Tree species diversity affects decomposition through modified micro-environmental conditions across European forests

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Summary

- Different tree species influence litter decomposition directly through species-specific litter traits, and indirectly through distinct modifications of the local decomposition environment. Whether these indirect effects on decomposition are influenced by tree species diversity is presently not clear.
- We addressed this question by studying the decomposition of two common substrates, cellulose paper and wood sticks, in a total of 209 forest stands of varying tree species diversity across six major forest types at the scale of Europe.
- Tree species richness showed a weak but positive correlation with the decomposition of cellulose but not with that of wood. Surprisingly, macroclimate had only a minor effect on cellulose decomposition and no effect on wood decomposition despite the wide range in climatic conditions among sites from Mediterranean to boreal forests. Instead, forest canopy density and stand-specific litter traits affected the decomposition of both substrates, with a particularly clear negative effect of the proportion of evergreen tree litter.
- Our study suggests that species richness and composition of tree canopies modify decomposition indirectly through changes in microenvironmental conditions. These canopy-induced differences in the local decomposition environment control decomposition to a greater extent than continental-scale differences in macroclimatic conditions.

Introduction

Changing biodiversity can lead to altered ecosystem-level processes, such as the decomposition of dead organic matter and its consequences for carbon (C) dynamics and nutrient recycling (e.g. Gessner *et al.*, 2010; Cardinale *et al.*, 2011). The majority of studies investigating how decomposition processes depend on biodiversity compared plant leaf litter mixtures to the respective single species litter. These studies frequently reported nonadditive effects, that is, different observed decomposition rates from those expected based on the monospecific leaf litter (Gartner & Cardon, 2004; Hättenschwiler *et al.*, 2005; Lecerf *et al.*, 2011). A common observation of leaf litter mixture experiments in terrestrial as well as in aquatic ecosystems is that, if nonadditive effects occur, they are related to species composition rather than the number of plant species represented in leaf litter mixtures (e.g. Ball *et al.*, 2008; Lecerf *et al.*, 2011; Barantal *et al.*, 2014; Handa *et al.*, 2014). These effects arise from the variation of species-specific physical and chemical litter traits represented in litter mixtures, as predicted theoretically by Epps *et al.* (2007), and reported empirically for example by Barantal *et al.* (2014) and Handa *et al.* (2014). By contrast, Grime's biomass ratio hypothesis (Grime, 1998) predicts that any litter composition effect is driven by community-weighted mean (CWM) traits (Garnier *et al.*, 2004), that is, the average trait values calculated from the species-specific values and the relative abundance of the species present in the mixture, which *a priori* excludes nonadditive effects.

Apart from these direct litter mixture-driven diversity effects on decomposition, the diversity of living plants can also modify the decomposition process indirectly via changes in understory environmental conditions and soil biota community composition (Wardle, 2006; Scherer-Lorenzen, 2008). These indirect effects of plant composition and diversity have been studied considerably less extensively and are poorly understood compared with the direct leaf litter quality-related effects of plant diversity. In a

tropical rainforest, for example, Barantal *et al.* (2011) found that litter mixture effects were more pronounced when litter mixtures decomposed in a forest stand where tree species composition matched that of the litter mixtures. This result emphasizes that the composition and diversity of living plant species have not only direct effects on C and nutrient cycling through the provision of distinct litter with specific physical and chemical characteristics but also indirect effects through modification of the decomposition environment. Yet, the indirect effects of living plant species composition and diversity on decomposition have not been studied in detail. In planted grassland plots of varying species diversity, Hector *et al.* (2000) reported an increased decomposition rate for standard grass litter with increasing species richness, but no effect of plant species composition. By contrast, Scherer-Lorenzen (2008) found no effect of plant species richness, but positive effects of functional diversity (i.e. the range of species-specific trait values observed in the community) on decomposition rates, using standard materials (cotton strips and wood sticks) within a grassland biodiversity experiment. Although relatively small in magnitude, these diversity effects on decomposition rates of standard materials demonstrated that decomposition is partially controlled by changes in the microenvironment which is influenced by the presence of living plants and their diversity. These indirect effects of species diversity may be more important in forest ecosystems, where the scope for such modifications of the decomposition environment is particularly great as a result of the longevity of trees and the highly complex canopy architecture, in comparison to grasslands. In particular, the relative abundance of tree species of distinct functional types, such as evergreen versus deciduous tree species, may have an important effect on the decomposition environment (Augusto *et al.*, 2015).

The presence and relative abundance of particular species and/or functional types of plants can influence the decomposition environment in various ways. Species-specific canopy characteristics can modify the microclimatic conditions via shading, interception of precipitation and wind break, all of which can affect the ground temperature, evapotranspiration and moisture conditions (Prescott, 2002; Eviner & Chapin, 2003; Milcu *et al.*, 2016). Microclimatic conditions on the forest floor may also be affected by the canopy structure and its effects on the penetration of sunlight (Hobbie *et al.*, 2006), and by the physical structure of the litter layer. Litter layer structure can modify decomposer activity, for example through changes in litter water-holding capacity (WHC) (Wardle *et al.*, 2003; Makkonen *et al.*, 2013). In addition to these immediate microclimatic effects, the long-term input of leaf litter may lead to local adaptation of the decomposer community and in turn to a higher efficiency of litter degradation, as suggested in the home-field advantage hypothesis (Gholz *et al.*, 2000; Ayres *et al.*, 2009; Milcu & Manning, 2011; Veen *et al.*, 2014). While decomposers probably respond to average concentrations of specific litter compounds in the litterfall, which is quantified by CWM traits, the decomposer community may also respond to the differences in the concentrations of these compounds among species, which is quantified by trait dissimilarity. For example, it was found that changing plant litter

diversity can modify the composition of microbial communities (Chapman & Newman, 2010; Ball *et al.*, 2014) and alter the composition and abundance of soil fauna communities (Chapman *et al.*, 1988; Blair *et al.*, 1990; Hansen & Coleman, 1998; Wardle, 2006).

Here, we specifically addressed the question of how tree species richness and composition affect decomposition through modifications of the decomposition environment in six different forest ecosystems composed of distinct tree species across a broad geographical range at the scale of Europe (Baeten *et al.*, 2013). In order to separate the effects of the decomposition environment from direct litter quality effects including any home-field advantage effects, we used two standard substrates: cellulose paper, as a readily degradable standard material accessible to a wide range of decomposers, and wood sticks, as a recalcitrant material accessible to a narrower range of decomposers. We hypothesized that the decomposition of the standard substrates (cellulose and wood) would depend, generally, on (H1) the tree species diversity and abundance of evergreen trees, and, more specifically, on (H2) factors controlling the microenvironmental conditions (site-specific macroclimatic conditions, plot-specific canopy closure and soil characteristics) as well as on (H3) the composition and diversity of the litterfall controlling the decomposer community composition.

