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Original article

Understanding earthworm – Collembola interactions and their importance for ecosystem processes needs consideration of species identity

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A B S T R A C T

Soil animals and their interactions exert strong effects on ecosystem processes, such as leaf litter decomposition and nitrogen (N) cycling, thereby contributing to ecosystem functioning and stability. The understanding of how and why certain species interact is important to predict the effect of soil animal communities on ecosystem processes. Species interactions are discussed as being facilitative, antagonistic or neutral. We investigated interactions between two earthworm (*Lumbricus terrestris*, *Aporrectodea caliginosa*) and two Collembola species (*Heteromurus nitidus* and *Protaphorura armata*), representing major soil decomposer taxa. The two earthworm species are representatives of the soil macrofauna, with *L. terrestris* living in permanent vertical burrows and feeding on leaf litter, and *A. caliginosa* living in non-permanent horizontal burrows and feeding predominantly on resources in organo-mineral soil. The Collembola species are representatives of the soil mesofauna, with *H. nitidus* predominantly colonizing the soil litter interface and feeding on litter associated resources, whereas *P. armata* colonizes deeper soil layers and mainly feeds on resources in organo-mineral soil. Therefore, the species were assumed to differ in two major traits, i.e. body size (macrofauna vs. mesofauna) and food microhabitat association ("litter-associated" vs. "soil-associated"). Mesocosms with natural forest floor containing one beech (*Fagus sylvatica*) sapling were set up and incubated in the laboratory for three months. ^{15}N labeled beech litter was added to follow the effect of detritivore animals on N cycling and N uptake by beech saplings. We hypothesized antagonistic interactions to dominate in species with similar body size or food microhabitat association via hampering the performance (biomass, abundance) of each other thereby reducing effects on leaf litter decomposition and N cycling. On the contrary, we expected species of different body size or food microhabitat association to facilitate each other's effects on ecosystem processes. In contrast to our expectation there was no clear relationship between similarity of body size or food microhabitat association and soil fauna effects on each other. Interactions between detritivores were not consensual with *L. terrestris* facilitating biomass gain of *A. caliginosa*, while its own biomass was reduced in presence of *A. caliginosa*. Additionally, ^{15}N incorporation into *A. caliginosa* and the two Collembola species decreased in presence of *L. terrestris*, irrespective of similarity of body size or food microhabitat association. Leaf litter decomposition was increased by *L. terrestris*, while none of the other species affected litter decomposition. Generally, ^{15}N incorporation into beech saplings was significantly increased in presence of *L. terrestris* or *H. nitidus*, but reduced in two species treatments due to antagonistic interactions. Interestingly, it was increased if *L. terrestris*, *A. caliginosa* and *P. armata* were present together, indicating facilitative interactions between these species. The results suggest that soil fauna interactions mainly vary with the identity of species and community composition rather than with similarity of traits. This highlights the complexity of soil fauna interactions and the difficulty to predict their effects on ecosystem processes, such as litter decomposition and N cycling, in species rich communities.

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1. Introduction

Biodiversity is considered to be a major determinant of ecosystem functioning and stability [1–3]. A considerable fraction of global biodiversity and species from virtually all taxonomic groups of microorganisms and invertebrates is found in soil [4], and soil animals are driving important ecosystem processes such as decomposition and nutrient turnover [5]. The majority of energy and nutrients obtained by plants is used for primary production and returned to soil as dead organic matter or detritus. In forest ecosystems up to 90% of the annual biomass production enters the soil and therefore the decomposer community as dead organic matter [6], mainly as aboveground litter [7,8], thereby returning nutrients to soil, most importantly nitrogen (N) and phosphorus (P). Most terrestrial ecosystems are limited by N [9,10], together with P and potassium, the main element that limits plant productivity [11]. Therefore, decomposition of litter material and the release and cycling of N bound in detritus are important for the continuous nutrient supply for soil animals, microorganisms and plants [12], and thereby for the productivity of terrestrial ecosystems [13].

