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Earthworm functional traits and interspecific interactions affect plant nitrogen acquisition and primary production

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ABSTRACT

We performed a greenhouse experiment to test how the functional diversity of earthworms, the dominant group of soil macro-invertebrates in many terrestrial ecosystems, affects nitrogen cycling and plant growth. Three species were chosen to represent a range of functional traits: *Lumbricus terrestris* (large, mainly detritivorous, makes vertical permanent burrows open at the surface), *Aporrectodea longa* (medium-large, feeds on both detritus and soil, makes burrows more branched than *L. terrestris*), and *Allolobophora chlorotica* (small, geophagous, makes ephemeral burrows below the soil surface). Mesocosms with ryegrass (*Lolium perenne*) were inoculated with none to all three species (similar total biomass), using an experimental design (Simplex) suited to partition single species and diversity effects. Two contrasting N sources, urea or mammalian dung, were labelled with ^{15}N so that the acquisition by plants and earthworms and recovery of applied ^{15}N could be estimated.

Over 3 months, plant production was higher with urea applications, but there were also species-specific earthworm effects: *A. chlorotica* and, to a lesser extent, *A. longa* increased shoot biomass, whereas *L. terrestris* increased root biomass. Earthworms did not affect soil N concentrations or leaching losses, whereas more N was leached under urea. *A. chlorotica* tended to increase dung-^{15}N recovery in grass shoots, but in interaction with *A. longa* had the opposite effect, possibly through increased N immobilization in the microbial biomass. Earthworms assimilated negligible amounts of urea-^{15}N but a substantial proportion (17% on average) of the dung-^{15}N, with no clear-cut differences between species. Our findings show that earthworm species may have similar trophic response to N sources and yet different effects on plant N uptake and primary production, and that inter-specific earthworm interactions can result in non-additive diversity effects.

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1. Introduction

There is mounting evidence that the diversity of soil animal decomposers is influential in ecosystem processes such as carbon and nutrient cycling (Gessner et al., 2010; Sheehan et al., 2006). However, it is not well known how such diversity can influence not only soil processes and biota, but also plant nutrient uptake and growth (Bardgett and Wardle, 2010). Earthworms are one of the abundant groups of soil fauna worldwide, and an example of ecosystem engineers due to their ability to modify the ecosystem physically (Jones et al., 1994). They have been linked to the provision of beneficial ecosystem services, such as soil fertility (Syers and Springett, 1984) and organic matter protection (Pulleman et al., 2005), but they can also be invasive species with the potential to change natural ecosystems dramatically (Nuzzo et al., 2009). There is a wide literature on the effects of earthworm presence on soil structure, nutrient dynamics and plant growth (Blouin et al., 2013; Lubbers et al., 2013; Scheu, 2003), and also an increasing body of studies on their plant-mediated effects on aboveground consumers (Wurst, 2010). Nevertheless, relatively scarce attention has been given to the role of earthworm diversity in ecosystem functioning, for instance in nutrient cycling and biological interactions.

Effects on decomposition and nutrient cycling arising from distinct earthworm species, and also from interactions with other

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animal decomposers, have been investigated in several studies (Hättenschwiler and Gasser, 2005; Heemsbergen et al., 2004; Postma-Blaauw et al., 2006; Sheehan et al., 2006 Zimmer et al., 2005), but, again, effects on plants are less explored. Discrete functional groups are commonly used to compare earthworms with ostensibly divergent traits, e.g. soil-feeding vs litter-feeding groups, but approaches that retain information on species identity are also valuable, because functional classifications should be treated with caution until tested (Petchey and Gaston, 2006). This is particularly relevant to earthworms because of the wide range of ecological traits in this taxon (Lee, 1985). In fact, it has been shown that even earthworm species usually included in the same group may differentially affect soil processes and other biota through niche partitioning and behavioural dissimilarities (Zhang et al., 2010; Zhao et al., 2013).

To investigate how the functional diversity of the earthworm assemblage affects mineral and organic N dynamics in a soil–plant system, we performed a greenhouse experiment in mesocosms with ryegrass monocultures (*Lolium perenne* L.) and different assemblages of up to three earthworm species. Three Lumbricidae species widely occurring in temperate regions (also through anthropogenic introduction) were chosen. *Allolobophora chlorotica* (Savigny) is a small endogeic earthworm (average individual fresh weight in our experiment 0.3 g) that lives near the soil surface, digging transient burrows while ingesting soil to feed on organic matter and microorganisms (Lee, 1985). *Lumbricus terrestris* L. is a much larger (3.4 g), anecic earthworm, it inhabits permanent vertical burrows in the soil, and feeds mainly on surface-deposited organic residues such as leaf litter and dung (Lee, 1985). *Aporrectodea longa* (Ude) is also anecic, closer in size (2.2 g) and ecological characteristics to *L. terrestris* than to *A. chlorotica*, but to some extent intermediate between more specialized detritivorous and soil-feeding forms (Schmidt et al., 1997); it also digs more branched tunnels than does *L. terrestris* (Eisenhauer et al., 2008). Hence, our species pool covers a range of functional traits, trophic and non-trophic. Interspecific trait dissimilarity, rather than other measures of diversity, is probably the real driver behind many biodiversity effects on ecosystem functioning (Dı'az and Cabido, 2001; Heemsbergen et al., 2004). In particular, we asked whether interactions between these three earthworm species with divergent traits will lead to synergistic effects on the plant–soil system.

