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Resolving the intricate role of climate in litter decomposition

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Summary paragraph

With ~60 Pg of carbon (C) released as CO_2 annually, the decomposition of dead organic matter feeds the major terrestrial global CO_2 flux to the atmosphere. Macroclimate control over this critical C flux facilitates the parametrization of the C cycle in Earth system models, and the understanding of climate change effects on the global C balance. Yet, the long-standing paradigm of climate control was recently challenged by the so far underestimated environmental heterogeneity at local scales, questioning the conceptual framework of thousands of decomposition studies and accuracy of current predictive models. Using three complementary decomposition experiments at European scale, we showed that macroclimate and litter characteristics largely control plant litter decomposition, reaffirming the role of macroclimate as integrative decomposition driver through direct environmental control and by influencing co-evolving local plant and decomposer communities. Neglecting this latter indirect effect, commonly-used standard litter types overrated micro-environmental control and failed to predict local decomposition of plot-specific litter. Our data help clarify a key question on the regulation of the global C cycle by identifying the relative role of control factors over decomposition and the scales at which they matter, and by highlighting sources of confusion in the literature.

Main text

The seminal synthesis by Swift et al.[1] laid the ground for the long-standing paradigm of the hierarchical control of organic matter decomposition dominated by climate, with only a secondary role by the biological components through the chemical and physical characteristics of the decomposing material, and a minor role by decomposer organisms[1–4]. The climate centred view was challenged by a synthesis across a large number of studies showing that characteristics of the decomposing material contribute considerably more to variation in decomposition than climate parameters[5]. More recently, a number of studies showed a surprisingly weak influence of climate parameters on decomposition across large spatial scales, when local environmental factors at the site and within-site scale were integrated in the analyses[6–9]. Collapsing within-site variability in decomposition into single mean values, as was usually done in large-scale studies, may misleadingly exacerbate the climate control over decomposition while underrating small local scale heterogeneity in environmental factors[6,7].

The uncertainty about the degree of climate control on decomposition – and thus, one of the most important global C fluxes – has important implications for the general understanding of the spatial patterns and mechanisms underlying decomposition, for model parametrization, and for accurate predictions of the consequences of climate change across spatial scales. We believe that much of this uncertainty comes from comparing apples with oranges, i.e., experiments and approaches that are not comparable or that answer different parts of the wider question. On the one hand, the majority of large-scale experiments across wide climatic gradients used only few standard litter types, often not naturally present nor produced at the experimental sites or even artificial[6,8–12]. By keeping litter characteristics constant, these studies evaluate the *decomposition environment*, but ignore litter characteristics that are shaped by site-specific environmental conditions and ecological interactions. On the other hand, studies including a representative range of litter types from a particular ecosystem at local scales are typically conducted at common sites, imperfectly matching natural conditions of the study plots, or even using artificial soil substrate[5,13–15]. By keeping the decomposition environment constant, these studies evaluate the litter *decomposability*, but ignore the wide range of environmental conditions and substantially contrasting decomposer communities due to differences in slope, exposition, soil characteristics and vegetation properties operating at local to global scales.

As a result, interactions between site-specific variability in litter characteristics and site-specific environmental conditions, including macroclimate, are rarely considered explicitly, especially at large spatial scales. While both types of experiments allowed considerable progress in understanding how environmental conditions and litter characteristics regulate decomposition, by disrupting the natural decomposition context, neither of them can evaluate the relative contribution of these factors comprehensively. A reasonable assumption is that *realistic decomposition* defined as the plant community-specific litter decomposing exactly where it was produced, could be predicted by both the *decomposition environment* and the litter *decomposability* assessed separately. However, this remains untested, and as we believe, is at the origin of considerable confusion in the understanding of the climate control of decomposition, which is problematic for a clear understanding of mechanisms and the scales at which they operate.

Here, we evaluate the relative importance of putative decomposition drivers on *realistic decomposition*, i.e., the decomposition of natural litter in its natural environment at the site of litter origin by disentangling the relative importance of the *decomposition environment* and *decomposability* on the *realistic decomposition*. We took advantage of an exceptionally well described network of more than 200 forest plots at a continental scale of Europe[16] to disentangle the controls by micro-environmental factors from macroclimate and litter characteristics with complementary approaches and experiments to study decomposition. Our data contribute to reconciling contrasting findings of past studies and to clarify the role of climate in decomposition. This will improve predictions of the consequences of ongoing climate change and the associated shift in species distribution on decomposition and the C cycle more generally.

We used a well-established network of six regions spanning a climatic gradient across Europe, each covering a range of different forests varying in tree species richness and composition at a regional scale within the six regions[16] (Fig. 1, Table S1) for three different decomposition experiments. In the first experiment, we assessed *realistic decomposition* with naturally occurring leaf litter that matched tree species richness and composition of the different plots within each region in contrast to one or a few litter types of dominant plants per site as commonly done. In the second experiment, we assessed the *decomposition environment* with two standard materials (paper sheets and wood sticks), which represented exactly the same composition of common and quantitatively important C compounds (water-soluble compounds, hemicelluloses, cellulose, and lignin – see detailed description in the Methods section) for decomposers, in all plots of variable species composition within all six regions. In the third experiment, we assessed the inherent *decomposability* of all naturally-occurring leaf litter combinations found along the climatic and vegetation gradients by measuring their decomposition in a common garden where none of the litter types occurred naturally (Fig. 1).

Results and discussion

Forest stand characteristics varied strongly among the six regions across Europe and at the regional scale among forest plots of each region, as documented by the detailed description of all plots of the European project FunDivEUROPE[16] (Table S1). The 26 different tree species or populations (for the species that are present at more than one site (e.g., *Pinus sylvestris*)) also varied strongly in a wide range of leaf litter characteristics resulting in marked differences in plot-specific litter characteristics among regions and among plots within regions (Fig. 2a). These differences in environmental parameters and litterfall characteristics among plots determined the plot-specific *decomposition environment* that was the main driver of the decomposition of the standard litter types[8] (Fig. 3a). Specifically, decomposition of the standard litter types correlated with the variance along the first axis of a principal component analysis (PCA) run with plot-specific values of litter characteristics, which was mostly determined by the differences in litter nutrient concentrations (Fig. 2a). Plot-specific leaf area index (LAI), a measure of canopy density, was the second variable that significantly explained the observed variation in decomposition of standard litter types (Fig. 3a, Table S2), but macroclimate had no significant influence despite the pronounced climatic differences among regions at the scale of Europe[8] (Table S1). This result supports the recent findings of much weaker macroclimate influence on decomposition than commonly assumed when variability at small local scales is accounted for[6,7]. Here, this small scale variability was determined by LAI, which captures part of the microclimatic conditions relevant for the composition and activity of decomposer communities[19,20], and by plot-specific litter characteristics that drives decomposer adaptation to recurrent resource availability[21,22].

The same litter characteristics varying along the first PCA axis that determined the *decomposition environment* via its long-term impact on decomposer communities[21,22] were also the major predictors of decomposition of all plot-specific leaf litter combinations in the common garden experiment (Fig. 3b, Table S2), thus determining *decomposability* of the various leaf litter types and combinations. The higher the concentrations of nitrogen (N), potassium (K), magnesium (Mg) and calcium (Ca), the faster the decomposition under the exact same environmental conditions. These findings agree with general knowledge on how different litter characteristics correlate with and predict decomposition[3,5].

