared to slightly depend on the N/P ratio of the proxy for the forest floor matrix ($p = 0.07$) while higher Mn concentration, negatively influenced plot performance ($p = 0.03$).

3.3. Substrate - matrix quality interactions

To evaluate the Substrate Quality-Matrix Quality Interaction (SMI) hypothesis, we assessed whether leaf litter decomposed faster or slower relative to home-field conditions and whether this response was influenced by differences in chemical composition between the incubated leaf substrate types and a proxy for the surrounding litter matrix at each incubation site (monoculture + mixtures). Linear mixed effects models (LMMs), incorporating substrate type and plot as random effects (marginal $R^2 = 0.27$), showed that higher differences in N/P ratio and Mn content positively affected Δ mass loss (Annex 10) over all incubation stands and leaf substrate types. When focusing on the eight leaf substrate types that are incubated in both the monoculture and mixed forest stands, higher differences in Ca content also positively influenced mass loss rates. Notice that for those eight species (Annex 1b) the intercept becomes significant, indicating substrates to significantly decompose faster (3.6%) at home than in other plots "away". Separate models for monoculture and mixed stands (Table 1) revealed similar significant effects. Higher chemical quality of the leaf substrate relative to the CWM litterfall of the incubation environment resulted in increased mass loss at away sites compared to home sites. A graphical representation of the SMI effects is provided in Annex 12, illustrating how specific chemical mismatches between substrate and matrix drive differences in decomposition rates.

As a sensitivity analysis (Annex 10), we tested whether the proxy-based substrate-matrix mismatch model was robust to inclusion of FF dry mass, used as a rough structural proxy for organic layer development. The proxy-based model performed substantially better than a model including FF mass alone (delta AIC = 16.1; likelihood ratio test: $\chi^2 = 22.05$, $df = 3$, $p < 0.001$). Adding FF dry mass to the proxy-based model did not improve model fit ($\chi^2 = 0.615$, $df = 1$, $p = 0.433$), nor did interactions between FF mass and the mismatch predictors ($\chi^2 = 0.841$, $df = 4$, $p = 0.933$). These results indicate that the observed proxy-based effects were not simply explained by variation in FF accumulation.

3.4. Disentangling leaf substrate effect from modulating environment on observed relative mass loss

Variation in relative mass loss was strongly shaped by both the identity of the incubated leaf substrate and the characteristics of the local forest environment. Among all predictors, leaf-substrate quality emerged as the dominant driver, explaining approximately 72.2% of the variance in mass loss (Fig. 6). Local forest conditions contributed

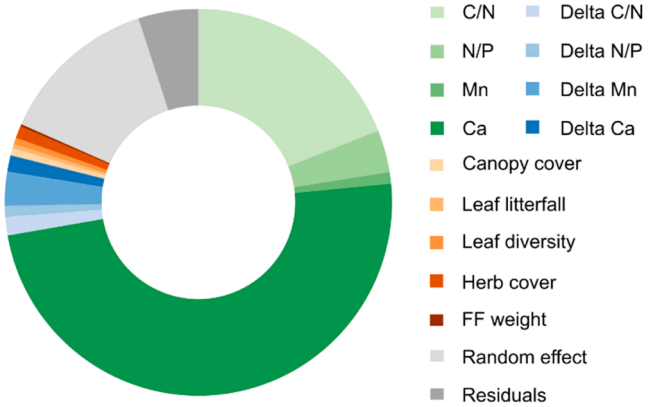

Fig. 6. Variance partitioning of the generalized linear mixed model (Annex 13) linking observed relative mass loss to leaf litter quality (green colors), difference in quality between the substrate and matrix (blue colors) and forest stand characteristics (red colors), while accounting for the hierarchical structure with random variable plot and substrate (grey colors).

additional explanatory power, partitioned into the chemical mismatch between leaf substrate and matrix (6.7%) and forest stand structural characteristics (2.7%).

The GLMM indicated that the random effects (substrate type and plot) accounted for an additional 13.4% of the variance, underscoring the context-dependent nature of decomposition dynamics. Approximately 5% of the variation in mass loss after one year of in situ incubation remained unexplained. Overall, the model (Annex 13) explained 81.6% of the variance (conditional $R^2 = 0.95$), with variance inflation factors below 3.2 for all predictors, indicating relatively low collinearity.

Among the fixed effects, leaf substrate calcium concentration was the most influential predictor, substantially increasing observed mass loss. Differences in N/P ratio and Mn content between the substrate and the proxy for the incubation environment also contributed significantly, further shaping modeled decomposition rates.

3.5. Interactions between litter quality and incubation environment

To assess the functional breadth, feeding flexibility, and canopy hypotheses, we fitted a GLMM including the interaction between leaf-substrate quality (rich vs. poor) and key environmental variables (Annex 15). Thereafter this model was extended with fixed variables focusing firstly on leaf substrate quality x matrix quality (Annex 16), secondly leaf substrate quality x forest characteristics (Annex 17) and lastly a full model (Annex 18).

The model in Annex 15 explained a large proportion of variation in relative mass loss ($R^2m = 0.732$, $R^2c = 0.956$). Relative mass loss differed strongly between leaf-quality classes: poor-quality litter decomposed substantially more slowly than rich-quality litter (Leaf quality - Poor: $\beta = -1.317 \pm 0.198$ SE, $p < 0.001$). On the response scale, this corresponds to an average mass loss of 77% for rich litter versus 47% for poor litter (intercept + poor effect). Among the environmental predictors, canopy cover showed a significant negative main effect ($p < 0.001$), indicating lower mass loss under denser canopies. Matrix Ca, Matrix C/N, yearly leaf litterfall, and forest floor mass had no detectable main effects (all $p > 0.35$).

Fig. 7 visualizes the interaction terms (Annex 15), accompanied by p-values and slope estimates indicating whether slopes differed significantly from zero. Symbols (dot, asterisk) denote significant interactions between substrate quality and the fixed predictors. For matrix Ca (Fig. 7a), high-quality substrates showed a positive but non-significant relationship with increasing matrix Ca ($p = 0.37$), whereas low-quality substrates exhibited a negative, non-significant slope ($p = 0.64$). An opposite pattern emerged for matrix C/N (Fig. 7b): low-quality substrates tended to decompose faster in matrices with higher C/N, indicative of more recalcitrant conditions, although this trend was also not statistically significant ($p = 0.28$).

The strongest and most significant interaction was observed for canopy cover (Fig. 7c). Mass loss of high-quality litter declined with increasing canopy closure, while low-quality litter showed a slight increase in mass loss under denser canopies. The interaction between substrate quality and yearly leaf-litterfall was marginally significant ($p = 0.089$; Fig. 7d; high-quality substrates generally benefited from greater litter inputs, whereas low-quality substrates showed reduced mass loss under similar conditions. Forest floor dry weight, included as a composite measure integrating matrix quality and annual litter inputs, did not show a significant interaction with substrate quality (Fig. 7e).

The GLMM extending on substrate quality and matrix quality interactions (Annex 16), showed that among the environmental variables, Mn in the CWM litterfall of the incubation matrix exerted a significant negative effect on relative mass loss ($\beta = -0.189 \pm 0.050$ SE, $p < 0.001$), while the proxy for matrix N/P showed a marginal negative trend ($p = 0.06$). CWM litterfall of the incubation matrix Ca and C/N had no detectable main effects (both $p > 0.40$). A single significant interaction indicated that the inhibitory effect of Mn on mass loss was weaker for poor quality litter than for rich litter (leaf quality × matrix Mn, $p = 0.04$).

