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RESEARCH ARTICLE

Context dependency of tree diversity effects on standardized substrates decomposition: Role of tree functional composition, mycorrhizal type and climatic conditions

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Abstract

1. Tree diversity influences litter decomposition both directly, through changes in litter quality and composition, and indirectly, by altering the local decomposition environment (LDE). However, the role of the LDE in shaping litter decomposition rates remains less explored than the direct effects.
2. A standardized decomposition experiment using cellulose and wood substrates was conducted over the course of a year across seven tree diversity experiments in Europe and North America to explore how tree diversity, through its influence on the LDE, impacts decomposition rates.
3. Tree functional diversity enhanced the decomposition rate of high-quality substrate (cellulose) but had no effect on the decomposition rate of low-quality substrate (wood). The impact of LDE was context-dependent, with decomposition rates being highest under favourable climatic conditions, such as moderate temperatures and high precipitation.
4. Contrary to the common assumption that litter decomposes faster in broadleaved and arbuscular (AM)-dominated stands, our findings show that decomposition was faster in mixtures containing coniferous species and ectomycorrhizal (EM)-associated trees, suggesting that LDE plays a larger role than initially thought.

5. *Synthesis*. This study highlights the crucial role of LDE in shaping decomposition rates. While tree functional diversity generally enhances decomposition under favourable climatic conditions, LDE played a more significant role than previously recognized in EM stands, suggesting that faster decomposition rates in AM stands are primarily due to litter quality. These findings emphasize the context-dependent nature of decomposition and the importance of considering LDE in understanding how tree diversity influences decomposition processes.

KEYWORDS
cellulose decomposition, litter quality, local decomposition environment, mycorrhizal type, species richness, tree functional diversity, wood decomposition

1 | INTRODUCTION

Over the last three decades, numerous studies have shown that litter decomposition rates increase with tree diversity (Gessner et al., 2010; Hättenschwiler et al., 2005; Mori et al., 2020). These findings primarily stem from studies examining direct effects of tree diversity through changes in litter diversity (Kou et al., 2020), the enhancement of decomposition via nitrogen transfers between litter types (Handa et al., 2014; Jewell et al., 2015; Liu et al., 2020) and the promotion of more diverse and active soil fauna and microbial communities (Hättenschwiler & Gasser, 2005). However, other studies have reported neutral or even negative effects of tree diversity on litter decomposition (Canessa et al., 2022; Chapman et al., 2013; Fujii et al., 2017), challenging the completeness of this pattern and suggesting that the outcome may strongly depend on environmental conditions, tree species identity or species-specific interactions (Barantal et al., 2011; Porre et al., 2020). Recently, it has been proposed that tree diversity can significantly influence litter decomposition indirectly by altering the 'local decomposition environment' (LDE), which is the environment in which decomposition occurs (Joly et al., 2023). These indirect effects encompass changes in total tree biomass and stand structure, which can affect local soil microclimate (Martin-Guay et al., 2022), as well as the diversity and composition of understorey vegetation and soil biota (Corcket et al., 2020; Gong et al., 2021; Korboulewsky et al., 2016). Furthermore, the effects of tree diversity on decomposition rates may be mediated by shifts in the interaction between litter quality and LDE (Joly et al., 2023). For instance, Joly et al. (2017) found across various European forests that the changes in microenvironmental conditions induced by tree diversity effects were stronger for high-quality (i.e. cellulose) litter than for low-quality (i.e. wood) litter, suggesting that litter quality is a central factor mediating how the LDE influences decomposition rates (Ge et al., 2013). However, it is still unclear how tree functional diversity and composition, for instance, via shifts in mycorrhizal associations or plant functional groups (Augusto et al., 2015; Phillips et al., 2013), interact with LDE to influence decomposition processes. Addressing this gap is essential for improving our understanding of how biodiversity shapes carbon and nutrient cycling in terrestrial ecosystems, particularly under changing climatic conditions.

Although tree diversity has been quantified primarily through tree species richness (e.g. Hector et al., 2000; Wardle et al., 1997), the incorporation of ecological traits and more complex relationships has significantly advanced our understanding of how diversity influences litter decomposition rates (Cornwell et al., 2008; Hättenschwiler et al., 2005; Scherer-Lorenzen et al., 2007). In particular, individual tree species differ in their functional traits (Violle et al., 2007), which influence ecosystem processes in different ways. As a result, approaches that focus on dissimilarity of functional traits in leaf litter offer valuable insights into the underlying mechanisms of tree diversity effects on litter decomposition (Jewell et al., 2017; Laganière et al., 2012; Meier & Bowman, 2008). For example, evergreen gymnosperms generally exhibit lower decomposition rates than deciduous angiosperms due to lower litter quality (e.g. certain morphological or chemical traits that inhibit decomposition) and higher interception of precipitation, leading to drier soil conditions (Augusto et al., 2015; Brunel et al., 2017; Gartner & Cardon, 2004; Hättenschwiler et al., 2005). Moreover, specific tree-mycorrhizal associations may differ in their effects on soil biogeochemistry (Keller et al., 2019; Phillips et al., 2013; Seyfried et al., 2021; Terrer et al., 2018). Trees associated with arbuscular mycorrhizal (AM) fungi tend to produce high-quality and fast-decomposing litter (Midgley et al., 2015), resulting in faster nutrient cycling in soils than for trees associated with ectomycorrhizal (EM) fungi (Lin et al., 2017; Read & Perez-Moreno, 2003). These differences in litter properties contribute to contrasting characteristics observed between AM- and EM-dominated stands in terms of soil microbial communities (Cheeke et al., 2017; Rosling et al., 2016), organic matter accumulation (Craig et al., 2018) and soil nutrient availability (Brzostek et al., 2015; Midgley & Phillips, 2016). However, while the effects of plant functional groups or mycorrhizal associations are primarily studied through the lens of litter quality (i.e. the 'direct effects' of tree species diversity), the 'indirect effects' of tree diversity on decomposition through the modification of the LDE have largely been overlooked. In particular, differences in tree composition, canopy packing and tree height are likely to influence light radiation and understorey vegetation composition (Corcket et al., 2020; Martin-Guay et al., 2022), which can subsequently affect temperature and moisture at the soil surface (Kovács et al., 2017; Williams et al., 2017), and

thus litter decomposition rates (Wang et al., 2022). However, it remains largely untested whether and how the functional role of tree diversity on LDE varies across different climatic contexts, pointing to a key uncertainty in our understanding of the interplay between local biotic effects and broader environmental gradients (Augusto et al., 2015; Guittar et al., 2016).

Climatic conditions have emerged as key modulators of the effects of tree diversity on litter decomposition, determining how biodiversity influences ecosystem processes across environmental gradients (Fanin et al., 2018; Jonsson & Wardle, 2008; Kou et al., 2020). For instance, using a comparative and observational approach across European forests, Ratcliffe et al. (2017) found that tree diversity effects on ecosystem functions intensified with greater water limitation, highlighting the role of biodiversity in sustaining ecosystem functioning under harsher climatic conditions. However, these effects are not universally observed and can depend on local environmental conditions at the plot scale (Prescott et al., 2020; Sohng et al., 2014). Reflecting this complexity, Maxwell et al. (2020) found that, in a temperate forest ecosystem, the negative impact of low water availability on decomposition could not be mitigated by the positive effects of mixing tree species. These contrasting results suggest that the relevance of factors influencing decomposition rates may vary with spatial scale (Joly et al., 2023), with macroclimate being essential for comparing tree diversity effects across regions or countries, while LDE likely plays a more crucial role at smaller scales (Aerts, 1997; Bradford et al., 2016; Wang et al., 2015). Furthermore, changes in LDE are likely more consequential under harsher climatic conditions, where improvements can significantly enhance decomposition limited by the macroclimate, whereas under favourable climates, such enhancements may have minimal observable effects (Fanin et al., 2020). Consequently, increased attention should be given to the various ways through which tree diversity may impact LDE, particularly regarding the interactive effects of macroclimate and LDE on litter decomposition.

