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Tree identity rather than tree diversity drives earthworm communities in European forests

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Highlights

- We studied earthworm communities in 6 European forest landscapes.
- Proportion of evergreen leaf litter negatively affected earthworm communities.
- Earthworm community response to leaf litter quality differed along a latitudinal gradient.
- Tree functional diversity had a positive effect on earthworms at continental scale.
- Litter quality was a stronger driver of earthworm communities than tree diversity.

ABSTRACT

Given the key role of belowground biota on forest ecosystem functioning, it is important to identify the factors that influence their abundance and composition. However, the understanding of the ecological linkage between tree diversity and belowground biota is still insufficient. Here we investigated the influence of tree diversity (richness, True Shannon diversity index, functional diversity) and identity (proportion of evergreen leaf litter and leaf litter quality) on earthworm species richness and biomass at a continental and regional scale, using data from a Europe-wide forest research platform (FunDivEUROPE) spanning six major forest types. We found a marked tree identity effect at the continental scale, with proportion of evergreen leaf litter negatively affecting total earthworm biomass and species richness, as well as their biomass per functional group. Furthermore, there were clear litter quality effects with a latitudinal variation in trait-specific responses. In north and central Europe, earthworm biomass and species richness clearly increased with increasing litter nutrient concentrations (decreasing C:N ratio and increasing calcium concentration), whereas this influence of litter nutrients was absent or even reversed in southern Europe. In addition, although earthworms were unaffected by the number of tree species, tree diversity positively affected earthworm biomass at the continental scale through functional diversity of the leaf litter. By focusing on tree leaf litter traits, this study advanced our understanding of the mechanisms driving tree identity effects and supported previous findings that litter quality, as a proxy of tree identity, was a stronger driver of earthworm species richness and biomass than tree diversity.

Keywords

FunDivEUROPE; litter functional traits; litter quality; soil fauna; species richness; tree functional diversity

1 INTRODUCTION

Among all soil biota, earthworms are considered key ecosystem engineers given their role in litter decomposition (Bonkowski et al., 1998; Holdsworth et al., 2012), bioturbation (Meysman et al., 2006; Bityutskii et al., 2016), water regulation (Blouin et al., 2013), nutrient cycling (Resner et al., 2015; Yang et al., 2015), soil carbon stocks and vertical distribution (Frouz et al., 2013; Vesterdal et al., 2013) and even seed germination (Forey et al., 2011). We studied the effect of tree species identity and diversity on the abundance and richness of these ecosystem engineers. Research on the aboveground-belowground relationship is highly valuable because of the importance of earthworms as ecosystem engineers in forest ecosystem functioning. They are important contributors to litter fragmentation and burial (Scheu, 1987; Staaf, 1987; Hättenschwiler and Gasser, 2005; Holdsworth et al., 2012) and have a fundamental influence on forest ecosystem dynamics (Satchell, 1983; Zicsi, 1983; Parkinson et al., 2004).

Earthworm biomass was reported to vary with tree species identity (Neiryneck et al., 2000; González et al., 2003; Sarlo, 2006) but also with plant functional groups: earthworm biomass and density was reported to increase with increased incidence of legumes in grassland communities (Milcu et al., 2008) and also with a conversion from conifer into mixed stands with broadleaved trees (Ammer et al., 2006; Salamon et al., 2008). One of the reasons for these relationships might be the difference in leaf litter quality, with higher leaf litter quality stimulating earthworm density and biomass. This litter quality effect has been demonstrated by common garden studies using tree monocultures that attributed differences in earthworm community structure to leaf litter quality (Muys et al., 1992; Neiryneck et al., 2000; Reich et al., 2005). Leaf litter can either directly affect earthworms by its nutrient concentration and carbon quality (Hendriksen, 1990; Rajapaksha et al., 2013) or indirectly by its influence on humus characteristics such as pH and habitat availability in the forest floor (Aubert et al., 2003; Aubert et al., 2006). Similar observations have been made in tropical agriculture where earthworm densities were negatively correlated with the lignin:N ratio of plant residues (Tian et al., 1993) and in grassland experiments where species with nitrogen-rich litter stimulated earthworm biomass and density (Milcu

et al., 2008) and affected earthworm species composition (Eisenhauer et al., 2009; Piotrowska et al., 2013).

As plant species vary in their litter traits, and in the way they occupy space and use resources, mixed assemblages are likely to have a different influence on the decomposer community compared to systems dominated by a single plant species. Several mechanisms have been proposed by which decomposers respond to differences in plant species diversity. Plant species diversity can affect the earthworm community by influencing the available plant biomass (resource quantity effect (Zaller and Arnone, 1999; Spehn et al., 2000)) or the quality of food resources (resource quality effect (Spehn et al., 2000; Milcu et al., 2006)). Plant species diversity can also influence the litter layer structure and consequently the microclimate conditions and microhabitat abundance and variety (Hättenschwiler et al., 2005), which is known to increase the abundance and diversity of soil fauna (Hansen and Coleman, 1998; Kaneko and Salamanca, 1999).

Since the presence of belowground biota can have important effects on forest ecosystem functioning (Lavelle et al., 2006; Bardgett and Wardle, 2010) it is important to have a greater understanding of the factors that influence their abundance and composition (De Wandeler et al., 2016), with tree diversity potentially being one of the key factors. Even though the number of studies on the effects of mixed forest stands on earthworm communities is increasing, very few studies were designed to investigate true tree species diversity effects (Korboulewsky et al., 2016). Many reports on diversity effects were from unbalanced studies, such as dilution series of one tree species: dilution of beech (Aubert et al., 2003; Cesarz et al., 2007; Jacob et al., 2009), dilution of Scots pine (Ammer et al., 2006) or dilution of spruce (Elmer et al., 2004; Salamon et al., 2008). In such studies, it is not possible to separate diversity from identity effects (Nadrowski et al., 2010). True diversity effects are more rarely reported and indicate positive tree species diversity effects on earthworm species richness (Chamagne et al., 2016), while others found no relationship with the earthworm community (Scheu et al., 2003; Schwarz et al., 2015).

In a previous study based on partly the same dataset (De Wandeler et al., 2016), we found that litter- and soil-related variables were more important for explaining earthworm incidence and biomass than

climatic variables. Here we extended the study to investigate the importance of different aspects of tree diversity on earthworm biomass and diversity. In this study we investigated: (i) how tree species diversity and proportion of evergreen leaf litter influences earthworm abundance and diversity, and (ii) which tree leaf litter traits affect earthworm abundance and diversity and whether their relative importance changes along a latitudinal gradient.