Adding forest stand related variables (Annex 17) changed previous findings to a lesser extent as leaf quality still had a significant interaction with the canopy cover. The main effect of canopy cover and herb cover became marginally significant. The full model is presented in Annex 18 and achieved $R^2m = 0.76$ and $R^2c = 0.96$. In this model only leaf litter quality and the interaction with canopy cover remained significant, possibly showing some overfitting (VIF 6.2).

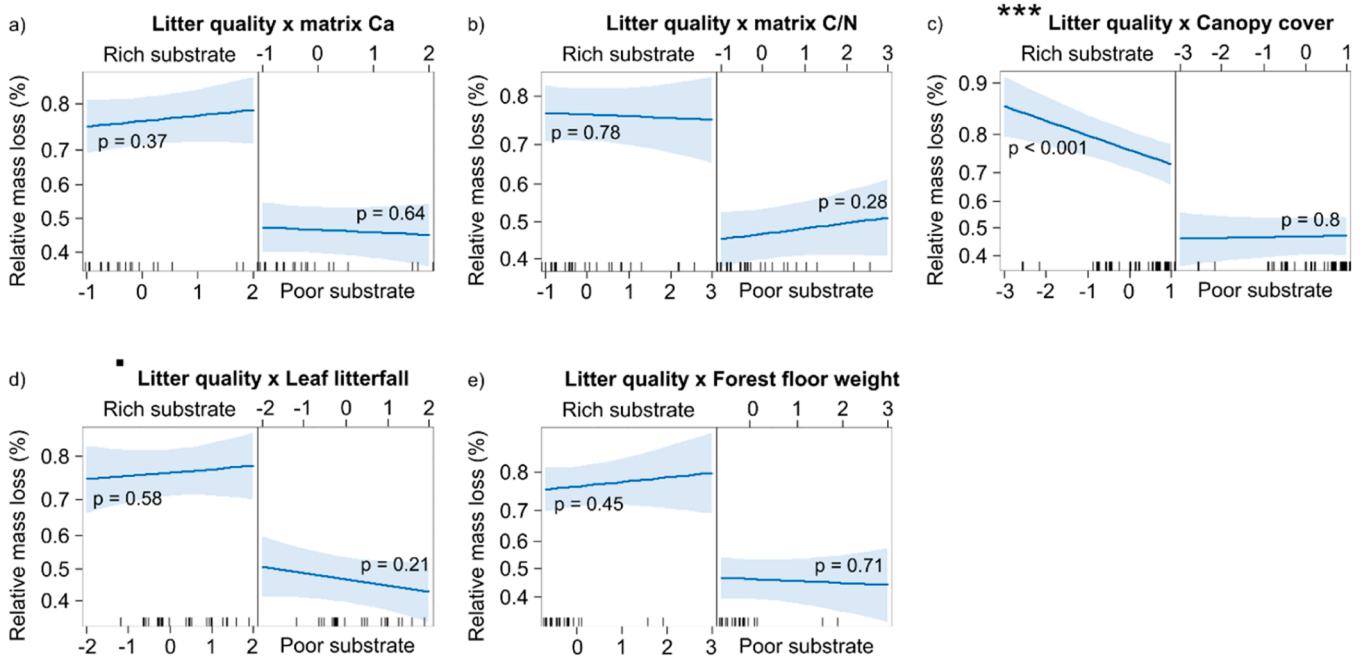

Fig. 7. GLMM relating relative mass loss to fixed variables and their interactions with leaf litter quality. P-values in the figure are illustrating if a slope is significantly different from zero.

4. Discussion

In this study, we showed that after a one-year incubation in the forest floor, leaf litter mass loss varied significantly between tree species. This high explanatory power (87.5%) likely reflects both the strong influence of leaf litter identity on decomposition and the deliberate selection of tree species spanning a wide functional trait gradient. Besides the large effect of tree species identity, large within species variability was observed, suggesting interaction between the leaf litter type and the proxy of the incubation environment, both in terms of stand structure and chemistry, even under shared soil and macroclimatic conditions. These results highlight that local stand characteristics and litter-environment interactions can modulate decomposition rates independently of climate and soil type.

4.1. Home field advantage

We accepted our first hypothesis, as a home-field advantage effect (Ayres et al., 2009; Gholz et al., 2000; Vivanco and Austin, 2008) was observed in this study. The effect, however, was very small with an average increased mass loss at home of 1.2% compared to away incubation sites. This value is slightly lower than what was reported in the recent meta-analysis of Shi et al. (2025), which could be expected, as macroclimatic and initial soil conditions in our study were comparable, meaning that the observed variation is primarily driven by tree-species effects rather than broad biome-level differences.

Firstly, it was evaluated whether there occurs an overall systematic home-field advantage (HFA) effect, by simply adding a categorical factor ("Home" vs. "Away") besides the leaf substrate type effect in the GLMM explaining relative mass loss (Annex 6). This categorical factor refers to whether the leaf substrate was incubated conspecific, i.e. beneath its own canopy (home) or heterospecific, i.e. under a different tree species' canopy (away). It did not show a significant effect, which suggests that possible HFA effects are context dependent. Besides ADH (Ma et al., 2023), multiple other related indices exist and are used in literature. We therefore briefly explored these indices and compared them with each other. We observed that they only varied slightly from each other and most often had the same direction (positive or negative effect). Most recently adopted metrics are those of Gießelmann et al. (2011); Perez et al. (2013), and Pugnaire et al. (2023), which extended the original approach of Ayres et al. (2009) from pairwise tree species comparison to multi-species experiments. Note that Pugnaire et al. (2023) used summed effects while the others corrected for sample size. In case of comparing decomposition rates across multiple studies, log-transformed response ratio can be used as well (Shi et al., 2025). To calculate those index-based approaches, a fully reciprocal design is required, which is met for monoculture stands but not for our leaf substrate incubations in mixed stands.

Whether litter decomposes faster "at home" than "away" remains debated over multiple studies, with evidence spanning positive (Ayres et al., 2009; Fanin et al., 2021; Veen et al., 2015), neutral (Ayres et al., 2006; Castillo-figueroa, 2024; Makkonen et al., 2012; van den Brink et al., 2023) or even negative (Pugnaire et al., 2023) HFA effects depending on ecosystem, substrate chemistry, and decomposer specialization. Relatively large differences (Fig. 5) were observed between leaf substrates and the incubation environments, suggesting that the outcome of decomposition studies (whether or not a HFA is observed) could mainly depend on the used tree species, especially when relatively limited numbers of tree species are used (Aponte et al., 2012; Lin et al., 2024; Midgley et al., 2015; Pearse et al., 2014; Zhang et al., 2008).

Our results indicated no consistent decomposition difference effect (Annex 8) over all tree species. This suggests no strong evidence for decomposer specialization to the local environmental conditions (Castillo-figueroa, 2024; Yang et al., 2025), although decomposer community composition was not directly assessed in this study. A possible explanation could partially be by the admixture of small proportions of other tree species (Chomel et al., 2015) and interaction of the herb layer leaf litter input (Wang et al., 2021a) weakening the HFA effects (Xue et al., 2025). Edaphic conditions (soil types and associated characteristics) and macroclimatic conditions can further modulate HFA (Daumal et al., 2024; Veen et al., 2015; Zhuang et al., 2022). In that way, the limited environmental contrast inherent to our experimental setup can dampen net HFA even when species specific HFA emerge.