The main objective of our study was to assess how the indirect effects of tree diversity on the 'litter decomposition potential' vary with environmental context, specifically through the modification of LDE, while disregarding litter quality differences among plots. To achieve this, we employed standardized litter (i.e. cellulose and wood) to evaluate decomposition rates in pure versus mixed forests and to study the different decomposition processes at play. Cellulose served as a proxy for easily decomposable substrates that are abundant during early decomposition stages, while wooden sticks represented more recalcitrant substrates that are prevalent during later decomposition stages (Joly et al., 2017). This approach enabled us to estimate the decomposition potential across both early and late stages. First, we hypothesized that the effect of tree diversity on decomposition rates would be greater for high-quality substrates than for low-quality substrates (H_1). We expected that the positive influence of tree diversity on LDE would be more pronounced for the easily decomposable substrates (i.e. cellulose), which directly benefit from improved local conditions (i.e. more humid microclimate) (Joly et al., 2017), while the more recalcitrant substrates (i.e. wooden sticks) would require specific functional abilities from soil decomposers that are less influenced by local conditions (Fanin et al., 2016). Second, we hypothesized that the effects of tree diversity on decomposition rates would depend on the climatic context, with greater effects observed under less favourable conditions (lower water availability and lower temperatures) (H_2). We anticipated that favourable climatic conditions might reduce the positive effects of tree diversity on decomposition rates, while modifications to the LDE (e.g. increased soil humidity) would enhance decomposition rates primarily in harsher environments (Ratcliffe et al., 2017). We conducted our study using tree diversity experiments specifically designed and planted to study the effects of tree species diversity on ecosystem functioning while minimizing confounding variables that may be present in natural forests. These experimental sites enable controlled comparisons and replications, providing a robust framework for assessing the impact of tree diversity on litter decomposition. We tested our hypotheses across a network of seven tree diversity experiments in Europe and North America, covering diverse ecological gradients. The main originality of this study lies in its experimental, multi-site approach using standardized litter types to isolate the effects of tree diversity on the LDE and its impact on decomposition across contrasting climatic contexts, thereby disentangling local influences from broader environmental drivers.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted on seven experiments in six countries: B-Tree (Austria), FORBIO Hechtel-Eksel (Belgium), FORBIO Gedinne (Belgium), ORPHEE (France), IDENT Freiburg (Germany), IDENT Macomer (Italy) and IDENT Sault Sainte-Marie (Canada). These sites represent various climate zones, including humid continental (Canada), oceanic (Belgium, France, and Germany), Mediterranean (Italy) and continental (Austria). This allowed for a comprehensive examination of tree diversity effects on litter decomposition across diverse environmental conditions. All the sites are part of the TreeDivNet network (Paquette et al., 2018; Verheyen et al., 2016). This international network of experimental forests was designed to investigate the effects of tree diversity on various ecosystem functions worldwide (www.treedivnet.ugent.be), by planting new tree communities with different levels of diversity on homogeneous sites to minimize the influence of confounding factors on ecosystem processes like decomposition. Experiments were installed between 2008 and 2014 (Table 1), resulting in sites ranging from 10 to 16 years old. Each site included at least three levels of species richness: monocultures, intermediate diversity (two-species mixtures) and high diversity (four- or six-species mixtures, depending on the site). We considered all the monocultures of the component species of the corresponding mixtures to enable comparisons between pure and mixed forests of different compositions (Table S1). Additionally, tree species were categorized based on their association with either

TABLE 1 Overview and characteristics for each study site.

Site name	Climatic zone	MAT (°C)	MAP (mm)	Soil type	Planting date	Plot numbers	Plot size (m^2)	Mean tree height (*year*)	Tree species selected	Species richness tested
B-Tree (AU)	Sub-semi-continental	9.6	635	Moist chernozem	2013	18	196	4.7 m (*2021*)	*A. platanoides*, *C. betulus*, *Q. robur*, *T. cordata*	1, 2, 4
FORBIO Hechtel-Eksel (BE)	Eu-oceanic	9.5	809	Dry sandy soil with gravel substrate	2012	22	1296	4.3 m (*2019*)	*B. pendula*, *L. kaempferi*, *P. menziesii*, *P. sylvestris*, *Q. petraea*	1, 2, 4
FORBIO Gedinne (BE)	Eu-oceanic	8.4	1051	Moderately dry stony loam	2010	22	1764	6.6 m (*2023*)	*A. pseudoplatanus*, *F. sylvatica*, *L. marschlinsii*, *P. menziesii*, *Q. petraea*	1, 2, 4
ORPHEE (FR)	Semi-hyper-oceanic	12.6	1000	Sandy podzol on sandstone bedrock	2008	20	400	5.8 m (*2021*)	*B. pendula*, *Q. robur*, *Q. ilex*, *P. pinaster*	1, 2, 4
IDENT Freiburg (DE)	Semi-continental	10.1	658	Shallow cambisol with high gravel content	2013	18	13	4.8 m (*2020*)	*A. platanoides*, *A. saccharum*, *B. papyrifera*, *B. pendula*, *Q. robur*, *Q. rubra*	1, 2, 6
IDENT Macomer (IT)	Euoceanic	13.6	888	Silt loam	2014	22	10.24	1 m (*2017*)	*A. monspessulanum*, *A. unedo*, *F. ornus*, *O. europea*, *P. latifolia*, *P. halepensis*, *P. pinaster*, *P. pinea*, *Q. ilex*, *Q. pubescens*, *Q. suber*	1, 2, 4
IDENT Sault Sainte-Marie (CA)	Eucontinental	4.8	806	Sandy loam	2013	22	10.24	3.44 m (*2020*)	*A. saccharum*, *B. papyrifera*, *L. laricina*, *P. glauca*, *P. strobus*, *Q. rubra*	1, 2, 4

Note: MAT, mean annual temperature and MAP, mean annual precipitation in 2022 and 2023. *Acer monspessulanum* (L., 1753), *A. platanoides* (L., 1753), *A. pseudoplatanus* (L., 1753), *A. saccharum* (Marshall, 1785), *Arbutus unedo* (L., 1753), *Betula papyrifera* (Marshall, 1785), *B. pendula* (Roth, 1788), *Carpinus betulus* (L., 1753), *Fagus sylvatica* (L., 1753), *Fraxinus ornus* (L. 1783), *Larix kaempferi* (Carrière, 1856), *L. laricina* (Koch, 1873), *L.*×*marschlinsii* (Coaz, 1917), *Phillyrea latifolia* (L., 1753), *Picea abies* (Karst, 1881), *P. pungens* var. *galuca* (Engelm, 1879), *Pinus pinaster* (Aiton, 1789), *P. pinea* (L., 1753), *P. strobus* (L., 1753), *P. sylvestris* (L. 1753), *Pseudotsuga menziesii* (Franco, 1950), *Quercus ilex* (L., 1753), *Q. petraea* (Liebl., 1784), *Q. pubescens* (Willd., 1796), *Q. pyrenaica* (Willd., 1805), *Q. robur* (L., 1753), *Q. rubra* (L., 1753) and *Tilia cordata* (Mill., 1768).

AM or EM fungi within each experiment. In total, we examined 26 different tree species and 144 forest plots across all seven sites, representing evergreen and deciduous conifers and broadleaves (Table 1).