Having identified the key factors determining the *decomposition environment* in a wide range of forest ecosystems across Europe, and the litter characteristics determining *decomposability* of the various leaf litter produced in these forests, we hypothesised that decomposition of the leaf litter naturally occurring in these plots can be predicted from the combination of *decomposition environment* and *decomposability*. We constructed an *a priori* model around this hypothesis (Fig. 4), which we tested using structural equation modelling (SEM) with inherent plot-specific litter characteristics affecting both, *decomposability* directly and the *decomposition environment* indirectly through the locally adapted decomposer community, and with forest stand density (LAI), soil parameters, and macroclimate further affecting the decomposition environment (Fig. 4). Similar to litter characteristics, we used principal component analysis to characterise the variability in a large number of soil parameters (Fig. 2b). The variance along the first PCA axis was mostly determined by differences in soil texture and that along the second PCA axis by differences in the C:N ratio of soil organic matter among the 194 plots.

The results from the SEM (Fig. 5) confirmed the importance of litter characteristics for litter *decomposability* that we determined with all plot-specific litter exposed at a common garden (Fig. 3b), and for the *decomposition environment* that we determined with standard litter types exposed in all plots (Fig. 3a). Variation in LAI positively correlated with the decomposition of standard litter in line with the results reported above, and thus, characterised the decomposition environment at the small local scale well, while soil parameters and macroclimate (here assessed with the "macroclimate index" calculated with temperature and precipitation data from all regions – see Methods for details) showed weak non-significant effects (Fig. 5). According to our hypothesis and our *a priori* model (Fig. 4), litter *decomposability* predicted the *realistic decomposition* of the natural litter in their plots of origin fairly well (Fig. 5). This confirms the strong effects of litter characteristics in a large reciprocal litter translocation experiment across four biomes, and the consistent ranking among 16 litter types regardless of their origin and site of decomposition in a previous study[3]. Our results further emphasise the key role of physicochemical litter characteristics as a general predictor of decomposition globally[5].

However, in contrast to our initial hypothesis, differences in the local *decomposition environment* captured by the variability in the decomposition of the standard litter types failed to predict the *realistic decomposition* of the natural litter in their plots of origin (Fig. 5). In fact, the initial SEM run according to our *a priori* model (Fig. 4) was rejected with a poor goodness-of-fit due to a missing path between macroclimate and *realistic* decomposition, which then accounted for the majority of the variance in *realistic decomposition* once included in the model (Fig. 5). Indeed, using linear mixed-effects models and model selections, we identified macroclimate, litter characteristics and their interactions explaining 68% of the variance in *realistic decomposition*, but none of the variables relevant for micro-environmental control were significant (Fig. 3c, Table S2). The apparent lack of control by the decomposition environment on *realistic decomposition* matches the observation that the decomposition of natural plot-specific litter varies independently of that of the standard litter types across all regions as well as within each region (Fig. 6a). This is noteworthy as both, plot-specific litter and standard litter were decomposing side-by-side under the exact same micro-environmental conditions during the same period of time. In other words, the decomposition of natural plot-specific litter is unpredictable from the decomposition of standard litter types keeping all other factors identical, and this was the case in all six regions (Fig. 6a) irrespective of the marked range in climate zones, soil parameters, and tree species identity.

Although the *realistic decomposition* was overall well predicted by *decomposability* and thus litter characteristics, the significant interactive effect between litter characteristics and macroclimate on decomposition of plot-specific litter in its plot of origin (Fig. 3c) indicates that the degree of litter characteristic control depends on macroclimate. Indeed, the stronger the climatic constraints (i.e., the lower the macroclimate index) across our study sites, the weaker the correlations between *realistic decomposition* on one side and common garden decomposition (Fig. 6b) and litter characteristics (Fig. 6c) on the other side. For example, the correlations were strong for the climatically more favourable sites in Germany and Poland, and weak for the climatically less favourable sites in Italy and Spain (Fig. 6c). Weaker effects of litter characteristics under more limiting climatic conditions have been proposed before[23,24], but Canessa et al.[25] recently showed in a detailed analysis with a large reciprocal translocation experiment that the relative importance of climate vs. litter characteristics depends on the range of both, climatic conditions and litter characteristics and change over time with ongoing decomposition.

The absence of any micro-environmental control and the strong direct macroclimate control over *realistic decomposition* contrasts with the growing critical reappraisal of the conventional view that macroclimate is the dominant driver of decomposition by studies that reported a strong effect of within-site variability on decomposition[6–9]. Because the within-region variability was likely more pronounced than that in previous studies, these contrasting results are even more noteworthy. Indeed, our study covered multiple forests differing in tree species composition, stand characteristics, and soil properties at regional scales (up to 150 x

150 km areas), as opposed to transects established within essentially the same type of vegetation and only small differences in soil properties at much smaller scales[6,9] (50 m to 2 km). What may explain these apparently conflicting results? The contrasting results may be related to our experimental design that differed from the vast majority of decomposition experiments in that the duration of decomposition varied among regions to reach similar ranges of litter mass loss (Table S1). This was a deliberate choice to assure the comparison of driving factors at roughly the same stage of decomposition, because the relative importance of multiple drivers is known to change with decomposition stage[25,26]. This means that our results are valid for the initial phase of decomposition, which received by far most of the attention in previous studies compared to late stage decomposition (but see[27,28]), and are thus relevant for the decomposition algorithms used in biogeochemical models. It will be important to explicitly address whether the dominance of macroclimate control over micro-environmental heterogeneity on realistic decomposition will persist through later stage decomposition, which is characterised by an apparent cessation of litter mass loss around 20% of initial mass with an increasing contribution of decomposition products over time[28] in future studies. Another consequence of our choice is that the common macroclimatic variables such as mean annual precipitation/temperature were no longer meaningful because the experiments covered different periods of the year. We thus calculated a macroclimate index as the ratio of precipitation to temperature (Lang's aridity index[18]), which has the advantage of integrating humidity and temperature, the two variables determining decomposer activity, for the exact period of decomposition at each of the six sites. While these climate variables reasonably well characterised macroclimatic conditions along our continental gradient of forest ecosystems, they may not be universal in predicting decomposition across biomes, particularly in ecosystems were high moisture can lead to anoxic conditions[29], or in drylands where UV-degradation and soil-litter mixing can lead to

decomposition-precipitation decoupling[30,31]. As there were no climate data available at the level of individual plots within the six regions, the relatively coarse-grained resolution of macroclimate at the level of regions did not allow to account for variability in climatic conditions within each region, which may explain an additional part of the remaining variability in decomposition. Still, our results clearly indicate that macroclimatic conditions explain the majority of the variability in decomposition of the naturally occurring litter. With the exception of particular conditions such as in peatlands and some drylands mentioned above[29–31], an even greater range of climatic conditions than covered in our study, for example by including tropical forests, may actually increase the contribution of macroclimate control to realistic decomposition[25].

An ecological explanation for our unexpected results may be related to the fact that the decomposition of naturally occurring litter was unpredictable by the decomposition of standard litter decomposing under the exact same conditions (Fig. 5, 6a). This is a critically important result because it suggests that the factors controlling decomposition differ for standard litter types, exacerbating in our study the relative importance of micro-environmental compared to macroclimatic factors. Decomposer organisms are sensitive to the kind of available organic matter at a given location within a forest, which affects its decomposition. For example, decomposers may process even naturally occurring leaf litter at substantially different rates depending on whether or not it is mixed with litter of co-occurring plant species[36,37], and the underlying mechanisms how litter mixing affects decomposer organisms may vary fundamentally depending on the context[33]. Similarly, the home-field advantage of locally produced litter decomposing locally is a regularly observed phenomenon[21,34,35], showing that disrupting the natural context of decomposing litter alters decomposition. These important and highly local effects on decomposition remain unaccounted for by using a standard litter type, that is common practice across different plots, sites, and regions, for example in studies evaluating the *decomposition environment*. Not all kinds of standard litter types may yield the same response and had we chosen a true leaf litter as standard material instead of paper sheets and wood sticks - which are highly representative for the major C sources available to decomposers in any ecosystem (i.e. water-soluble compounds, cellulose, hemicelluloses, and additionally lignin in the case of wood sticks), but essentially nutrient free - the results may well have been different. However, the use of a true leaf litter as standard material could make the comparison across plots and regions more problematic. The physical and chemical characteristics of a standard leaf litter type would be more or less different from plot- and region-specific native leaf litter, with decomposers being more or less familiar with the characteristics of the standard leaf litter type. The substrate quality - matrix quality interaction hypothesis as an extension of the home-field advantage hypothesis predicts a continuum from positive to negative interactions between specific litter types and decomposer communities as specific litter types (i.e. standard leaf litter) and the plot-specific litter become increasingly dissimilar in their characteristics[22]. Such bias by a randomly variable proximity of standard leaf litter with plot-specific litter characteristics and its appreciation by the local decomposer community may shift the predictability of realistic decomposition by standard leaf litter decomposition in any direction depending on the choice of the standard leaf litter and the kind and range of ecosystems studied.