Given that earthworm abundances and species diversity can be influenced by plant species identity, plant functional traits and plant diversity-related mechanisms, we hypothesise that in mixed forests, earthworm abundance and species diversity may be affected by (1) the functional diversity of the tree species community rather than tree species richness or true Shannon diversity and (2) the dominant leaf litter trait values within a tree species community. The first hypothesis is related to the food web theory that predicts increased diversity of higher trophic levels with increased producer diversity (Knops et al., 1999; M. Haddad et al., 2001). The producer diversity in the context of this study was quantified by the functional dispersion of the tree species community (FDis), as proposed by Laliberté and Legendre (2010), and refers to the diversity of litter types serving different ecological functions in terms of food and structural habitat. The second hypothesis is related to the ‘mass-ratio hypothesis’ (Grime, 1998) stating that ecosystem processes are mainly determined by the functional identity of the dominant species. The functional identity of the dominant species can be quantified by the community-weighted mean of tree leaf litter trait values (CWM, Garnier et al. (2004)). Furthermore, we expected context dependency (Fridley, 2003; Tedersoo et al., 2016; Eisenhauer and Powell, 2017); the relationships between earthworm abundance and species diversity with the different leaf litter traits could change with environmental conditions, as previously found for the relationship of moisture availability with mites and nematodes (Sylvain et al., 2014).

The link between above- and belowground communities was studied in a European network of mature forest plots that was especially designed to explore the relationship between biodiversity and ecosystem functioning (Baeten et al., 2013) and allowed us to assess the effects of tree species diversity (species richness, True Shannon diversity index, functional diversity) while controlling for the effects of tree species identity and abiotic environmental variables. Unlike most research on tree species identity

effects, we went beyond tree species identity as an explanatory variable and focused on the role of tree leaf litter traits, further described as ‘litter quality’.

2 MATERIAL AND METHODS

2.1 STUDY AREA

The six studied regions span most of the European bioclimatic gradient and represent major European forest types including boreal forest (North Karelia, Finland), temperate mixed coniferous and broadleaf forest (Białowieża, Poland), temperate deciduous forest (Hainich, Germany), mountainous deciduous forest (Râșca, Romania), thermophilous deciduous forest (Colline Metallifere, Italy) and Mediterranean mixed forest (Alto Tajo, Spain) (see FunDivEUROPE research platform in Baeten et al. (2013); Appendix I, Fig. S1). These six regions are the basis for the FunDivEUROPE exploratory platform, which was specifically designed to assess biodiversity-ecosystem function relationships along tree species richness gradients in mature forests. Each studied region includes between 28 and 43 selected plots (30 x 30 m) with different combinations of a fixed set of locally dominant tree species (the so called target species). The established plots ranged in tree species richness from one to five species per plot. Three important criteria were applied in designing this platform. First, to ensure evenness in the tree species composition of the plots, a lower limit of 60% of maximum evenness based on basal area was set. Second, the research platform was designed in such a way that the admixture of non-target species was minimised. The basal area of the admixed species was generally kept below 5% of the total basal area, with a maximum of ca. 10%. Third, plots within a region were selected to minimise differences in soil related conditions, such as bedrock type, soil type, texture and depth. In total, the platform consists of 209 plots with 16 target tree species, some of them occurring in multiple regions. The species pool comprised conifers, deciduous broadleaved and evergreen broadleaved trees. For more details on the design of the platform consult Appendix II (Appendix II, Table S1) and Baeten et al. (2013).

2.2 DATA COLLECTION

ASSESSMENT OF EARTHWORM COMMUNITY PROPERTIES

Earthworm sampling was carried out in spring 2012 in Italy, Germany and Finland, and in autumn 2012 in Poland, Romania and Spain. We scheduled earthworm sampling in spring or autumn because of their requirement for humid soil conditions and positive temperatures (Berry and Jordan, 2001; Holmstrup, 2001; Baker and Whitby, 2003; Eggleton et al., 2009). In spite of this principle, our sampling campaign in Romania and Italy was characterized by extended drought periods prior to sampling, which negatively influenced the sampling success. Plum and Filser (2005) estimated that it takes about half a year for an earthworm population to recover after a disturbance. Consequently, it could be that regions affected by recent drought had not fully recovered yet, resulting in lower earthworm abundance. Therefore our results may have been influenced by unusually low earthworm abundances in Italy and Romania resulting from unpredictable drought events preceding the respective sampling periods. However, such stochastic effects of climate variability on the results could only be evaluated by repeated sampling campaigns over several years, which was impossible within the context of this study. All 209 plots of the FunDivEUROPE exploratory platform were sampled once.

Plots were divided in nine (10 x 10 m) subplots. In each plot, one earthworm sample was taken in the central subplot (Appendix I, Fig. S2). Sampling close to tree stems was avoided and in mixed stands performed in the inter-space between different tree species. Earthworms were sampled by means of a combined method. First, litter (OL and OF horizon, Zanella et al. (2011)) was hand sorted over an area of 25 x 25 cm to focus on epigeic earthworm species. Second, litter was removed over a larger area of 100 x 50 cm in order to effectively apply an ethological extraction of earthworms using a mustard suspension to focus on anecic species (Valckx et al., 2011). Third, hand sorting of a soil sample from an area of 25 x 25 cm and 20 cm depth was performed in the middle of the 100 x 50 cm area to focus on endogeic species. Collected earthworms were preserved in ethanol (70%) for two weeks, transferred to a 5% formaldehyde solution for fixation (until constant weight), after which they were transferred back to ethanol (70%) for preservation for at least one month. Upon identification, all earthworms were individually weighed, including gut content, and identified to species level with the use of different identification keys (Bouché, 1972; Sims and Gerard, 1999; Csuzdi and Zicsi, 2003; Pop et al., 2012) or

primary literature. Earthworm individuals that could only be identified at the level of the ecological group (0.5 %) or genus level (64%), which were mostly juveniles, were pro rata assigned to species based on their biomass. The earthworm biomass data obtained from the three sampling techniques were converted to 1 m² and then summed to obtain the earthworm biomass in gram per m² (total biomass and biomass of the three functional groups) (Appendix I, Fig. S3). Earthworm individuals were appointed to one of the three functional groups defined by Bouché (1977): epigeic, endogeic or anecic. Plot-level earthworm species richness was calculated as the total number of earthworm species obtained from the three collection methods (Appendix II, Table S2).

TREE DIVERSITY, EVERGREEN PROPORTION AND LITTER QUALITY VARIABLES

In all 209 plots, tree leaf litter of all target tree species was collected with litter traps to estimate tree leaf litter biomass per species per plot (De Wandeler et al., 2016). The litter was then used to determine tree species specific leaf litter C:N ratio and calcium concentration per plot (Appendix III). Fourteen additional leaf litter traits (Appendix IV) were determined from freshly fallen leaf litter of each species at regional level at several locations around the plots (De Wandeler et al., 2016).