2.2 | Decomposition experiment

Standardized substrates were used to build litterbags in order to examine the influence of tree diversity on decomposition rates at each site (Gottschall et al., 2019; Hu et al., 2021). We selected cellulose discs and wooden sticks as proxies for the potential decomposition rates of nutrient-free substrates, chosen to represent different dominant material types at different decomposition stages (i.e. early vs late decomposition stage for cellulose and wood, respectively). The decision to use these two standard materials rather than leaf litter was made to test the effects of the LDE provided by each experimental plot on decomposition, thus avoiding any direct effect of litter mixture or 'home field advantage' on decomposition (Fanin et al., 2021; Joly et al., 2017; Scherer-Lorenzen, 2008). It is important to stress that, because standardized litters do not mimic leaf litter (Joly et al., 2023), their decomposition should not be used to estimate the decomposition rate of leaf litter in the field. Cellulose paper was chosen because it is highly degradable and accessible to a wide range of decomposer organisms (Štursová et al., 2012). The samples consisted of individual cellulose paper disks of 125 mm in diameter, 205 µm in thickness and composed of 98% cellulose (Whatman filter paper, Grade 4). Wooden sticks were selected as a more recalcitrant material due to their larger proportion of lignin, which represents a more complex structure than cellulose and hemicelluloses (Meshitsuka & Isogai, 1996). This composition restricts accessibility primarily to a limited group of decomposer organisms capable of enzymatically degrading lignocellulosic complexes (Fanin et al., 2020). The wooden lolly sticks used (110 × 0.2 × 10 mm, Sinsally manufacturer) were uniformly made from *Populus* sp. The initial mass of substrates was measured using air-dry material, with some subsamples ($n = 20$) further dried at 65°C for 48 h and reweighed to establish a correction factor for dry mass. Each litterbag (0.17 m × 0.14 m with a fine mesh size of 38 µm) was filled with the standardized substrates, half of which contained only cellulose (~1.63 g) and the other half only wood (~1.76 g). Two litterbags were installed at the top of the mineral soil layer after removing the organic litter at that location. All plot compositions were replicated twice per site (Table S1). The bags were placed in the centre of each plot, evenly distributed at maximum diversity with respect to the four or six immediate tree neighbours to capture representative variability at the site scale. A total of 872 litterbags were incubated across the seven sites.

All the litterbags were recovered after about 1 year of incubation (between May 2022 and October 2023) and were carefully collected, dry-cleaned and dried at 65°C for 48 h. The mass of the standardized material remaining within bags was recorded, assuming that the bag itself did not lose any material. Using the percentage of mass loss, we calculated the decomposition constant k to standardize the different sampling dates across sites, for cellulose and wood sticks separately, as:

$$\%\,\text{mass loss} = 100 - 100 \times e^{-kt} \quad (1)$$

where t corresponds to the total number of days of incubation and k representing the decomposition rate (year^{-1}) (Olson, 1963).

2.3 | Response variables

We used two metrics as response variables: the decomposition rate 'k' (year^{-1}) and the net biodiversity effect (NBE) on decomposition calculated for cellulose and wood independently. We calculated NBE as the difference between mean observed values of the decomposition rate in the mixtures and their expected values based on their mean values in the monocultures of component tree species from the same site and the relative proportion of tree species in the mixed plots (Loreau & Hector, 2001):

$$\text{NBE} = \left(X_{\text{mx}} - \sum p_i X_{\text{mo}-i}\right) / \sum p_i X_{\text{mo}-i} \quad (2)$$

where X_{mx} = mean decomposition rate in mixture; X_{mo} = mean decomposition rate in monoculture plot i; and p_i is the proportion of the tree species i in the mixture (% basal area of each tree species in the mixture). We calculated NBE values for each site, with positive NBE values indicating that decomposition rates were higher in mixed forests than expected based on the monocultures of each tree species. Each NBE value was calculated per tree species mixture within a site, based on two replicate plots of the mixture and two replicate monoculture plots for each of its component species at the same site. This approach ensured that each NBE value integrates data from four or more plots (depending on the number of species in the mixture), representing the plot-level variation within each experimental site.

2.4 | Explanatory variables

We used several explanatory variables to assess their relative importance in decomposition rates, namely '*functional composition*', '*mycorrhizal association type*', '*richness level*' and '*functional dissimilarity*' (FD) for the effect of tree diversity; and '*climate factor*' and '*tree height*' for the effect of environmental context. '*Tree height*' was calculated as the mean tree height of trees at the plot scale and used as a proxy for tree biomass and sunlight interception in order to consider whether the effects of tree diversity on decomposition rates were mediated by differences in standing biomass. While tree height is often correlated with stand age, it is important to recognize that this relationship can be non-linear and influenced by factors such as species-specific growth rates, site conditions and environmental disturbances, particularly in younger stands. '*Richness level*' is an ordinal variable representing three levels of tree species richness in the plot, that is, 'Pure' in monoculture stands, 'Intermediate' for two-species mixtures and 'High' for mixtures of four or six

species. This ordinal grouping was used instead of continuous species richness to account for the variation in richness across sites (e.g. maximum richness ranging from 4 to 6 species), ensuring more balanced representation and better comparability among sites in the cross-site analysis. '*Functional composition*' is a categorical variable representing the tree composition of the plot as 'monoculture angiosperm', 'monoculture gymnosperm', 'mixed angiosperm', 'mixed gymnosperm' and 'mixed angiosperm and gymnosperm'. The '*mycorrhizal association type*' corresponds to the different mycorrhizae types associated with tree species including 'AM' for arbuscular mycorrhizal fungi, 'EM' for ectomycorrhizal fungi and the combination 'EM.AM' when both are present in the mixture (Wang & Qiu, 2006). The '*FD*' between the different tree species in mixed plots was calculated based on five functional leaf traits highly related to decomposition (Pietsch et al., 2014): leaf carbon-to-nitrogen ratio, leaf nitrogen content, leaf phosphorus content, leaf dry matter content and specific leaf area. This combination provided a comprehensive representation of functional diversity and a nuanced understanding of ecological variability, as each trait contributes distinct and valuable information related to plant functional strategies. Mean trait values per species were obtained from the literature and highly related to decomposition (see PCA of the traits in Figure S1). The FD was weighted by the relative abundance of tree species (based on basal area), and computed using the *fdisp* function in the package FD (Laliberté et al., 2014). First, the *fdisp* function constructs a trait matrix *T* where rows represent species and columns represent traits. The pairwise distance d_{ij} between species *i* and *j* is computed using a distance metric, such as Euclidean distance:

$$d_{ij} = \sqrt{\sum_{k=1}^{m} (T_{ik} - T_{jk})} \quad (3)$$

where *m* is the number of traits. The function then aggregates these distances to produce a dissimilarity matrix *D* for communities, which reflects the degree of functional diversity. The variable '*climate factor*' was calculated according to the formula (Augusto et al., 2017):

$$f_{\text{climate}} = 0.4565 \times (I_{\text{LT}})^{0.4466} \quad (4)$$

where I_{LT} is a climate index well tested at global scale (Adair et al., 2008) and computed as follows:

$$I_{\text{LT}} = f_{T^\circ\text{C}} \times f_{\text{H}_2\text{O}} \quad (5)$$

$$f_{T^\circ\text{C}} = 0.5766 \times \exp\left[308.56 \times \left(\frac{1}{56.02} - \frac{1}{(273 + T_i) - 227.13}\right)\right] \quad (6)$$

$$f_{\text{H}_2\text{O}} = \frac{1}{1 + \left(30 \times \exp\left(-8.5 \times \left(\frac{\text{PPT}_i}{\text{PET}_i}\right)\right)\right)} \quad (7)$$

where T_i, PPT_i and PET_i are the monthly mean values for air temperature, precipitation and potential evapotranspiration (Thornthwaite method). Local climate data were extracted from the WorldClim database (http://www.worldclim.org; Hijmans et al., 2005; Anderson-Teixeira et al., 2015). Mean annual temperatures during the decomposition experiment period across the sites ranged from 4.8°C to 13.6°C and mean annual precipitation ranged from 635 to 1051 mm (Table 1). The 'climate factor' (f_{climate}; Equation 4) increases with water availability and warmer temperatures, which are expected to favour biological activity and therefore, decomposition (Augusto et al., 2017). Unfortunately, we did not have direct soil measurements from the sites to avoid confounding effects of soil characteristics and climate across sites, but we were able to verify that the climate factor was not correlated with soil pH (Figure S2).