Potential interactions between a given standard litter and the naturally present litter, which vary depending on the local context, further complicate the interpretation of the data from decomposition of standard materials and their relevance for local decomposition processes. This may then result in a disconnected variability in the data of standard material decomposition and natural litter decomposition as observed in our study (Fig. 6a, Fig. S2), making the identification and quantification of the relevant control factors of decomposition based on standard material very difficult and even erroneous. Regardless of the specific underlying mechanisms, this disconnect between standard litter and natural litter decomposition raises doubts over the validity of conclusions drawn from studies that use standard litter, such as tree litter[10], agricultural litter[9], wood[6,8], tea-bags[12,36], bait lamina[37], or cotton strips[38], as a way of evaluating the decomposition environment in contrasting ecosystems. Fixing one parameter to isolate the effect of a second parameter of interest is certainly one of the most effective methods in ecology to disentangle the contribution of multiple drivers to ecosystem processes, but when these parameters are not independent from each other the conclusions become erroneous. In our study, for example, we demonstrated that the relative contribution of macroclimate in the control of decomposition changes fundamentally between plot-specific litter and standard materials. This does not mean that the recently shown impact of the micro-environment[6,7] as a driver of decomposition is irrelevant. On the contrary, micro-environmental factors remain critically important and differences in humidity and temperature that were not perfectly accounted for by the proxy of canopy density (LAI) used in our study for example, may likely account for part of the unexplained variance in our models.

Collectively, the simultaneous evaluation of the *decomposition environment*, litter *decomposability* and *realistic decomposition* (Fig. 5) across gradients of distinct climatic conditions and vegetation allowed identifying the relative role of different drivers of decomposition more accurately than it was possible previously. Specifically, our results clarify the role of macroclimate as a dominant decomposition driver by demonstrating its integrative impact through direct (environmental conditions) and indirect (by determining local plant and decomposer communities) effects. This approach of combined experiments used here helps to reconcile conflicting views of the role of climate in decomposition by highlighting the critical importance of methodological choices that have a large impact on the results and how they are interpreted, which is presently not sufficiently acknowledged. The widely used experiments with one or a few standard materials as common litter types across study sites of variable spatial scales may produce misleading results when evaluating the role of the decomposition environment. Our study contributes to consolidating the role of climate as a key driver of decomposition and to the robustness of predictions of the consequences of ongoing climate-change on the global C cycle.

Methods

Experimental design. We performed three complementary decomposition experiments to disentangle the relative contribution of (1) the decomposition environment and (2) the litter decomposability on (3) the decomposition of litter where it naturally occurs, at a continental scale (Fig. 1). To do so, we used the FunDivEUROPE exploratory platform[16] which spans across six major European forest ecosystems (region hereafter) ranging from Mediterranean forests in Spain to boreal forests in Finland. In each region, we selected 28 to 43 mature forest plots differing in species richness and composition (from monospecific plots up to five co-occurring tree species) at regional scale (in an area of up to 150 x 150 km), in which we established 30 x 30 m plots. This led to 209 forest plots representing 110 different tree species mixtures. Within each region, major environmental variables were held as constant as possible (e.g., geology, soil types), ensuring that the effect of tree species composition and diversity was not confounded with soil- and stand-related factors, and the final selection of plots was done by a random draw from a pool of suitable plots[16]. The *decomposition environment* effect was evaluated by isolating the control of environmental conditions on decomposition from co-variation in litter characteristics. This was done by placing standard litter types (paper sheets and wood sticks – see next section for characteristics) in all plots across all regions (*Decomposition environment* experiment, hereafter). The results of the standard litter decomposition were previously published independently[8]. Litter *decomposability* was evaluated by isolating the control of litter characteristics on decomposition from covariation in environmental conditions. We did this by placing all 110 litter mixtures with species composition matching that of all plots included in our study to decompose in a common garden (*Decomposability* experiment, hereafter). This common garden was set up in Montpellier (43° 38' N, 3° 51' E), France to be geographically separate from the focal sites, in an old field rather than a forest to avoid potential home-field advantage effects on any of the used tree leaf litter[21]. To evaluate the combined control of litter decomposability and decomposition environment on the decomposition of litter where it naturally occurs, we placed the plot-specific litter mixture of the plot-specific species composition in each of our established 30 x 30 m plots (*Realistic* experiment, hereafter). In each region, the *Realistic decomposition* and *Decomposition environment* experiments occurred simultaneously, while the *Decomposability* experiment in the common garden was started a little after the start of the field experiments (see Table S1 for the exact start and end date of each experiment).

Decomposition experiments. For the *Realistic* experiment, we filled litterbags with 10 g of air-dried leaf litter consisting of a litter mixture with equal proportions of litter from each tree species present in each of the plots. For the *Decomposability* experiment, litterbags containing the same plot-specific litter mixtures from the *Realistic* experiment were prepared. For these two experiments, we used freshly senesced leaf litter from all target tree species of the FunDivEUROPE exploratory platform collected at tree species-specific peak leaf litter fall between October 2011 and November 2012, in close vicinity of the experimental plots (see Joly *et al.*[8] for further details). For the *Decomposition environment* experiment, we used two types of standard litter differing in physicochemical characteristics. First, we filled litterbags with individual paper sheets (10 g, non-recycled, total chlorine-free printing paper) with a size of 297 x 420 mm (A3) folded into the litterbags, representing a comparatively readily degradable material accessible to a wide variety of decomposer organisms. These sheets consisted of 16% water-soluble compounds, 4% hemicelluloses and 80% cellulose[8]. Second, we used wooden sticks (tongue depressors, 152 x 17 x 2 mm) made of *Betula pendula* wood, representing a more recalcitrant material consisting of lignin intimately associated with cellulose and hemicelluloses. These wooden sticks consisting of 9.5% water-soluble compounds, 26% hemicelluloses, 52.5% cellulose, and 12% lignin[8], and were placed directly on the soil without litterbags. For litter and paper sheets, we used litterbags (15 x 15 cm) constructed from polyethylene fabrics of two different mesh sizes. For the bottom side of the litterbags we used a small mesh (0.5 x 0.5 mm) to minimise losses of fragments. For the upper side, we used a large mesh (5 x 8 mm) to allow access to all classes of soil fauna. This access was important as soil fauna has been shown to have an important effect on decomposition[39]. For all experiments, initial mass was determined with air-dry material, with subsamples additionally dried at 65°C for 48 h and reweighed to obtain an oven-dry mass correction factor. For the *Realistic* and *Decomposition environment* experiments respectively, we placed three litterbags filled with the plot-specific leaf litter, three litterbags filled with paper sheets, and three wooden sticks side by side within a 1 m^2 homogeneous area within each of the established 30 x 30 m plots, on the bare soil after the natural litter layer had been locally removed. The three replicates of each decomposing material were fully randomised within the homogeneous area, were considered to experience the same micro-environmental conditions, and used as analytical replicates. For the *Decomposability* experiment, we used a randomised complete block design, with all litter mixtures being replicated in four blocks. For all experiments, we retrieved litterbags when the most rapidly decomposing species within each region reached 40-50% mass loss (evaluated with an extra set of litterbags harvested regularly). Consequently, the duration of litter incubation varied from 190 days in Germany to 605 in Spain. This procedure ensured that litter was sampled at similar decomposition stages across all sites (Table S1), which is particularly important when assessing the relative role of different control factors that changes during the decomposition process as a function of the decomposition stage and not as function of time, thus enabling meaningful comparisons of decomposition driver contribution[26]. Harvested decomposed materials were dried at 65 °C, cleaned of pieces of wood, stones or other foreign material that occasionally got into the litterbags, and weighed. To correct for potential soil contamination during decomposition in the field, litter and paper sheets samples were ground with a Cyclotec Sample Mill (Tecator, Höganäs, Sweden) and their ash content determined, and their mass loss rates expressed based on ash-free litter mass. To account for the differences in the incubation durations of field exposure between the different regions, we expressed decomposition as a litter mass loss rates rather than just litter mass losses. These litter mass loss rates were expressed as the ratio of mass lost per amount of initial mass per day of incubation (mg g^{-1} day^{-1}), calculated as followed: Mass loss rates = [1000 x (Initial mass – Final mass)/Initial mass] / Days of incubation. We considered the 28 (Romania) to 43 (Poland) different plots per region as replicates for the *decomposition environment* and the *realistic decomposition* experiments, using the three litterbags of natural leaf litter and paper sheets, and the three wood sticks decomposing side by side as analytical replicates. Their values, thus, were averaged and mean values used for the analyses. For the *decomposition environment* experiment, standard litter mass loss rate was computed for each plot as the average mass loss rates of paper sheets and wood sticks.