Materials and Methods

Study sites

The experiment was conducted within the FunDivEUROPE exploratory platform consisting of permanent forest plots in six different European countries, specifically established in order to evaluate the effects of tree diversity on ecosystem functioning in mature European forests (Baeten *et al.*, 2013). This network of forest plots was established in 2011 and includes 209 plots (each 30×30 m) of mature forest distributed among six sites across Europe. The six field sites represent major European forest types and include boreal forests in Finland, hemi-boreal forests in Poland, beech forests in Germany, mountainous beech forests in Romania, thermophilous deciduous forests in Italy and Mediterranean mixed forests in Spain. Within each site, between 28 and 43 plots were selected (Finland: 28; Poland: 43; Germany: 38; Romania: 28; Italy: 36; Spain: 36), containing different combinations of locally dominant tree species, with species richness ranging from one to three in Finland, from one to four in Romania, Germany and Spain, and from one to five in Italy and Poland. There were a total of 18 different species and subspecies across all sites, including evergreen conifers as well as both deciduous and evergreen broadleaves (see Baeten *et al.*, 2013 and Table 1 for species identity). Within a site, each target species was represented at all species richness levels. To allow meaningful comparisons among species composition treatments and species richness levels, plots within each site were selected to have environmental conditions (altitude, topography and soil characteristics) and developmental stage (mid to late stem exclusion stage) as similar as possible. Management practices and/or pure random species

Table 1 (a) Characteristics of each of the six sites from the exploratory platform, and (b) start, end and total duration of the incubation period, average mass loss (%) and mass loss rates (mg g^{-1} d^{-1}) of cellulose paper and wood sticks

	Finland	Poland	Germany	Romania	Italy	Spain
(a) Site characteristics						
Latitude, longitude (°)	62.6, 29.9	52.8, 23.9	51.1, 10.5	47.3, 26.0	43.2, 11.2	40.7, −1.9
Mean annual temperature (°C)	2.1	6.9	6.8	6.8	13	10.2
Mean annual precipitation (mm)	700	627	775	800	850	499
Average daily temperature (°C)	6.06	3.52	2.4	11.05	15.88	10.12
Average daily precipitation (mm)	1.97	1.56	1.36	1.62	3.00	2.32
Target species	Betula pendula Picea abies Pinus sylvestris	Betula pendula Carpinus betulus Picea abies Pinus sylvestris Quercus robur	Acer pseudoplatanus Fagus sylvatica Fraxinus excelsior Picea abies Quercus sp.	Abies alba Acer pseudoplatanus Fagus sylvatica Picea abies	Castanea sativa Ostrya carpinifolia Quercus cerris Quercus ilex Quercus petraea	Quercus faginea Quercus ilex Pinus nigra Pinus sylvestris
Tree species richness levels	1, 2, 3	1, 2, 3, 4, 5	1, 2, 3, 4	1, 2, 3, 4	1, 2, 3, 4, 5	1, 2, 3, 4
Average leaf area index (m^2 m^{-2})	2.78 ± 0.15	5.60 ± 0.19	6.42 ± 0.21	5.73 ± 0.12	3.92 ± 0.16	1.71 ± 0.12
Average litterfall (g m^{-2} yr^{-1})	175.5 ± 8.6	280.2 ± 8.7	159.7 ± 12.9	211.5 ± 14.5	290.4 ± 14.6	125.8 ± 9.2
Soil type	Podzol	Cambisol/Luvisol	Luvisol/Cambisol	Eutric cambisol	Cambisol	Calcic cambisol
Soil C : N ratio	24.2 ± 0.7	17.0 ± 0.3	13.1 ± 0.2	14.0 ± 0.2	19.1 ± 0.6	20.1 ± 1.1
Soil pH	3.76 ± 0.05	3.84 ± 0.05	5.45 ± 0.16	4.62 ± 0.12	4.79 ± 0.18	6.93 ± 0.09
(b) Response variable						
Incubation start	June 2012	September 2012	October 2012	July 2012	June 2012	September 2012
Incubation end	October 2013	June 2013	April 2013	September 2013	July 2013	April 2014
Incubation length (d)	471	269	190	424	407	605
Cellulose mass loss (%)	39.3 ± 4.2	38.3 ± 3.2	33.2 ± 3.1	39 ± 3.5	45.2 ± 3.3	30.4 ± 3.6
Wood mass loss (%)	28.4 ± 2.3	9.4 ± 0.7	7.2 ± 0.6	14.5 ± 1.1	20 ± 1.7	14 ± 1.3
Cellulose mass loss rate (mg g^{-1} d^{-1})	0.84 ± 0.09	1.48 ± 0.12	1.75 ± 0.16	0.93 ± 0.08	1.11 ± 0.08	0.50 ± 0.06
Wood mass loss rate (mg g^{-1} d^{-1})	0.60 ± 0.05	0.36 ± 0.03	0.38 ± 0.03	0.34 ± 0.03	0.49 ± 0.04	0.23 ± 0.02

Average daily temperature and precipitation are computed over the exact site-specific incubation period. Average leaf area index, total litterfall, soil carbon : nitrogen (C : N) ratio, and pH indicate the average of all plots per site (± SE).

assembly were thus the key drivers of the diversity gradients. Within each site, covariation between environmental factors (e.g. soil parameters and topography) and species richness levels was strictly avoided. In addition, the plots were chosen based on similar relative abundances among species in mixtures. A detailed description of site selection and experimental set-up is available in Baeten *et al.* (2013).

Experimental design

Two common substrates, cellulose paper and wood sticks, were chosen to test the indirect effects of tree species diversity on rates of decomposition across all species diversity gradients at all six sites. These two standard materials were chosen rather than leaf litter material to avoid any direct effects of litter quality on decomposition, as any leaf litter chosen could potentially have trait similarities to the leaf litter of site-specific tree species. Cellulose paper represents a comparatively readily degradable material accessible to a wide variety of decomposer organisms. It consisted of individual cellulose sheets (nonrecycled, total chlorine-free printing paper) with a size of 297×420 mm (A3). The paper consisted of 16% water-soluble compounds, 4% hemicelluloses and 80% cellulose (determined by the Van Soest & Wine (1967) protocol of fiber analysis). One sheet of an average air-dry weight of 10 g was folded to one-sixth of its initial size, and then placed in an individual litterbag. Litterbags had a size of 15×15 cm, and were constructed from polyethylene fabrics of two different mesh sizes. For the bottom side of the litterbags we used a small mesh width of 0.5×0.5 mm to minimize losses of fragments, while for the upper side we used a large mesh width of 5×8 mm to allow free access to the soil fauna, including macrofauna. Wood sticks represent a more recalcitrant material containing lignin that is intimately associated with cellulose and hemicelluloses (Petterson, 1984), rendering the latter accessible to a relatively small subset of decomposer organisms capable of enzymatically breaking down ligno-cellulose complexes. They were wooden tongue depressors ($152 \times 17 \times 2$ mm) made of *Betula pendula* wood and consisted of 9.5% water-soluble compounds, 26% hemicelluloses, 52.5% cellulose, and 12% lignin (determined by the Van Soest & Wine (1967) protocol of fiber analysis). These sticks, with an average air-dry weight of 2.5 g, were placed directly on the soil without litterbags. Initial mass was determined with air-dry material, with subsamples additionally dried at 65°C for 48 h and reweighed to obtain a 65°C dry mass correction factor. Within each individual plot, we randomly placed three litterbags each containing one cellulose sheet, and three wood sticks in direct contact with the soil surface after removing the naturally occurring litter within a 1-m^2 area. Litterbags and wood sticks were then fixed to the ground with chicken wire covering the entire 1-m^2 surface. This method is also an effective protection against the disturbing activity of animals such as wild boar (*Sus scrofa*). The material was retrieved after a period of field exposure varying from 190 d (at the German site) to 605 d (at the Spanish site; Table 1), when cellulose paper decomposition reached 30–45%

