RESEARCH ARTICLE

Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna

Shixing Zhou[1,2] | Olaf Butenschoen[2,3] | Sandra Barantal[4] | Ira Tanya Handa[4,5] | Marika Makkonen[6] | Veronique Vos[7] | Rien Aerts[6] | Matty P. Berg[8,9] | Brendan McKie[10,11] | Jasper Van Ruijven[7] | Stephan Hättenschwiler[4] | Stefan Scheu[2,12]

[1]Sichuan Province Key Laboratory of Ecological Forestry Engineering on the Upper Reaches of Yangtze River, College of Forestry, Sichuan Agricultural University, Chengdu, People's Republic of China; [2]J.F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany; [3]Senckenberg Biodiversität und Klima Forschungszentrum, Frankfurt am Main, Germany; [4]Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), CNRS, Univ Montpeller, Univ Paul Valéry Montpellier 3, EPHE, IRD, Montpellier Cedex 5, France; [5]Département des Sciences Biologiques, Université du Québec à Montréal, Succursale Centre-ville, Montréal, QC, Canada; [6]Department of Ecological Science, Section Systems Ecology, VU University Amsterdam, Amsterdam, The Netherlands; [7]Plant Ecology and Nature Conservation, Wageningen University and Research Centre, Wageningen, The Netherlands; [8]Department of Ecological Science, Section Animal Ecology, VU University Amsterdam, Amsterdam, The Netherlands; [9]Groningen Institute of Evolutionary Life Science, Community and Conservation Ecology Group, University of Groningen, Groningen, The Netherlands; [10]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden; [11]Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden and [12]Center of Biodiversity and Sustainable Land Use, University of Göttingen, Göttingen, Germany

Correspondence
Shixing Zhou
Email: szhou@sicau.edu.cn; djyzsx@163.com

Abstract

1. At broad spatial scales, the factors regulating litter decomposition remain ambiguous, with the understanding of these factors largely based on studies investigating site-specific single litter species, whereas studies using multi litter species mixtures across sites are rare.

2. We exposed in microcosms containing single species and all possible mixtures of four leaf litter species differing widely in initial chemical and physical characteristics from a temperate forest to the climatic conditions of four different forests across the Northern Hemisphere for 1 year.

3. Calcium, magnesium and condensed tannins predicted litter mass loss of single litter species and mixtures across forest types and biomes, regardless of species richness and microarthropod presence. However, relative mixture effects differed among forest types and varied with the access to the litter by microarthropods. Access to the microcosms by microarthropods modified the decomposition of individual litter species within mixtures, which differed among forest types independent of litter species richness and composition of litter mixtures. However, soil microarthropods generally only little affected litter decomposition.

Shixing Zhou and Olaf Butenschoen have equal first author position.

Stephan Hättenschwiler and Stefan Scheu have equal last author position.

4. *Synthesis*. We conclude that litter identity is the dominant driver of decomposition across different forest types and the non-additive litter mixture effects vary among biomes despite identical leaf litter chemistry. These results suggest that across large spatial scales the environmental context of decomposing litter mixtures, including microarthropod communities, determine the decomposition of litter mixtures besides strong litter trait-based effects.

1 | INTRODUCTION

Decomposition of plant litter in terrestrial ecosystems is a central process in the global carbon (C) cycle (Chapin, Matson, & Vitousek, 2011), and releases ten times more C to the atmosphere than what is released by anthropogenic fossil fuel combustion (Prentice et al., 2001). Reflecting its importance in the C cycle and in energy and nutrient transfer in decomposer food webs, litter decomposition and the relative contribution of the various controlling factors including climate, litter quality and the diversity and composition of soil decomposer communities have been extensively studied (Aerts, 1997; Cornwell et al., 2008; García-Palacios, Shaw, Wall, & Hattenschwiler, 2016; Wall et al., 2008). However, these controlling factors operate at different spatial scales and interact with each other. To truly facilitate generalizations at large spatial scales and underpin predictions on the consequences of anthropogenic impacts on both biodiversity and climate for ecosystem functioning it is necessary to investigate the driving factors of litter decomposition across different types of ecosystems (Bradford et al., 2016; Djukic et al., 2018; Makkonen et al., 2012). Previous gradient studies across latitudes and biomes have widely improved our knowledge on drivers of leaf litter decomposition across large spatial scales (Boyero et al., 2017; Gholz, Wedin, Smitherman, Harmon, & Parton, 2000; Handa et al., 2014; Makkonen et al., 2012; Parton et al., 2007; Tiegs et al., 2019; Woodward et al., 2012). However, the generality of the results of these studies remained limited as the litter materials used varied among biomes or ecosystem types, and often only site-specific single litter species were used (Djukic et al., 2018; Gessner et al., 2010) preventing identification of common litter traits for litter decomposition across spatial scales and biomes.

At the global scale, variations in climate exert a predominant control on basic ecological processes, with mean annual temperature, mean annual precipitation and the resulting actual evapotranspiration shown to be key drivers of litter decomposition and nutrient dynamics (Aerts, 1997; Berg et al., 1993; Bradford et al., 2016; Gholz et al., 2000; Woodward et al., 2012). However, recent studies indicate that leaf litter characteristics affect litter decomposition rates and nutrient cycling more strongly than climatic variables. Two meta-analyses (Cornwell et al., 2008; Zhang, Hui, Luo, & Zhou, 2008) and a cross-biome litter transplant study (Makkonen et al., 2012)

have reported that litter identity explains more variation in leaf litter decomposition than climatic variables or abiotic and biotic soil characteristics. These litter identity effects mostly were interpreted based on few, commonly measured traits such nitrogen (N), C and lignin concentrations (Adair et al., 2008; Hättenschwiler & Jørgensen, 2010), which have been assumed to exert the strongest control on litter decomposition rates. However, there is increasing evidence that other litter traits regulating decomposer and enzyme activities, including concentrations of plant secondary compounds as well as micronutrients such as calcium (Ca), magnesium (Mg) and manganese (Mn), can be more important in driving litter decomposition than the more commonly used nutrient and C quality traits (Berg et al., 2017; Berg, Steffen, & McClaugherty, 2007; García-Palacios, McKie, Handa, Frainer, & Hattenschwiler, 2016; Guerrero-Ramírez et al., 2016; Makkonen et al., 2012; Pérez-Harguindeguy et al., 2000; Vaieretti, Harguindeguy, Gurvich, Cingolani, & Cabido, 2005). Therefore, to better understand the underlying drivers of litter identity effects on decomposition, and how they interact with climate at large spatial scales and across biomes, decomposition studies should assess a large number of leaf litter traits, including those that, like micronutrients, are not commonly considered.

The importance of soil fauna for litter decomposition has long been recognized (Hättenschwiler & Gasser, 2005; Hättenschwiler, Tiunov, & Scheu, 2005; Seastedt, 1984). Soil fauna has been shown to generally increase leaf litter mass loss in a variety of ecosystems and climate zones, despite that soil fauna abundance and activity varies with climatic conditions and leaf litter quality (Anderson, Ineson, & Huish, 1983; García-Palacios, Maestre, Kattge, & Wall, 2013; Handa et al., 2014; Hättenschwiler & Jørgensen, 2010; Makkonen et al., 2012; Wall et al., 2008). However, the role of soil fauna in global litter decomposition models has been largely ignored and this might be one of the reasons for the limited ability of these models to explain global decomposition patterns (García-Palacios et al., 2013; Parton et al., 2007; Wall et al., 2008). At the global scale, Wall et al. (2008) found that including soil fauna effects resulted in a 7% improvement in the variance explained by climatic predictors in global decomposition models. Moreover, a meta-analysis conducted by García-Palacios et al. (2013) has reported that soil fauna consistently enhance litter decomposition at both global and biome scales by an average of 27%. In general, macrofauna, such as millipedes

and earthworms, act directly on litter decomposition as detritivores, but soil microarthropods, such as collembolans and oribatid mites, may also strongly impact litter decomposition by modifying the activity and composition of saprotrophic fungal communities (García-Palacios, Shaw, et al., 2016; Tordoff, Boddy, & Jones, 2008; Wal, Geydan, Kuyper, & Boer, 2013). The majority of previous studies addressing fauna effects on leaf litter decomposition focused on how variable litter quality (i.e. different litter species that varied widely in traits; García-Palacios, Shaw, et al., 2016; Hättenschwiler & Jørgensen, 2010; Makkonen et al., 2012) or climate conditions (i.e. decomposition in a variety of ecosystems and climate zones; García-Palacios, Shaw, et al., 2016; Wall et al., 2008) determine the relative impact of fauna. Moreover, measuring the effects of soil fauna on leaf litter decomposition was typically done using single species experiments, largely neglecting that litter layers of the majority of ecosystems are composed of leaf litter from different plant species from which soil animals can choose their diet (Gessner et al., 2010). In fact, in leaf litter mixtures, the abundance and diversity of soil animals has been found to vary with litter species identity (Wardle, Yeates, Barker, & Bonner, 2006). Further, feeding activity and structure of decomposer communities have been shown to vary with leaf litter composition exerting feedbacks to decomposition processes (Hättenschwiler et al., 2005; Wardle et al., 2006). However, studies evaluating the importance of litter diversity in the regulation of fauna effects are comparatively rare (but see García-Palacios, McKie, et al., 2016; García-Palacios, Shaw, Wall, & Hattenschwiler, 2017; Handa et al., 2014), and therefore consequences of litter diversity for litter decomposition remain difficult to predict (García-Palacios, McKie, et al., 2016; Hättenschwiler et al., 2005; Tresch et al., 2019).

Mixtures of leaf litter from different co-occurring plant species often decompose at different rates than predicted from the respective decomposition of single leaf litter species (Gartner & Cardon, 2004; Gessner et al., 2010; Hättenschwiler et al., 2005). When decomposing in mixtures abiotic and biotic interactions between litter species can change decomposition processes due to several non-exclusive mechanisms resulting in accelerated or decelerated mass loss of litter mixtures or component litter species (Gessner et al., 2010; Hättenschwiler & Gasser, 2005). For example, in mixtures leaching and transfer of nutrients and inhibitory compounds between litter species can result in synergistic and antagonistic leaf litter mixing effects (Butenschoen et al., 2014; Handa et al., 2014; Lummer, Scheu, & Butenschoen, 2012). Moreover, improved microclimatic conditions in mixtures comprising litter species characterized by different physical functional traits can change litter decomposition rates (Makkonen et al., 2012; Makkonen, Berg, van Logtestijn, van Hal, & Aerts, 2013; Wardle, Bonner, & Nicholson, 1997). In addition, leaf litter composition can change the feeding activity and composition of decomposer communities altering litter decomposition in leaf litter mixtures (Hättenschwiler & Bretscher, 2001; Hättenschwiler et al., 2005; Santonja, Fernandez, et al., 2017; Vos, van Ruijven, Berg, Peeters, & Berendse, 2011). All these different mechanisms have been found to explain non-additive mixing effects on litter decomposition in a wide variety of ecosystems and biomes (Currie

et al., 2010; Makkonen et al., 2013; Santonja, Rancon, et al., 2017; Schindler & Gessner, 2009). However, as the environmental context, decomposer access and litter species all vary among individual studies, it is presently difficult to assess the generality of the various mechanisms described for non-additive litter mixture effects.