Substrate quality, represented by C/N and Ca concentrations did not have a clear effect in influencing the direction and magnitude of home-field advantage. On the other hand, leaf nutrient balance (N/P) was significantly influencing home decomposition differences. Similar outcomes were found by Hu et al. (2021) who indicated that leaf P content could interact with the observed HFA effects by influencing the soil meso- and micro-faunal communities, besides other factors such as soil type, temperature, and humidity (Chen et al., 2025). As noted above, higher-than-average precipitation during our one-year incubation period may have influenced the observed HFA outcomes. Soil moisture is a key driver of soil microbial activity, which in turn can enhance litter decomposition (Liu et al., 2021). Importantly, litter types do not respond equally to variation in soil moisture (Petraglia et al., 2019). High-quality litter tends to show a stronger increase in mass loss under wetter conditions compared to low-quality litter, likely due to greater leaching of water-soluble compounds during the early stages of decomposition (Blume-Werry et al., 2021).

4.2. Substrate-matrix interaction

The SMI framework extends the HFA concept, including mixed forest stands and litters, by proposing that decomposition is driven not only by the identity of the incubated leaf substrate but the quality mismatch between the substrate and its receiving environment (Fanin et al., 2021; Freschet et al., 2012). Our second hypothesis, i.e. stronger contrasts between substrate and matrix quality will reduce mass loss rates, can only be partially accepted. Rather than absolute quality differences |substrate - matrix| explaining variation, our results indicate directional, trait-specific effects. However, our "matrix chemistry" was based on a proxy, i.e. chemistry of fresh canopy leaf litter, community weighted based on annual leaf litterfall amounts, and not on measured forest floor chemistry. Consequently, the inferred substrate-matrix interactions should be interpreted as proxy-based patterns rather than direct tests of the SMI framework sensu Freschet et al. (2012).

Across both monoculture and mixed stands, mass loss differences between home and away sites were consistently shaped by stoichiometric and micronutrient mismatches. ΔN/P emerged as the strongest predictor (Table 1), with litter decomposing relatively faster in forest stands with lower N/P ratios than the incubated leaf substrate, which is consistent with broader evidence that P availability and N/P balance can constrain microbial enzyme production and decomposition efficiency (Fanin et al., 2016b; Li et al., 2024), although these mechanisms cannot be directly evaluated here due to absence of decomposer community measurements. ΔMn seem to significantly influence mass loss differences where incubated leaf substrates higher in Mn content than the surrounding matrix Mn content (represented by a proxy), decomposed more rapidly away from home. This pattern is consistent with literature highlighting the role of Mn in oxidative processes related to lignin degradation (Berg et al., 2015; Keiluweit et al., 2015; Santos and Herndon, 2023), but given the absence of direct measurements of enzyme activity or decomposer communities, this interpretation remains inferential. Notably, this interpretation differs from the negative relationship observed between matrix Mn concentration and overall mass loss, indicating that Mn may play multiple, context-dependent roles during decomposition that cannot be disentangled with the current data. The negative relationship between matrix Mn concentration and litter mass loss suggests that Mn effects are not straightforward. While Mn has been linked to oxidative decomposition processes (Li et al.,

2019), its role may vary across decomposition stages and environmental contexts. Because our measurements focus on relatively early-stage mass loss, these contrasting patterns cannot be assigned to a single mechanism, and should be interpreted cautiously

In contrast, ΔC/N did not explain variation in mass loss differences in monocultures and showed only a non-significant trend in mixed stands (Table 1). Notably, the mixed-stand model exhibited a significant negative intercept, suggesting that, after accounting for trait mismatches, litter decomposes more slowly under mixed canopies than in its monospecific homefields. This may reflect structural or biochemical features of the selected mixed stands, potentially linked to their generally lower Ca content and higher N/P ratios (Annex 4), that create environments less favourable for rapid decomposition compared to the broader conditions represented in monocultures.

4.3. Leaf substrate quality is the primary driver of mass loss

Unsurprisingly, variance partitioning (Fig. 6) showed that leaf litter chemical composition was the primary driver of variation in observed relative mass loss (72.2%) with similar high values observed by Canessa et al. (2021) and Castillo-Figueroa et al. (2025) at other contextual sites. Differences in leaf substrate quality, the incubation environment (6.7%), and other stand structural characteristics (2.7%) also contributed significantly, but to a lesser extent. This was also observed by Yang et al. (2022) who found that variation in litter quality had a considerably larger effect on litter decomposition than the fauna and decomposition site. Litter quality, more precisely the initial Mg concentration and lignin/P ratio, were in that study significantly related to the decomposition constant.

Our findings support the growing recognition in literature that microbial activity and accelerated litter decomposition are closely linked to BC availability, particularly Ca and Mg (Aponte et al., 2012; Cassart et al., 2020; Desie, 2020). In our dataset, however, Ca and Mg were strongly collinear, and only calcium was retained in the final models. In contrast, the predictive power of the litter C/N ratio was weaker in our study, possibly reflecting elevated nitrogen availability in our study region due to atmospheric deposition, which can strongly impact observed decomposition rates and home-field advantage effects (Li et al., 2017; Yin et al., 2022). This could also relate to the theory of Liebig of the most limiting resource (von Liebig, 1840), indicating that depending on the environment, different elements could act as explanatory (Desie et al., 2020). Other leaf traits, such as leaf toughness, waxes, cutting, tannins, could reflect decomposability maybe better (Berg, 2018) than C/N ratios, for example.

The negative relationship between matrix Mn concentration and litter mass loss contrasts with the frequently reported positive role of Mn in lignin degradation (Berg et al., 2015; Keiluweit et al., 2015). However, Vivanco and Austin (2019) indicated no relation between leaf litter Mn and mass loss. As our measurements primarily reflect relatively early-stage mass loss, Mn-mediated effects in late-stage decomposition dynamics (Berg et al., 2007) may not yet have been profound. Additionally, high Mn in litter may reflect acid site conditions that independently slow decomposition (Santos and Herndon, 2023) or causes phytotoxicity (Li et al., 2019). So focussing on one chemical element may produce inconsistent results when other elements could become limited in relation to Liebig's law (Desie et al., 2020).

Contrary to the findings of Bourdin et al. (2025), we did not find enhanced decomposition rates under mixed stands, nor did the fixed variable “leaf diversity” exert a strong influence in our models. This result aligns with a growing body of literature showing that mixing effects on decomposition are often inconsistent and strongly context-dependent, rather than universally positive (e.g., (Gessner et al., 2010; Zhou et al., 2020), although earlier work suggested more general positive diversity effects on decomposition (Hättenschwiler, 2005). Although higher diversity has been shown to be related to increased soil microbial biomass, it remains unclear how tree diversity affects higher trophic levels involved in litter decomposition (Strukelj et al., 2021). Because our litterbags allowed access to macro decomposers, their effects on mass loss likely overrode any subtle litter-diversity effects (Dou and Lin, 2026), suggesting that the absolute quality of the surrounding matrix may be a dominant driver, which influences, for example, earthworm abundance and macrofaunal activity, a more dominant driver of decomposition patterns. Additionally, our monoculture plots were selected to cover a wide range of leaf chemical traits (Annex 4), which may have reduced the relative contrast between monocultures and mixtures.

4.4. Modulating mechanisms

Our third hypothesis, i.e. that tree-canopy characteristics and matrix quality modulate decomposition by shaping decomposer functional breadth, feeding flexibility, and responses to litter availability, can only be partially accepted. Although interactions between substrate quality and environmental variables were detected, they were generally not statistically significant. Nevertheless, several directional patterns were consistent with the underlying mechanisms we expected. For example, recalcitrant environments with high matrix C/N ratios tended to enhance the decomposition of poor quality litter, while nutrient rich matrices (low C/N) appeared to suppress the decomposition of recalcitrant substrates, while the reverse was observed for Ca content (Fig. 7), however the modelled interactions were not significant (Annex 16). These directional patterns suggest potential mechanisms related to functional breadth hypothesis (Fanin et al., 2016a; Keiser et al., 2014; Osburn et al., 2022; Palmer et al., 2025), but the lack of statistically significant interactions means that this interpretation remains speculative in our study.

