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

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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.

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

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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 (Neirynck 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; Neirynck 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; 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 (Râşca, 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 × 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,