While the relevant environmental variability within each region played out at the scale of individual plots that varied in the quantified tree species composition, stand characteristics, and soil properties, we acknowledge that decomposition rates of individual litterbags and wood sticks varied also to some degree. Averaging across the three (analytical) replicates does not allow for within-plot variability thereby reducing the overall variability within regions and inflating the variability among regions, respectively[7]. We evaluated the effect of averaging across the three (analytical) replicates of litterbags and wood sticks on the variability explained by each spatial scale by comparing the amount of variance explained by differences amongst regions, when either using mean values or using the individual values of the three (analytical) replicates (Table S3). This showed that the averaging of analytical replicates inflated the variability among regions by 4% only, for both the standard litter and the natural litter, and thus did not significantly affect our conclusions. In our analyses, we did not include the variability among the three (analytical) replicates of litterbags and wood sticks within each plot for the following reasons: (i) our experimental design aimed at quantifying the variability in the decomposition environment within each region at the plot level, (ii) we cannot disentangle the part of the variability among individual litterbags and wood sticks due to microscale environmental differences from that due to analytical error, and (iii) because replicates of naturally-occurring and standard litter were not paired, but fully randomised within the 1 m^2 area, preventing us from associating replicate values with one another and analysing them accordingly in our statistical models.

Definition of spatial scales

According to our experimental design, we here use the term "macroclimate" to refer to differences in average climatic conditions between the six different regions, and the term "micro-environmental conditions" to refer to differences in environmental/climatic conditions among the different forest plots of 30 x 30 m established at a regional scale within the six regions during the FunDivEUROPE project[16]. For a study in forests, this plot size was small enough to define plots with contrasting plant species composition and for relatively homogenous conditions, and big enough for the contrasting plant species compositions having an impact on the multiple variables measured. Variation in decomposition at smaller, sub-plot scales was not considered.

Decomposition drivers: litter, soil and climate. The different litter mixtures from all plots were characterised by a series of chemical and physical leaf litter parameters on litter from each tree species from each region. Chemical parameters included elemental composition (carbon (C), Nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg) and potassium (K)), carbon fractions (lignin, cellulose, hemicellulose and water-soluble compounds), secondary metabolite concentrations (condensed tannins, total phenolics) and pH. We added water-holding capacity (WHC) of the litter as a physical parameter (see details for the measurement off litter characteristics in Joly *et al.*[8]). We used these data to compute, for each litter characteristic, its average value in the litter mixture of each plot (p) based on its tree community composition (presence/absence) using the community-weighed mean calculated as follows[40]:

$$Trait_p = \sum_{i=1}^{n} p_i \, x \, trait_i$$

where p_i is the relative abundance (presence/absence) of species $\underline{i}$ to the litter mixture. To visualise how 15 physicochemical litter characteristics were related and how their values differed between plots and regions, we used a principal component analysis (PCA) with all variables centred and standardised prior to ordination. To characterise the soil parameters, we measured a series of soil properties in all plots. Soil properties included pH and C:N ratios of the forest floor and of the top 0-10 cm mineral soil layer below the forest floor layer, as well as the texture of the top 0-10 cm of the mineral soil. Soil sampling and details of pH and C:N ratios measures can be found in Dawud *et al.*[17]. Soil texture was determined by the laser diffraction method. Similar to litter characteristics, we visualised how the seven soil parameters were related using a PCA. To characterise the canopy density that can modulate the microclimatic conditions on the forest floor, we used plot-specific leaf area index (LAI; m^2/m^2). Details of LAI measures can be found in Pollastrini *et al.*[41]. To characterise macroclimatic conditions at the site level during the respective incubation periods, we collected daily meteorological data (mean temperature, precipitation and potential evapotranspiration) from of the CGMS database of interpolated data (AGRI4CAST, http://mars.jrc.ec.europa.eu/mars). We used these variables to compute two climatic variables, including a macroclimate index (Lang's aridity index[18]) as the ratio of cumulated precipitation to cumulated daily mean temperature, and the UNEP's aridity index[18] as the ratio of cumulated precipitation to cumulated potential evapotranspiration, both computed over the specific period of litterbag exposure at each region.

Data analyses. Due to missing data from one of the three decomposition experiments, fifteen plots were removed from the dataset, leaving a total 194 plots (Table S1). For all data analyses described below (including structural equation modelling and model selection), to account for the non-independence of plots of the FunDivEUROPE exploratory platform within each region, we considered differences in regions, differences in tree species composition within region, and differences in plot identity for each tree species composition within region, by including region, tree species composition and plot identity as random factors, using the following R syntax: (mass loss rates ~ predictor_a + (. . .) + predictor_n + (1|region/composition/plot)), using mixed-effect models. We used the R software, v.3.6.1[42] for all statistical analyses, the *lme4* package[43] for all mixed-effect models, and the *PiecewiseSEM* package[44] for structural equation modelling.

Structural equation modelling: To test our a priori model (Fig. 4), we constructed a structural equation model (SEM) to evaluate (1) the controls of macroclimate, soil characteristics and vegetation characteristics on the decomposition environment, (2) the controls of litter characteristics on litter decomposability and (3) the combined control of decomposition environment and litter decomposability over the decomposition of litter where it naturally occurs. To do so, we combined the data from the three decomposition experiments by attributing the decomposability of litter mixtures (measured in the common garden experiment) to the plots where they naturally occur. For vegetation characteristics we used the leaf area index and litter characteristics defined as the litter mixture coordinates on the two first axes of a PCA including mixtures from all plots and all litter characteristics (named “Litter PC1” and “Litter PC2). For soil parameters, we used the two first axes of a PCA including all soil parameters from all plots (named “Soil PC1” and “Soil PC2). For macroclimate, we used a macroclimate index (Lang’s Aridity index, which is the ratio of cumulated precipitation to cumulated temperature). Poor goodness-of-fit upon fitting the model based on the *a priori* model (Fig. 4) revealed the omission of an important relationship between macroclimate and the decomposition of plot-specific litter in its plot of origin. We also constructed an alternative SEM with an alternative index for the macroclimate (UNEP’s aridity index: ratio of precipitation to potential evapotranspiration[18]) which yielded similar results (Fig. S1).