Canopy structure exerted a clearer influence. Increasing canopy cover significantly reduced mass loss, especially for high-quality substrates. This pattern aligns with plant resource-use strategies described in the leaf economic spectrum (de la Riva et al., 2019), where denser canopies can reduce throughfall, limit leaching of soluble components, and alter forest floor moisture regimes (Zhang et al., 2024). Such microclimatic constraints likely reduced decomposer activity at the forest floor, resulting in slower decomposition under closed canopies. This effect however is not necessarily universal and depend on the incubated litter type as dense canopies may influence decomposition activity by moderating temperature fluctuations and increasing soil moisture levels through reduced soil surface evaporation (Joly et al., 2017; Von Arx et al., 2013; Zhang et al., 2022), possibly enhancing labile litter species decomposition. On the other hand, open canopies can increase decomposition in of recalcitrant litter species through enhanced photodegradation (Almagro et al., 2016; Wang et al., 2021b).

Litter availability introduced an additional, though subtle, environmental modulation (Sayer et al., 2020). Higher annual litterfall slightly increased decomposition of rich litter but tended to reduce mass loss of poor litter, although the interaction remained marginal ($p = 0.089$). A similar pattern has been noted by Beugnon et al. (2023), partly linked to increased canopy density and leaf biomass production in diverse stands (Nickmans et al., 2019). This pattern is conceptually consistent with the feeding-flexibility hypothesis, where decomposers in abundant litter environments favor high-quality resources (Briones, 2014), whereas low litter availability may induce a more generalist, “hungry” community response, reducing selectivity and allowing poorer substrates to decompose at relatively higher rates. Although no direct measurements of decomposer behavior or community structure were available to test this mechanism.

Taken together, our results suggest that functional breadth, canopy-mediated microclimatic effects, and litter-availability mechanisms all contribute to shaping decomposition, but their influence is subtle compared with the dominant role of substrate quality. Environmental interactions thus appear present but secondary, modifying rather than overriding the strong intrinsic differences in decomposability between

rich and poor leaf litter.

4.5. Study limitations

Although widely used, litterbag experiments may yield biased estimates of litter decomposition in natural environments, as they capture only part of the full decomposition continuum, both in time (Jewell et al., 2017) and in actual forest floor conditions. The effect of mesh size has been studied several times, and litter mass loss varied significantly among different mesh sizes (Patoine et al., 2020; Peng et al., 2022a). The role of mesh size and the associated access of soil fauna have been indicated to be critical in decomposition studies (Zhu et al., 2025). Depending on the mesh size used, different organisms are allowed to participate in the decomposition process (Makkonen et al., 2012; Yang et al., 2022), illustrating the effect of meso- and macro-fauna communities on decomposition (Peng et al., 2022a). Small-mesh bags underestimate mass loss by excluding soil macrofauna activity, whereas large-mesh bags overestimate mass loss by failing to account for material transformed into faeces that remains undecomposed or is transferred outside the bags for subsequent decomposition in the forest floor or mineral soil (Prescott and Vesterdal, 2021). However, a substantial amount of plant residues can be converted by soil fauna into faeces, significantly impacting the decomposition process (Frouz, 2018). To accommodate this, our litterbags were constructed with two different mesh sizes: a fine mesh (0.5 mm) at the bottom and a coarser mesh (2 mm) at the top of the litterbags, which allowed for greater access by both soil fauna and microbial decomposers while minimizing particle loss. This design better mimics natural field conditions and captures a more complete range of decomposition processes, thereby providing a more realistic assessment of potential HFA effects (Zhang et al., 2024). During the opening and cleaning of the litterbags, we found faunal faeces and earthworms inside the litterbags, illustrating accessibility of the used dual mesh size. Caution is needed on the effect of changing abiotic conditions inside the litterbags compared to the forest floor; as water beads could form, however, between different mesh sizes, microclimatic differences are limited (Bokhorst and Wardle, 2013).

It should be noted that leaf chemical composition was determined on freshly collected, dried leaves, whereas litterbags were filled with material from pooled annual litterfall traps. Such litter may contain lower nutrient concentrations due to leaching and nutrient reallocation during senescence, which could slightly alter trait-decomposition relationships or model performance. Nevertheless, this approach closely reflects the material entering natural decomposition pathways and is commonly used in field-based litter decomposition studies (Guo et al., 2024).

Although *Q. robur* has a long historical presence at the site (Huvenne et al., 2020), our results do not indicate a strong, site-wide legacy effect on decomposition dynamics. Instead, Q. robur exhibited a clear positive HFA (Fig. 5a), and its home stand tended to enhance the decomposition of several other litter types. This pattern may reflect local stand level conditions currently play a stronger role than potential historical legacies, although such legacy effects were not directly assessed in this study. More generally, soil legacy effects can persist over long timescales (Palmer et al., 2025), but are often spatially heterogeneous, making their influence difficult to disentangle from present-day stand characteristics. Because this study did not include direct measurements of decomposer communities (microbial or faunal), all interpretations regarding decomposer specialization, functional breadth, or enzyme-mediated mechanisms should be considered as plausible but untested explanations of the observed patterns.

In addition, plot selection posed constraints: due to stand structure and edge effects in the forest, target species often occurred in relatively small or spatially clustered groups. As a result, almost no fully pure monoculture stands, and no controlled 50–50 species mixtures were available. This limitation may have reduced the contrast between "mixture" and "monoculture" conditions and could partly explain the non-significant mixing effects on mass-loss rates. However, by modelling species-level traits and community-weighted mean (CWM) traits, we accounted for the actual species composition and relative abundances in each plot, thereby integrating the realized forest conditions into our analyses. In forest with higher degree of litter mixture, observed HFA effects may weaken possibly through adaptations within the detrital community to various leaf litter sources (Chomel et al., 2015). On the other hand, Yang et al. (2025) noted that dominant tree species were shaping soil fauna composition and nutrient cycling suggesting a driving role of the dominant tree species compared to rare species in the mix on decomposition rates of the incubated leaf litter (Yang et al., 2025).

5. Conclusion

This study demonstrates that, under shared macroclimate and soil type, leaf litter decomposition is dominated by tree species identity and leaf litter chemical composition, with weaker but meaningful modulation by forest stand characteristics and the approximation for the receiving environment. This aligns with the broad consensus that plant traits are the predominant control on decomposition within biomes (Aerts, 1997; Cornelissen et al., 2007; Makkonen et al., 2012).

We detected a modest home-field advantage (HFA) of 1.2%, but with clear species-specific variation, consistent with the view that HFA is context dependent and not universally expressed (Ayres et al., 2009; Pugnaire et al., 2023; Veen et al., 2015). Trait-based directional matching between incubated leaf substrate and CWM annual leaf litterfall, particularly involving differences in N/P ratio and Mn content were associated with home and away differences, supporting the idea that litter-environment interactions can shape decomposition rates beyond leaf litter identity alone (Freschet et al., 2012; Perez et al., 2013). At the same time, the interpretation of our SMI (Substrate Quality-Matrix Quality Interaction framework) results should remain cautious because the litter matrix chemistry was approximated using CWMs of fresh leaf traits, rather than measured forest floor organic layer chemistry. The forest floor integrate decades of transformed litter inputs, and these transformations could shift stoichiometry and element availability relative to fresh leaf proxies (Berg and McClaugherty, 2014; Guo et al., 2024; Prescott and Vesterdal, 2021).