2.5 | Data analysis

We assessed the context-dependent effects of tree diversity on decomposition rates in five separate analyses, explicitly designed to test our two main hypotheses (H_1 and H_2). First, we tested the significance of overall $\text{NBE}_{\text{cellulose}}$ and NBE_{wood} across all sites by testing if the 95% confidence interval was significantly different from zero. This test allowed us to evaluate whether, on average, tree diversity had a significant indirect effect on decomposition rates across the network. Second, we tested the relationships between NBE and climate factor and tree height across the different sites by using univariate linear tests. Each NBE value was treated as an independent observation. These tests addressed H_2 by exploring whether the magnitude and direction of NBE varied with the climatic context or stand structure (i.e. tree height). Third, we used linear mixed-effect models in order to test the effect of tree diversity on $k_{\text{cellulose}}$ and k_{wood}. For each substrate, we tested the fixed effects of *functional composition*, *mycorrhizal association type* and *richness level* in separate models. All the models controlled for the fixed effect of climate factor and tree height, and included *Site* as a random factor. Models for continuous variables were fitted using the '*lmer*' function from the R package '*lme4*' (Bates et al., 2015). For models testing the effect of '*mycorrhizal association type*', we used a subset of sites excluding those that presented only one type of mycorrhiza (i.e. EM only for ORPHEE and FORBIO Hechtel-Eksel). For models testing the effect of *functional composition*, we excluded the 'Mixed gymnosperm' treatment as these plots were present in only two sites (i.e. FORBIO Gedinne and FORBIO Hechtel-Eksel). These models served two purposes: (i) to test Hypothesis H_1, that is, whether the effects of tree diversity on decomposition rates differ between high-quality (cellulose) and low-quality (wood) substrates, and (ii) to assess the influence of stand-level diversity-related variables on decomposition rates. This allowed us to investigate how different facets of tree diversity influence the LDE, and thus contribute to changes in decomposition dynamics. Fourth, we tested the combined effect of FD and climate factor on the sign of $\text{NBE}_{\text{cellulose}}$ and NBE_{wood} using a binomial generalized linear model, as the

analysis focused on the binary nature of the response variable (positive vs negative NBE values). We fitted the models that included interactions between the climate factor and FD, with '*Site*' as a random effect to account for differences across the seven experiments and plot-level replications, using the '*glmer*' function from the R package '*lme4*' for categorical response variables (Bates et al., 2015). All continuous predictor variables were scaled and centred prior to modelling to make their coefficients comparable (Schielzeth, 2010). We simplified the models by sequentially removing the non-significant interactions (Barr et al., 2013). This analysis directly tested H_2 by examining how climate modulates the direction (positive or negative) of tree diversity effects on decomposition, and whether functional diversity reinforces or buffers these effects under different environmental contexts. Fifth, we built a structural equation model (SEM) for each substrate to test the direct and indirect fixed effects of *FD*, *climate factor* and *tree height* on $k_{substrate}$ based on our a priori global path model (Figure 5a) and to identify statistically significant relationships. SEMs included *Site* as a random factor. We evaluated the probability that none of the paths missing from the hypothesized network contained useful information using Shipley's test of direct separation (Shipley, 2009) as implemented in the '*piecewiseSEM*' R package (Lefcheck, 2016). The best model was selected as a valid reflection of reality if a chi-square test of Fisher's *C* statistic yielded a *p* value >0.05. These SEMs served to integrate both H_1 and H_2, by simultaneously testing how tree diversity (via FD), tree height and climate influence decomposition, and how these variables interact directly or indirectly. All analyses were based on 144 forest plots (two replicates per composition per site), and 872 decomposition bags (436 for each substrate type) across the seven experimental sites. All models are described in Table S2. All statistical analyses were performed using the R software version 4.3.1 (R Core Team, 2019).

3 | RESULTS

3.1 | Decomposition rates and NBEs across sites

The average decomposition rate $k_{cellulose}$ across sites over 1 year was $2.40 \pm 0.11\ year^{-1}$ (mean ± standard error), while average k_{wood} was $0.44 \pm 0.02\ year^{-1}$ (Figure S3A,B). Decomposition rates varied widely among different sites, with the highest decomposition rates in temperate, humid climates represented by the Belgian sites with an average of $2.19 \pm 0.22\ year^{-1}$ for FORBIO Gedinne and $2.19 \pm 0.24\ year^{-1}$ for Forbio Hechtel-Eksel and the German site (IDENT-Freiburg). The decomposition was slower in colder climates represented by the Austrian (B-Tree) and Canadian (IDENT Sault Sainte-Marie) sites, and slowest in oceanic and dry Mediterranean climates, for the French (ORPHEE) and Italian (IDENT-Macomer) sites with an average of 0.78 ± 0.08 and $0.62 \pm 0.06\ year^{-1}$, respectively (Figure S3A,B).

The overall mean $NBE_{cellulose}$ was positive, with a confidence interval that did not bracket zero ($0.05 \pm$CI [0.01; 0.09]), indicating a significant increase in decomposition rates in mixed plots compared to the expected value (Figure 1a). NBE_{wood} was not significantly different from zero ($0.00 \pm$CI [−0.08; 0.08]) (Figure 1b).

3.2 | Relationships between climate factor or tree height and NBEs

We found that $NBE_{cellulose}$ was positively influenced by the climate factor (i.e. numerical index that increases with a more favourable climate for decomposition) ($r^2 = 0.30$; Figure 2a). By contrast, the relationship between NBE_{wood} and the climate factor was not significant (Figure 2b). $NBE_{cellulose}$ ($r^2 = 0.26$; Figure 2c) and NBE_{wood} ($r^2 = 0.14$; Figure 2d) significantly increased with tree height, our proxy of tree biomass.

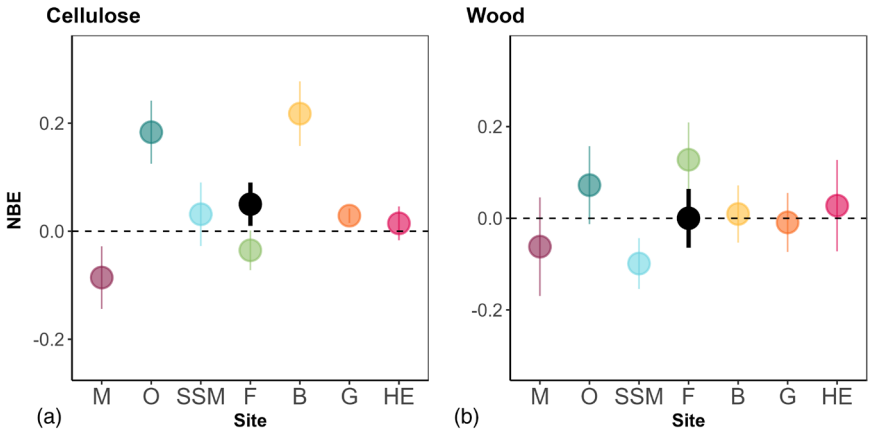

FIGURE 1 Net tree biodiversity effect (NBE) on decomposition rates ($k_{substrate}$; $year^{-1}$) for (a) cellulose, and (b) wood. Coloured symbols with bars represent the mean ± standard error of each site. Black symbols with bars represent the mean ± confidence interval. Sites are presented in order of increasing latitude. B, B-Tree [yellow]; F, IDENT Freiburg [green]; G, FORBIO Gedinne [orange]; HE, FORBIO Hechtel-Eksel [red]; M, IDENT Macomer [purple]; O, ORPHEE [dark blue]; SSM, IDENT Sault Sainte-Marie [light blue].