For each plot we calculated three diversity indices, an evergreen proportion metric, and five leaf litter quality indices. We estimated the variables based on leaf litter mass abundance, rather than tree species basal area, because earthworms are directly and indirectly dependent on leaf litter for food and habitat opportunity (Sims and Gerard, 1999; Curry, 2004; Edwards, 2004). The basal area of tree species within plots was highly correlated with their corresponding litter mass (Pearson's correlation coefficient $r_p=0.96$; $P < 0.001$). The diversity indices were: 1) tree species richness (the number of target trees); 2) True Shannon index (exponent of Shannon diversity index; (Jost, 2006)); and 3) functional dispersion, calculated as a proxy of tree functional diversity. Functional dispersion measures the distance between tree species in a multivariate functional trait space (Laliberté and Legendre, 2010), with high values indicating that the tree species are more functionally dissimilar from each other. It was calculated in R with the *dbFD* function from the FD package (Laliberté et al., 2014), based on five relevant tree litter quality traits (C:N, C:P, calcium and lignin concentration and litter water holding capacity), weighted by the species' leaf litter mass. Traits were selected out of a pool of 18 measured litter traits by means

of PCA and pairwise correlations to select five traits that optimally represented the litter trait space and are minimally correlated (see Appendix IV for details). The evergreen proportion metric represents the proportion of evergreen leaf litter in the total litterfall of a plot. In five of the six regions, evergreen tree species were coniferous, while *Quercus ilex*, an evergreen angiosperm, occurred in Italy and Spain. As leaf litter quality indicators, the community weighted means (CWM) of the same five litter traits were calculated per plot. These CWM traits quantify the dominant trait values within a community by summarising the functional composition of single traits (Ricotta and Moretti, 2011). More details about the leaf litter mass collection can be found in De Wandeler et al. (2016).

ABIOTIC VARIABLES

Four abiotic variables were recorded in each plot: soil pH (0-10 cm horizon), soil depth, stoniness and a Heat Load index. A composite sample of nine subsamples was analysed to determine the soil pH of the 0-10 cm layer (cf. (Dawud et al., 2016)). Soil pH (CaCl₂) of the mineral soil was determined with 0.01 M CaCl₂ solution at a ratio of 1:2.5, using 827 pH lab (Metrohm AG, Herisau, Switzerland) after the soil was dried to constant weight (55°C) and sieved through a 2 mm diameter mesh. Soil depth to bedrock (cm) was measured in each plot using a soil auger or taken from literature (Guckland et al., 2009). Stone content of the soil was estimated with the “iron-rod” method by Viro (1952) and the empirical equation presented by Tamminen and Starr (1994). Heat load index, as a proxy for climate variation within regions, was calculated according to McCune and Keon (2002) where plot specific values for latitude, slope and aspect were used to feed and calculate following equation 3: Heat load index = $0.339 + 0.808 * \text{COS}(\text{latitude}) * \text{COS}(\text{slope}) - 0.196 * \text{SIN}(\text{latitude}) * \text{SIN}(\text{slope}) - 0.482 * \text{COS}(\text{aspect}) * \text{SIN}(\text{slope})$. To prevent correlation with latitude, plot-level heat load index values were scaled by the region maximum. The heat load index reflects the heat load that a particular location receives due to annual direct incidence radiation. The higher the value, the greater the heat load and the warmer that location will be.

2.3 STATISTICAL ANALYSIS

EARTHWORM RESPONSE VARIABLES

The earthworm community was represented by five different response variables: total earthworm biomass, biomass of epigeic, endogeic and anecic species and community species richness. Biomass data (g/m^2) were $[\log_{10}(x_{ij} + d) - c]$ transformed, where $c = \text{Trunc}(\log_{10}(\text{Min}(x)))$ and $d = 10^{(c)}$ following McCune et al. (2002) to meet the requirements of homogeneity and normality of residuals. This specific transformation tends to preserve the original order of magnitude in data and was preferred above the more commonly used $\log_{10}(x+1)$ since our lowest non-zero value of x differs from one by more than an order of magnitude, which would distort the relationship between zeros and other values in our dataset. As in De Wandeler et al. (2016) up to eight plots of the 209 were removed to prevent outliers and probable recording errors unduly influencing the results. In addition, we used a rarefaction procedure (rarefy function in the vegan package (version 2.4-3) (Oksanen et al., 2007)) to investigate the potential confounding effect of earthworm abundance on earthworm species richness estimations. Given that the rarefied earthworm richness values were highly correlated with the original species richness variable (Pearson's correlation coefficient $r_p=0.96$; $P < 0.001$) we chose to use the widely used and easy to understand earthworm species richness values.

TREE DIVERSITY, EVERGREEN PROPORTION AND LITTER QUALITY EFFECTS

In order to investigate tree diversity, evergreen proportion and litter quality effects we applied information-theory based analyses (Burnham et al., 2011). These analyses use different approaches to data analysis and inference compared to the traditionally used null hypothesis testing of the frequentist approach (Anderson et al., 2001). The potential effect of tree diversity indices and proportion of evergreen leaf litter on the earthworm community was tested using mixed-effects models for all regions together (continental scale) and each region separately (regional scale). The covariates (soil pH, soil depth, stoniness and heat load index) and random effects of tree species composition and region were included in all models. Tree species composition was included as random effect and was a categorical variable with 90 levels at the continental scale (one level for each tree species combination in this study). In each region, every tree species composition was represented 2 – 4 times, except the two- and three-species mixtures in the regions with a pool of five species. The species composition random effect term accounted for the non-independence of plots with the same species composition. Composition was

nested within region to account for regional phenotypic plasticity of the litter quality. For the analysis within the separate regions, 'region' was deleted from the random structure. Our null model contained only the covariates and the random error structure whilst the full model contained two additional explanatory variables: a single diversity index and the proportion of evergreen leaf litter. Before analysis, all explanatory variables were standardised to zero mean and standard deviation of 0.5 (Schielzeth, 2010). The three explanatory tree diversity indices (species richness, True Shannon Index and functional dispersion) were strongly correlated (variance inflation factor (VIF) > 5 and all pairwise correlations $r_p > 0.65$). Therefore separate models were constructed for each diversity index: [R-syntax of the full model: $y \sim \text{Diversity index} + \text{Evergreen proportion} + \text{Covariates}$, random = $\sim 1 \mid \text{Region/Composition}$]. We used an information theory approach to select the best model based on Akaike's information criterion by removing each predictor variable (diversity index and proportion of evergreen leaf litter) in turn from the model. We corrected for small sample sizes (AICc) using the *SelMod* function in the *pgriness* package (version 1.6.4) (Giraudoux, 2015). Among the best fitting models, the minimum adequate model (MAM) was that with the lowest number of estimable parameters (K) within 2 AICc units of the model with the lowest AICc. Differences in AICc scores (Δ_i) > 2 can be interpreted as indicating strong support for the MAM compared to poorer models (Burnham and Anderson, 2002). All four covariates were kept in the continental models, but to minimise over-parameterisation in the regional scale models, the number of covariates per model was reduced to the two that explained the most variation in the response variable.

