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Drivers of earthworm incidence and abundance across European forests

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ABSTRACT

Earthworms have a significant influence on the structure, composition and functioning of forest ecosystems, but in spite of their role as ecosystem engineers, little is known on the factors controlling their distribution across European forests. Optimised sampling techniques, as well as more advanced statistical tools and geographical information systems have facilitated studies at the landscape scale. But these, and even larger-scale studies, are scarce due to data limitations, taxonomic inconsistencies and practical issues in linking existing databases. In this continental-scale field-based study we used boosted regression tree modelling to identify and evaluate the relative importance of environmental factors explaining earthworm incidence (presence/absence) and abundance (density and biomass) in European forests. To parameterise our models earthworms were sampled in six forest landscapes along a latitudinal gradient from the boreal north to the Mediterranean south in spring or autumn of 2012, together with several environmental variables. Earthworms were sampled using a combined method of mustard extraction and hand sorting of litter and a soil monolith, after which they were weighed and identified to functional group (epigeic, endogeic and anecic). We found that litter- and soil-related variables best explained earthworm incidence and biomass in European forests, leaving only a minor role to climate-related variables. Among the litter related variables, understory vegetation played an important role in explaining earthworm incidence and abundance. The relative importance of explanatory variables differed between models for incidence, density and biomass and between earthworm functional groups. Our results suggested that threshold values for soil C:N ratio, forest floor pH and understory plant biomass and plant nutrient concentrations have to be attained before earthworms can occur. Beyond these threshold values, variables like soil C:N ratio, tree litter C:P ratio and forest floor mass further

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explain earthworm biomass. Mechanisms behind these observations are discussed in the light of future earthworm distribution modelling at continental scale.

1. Introduction

Earthworms are known as ecosystem engineers modifying the physical, chemical and biological soil properties (Blouin et al., 2013). They contribute to ecosystem functioning by changing soil porosity, by controlling the rate of organic matter decomposition and nutrient release, and consequently also indirectly influence primary production (Scheu and Wolters, 1991; Lavelle and Spain, 2001; Scheu, 2003; Edwards, 2004). Based on their ecology, Bouché (1977) classified earthworm species into three ecological groups, namely epigeic, endogeic and anecic earthworms. These functional groups have a different behaviour, and thus affect ecosystem functioning differently (Lavelle and Spain, 2001). Epigeic earthworms are rather small-sized species that live within the litter layer on the soil surface or within the uppermost part of the mineral soil and they feed on plant litter. Endogeic earthworms are geophagous species of generally intermediate size that live in a network of subhorizontal burrows in the mineral soil. Anecic earthworms finally, are large earthworm species that live in deep (semi) permanent vertical burrows in the mineral soil and feed on leaf litter that they drag into their burrows. Representing the greatest animal biomass component in most European forest soils (Lavelle and Spain, 2001), earthworm community composition and activity can have major consequences for the structure, composition and functioning of forest ecosystems (Hale et al., 2006; Lukac and Godbold, 2011). It is therefore highly relevant to know how environmental variables affect the incidence and abundance of earthworms (Schröder, 2008).

The composition of earthworm communities and their distribution can be studied at different spatial scales, e.g. local, landscape or continental scale. It is likely that factors influencing earthworm presence are scale-dependent (Schröder, 2008). At the local scale, earthworm incidence and abundance in forests has been shown to be influenced by soil moisture conditions (Whalen and Costa, 2003), soil texture (Fragoso and Lavelle, 1987), soil pH (Ma, 1984), litter quantity (Jordan et al., 2000; Nachtergale et al., 2002), and litter type (Peterson et al., 2001). At the landscape and continental scales, soil pH (Ammer et al., 2006; Moore et al., 2013) and litter type (Muys and Lust, 1992; Vahder and Irmler, 2012) remain influential, but variables such as climate (Rutgers et al., 2015), land use history (Räty and Huhta, 2004) and dispersal possibilities (Räty and Huhta, 2004; Suárez et al., 2006; Shartell et al., 2013) become more important (Lavelle and Spain, 2001). Earthworm distribution at local scales has been studied in depth in most terrestrial ecosystems and bioclimatic regions worldwide (e.g. Fragoso and Lavelle, 1987; Peterson et al., 2001; Whalen and Costa, 2003; Suárez et al., 2006). More recently, a next generation of larger-scale studies has been stimulated by the availability of new sampling and species identification techniques, more advanced statistical tools and geographical information systems (Decaëns, 2010; Birkhofer et al., 2012; Shartell et al., 2013; Pansu et al., 2015). Despite these recent advancements and the importance for synthetic data analysis at larger spatial scales in soil ecology, only a few studies on earthworm distribution have exceeded the landscape scale (Lindahl et al., 2009; Decaëns, 2010; Rutgers et al., 2015). Studies at larger scales can provide new insights about the drivers of the abundance and composition of soil macrofauna communities, but these are challenging for a number of reasons (Schröder, 2008; Cameron et al., in press). A standardised sampling executed over a large scale is costly, logistically, and often physically, demanding. Compiling datasets from different studies could therefore be an alternative solution. However, as Cameron et al. (in press) summarise, compiled datasets often suffer from data limitations due to differing sampling techniques, taxonomic inconsistencies and practical issues with linking and transferring databases.

In this paper we present the results of a continental-scale field-based study on earthworm incidence and abundance in mature forests. The objective of this research was to identify and evaluate the relative importance of a set of abiotic environmental variables (climate and soil parameters) and biotic variables such as vegetation composition and forest stand characteristics in explaining earthworm incidence and abundance in European forests. We evaluated the incidence and abundance of earthworm communities and the different functional groups of earthworms (epigeic, endogeic and anecic). As our sampling locations were spread along a latitudinal gradient from boreal to Mediterranean regions in Europe, covering distinct climate types (Peel et al., 2007), we hypothesised that earthworm community characteristics are primarily driven by climatic factors. Furthermore, since the three earthworm functional groups occupy different niches in the forest soil system and have distinct feeding behaviours (Bouché, 1977; Sheehan et al., 2008; Ferlian et al., 2014), we expected that the relative importance of the different control factors would differ between the three functional groups. We hypothesised that the incidence and abundance of endogeic species would primarily be explained by soil quality related factors, while that of epigeic and anecic species would be more influenced by litter quality parameters. This study extends on previous research at the landscape scale (Palm et al., 2013; Shartell et al., 2013; Marchán et al., 2015) by investigating earthworm community characteristics in mature forests at a continental scale. This research overcomes most of the aforementioned problems with large scale data sets, as all data were collected within a single study in the same standardised way, species were identified to the same taxonomic level and compiled into one single database.

2. Material and methods

2.1. Study sites

Sampling took place in the exploratory platform of the FunDivEUROPE project (Baeten et al., 2013). This platform was designed to assess biodiversity-ecosystem function relationships along a tree species richness gradient in mature forests. The six studied forest landscapes (hereafter called sites) in this platform span most of the European bioclimatic gradient and represent major European forest types including the boreal forest (North Karelia, Finland), hemiboreal forest (Białowieża, Poland), temperate beech forest (Hainich, Germany), mountain beech forest (Râsça, Romania), thermophilous deciduous forest (Colline Metallifere, Italy) and Mediterranean-mixed forest (Alto Tajo, Spain) (Appendix 3, Fig. S1).

Each study site included between 28 and 43 selected plots (30 × 30 m) with different combinations of a fixed set of locally