From a management perspective, our findings highlight that large differences in leaf litter decomposition rates arise from tree species identity, reflecting a trade-off between rapid nutrient cycling and longer-term soil carbon stabilization (Prescott, 2010; Prescott and Vesterdal, 2021). This points to trait-based tree species selection and the mixing of species with complementary leaf litter traits as practical levers to steer litter turnover and carbon storage, while recognizing that increasing tree species richness alone will not universally accelerate decay (Bourdin et al., 2025; Handa et al., 2014). Canopy structure can further modulate decomposition, but likely in a context-dependent manner through microclimatic buffering and moisture constraints that interact with leaf litter quality (Joly et al., 2017; Wang et al., 2021b; Zhang et al., 2024).

Given that our results emphasize functional traits as primary drivers of decomposition, they also inform current debates in climate-smart forestry. Strategies such as tree species mixtures and assisted migration aim to sustain forest functioning under rapid climate change (Paquette et al., 2018; Stanturf et al., 2024; Williams and Dumroese, 2013). In our common garden setting, several non-native species exhibited decomposition dynamics comparable to native species, suggesting that for litter mass loss, functional traits may outweigh species origin and could help sustain targeted ecosystem functions under changing climates (Nyssen et al., 2024; Van Meerbeek et al., 2025). However, comparable decomposition does not imply full ecological equivalence, as non-native tree species may involve trade-offs and alter broader ecosystem functioning (Beugnon et al., 2025; Castro-díez et al., 2025; Gessler et al., 2026; Wenglein et al., 2024). Future research should therefore assess whether long-established non-native species support

comparable associated biodiversity and ecosystem interactions relative to native-dominated stands.

CRediT authorship contribution statement

Quentin Ponette: Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Bart Muys:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **Karen Vancampenhout:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **Rune Melis:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Joachim López:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, 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 licenced 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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Annex 1. : Experimental setup in the monoculture stands a) and mixed stands b) with "o" indicating leaf substrate that is known/ native to the incubation plot. Abbreviation for the tree species are: Corylus colurna (C. col), Juglans cinerea (J. cin), Alnus cordata (A. cor), Larix kaempferi (L. kae), Pinus nigra (P. nig), Quercus robur (Q. rob), Tilia americana (T. ame), Acer saccharum (A. sac), Betula alleghaniensis (B. all), Tsuga canadensi (T. can)s, Thuja plicata (T. pli), Fagus sylvatica (F. syl), Abies homolepis (A. hom), Pseudotsuga menziessii (P. men), Quercus rubra (Q. rub), Abies alba (A. alb), Quercus palustris (Q. pal), Carpinus betulus (C. bet), Castanea sativa (C. sat)

a)				Monospecific tree stand environments											
				Shade intolerant						Shade tolerant					
				Rich litter environment			Poor litter environment			Rich litter environment			Poor litter environment		
				C. col	J. cin	A. cor	L. kae	P. nig	Q. rob	T. ame	A. sac	B. all	T. can	T. pli	F. syl
Mono specific litters in litterbags	Shade intolerant	Rich litter	C.col	oo	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
			J. cin	xx	oo	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
			A. cor	xx	xx	oo	xx	xx	xx	xx	xx	xx	xx	xx	xx
		Poor litter	L. kae	xx	xx	xx	oo	xx	xx	xx	xx	xx	xx	xx	xx
			P. nig	xx	xx	xx	xx	oo	xx	xx	xx	xx	xx	xx	xx
			Q. rob	xx	xx	xx	xx	xx	oo	xx	xx	xx	xx	xx	xx
	Shade tolerant	Rich litter	T. ame	xx	xx	xx	xx	xx	xx	oo	xx	xx	xx	xx	xx
			A. sac	xx	xx	xx	xx	xx	xx	xx	oo	xx	xx	xx	xx
			B. all	xx	xx	xx	xx	xx	xx	xx	xx	oo	xx	xx	xx
		Poor litter	T. can	xx	xx	xx	xx	xx	xx	xx	xx	xx	oo	xx	xx
			T. pli	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	oo	xx
			F. syl	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	oo

b)				Monospecific tree stand environments											
				Gymnosperm		Gymnosperm + Angiosperm				Angiosperm + Angiosperm					
				Poor + Poor		Poor + Poor		Poor + Rich		Poor + Poor		Poor + Rich		Rich + Rich	
				L. kae + A. hom	T. pli + P. men	T. can + Q. rub	A. alb + F. syl	A. cor + P. nig	A. sac + T. can	Q. rob + F. syl	Q. rub + Q. pal	A. sac + Q. rub	Q. rob + C. bet	T. ame + B. all	C. sat + A. cor
Mono specific litters in litterbags	Angio-sperm	Rich litter	A. cor	xx	xx	xx	xx	oo	xx	xx	xx	xx	xx	xx	oo
			A. sac	xx	xx	xx	xx	xx	oo	xx	xx	oo	xx	xx	xx
		Poor litter	Q. rob	xx	xx	xx	xx	xx	xx	oo	xx	xx	oo	xx	xx
			F. syl	xx	xx	xx	oo	xx	xx	oo	xx	xx	xx	xx	xx
	Gymno-sperm	Poor litter	P. nig	xx	xx	xx	xx	oo	xx	xx	xx	xx	xx	xx	xx
			L. kae	oo	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx
			T. can	xx	xx	oo	xx	xx	oo	xx	xx	xx	xx	xx	xx
			T. pli	xx	oo	xx	xx	xx	xx	xx	xx	xx	xx	xx	xx

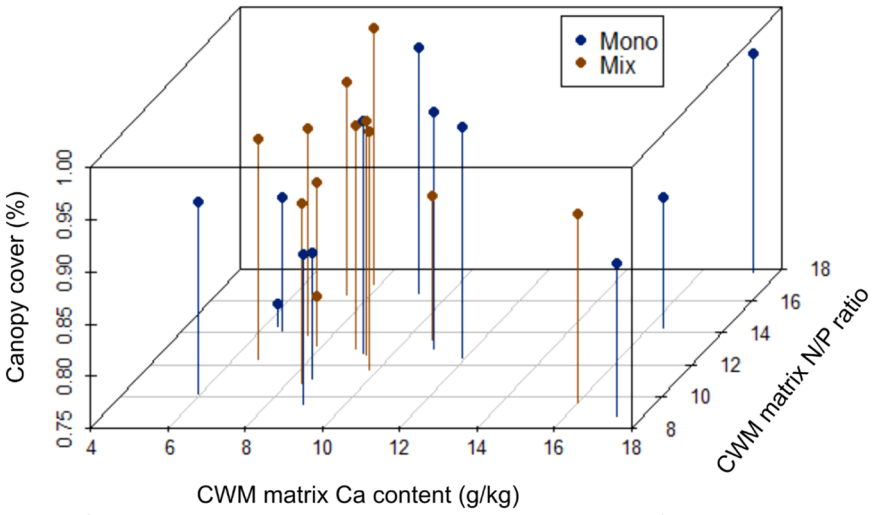
Annex 2. : Plot characteristics of the 24 selected forest stands (Fig. 2) with the first 12 stands presumed monospecific and the later 12 mixed forest stands. Dom. Tree Sp. Indicates the most abundant tree species in the year-round leaf litterfall collection with percentages indicating shares. The abbreviation "FF" indicates the ectorganic layer or "forest floor". Leaf diversity was calculated following the functional dispersion theory (Laliberte and Legendre, 2010). Chemical compositions (last four columns) are community weighted means of the observed leaf litterfall