of initial mass loss, and wood stick decomposition reached 7–28% of initial mass loss. These different incubation lengths ensured that standard materials were sampled at relatively similar decomposition stages across all sites, enabling meaningful comparisons. Site-specific harvest times were determined by following decomposition dynamics in additional litterbags that were regularly harvested. After retrieval from the field, the remaining cellulose sheets and wood sticks were dried at 65°C and weighed. Cellulose was ground to obtain a uniform particle size of 1 mm (Cyclotec Sample Mill; Tecator, Höganäs, Sweden). To correct for potential soil contamination during decomposition in the field, we determined the ash content on subsamples of undecomposed cellulose, and on the remaining cellulose material at final harvest of each individual sample. We then calculated cellulose mass loss using ash-free 65°C dry masses. Wood sticks were cleaned manually because adhering soil particles could be brushed off easily and their mass losses calculated on the basis of 65°C dry masses. For both standard materials, mass loss rates were expressed as the ratio of mass lost per amount of initial mass per day of incubation ($mg\,g^{-1}\,d^{-1}$), calculated as follows: mass loss rates = (1000 × (initial mass − final mass)/initial mass)/days of incubation. To account for the nonindependence of within-plot replicates, and to avoid pseudo-replication, their values were averaged and mean values used for the analyses, leading to a total of 418 values (two substrates × (28 + 28 + 36 + 36 + 38 + 43 = 209 plots)).

Site and stand characteristics

To characterize the climatic conditions for each site during the respective exact incubation periods of standard materials, we collected daily meteorological data (daily mean temperature, precipitation and potential evapotranspiration) from the CGMS database of interpolated data (AGRI4CAST; http://mars.jrc.ec.europa.eu/mars). We then computed the average of these data per day of the site-specific duration of incubation. Also, using the mean monthly precipitation, and minimum and maximum monthly temperatures, we computed the Climate Decomposition Index (CDI) over the incubation period, using the Lloyd & Taylor (1994) temperature function, following the equations presented in Adair *et al.* (2008). As an index of water availability per degree of temperature, which may be particularly informative for the decomposition process, we computed an additional climatic index by dividing the cumulated precipitation over the entire incubation period by the summed daily mean temperature.

Canopy density was estimated using the plot-specific leaf area index (LAI; $m^2\,m^{-2}$) (see Pollastrini *et al.*, 2016). As indicators of soil properties, we used the carbon : nitrogen (C : N) ratio and pH of the upper mineral soil layer (below the forest floor layer), at 0–10 cm. Nine soil cores were collected per plot and chemical analyses were performed on a composite sample of these cores. Soil samples were dried at 55°C until constant weight and sieved through a 2-mm sieve to separate coarse material and roots from the fine soil. These subsamples of fine soil were ground with a Planetary Ball Mill PM 400 (Retsch, Haan, Germany) into finer

particles. Soil pH was measured in a 0.01 M CaCl₂ suspension at a ratio of 1 : 2.5 using 827 pH lab (Metrohm AG, Herisau, Switzerland). Subsamples of fine soil were ground with a Planetary Ball Mill PM 400 into finer particles and C and N were analyzed with a FLASH 2000 Soil CN Analyzer (Thermo Fisher Scientific, Milan, Italy). All soil analyses were performed in the laboratory of the Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark.

Species-specific annual leaf litterfall was estimated by installing five litter traps in a regular grid within each individual plot. Litter traps were constructed with nylon mesh suspended from hoops *c.* 1 m above the ground, each covering a collection surface of 0.5 m². They were regularly emptied over one entire year. Collected litter was pooled by plot and sorted by species and type (i.e. leaves, reproductive parts and twigs) of litter. Leaf litter was then weighed for each species at each collection date. For each plot, subsamples of each species were weighed, dried at 65°C and reweighed, to apply a correction factor to total air-dry mass to obtain '65°C dry masses'.

For the measurement of leaf litter chemical and physical characteristics, we collected freshly fallen leaf litter of each species at peak leaf litterfall between October 2011 and November 2012 (depending on species-specific leaf fall phenology) at the site level at several locations around the experimental plots. The litter was air-dried and kept dry until the analyses. We measured the following leaf litter quality traits for all tree species of each site: elemental composition (C, N, phosphorus (P), calcium (Ca), magnesium (Mg) and potassium (K)), carbon fractions (lignin, cellulose, hemicellulose and water-soluble compounds), the concentrations of secondary metabolites (condensed tannins, total phenolics and soluble phenolics), pH, specific leaf area (SLA) and WHC. Chemical and physical litter traits were measured as described in Joly *et al.* (2015) in the laboratory of CEFE, Montpellier, France. Using species-specific litter quality traits and the plot-specific annual litterfall of each species present in that particular plot, we computed the community-weighted mean of annual litterfall for each litter trait following Garnier *et al.* (2004), and the functional dissimilarity using Rao's quadratic entropy (Botta-Dukát, 2005). The CWM traits of plots (*p*) were calculated as follows:

$$\text{Trait}_p = \sum_{i=1}^{n} p_i \times \text{trait}_i$$

where p_i is the relative contribution (mass) of species i to the total litterfall. The trait dissimilarity (Rao's quadratic entropy), that is, the dissimilarity in litter trait values among species present in the litterfall, was calculated trait by trait, as follows:

$$\text{Rao}_{ij} = \sum_{i=j}^{n} \sum_{j=1}^{n} \rho_i \rho_j d_{ij},$$

where ρ_i and ρ_j are the relative contributions (masses) of species i and j, respectively, and d_{ij} is the trait dissimilarity coefficient based on the Euclidean distance between two species i and j in the functional trait space.

Data analysis

We used linear mixed-effects models to test separately the effects of (H1) tree species diversity and functional composition, (H2) microenvironmental conditions, and (H3) functional composition and diversity of the litterfall on cellulose paper and wood stick mass loss rates. Retained variables from H2 and H3 were then included in a combined model. As variables from H1 were not independent from those used in the models to test H2 and H3, they were not included in the global model.

H1: tree species diversity and abundance of evergreen trees

To test the general effect of tree species diversity and evergreen tree abundance, we modeled mass loss rates as a function of tree species richness and percentage of evergreen basal area. Evergreen was selected as the functional type as it is represented in different abundance at all sites (conifers absent from the Italian site), and because evergreen broadleaves and conifers share similar characteristics of interest for our study, including leaf fall phenology and litter characteristics. Indeed, the longer leaf life span of all evergreen compared with deciduous trees led to lower SLA and associated lower decomposability (Cornelissen, 1996).

H2: microenvironmental conditions

To test whether microenvironmental conditions affected decomposition, we modeled mass loss rates as a function of soil characteristics (pH and C : N ratio of the 0–10 cm soil layer) and microclimatic conditions. We considered that both plot canopy density, estimated with plot-specific LAI, and site-specific macroclimatic indices would determine microclimatic conditions. For site-specific macroclimatic indices, we used both average daily temperature and precipitation, or CDI, or the ratio of precipitation per degree of temperature. Because these climatic indices are not independent, we separately included them in the model with LAI and soil characteristics, and reported the model explaining the largest amount of variance.