Model selection: To determine the direct control of explanatory variables on decomposition for the common garden (litter PC1 and litter PC2), standard litter (all variables) and realistic (all variables) experiments, separately, we used backward stepwise selection. We modelled mass loss rates as a function of these variables and removed least significant terms until we reached the best-fitting model determined by lowest AIC. For realistic decomposition, we also included in the full model the interaction between litter characteristics and (1) macroclimatic variable, (2) soil properties, and (3) LAI, as we observed that the relationship between realistic decomposition and decomposability varied by region suggesting an interaction between litter characteristics and environmental variables. To ensure the absence of collinearity issue, we checked for collinearity in all our models through variance inflation factor values.

Data availability

The data sets generated in this study are available from the University of Stirling's online data repository (http://hdl.handle.net/11667/205).

Code availability

The R code used to analyse the data sets of this study is available from the corresponding author on request.

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Author contribution

S.H., F.-X.J. and M.S.-L. designed the experiments, and S.H. and M.S.-L. acquired funding. F.-X.J. collected and analysed the decomposition data. F.-X.J. and S.H. led the writing of the manuscript and M.S.-L. contributed to the drafts.

Competing interests

The authors declare no competing interests.

Figure legends

Figure 1 | Conceptual framework and design of the experiments. The plot network consists of 209 forest plots (each 30 x 30m) established in six different regions across Europe, from Mediterranean-type forests in Spain to boreal-type forests in Finland. There were 28 to 43 plots in each region varying in tree species richness (from one to five species) and composition. In each plot, decomposition of litter of canopy trees from the plot was assessed to estimate the *realistic decomposition*. Alongside this naturally occurring litter, we also added common standard material (wood sticks and paper sheets) to each plot to assess the influence of the *decomposition environment*. We additionally placed plot-specific litter combinations from all plots in a common garden (located in Montpellier, France) to assess the *decomposability* of each litter. Fifteen plots were removed from the dataset due to missing data from one of the three decomposition experiments, leaving a total 194 plots with their own plot-specific litter combination.

Figure 2 | Litter and soil characteristics. Principal component analyses of (a) litter characteristics and (b) soil parameters, represented as black arrows, for all 194 plots considered for further analyses. Coloured convex hulls contain all plots from each region.

Litter characteristics were determined for each species at the region level. In each region, plot-specific litter characteristics were estimated as the mean values of the component species present in each plot[8]. Soil parameters were measured for each individual plot on a composite sample of nine soil samples collected with each of the 30 x 30 m plots[17]. NB: The number of symbols in (a) is somewhat inferior to the number of plots since replicated tree species combinations resulted in the same mean values of litter characteristics.

Figure 3 | Dominant drivers of (a) *decomposition environment,* (b) *decomposability,* and (c) *realistic decomposition*. Slope coefficients (mean ± SE; n = 194) of terms and interactions retained in the best model (linear mixed effects models) explaining decomposition rates in the three experiments (a) standard litter in natural environment (*decomposition environment*), (b) natural litter in common garden (*decomposability*) and (c) natural litter in its natural environment (*realistic decomposition*). NB: Litter PC1: litter scores on the first axes of the PCA including 18 litter physicochemical characteristics; LAI: leaf area index; Macroclimate Index: ratio of cumulated precipitation (mm) to cumulated mean daily temperature (°C) over the incubation period (Lang's Aridity Index[18]), with high values indicating more favourable macroclimatic conditions for decomposition. r^2m is the marginal r^2, i.e., the variance explained by the fixed factors; r^2c is the conditional r^2, i.e., the variance explained by both fixed factors and random factors (plot, tree species composition, and region).

Figure 4 | *A priori* model of the drivers of realistic decomposition. We hypothesised that the decomposition of litter where it naturally occurs (*realistic decomposition*) depends on (1) the litter *decomposability* and (2) the *decomposition environment*. We further hypothesised that litter decomposability is determined by the litter characteristics[5], and that the decomposition environment is determined by the characteristics of the litterfall[8], exerting a long-term control over the decomposer community, the canopy density affecting plot-specific climatic conditions, and by macroclimate and soil characteristics[8].

Figure 5 | Structural Equation Model based on the *a priori* model. Structural equation model representing the effects litter characteristics (Litter PC1 and Litter PC2), canopy density (LAI), soil characteristics (Soil PC1 and Soil PC2) and macroclimate (Aridity Index) on *in situ* natural litter decomposition (*realistic decomposition*) through their effects on the *decomposition environment* (*in situ* standard litter decomposition) and litter *decomposability* (common garden natural litter decomposition). Solid lines represent significant relationships. Arrow widths are proportional to relative strengths of path coefficients. The model global goodness-of-fit (Fisher's C statistic) is 27.471 ($P = 0.123$). Litter PC1/PC2: litter scores on the first two axes of the PCA including 18 litter physicochemical characteristics; LAI: leaf area index; Soil PC1/PC2: soil scores on the first two axes of the PCA including 7 soil characteristics; Macroclimate Index (Lang's Aridity Index[18]): ratio of cumulated precipitation (mm) to cumulated mean daily temperature (°C) over the incubation period with low values indicating less favourable climatic conditions. $^{***}P < 0.001$, $^{**}P < 0.01$. r^2m is the marginal r^2, i.e., the variance explained by the fixed factors reported on the figure; r^2c is the conditional r^2, i.e., the variance explained by both fixed factors and random factors (plot, tree species composition, and region).

Figure 6 | Bivariate relations between realistic decomposition, decomposition environment, decomposability, macroclimate and litter characteristics. Relationship between decomposition (mass loss rate) in the realistic experiment and (a) decomposition in the standard litter experiment, (b) decomposition in the common garden experiment, and (c) litter characteristics, derived from linear mixed-effects models. Individual symbols represent data from individual plots. Litter PC1: litter scores on the first axis of the PCA including 18 litter physicochemical characteristics. Macroclimate Index: ratio of cumulated precipitation (mm) to cumulated mean daily temperature (°C) over the incubation period with low values indicating less favourable climatic conditions (Lang's Aridity Index[18]). In (c), differences in litter climate are represented by a colour gradient. Black lines indicate the regression lines across all regions. Coloured lines indicate regression lines for each region (a, b), or climate (c). Different slopes between coloured and black lines designate a significant interaction between the explanatory variable and the region variable (b) and macroclimate (c), respectively. r^2m is the marginal r^2, i.e., the variance explained by the fixed factors; r^2c is the conditional r^2, i.e., the variance explained by both fixed factors and the random factor 'Region'.