Units			[%]	[g/m^2]	[g/m^2]	[g/m^2]	Functional dispersion	[g/kg]	[g/kg]	[g/kg]	[g/kg]
Plot	Dom. tree sp.	Secondary tree sp.	Canopy cover	Leaf litterfall	Herb weight	FF weight	Leaf diversity	C/N	N/P	Mn	Ca
1	*Alnus cordata (67%)*		0.98	553.8	51.8	487.6	1.79	15.30	12.98	1.16	10.96
2	*Acer saccharum (99%)*		0.97	555.1	9	706.4	0.00	20.10	12.45	2.81	11.88
3	*Betula alleghaniensis (82%)*		0.97	459.7	40.6	262	0.56	19.52	12.76	3.92	9.21
4	*Corylus colurna (83%)*		0.88	463.4	74.4	315.8	0.91	19.97	14.34	1.03	16.36
5	*Fagus sylvatica (67%)*		0.98	518.8	28	1088	2.00	19.92	16.50	1.23	9.20
6	*Juglans cinerea (98%)*		0.96	456.8	266.4	814.8	0.00	15.80	17.82	1.07	17.35
7	*Larix kaempferi (97%)*		0.88	314.1	653.4	6578	0.00	20.51	14.14	2.01	6.57
8	*Pinus nigra (81%)*		0.77	545.2	679.4	1464.2	1.22	30.90	14.45	0.85	6.32
9	*Quercus robur (80%)*		0.87	432.5	552.2	1128	0.91	16.74	11.17	1.21	8.51
10	*Tilia americana (83%)*		0.90	441.2	139	336.8	0.52	15.84	8.80	0.31	17.33
11	*Tsuga canadensis (88%)*		0.93	460.8	143.8	3863.8	0.00	27.75	10.15	1.56	5.94
12	*Thuja plicata (97%)*		0.89	436.8	10.4	1135.2	0.14	39.25	9.51	0.81	8.91
13	*Tilia americana (70%)*	*B. alleghaniensis (15%)*	0.93	391.0	109.6	522.2	1.51	16.88	9.65	0.99	15.99
14	*Castanea sativa (70%)*	*A. cordata (20%)*	0.95	508.9	203.8	683.6	1.27	18.90	16.43	0.80	7.35
15	*Quercus robur (53%)*	*C. betulus (40%)*	0.97	599.4	26	957.8	1.67	18.24	12.12	2.10	9.88
16	*Quercus rubra (49%)*	*A. saccharum (35%)*	0.89	582.0	339.2	461.4	1.23	22.10	13.54	1.92	10.67
17	*Fagus sylvatica (70%)*	*Q. robur (31%)*	0.99	514.5	7.2	808	1.51	30.03	10.11	0.40	15.28
18	*Quercus palustris (64%)*	*Q. rubra (31%)*	0.95	621.5	126.4	476.8	0.34	19.70	13.87	1.77	7.32
19	*Acer saccharum (62%)*	*T. canadensis (34%)*	0.98	478.8	15.2	783.4	0.86	22.74	11.65	2.39	9.79
20	*Pinus nigra (58%)*	*A. cordata (38%)*	0.79	466.3	439.6	1098.8	2.02	26.31	13.36	0.91	7.78
21	*Abies alba (73%)*	*F. sylvatica (20%)*	0.96	460.1	13.8	1073.6	1.32	29.25	12.37	2.19	6.65
22	*Quercus rubra (60%)*	*T. canadensis (29%)*	0.96	575.2	12	1270.2	1.13	23.84	13.03	1.53	8.90
23	*Thuja plicata (74%)*	*P. menziessii (22%)*	0.92	551.1	0.6	1574.2	1.05	36.78	10.84	0.96	8.38
24	*Larix kaempferi (54%)*	*A. homolepis (30%)*	0.91	312.2	198.4	4397.2	1.77	25.79	13.24	1.60	7.82

Annex 3. : Leaf substrate characteristics, used in the incubated litterbags. AM = arbuscular mycorrhiza, EcM = ectomycorrhizal association. Tree type is based on a categorization angiosperms - gymnosperms. Chemical elements Manganese and Calcium are given in [g/kg] dry matter. Ranks were based on initial literature research and match quite well with measured C/N and Ca content of the leaf substrates

Substrate type	Mycorrhiza	Type	Shade tolerance	C/N	N/P	Mn	Ca	Type
Acer saccharum	AM	Angio.	4.76	20.10	12.45	2.81	11.88	Rich
Alnus cordata	AM	Angio.	1.83	14.07	10.05	1.09	11.93	Rich
Betula alleghaniensis	EcM	Angio.	3.17	18.72	13.01	4.14	9.52	Rich
Corylus colurna	EcM	Angio.	1.35	20.11	13.24	0.99	18.05	Rich
Fagus sylvatica	EcM	Angio.	4.56	18.13	20.32	1.37	7.49	Poor
Juglans cinerea	AM	Angio.	1.88	15.80	17.82	1.07	17.35	Rich
Larix kaempferi	EcM	Gymno.	1.38	20.51	14.14	2.01	6.57	Poor
Pinus nigra	EcM	Gymno.	2.1	34.44	15.37	0.80	5.14	Poor
Quercus robur	EcM	Angio.	2.45	16.01	9.70	1.20	8.56	Poor
Thuja plicata	AM	Gymno.	4.73	39.49	9.42	0.78	8.97	Poor
Tilia americana	EcM	Angio.	3.98	15.82	8.67	0.18	18.64	Rich
Tsuga canadensis	EcM	Gymno.	4.83	27.75	10.15	1.56	5.94	Poor

Annex 4. : 3D scatterplot representing the experimental setup with characteristics of the decomposition environments, divided into monocultures (blue) and mixtures (brown) with values given in Annex 2



Annex 5. : Relative mass loss was related to substrate type over all plots using GLMMTMB with a beta distribution and logit link. Reported model intercepts and estimated deviations are therefore on the logit scale and do not directly match the raw relative mass loss values. Pinus nigra performed as the reference level for the other substrate type estimates and plot was added as a random variable. ($R^2m = 0.8746$ and $R^2c = 0.9412$). The letters in the last column represent significant differences between leaf substrate mass loss

	Estimate	Std. Error	z value	Pr(>|z|)		
(Intercept)	0.006	0.077	0.08	0.94		b
Tsuga canadensis	−0.158	0.093	−1.69	0.09	.	b
Larix kaempferi	−0.294	0.094	−3.13	< 0.01	**	ab
Fagus sylvatica	−0.309	0.095	−3.25	< 0.01	**	ab
Quercus robur	0.415	0.094	4.44	< 0.001	***	c
Thuja plicata	−0.504	0.096	−5.26	< 0.001	***	a
Betula alleghaniensis	0.683	0.119	5.72	< 0.001	***	cd
Acer saccharum	0.968	0.098	9.88	< 0.001	***	d
Alnus cordata	1.015	0.099	10.25	< 0.001	***	d
Juglans cinerea	1.050	0.125	8.44	< 0.001	***	d
Corylus colurna	1.821	0.142	12.83	< 0.001	***	e
Tilia americana	1.627	0.136	11.92	< 0.001	***	e

Annex 6. : Anova of the relative mass loss was related to leaf substrate type, incubation location (home- away) and the interaction between leaf substrate type and incubation location over all plots using GLMMTMB with a beta distribution and logit link. Plot was added as a random variable. ($R^2m = 0.8787$ and $R^2c = 0.9419$)

	Chisq	Df	Pr(>Chisq)	
(Intercept)	137.34	1	< 0.001	***
Substrate type	803.96	11	< 0.001	***
Incubation (home – away)	0.08	1	0.78	
Substrate: Incubation	4.94	11	0.93	