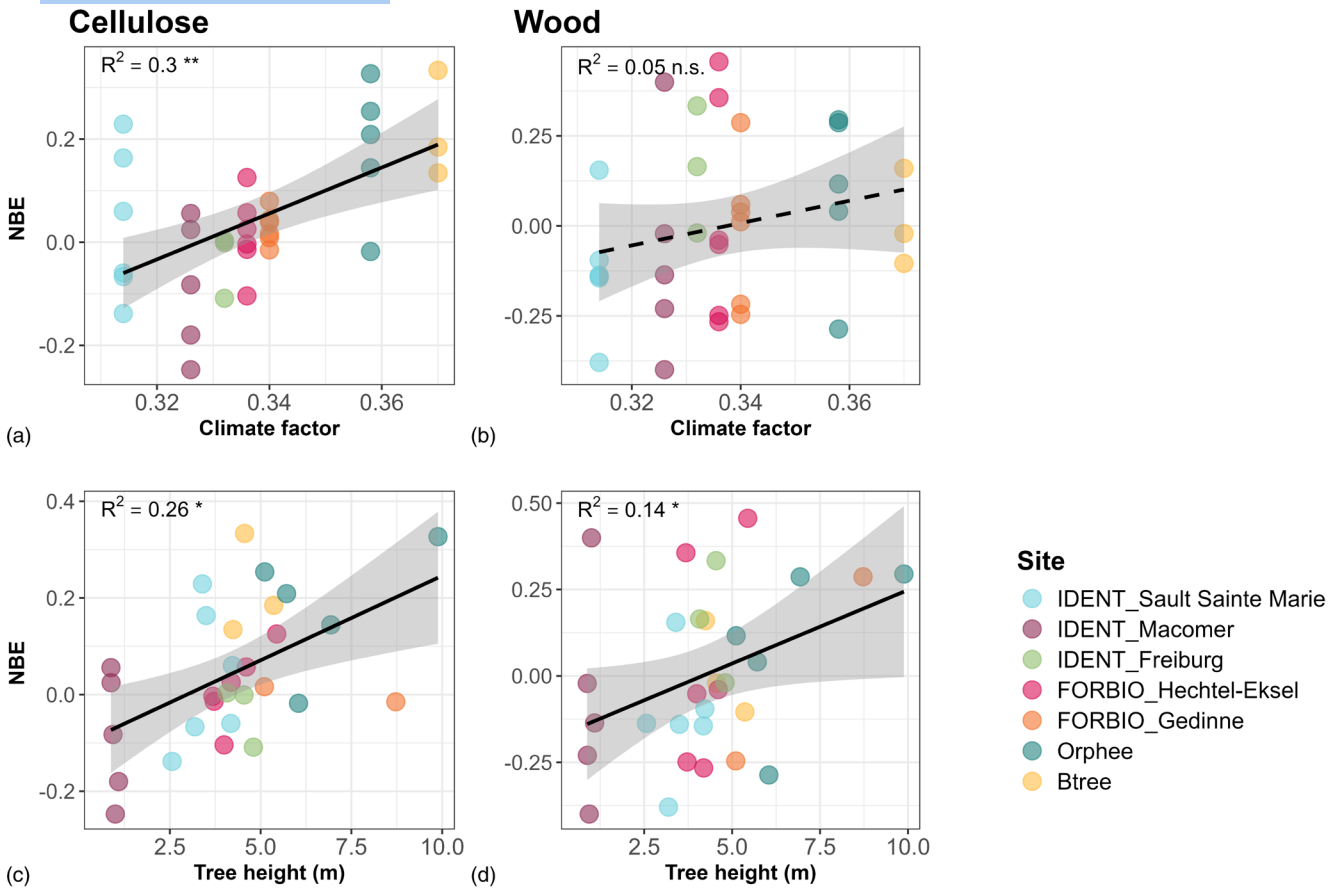

FIGURE 2 Effect of climate factor (top) and tree height (bottom) on the net biodiversity effect (NBE) on decomposition rates for (a, b) cellulose (left) and (c, d) wood substrates (right). Symbol colours represent the sites. Solid and dashed lines represent a significant and insignificant relationship, respectively (significance levels $^{*}p < 0.05$ and $^{**}p < 0.01$). The coefficient of determination (R^2) indicates the proportion of variance explained.

3.3 | Effect of functional composition, mycorrhizal type and tree richness on decomposition

We found that $k_{cellulose}$ was significantly influenced by the functional composition, the type of associated mycorrhiza and the level of tree richness of the stand, and this even when considering climate factor or tree height as co-variables (Figure 3). Overall, we found that $k_{cellulose}$ was greater in plots containing gymnosperms (pure or mixed with angiosperms) (Figure 3A). We found a similar result for k_{wood}, with higher decomposition rates in plots containing gymnosperms (Figure 3B). No effects of climate factor and tree height as co-variables were found in these two models. When assessing the effect of mycorrhizal type, we found that $k_{cellulose}$ was significantly higher in EM-dominated stands (pure EM or mixed with AM) (Figure 3C). The co-variable tree height and its interaction with climate factor also explained a significant proportion of the variation in this model. However, we did not find an effect of mycorrhizal type on k_{wood} (Figure 3D). We found higher decomposition rates for $k_{cellulose}$ for the high category of tree species richness compared to the monoculture (Figure 3E; Figure S4). The co-variable tree height was also a significant factor, but no effect of tree species richness was found on k_{wood} (Figure 3F).

3.4 | Context-dependent effects of functional diversity composition across different climatic conditions

Overall, we observed a contrasting effect of FD on NBE for cellulose and wood decomposition in mixtures that depended on climate (Figure 4). Specifically, FD positively influenced NBE for cellulose decomposition, with the percentage of positive NBE increasing from 34% under low FD and unfavourable climate conditions (i.e. bottom left quadrant) to 62% under high FD and unfavourable climatic conditions (i.e. top right quadrant). In contrast, for wood decomposition, the percentage of positive NBE decreased from 41% to 12% between the same quadrants. Additionally, we found a clear positive influence of the climate factor for both substrates. The highest proportion of positive NBE for both substrates was found under high FD and favourable climatic conditions.