To prevent over-parameterised models the tree litter quality analysis was carried out separately, using a different modelling approach. At both the continental and regional scale a global model was defined for each earthworm response variable. We used a mixed-effects model with leaf litter CWM traits, covariates and a random term: [R-syntax: $y \sim \text{Trait}_1 + \text{Trait}_2 + \dots + \text{Trait}_p + \text{Covariates} + (1 \mid \text{Region/Composition})$]. At the regional scale however, multicollinearity between several litter trait variables occurred. A variance inflation factor (VIF) analysis was therefore performed to drop variables with a too high VIF score so that all individual VIF < 5 and median VIF < 3 (Zuur et al., 2010). By means of the *dredge* function in the *MuMIn* package (version 1.15.6) (Bartoń, 2015) all possible

combinations of candidate models that can be built with litter trait variables from the global model were built with maximum-likelihood estimation and ranked using AICc. To account for model uncertainty, we performed full model averaging of parameter estimates across all models with $\Delta\text{AICc} < 2$ (Burnham and Anderson, 2002), after which model estimates and confidence intervals were calculated (Grueber et al., 2011). Relative variable importance values (RI) per variable were calculated as the sum of Akaike weights over all models from the top model set including the variable. To minimise over-parameterisation in the regional scale models (Grueber et al., 2011), only two covariates and two litter trait variables were included per candidate model. In order to be able to compare diversity, evergreen proportion and litter quality effects the same two covariates were used per region.

To model the two response variables of this study, earthworm biomass and species richness, we used linear and generalised linear mixed-effects models, respectively (*lme* in the nlme and *glmer* in lme4 package (Bates et al., 2016; Pinheiro et al., 2016)). Model assumptions of normality and homogeneity of residuals were checked and improved by either changing the model type (linear instead of generalised linear mixed-effects modelling) or by adding a variance function (Zuur et al., 2009; Cleasby and Nakagawa, 2011) if necessary. To examine whether litter quality variables were stronger drivers of earthworm biomass and richness than tree diversity, model R^2 values were calculated as likelihood ratio-based R^2 (Magee, 1990) using the *r.squaredLR* function in the MuMin package.

At the continental scale, anecic earthworm biomass could not be analysed due to the small number of plots where anecic species were found. In addition, due to very low sample sizes, the Romanian and Spanish regions were removed from the epigeic biomass model and the Finnish region was removed from the endogeic biomass model. Several regional scale models could not be fitted due to low sample sizes (earthworm individuals present in <40% of the plots), we therefore decided to analyse the endogeic earthworm biomass for the German, Italian, Polish, Romanian and Spanish region and the biomass of each individual earthworm functional group for the German region only.

Since earthworm distribution can change over smaller spatial scales than the selected research plots of 30 x 30 m (Valckx et al., 2009), tree diversity, evergreen proportion and leaf litter quality effects were

also investigated at the neighbourhood level (5 m radius surrounding the earthworm sampling locations). In general, the model results were similar to the results at plot level. Details about the neighbourhood analysis and results can be found in Appendix V.

3 RESULTS

3.1 TREE DIVERSITY AND EVERGREEN PROPORTION EFFECTS

At the continental scale, across the six regions, tree functional diversity (based on functional dispersion) had a positive effect on the total earthworm biomass (Fig. 1a). However, the magnitude of the effect was very small and explained only 1% of the total variation in earthworm biomass. A positive effect of tree functional diversity was also visible in the other earthworm response variables (species richness, and epigeic and endogeic biomass), but was not well supported by our model selection results (Appendix II, Table S4-S5). There was little support for a taxonomic tree diversity effect, as the null model was always better than the models including the tree richness or True Shannon index (Appendix II, Table S3-S5). Compared to the diversity indices, the proportion of evergreen leaf litter in the forest stands had a stronger effect on the earthworm response variables and negatively affected both total earthworm biomass, species richness as well as their functional group biomass (epigeic and endogeic) (Fig. 1b and Appendix II, Table S3-S5). In most cases the support was strong ($\Delta AICc > 2$ compared to the null model), but it still explained only 1.7% to 3.6% of the variation in the models (Appendix II, Table S3-S5). When the evergreen leaf litter and tree functional diversity variables were tested together in one model we found an additional effect of tree functional diversity on top of the evergreen proportion effect on total earthworm biomass, together they explained 4.2% of the total variation (Appendix II, Table S3).