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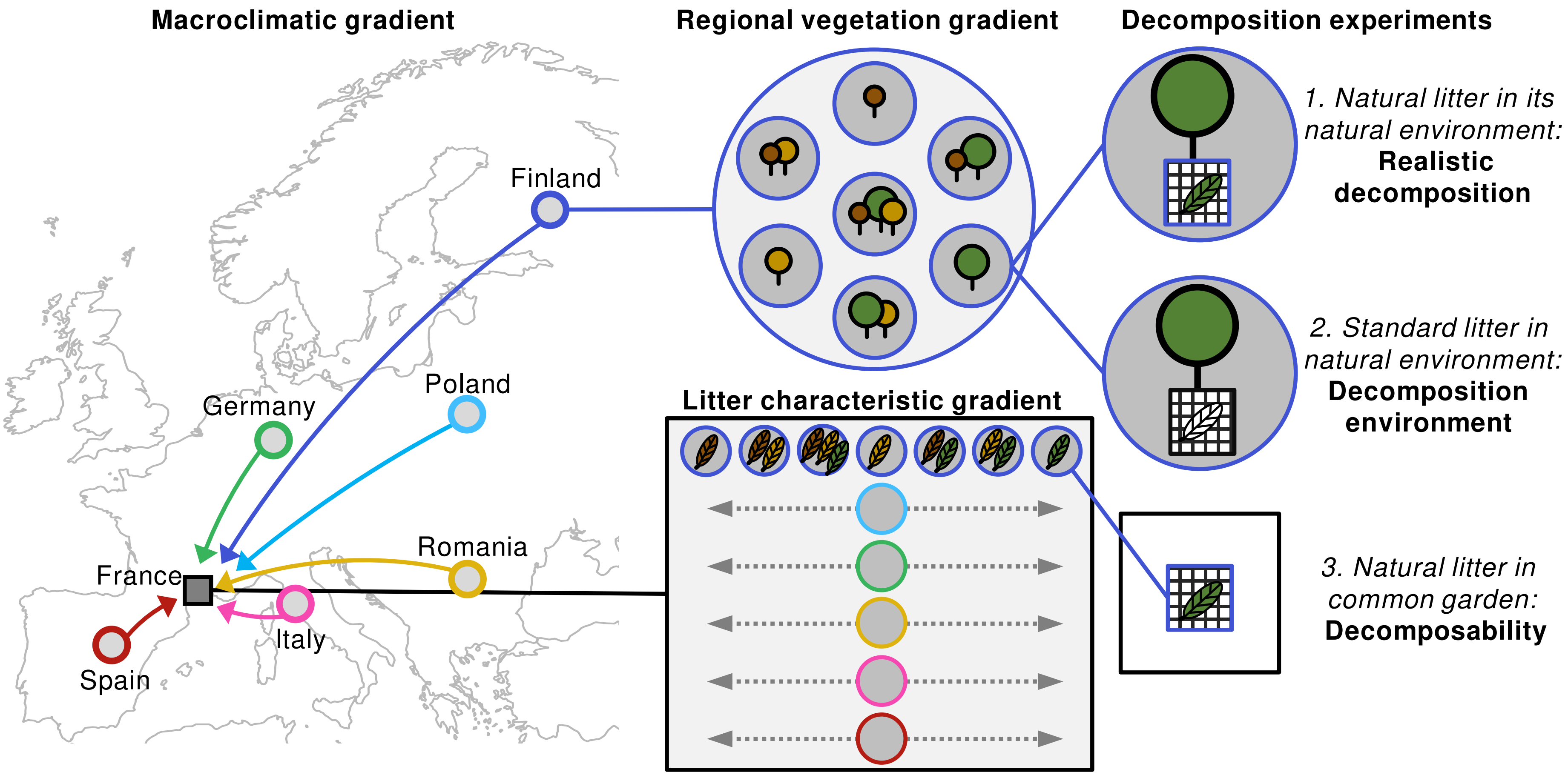
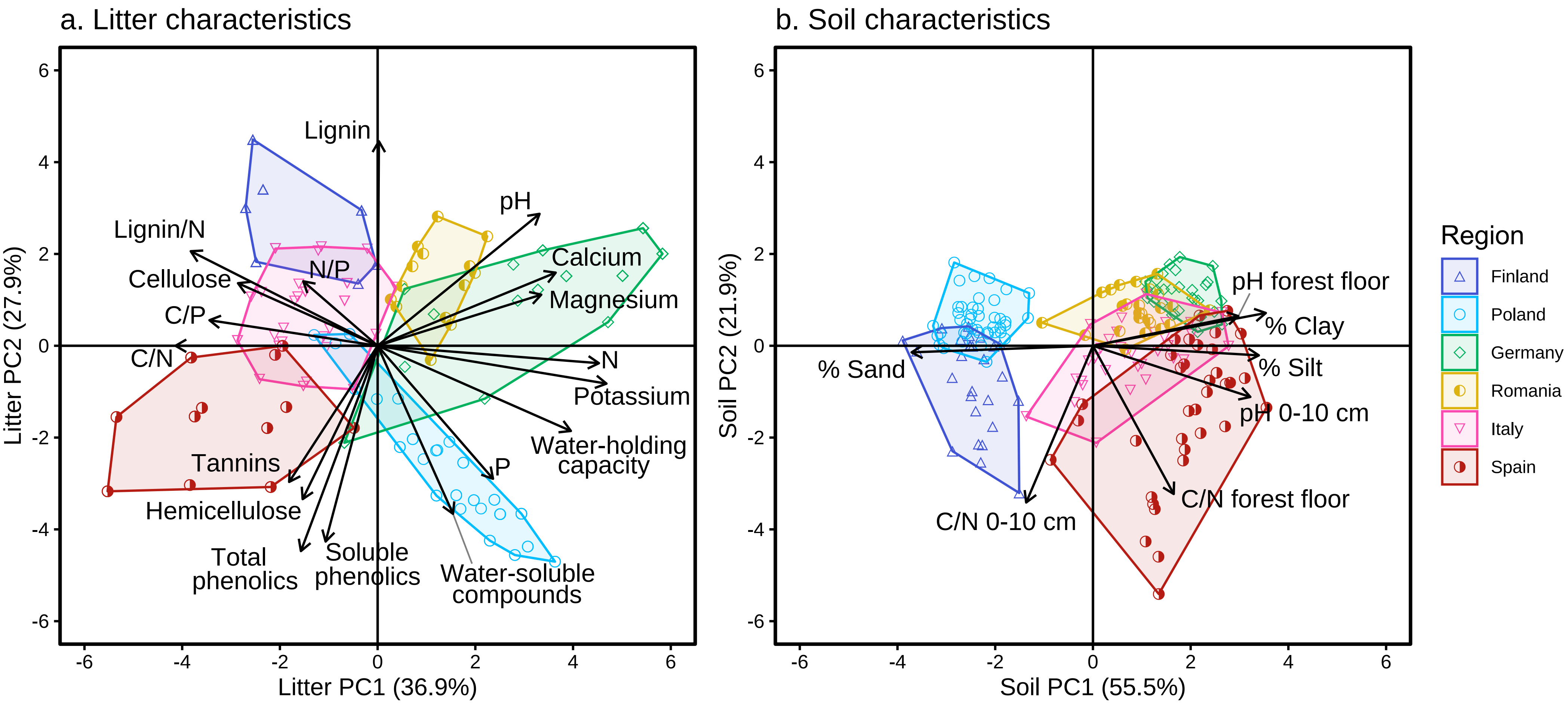