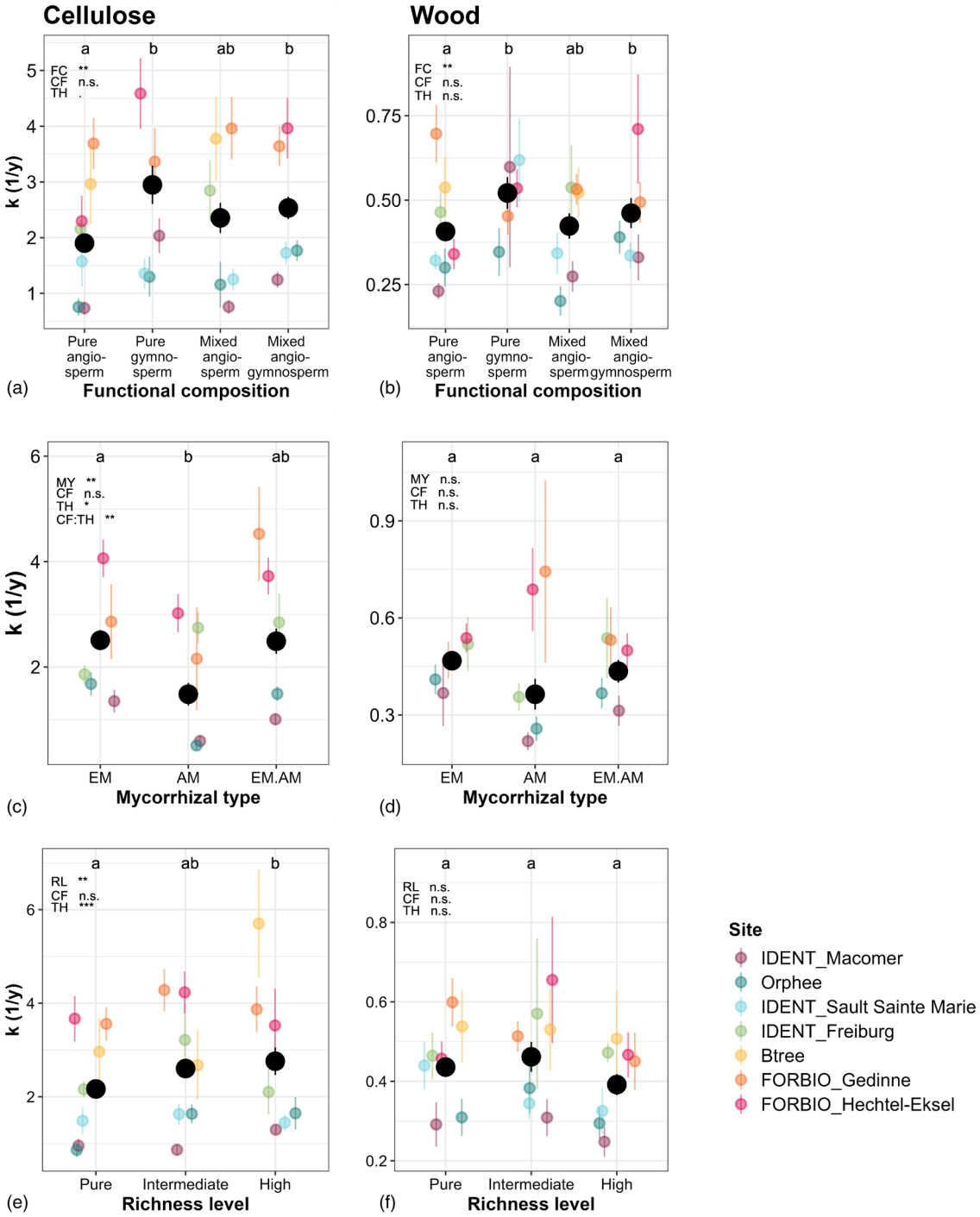

FIGURE 3 Effect of functional tree composition (a, b), mycorrhizal type (c, d) and species richness (f) on the decomposition constant (*k*) for cellulose (left) and wood substrates (right). Mycorrhizal type corresponds to ectomycorrhizal species (EM), arbuscular mycorrhizal species (AM) and mixtures of both (EM.AM). *Richness level* representing 'Pure' in monoculture stands, 'Intermediate' in 2-sp mixtures and 'High' for 4-sp or 6-sp mixtures. Symbol colours represent the sites. Colour symbols with bars correspond to mean ± standard error values per site. Black symbols with bars correspond to mean ± se by tree diversity level. Significance effect levels (*$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$) and marginal trends ($0.05 < \cdot p < 0.01$) represented by a dot (.) are indicated for each corresponding variable: CF, *climate factor*; FC, *functional composition*; MY, *mycorrhizal type association type*; RL, *richness level* and TH, *tree height*. Different letters indicate statistically significant differences between groups based on mixed models followed by post hoc comparisons ($p < 0.05$).

The two structural equation models represented the data well as no missing paths were identified (Fisher's $C = 0.3$, df = 2, $p = 0.87$ for the cellulose model and for Fisher's $C = 0.8$, df = 2, $p = 0.66$ for the wood model). For the cellulose model, only two of the four tested links were significant (Figure 5b): LDE was positively influenced by tree FD and tree height. The fixed effects explained 37% of the

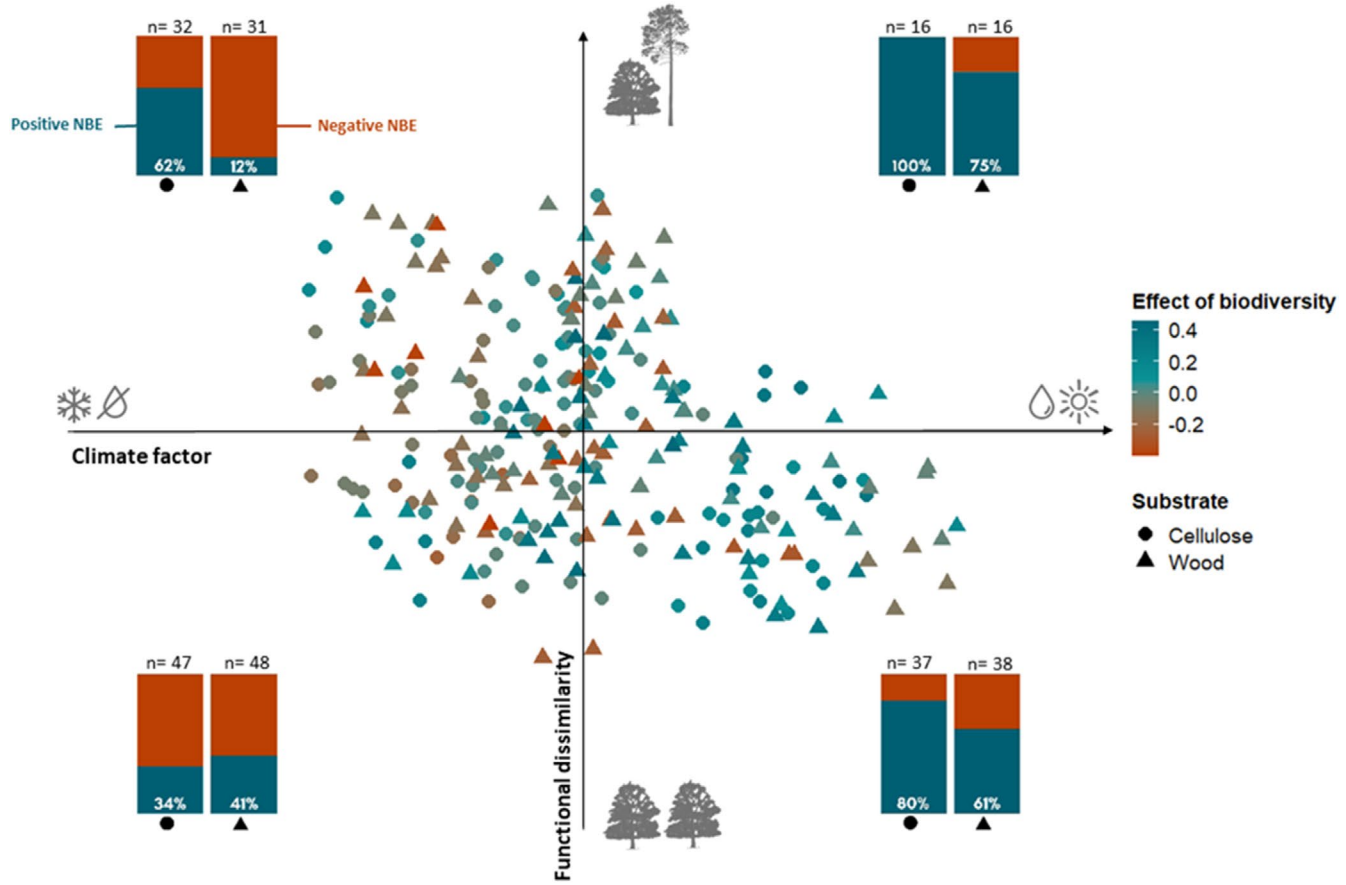

FIGURE 4 Bi-dimensional representation of the combined effects of climate factor and functional dissimilarity (FD) on $NBE_{cellulose}$ (●) and NBE_{wood} (▲) in mixtures. The first axis represents the climate factor, from an unfavourable to a favourable (higher water availability and warmer temperatures) climate for decomposition. The second axis represents increasing FD between tree species in mixtures. Colours represent the strength and sign of the NBE: green for positive and orange for negative effects. Symbols correspond to the substrate: cellulose (●) or wood (▲). In each quadrant, bar plots display the percentage of positive (blue) and negative (orange) NBE values for each substrate. This figure is based exclusively on the subset of data from mixed-species plots.

variation in diversity effects on cellulose decomposition, and random effects explained an additional 8%. For the wood model, none of the tested paths were significant. The fixed effects explained 18% of the overall variation in diversity effects on wood decomposition, while random effects contributed marginally.