Annex 7. : Relative mass loss was related to leaf substrate quality over all plots using GLMMTMB with a beta distribution and logit link

$R^2m = 0.743$; $R^2c = 0.949$	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	0.396	0.095	4.16	< 0.001	***
C/N	−0.153	0.109	−1.40	0.16	
N/P	−0.110	0.087	−1.27	0.20	
Mn	0.083	0.083	1.00	0.32	
Ca	0.548	0.098	5.62	< 0.001	***

Annex 8. : Additional Decomposition at Home index (ADHi), calculated following (Ma et al. 2023), with Home Decomposition Difference (HDDi) and Away Decomposition Difference (ADDi) for all twelve monoculture stands x leaf litter substrates. The last column gives the average mass loss differences per leaf substrate Sum(Home – Away) / 11

Species	HDDi	ADDi	ADHi	Delta mass loss
A. cordata	2.07	1.57	3.53	5.18
A. saccharum	1.22	1.09	−0.17	−4.07
B. alleghaniensis	0.48	0.47	−1.30	−5.43
C. colurna	3.67	2.78	7.51	5.25
F. sylvatica	−2.38	−2.43	−0.93	−10.19
J. cinerea	1.64	1.30	2.06	−6.18
L. kaempferi	−2.28	−2.30	−1.24	−1.26
P. nigra	−1.48	−1.55	−0.76	2.71
Q. robur	0.86	0.00	7.19	12.83
T. americana	1.52	2.48	−11.03	−1.25
T. canadensis	−1.39	−2.09	5.64	7.27
T. plicata	−2.36	−2.88	3.76	9.38
Average (%)			**1.19**	**1.19**

Annex 9. : Left: decomposition difference (delta mass loss) for each substrate type linked to substrate quality. Right: plot performance (delta mass loss) linking how substrates behaved to matrix quality

	LMM Substr $R^2m = 0.223$, $R^2c = 0.498$					LMM Plot $R^2m = 0.071$, $R^2c = 0.5$				
	Estim.	Std. Error	t value	p-value		Estim.	Std. Error	t value	p-value	
(Intercept)	0.026	0.017	1.55	0.15		−0.020	0.022	−0.92	0.12	
C/N	−0.003	0.018	−0.17	0.87		−0.002	0.012	−0.20	0.84	
N/P	−0.050	0.014	−3.44	0.01	*	−0.020	0.011	−1.94	0.07	.
Mn	−0.021	0.016	−1.34	0.22		−0.014	0.012	−1.17	0.26	
Ca	−0.024	0.014	−1.78	0.12		−0.025	0.010	−2.43	0.03	*

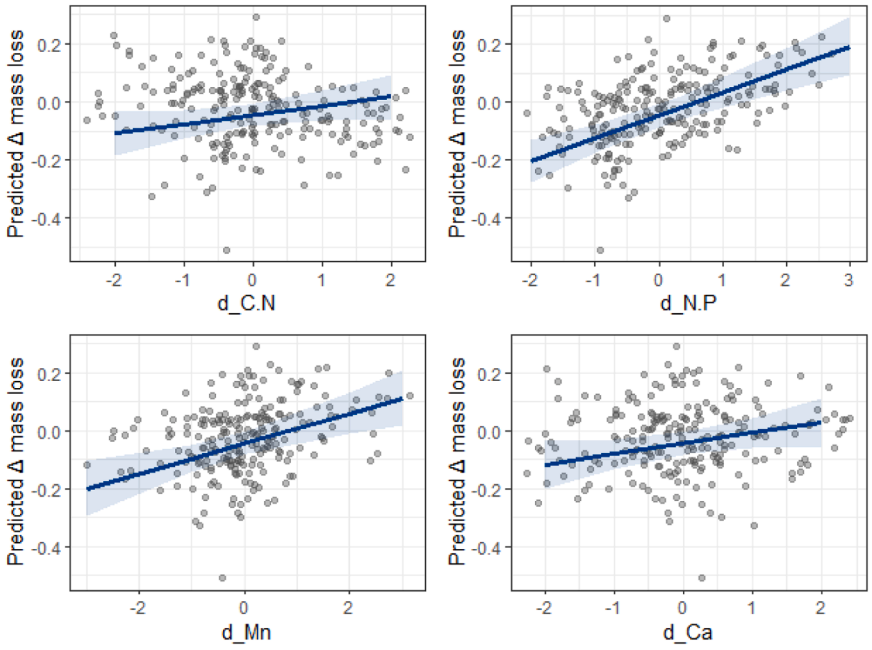
Annex 10. : LMM linking differences in relative mass loss (Away plot – home plot) to the difference in litter quality (substrate – matrix) with leaf substrate type and plot as random variables for left: all substrates in all plots (228 observations) and right: the eight substrates incubated in both mono and mixture stands (184 observations)

	LMM all spp $R^2m = 0.272$, $R^2c = 0.476$					LMM 8 spp $R^2m = 0.376$, $R^2c = 0.512$				
	Estim.	Std. Error	t value	p-value		Estim.	Std. Error	t value	p-value	
(Intercept)	−0.026	0.015	−1.70	0.11		−0.036	0.013	−2.80	0.02	*
Delta C/N	0.007	0.015	0.45	0.66		0.018	0.013	1.40	0.20	
Delta N/P	0.050	0.012	3.98	< 0.001	***	0.072	0.011	6.51	< 0.001	***
Delta Mn	0.038	0.012	3.22	< 0.01	**	0.040	0.011	3.64	< 0.01	**
Delta Ca	0.026	0.013	1.95	0.06	.	0.029	0.013	2.32	0.03	*

Annex 11. : Sensitivity analysis adding forest floor dry weight to the proxy-based model of Annex 9 for all plots and all species. Model delta represents the original model, model 2 adds the fixed factor FF weight, model 3 add the interaction between the fixed factors and FF weight, model 3 only used FF weight as the explanatory variable

Anova	npar	AIC	BIC	logLik	−2*LOG(L)	Chisq	Df	Pr (>Chisq)	
Model delta 3	5	−434.7	−417.3	222.37	−444.74				
Model delta	8	−450.8	−422.9	233.39	−466.79	22.05	3	< 0.001	***
Model delta 1	9	−449.4	−418.1	233.7	−467.4	0.62	1	0.433	
Model delta 2	13	−442.2	−397	234.12	−468.24	0.84	4	0.933	

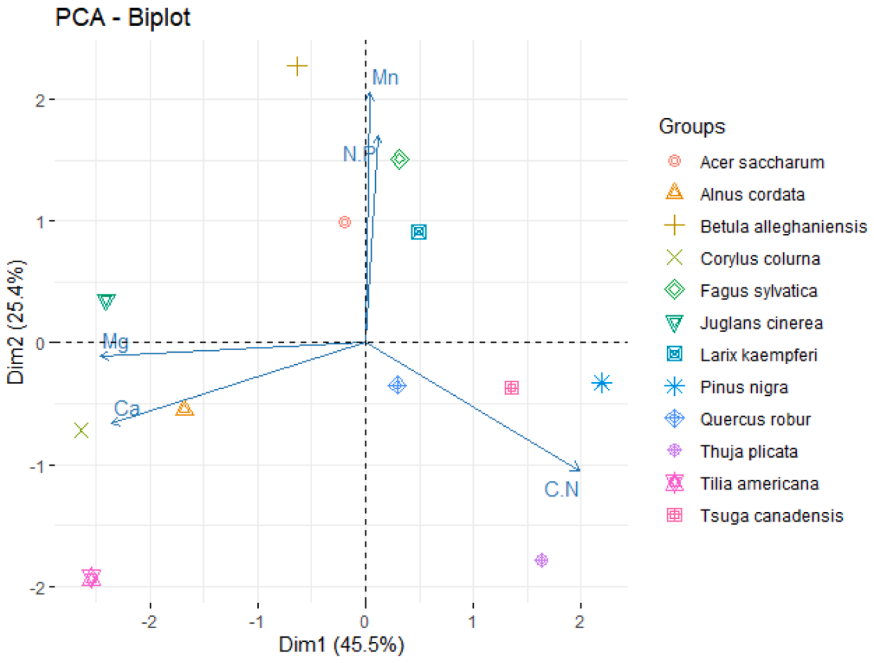
Annex 12. : Blue lines present the predicted effects by the LMM while gray dots are indicating the raw data points. Difference in chemical "quality" between the incubated substrate and the local matrix (forest floor) of the monoculture and mixture stands are given on on the x-axis. Positive values indicate an improved mass loss away than at the home sites