Rather than using factorial combinations of earthworm species presence-absence, we established a "continuous" range of species assemblages at fixed overall biomass. This experimental framework, which has been successfully used in recent studies on plants and soil animal decomposers (O'Hea et al., 2010; Piotrowska et al., 2012; Sheehan et al., 2006), allowed us to separate the contribution of species identity and interspecific interactions (diversity effects) to an ecosystem process. Furthermore, as the relationship between soil animal decomposers, nutrient cycling and plants is likely to depend on the form in which nutrients enter the belowground system, we included two distinct N sources, dung and urea. From an agricultural perspective, dung and urea simulate organic and mineral fertilization, respectively, but they also exemplify common N sources in natural grasslands, i.e. mammalian faeces and urine. We hypothesized that earthworms would incorporate more N from the dung than the urea fertilizer, and increase plant growth with both types but in particular with dung. We expected such effects to be more pronounced in communities in which an anecic and an endogeic coexisted; the posited mechanism is that the anecic species would directly incorporate dung belowground, and also assimilate more dung-derived N in their bodies through direct feeding, whereas *A. chlorotica* would mix the buried dung with soil, making its nutrients more available to plant roots. We also hypothesized that earthworms would increase N losses through

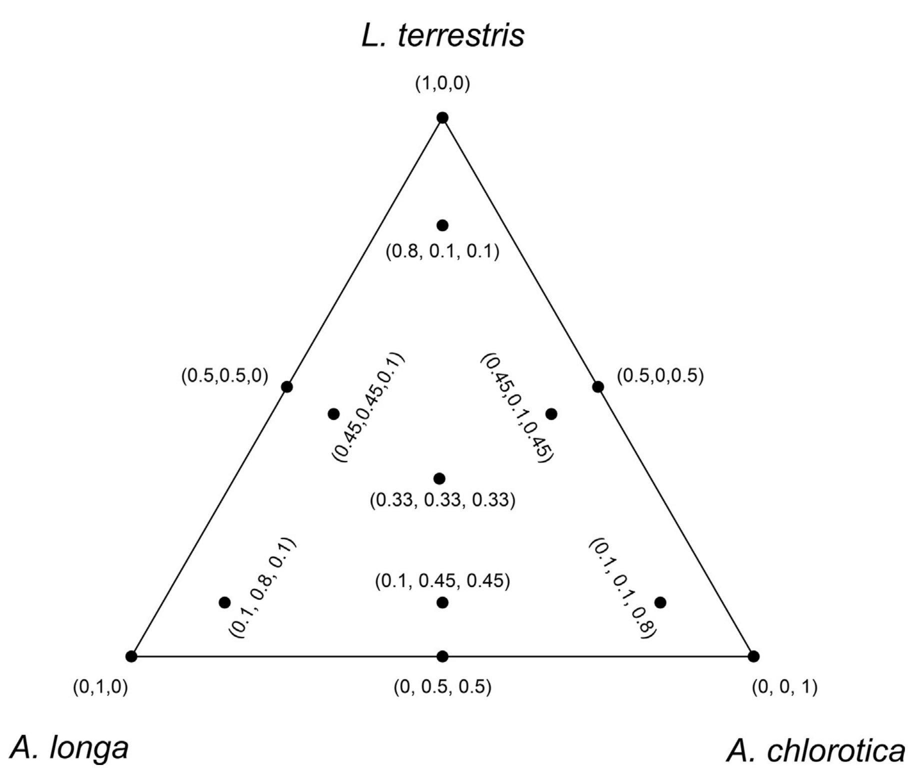

Fig. 1. Diagram of the Simplex design that guided the biomass proportions in earthworm species assemblages. The vertices of the triangle are the single-species treatments, the points on the sides are the two-species mixtures, and the others correspond to various three-species combinations, in the order *L. terrestris*, *A. longa*, *A. chlorotica*. For instance, (0.1, 0.1, 0.8) indicates mesocosms in which *L. terrestris* and *A. longa* each accounted for 10% of the earthworm biomass, while *A. chlorotica* made up 80%.

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