4 | DISCUSSION

Using a decomposition experiment with standardized substrates across seven sites in Europe and North America, we evaluated the indirect effect of tree diversity on litter decomposition through its impact on the LDE. We found a positive effect of species richness and functional diversity on the decomposition rates of the high-quality cellulose substrate, but not on the low-quality wood substrate. Contrary to the common view that decomposition is faster under broadleaf and AM-dominated stands, we found that the decomposition of standardized substrates was higher under coniferous and EM-dominated stands. Lastly, we found that the positive effects of functional diversity were more pronounced under more favourable climatic conditions (i.e. moderate temperatures and high water availability), highlighting that the indirect effects of tree diversity on decomposition via the LDE are context-dependent.

4.1 | Effect of tree diversity, composition and structure on decomposition rates

In support of our first hypothesis, we found that the effect of tree diversity on decomposition rates was greater for high substrate quality (i.e. cellulose) than for low substrate quality (i.e. wood), which may reflect both the inherent differences in substrate degradability and the fact that cellulose decomposition represents an earlier stage in the process, where local conditions may play a more immediate role. This result is consistent with previous studies showing that decomposition of high-quality substrates may directly benefit from improved local conditions (Joly et al., 2017), whereas low-quality substrates also require specific soil biota to decompose (Fanin et al., 2020). However, our analysis did not reveal a relationship between

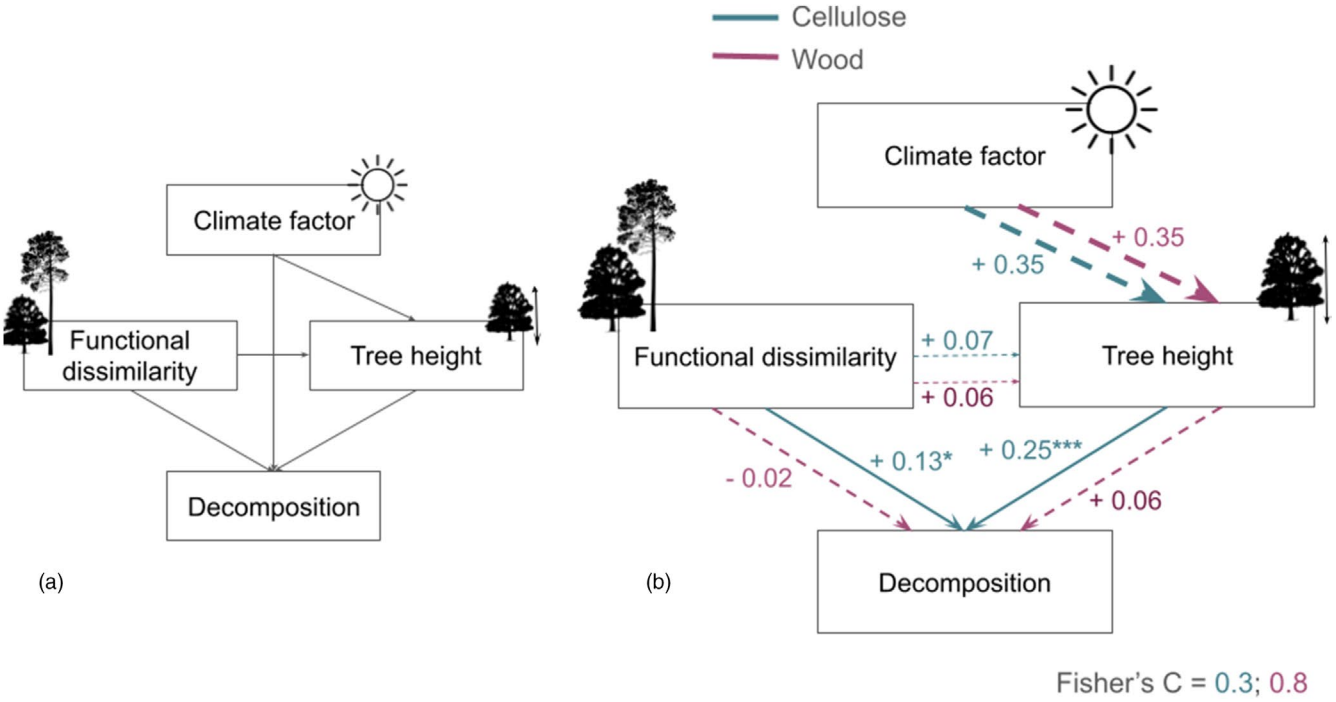

FIGURE 5 Direct and indirect effects of climate factor, functional dissimilarity and tree height on decomposition rate. (a) Theoretical *a priori* model. (b) Structural equation model for cellulose (green) and wood (purple). The thickness of the arrows is proportional to the model coefficient parameter estimate. Standardized estimates for each response variable are indicated next to each arrow. Continuous arrows represent significant ($p < 0.05$) relationships. Dashed arrows represent non-significant ($p > 0.05$) relationships. Significance levels are indicated as $p < 0.1$, $^{*}p < 0.05$ and $^{***}p < 0.001$.

LDE and wood decomposition. This may be due to the relatively short study period (1 year), as only 35% of wood mass was lost, and longer durations (e.g. 2–3 years) may be required for such patterns to emerge.

The effect of tree diversity on decomposition was essentially related to the functional composition of the tree mixture, which can mainly be explained by two non-exclusive and complementary effects. First, species mixtures with complementary traits can accelerate decomposition by providing a wider range of substrates for soil biota (Hättenschwiler et al., 2011; Njoroge et al., 2023), which can in turn favour a greater functional diversity of soil decomposers to decay various litter types (Coulis et al., 2015; Gessner et al., 2010). This may be due to the fact that a greater diversity of litter species can stimulate local microbial decomposition by enhancing both litter quality and quantity (Beugnon et al., 2023), and by creating new microhabitats that support more diverse decomposer communities compared to monocultures (Chapman & Newman, 2010). Alternatively, a greater functional diversity of tree species can create a more heterogeneous and dense forest cover, reducing light penetration and enhancing microclimatic conditions, such as increasing soil moisture (i.e. 'canopy packing hypothesis'; Jucker et al., 2015; Williams et al., 2017). These improved conditions can, in turn, promote decomposer activity and accelerate litter decomposition rates (Manzoni et al., 2012), although this mechanism warrants further empirical investigation to be confirmed. In addition to previously identified mechanisms of nutrient transfers among leaf litter of different tree species (Porre et al., 2020), our results confirm the findings of previous studies showing that functional diversity is the key to understanding and predicting litter decomposition rates (Joly et al., 2017; Scherer-Lorenzen, 2008), reinforcing the idea that tree diversity can promote litter decomposition by enhancing the LDE.

4.2 | LDE is more favourable in mixtures including gymnosperms and EM-associated trees

It is commonly assumed that litter decomposition of gymnosperm and EM-associated trees is slower than that of angiosperm and AM-associated trees (Chomel et al., 2015; Fanin et al., 2020; Pietsch et al., 2014), primarily because gymnosperms and EM-associated trees tend to create less favourable decomposition conditions. This is due to a combination of factors, including the lower litter quality of evergreen gymnosperms, which often exhibit traits such as higher chemical or morphological defences that inhibit decomposition, as well as their higher interception of precipitation, leading to drier soil conditions that further hinder decomposition (Augusto et al., 2015; Brunel et al., 2017; Gartner & Cardon, 2004; Hättenschwiler et al., 2005). Slower decomposition rates may, in turn, increase organic matter accumulation and slow nutrient recycling, which can also impact tree growth and soil fertility (Sariyildiz & Anderson, 2003). Contrary to this view, we found that the decomposition of standardized litter was faster in mixtures that included

coniferous species and EM-associated trees (Figure 3). Although these results may appear confounding, given that the conifers in our study are all associated with EM fungi, our findings suggest that the differences in decomposition rates between EM and AM plant species reported in the literature are primarily driven by differences in litter quality (Phillips et al., 2013). This is particularly true given that gymnosperms are known to produce relatively low quality and more recalcitrant litter compared to angiosperms (Augusto et al., 2015; Bray & Gorham, 1964). Nevertheless, based on our standardized approach, we exclude the possibility that LDE is inherently less favourable under EM-associated canopies. Instead, we propose that the faster decomposition rates in mixtures containing gymnosperms and EM-associated trees could be driven by the presence of microbial communities potentially better adapted to decompose recalcitrant substrates. This idea is supported by previous studies showing changes in microbial community composition and activity in response to different litter types (Bourget et al., 2023; Fanin et al., 2014; Priha et al., 2001), which may in turn favour a broader functional breadth to decay various litter types in poor litter environments (Keiser et al., 2014; Fanin et al., 2016). In line with these results, Desie et al. (2023) found higher decomposition rates of standardized litter under gymnosperms in young European plantations, further emphasizing that tree species can significantly influence decomposition rates through both direct effects on litter quality and indirect effects on microenvironmental conditions. Altogether, our findings indicate that the relatively slower decomposition rates observed in gymnosperms and EM-associated tree communities are primarily driven by litter quality rather than inherent environmental factors, and that the LDE is not necessarily more favourable in mixtures including only angiosperm and AM-associated trees.