Here, we conducted a field experiment investigating the drivers of leaf litter decomposition in four different forests, across a latitudinal gradient covering four major biomes of the Northern Hemisphere, including the subarctic, the boreal, the temperate and the Mediterranean biome. Using the same species pool across all biomes, we investigated the relative importance of leaf litter identity, diversity (i.e. richness or composition of litter species in mixtures) and the decomposer food web composition (i.e. presence or absence of microarthropods) as drivers of litter decomposition rates under variable environmental conditions across Europe. In field microcosms, we incubated four leaf litter species from common temperate forest tree species, differing widely in initial chemical and physical litter characteristics, in single species and all possible multispecies mixtures. We used microcosms set up in the field with two different mesh sizes, to manipulate access by microarthropods to further evaluate the importance and generality of the impact of soil microarthropods in driving litter mixture effects on litter decomposition. Using the same four leaf litter species and keeping the same litter mixtures in all four forest types allowed for testing of the generality litter mixing effects under variable environmental conditions and decomposer food web structure independently from differences in site-specific initial litter quality. Based on the well-documented dominant litter quality control on decomposition compared to other drivers such as climate, soil characteristics and decomposer communities (Cornwell et al., 2008; Makkonen et al., 2012), we hypothesized that (a) litter identity and mixture effects remain constant across the wide continental gradient covered in our study, and (b) across biomes, litter decomposition can be predicted from a common set of initial litter traits. Additionally, we hypothesized that (c) soil microarthropods increase litter decomposition in similar ways across all studied forests irrespective of species identity and non-additive mixture effects.

2 | MATERIALS AND METHODS

2.1 | Study sites and plant material

The experiment was set up in four forests belonging each to a different biome (i.e. subarctic, boreal, temperate and Mediterranean), spanning a latitudinal gradient of about 3,000 km from Northern Sweden to Southern France (Figure 1). Forests at the study sites were minimally impacted by human activities and varied widely in plant species diversity and composition. The dominant tree species at the subarctic is *Betula pubescens*, at the boreal site *B. pubescens* and *Picea abies*, at the temperate site *Fagus sylvatica* and at the Mediterranean site *Quercus ilex* and *Fraxinus angustifolia*. The forests encompassed a modest range of soil pH, but differed widely in soil C and N concentrations (from 3.63% to 27.36% and 0.39% to 1.14%
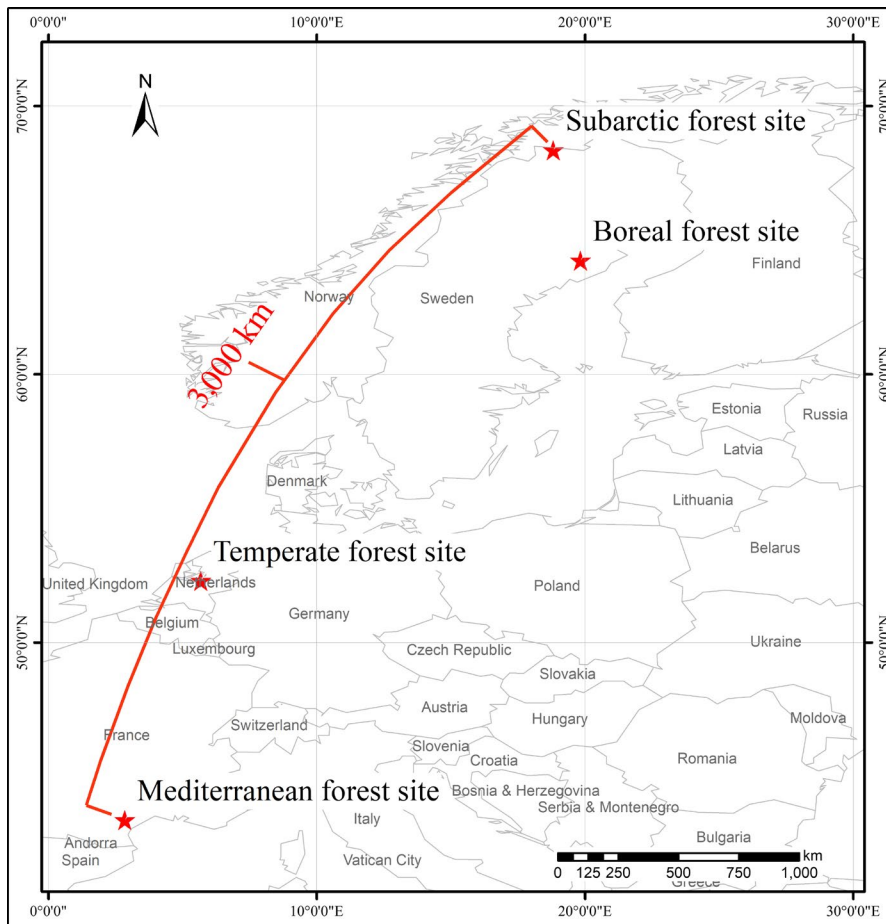
FIGURE 1 Study sites located in four different forest ecosystems, the subarctic, boreal, temperate and Mediterranean, along a large latitudinal gradient in the Northern Hemisphere [Colour figure can be viewed at wileyonlinelibrary.com]

dry weight, respectively; for details on analyses of soil properties see Handa et al., 2014) and varied in mean annual temperature, mean annual precipitation and seasonality (Table S1; calculated based on data from 1998 to 2008 from the closest possible meteorological station).

Four different leaf litter species of common temperate forest trees were chosen for this study: alder *Alnus glutinosa* (L.) Gaertn., grey willow *Salix cinerea* L., beech *F. sylvatica* L. and holly *Ilex aquifolium* L. The four leaf litter species differed broadly in chemical and physical litter traits (Table 1; for details on analyses of litter traits see Makkonen et al., 2012). The selected four species only occurred in the temperate forest restricting potential home-field advantage effects to the temperate forest site and avoiding it in the subarctic, boreal and Mediterranean forest sites. Leaf litter was collected during the time of litter fall in autumn 2006 at the temperate forest site in the Netherlands using litter traps placed at time of leaf fall. Freshly fallen senesced leaf litter of *A. glutinosa*, *S. cinerea* and *F. sylvatica* were collected every second day, whereas leaf litter of *I. aquifolium* was obtained by cutting branches in the field and simulating senescence by air-drying and allowing laves to fall off from the branches in the laboratory during a period of three to four weeks (Handa et al., 2014; Makkonen et al., 2012). López-Rojo et al. (2018) found that the N concentration of *I. aquifolium* leaves collected from branches did not significantly differ from senescent leaves which are shed in the field. After collection, the litter was dried at 40°C for one

week. Leaf litter from each species was pooled and homogenized. Leaves with signs of herbivory, fungal attack or galls were excluded.

2.2 | Experimental design

There were 15 different litter treatments, including four single species (monocultures) and all possible combinations of 2-species (six), 3-species (four) and 4-species (one) mixtures. Leaf litter mixtures were prepared in the laboratory and transported in individual plastic bags to all four forest sites in autumn 2008. The leaf litter was exposed in the field using custom-made microcosms constructed of polyethylene tubes (height 90 mm, diameter 150 mm) and covered with 50 μm mesh at the bottom and a lid covered with 50 μm mesh on top to prevent entry of extraneous litter while allowing water to pass. Two windows (50 × 180 mm) were cut at the side of the microcosms and covered either with 50 μm mesh, allowing microorganism and microfauna passing through or 1 mm mesh, additionally allowing entry of microarthropods (Bradford, Tordoff, Eggers, Jones, & Newington, 2002; Handa et al., 2014; Makkonen et al., 2012). We chose to use microcosms rather than litterbags to avoid compression of litter that can alter microclimatic conditions and faunal activity. We filled each microcosm with 8 g dry weight leaf litter with mixtures containing equal amounts of each litter type. At each forest site we

TABLE 1 Litter quality traits of the four litter species studied (±*SD*). Initial concentrations (% dry weight) of carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), water soluble carbon (WSC), cellulose (Cell), hemicelluloses (Hcell), lignin (Lig), soluble phenolics (S-Phen), total phenolics (T-Phen), condensed tannins (Tan) and water saturation capacity (Wsat, % H_2O), tri-dimensionality (3D, cm^{-2} in number of leaves cm^{-3}), specific leaf area (SLA; cm^2/g dry weight), leaf toughness (Tough; g H_2O), tensile strength (Ten; N cm^{-1}) and pH of *Alnus glutinosa*, *Salix cinerea*, *Fagus sylvatica* and *Ilex aquifolium*. Different superscript letters indicate significant differences among litter species using single factorial ANOVA and Tukey's HSD-Test ([a]indicates the highest value of each litter trait)