H3: litterfall composition and diversity

Litterfall quantity and abundance of evergreen litter To further test whether potential effects of the percentage of evergreen basal area (H1) on mass loss rates were related to the proportion of evergreen leaf litter in the total litterfall, and whether potential effects of LAI (H2) were driven by the amount of litterfall rather than canopy closure, we modeled mass loss rates as a function of the percentage of evergreen litter in the litterfall and total amount of litterfall.

Litterfall functional quality and dissimilarity The role of litterfall characteristics in decomposition was assessed by separately testing the effect of the plot-specific mean litter traits (CWM), and the plot-specific litter trait dissimilarity (Rao), using multivariate linear mixed models. Given the high number of litter traits measured, we preselected five traits for the calculation of CWM and trait dissimilarity (Rao) using the 'RandomForest' function of the package RANDOMFOREST, which classifies

predictor variables by importance (Cutler *et al.*, 2007). In the case of high collinearity between two selected traits ($r > 0.6$), we replaced the lower ranked of the two traits by the next ranked one. We compared the model outputs based on these preselected traits, with those based on five traits selected based on *a priori* expected importance as drivers of decomposition (namely the concentrations of cellulose, condensed tannins, lignin : N, and P, and WHC). The models with the traits selected based on expected importance explained systematically less variance than those based on 'RandomForest' preselection, and are thus not reported here. The combined effects of CWM and functional trait dissimilarity were tested by modeling decomposition rates as a function of both the CWM and Rao values previously kept in the best models with only CWM and Rao, respectively.

H2 and H3: microenvironmental conditions and litterfall

To assess the total amount of variance explained by factors related to microclimatic conditions, soil quality or litterfall characteristics, we modeled mass loss rates as a function of variables retained in the previous models after model selection. As variables from H3(a) and H3(b) are not independent, we first combined variables retained from H2 and H3(a), and then those from H2 and H3(b).

We used the R software, v.3.1.2 (R Core Team, 2014) for all statistical analyses, and the LME4 package to fit mixed-effect models. To account for the nonindependence of plots within each site and for differences in tree species composition among the different regions of the exploratory platform, site and tree species composition within sites were included as random factors in all models, using the following R syntax: (mass loss rates ~ predictor$_a$ + (...) + predictor$_n$ + (1|site/composition)). Model selection was performed using the 'dredge' function of the MuMIn package, which ranks all candidate models (all possible combinations of explanatory variables included in the full model) based on lowest Akaike information criteria (AICcs). We then computed the r^2 of the most parsimonious model using the 'R.SQUAREDGLMM' function of the MuMIn package, as proposed by Johnson (2014), and reported the marginal r^2 that represents the variance explained by fixed factors. Additionally, for each explanatory variable included in the full model, we reported its relative importance as the summed AIC weights (sum of AIC weights over all models including the explanatory variable), as proposed in Burnham & Anderson (2002). Because including interactions between explanatory variables and site systematically led to higher AICcs, we did not report the site-specific relations. Mass loss rates were logit-transformed (Warton & Hui, 2011) before analyses to ensure normal distribution and homoscedasticity of residuals.

Results

Effects of tree stand diversity and functional composition on decomposition

Across sites, cellulose mass loss rates were lowest in the Mediterranean mixed forests in Spain (0.50 ± 0.06 mg g^{-1} d^{-1}) and

peaked in temperate forests in Germany (1.75 ± 0.16 mg g^{-1} d^{-1}; Table 1). Wood mass loss rates were also lowest in Spain (0.23 ± 0.02 mg g^{-1} d^{-1}), but they peaked in the boreal forests in Finland (0.60 ± 0.05 mg g^{-1} d^{-1}; Table 1). Cellulose mass loss rates increased with tree species richness; however, this trend was only marginally significant and accounted for only a small amount of variance ($R^2 = 0.02$; $P = 0.053$; Fig. 1a). Wood mass loss rates showed no differences among tree species richness levels (Fig. 1d). Compared with tree species richness, the relative basal area of evergreen trees in the forest stands was more closely related to decomposition and negatively correlated with both cellulose ($R^2 = 0.11$; $P < 0.001$; Fig. 1c) and wood mass loss rates ($R^2 = 0.05$; $P < 0.001$; Fig. 1d). When combined in one model, species richness and relative basal area of evergreen trees were both retained in the most parsimonious model for cellulose mass loss rates (but not for wood mass loss rate), explaining 13% of the variance (Table 2).

Effects of microenvironmental conditions

Plot-specific soil characteristics including pH and C : N ratio of the 0–10 cm soil layer were not related to cellulose mass loss rates across all sites (Table 2), but cellulose mass loss rates positively correlated with plot-specific LAI and site-specific macroclimatic conditions when the latter were expressed as the ratio of precipitation per degree of temperature ($R^2 = 0.22$; Table 2). In equivalent models including other indices or specific climatic variables (i.e. CDI, or mean daily temperature and precipitation), LAI was retained as the only variable in the most parsimonious model, accounting for 13% of the variance (Fig. 2a). In contrast to cellulose, wood mass loss rates were negatively related to the plot-specific soil C : N ratio, explaining 4% of the variance (Table 2), while none of the site-specific macroclimatic variables or plot-specific LAI was retained in the most parsimonious model for wood mass loss rates (Table 2; Fig. 2b), indicating that wood stick decomposition was not significantly affected by microclimatic conditions.

