Original article

Non-significant tree diversity but significant identity effects on earthworm communities in three tree diversity experiments

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ABSTRACT

There is mounting evidence that the functioning of an ecosystem is highly connected to the diversity of its biota. However, the influence of biodiversity on ecosystem functions in terrestrial ecosystems has mainly been investigated in grassland. In contrast, forests have long been neglected in this context, though their functional relevance is undoubted. This study investigated the effects of different tree diversity indices (species richness, species evenness, functional diversity) and of tree species identity on earthworm communities in three distinct eight to ten years-old tree diversity experiments.

Consistently in all three experiments we found no significant relationships between tree diversity indices and earthworms, whereas they were significantly affected by tree species identity. European larch (*Larix decidua*) and Norway spruce (*Picea abies*) had strong and consistent negative effects on earthworms, while the presence of oak (*Quercus petraea* and *Quercus robur*) and Scots pine (*Pinus sylvestris*) increased earthworm abundance and biomass significantly, but effects were inconsistent. Soil pH was only a poor explanatory variable for tree identity effects. The results indicate that tree identity, but not tree diversity drives earthworm communities in young tree stands. The negative effects of larch and spruce may be due to rather low palatability of their litter and to the dense canopy structure reducing soil moisture and temperature, while we found limited support for soil acidification effects. Future studies should consider litter and root traits of trees, and both the effects of trees and herbaceous plants in the understory to explain variations in ecological communities and ecosystem processes.

1. Introduction

Over the last years there has been growing evidence that biodiversity has positive effects on various ecosystem functions [1—3]. In real nature, however, changing biodiversity is not only a result of species extinctions and invasions, but also of changing dominance structures, indicating the need to understand how evenness or dominance of species influences ecosystem functions [4]. In addition, focusing only on species diversity neglects other levels of organization contributing to biodiversity. In particular trait-based approaches have gained in importance as functional traits of species rather than their pure number seem to determine ecosystem functions [5,6]. The dissimilarity of traits may result in niche differentiation and thus a higher resource use efficiency, while evenness is likely to enhance such complementarity effects [7].

Our understanding of the relative importance of different diversity measures, and the biodiversity—ecosystem functioning relationship in terrestrial ecosystems is mainly based on experiments in microcosms, mesocosms, and grasslands [1,2]. In contrast, forests as long-lived systems have long been neglected by functional biodiversity research. Due to their ecological and socioeconomic significance [8—10] and to complement findings in natural and semi-natural woods, some experiments were established in

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recent years that created longer gradients of tree diversity by planting new forest communities [9,11,12].

Through their physical structure and especially their above- and belowground litter inputs, trees have large impacts on chemical, physical, and biological properties of the soil system [13,14], where complex detrital food webs in turn recycle nutrients for plant biomass production. Different tree species are likely to vary in their influence on soil organisms and the processes driven by them [15]. Compared to monospecific litter, increasing litter diversity may improve nutrient availability and microclimatic conditions for microbial decomposers and detritivores, thus, resulting in accelerated decomposition of the constituent litter species [16—18]. It was found that such litter diversity effects determine decomposition rates to a large extent through their impacts on soil macrofauna [19].

We investigated tree diversity and tree identity effects on earthworms, which are key organisms in the soil with strong influences on soil physical, chemical, and biological properties [20,21]. They often dominate the biomass of soil fauna and represent main contributors to litter fragmentation and burial [19,22,23]. According to their burrowing and feeding behavior, earthworms are assigned to the three ecological groups anecics, epigeics, and endogeics [24]. Several studies revealed that size and structure of earthworm communities depend on the identity of the present tree species [25—28], probably due to differences in litter palatability and soil chemistry. In grasslands, earthworm density and biomass have been found to increase in the presence of nitrogen (N)-rich litter material [29—31], whereas endogeic earthworms may rather be carbon (C)-limited in forests [32,33]. In addition, litter C/N ratio and polyphenol content were suggested to determine litter palatability [34], with potential impacts on earthworms. Satchell [35] reported earthworms to selectively feed on litter material with high soluble carbohydrate content with freshly fallen litter of some tree species becoming only palatable after microbial decay.

Most previous studies investigating tree diversity effects on soil organisms considered only mixtures of barely more than two tree species. Thus, little is known about the effects of tree diversity on earthworm communities. Only a few studies investigated earthworms in more diverse tree stands and found earthworm abundance to be positively related to the number of tree species [36—38]. However, these studies used a diversity gradient based on the dilution of beech dominance and thus were not able to separate identity from diversity effects [8]. In contrast, using a more balanced design, studies on other soil invertebrates revealed that tree species identity and not diversity is a driving factor in structuring soil animal communities [39—41].