Parameter	A. glutinosa	S. cinerea	F. sylvatica	I. aquifolium
C	47.83 ± 0.45[a]	47.75 ± 0.75[a]	48.04 ± 0.54[a]	46.78 ± 0.33[a]
N	2.49 ± 0.08[a]	1.23 ± 0.07[c]	1.03 ± 0.06[d]	1.69 ± 0.07[b]
P	0.08 ± 0.01[c]	0.11 ± 0.01[b]	0.06 ± 0.01[d]	0.16 ± 0.01[a]
K	0.28 ± 0.04[c]	0.69 ± 0.05[a]	0.55 ± 0.05[b]	0.77 ± 0.07[a]
Ca	1.59 ± 0.12[a]	1.31 ± 0.02[b]	0.73 ± 0.07[c]	1.69 ± 0.11[a]
Mg	0.24 ± 0.03[b]	0.23 ± 0.01[b]	0.09 ± 0.01[c]	0.52 ± 0.04[a]
Na	0.14 ± 0.02[b]	0.19 ± 0.02[a]	0.09 ± 0.01[c]	0.03 ± 0.01[d]
WSC	41.77 ± 5.23[ab]	44.2 ± 2.60[ab]	35.34 ± 3.27[b]	50.97 ± 5.68[a]
Cell	23.8 ± 2.58[a]	17.17 ± 1.16[a]	20.47 ± 1.31[a]	22.59 ± 4.70[a]
Hcell	15.03 ± 1.36[b]	14.43 ± 1.74[b]	21.67 ± 0.50[a]	15.84 ± 0.64[b]
Lig*	19.4 ± 3.04[a]	24.19 ± 1.65[a]	22.53 ± 1.92[a]	10.59 ± 0.63[b]
3D	0.03 ± 0.02[b]	0.18 ± 0.03[a]	0.07 ± 0.02[b]	0.03 ± 0.00[b]
Tough	100.36 ± 17.36[b]	126.86 ± 13.46[b]	130.31 ± 5.50[b]	570.23 ± 27.63[a]
SLA	153.81 ± 19.75[b]	149.74 ± 4.47[b]	275.66 ± 27.01[a]	79.57 ± 6.52[c]
Wsat	224.04 ± 36.04[a]	185.95 ± 30.78[a]	235.55 ± 54.21[a]	190.09 ± 91.47[a]
Ten	3.71 ± 0.26[c]	1.74 ± 0.48[c]	8.72 ± 0.42[b]	16.18 ± 1.75[a]
S-Phen	1.63 ± 0.29[b]	4.64 ± 0.89[a]	3.39 ± 1.01[ab]	3.79 ± 0.22[a]
T-Phen	3.51 ± 0.73[b]	8.65 ± 1.29[a]	8.78 ± 1.36[a]	4.63 ± 0.49[b]
Tan	0.29 ± 0.08[b]	2.73 ± 0.47[a]	2.77 ± 0.50[a]	0.13 ± 0.01[b]
pH	5.32 ± 0.20[bc]	5.17 ± 0.04[c]	5.65 ± 0.07[a]	5.53 ± 0.06[ab]

*In this study, lignin refers to the portion determined as acid-unhydrolysable residue (AUR).

installed 90 microcosms (15 litter treatments × 2 mesh sizes × 3 replicates) arranged in three randomized blocks, resulting in a total of 360 microcosms and an overall replication of 12 microcosms per treatment combination. Using the same four leaf litter species and keeping the same litter mixtures in all four forest types allowed us to investigate the same litter traits and mixture effects across the broad environmental gradient. Note that using the same species pool was a prerequisite to assess litter identity and diversity effects on decomposition independently from the differences in site-specific environmental conditions and decomposer communities (García-Palacios et al., 2017; Madritch & Cardinale, 2007). The 30 microcosms per block were separated from each other by at least 50 cm and randomly distributed within each block; blocks were spaced at least 20 m at each forest site. Before microcosms were installed, the local litter layer underneath the microcosms was carefully removed. Microcosms were placed into the local litter layer at the same depth as the natural litter layers outside the microcosms, to ensure the microcosms were integrated with the existing litter layer and facilitate colonization by decomposers.

After approximately 1 year (49–51 weeks, see Table S1), microcosms were retrieved from the field. Microcosms were opened on site, leaf litter was removed and transported in individual plastic bags to the laboratory. Litter mixtures were sorted to component species to assess individual litter species mass loss in mixtures. Attached mineral material was brushed off and litter was dried at 65°C for 2 days.

2.3 | Calculations and statistical analysis

Two blocks, one at the boreal and one at the temperate site, had to be dropped from the analyses due to destruction of microcosms by mammals, resulting in a total of 300 intact microcosms at harvest. Leaf litter mass loss (ML) was calculated as percentage of total initial mass as $ML = ((m_0 - m_1)/m_0) \times 100$, with m_0 the initial dry weight of individual litter species and m_1 the dry weight of individual leaf litter species at harvest; ML was uniformly calculated on the basis of 52 weeks (1 year) assuming linearity of mass loss rates (Table S1). To detect any non-additive mixture effects on litter mass loss, we calculated the relative mixture effect $RME (\%) = ((m_{obs} - m_{exp})/m_{exp}) \times 100$ for each mixture, with m_{obs} the observed mass loss of the litter mixture and m_{exp} the expected mass loss of the same litter mixture calculated as the mean mass loss of the component litter species decomposing in single litter species microcosms at each site (Wardle et al., 1997). Deviations from zero indicate non-additive mixture effects with positive and negative values referred to as synergistic and antagonistic effects respectively (Butenschoen et al., 2014). To explore the mechanisms underlying non-additive effects in litter mixtures, we compared individual mass loss of litter species in mixtures to the average mass loss of litter species in single litter species microcosms and calculated relative individual performance as $RIP (\%) = ((m_{obs-mix} - m_{obs-sing})/m_{obs-sing}) \times 100$, with $m_{obs-mix}$ the observed mass loss of individual litter species in mixtures and $m_{obs-sing}$ the observed mass loss of the same litter species in single litter species at each site.

Before the main analysis, we used a one-way ANOVA to test the effect of block for each forest type separately. As the effect of block was not significant for any forest type, block was excluded from further analyses. Variations in single leaf litter species mass loss (% of initial, arcsine square-root transformed) were analysed with full factorial ANOVAs (GLM; type III sum of squares) with the factors forest type (FT; subarctic [Sub], boreal [Bor], temperate [Temp] and Mediterranean [Med]) treated as random factor and litter species identity (SI; *A. glutinosa* [A], *S. cinerea* [S], *F. sylvatica* [F] and *I. aquifolium* [I]) and soil fauna community (M; presence and absence of microarthropods) as fixed factors.

Partial least square (PLS) regressions were used to assess the relative importance of initial chemical and physical leaf litter traits for leaf litter mass loss incubated in single litter species and litter mixtures. Litter traits of the mixtures were calculated from individual species contributing to the mixture as community-weighted mean traits (García-Palacios, McKie, et al., 2016). We used PLS regressions instead of multiple linear regressions because PLS regression is based on the linear conversion of a large number of predictors to a small number of orthogonal factors, thereby eliminating multi-collinearity between predictors (Geladi & Kowalski, 1986). First, we used the complete set of 20 chemical and physical litter traits as predictors to conduct regressions. Then, a reduced set of litter traits which had the highest explanatory power in the full model were used to investigate if litter mass loss can be explained by a consistent set of traits. The relative importance of individual predictors in the model was estimated by the variable of importance of projection (VIP), with VIP > 1 indicating significant contribution of predictors to variations in the dependent variable (Andersen & Bro, 2010). Model strength was assessed by the variance of the dependent variable that is explained by the model (R^2Y) and the variance of the set of predictors used for the model (R^2X).

Analysis of variance models based on sequential sums of squares (GLM; type I sum of squares) were used to inspect for effects of FT (forest type), M (microarthropods), litter species richness (SR; 2, 3 and 4 species), litter species composition (SC; AS, AF, AI, SF, SI, FI, ASF, SFI, FIA, IAS and ASFI) and their interactions on relative mixture effects (RME) on mass loss. The relative individual performance (RIP) of individual litter species mass loss within mixtures was analysed with a similar model (ANOVA; type I sum of squares) with FT, SI, SR, SC and M as main factors and their interactions. In addition, we used Student's *t* tests to inspect if RIP of litter species and RME on litter mass loss significantly differed from zero and between soil community treatments.

Prior to statistical analyses, data were inspected for homogeneity of variance using Levene test and $\log(x + 1)$ transformed if necessary. Data on litter mass loss were arcsine square-root transformed prior to the analysis. Means presented in text and figures represent back-transformed means of the log transformed and arcsine square-root transformed data. Analyses of variance and comparisons of means (Tukey's HSD test, $p < 0.05$), and Student's *t* tests were performed using SPSS (Version 20.0.0; SPSS Inc.). PLS regressions were performed using TANAGRA 1.4.50 (Rakotomalala, 2005).

3 | RESULTS

3.1 | Single litter species

Litter mass loss of single litter species ranged from 15% for *F. sylvatica* incubated in the subarctic biome to 62% for *I. aquifolium* incubated in the temperate biome (Figure 2). Forest type explained 31% of the variance in litter mass loss (Table 2). Averaged across litter species and soil fauna community treatments, litter mass loss increased from the subarctic forest (25 ± 7%), to the boreal and Mediterranean forests (both 34 ± 12%) and was highest in the temperate forest (45 ± 12%). Species identity explained 59% of the variance in litter mass loss (Table 2). Averaged across forest types and soil fauna community treatments litter mass loss increased from *F. sylvatica* (20 ± 7%) to *S. cinerea* (30 ± 7%) to *A. glutinosa* (37 ± 5%) to *I. aquifolium* (46 ± 12%). These interspecific differences depended somewhat on the site of incubation as indicated by the significant FT × SI interaction, but did not differ in response to microarthropod access. However, the variance accounted for by the FT × SI interaction was small (6% variance explained; Table 2; Figure 2) compared to that of litter species identity and forest type.

3.2 | Litter mixtures

Neither species richness nor species composition of the litter mixtures nor any interactions with the other factors we tested significantly affected RME (Table 3), indicating that none of the specific litter mixtures systematically increased or decreased decomposition of litter mixtures as compared to the prediction based on the
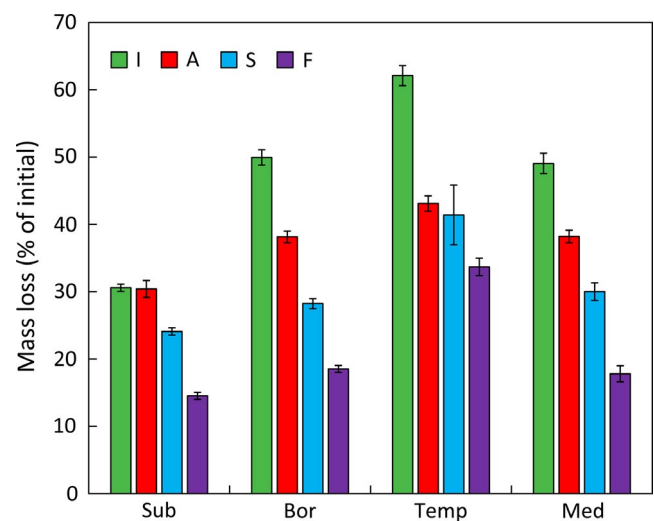
FIGURE 2 Litter mass loss (% of initial) of *Ilex aquifolium* (I), *Alnus glutinosa* (A), *Salix cinerea* (S) and *Fagus sylvatica* (F) incubated as single litter species in the subarctic (Sub), boreal (Bor), temperate (Temp) and Mediterranean forest (Med; Mean ± *SE*). Data are pooled across soil fauna treatments. Means of six replicates in the subarctic and Mediterranean forest, and four in the temperate and boreal forest (see Section 2) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Three factorial ANOVA table (Type III sum of squares) for the response of litter mass loss (% of initial, arcsine-square-root transformed) in single litter species microcosms to forest type (FT), litter species identity (SI) and soil fauna community composition (M) and their interactions. *df*, degrees of freedom; *SS*, Type III sum of squares; *SS%*, percentage of variance explained; *MS*, mean square; *F*, *F* statistics; *p*, statistical significance. Significant effects are given in bold