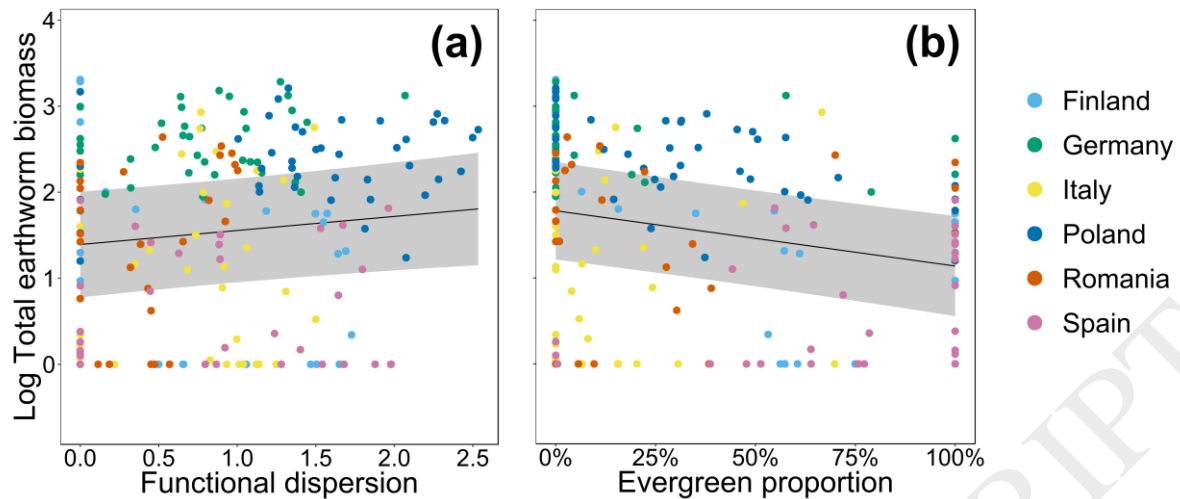


Figure 1. Effect of (a) functional dispersion of tree litter and (b) proportion of evergreen leaf litterfall on the total earthworm biomass. Lines and shaded areas represent predicted responses and corresponding 95% confidence intervals (CI) based on the respective models with respectively functional dispersion and proportion of evergreen leaf litterfall as fixed effect, tree species composition nested within region as random effect, and all other covariates set to their mean value across all the plots. Grey shaded areas represent 95% CIs of the predictions pooled across regions. Biomass data (g/m^2) are $[\log_{10}(x_{ij} + d) - c]$ transformed, where $c = \text{Trunc}(\log_{10}(\text{Min}(x)))$ and $d = 10^{(c)}$. Colours of the circles represent the different regions (light blue = Finland, green = Germany, yellow = Italy, dark blue = Poland, Red = Romania, pink = Spain).

At the regional scale, there was little support for the importance of the tree diversity indices (species richness, True Shannon Index and functional dispersion) in explaining variation in the earthworm response variables (total biomass, species richness and functional groups of earthworms). After model selection, either the null model was the best model or models including a diversity variable had the smallest AICc but were within two AICc units of the null model. We found a weak negative effect of tree species taxonomic diversity in the Polish region, suggesting a decreasing total earthworm biomass as tree species diversity increased (Appendix II, Table S3). In the German region, evidence of a weak positive effect of the True Shannon's tree diversity index and a tree functional diversity effect were identified for epigeic and anecic biomass, but not for the endogeic biomass. Whereas only 1 % of the total variation was explained by tree diversity variables in the endogeic models, up to 7% and 10% were explained in the epigeic and anecic models, respectively (Appendix II, Table S6). In general, endogeic biomass was not related to tree diversity variables in any of the studied regions (Appendix II, Table S7).

Consistent with the diversity variables, we found little support for the importance of the proportion of evergreen leaf litter at regional scale. The exception was the Finnish region where the proportion of evergreen leaf litter explained 28% and 9% of the variation in the total earthworm biomass and species richness, respectively. The total earthworm biomass and species richness in the Finnish region decreased with increasing proportion of evergreen leaf litter.

3.2 TREE LITTER QUALITY EFFECTS

At the continental scale there was strong evidence for a positive effect of the water holding capacity (WHC) of the litter and a negative effect of the litter C:P ratio on the total earthworm biomass and species richness (Table 1, Fig. 2 and 3). In addition we found significant effects of litter C:N ratio, calcium and lignin on the total earthworm biomass, however their relative importance was low (Appendix II, Table S8).

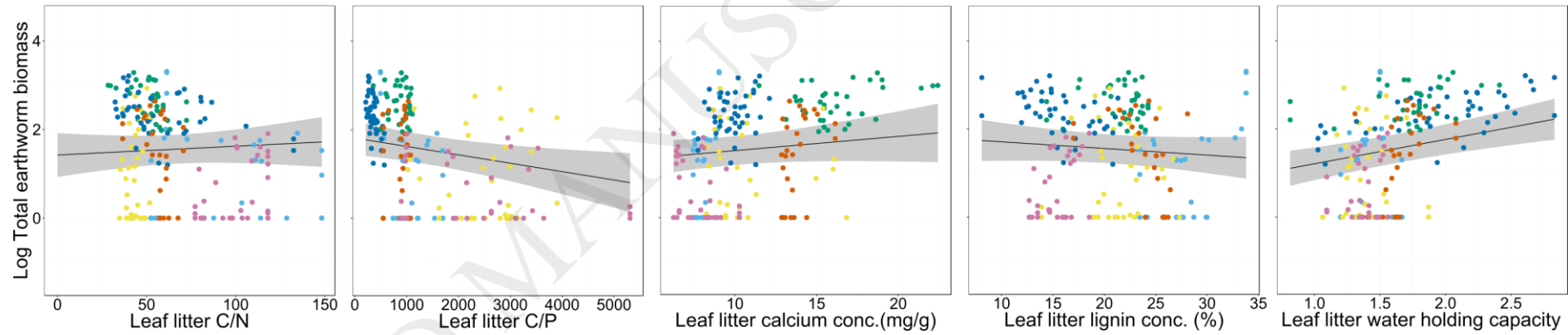


Figure 2. Effect of tree leaf litter traits on the total earthworm biomass. Lines and shaded areas represent predicted responses and corresponding 95% confidence intervals (CI) based on the respective models with the respective litter trait as fixed effect, tree species composition nested within region as random effect, and all other litter traits and covariates set to their mean value across all the plots. Grey shaded areas represent 95% CIs of the predictions pooled across region. Biomass data (g/m^2) are $[\log_{10}(x_{ij} + d) - c]$ transformed, where $c = \text{Trunc}(\log_{10}(\text{Min}(x)))$ and $d = 10^{(c)}$. Colours of the circles represent the different regions (light blue = Finland, green = Germany, yellow = Italy, dark blue = Poland, Red = Romania, pink = Spain).

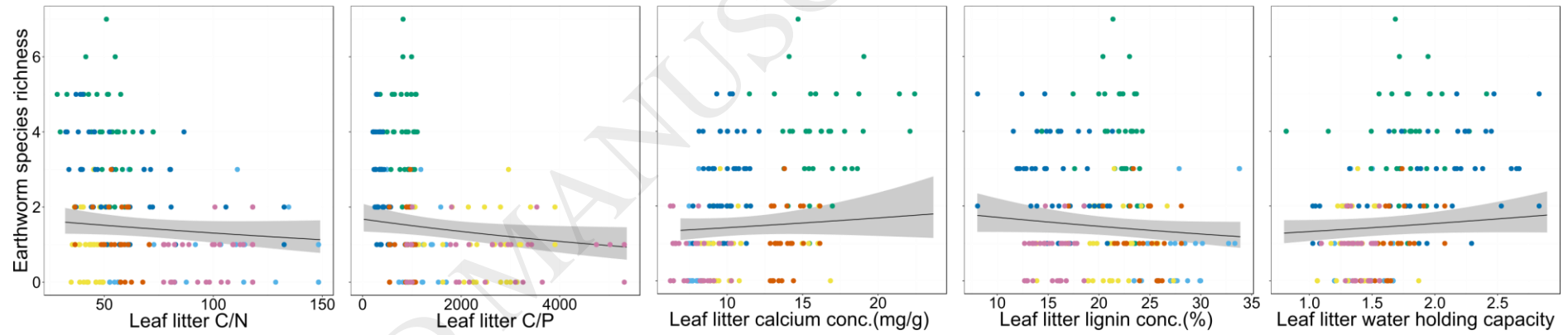


Figure 3. Effect of tree leaf litter traits on the earthworm species richness. Lines and shaded areas represent predicted responses and corresponding 95% confidence intervals (CI) based on the respective models with the respective litter trait as fixed effect, region as random effect, and all other litter traits and covariates set to their mean value across all the plots. Grey shaded areas represent 95% CIs of the predictions pooled across regions. Colours of the circles represent the different regions (light blue = Finland, green = Germany, yellow = Italy, dark blue = Poland, Red = Romania, pink = Spain).