The impact of leaf litterfall

Total plot-specific annual litterfall was not related to cellulose and wood mass loss rates (Table 2). By contrast, the relative amount of evergreen leaf litter in the annual litterfall was negatively related to both cellulose and wood mass loss rates (Fig. 3). In addition, the litterfall quality was significantly related to mass loss rates of both cellulose and wood sticks. Among the five traits preselected based on their calculated importance, the CWM of specific leaf area and Mg concentration were retained in the most parsimonious model, collectively accounting for 19% of the variance in cellulose mass loss rates (Table 3). The CWMs of these two traits were both positively related to cellulose mass loss rates. Wood decomposition was driven by a different set of traits, with CWMs of the concentrations of condensed tannins and cellulose negatively correlated, and CWM of lignin concentration positively correlated with wood mass loss rates, altogether explaining 20% of the total variance. Compared with CWMs, the functional dissimilarity of litter traits as measured by Rao's quadratic entropy (Rao) was less closely related to mass loss rates (Table 3).
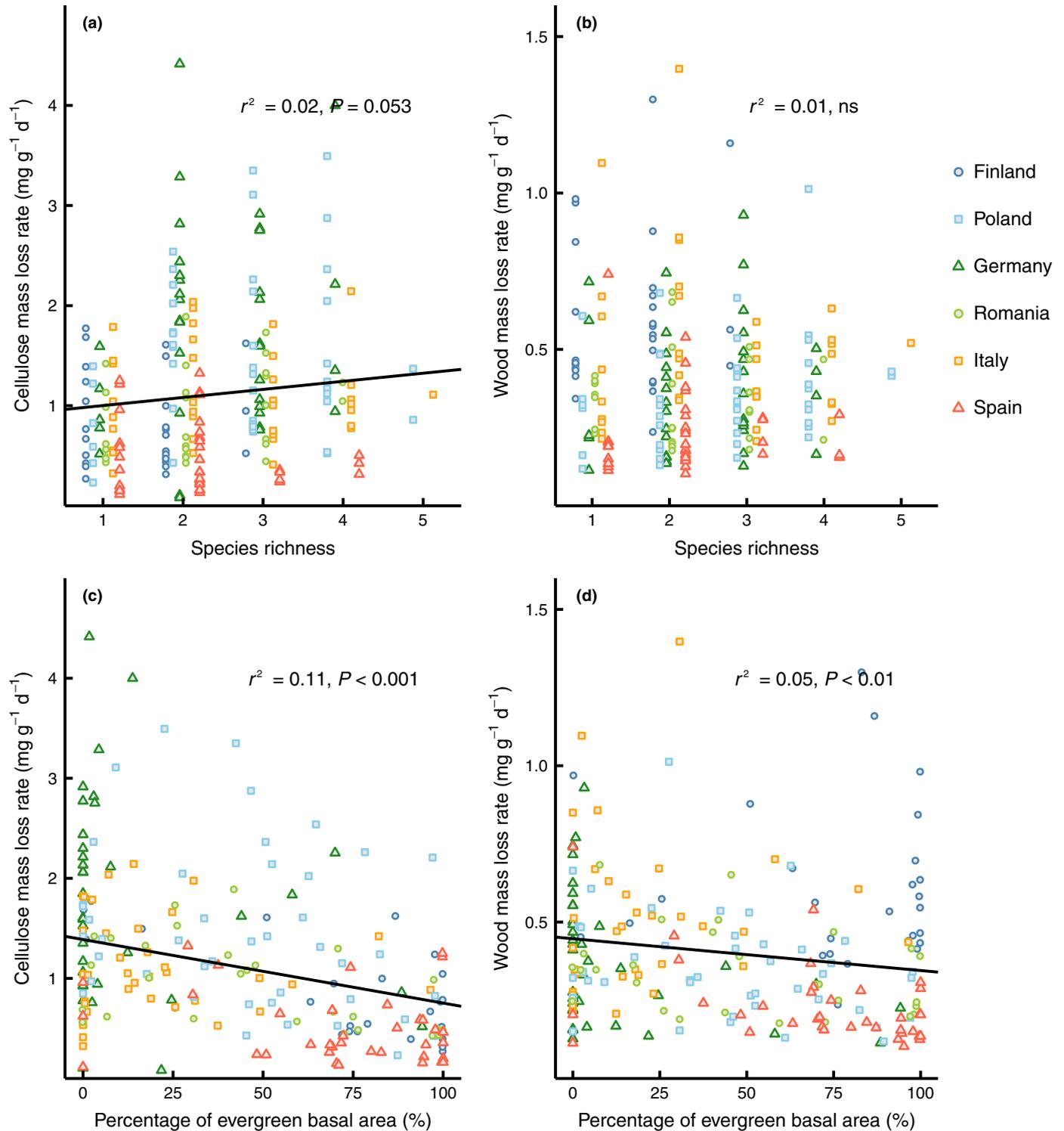
Fig. 1 Mass loss rate of (a) cellulose paper and (b) wood sticks as a function of the tree species richness, and of (c) cellulose paper and (d) wood sticks as a function of the percentage of evergreen basal area. The black lines indicate the regression lines across all sites, if slope is significantly different from zero, with site as a random factor. Points on the species richness axis are offset for clarity. ns, nonsignificant.

Dissimilarity in the concentration of water-soluble compounds and in lignin : N ratio accounted for 9% of the variance in cellulose mass loss rates. By contrast, wood mass loss rates were much less closely related to the functional dissimilarity of litterfall, with only a small negative relationship with the dissimilarity in the concentration of total phenolics. Combined models that included CWM and dissimilarity of litter traits explained a total variance of 27% of cellulose mass loss rates. However, litter trait dissimilarity was not retained in the combined model for wood mass loss rates.

Table 2 Output of multiple linear mixed models testing the effects of (H1) stand diversity, (H2) microenvironmental conditions, (H3a) litterfall characteristics, and the combined effects of (H2) and (H3a) retained variables on cellulose and wood mass loss rates

	Cellulose mass loss rate				Wood mass loss rate			
	Slope (± SE)	$\sum w_i$	R^2	AICw	Slope (± SE)	$\sum w_i$	R^2	AICw
H1:stand diversity								
Species richness	**0.08 (±0.04)**	0.67	0.13	0.667	0.04 (±0.03)	0.43		
Proportion of evergreen basal area (%)	**−0.61 (±0.14)**	1			**−0.32 (±0.11)**	0.97	0.05	0.55
H2: microenvironmental conditions								
Precipitation per degree of temperature (mm °C^{-1})	**0.95 (±0.61)**	0.52	0.22	0.23	−0.33 (±0.92)	0.26		
Leaf area index (m^2 m^{-2})	**0.12 (±0.04)**	0.96			0.03 (±0.03)	0.37		
Soil C : N (0–10 cm)	−0.01 (±0.01)	0.41			**−0.02 (±0.01)**	0.92	0.04	0.24
Soil pH (0–10 cm)	−0.01 (±0.06)	0.26			−0.05 (±0.04)	0.44		
H3(a): litterfall control								
Proportion of evergreen litterfall (%)	**−0.78 (±0.14)**	1.00	0.16	0.61	**−0.28 (±0.11)**	0.96	0.05	0.65
Total litterfall (g m^{-2})	−0.00 (±0.00)	0.39			0.00 (±0.00)	0.34		
H2 and H3(a): microenvironment and litterfall								
Precipitation per degree day (mm °C^{-1})	**0.74 (±0.43)**	0.54	0.39	0.540				
Leaf area index (m^2 m^{-2})	**0.11 (±0.03)**	0.99						
Proportion of evergreen litterfall (%)	**−0.73 (±0.12)**	1.00			**−0.26 (±0.10)**	0.93	0.08	0.60
Soil C : N (0–10 cm)					**−0.02 (±0.01)**	0.67		

For each group of explanatory variables, we report the slope (± SE) of each variable and its relative importance (sum of Akaike information criterion (AIC) weights ($\sum w_i$) over all models including the explanatory variable bound between 0 (not important) and 1 (relevant)). We also report the r^2 of the most parsimonious model and its AIC weight (AICw). The variables retained in the most parsimonious models are in bold and indicated with the black vertical line. C, carbon; N, nitrogen.