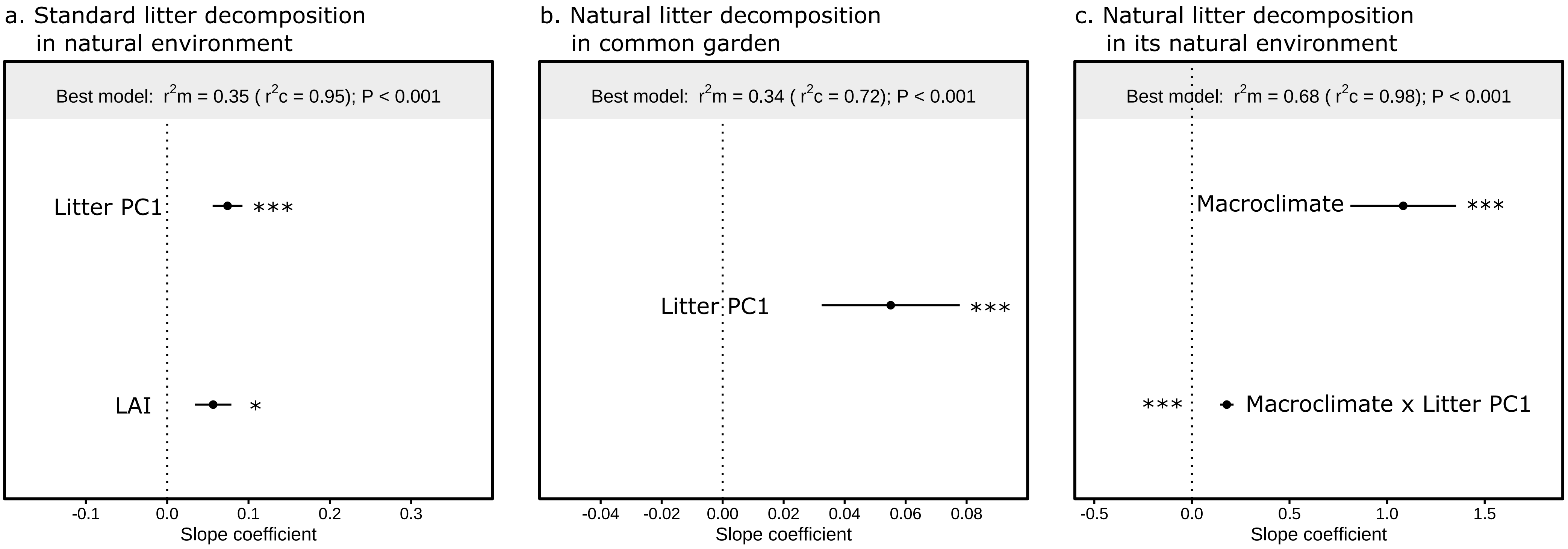
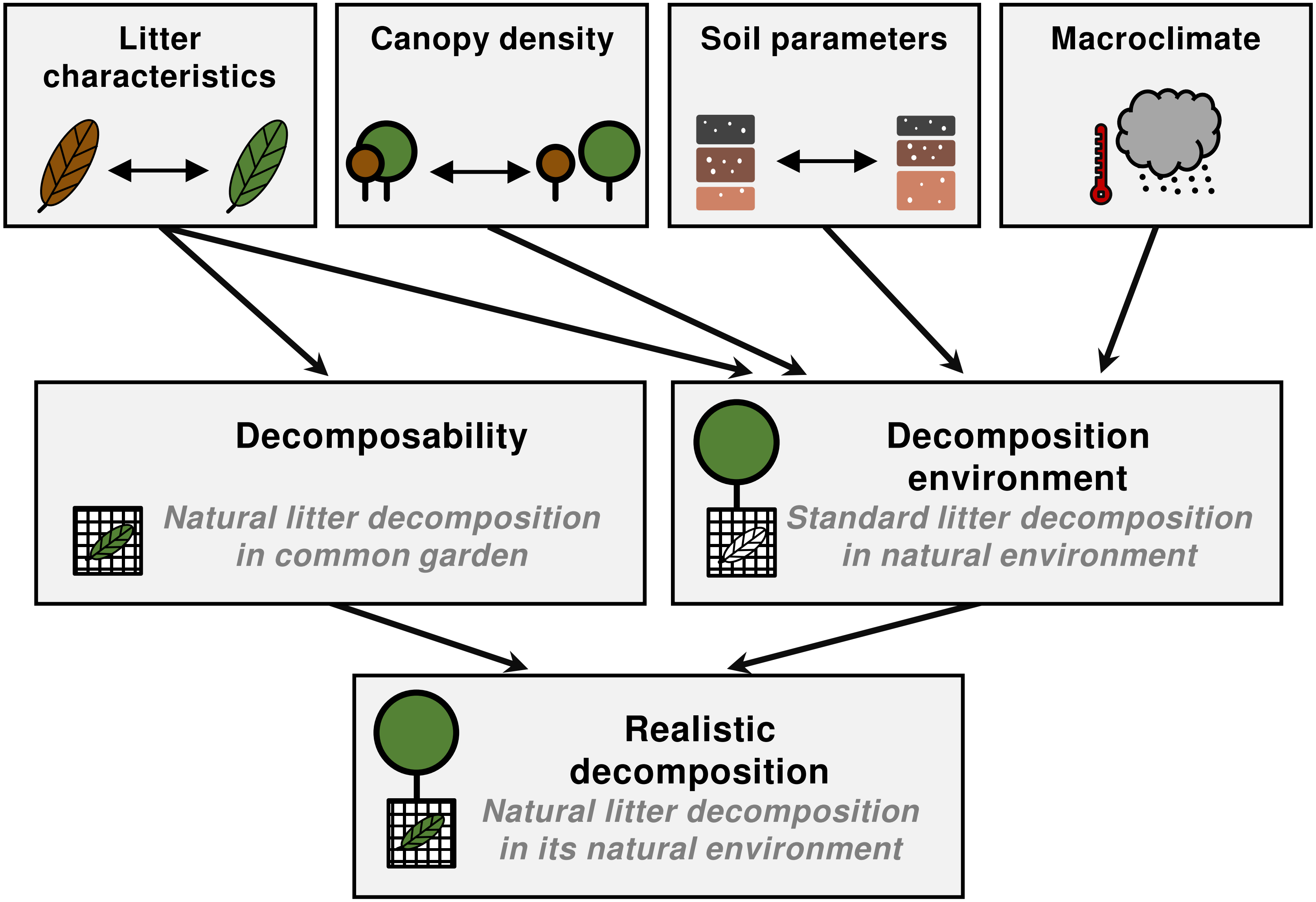
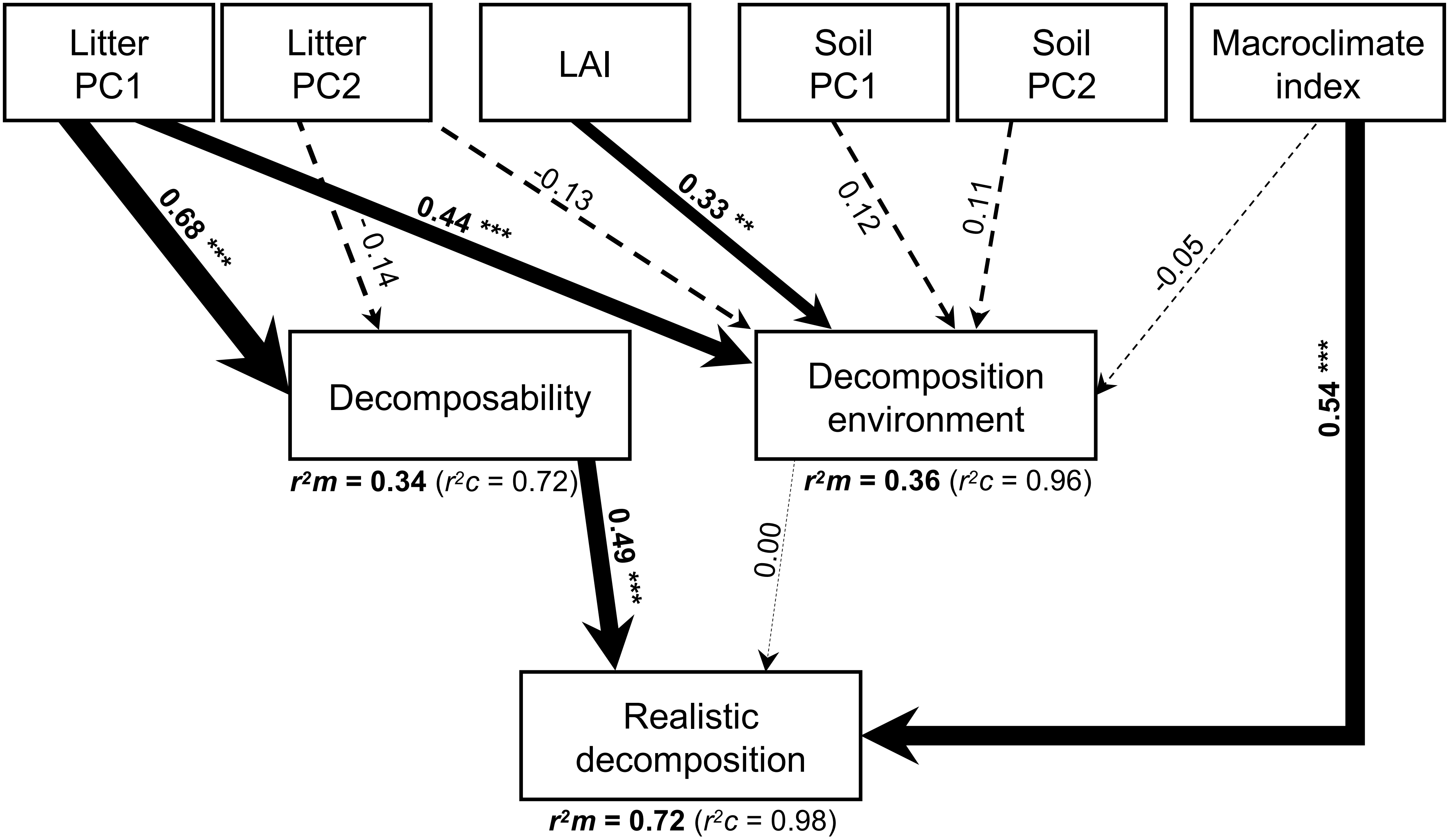
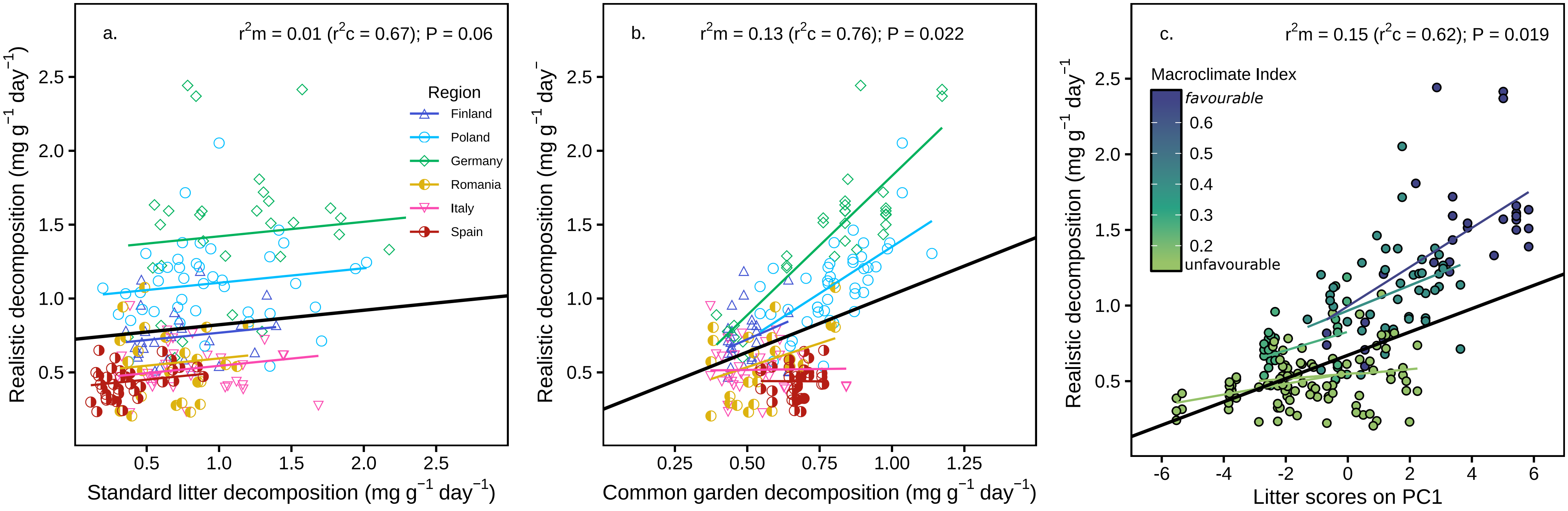