Effect	df	SS	SS%	MS	F	p
Forest type (FT)	3	0.45	30.94	0.15	13.3	**0.0006**
Species identity (SI)	3	0.86	58.89	0.29	32.3	**<0.0001**
Fauna community composition (M)	1	<0.01	<0.01	<0.01	<0.1	0.9502
FT × SI	9	0.08	5.60	0.01	20.1	**<0.0001**
FT × M	3	0.01	0.55	0.00	5.9	**0.0161**
SI × M	3	<0.01	0.14	<0.01	1.5	0.2799
FT × SI × M	9	<0.01	0.28	<0.01	0.4	0.9222
Residuals	48	0.05	3.60	<0.01		

TABLE 3 ANOVA table (GLM Type I sum of squares) for the response of relative mixture effects on litter mass loss (log transformed) to forest type (FT), litter species richness (SR), litter species composition (SC) and soil fauna community composition (M) and their interactions. *df*, degrees of freedom; *SS*, Type I sum of squares; *MS*, mean square; *F*, *F* statistics; *p*, statistical significance. Significant effects are given in bold

Effect	df	SS	MS	F	p
Forest type (FT)	3	16.34	5.45	7.9	**<0.0001**
Species richness (SR)	2	1.83	0.91	1.3	0.2677
Species composition (SC)	8	8.40	1.05	1.5	0.1525
Fauna community composition (M)	1	0.31	0.31	0.4	0.5037
FT × SR	6	1.27	0.21	0.3	0.9313
FT × SC	24	11.80	0.49	0.7	0.8269
FT × M	3	10.78	3.59	5.2	**0.0019**
M × SR	2	1.39	0.69	1.0	0.3666
M × SC	8	2.20	0.27	0.4	0.9184
FT × SR × M	6	1.19	0.20	0.3	0.9410
FT × SC × M	24	19.82	0.83	1.2	0.2499
Residuals	132	90.53	0.69		

respective species decomposing in monoculture. However, the relative mixture effect differed among the four forest ecosystems, with the difference varying with microarthropod access (Table 3). Indeed, litter mixtures decomposed somewhat more slowly than predicted in the subarctic and temperate forests, but litter mixing had no effect in the boreal and Mediterranean forests (Figure 3). In the subarctic forest the RME changed from an overall positive effect without microarthropods (RME = +1.51%, t_{33} = 0.90), though not significant, to a negative RME when microarthropods had access to the microcosms (RME = −6.77%, t_{33} = −3.81***; Figure S1). This pattern was opposite in the temperate forest, with a strong antagonistic mixture effect without microarthropods (RME = −8.71%, t_{22} = −5.43***), which was attenuated and was no longer significant when microarthropods had access to the microcosms (RME = −2.67%, t_{22} = −1.32; Figure S1).

Similar to the RME, mass loss of individual litter species within mixtures was not affected by leaf litter species richness or composition (Table 4). However, mass loss of different litter species was distinctively influenced by litter mixing, which also depended on the type of forest and the presence of microarthropods as indicated by the significant B × SI × M interaction (Table 4). In general, in mixtures *F. sylvatica* (mean RIP = −5.29%, t_{140} = −2.91*) and *S. cinerea* (mean RIP = −3.17%, t_{140} = −2.97*) decomposed slightly slower, and *A. glutinosa* (mean RIP = +1.64%, t_{140} = +1.36) and in

particular *I. aquifolium* (mean RIP = +2.05%, t_{140} = +2.72*) slightly faster as compared to single species incubations (Figure 4). Mass loss of individual litter species in mixtures was significantly lower as compared to single litter species incubations in the temperate and subarctic forests, particularly for *F. sylvatica* and *S. cinerea* (Figure 4), which also explained the negative RME in these two forests (see above). The impact of microarthropods was minor, with the interactions with forest type and litter species identity being primarily due to a negative effect of soil microarthropods on *A. glutinosa* mass loss in the subarctic forest and positive effects on *A. glutinosa* mass loss in the temperate and Mediterranean forests (Figure S2).

3.3 | Litter traits and decomposition patterns

In single litter species and litter mixtures the set of predictors explaining interspecific variation in litter mass loss differed between forest types, but initial concentrations of Mg, Ca and condensed tannins in the litter were among the best predictors of mass loss across forest types (Table 5). Regression models using only these three leaf litter traits explained the great majority of the variation in litter mass loss in the subarctic (77% of total in monoculture and 59% in
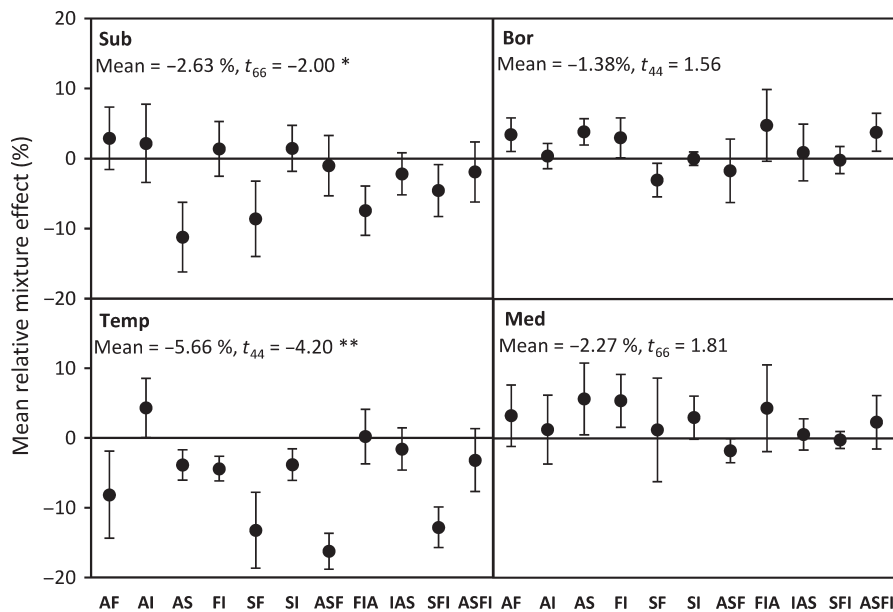
FIGURE 3 Relative mixture effects on leaf litter mass loss for 11 different litter mixtures incubated in the subarctic (Sub), boreal (Bor), temperate (Temp) and Mediterranean forest (Med; Mean ± SE). Data are pooled across soil fauna treatments. Means of six replicates for each litter combination in the subarctic and Mediterranean forest, and four in the temperate and boreal forest (see Section 2). See Figure 2 for abbreviations of litter species. Asterisks indicate significant deviations from zero (Student's t tests; *<0.05, **<0.001, ***<0.0001)

TABLE 4 ANOVA table (GLM Type I sum of squares) for the response of relative individual performance (log transformed) to forest type (FT), litter species identity (SI), litter species richness (SR), litter species composition (SC) and soil fauna community composition (M) and their interactions. df, degrees of freedom; SS, Type I sum of squares; MS, mean square; F, F statistics; p, statistical significance. Significant effects are given in bold

Effect	df	SS	MS	F	p
Forest type (FT)	3	24.34	8.11	8.9	**<0.0001**
Species identity (SI)	3	18.30	6.10	6.7	**0.0002**
Species richness (SR)	2	2.21	1.10	1.2	0.2975
Species composition (SC)	8	4.97	0.62	0.7	0.7066
Fauna community composition (M)	1	0.69	0.69	0.8	0.3841
FT × SI	9	29.97	3.33	3.7	**0.0002**
FT × SR	6	1.89	0.32	0.3	0.9118
FT × SC	24	19.70	0.82	0.9	0.5985
FT × M	3	13.79	4.60	5.1	**0.0019**
SI × SR	6	4.59	0.77	0.8	0.5377
SI × SC	8	4.07	0.51	0.6	0.8112
SI × M	3	2.35	0.78	0.9	0.4606
M × SR	2	3.19	1.60	1.8	0.1737
M × SC	8	3.88	0.48	0.5	0.8316
FT × SI × M	9	26.68	2.96	3.3	**0.0007**
Residuals	464	421.80	0.91		

FIGURE 4 Relative individual performance mass loss of *Ilex aquifolium* (I), *Alnus glutinosa* (A), *Salix cinerea* (S) and *Fagus sylvatica* (F) incubated in mixtures in the subarctic (Sub), boreal (Bor), temperate (Temp) and Mediterranean forest (Med; Mean ± SE). Data are pooled across soil fauna treatments. Means of 42 replicates in the subarctic and Mediterranean forest, and 28 replicates in the temperate and boreal forest (see Section 2). Asterisks indicate significant deviations from zero (Student's t tests; *<0.05, **<0.001, ***<0.0001) [Colour figure can be viewed at wileyonlinelibrary.com]

Regulating factors of litter decomposition may differ between decomposition stages (Berg, 2014; Hättenschwiler et al., 2005) and in our study this may particularly apply to *I. aquifolium* with high mass loss (up to 62%) compared to the other three litter species with mass loss <40% (Figure 2). To inspect this potential effect, we excluded *I. aquifolium* and only used the three litter species likely being at a similar decomposition stage. In this analysis initial Mg, Ca and condensed tannins remained to be the best predictors of mass loss across forest types. Similar to when *I. aquifolium* was included, regression models using only these three

mixture), boreal (92% in monoculture and 81% in mixture), temperate (79% in monoculture and 73% in mixture) and Mediterranean forests (90% in monoculture and 75% in mixture; Table 6). Relationships between mass loss and all litter quality traits analysed are visualized in Figure S3.
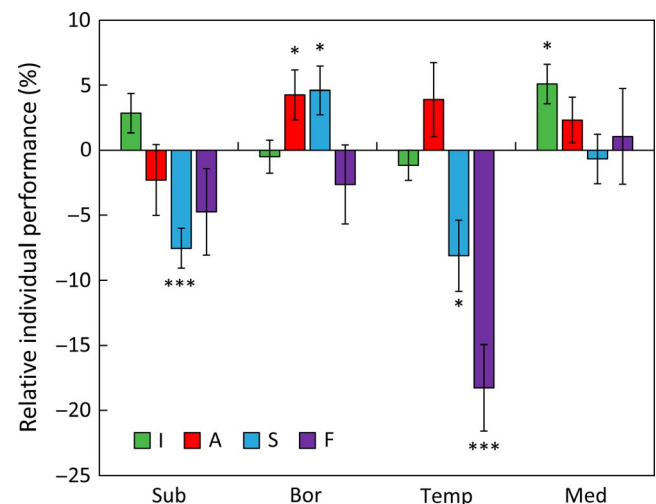
TABLE 5 Results of partial least square regressions for the effects of physical and chemical litter traits on litter mass loss (% of initial, arcsine-square-root transformed) in single litter species and litter mixtures microcosms across four forest types and separately in the subarctic (Sub), boreal (Bor), temperate (Temp) and Mediterranean forest (Med). R^2X = variance of predictors in the models. R^2Y = variance of the dependent variable explained by the models. Predictors most relevant in the models (VIP > 1) are given in bold. Full names of litter traits are given in Table 1