Combined effects of microenvironmental conditions and litterfall characteristics

The combination of variables controlling microclimatic conditions (i.e. canopy density (LAI) and macroclimatic variables (ratio of precipitation per degree of temperature)) and litterfall functional type (percentage of evergreen litter in annual litterfall) in one global model explained a total of 39% of variance in cellulose mass loss rates (Table 2). When the variable 'litterfall functional type' was replaced in this global model with litterfall quality, both expressed as CWM and functional dissimilarity (Rao), a total of 41% of variance in cellulose mass loss rates was explained (Table 3). In this
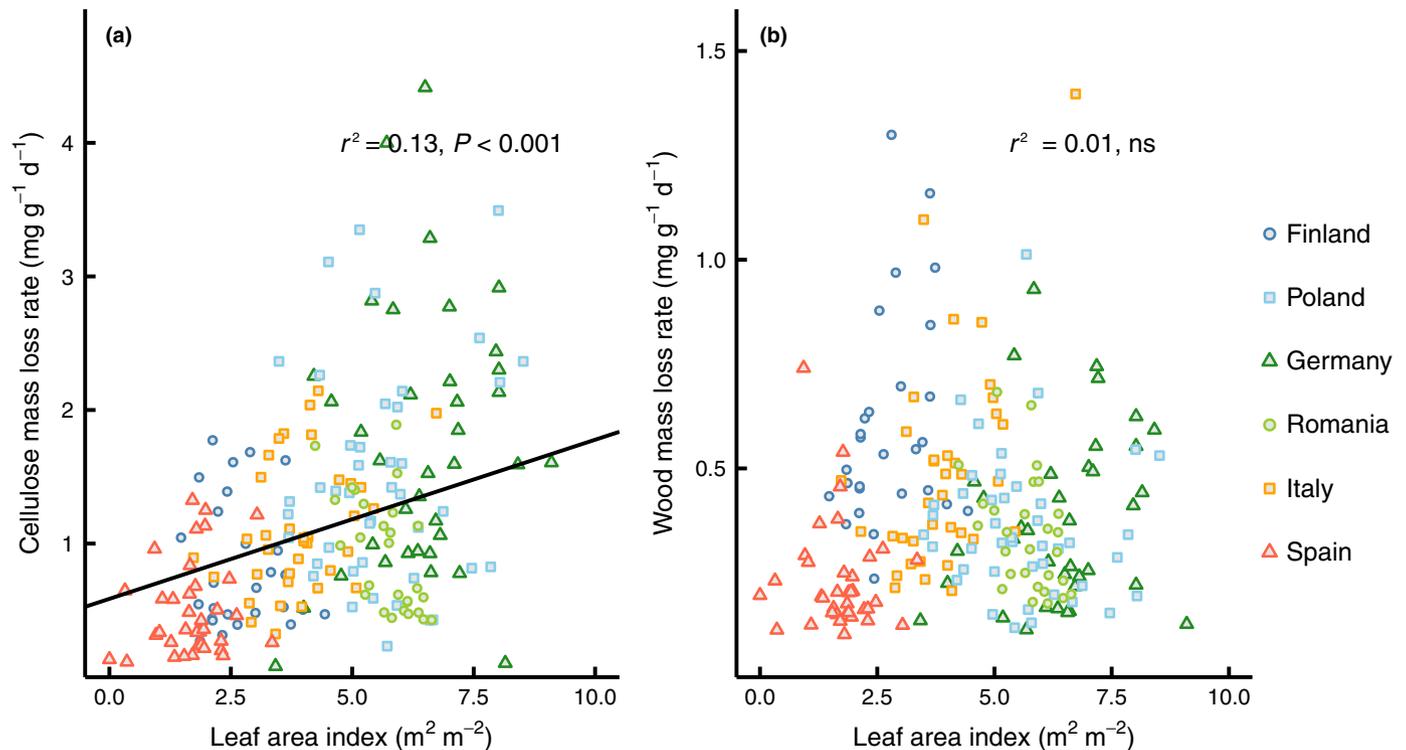

Fig. 2 Mass loss rate of (a) cellulose paper and (b) wood sticks as a function of plot-level leaf area index (m^2 m^{-2}). The black lines indicate the regression lines across all sites, if slope is significantly different from zero, with site as a random factor. ns, nonsignificant.
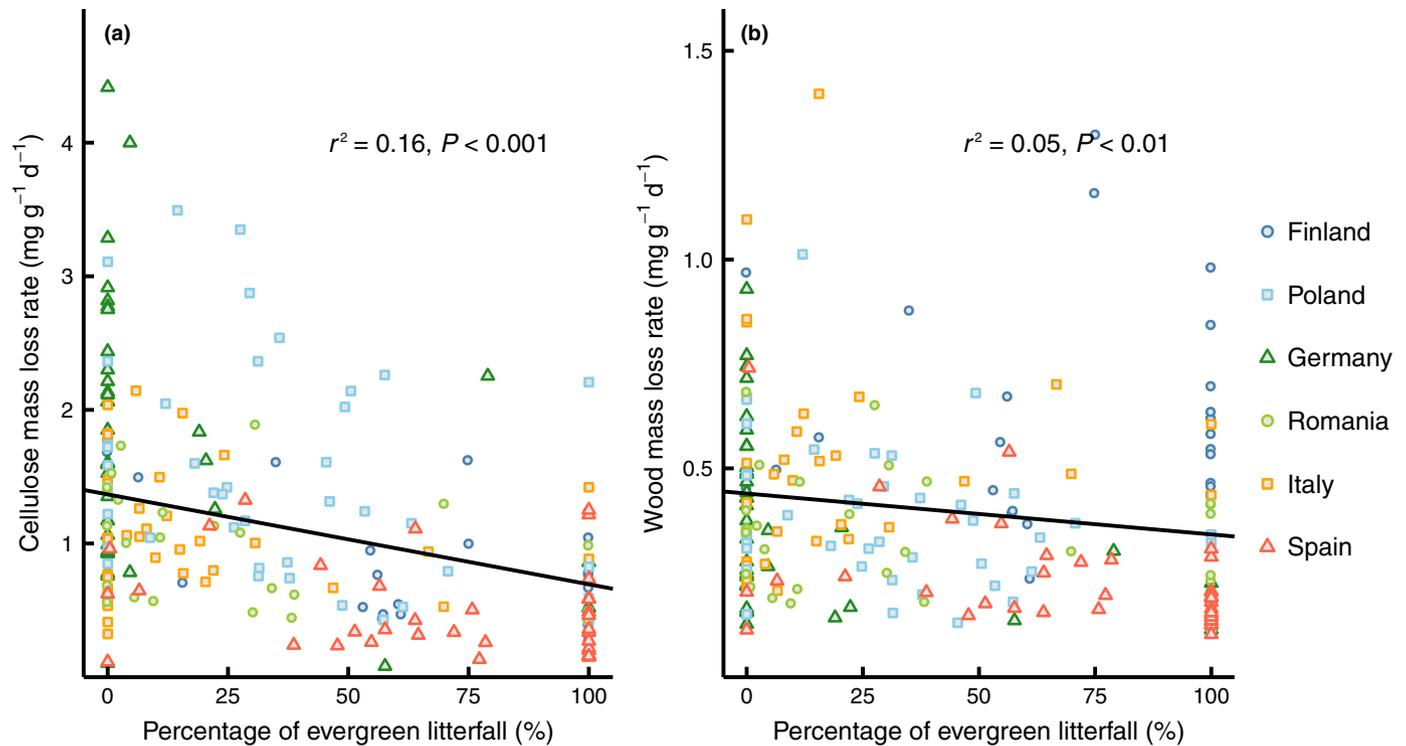
Fig. 3 Mass loss rate of (a) cellulose paper and (b) wood sticks as a function of the percentage of evergreen litter. The black lines indicate the regression lines across all sites, with site as a random factor.

best-fitting model, none of the macroclimate variables were retained, while plot-specific LAI and all formerly identified litterfall traits were kept except for the dissimilarity in water-soluble compounds (Table 3). As for wood mass loss rates, the combination of the soil C : N ratio and the percentage of evergreen litterfall in one model explained a total of 8% of variance (Table 2). When litterfall functional type was replaced by the retained litterfall CWMs, the soil C : N ratio was not kept in the model, while CWMs of tannins, lignin and cellulose were retained (Table 3).