Table 1. Simplified reproduction of the model parameter estimates and their relative importance demonstrating the effect of litter quality traits on a) total earthworm biomass and b) earthworm species richness for the continental and six regional scale models. The arrows represent the direction of the averaged parameter estimates of the best candidate models and the values right of the arrows represent their relative importance values. Detailed results of the parameter estimates can be found in Appendix II, Table S8-S12. Parameters that were retained in the best candidate models are represented with a black arrow. Parameters that were not included in the analysis due to multicollinearity issues, but that showed high correlations with variables that were retained in the best candidate models have grey arrows (Appendix II, Table S15). Parameters that were included in the model, but not retained in the best candidate models are indicated with a hyphen. Parameters that were highly correlated with parameters that were not retained in the best candidate models are left blank.

Model parameters	CONTINENTAL	FINLAND	GERMANY	ITALY	POLAND	ROMANIA	SPAIN
a) Total earthworm biomass							
C:N ratio	↗ 0.13		↘ 1	-	-	↘ 0.31	↗ 0.67
C:P ratio	↘ 0.80	↘	↘ 0.33		↘	-	-
Calcium	↗ 0.16	↗ 1	-	-	↗	-	↘ 0.67
Lignin	↘ 0.16	↗	-		-	↘ 1	↗
Water holding capacity	↗ 1	-	↗	-		↗	↗ 0.22
b) Earthworm species richness							
C:N ratio	↘ 0.49	↘	↘ 0.98	-	↘	0.30	↘
C:P ratio	↘ 0.21	↘	↘ 0.31		↘	-	-
Calcium	↗ 0.09	↗ 0.69	-	-	-	↗ 0.23	-
Lignin	↘ 0.09	↗	↘ 0.16		-	↘ 0.21	
Water holding capacity	↗ 0.54	↘ 0.27	↗	-		↗	-

↗ : Earthworm biomass/species richness increases with increasing model parameter value

↘ : Earthworm biomass/species richness decreases with increasing model parameter value

Table 2. Simplified reproduction of the model parameter estimates and their relative importance demonstrating the effect of litter quality traits on earthworm functional group biomass (epigeic, endogeic and anecic) for continental scale models. Anecic models could not be fitted due to a too low amount of plots where anecic species were present. (cf. Table 1 for details)

Model parameters	Epigeic	Endogeic	Anecic
C:N ratio	-	-	NA NA
C:P ratio	↘ 0.20	↘ 0.55	NA NA
Calcium	-	-	NA NA
Lignin	↗ 0.32	↘ 0.45	NA NA
Water holding capacity	↗ 1	↗ 1	NA NA

↗ : Earthworm biomass increases with increasing model parameter value

↘ : Earthworm biomass decreases with increasing model parameter value

Table 3. Simplified reproduction of the model parameter estimates and their relative importance demonstrating the effect of litter quality traits on endogeic earthworm biomass for the continental and regional scale models that had sufficient endogeic earthworms. (cf. Table 1 for details)

Model parameters	CONTINENTAL	FINLAND	GERMANY	ITALY	POLAND	ROMANIA	SPAIN
C:N ratio	-	NA NA	↘ 1	-	-	-	↗
C:P ratio	↘	0.20 NA NA	-	-	-	-	-
Calcium	-	NA NA	-	-	-	-	↘ 0.63
Lignin	↘	0.32 NA NA	-	-	↘ 0.40	-	↗
Water holding capacity	↗	1 NA NA	↗	-	↗	-	-

↗ : Earthworm biomass increases with increasing model parameter value

↘ : Earthworm biomass decreases with increasing model parameter value

Table 4. Simplified reproduction of the model parameter estimates and their relative importance demonstrating the effect of litter quality traits on earthworm functional group biomass (epigeic, endogeic and anecic) for the German region. (cf. Table 1 for details)

Model parameters	Epigeic	Endogeic	Anecic
C:N ratio	↘ 1	↘ 1	↘ 0.42
C:P ratio	↘ 1	-	↘ 0.13
Calcium	-	-	↗ 0.42
Lignin	-	-	↘ 0.13
Water holding capacity	↗	↗	↗

↗ : Earthworm biomass increases with increasing model parameter value

↘ : Earthworm biomass decreases with increasing model parameter value

Table 5. Likelihood ratio R^2 of the total earthworm biomass null models (Biomass ~ 1 + Covariates + Random effect) and respective diversity (Biomass ~ Diversity index + Covariates + Random effect), proportion of evergreen leaf litter (Biomass ~ Evergreen proportion + Covariates + Random effect) and litter quality models (Biomass ~ Litter quality traits + Covariates + Random effect). The litter quality models are the best models after model selection (see section 2.4 for details). The last column (Litter quality traits) describes which traits were included in the best litter quality model. All models were fitted with restricted maximum likelihood estimation.

Model scale	Null model	Diversity			Identity		
		Richness	Shannon	FDis	Evergreen	Litter quality	Litter quality traits
Continental	0.575	0.575	0.576	0.585	0.611	0.624	C:P ratio + WHC
Finland	0.289	0.284	0.304	0.297	0.565	0.715	Calcium
Germany	0.049	0.054	0.128	0.105	0.077	0.269	C:N ratio
Italy	0.092	0.177	0.176	0.151	0.094	0.092	-
Poland	0.568	0.612	0.59	0.573	0.573	0.568	-
Romania	0.24	0.281	0.267	0.305	0.286	0.494	Lignin
Spain	0.04	0.059	0.089	0.041	0.079	0.139	Calcium

At the continental scale epigeic and endogeic earthworm biomass were positively correlated with litter water holding capacity (Table 2). In addition, both groups showed a negative correlation with C:P ratio but opposite relationships with litter lignin concentration, with epigeic biomass increasing and endogeic biomass decreasing with increasing lignin concentration.