	Gradient		Sub		Bor		Temp		Med	
	Monoculture	Mixture	Monoculture	Mixture	Monoculture	Mixture	Monoculture	Mixture	Monoculture	Mixture
Predictor	*VIP*		*VIP*		*VIP*		*VIP*		*VIP*	
Ca	**1.40**	**1.35**	**1.57**	**1.46**	**1.36**	**1.32**	**1.15**	**1.22**	**1.40**	**1.37**
Mg	**1.35**	**1.34**	**1.22**	**1.26**	**1.34**	**1.32**	**1.41**	**1.37**	**1.35**	**1.35**
Tan	**1.27**	**1.31**	**1.33**	**1.39**	**1.30**	**1.33**	**1.07**	**1.22**	**1.27**	**1.28**
WSC	**1.34**	**1.27**	**1.27**	**1.23**	**1.29**	**1.24**	**1.34**	**1.28**	**1.33**	**1.31**
C	**1.23**	**1.24**	0.99	**1.10**	**1.24**	**1.24**	**1.40**	**1.33**	**1.23**	**1.24**
P	**1.23**	**1.18**	**1.08**	**1.07**	**1.20**	**1.14**	**1.34**	**1.24**	**1.23**	**1.21**
Lig	**1.20**	**1.25**	0.97	**1.14**	**1.24**	**1.28**	**1.31**	**1.33**	**1.19**	**1.23**
T-Phen	**1.15**	**1.19**	**1.32**	**1.34**	**1.18**	**1.22**	0.87	**1.06**	**1.16**	**1.17**
Tough	**1.05**	**1.08**	0.71	0.88	**1.07**	**1.08**	**1.31**	**1.22**	**1.04**	**1.07**
Hcell	**1.03**	0.92	**1.36**	**1.09**	0.94	0.86	0.71	0.74	**1.05**	0.97
N	0.90	0.91	**1.23**	**1.15**	0.90	0.93	0.47	0.70	0.91	0.90
Cell	0.73	0.83	0.75	0.91	0.81	0.90	0.56	0.78	0.73	0.78
Wsat	0.70	0.58	0.63	0.49	0.62	0.51	0.82	0.63	0.70	0.65
Ten	0.64	0.73	0.19	0.49	0.71	0.76	0.99	0.92	0.62	0.69
3D	0.55	0.68	0.44	0.68	0.65	0.76	0.52	0.70	0.54	0.61
Na	0.52	0.63	0.09	0.42	0.61	0.69	0.84	0.82	0.50	0.58
pH	0.28	0.13	0.71	0.35	0.16	0.06	0.08	0.07	0.29	0.20
K	0.26	0.21	0.11	0.05	0.23	0.17	0.67	0.41	0.25	0.24
S-Phen	0.18	0.26	0.43	0.47	0.23	0.32	0.17	0.10	0.19	0.21
R^2X	0.50	0.50	0.48	0.49	0.50	0.50	0.50	0.50	0.50	0.50
R^2Y	0.58	0.33	0.84	0.65	0.97	0.90	0.85	0.80	0.91	0.78

TABLE 6 Results of partial least square (PLS) regressions for the effects of fixed subsets of litter traits on litter mass loss (% of initial, arcsine-square-root transformed) in single litter species and litter mixtures microcosms across four forest types and separately in the subarctic (Sub), boreal (Bor), temperate (Temp) and Mediterranean (Med) forest. Full names of litter traits are given in Table 1; see Table 5 for abbreviations of PLS regression parameters

	Gradient		Sub		Bor		Temp		Med	
	Monoculture	Mixture	Monoculture	Mixture	Monoculture	Mixture	Monoculture	Mixture	Monoculture	Mixture
Predictor	*VIP*		*VIP*		*VIP*		*VIP*		*VIP*	
Ca	1.03	1.02	1.15	1.10	1.01	1.02	0.88	0.95	1.03	1.02
Mg	1.00	1.01	0.89	0.95	1.00	1.02	1.08	1.06	0.99	1.00
Tan	0.97	0.97	0.94	0.93	0.97	0.96	1.03	0.99	0.98	0.97
R^2X	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92	0.92
R^2Y	0.57	0.31	0.77	0.59	0.92	0.81	0.79	0.73	0.90	0.75

leaf litter traits also explained the great majority of the variation in litter mass loss in the subarctic (93% of total in monoculture and 66% in mixture), boreal (97% in monoculture and 90% in mixture), temperate (41% in monoculture and 75% in mixture) and Mediterranean forests (91% in monoculture and 80% in mixture; Table S3).

4 | DISCUSSION

4.1 | Single litter species decomposition

In support of our first hypothesis, the four different litter species used in our study differed considerably in their mass loss

across biomes, but mass loss of the different species was consistent across biomes, indicating that leaf litter mass loss primarily depends on leaf litter species identity and local environmental context. Contrary to our third hypothesis, however, litter mass loss was little affected by the access of microarthropods to mesocosms, indicating that microarthropods little affected litter decomposition.

In general, leaf litter mass loss in single species treatments was lowest in *F. sylvatica* (15%) and highest in *I. aquifolium* (62%), but the reported significant interaction between forest type and litter species identity suggests that species differences also depended on site-specific conditions. Interestingly, the differences among the four species were pronounced and consistent in the three forest types where the species used for our decomposition study do not occur naturally (subarctic, boreal and Mediterranean), but were attenuated at the site of origin. In particular, the two slowly decomposing species *F. sylvatica* and *S. cinerea* decomposed comparatively more rapidly at their site of origin, resulting in home-field advantage effects. The observed home-field advantage effects may have been due to the decomposer community being adapted to the specific litter species, potentially facilitating the decomposition of otherwise relatively slow-decomposing litter species (Ayres et al., 2009). However, a previous study with a reciprocal transplant approach using 16 different litter species, including the same four species used in our study, did not show home-field advantage in the respective sites of origin (Makkonen et al., 2012). Another large-scale study including different litter species also observed consistent differences in decomposition across different sites irrespective of litter origin (Parton et al., 2007), supporting the assumption of fundamental litter quality constraints on decomposers regardless of litter origin. However, because we lost one block in the temperate forest, we cannot exclude a potential bias due to low replication since high decomposition of *F. sylvatica* and *S. cinerea* monospecific litter in the remaining two blocks might reflect slightly more favourable micro-environmental conditions. Furthermore, considering that the Mediterranean forest may be limited by rainfall, while the other three northern sites (i.e. subarctic, boreal, temperate forests) may be limited by temperature, we checked for consistency when excluding Mediterranean site. Species identity explained the majority of the variance in litter mass loss (49%), with the effect of microarthropod access being non-significant (Table S2); overall, supporting the main results and conclusions of the study including all four sites.

Although litter mass loss was little affected when microarthropods had access to the microcosms, the microarthropod effect varied among forest types, which appeared to be a consequence of rather slower mass loss in the subarctic forest when microarthropods had access. The observed negative effect of microarthropod on decomposition could mean that grazing on fungal hyphae by microarthropods disrupted decomposer communities in the subarctic forest more than in other forests, leading to rather slower decomposition contrary to what has been shown previously (Scheu, Ruess, & Bonkowski, 2005; Seastedt, 1984). Our findings are in

contradiction to previous studies demonstrating a largely consistent positive effect of soil fauna on litter mass loss at a global scale (García-Palacios et al., 2013; Wall et al., 2008). These latter meta-analyses, however, did not discriminate clearly among different groups of fauna and included also studies allowing access by macrofauna, which were excluded with our mesh width of 1 mm. Indeed, in previous studies using three different mesh sizes to partition microarthropod and macrofauna effects, comparatively small effects of microarthropods were reported, in line with our results, whereas stronger effects occurred when macrofauna additionally had access (Handa et al., 2014; Makkonen et al., 2012). Importantly, the lack of effects of microarthropods on litter decomposition might have been due to the use of standard litter from one biome exposed across biomes. In fact, there is evidence that the decomposer community may preferentially process litter of native plant species rather than litter of foreign species (Asplund et al., 2018; Freschet, Aerts, & Cornelissen, 2012).

4.2 | Litter mixture effects

In contrast to our first hypothesis, RME differed among forest types, suggesting that non-additive effects on litter decomposition are not only determined by species-specific litter properties within mixtures, but also depend on environmental context. The different litter species included in the mixtures differed strongly in their response to litter mixing, independently of litter species richness or composition of the mixtures. Furthermore, the presence of microarthropods modified litter mixture effects on decomposition only weakly, which is contrary to our expectation that a more complete decomposer community should amplify mixture effects, but is in line with the overall weak effect of the presence of microarthropods we reported for single litter species decomposition.