Discussion

Indirect biotic control

In line with a previous study of standard substrate decomposition in a grassland diversity experiment (Hector *et al.*, 2000), we found a positive, but weak and statistically only marginally significant, effect of tree species richness on cellulose mass loss rates. Species richness only poorly captures trait-related aspects of diversity, and, in another grassland study, Scherer-Lorenzen (2008) reported positive effects of measures of trait diversity of the plant community on the decomposition of standard material (cotton strips and wood sticks), but no effect of plant species richness. In our study, the proportion of evergreen trees in the forest stands clearly played a more important role in decomposition than species richness. The decay of both materials correlated negatively with the relative basal area of evergreen trees, accounting for 11% and 5% of variance in mass loss rates for cellulose and wood, respectively. At all six forest sites, evergreen species were all coniferous, with the exception of *Quercus ilex* which

occurred in Italy and in Spain. A similar negative effect of coniferous trees independent of their own leaf litter, that is generally of rather poor quality and of slow decomposition (Berg & McClaugherty, 2008), was recently documented by Chomel *et al.* (2015), who observed lower decomposition of cellulose in a spruce (*Picea glauca*) plantation, compared with a poplar (*Populus maximowiczii × P. balsamifera*) plantation. The negative effect of evergreen species on decomposition may have different causes. In a recent review, Augusto *et al.* (2015) reported that, relative to evergreen coniferous species, deciduous angiosperms produce higher soil pH and permit higher rates of throughfall resulting in wetter soil conditions. In addition, leaf litter chemical properties of deciduous broadleaf trees may induce higher soil moisture and more favorable conditions for decomposer organisms. In our study, soil parameters had no (pH) or only very small (C : N for wood but not for cellulose decomposition) effects on decomposition. However, the amount of variance in cellulose mass loss rates explained increased from 11% to 16% when the relative abundance of evergreen trees was expressed based on the amount of litterfall rather than basal area. This indicates that the proportion of evergreen trees modifies the decomposition environment primarily through litterfall characteristics.

In fact, accounting specifically for litterfall quality effects improved the prediction of cellulose and wood mass loss to 19% and 20% of total variance explained, respectively. Such control of litterfall quality supports the view that the locally produced leaf litter exerts a selective pressure on the decomposer community beyond immediate direct litter quality effects (Ayres *et al.*, 2009; Freschet *et al.*, 2012). Our models retained mean SLA and Mg concentrations of the local litterfall as predictors for cellulose

Table 3 Output of multiple linear mixed models testing the effects of (community-weighted mean, CWM) mean plot-specific functional quality traits, (Rao) functional traits dissimilarity, (H3b) the combined effects of retained CWM and Rao traits, and (H2 and H3b) the combined effects of H2 and H3(b) retained variables on cellulose and wood mass loss rates

	Cellulose mass loss rate					Wood mass loss rate			
	Slope (± SE)	$\sum w_i$	R^2	AICw		Slope (± SE)	$\sum w_i$	R^2	AICw
CWM: litterfall quality (CWM)									
Specific leaf area	**0.03 (±0.01)**	0.93	0.19	0.19	Lignin	**0.03 (±0.01)**	0.89	0.20	0.27
Magnesium	**0.12 (±0.07)**	0.62			Tannins	**−0.02 (±0.01)**	0.70		
Cellulose	−0.04 (±0.03)	0.50			Cellulose	**−0.03 (±0.02)**	0.60		
Water-soluble compounds	−0.02 (±0.01)	0.41			Specific Leaf Area	0.01 (±0.01)	0.56		
C : N	−0.00 (±0.00)	0.39			C : N	0.00 (±0.00)	0.37		
Rao: litterfall dissimilarity (Rao)									
Water-soluble compounds	**0.51 (±0.17)**	0.97	0.09	0.20	Total phenolics	**−0.34 (±0.17)**	0.64	0.01	0.20
Lignin : N	**−0.18 (±0.17)**	0.54			C : P	0.07 (±0.07)	0.38		
Soluble phenolics	−0.13 (±0.21)	0.41			Lignin : N	0.09 (±0.12)	0.31		
Magnesium	−0.13 (±0.14)	0.37			pH	0.07 (±0.12)	0.28		
Cellulose	−0.02 (±0.08)	0.28			Cellulose	−0.00 (±0.05)	0.26		
H3(b): litter quality (CWM) and dissimilarity (Rao)									
Specific leaf area (CWM)	**0.03 (±0.01)**	0.90	0.27	0.28	Tannins (CWM)	**−0.02 (±0.01)**	0.90	0.20	0.38
Magnesium (CWM)	**0.14 (±0.07)**	0.74			Lignin (CWM)	**0.03 (±0.01)**	0.90		
Water-soluble compounds (Rao)	**0.22 (±0.12)**	0.70			Cellulose (CWM)	**−0.04 (±0.02)**	0.85		
Lignin : N (Rao)	**−0.24 (±0.11)**	0.59			Total phenolics (Rao)	−0.17 (±0.12)	0.49		
H2 and H3(b): microenvironment and litterfall									
Precipitation per degree day (mm °C^{-1})	0.38 (±0.48)	0.37			Tannins (CWM)	**−0.02 (±0.01)**	0.85	0.20	0.4
Leaf area index (m^2 m^{-2})	**0.09 (±0.03)**	0.97	0.41	0.16	Lignin (CWM)	**0.03 (±0.01)**	0.85		
Specific leaf area(CWM)	**0.03 (±0.01)**	0.94			Cellulose (CWM)	**−0.03 (±0.02)**	0.81		
Magnesium (CWM)	**0.13 (±0.06)**	0.67			Soil C : N (0–10 cm)	−0.01 (±0.01)	0.48		
Lignin : N (Rao)	**−0.21 (±0.11)**	0.62							
Water-soluble compounds (Rao)	0.14 (±0.12)	0.38							

For each group of variables, we report the slope (± SE) of each variable and its relative importance (sum of Akaike information criterion (AIC) weights ($\sum w_i$) over all models including the explanatory variable bound between 0 (not important) and 1 (relevant)). We also report the r^2 of the most parsimonious model and its AIC weight (AICw). The variables retained in the most parsimonious models are in bold and indicated with the black vertical line. C, carbon; N, nitrogen; P, phosphorus.

mass loss rates. Evergreen leaves typically have a lower SLA than deciduous leaves, with longer life spans and associated lower decomposability (Cornelissen, 1996). The SLA encapsulates several litter characteristics such as WHC, leaf toughness and sometimes the concentrations of secondary metabolites, which all influence decomposition (Berg & McClaugherty, 2008). Moreover, litterfall SLA was found to correlate positively with earthworm biomass (De Wandeler *et al.*, 2016). Litter Mg concentration was also found to be an important trait associated with litter decomposition across biomes previously (Makkonen *et al.*, 2012; García-Palacios *et al.*, 2015). Soil fauna depends particularly on Mg which plays an important role in enzyme functions and growth (Klasing *et al.*, 2005). Additionally, litter Mg and Ca were highly correlated in our study, and Ca was previously shown to favor decomposer abundance, especially that of earthworms (Reich *et al.*, 2005).