Annex 13. : GLMM linking relative mass loss to fixed variables describing leaf substrate quality, matrix quality and forest stand structure with substrate type and plot as random variables. (VIF <3.17)

$R^2m = 0.816$; $R^2c = 0.95$	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	0.411	0.083	4.96	< 0.001	***
C/N	−0.158	0.117	−1.35	0.18	
N/P	−0.174	0.096	−1.81	0.07	.
Mn	0.010	0.080	0.12	0.90	
Ca	0.519	0.107	4.87	< 0.001	***
Delta C/N	−0.096	0.072	−1.34	0.18	
Delta N/P	0.207	0.067	3.09	< 0.01	**
Delta Mn	−0.249	0.064	−3.91	< 0.001	***
Delta Ca	0.009	0.070	0.13	0.89	
Canopy cover	−0.027	0.052	−0.52	0.61	
Leaf litterfall	0.024	0.046	0.52	0.60	
Leaf diversity	−0.048	0.038	−1.27	0.20	
Herb cover	0.079	0.047	1.69	0.09	.
Forest floor weight	0.058	0.056	1.05	0.29	

Annex 14. : PCA plot illustrates the chemical composition of the used leaf litter substrates. The first PCA axis (Dim1) was used to determine the categorical variable "leaf quality", negative PCA values are 'rich litter', positive values are indicated as 'poor litter'



Annex 15. : GLMM relating relative mass loss to matrix quality, incubation environmental characteristics and the interaction between the incubated leaf substrate with the other fixed variables with fixed variables selected based on initial hypotheses (VIFs <3.9)

$R^2m = 0.732$; $R^2c = 0.956$	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.185	0.146	8.10	< 0.001	***
Leaf quality (Poor)	−1.317	0.198	−6.65	< 0.001	***
Matrix Ca	0.067	0.074	0.90	0.37	
Matrix C/N	−0.018	0.064	−0.28	0.78	
Canopy cover	−0.221	0.059	−3.73	< 0.001	***
Yearly leaf litterfall	0.042	0.076	0.55	0.58	
Forest floor weight	0.065	0.085	0.76	0.45	
Leaf quality (Poor): Matrix Ca	−0.097	0.067	−1.46	0.15	
Leaf quality (Poor): Matrix C/N	0.078	0.057	1.36	0.17	
Leaf quality (Poor): Canopy cover	0.234	0.053	4.38	< 0.001	***
Leaf quality (Poor): Yearly leaf litterfall	−0.119	0.070	−1.70	0.09	.
Leaf quality (Poor): Forest floor weight	−0.093	0.076	−1.22	0.22	

Annex 16. : GLMM relating relative mass loss to matrix quality and the interaction of the incubated leaf substrate with the incubation environment ~ matrix quality. (VIF<2.97)

$R^2m = 0.743$; $R^2c = 0.953$	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.199	0.145	8.25	< 0.001	***
Leaf quality (Poor)	−1.332	0.199	−6.69	< 0.001	***
Matrix Ca	−0.049	0.058	−0.85	0.40	
Matrix C/N	−0.034	0.063	−0.54	0.59	
Matrix N/P	−0.097	0.052	−1.88	0.06	.
Matrix Mn	−0.189	0.050	−3.77	< 0.001	***
Leaf quality (Poor): Matrix Ca	−0.021	0.059	−0.36	0.72	
Leaf quality (Poor): Matrix C/N	0.029	0.062	0.46	0.64	
Leaf quality (Poor): Matrix N/P	0.015	0.052	0.28	0.78	
Leaf quality (Poor): Matrix Mn	0.101	0.050	2.03	0.04	*

Annex 17. : GLMM relating relative mass loss to matrix quality and the interaction of the incubated leaf substrate with characteristics of the incubation environment. (VIF<3.06)

$R^2m = 0.734$; $R^2c = 0.955$	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.195	0.147	8.14	< 0.001	***
Leaf quality (Poor)	−1.325	0.199	−6.65	< 0.001	***
Canopy cover	−0.130	0.072	−1.79	0.07	.
Yearly leaf litterfall	0.009	0.068	0.13	0.90	
Leaf diversity	−0.013	0.054	−0.25	0.80	
Herb cover	0.118	0.070	1.69	0.09	.
Forest floor weight	0.017	0.066	0.25	0.80	
Leaf quality (Poor): Canopy cover	0.138	0.066	2.10	0.04	*
Leaf quality (Poor): Yearly leaf litterfall	−0.055	0.064	−0.87	0.38	
Leaf quality (Poor): Leaf diversity	0.015	0.050	0.29	0.77	
Leaf quality (Poor): Herb cover	−0.093	0.063	−1.47	0.14	
Leaf quality (Poor): Forest floor weight	0.000	0.060	0.00	1.00	

Annex 18. : GLMM relating relative mass loss to matrix quality, incubation environmental characteristics and the interaction between the incubated leaf substrate with the other fixed variables (VIFs <6.2)

$R^2m = 0.759$; $R^2c = 0.956$	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.190	0.143	8.30	< 0.001	***
Leaf quality (Poor)	−1.320	0.197	−6.69	< 0.001	***
Matrix Ca	−0.011	0.083	−0.13	0.89	
Matrix C/N	−0.059	0.074	−0.80	0.42	
Matrix N/P	−0.081	0.052	−1.57	0.12	
Matrix Mn	−0.117	0.060	−1.96	0.05	.
Canopy cover	−0.121	0.076	−1.59	0.11	
Yearly leaf litterfall	0.040	0.070	0.58	0.56	
Leaf diversity	−0.037	0.062	−0.60	0.55	
Herb cover	0.076	0.070	1.08	0.28	
Forest floor weight	0.042	0.083	0.50	0.61	
Leaf quality (Poor): Matrix Ca	−0.090	0.086	−1.05	0.29	
Leaf quality (Poor): Matrix C/N	0.077	0.077	1.01	0.31	
Leaf quality (Poor): Matrix N/P	0.016	0.054	0.29	0.78	
Leaf quality (Poor): Matrix Mn	0.003	0.062	0.05	0.96	
Leaf quality (Poor): Canopy cover	0.203	0.079	2.56	0.01	*
Leaf quality (Poor): Yearly leaf litterfall	−0.114	0.072	−1.58	0.11	
Leaf quality (Poor): Leaf diversity	0.010	0.064	0.16	0.88	
Leaf quality (Poor): Herb cover	−0.039	0.073	−0.53	0.59	
Leaf quality (Poor): Forest floor weight	−0.080	0.086	−0.93	0.35	

Data availability

Data will be made available on request.

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