Similar to the results of our study Madritch and Cardinale (2007) found non-additive effects on litter mixture decomposition to also depend on the environmental context and not only on species-specific properties of litter within mixtures. In their study, they found that the effects of leaf litter diversity were non-additive and the exact nature of these effects were spatially variable because the performance of individual litter species changed across the heterogeneous landscape. In our study, the non-additive mixture effects were only significant in two out of the four forest types studied and they were predominantly negative. Surprisingly, these antagonistic effects were particularly strong in the temperate forest, the site of origin of the litter, and somewhat less in the subarctic forest. In the other two sites of boreal and Mediterranean forests, mixing had no effect on litter mass loss. We would have expected that long-term adaptation of local decomposer communities should rather favour synergistic litter mixture effects at the site of origin of the litter as it was reported for a tropical forest (Barantal, Roy, Fromin, Schimann, & Hättenschwiler, 2011). However, the ability of the decomposer community to respond to a range of litter qualities may be restricted due to adaptation to local low-quality litter (Austin,

Vivanco, Gonzalez-Arzac, & Perez, 2014) and this may result in complementary or antagonistic effects of home-field advantage in decomposing litter mixtures. There could be several reasons for the unexpected results reported here. On one hand, antagonistic effects can be attributed to interactions with inhibitory fungal substances or plant secondary compounds (e.g. polyphenols), which vary in their occurrence among different species (Gessner et al., 2010; Trogisch, He, Hector, & Scherer-Lorenzen, 2016). Since we used the same litter species, litter-inherent secondary compounds were the same at all sites and indeed could have favoured antagonistic effects at sites where these compounds are not naturally present such as in the subarctic forest. On the contrary, the adaptation of local decomposer organisms to these compounds in the temperate forest is expected to reduce antagonistic effects unlike what we observed here. On the other hand, since we harvested the litter at all sites after a fixed amount of time, another explanation for our results could be varying non-additive effects depending on the decomposition stage (Lecerf et al., 2011), which was more advanced in the temperate forest as compared to the other forests. However, since decomposition was least advanced in the subarctic forest, the other site with antagonistic mixture effects, it seems unlikely that the same mechanism is at work, although mixture effects on decomposition have been shown to change during incubation (Lecerf et al., 2011; Srivastava et al., 2009) and to predominate at early or late stages of litter decomposition (Butenschoen et al., 2014; Chen, Peng, D'Antonio, Li, & Ren, 2013; Wu, Li, & Wan, 2013). Finally, we cannot exclude the possibility that due to low replication, especially in the temperate forest, monospecific litter decomposition might have been overestimated as indicated by the particular high mass loss in *F. sylvatica* and *S. cinerea* single species microcosms in the temperate forest. The low replication would then lead to an artificially strong antagonistic effect in litter mixtures, which may explain the contrasting results of our study with a previous, better replicated, study using the same litter species (Handa et al., 2014). Overall, however, our results indicate that litter mixture effects vary among forest types despite identical leaf chemistry, but the mechanisms underlying the antagonistic mixture effects need further investigation. Knowledge on the functional breadth and importance of soil organisms for litter decomposition will facilitate uncovering these mechanisms (Austin et al., 2014).

The different litter species included in the mixtures differed strongly in their responses to litter mixing, independently of litter species richness or composition of the mixtures. These differences were mainly the result of slower decomposition in the mixtures of the two more slowly decomposing species *F. sylvatica* and *S. cinerea*, and faster decomposition of the two more rapidly decomposing species *A. glutinosa* and *I. aquifolium*. The faster decomposition of the latter two species could indicate preferential decomposition of more easily decomposable litter when there is a choice in litter mixtures. Such choice effects have been observed in previous studies with litter feeding detritivores showing preferentially feeding or avoiding of certain litter species in mixtures (Hättenschwiler & Bretscher, 2001; Hättenschwiler & Gasser, 2005; Vos et al., 2011). In this study, detritivorous macrofauna did not have access to the

microcosms, suggesting that the microbial community, the ultimate actor in the decomposition process, could also preferentially process some high quality litter in mixtures (Butenschoen et al., 2014; Santonja, Rancon, et al., 2017). However, it remains unclear whether this effect was due to changes in the activity or composition of microbial communities in response to mixing, as we did not analyse microbial parameters on constituent leaf litter species, which could be a valuable measure for a better mechanistic understanding of leaf litter mixing effects on decomposition in future studies.

Although the presence of microarthropods modified litter mixture effects on decomposition only weakly, their effect varied among biomes. In the subarctic and the temperate forest, microarthropod communities altered the observed antagonistic mixture effects towards stronger (subarctic forest) and weaker (temperate forest) effects, which may be explained by their distinct interactions with microbial communities depending on the environmental context, microbial community composition or decomposition stage as discussed above. These patterns were also observed for individual species within the litter mixtures, suggesting that microarthropod effects on litter decomposition change with plant litter diversity. For instance, *A. glutinosa* mass loss was reduced by microarthropods in the subarctic forest, but enhanced in the temperate and Mediterranean forests. Likewise, mass loss of *S. cinerea* and *F. sylvatica* was lower in the subarctic and the boreal forest, respectively, when microarthropods were present, but not in any other forest. All these microarthropod effects are likely indirect via imposed modifications of microbial activity and/or composition, but remain poorly understood. More generally, the wider geographical patterns of the distribution of soil fauna and their impact on decomposition and related ecosystem processes are also weakly documented and understood (Fierer, Strickland, Liptzin, Bradford, & Cleveland, 2009; Wu et al., 2011). However, differences in soil fauna communities and nutritional constraints across biomes likely contributed to the variable effects of soil microarthropods across forest types and litter species in this study.

4.3 | Consistent litter traits control decomposition

In support of our second hypothesis, using common litter from a temperate forest across biomes, we identified a set of easy to measure litter traits, i.e. concentrations of Mg, Ca and condensed tannins, explaining most of the variation in mass loss both in single litter species and litter mixtures across and among the different forests along the large latitudinal range. The strong litter identity effect confirms the important control of litter-specific initial quality in driving decomposition independently of any additional differences in environmental conditions and decomposer communities shown before (Makkonen et al., 2012). The fact that the initial concentrations of Mg, Ca and condensed tannins of litter accounted for most of the variability in mass loss also held if the species which by the end of the experiment potentially being at a later stage of decay, i.e. *I. aquifolium*, was excluded. Magnesium is not

commonly among the main predictors of leaf litter decomposition, in part because it is measured less regularly in litter decomposition studies compared to other traits such as N concentration or its ratio with C and lignin (Berg, 2014; García-Palacios, McKie, et al., 2016). However, more recent studies also identified Mg as key trait that strongly and positively affects decomposition in different ecosystems (García-Palacios, McKie, et al., 2016; Joly et al., 2017; Makkonen et al., 2012). Magnesium is essential to all living cells, as Mg is involved with critically important compounds such as DNA, RNA and ATP and is of prime importance for the functioning of many enzymes (Council, 2005; Gottschalk, 2012), suggesting that high Mg concentrations support microbial activity and enhance leaf litter mass loss. Positive correlations between initial Ca concentration and litter decomposition have also been reported previously (Berg et al., 2017; Hobbie et al., 2006; Joly et al., 2017; Makkonen et al., 2012). Calcium stimulation was proposed to act indirectly via soil pH or by directly stimulating earthworm activity (Reich et al., 2005) and cuticle construction of oribatid mites (Gist & Crossley, 1975; Norton & Behan-Pelletier, 1991). Because macrofauna had no access to our field microcosms and because we studied decomposition over a relatively short time span, which is not sufficient to change soil pH values, our data indicate that microorganisms responded positively to Ca in decomposing litter. In fact, liming experiments have found strong stimulation of litter decomposition rates after Ca addition to forest floors (McCay, Cardelús, & Neatrour, 2013) and streams (McKie, Petrin, & Malmqvist, 2006), especially in ecosystems in which ambient Ca concentrations are low (García-Palacios, McKie, et al., 2016). We also found concentrations of condensed tannins to be strongly and negatively related to mass loss in our regression models as tannins are known to slow down decomposition as they can be unpalatable to decomposers through their toxicity or by binding with dietary proteins or digestive enzymes (Coulis, Hättenschwiler, Rapior, & Coq, 2009; Makkonen et al., 2012). Moreover, condensed tannins may also slow decomposition and N mineralization by forming recalcitrant complexes with organic N (Madritch & Lindroth, 2015). In our study, condensed tannins were measured using the butanol-HCl method according to Porter, Hirstich, and Chan (1985) and Waterman and Mole (1994); as there are many methods for quantifying tannins with their efficiency varying between species our results, however, have to be interpreted with care. Supporting previous findings, our results suggest that mass loss in leaf litter species can be predicted by a basic set of litter traits, which are consistent across biomes (Cornwell et al., 2008; Joly et al., 2017; Makkonen et al., 2012; Parton et al., 2007). Remarkably, leaf litter traits that received little attention in previous studies were of major importance in our regression models, whereas traits commonly used in decomposition models, e.g. N concentration and C-to-N ratio, had only minor explanatory power. Although the four litter species used were selected to cover a wide range of litter traits, at least in part these discrepancies might be due to the fact that we only used four litter species, whereas previous studies such as Makkonen et al. (2012) and Joly et al. (2017) included a

wider range of species likely including a wider range of litter traits. In the future, more traits should be included, such as Mn, a cofactor and regulator of lignin-decay enzymes produced by fungi (Berg et al., 2007; Whalen, Smith, Grandy, & Frey, 2018), and other elements including heavy metals (e.g. lead, cadmium and chromium) potentially affecting the formation of stable humus compounds (Berg, 2014). Moreover, to better understand and predict biogeochemical cycles at large scales, expanding the scope of trait-based approaches is needed and a wider range of litter species needs to be included.

In line with the very consistent effects of plant litter identity and functional traits on decomposition of single litter species across biomes (Makkonen et al., 2012), in our study three litter traits predicted litter mass loss of single litter species and mixtures very well across forest types and biomes, regardless of species richness and microarthropod presence. The results suggest that the role of litter traits for decomposition across biomes is invariant of litter mixture effects. However, differences in RME among forest types suggest that non-additive effects are an important component of the decomposition of litter in mixtures and these effects cannot be predicted easily from species-specific litter traits, indicating that even if the initial leaf litter characteristics are identical local environmental conditions modify litter decomposition processes in mixtures. Overall, the results of our study suggest that the environmental context of decomposing litter mixtures, including microarthropod communities, determine the decomposition of litter mixtures besides strong litter trait-based effects.

5 | CONCLUSIONS

Results of our litter decomposition study across a large latitudinal gradient and four forest types, indicate that, at least during the initial stage of decomposition, leaf litter mass loss primarily depends on leaf litter species identity and local environmental context, whereas litter diversity and the access to the litter by microarthropods had mostly minor effects on litter decomposition. As expected from the distinct initial quality, the four litter species used in our study differed considerably in their mass loss after approximately 1 year of field exposure and this was consistent across forest types over this large latitudinal gradient. RME differed among forest types, suggesting that non-additive effects on litter decomposition are not only determined by species-specific litter properties within mixtures, but also depend on environmental context. The different litter species included in the mixtures differed strongly in their responses to litter mixing, independently of litter species richness or composition of the mixtures. Notably, using common litter from a temperate forest across biomes we identified a set of easy to measure litter traits, i.e. concentrations of Mg, Ca and condensed tannins, explaining most of the variation in mass loss both in single litter species and litter mixtures. Our results also suggest limited impact of soil microarthropods on microbial-driven decomposition processes, but this may differ

in native litter species of individual forest types. More functional groups of litter species from a wider range of forest types as well as microbial parameters in decomposing leaf litter are needed to advance our understanding of driving factors of litter decomposition across biomes and to explore the generality of these findings allowing to improve predictions on how changes in plant species diversity impacts C dynamics in terrestrial ecosystems.