Unlike cellulose, wood decomposition was affected by the concentration of lignin in the local litterfall. This positive effect of lignin on wood decay suggests that the chemical similarity between the standard substrate and the locally occurring litter may favor its decomposition. This is in line with the substrate-matrix hypothesis (Freschet *et al.*, 2012) predicting that substrates of low quality (such as the wood sticks used here) decompose more rapidly on a soil that regularly receives similarly

recalcitrant litter. Enhanced decomposition of low-quality substrates may apply to recalcitrant compounds such as lignin, but not to inhibitory compounds such as condensed tannins, as indicated by the negative effect of concentration of condensed tannins on wood mass loss rates. Condensed tannins may suppress fauna activity, as has been shown for a tropical rainforest with quite large negative effects of condensed tannins on the fauna contribution to decomposition (Coq *et al.*, 2010).

The more important effect of community-weighted mean litterfall quality than litter quantity on the decomposition of two distinct substrates we found here suggests that the physical and chemical characteristics of litterfall regulate the local decomposer communities, and thereby alter the decomposition environment, as also found in a grassland study quantifying indirect effects of plant diversity on decomposition (Scherer-Lorenzen, 2008).

However, in addition to community-weighted mean traits of plot-specific litterfall, the dissimilarity in quality traits explained another 9% of the variance in cellulose mass loss rates. Specifically, the dissimilarity in the concentrations of water-soluble compounds was positively correlated with the decomposition of cellulose. In a previous study, Joly *et al.* (2016) reported that litter of different tree species provided leachates of both varying amount and varying quality, suggesting that water-soluble compound dissimilarity is also related to distinct leachates quality.

Combined differences in the quantity and quality of water-soluble compounds may provide complementary resources for decomposers that then may break down the exposed cellulose more efficiently.

Collectively, our data from six different European forests suggest that the relative abundance of evergreen trees and the litterfall characteristics of community-weighted mean SLA and Mg concentration and dissimilarity in water-soluble compound concentrations affect the decomposition environment in concert, accounting for up to 27% of total variance in the decomposition of standard materials.

Indirect abiotic control

In our continental-scale study, the decomposition rate of cellulose was surprisingly little affected by macroclimatic differences across Europe, while that of wood was not affected at all. This is all the more surprising given that we explored a variety of different climatic indices (average temperature, precipitation, potential evapotranspiration, climatic decomposition index and ratio of precipitation per degree of temperature) computed with climatic data corresponding to the exact site-specific incubation period. These results question the generality of climate as the main driver of decomposition at large spatial scales (Meentemeyer, 1978; Berg *et al.*, 1993; Aerts, 1997; Zhang *et al.*, 2008). In fact, in a reanalysis of the classical cross-biome decomposition study by Berg *et al.* (1993), Bradford *et al.* (2016) argued that the design and analysis of broad-scale experiments may inflate the importance of macroclimate by ignoring site-specific variation in microclimatic conditions that may be disconnected from macroclimate to some degree. In agreement with these conclusions, the plot-level environmental characteristics in our study apparently overrode the importance of macroclimate. Compared with site-specific temperature and precipitation, the plot-specific differences in canopy density and its effects on microenvironmental conditions accounted for more of the overall variance in cellulose decomposition (Table 3; Fig. 2a). We evaluated only the initial stage of decomposition, and the relative importance of microclimatic drivers could increase during later stages of litter decay (García-Palacios *et al.*, 2016). However, the proportion of lignin increases with ongoing decay, and lignin-rich litter decomposition has been found to be less sensitive to climatic conditions than lignin-poor litter decomposition (Berg, 2000).

We acknowledge that LAI, used in our study as a surrogate for microclimatic conditions, may be only a rough proxy, and that measurements of humidity and temperature in the litter layer would be more precise, but were logistically not realistic across the 209 plots spread across Europe. Moreover, our positive correlation between LAI and decomposition rates contrasts with results of Hobbie *et al.* (2006), who reported an increased mean annual soil temperature and decomposition in plots with higher light penetration in a common garden experiment. However, in their study, the monospecific coniferous stands had the lowest light penetration, and thus highest LAI, which in the light of our results may have been confounded with potential negative effects on decomposition through the quality of the local litter input. Our results rather suggest that denser canopies may favor decomposition by attenuating temperature fluctuation and by increasing soil moisture through reduced soil surface evaporation, as was suggested previously (von Arx *et al.*, 2013). It is important to note that the amount of litterfall, which correlates positively with stand LAI, had no effect on cellulose decomposition. This suggests that the LAI-driven effect on microclimatic conditions rather than the amount of litterfall affected cellulose decomposition. This control of canopy density may depend not only on tree species composition and associated distinct canopy architectures and leaf positions among species, but also on the stand-level tree species diversity. Indeed, Pretzsch (2014) reported that canopy space filling can increase with the number of species as a result of complementarity in crown shapes. In another study using the FunDivEUROPE forest plot network, Jucker *et al.* (2015) actually reported increased canopy packing efficiency with increasing species richness. This suggests that the positive effect of canopy closure we observed may also result from increasing tree species richness, which is in line with the positive, although weak, species richness effect we reported for cellulose decomposition.

With a direct impact on the activity and abundance of soil fauna and microorganisms, soil characteristics (e.g. pH and nutrient status) also contribute importantly to the control of decomposition (Berg & McClaugherty, 2008). Differences in soil properties may arise from different parent material, as well as from the long-term influence of plant species composition (Vesterdal *et al.*, 2008; Dawud *et al.*, 2016). In fact, Vesterdal *et al.* (2008) showed that soil C and N contents were affected by the quality of the foliar litterfall. However, the soil properties of topsoil pH and C : N ratio that we evaluated here had no direct effect on cellulose mass loss rates, while C : N ratio had a minor negative effect on wood mass loss rates, which is in line with the findings of Vesterdal (1999) reporting a limited effect of soil properties on decomposition compared with litter quality. Such limited effects of soil nutrient status on decomposition indicate that the quality and diversity of the litterfall affects the decomposer community directly, rather than indirectly through modification of soil properties.

Conclusions

We present clear evidence demonstrating the importance of indirect controls of tree species diversity on decomposition through changes in canopy density and in litterfall quality and diversity across different forest types of Europe. While climate is often assumed to be the dominant controlling factor for litter decomposition across large spatial scales, the macroclimatic conditions played a minor role in this European-scale study. This suggests that the microenvironmental conditions modified by tree species composition and diversity override the impact of macroclimate, at least during the early stage of decomposition covered by our study. The diversity of tree communities, in particular with respect to the inclusion of evergreen species, may affect biogeochemical cycling in European forests through modifications of microenvironmental conditions more than currently

acknowledged and in addition to litter mixing effects. In light of our results, we advocate that broad-scale decomposition studies should systematically consider environmental variation at small local scales in order to disentangle the relative importance of direct and indirect effects of vegetation structure from the importance of macroclimatic conditions. Particularly, the often overlooked composition and diversity of living plants appear to be important factors to consider in litter decomposition studies.

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Author contributions

S.H., F-X.J. and M.S-L. designed the experiment. F-X.J. and L-K.J. collected the decomposition data and F.B., S.M.D., S.M., M.P., K.R-R., M.S-L. and L.V. provided data on explanatory variables. F-X.J. and A.M. analyzed the data. F-X.J., A.M. and S.H. wrote the paper and all other authors commented on the paper.

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