At the regional scale we observed similar responses for total earthworm biomass in the Finnish, German and Polish regions. However, in the Spanish region relationships with litter nutrient traits were reversed (Table 1a), total earthworm biomass was higher in plots with higher litter C:N ratio and lower in plots with a higher litter calcium concentration. In contrast, water holding capacity was positively related to earthworm biomass in Spain as in Germany and Romania. In general, all litter quality traits that were retained in the averaged top model sets at the regional scale, showed similar directional responses for both total earthworm biomass and species richness (Table 1). Moreover, there were strong correlations between earthworm biomass and species richness ($r_p = 0.88 - 0.51$). Nevertheless, we found differences in the relative importance of the explanatory variables (Appendix II, Table S8-S9). In contrast to total earthworm biomass where no such relationships were detected, earthworm species richness decreased with increasing litter water holding capacity in the Finnish region, increasing lignin concentration in the German region and increasing C:N ratio in the Polish region (Table 1b). We found little support for an effect of litter quality on endogeic biomass (Table 3). However, litter quality appeared to have opposite effects on endogeic earthworm biomass in the Spanish region and the temperate forest regions in Germany and Poland.

When we compared earthworm functional group models in the German region, we found support in all functional groups for a negative relationship between earthworm biomass and litter C:N ratio and an increase in earthworm biomass in forest plots with litter with a higher water holding capacity ($r_p = -0.8$; WHC~C:N) (Table 4). Lignin and litter calcium concentration were only related to anecic earthworm biomass in the German forest region.

3.3 COMPARING IMPORTANCE OF SPECIES DIVERSITY, EVERGREEN PROPORTION AND LITTER QUALITY EFFECTS

Litter quality traits explained a larger proportion of the variation in total earthworm biomass than the proportion of evergreen leaf litter and any of the tree diversity indices. This is clearly indicated in the continental and most regional models (Table 5) by higher R^2 values for the litter quality models in comparison with the evergreen proportion and diversity models. Similarly, the variation in the biomass of earthworm functional groups was generally better explained by tree litter quality traits than by the proportion of evergreen leaf litter or tree diversity (Appendix II, Table S14). The results of the earthworm species richness models were less consistent: At the continental scale and in the Finnish region the proportion of evergreen leaf litter explained the highest amount of variation in species richness. However, in the German region litter quality was the best predictor, while in the other regions R^2 values were much lower and their differences between predictor variables small (Appendix II, Table S13).

4 DISCUSSION

4.1 TREE DIVERSITY AND EVERGREEN PROPORTION EFFECTS

We found little support for the importance of tree diversity on earthworm biomass and species richness, at either the regional or continental scale. Nevertheless, functional dispersion as a proxy for tree functional diversity contributed to explain total earthworm biomass at the continental scale. Our findings are largely consistent with the findings of Schwarz et al. (2015) who found no significant relationships between tree diversity indices and earthworm abundance and species richness in young tree diversity experiments (8-10 years old). These forest experiments, however, might have been too young to allow the trees to create changes in soil properties that could facilitate earthworm abundance or species richness. In contrast, Chamagne et al. (2016) reported a significant positive True Shannon diversity effect on earthworm species richness in mature forests in the Czech Republic. They reasoned that earthworm species might be specialized on certain tree species, which results in higher earthworm species richness when these tree species occur together in a mixture. In addition, the effect of litter functional diversity on earthworm biomass observed in this study echoes results from another study from the FunDivEUROPE platform, wherein the effect of the overall decomposer community on

decomposition was partly driven by the litter functional diversity (Joly et al., 2017). It is not clear why functional diversity was only significant at the continental scale. In this case there can be several reasons why different conclusions can be drawn from effects acting on different scales. (i) Environmental and earthworm biomass gradients might be longer at the continental scale compared to the regional scale. (ii) A larger sample of the continental model can also result in higher statistical power. (iii) Factors other than functional diversity are more important at the regional scale, such as differences in soil characteristics that were not covered by our covariates. Only after accounting for such hidden differences in the random factor “region”, functional diversity signals emerged at the continental scale.

Tree diversity (both True Shannon index and functional diversity) was more important for detritivore earthworm biomass (epigeic and anecic species) than for geophagous biomass (endogeic species), in the German region. This is consistent with the different feeding behaviour of the two groups (Hendriksen, 1990): detritivore earthworm species mainly feed on surface litter, while geophagous species feed on organic matter in the organo-mineral horizon.

The negative trends in the tree diversity-total earthworm biomass relationships in Poland and Finland are most probably caused by litter quality or tree species identity effects, where one or two tree species with leaf litter rich in N, P and several base cations have a decisive impact on the soil (Cesarz et al., 2016) and thus could diversify the soil ecosystem in these poorly buffered sandy soils (Reich et al., 2005). A certain proportion of good quality litter seems to be necessary in this poorly buffered system to bring the soil nutrient conditions to a certain level that earthworm biomass can increase significantly. This mechanism is similar to the threshold effect observed by De Wandeler et al. (2016) where a threshold value for several litter and soil variables had to be attained before earthworms can occur. It can also be interpreted as a selection effect of tree diversity: if only a few species with good litter quality occur in the species pool, the proportion of low quality litter increases as the tree diversity increases.

In this study the evergreen proportion effect was a more important factor in explaining earthworm biomass and species richness than tree diversity. At the continental scale we observed a negative effect of the proportion of evergreen leaf litter on the earthworm community and hereby confirm results of

previous studies in Europe and North America (González et al., 2003; Scheu et al., 2003; Elmer et al., 2004; Ammer et al., 2006). The mechanism behind this negative relationship is most probably a litter quality effect. Evergreen leaf litter is generally lower quality litter in terms of low nutrient content and high lignin content and therefore less preferred by soil organisms (Korboulewsky et al., 2016), which in turn slows down litter decomposition and promotes soil acidification (Augusto et al., 2002; De Schrijver et al., 2012). Even though this negative effect of the proportion of evergreen leaf litter on the earthworm community was observed in northern Europe, our results indicate that it might not hold true in southern Europe where the more arid climate and the presence of broadleaved angiosperm trees in the evergreen functional group (*Q. ilex*) may alter this effect (section 5.3. and Appendix II, Table S3-S4).