AUTHORS' CONTRIBUTIONS

S.S., O.B. and S.H. initiated the idea and designed the study; O.B., S.B., I.T.H., M.M. and V.V. conducted the research and collected the data; S.Z. and O.B. performed statistical analysis; S.Z., O.B. and S.S. drafted the manuscript with contributions from I.T.H., M.P.B., S.H. and B.M. and all authors contributed substantially to the revisions.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository http://doi.org/10.5061/dryad.9cnp5hqdk (Zhou et al., 2020).

ORCID

Shixing Zhou https://orcid.org/0000-0003-4228-4227
Olaf Butenschoen https://orcid.org/0000-0003-1866-9805
Sandra Barantal https://orcid.org/0000-0002-0663-0914
Ira Tanya Handa https://orcid.org/0000-0002-7272-031X
Rien Aerts https://orcid.org/0000-0001-6694-0669
Matty P. Berg https://orcid.org/0000-0001-8442-8503
Brendan McKie https://orcid.org/0000-0002-1796-9497
Jasper Van Ruijven https://orcid.org/0000-0003-0003-2363
Stefan Scheu https://orcid.org/0000-0003-4350-9520

REFERENCES

Adair, E. C., Parton, W. J., Del Grosso, S. J., Silver, W. L., Harmon, M. E., Hall, S. A., … Hart, S. C. (2008). Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. *Global Change Biology*, 14, 2636–2660. https://doi.org/10.1111/j.1365-2486.2008.01674.x

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos*, 79, 439–449. https://doi.org/10.2307/3546886

Andersen, C. M., & Bro, R. (2010). Variable selection in regression—A tutorial. *Journal of Chemometrics*, 24, 728–737. https://doi.org/10.1002/cem.1360

Anderson, J., Ineson, P., & Huish, S. (1983). Nitrogen and cation mobilization by soil fauna feeding on leaf litter and soil organic matter from deciduous woodlands. *Soil Biology and Biochemistry*, 15, 463–467. https://doi.org/10.1016/0038-0717(83)90012-3

Asplund, J., Kauserud, H., Bokhorst, S., Lie, M. H., Ohlson, M., & Nybakken, L. (2018). Fungal communities influence decomposition rates of plant litter from two dominant tree species. *Fungal Ecology*, 32, 1–8. https://doi.org/10.1016/j.funeco.2017.11.003

Austin, A. T., Vivanco, L., Gonzalez-Arzac, A., & Perez, L. I. (2014). There's no place like home? An exploration of the mechanisms behind plant litter-decomposer affinity in terrestrial ecosystems. *New Phytologist*, 204(2), 307–314. https://doi.org/10.1111/nph.12959.

Ayres, E., Steltzer, H., Simmons, B. L., Simpson, R. T., Steinweg, J. M., Wallenstein, M. D., … Wall, D. H. (2009). Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biology and Biochemistry*, 41, 606–610. https://doi.org/10.1016/j.soilbio.2008.12.022

Barantal, S., Roy, J., Fromin, N., Schimann, H., & Hättenschwiler, S. (2011). Long-term presence of tree species but not chemical diversity affect litter mixture effects on decomposition in a neotropical rainforest. *Oecologia*, 167, 241. https://doi.org/10.1007/s00442-011-1966-4

Berg, B. (2014). Decomposition patterns for foliar litter – A theory for influencing factors. *Soil Biology and Biochemistry*, 78, 222–232. https://doi.org/10.1016/j.soilbio.2014.08.005

Berg, B., Berg, M. P., Bottner, P., Box, E., Breymeyer, A., de Anta, R. C., … de Santo, A. V. (1993). Litter mass loss rates in pine forests of Europe and Eastern United States: Some relationships with climate and litter quality. *Biogeochemistry*, 20, 127–159. https://doi.org/10.1007/BF00000785

Berg, B., Johansson, M.-B., Liu, C., Faituri, M., Sanborn, P., Vesterdal, L., … Ukonmaanaho, L. (2017). Calcium in decomposing foliar litter – A synthesis for boreal and temperate coniferous forests. *Forest Ecology and Management*, 403, 137–144. https://doi.org/10.1016/j.foreco.2017.08.022

Berg, B., Steffen, K., & McClaugherty, C. (2007). Litter decomposition rate is dependent on litter Mn concentrations. *Biogeochemistry*, 82, 29–39. https://doi.org/10.1007/s10533-006-9050-6

Boyero, L., Graça, M. A. S., Tonin, A. M., Pérez, J., J. Swafford, A., Ferreira, V., … Pearson, R. G. (2017). Riparian plant litter quality increases with latitude. *Scientific Reports*, 7, 10562. https://doi.org/10.1038/s41598-017-10640-3

Bradford, M. A., Berg, B., Maynard, D. S., Wieder, W. R., Wood, S. A., & Cornwell, W. (2016). Understanding the dominant controls on litter decomposition. *Journal of Ecology*, 104, 229–238. https://doi.org/10.1111/1365-2745.12507

Bradford, M. A., Tordoff, G. M., Eggers, T., Jones, T. H., & Newington, J. E. (2002). Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos*, 99, 317–323. https://doi.org/10.1034/j.1600-0706.2002.990212.x

Butenschoen, O., Krashevska, V., Maraun, M., Marian, F., Sandmann, D., & Scheu, S. (2014). Litter mixture effects on decomposition in tropical montane rainforests vary strongly with time and turn negative at later stages of decay. *Soil Biology and Biochemistry*, 77, 121–128. https://doi.org/10.1016/j.soilbio.2014.06.019

Chapin, I. F. S., Matson, P. A., & Vitousek, P. (2011). *Principles of terrestrial ecosystem ecology*, New York, NY: Springer.

Chen, B., Peng, S., D'Antonio, C. M., Li, D., & Ren, W. (2013). Non-additive effects on decomposition from mixing litter of the invasive *Mikania micrantha* HBK with native plants. *PLoS ONE*, 8, e66289.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., … Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, 11, 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Coulis, M., Hättenschwiler, S., Rapior, S., & Coq, S. (2009). The fate of condensed tannins during litter consumption by soil animals. *Soil Biology and Biochemistry*, 41, 2573–2578. https://doi.org/10.1016/j.soilbio.2009.09.022

Council, N. R. (2005). *Mineral tolerance of animals: Second revised edition, 2005*. Washington, DC: The National Academies Press.

Currie, W. S., Harmon, M. E., Burke, I. C., Hart, S. C., Parton, W. J., & Silver, W. (2010). Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale. *Global Change Biology*, 16, 1744–1761. https://doi.org/10.1111/j.1365-2486.2009.02086.x

Djukic, I., Kepfer-Rojas, S., Schmidt, I. K., Larsen, K. S., Beier, C., Berg, B., … Tóth, Z. (2018). Early stage litter decomposition across biomes. *Science of the Total Environment*, 628–629, 1369–1394. https://doi.org/10.1016/j.scitotenv.2018.01.012

Fierer, N., Strickland, M. S., Liptzin, D., Bradford, M. A., & Cleveland, C. C. (2009). Global patterns in belowground communities. *Ecology Letters*, 12, 1238–1249. https://doi.org/10.1111/j.1461-0248.2009.01360.x

Freschet, G. T., Aerts, R., & Cornelissen, J. H. (2012). Multiple mechanisms for trait effects on litter decomposition: Moving beyond home-field advantage with a new hypothesis. *Journal of Ecology*, 100, 619–630. https://doi.org/10.1111/j.1365-2745.2011.01943.x

García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. *Ecology Letters*, 16, 1045–1053. https://doi.org/10.1111/ele.12137

García-Palacios, P., McKie, B. G., Handa, I. T., Frainer, A., & Hattenschwiler, S. (2016). The importance of litter traits and decomposers for litter decomposition: A comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology*, 30, 819–829. https://doi.org/10.1111/1365-2435.12589

García-Palacios, P., Shaw, E. A., Wall, D. H., & Hattenschwiler, S. (2016). Temporal dynamics of biotic and abiotic drivers of litter decomposition. *Ecology Letters*, 19, 554–563. https://doi.org/10.1111/ele.12590

García-Palacios, P., Shaw, E. A., Wall, D. H., & Hattenschwiler, S. (2017). Contrasting mass-ratio vs. niche complementarity effects on litter C and N loss during decomposition along a regional climatic gradient. *Journal of Ecology*, 105, 968–978. https://doi.org/10.1111/1365-2745.12730

Gartner, T. B., & Cardon, Z. G. (2004). Decomposition dynamics in mixed-species leaf litter. *Oikos*, 104, 230–246. https://doi.org/10.1111/j.0030-1299.2004.12738.x

Geladi, P., & Kowalski, B. R. (1986). Partial least-squares regression: A tutorial. *Analytica Chimica Acta*, 185, 1–17. https://doi.org/10.1016/0003-2670(86)80028-9

Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology & Evolution*, 25, 372–380. https://doi.org/10.1016/j.tree.2010.01.010

Gholz, H. L., Wedin, D. A., Smitherman, S. M., Harmon, M. E., & Parton, W. J. (2000). Long-term dynamics of pine and hardwood litter in contrasting environments: Toward a global model of decomposition. *Global Change Biology*, 6, 751–765. https://doi.org/10.1046/j.1365-2486.2000.00349.x

Gist, C. S., & Crossley, D. A. (1975). The litter arthropod community in a southern appalachian hardwood forest: Numbers, biomass and mineral element content. *The American Midland Naturalist*, 93, 107–122. https://doi.org/10.2307/2424109

Gottschalk, G. (2012). *Bacterial metabolism*, New York, NY: Springer.