Macroclimatic gradient
Regional vegetation gradient
Decomposition experiments
Finland
Poland
Germany
Romania
France
Italy
Spain
Litter characteristic gradient
1. Natural litter in its natural environment: **Realistic decomposition**
2. Standard litter in natural environment: **Decomposition environment**
3. Natural litter in common garden: **Decomposability**


a. Litter characteristics
b. Soil characteristics
Litter PC2 (27.9%)
Litter PC1 (36.9%)
Soil PC2 (21.9%)
Soil PC1 (55.5%)
6
4
2
0
-2
-4
-6
Lignin
pH
Lignin/N
N/P
Cellulose
Calcium
Magnesium
C/P
C/N
N
Potassium
Water-holding capacity
P
Tannins
Hemicellulose
Total phenolics
Soluble phenolics
Water-soluble compounds
pH forest floor
% Clay
% Sand
% Silt
pH 0-10 cm
C/N forest floor
C/N 0-10 cm
Region
Finland
Poland
Germany
Romania
Italy
Spain


a. Standard litter decomposition in natural environment
Best model: $r^2m = 0.35$ ($r^2c = 0.95$); P < 0.001
Litter PC1
***
LAI
*
-0.1
0.0
0.1
0.2
0.3
Slope coefficient
b. Natural litter decomposition in common garden
Best model: $r^2m = 0.34$ ($r^2c = 0.72$); P < 0.001
Litter PC1
***
-0.04
-0.02
0.00
0.02
0.04
0.06
0.08
Slope coefficient
c. Natural litter decomposition in its natural environment
Best model: $r^2m = 0.68$ ($r^2c = 0.98$); P < 0.001
Macroclimate
***
***
Macroclimate x Litter PC1
-0.5
0.0
0.5
1.0
1.5
Slope coefficient


Litter characteristics
Canopy density
Soil parameters
Macroclimate
Decomposability
Natural litter decomposition in common garden
Decomposition environment
Standard litter decomposition in natural environment
Realistic decomposition
Natural litter decomposition in its natural environment


Litter PC1
Litter PC2
LAI
Soil PC1
Soil PC2
Macroclimate index
0.68 ***
-0.14
0.44 ***
-0.13
0.33 **
0.12
0.11
-0.05
0.54 ***
Decomposability
Decomposition environment
r^2m = 0.34 (r^2c = 0.72)
r^2m = 0.36 (r^2c = 0.96)
0.49 ***
0.00
Realistic decomposition
r^2m = 0.72 (r^2c = 0.98)


a.
r²m = 0.01 (r²c = 0.67); P = 0.06
Region
Finland
Poland
Germany
Romania
Italy
Spain
Realistic decomposition (mg g⁻¹ day⁻¹)
2.5
2.0
1.5
1.0
0.5
0.5
1.0
1.5
2.0
2.5
Standard litter decomposition (mg g⁻¹ day⁻¹)
b.
r²m = 0.13 (r²c = 0.76); P = 0.022
Realistic decomposition (mg g⁻¹ day⁻
2.5
2.0
1.5
1.0
0.5
0.25
0.50
0.75
1.00
1.25
Common garden decomposition (mg g⁻¹ day⁻¹)
c.
r²m = 0.15 (r²c = 0.62); P = 0.019
Macroclimate Index
favourable
0.6
0.5
0.4
0.3
0.2
unfavourable
Realistic decomposition (mg g⁻¹ day⁻¹)
2.5
2.0
1.5
1.0
0.5
-6
-4
-2
0
2
4
6
Litter scores on PC1