4.2 LITTER QUALITY EFFECTS

Several litter trait effects were similar for total earthworm biomass and richness, both at the continental and regional scale. Earthworm biomass and species richness both increased with decreasing C:N and C:P ratios and increasing water holding capacity and calcium concentration in all but the southern (Italian and Spanish) regions. These effects of tree litter calcium concentration and C:N and C:P ratios on earthworm biomass are in concordance with earlier research by De Wandeler et al. (2016) at a continental scale and with many other local scale studies (Reich et al., 2005; Holdsworth et al., 2012; Ott et al., 2014; Cesarz et al., 2016; Yatso and Lilleskov, 2016). A high litter calcium concentration, high water holding capacity and low C:N and C:P ratios create favourable conditions that stimulate microbial decomposer abundance and consequently the recycling of other important nutrients, resulting in an increased nutrient availability (Gosz et al., 1973; Bardgett, 2005; Manzoni et al., 2012). Nevertheless, the mechanisms behind these relationships could be diverse: Litter calcium can influence soil pH (Reich et al., 2005) and as a consequence indirectly increase earthworm richness and biomass by allowing acidophobic species to occur. This is especially important in a sandy soil with low pH values, consistent with those recorded in the Finnish and Polish plots (Ammer et al., 2006). More calcium-rich litter generally means more easily digestible food with high macronutrient concentrations, which can also more directly support a higher earthworm biomass (Lavelle et al., 1995; Reich et al., 2005; Cesarz et al., 2016). In addition, it is known that some species, mainly litter feeders (Pearce,

1972), need calcium to supply their well-developed calciferous glands, that produce calcium carbonate (Canti and Pearce, 2003). CaCO_3 production in these earthworms is probably related to pH regulation of blood and tissue fluids when soil CO_2 levels are high (Versteegh et al., 2014). The fact that litter calcium was an important variable explaining variation only in anecic earthworm biomass in the German region could be related to their stronger dependence on litter as a food source and, at the same time, their need for calcium to regulate pH levels in the blood.

As expected we found a decrease in total earthworm biomass and species richness with increasing litter lignin concentration and decreasing water-holding capacity. In contrast, we found the opposite patterns in the Finnish region. Increasing earthworm biomass and species richness with increasing litter lignin concentration and decreasing water-holding capacity might seem counterintuitive, but in the Finnish forest region lignin was highly positively correlated with litter calcium concentration across the three tree species ($r_p=0.98$) and negatively with C:N and C:P ratio (respectively $r_p= -0.73$ and $r_p= -0.95$, Appendix II, Table S15). It confirms earlier observations that as soon as a sufficient amount of macronutrients are present (threshold effect, see De Wandeler et al. (2016)), other litter traits like lignin and WHC become less important (Rajapaksha et al., 2013). The opposite relationships of the epigeic and endogeic earthworm biomass with the litter lignin concentration across regions was against our expectations as leaf litter high in lignin is generally considered hard to decompose (Hobbie et al., 2006; Berg and McClaugherty, 2008) and high-lignin substrate is not preferred by earthworms (Kasurinen et al., 2007). However, the relative importance of litter lignin concentration for epigeic earthworm biomass was small (Appendix II, Table S10), and this positive relationship with lignin disappeared when the Italian plots were excluded from the analysis. Drought earlier in the season, in the Italian region might have contributed to this rather unexpected result at a continental scale.

4.3 LATITUDINAL VARIATIONS IN EARTHWORM BIOMASS RESPONSE TO LITTER QUALITY

A latitudinal variation in trait specific responses was observed for total and endogeic earthworm biomass, but also for earthworm species richness. Consistent with Reich et al. (2005), who associated

increased earthworm abundance and diversity to calcium-rich litter in Poland, we observed increasing earthworm biomass and species richness with increasing litter nutrient concentrations (low C:N ratio and high calcium concentration; Table 1) in north and central Europe (Finland, Poland, Germany, Romania). In southern Europe, earthworms seemed less dependent on nutrient-rich litter. We found endogeic earthworm biomass to even decrease with increasing leaf litter nutrient concentration in the Spanish forest region (Table 3). This is inconsistent with the well-accepted hypothesis that earthworms prefer to ingest litter with high nutrient concentrations (Hendriksen, 1990; Rajapaksha et al., 2013). This contrasting relationship of endogeic earthworm biomass with leaf litter nutrient concentration in Spain could have several reasons. On the one hand, litter nutrient concentrations are less important to endogeic earthworms in nutrient rich soil (Cesarz et al., 2016). On the other hand, the higher temperatures in the Italian and Spanish regions may facilitate the mutual digestion system of the earthworm species (Lavelle et al., 1995). However, the most important explanation as to why endogeic earthworm biomass decreases with increasing leaf litter nutrient concentration in Spain is probably the correlation of nutrient rich litter with very dry soil conditions that negatively impact the earthworm community. This reasoning is based on our assumption that calcium-rich litter in Spain indicates shallow soils on calcareous bedrock that results in temporally very dry conditions and sparse vegetation.

4.4 IMPORTANCE OF TREE DIVERSITY VERSUS TREE IDENTITY EFFECTS FOR EARTHWORMS

We found that litter quality was a stronger driver of earthworm biomass than tree diversity, as reported by Schwarz et al. (2015). At the continental scale and in the Finnish and German region, tree identity (evergreen proportion and litter quality) rather than tree diversity was driving earthworm species richness. Herewith, our results contradict findings of Chamagne et al. (2016) who found that tree species richness rather than differences in litter quality affected the earthworm diversity. However, the range of litter traits of the four tree species studied by Chamagne et al. (2016) is smaller than in our study and might not have been large enough to detect litter quality effects in the studied forest soil.

5 CONCLUSION

Overall, our study showed that covering the large geographic area and the multitude of factors considered advances our understanding of tree diversity and identity effects on earthworm communities. By focusing on tree leaf litter traits, this study provided greater insight into the mechanisms driving tree identity effects. We specifically found a latitudinal variation in earthworm biomass response to tree leaf litter quality. Furthermore, by making use of a research platform that allowed unconfounded tree species diversity tests, this study supports previous findings that litter quality, as a proxy of tree identity, was a stronger driver of earthworm biomass than tree species diversity. In addition, of the three diversity indices tested (richness, True Shannon diversity index, functional diversity), tree functional diversity positively affected earthworm biomass at the continental scale. This study was however limited to the diversity and litter quality effects of trees as they were assumed to be the main players in the forest ecosystem in terms of litter production, although the ground was often covered with herbaceous plants or shrubs in most of the studied regions. Previous research highlighted the link between earthworm distribution and the presence, biomass and nutrient quality of understory vegetation, and we therefore encourage future tree diversity research to incorporate understory vegetation in their study.

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SUPPLEMENTARY MATERIAL

Appendix I: Additional figures (S1-S3)

Appendix II: Additional tables (S1-S15)

Appendix III: Determination of leaf litter C:N ratio and calcium concentration

Appendix IV: Variable reduction procedure to optimally represent the litter trait space

Appendix V: Analysis and results at neighbourhood level

Appendix VI: References

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