Guerrero-Ramírez, N. R., Craven, D., Messier, C., Potvin, C., Turner, B. L., & Handa, I. T. (2016). Root quality and decomposition environment, but not tree species richness, drive root decomposition in tropical forests. *Plant and Soil*, 404, 125–139. https://doi.org/10.1007/s11104-016-2828-y

Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., … Hattenschwiler, S. (2014). Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, 509, 218–221. https://doi.org/10.1038/nature13247

Hättenschwiler, S., & Bretscher, D. (2001). Isopod effects on decomposition of litter produced under elevated CO_2, N deposition and different soil types. *Global Change Biology*, 7, 565–579. https://doi.org/10.1046/j.1365-2486.2001.00402.x

Hättenschwiler, S., & Gasser, P. (2005). Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 1519–1524. https://doi.org/10.1073/pnas.0404977102

Hättenschwiler, S., & Jørgensen, H. B. (2010). Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. *Journal of Ecology*, 98, 754–763. https://doi.org/10.1111/j.1365-2745.2010.01671.x

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 36, 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Hobbie, S. E., Reich, P. B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., & Karolewski, P. (2006). Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology*, 87, 2288–2297. https://doi.org/10.1890/0012-9658(2006)87[2288:TSEODA]2.0.CO;2

Joly, F.-X., Milcu, A., Scherer-Lorenzen, M., Jean, L.-K., Bussotti, F., Dawud, S. M., … Hättenschwiler, S. (2017). Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. *New Phytologist*, 214, 1281–1293. https://doi.org/10.1111/nph.14452

Lecerf, A., Marie, G., Kominoski, J. S., LeRoy, C. J., Bernadet, C., & Swan, C. M. (2011). Incubation time, functional litter diversity, and habitat characteristics predict litter-mixing effects on decomposition. *Ecology*, 92, 160–169. https://doi.org/10.1890/10-0315.1

López-Rojo, N., Martínez, A., Pérez, J., Basaguren, A., Pozo, J., & Boyero, L. (2018). Leaf traits drive plant diversity effects on litter decomposition and FPOM production in streams. *PLoS ONE*, 13, e0198243. https://doi.org/10.1371/journal.pone.0198243

Lummer, D., Scheu, S., & Butenschoen, O. (2012). Connecting litter quality, microbial community and nitrogen transfer mechanisms in decomposing litter mixtures. *Oikos*, 121, 1649–1655. https://doi.org/10.1111/j.1600-0706.2011.20073.x

Madritch, M. D., & Cardinale, B. J. (2007). Impacts of tree species diversity on litter decomposition in northern temperate forests of Wisconsin, USA: A multi-site experiment along a latitudinal gradient. *Plant and Soil*, 292, 147–159. https://doi.org/10.1007/s11104-007-9209-5

Madritch, M. D., & Lindroth, R. L. (2015). Condensed tannins increase nitrogen recovery by trees following insect defoliation. *New Phytologist*, 208, 410–420. https://doi.org/10.1111/nph.13444

Makkonen, M., Berg, M. P., Handa, I. T., Hattenschwiler, S., van Ruijven, J., van Bodegom, P. M., & Aerts, R. (2012). Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecology Letters*, 15, 1033–1041. https://doi.org/10.1111/j.1461-0248.2012.01826.x

Makkonen, M., Berg, M. P., van Logtestijn, R. S., van Hal, J. R., & Aerts, R. (2013). Do physical plant litter traits explain non-additivity in litter mixtures? A test of the improved microenvironmental conditions theory. *Oikos*, 122, 987–997. https://doi.org/10.1111/j.1600-0706.2012.20750.x

McCay, T. S., Cardelús, C. L., & Neatrour, M. A. (2013). Rate of litter decay and litter macroinvertebrates in limed and unlimed forests of the Adirondack Mountains, USA. *Forest Ecology and Management*, 304, 254–260. https://doi.org/10.1016/j.foreco.2013.05.010

McKie, B. G., Petrin, Z., & Malmqvist, B. (2006). Mitigation or disturbance? Effects of liming on macroinvertebrate assemblage structure and leaf-litter decomposition in the humic streams of northern Sweden. *Journal of Applied Ecology*, 43, 780–791. https://doi.org/10.1111/j.1365-2664.2006.01196.x

Norton, R. A., & Behan-Pelletier, V. M. (1991). Calcium carbonate and calcium oxalate as cuticular hardening agents in oribatid mites (Acari: Oribatida). *Canadian Journal of Zoology*, 69, 1504–1511. https://doi.org/10.1139/z91-210

Parton, W., Silver, W. L., Burke, I. C., Grassens, L., Harmon, M. E., Currie, W. S., ... Fasth, B. (2007). Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*, 315, 361–364. https://doi.org/10.1126/science.1134853

Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J. H., Vendramini, F., Cabido, M., & Castellanos, A. (2000). Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant and Soil*, 218, 21–30.

Porter, L. J., Hirstich, L. N., & Chan, B. G. (1985). The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin. *Phytochemistry*, 25, 223–230. https://doi.org/10.1016/S0031-9422(00)94533-3

Prentice, I. C., Farquhar, G., Fasham, M., Goulden, M., Heimann, M., Jaramillo, V., ... Wallace, D. (2001). *The carbon cycle and atmospheric carbon dioxide*. Cambridge, UK: Cambridge University Press.

Rakotomalala, R. (2005). TANAGRA: un logiciel gratuit pour l'enseignement et la recherche. *Actes de EGC'2005, RNTI-E-3*, 2, 697–702.

Reich, P. B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S. E., Eissenstat, D. M., ... Tjoelker, M. G. (2005). Linking litter calcium, earthworms and soil properties: A common garden test with 14 tree species. *Ecology Letters*, 8, 811–818. https://doi.org/10.1111/j.1461-0248.2005.00779.x

Santonja, M., Fernandez, C., Proffit, M., Gers, C., Gauquelin, T., Reiter, I. M., ... McCulley, R. (2017). Plant litter mixture partly mitigates the negative effects of extended drought on soil biota and litter decomposition in a Mediterranean Oak Forest. *Journal of Ecology*, 105, 801–815. https://doi.org/10.1111/1365-2745.12711

Santonja, M., Rancon, A., Fromin, N., Baldy, V., Hättenschwiler, S., Fernandez, C., ... Mirleau, P. (2017). Plant litter diversity increases microbial abundance, fungal diversity, and carbon and nitrogen cycling in a Mediterranean shrubland. *Soil Biology and Biochemistry*, 111, 124–134. https://doi.org/10.1016/j.soilbio.2017.04.006

Scheu, S., Ruess, L., & Bonkowski, M. (2005). Interactions between microorganisms and soil micro-and mesofauna. *Microorganisms in soils: Roles in genesis and functions* (pp. 253–275). Berlin, Heidelberg: Springer.

Schindler, M. H., & Gessner, M. O. (2009). Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology*, 90, 1641–1649. https://doi.org/10.1890/08-1597.1

Seastedt, T. (1984). The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology*, 29, 25–46. https://doi.org/10.1146/annurev.en.29.010184.000325

Srivastava, D. S., Cardinale, B. J., Downing, A. L., Duffy, J. E., Jouseau, C., Sankaran, M., & Wright, J. P. (2009). Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology*, 90, 1073–1083. https://doi.org/10.1890/08-0439.1

Tiegs, S. D., Costello, D. M., Isken, M. W., Woodward, G., McIntyre, P. B., Gessner, M. O., ... Zwart, J. A. (2019). Global patterns and drivers of ecosystem functioning in rivers and riparian zones. *Science Advances*, 5(1), eaav0486. https://doi.org/10.1126/sciadv.aav0486

Tordoff, G. M., Boddy, L., & Jones, T. H. (2008). Species-specific impacts of collembola grazing on fungal foraging ecology. *Soil Biology and Biochemistry*, 40, 434–442. https://doi.org/10.1016/j.soilbio.2007.09.006

Tresch, S., Frey, D., Le Bayon, R. C., Zanetta, A., Rasche, F., Fliessbach, A., & Moretti, M. (2019). Litter decomposition driven by soil fauna, plant diversity and soil management in urban gardens. *Science of the Total Environment*, 658, 1614–1629. https://doi.org/10.1016/j.scitotenv.2018.12.235

Trogisch, S., He, J.-S., Hector, A., & Scherer-Lorenzen, M. (2016). Impact of species diversity, stand age and environmental factors on leaf litter decomposition in subtropical forests in China. *Plant and Soil*, 400, 337–350. https://doi.org/10.1007/s11104-015-2737-5

Vaieretti, M., Harguindeguy, N. P., Gurvich, D., Cingolani, A., & Cabido, M. (2005). Decomposition dynamics and physico-chemical leaf quality of abundant species in a montane woodland in central Argentina. *Plant and Soil*, 278, 223–234. https://doi.org/10.1007/s11104-005-8432-1

Vos, V. C., van Ruijven, J., Berg, M. P., Peeters, E. T., & Berendse, F. (2011). Macro-detritivore identity drives leaf litter diversity effects. *Oikos*, 120, 1092–1098. https://doi.org/10.1111/j.1600-0706.2010.18650.x

Wal, A., Geydan, T. D., Kuyper, T. W., & Boer, W. (2013). A thready affair: Linking fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiology Reviews*, 37, 477–494. https://doi.org/10.1111/1574-6976.12001

Wall, D. H., Bradford, M. A., St. john, M. G., Trofymow, J. A., Behan-pelletier, V., Bignell, D. E., ... Zou, X. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, 14, 2661–2677. https://doi.org/10.1111/j.1365-2486.2008.01672.x

Wardle, D., Bonner, K., & Nicholson, K. (1997). Biodiversity and plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos*, 247–258. https://doi.org/10.2307/3546010

Wardle, D., Yeates, G., Barker, G., & Bonner, K. (2006). The influence of plant litter diversity on decomposer abundance and diversity. *Soil Biology and Biochemistry*, 38, 1052–1062. https://doi.org/10.1016/j.soilbio.2005.09.003

Waterman, P. G., & Mole, S. (1994). *Analysis of phenolic plant metabolites – Methods in ecology*. Oxford: Blackwell Scientific Publications.

Whalen, E. D., Smith, R. G., Grandy, A. S., & Frey, S. D. (2018). Manganese limitation as a mechanism for reduced decomposition in soils under atmospheric nitrogen deposition. *Soil Biology and Biochemistry*, 127, 252–263. https://doi.org/10.1016/j.soilbio.2018.09.025

Woodward, G., Gessner, M. O., Giller, P. S., Gulis, V., Hladyz, S., Lecerf, A., ... Chauvet, E. (2012). Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science*, 336, 1438–1440. https://doi.org/10.1126/science.1219534

Wu, D., Li, T., & Wan, S. (2013). Time and litter species composition affect litter-mixing effects on decomposition rates. *Plant and Soil*, 371, 355–366. https://doi.org/10.1007/s11104-013-1697-x

Wu, L., Feinstein, L. M., Valverde-Barrantes, O., Kershner, M. W., Leff, L. G., & Blackwood, C. B. (2011). Placing the effects of leaf litter diversity on saprotrophic microorganisms in the context of leaf type and habitat. *Microbial Ecology*, 61, 399–409. https://doi.org/10.1007/s00248-010-9760-0

Zhang, D., Hui, D., Luo, Y., & Zhou, G. (2008). Rates of litter decomposition in terrestrial ecosystems: Global patterns and controlling factors. *Journal of Plant Ecology*, 1, 85–93. https://doi.org/10.1093/jpe/rtn002

Zhou, S., Butenschoen, O., Barantal, S., Handa, I. T., Makkonen, M., Vos, V., ... Scheu, S. (2020). Data from: Decomposition of leaf litter mixtures across biomes: The role of litter identity, diversity and soil fauna. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.9cnp5hqdk

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.