The present study was conducted in three distinct eight to ten years-old tree diversity experiments in Central Germany, to simultaneously investigate the influences of tree diversity and identity on earthworm communities. As all experiments differed in their design, we were able to consider three different measures of diversity: (1) tree species richness, (2) functional diversity [42], and (3) evenness. To understand the underlying mechanisms of potential diversity and identity effects we tested for the influence of soil pH.

According to results from grassland studies [43—45], we expected tree functional diversity to be the best predictor of earthworm community structure (hypothesis 1) as functional characteristics of the tree species may be more important than richness *per se*. Further, we hypothesized that tree identity effects are stronger than tree diversity effects [8] (hypothesis 2) as certain traits, such as leaf litter nutrient concentrations or impacts on soil pH, may have stronger effects than trait diversity/dissimilarity.

2. Materials and methods

2.1. Experimental setup

Earthworms were sampled in three different tree diversity experiments in Central Germany, which consisted of several plots being planted with a certain number of trees out of distinct species pools to generate different diversity levels (Fig. 1). Two experimental sites, BIOTREE-FD and BIOTREE-SIMPLEX, both in Thuringia, are part of the BIOTREE experiment [9], while the third sampling campaign was performed in the Kreinitz experiment in Saxony [46]. All experiments belong to an international network of tree diversity experiments (TreeDivNet, see www.treedivnet.ugent.be).

The BIOTREE-FD site (Fig. 1A, D) was established on a former pasture near Bechstedt in Thuringia, Germany in winter 2003/2004. Mean annual temperature is 7.9 °C, and annual precipitation is 553 mm. The bedrock consists of limestone, and pH is about 6.9 (Table 1). The biological subtypes vary between Eumull and Oligomull [47]. On a total area of 9 ha 25 hexagonal plots of 1700 m^2 were installed. The plots were planted with a constant number of four tree species out of a pool of 16 species to establish a gradient in functional diversity by simultaneously avoiding species richness effects. According to the method by Petchey and Gaston [42], an index of functional diversity was calculated by using nine relevant traits of the tree species, such as leaf type, crown and root architecture, and litter C/N ratio (see Scherer-Lorenzen et al. [9] for details). In each plot species were planted in groups of 20 individuals, whereas each species was planted in eleven groups per plot. Trees used for planting had an age between three and four years. The tree-to-tree distance was 1 m within a planting row, and 2 m between planting rows, being equivalent to a planting density of 5000 trees ha^{-1}. Here earthworms were sampled on 24 plots with three spatial replicates per plot (72 extractions in total). Replicates were always placed between groups of three different tree species, while assuring that all four species per plot were similarly included in the three combinations.

The BIOTREE-SIMPLEX site (Fig. 1B, E) near Kaltenborn, Germany was used as cropland until 1975 and grassland until the establishment in 2003/2004. Mean annual temperature is 7.8 °C, and precipitation is 650 mm. The bedrock belongs to the Lower Buntsandstein formation and leads to a rather low cation exchange capacity [9]. Therefore, soil pH is low in the upper soil horizons compared to the other sites (Table 1). Similar to BIOTREE-FD, the biological subtypes vary between Eumull and Oligomull [47]. The SIMPLEX site comprises 36 plots of 16 × 16 m, differing in tree density and dominance structure. Here, we sampled earthworms only in the 18 plots with high tree densities (with three spatial replicates per plot; 54 extractions in total), which were created by tree-to-tree distances of 1 m within and 1.5 m between planting rows, equivalent to a planting density of 6667 trees ha^{-1}. Here, also three to four year-old saplings were used for planting. All plots were planted with the same four species, but in different proportions. Two plots were established with equal proportions of all species, i.e. 25:25:25:25, eight plots with one dominant species, i.e. 70:10:10:10, and eight plots with one subordinate species, i.e. 10:30:30:30 (see also Lei et al. [48]). Due to the high density of randomly distributed tree species spatial replicates per plot could be placed randomly.

The Kreinitz experiment (Fig. 1C, F) near Kreinitz, Germany was established on a former arable field, which had been abandoned from the early 1990s to 2005, when the trees were planted. Mean annual temperature is 8.4 °C, and precipitation is 575 mm. The soil consists mainly of loose and partly gravelly sandy alluvial deposits [49], and soil pH is about 5.5. Two fast decomposing and two slowly decomposing deciduous tree species and two slowly decomposing