Despite these new insights into the LDE, our approach does not permit an assessment of the 'home field advantage' (i.e. HFA; Ayres et al., 2009; Veen et al., 2015). As such, the specialization of microbial communities may reduce the differences in decomposition rates observed in this study, particularly if AM-associated microbial communities are more efficient at decomposing litter from trees associated with AM, thereby mitigating the decomposition lag observed in AM-dominated plots. While HFA is typically considered more pronounced for low-quality litter (Pugnaire et al., 2023), a number of recent studies have shown that it can also occur with high-quality litter (Li et al., 2017; Lin et al., 2019). This could be due to faster microbial community succession due to priority effects (Fukami, 2015), which is likely more pronounced for high-quality litter (i.e. from AM-associated trees) when microclimate or soil properties are favourable (Fanin et al., 2021). Decomposition rates in AM communities may also depend on how well litter quality matches its environment (Freschet et al., 2012), as this 'match' can facilitate the establishment of specialized decomposers and enhance decomposition rates. Although these hypotheses remain to be tested, understanding the relationships between microbial decomposers and their substrates is crucial, as shifts in the LDE may influence the strength of plant–microbe interactions and potentially alter decomposition dynamics across different tree communities.

4.3 | Context-dependency of tree diversity effects

In contrast to our second hypothesis, we found that the effect of tree diversity on decomposition rates was greater under more favourable climatic conditions for both substrates. These results contradict the idea that complementarity effects among trees are stronger when environmental conditions are harsher for decomposition (Ratcliffe et al., 2017). Instead, they suggest that tree diversity may not offset the negative effects of an unfavourable climate by improving the LDE. Although one could expect that the effect of favourable climate would be due to an enhancement of biological and chemical processes affecting decomposition, for instance, by reducing abiotic stress and increasing nutrient availability, we found instead that climate tended to have an indirect effect on the LDE through increased tree height, even though this effect was only marginally significant in our final model. Such an effect can be due to an increase in litter quantity in larger trees shedding more leaves or modifying microclimatic conditions at the soil surface (Beugnon et al., 2023; Hättenschwiler et al., 2005), which in turn can further stimulate soil microbial activity in sites where trees are taller (Madrigal-González et al., 2016; Mina et al., 2018). As such, our results suggest that the potential synergies generated by tree functional diversity are fully realized under optimal growth conditions, whereas the negative effects of excessively high temperatures and/or low water availability cannot be compensated by the positive effects of tree species mixing. Interestingly, our results also reveal a differential impact of tree diversity on wood decomposition depending on climate and tree dissimilarity. While the positive effects of tree diversity on cellulose decomposition were strongest in favourable climates and in plots with greater tree dissimilarity, we observed that in unfavourable climates, greater FD negatively affected the relationship between tree diversity and wood decomposition. This suggests that under harsher conditions, the complementary effects of functionally dissimilar trees may not be as beneficial for decomposing recalcitrant substrates like wood, a substrate for which the specificity of the decomposers involved could be more important.

4.4 | Mechanisms of plant–soil interactions through LDE and future directions

The results of our multi-site diversity experiment contribute to a better understanding of the mechanisms of plant–soil interactions, and highlight the importance of LDE on decomposition rates. In addition to previously identified mechanisms revealing that species richness and composition of tree canopies modify decomposition indirectly through changes in microenvironmental conditions (Joly et al., 2017), our results highlight that functional diversity had comparatively large effects on LDE. We propose that this is due to enhanced complementarity among functionally diverse species, which can create more heterogeneous microhabitats and promote decomposer communities better adapted to a broader range of litter types (Hättenschwiler et al., 2011). This effect was particularly

pronounced under optimal conditions for tree growth, as larger trees provided more resources that support a greater diversity and activity of soil decomposers (Beugnon et al., 2023; Chapman & Newman, 2010). Furthermore, although the quality of plant litter is higher under angiosperms and AM-associated trees (Augusto et al., 2015), we found that LDE was more favourable under gymnosperms and EM-associated trees. This result suggests that studying LDE is crucial for understanding the underlying mechanisms of litter decomposition and disentangling the distinct roles of litter quality and environmental factors (Joly et al., 2023). However, it is important to note that the effect of gymnosperms on litter decomposition may vary depending on the species and climate considered (Augusto et al., 2015). Therefore, while our findings may apply to temperate regions, they are likely not directly applicable to other climatic regions. Finally, it should be emphasized that the differential effect between cellulose and wood may partly be due to the duration of in situ incubation, perhaps too short for wood litter, or by the fact that our experiment was carried out in relatively young planted forests, with a strong disparity in tree height among sites, partly due to differences in stand age. If local diversity effects increase with tree height, we can expect the LDE to be higher for wood in mature forests where the trees are taller, but this hypothesis remains to be tested. Future research should also incorporate additional factors such as soil properties, microbial communities and forest management practices to provide a more comprehensive understanding of the mechanisms driving litter decomposition in non-experimental, diverse forest ecosystems.

5 | CONCLUSION

Our study sheds new light on the indirect effects of tree diversity on litter decomposition through its impact on the LDE. Our findings align with previous studies that highlighted the role of tree diversity in enhancing decomposition rates of easily decomposable substrates by improving local environmental conditions. However, our observation that the positive effects of functional diversity on decomposition are more significant under favourable climatic conditions challenges the hypothesis that local biodiversity effects are stronger under harsher climates and the view that biodiversity could alleviate the negative impacts of climate change. Our results further underscore the importance of considering both litter quality and environmental factors in decomposition studies. We conclude that managing tree species diversity, particularly functional diversity, can be a valuable strategy to enhance decomposition processes in forests, especially in contexts where improving nutrient cycling or supporting soil microbial activity is a priority.

AUTHOR CONTRIBUTIONS

Nicolas Fanin and Bastien Castagneyrol conceived and designed the research. Nicolas Fanin led the project with the help of Laurent Augusto, Mark R. Bakker and all co-authors. Audrey Bourdin led the data analysis and code curation in collaboration with Nicolas Fanin. Audrey Bourdin wrote the first draft of the manuscript, with significant revisions and improvements by Nicolas Fanin. Laurent Augusto and François-Xavier Joly made substantial contributions to improving the initial version of the manuscript. All authors contributed to the finalization and revision of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70189.

DATA AVAILABILITY STATEMENT

The dataset is publicly available at the following DOI: https://doi.org/10.57745/OQHO2D (Bourdin et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Geographic coordinates of sites and plots composition.

Table S2. Results of statistical models for NBE and *k*.

Figure S1. Principal component analysis of the traits used for functional dissimilarity calculation.

Figure S2. Relationship between soil pH and climate factor.

Figure S3. Mean decomposition rate (*k*, $year^{-1} \pm SE$) by site for both substrates.

Figure S4. Decomposition rate (*k*) of cellulose and wood in relation to tree richness level by site.

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