Earthworms and Collembola are among the most important and abundant soil invertebrate taxa involved in decomposition and nutrient cycling [14–16]. Earthworms modify physical, chemical and biological properties of the soil, feed on and incorporate litter into the soil, and mingle organic material and mineral soil, thereby increasing decomposition processes and nutrient cycling [14,17,18]. Collembola are among the most abundant and best studied microarthropods [15,16,19]. Although classically viewed as typical fungivores, Collembola are trophically diverse and feed on a variety of food materials including fungi, but also plants, algae, detritus, bacteria and even other soil animals [20–22]. Since soil animals affecting decomposition and nutrient cycling are part of complex trophic and non-trophic networks, their influence on ecosystem processes is modified by interactions between them [4,23]. Previous studies on the effects of earthworms on Collembola [24–26] suggest those effects to vary from antagonistic over neutral to facilitative. The variability in the effects is likely due to differences in the traits of the investigated earthworm species, such as body size, distribution within the soil and resource use, that indirectly influence their individual performance [27–29]. However, even earthworms with similar traits may exert different effects on Collembola [27]. This suggests that not only the traits of earthworms, but also those of Collembola are important for their interactions.

The similarity of traits is assumed to be the main factor influencing effects of soil animals on each other [30]. This is supported by Uvarov [31] who found competition and therefore antagonistic interactions between earthworm species to increase with increasing trait similarity. Moreover, Heemsbergen et al. [30] found different macrofauna detritivores to antagonistically affect their respective effect on the rate of ecosystem processes with increasing similarity of traits. In contrast, animal species with dissimilar traits facilitated each other's influence on e.g., the rate of leaf litter mass loss [30]. We investigated if these relationships also apply for interactions between macrofauna and mesofauna detritivores. We conducted a full factorial mesocosm experiment in the greenhouse with two earthworm species (*Lumbricus terrestris*, *Aporrectodea caliginosa*) and two Collembola species (*Heteromurus nitidus*, *Protaphorura armata*), representing macro- and mesofauna, respectively, i.e. differing strongly in body size. *L. terrestris* and *H. nitidus* colonize predominantly the litter - soil interface and feed on resources associated with litter and therefore were taken to represent “litter-associated” species. In contrast, *A. caliginosa* and *P. armata* predominantly live in organo-mineral soil and feed on resources in soil and therefore were taken to represent “soil-associated” species [14,15]. Beech saplings and ^{15}N labeled beech litter were introduced into the mesocosms to allow investigating the importance of soil fauna interactions for ecosystem processes, i.e. leaf litter decomposition and nitrogen cycling. The experiment was run for three months.

We hypothesized that (1) effects of “litter-associated” species on ecosystem processes, e.g. litter decomposition and ^{15}N cycling, exceed those of “soil-associated” species. Further, we hypothesized that (2) soil animals with similar body size (macrofauna vs. mesofauna) and food microhabitat association (“litter-associated” vs. “soil-associated”) interact antagonistically, thereby reducing the performance (biomass, abundance) of each other, while species with dissimilar traits were assumed to interact in a facilitative way. Accordingly, we hypothesized that (3) the effects of single soil animal species on litter decomposition and ^{15}N cycling are reduced by species with similar traits due to antagonistic interactions and increased by dissimilar species that interact in a facilitative way.

2. Material and methods

2.1. Soil and plant material

Soil samples were taken in April 2012 in a 150 year old deciduous forest in the vicinity of Göttingen (51°26′27″N, 10°01′03″O, 340 m a.s.l., Lower Saxony, Germany). The region has a continental climate with a mean annual temperature of 8.7 °C and a mean annual precipitation of 644 mm (30 year average; Göttingen Weather Station; http://www.wetterstation-goettingen.de). The forest is dominated by oak (*Quercus petraea*) and beech (*Fagus sylvatica*) that represent 95% of all tree individuals and that are interspersed by single individuals of larch (*Larix decidua*), spruce (*Picea abies*), pine (*Pinus sylvestris*), willow (*Salix* spec.) and birch (*Betula* spec.). The understory is species rich and dominated by jewelweed (*Impatiens* spec.), stinging-nettle (*Urtica urens*) and lady fern (*Athyrium filix-femina*). The soil is an oligotrophic brown earth from bunter composed of mull to mull like moder humus, that represents a humus form in between mull and moder and mineral soil (Ah horizon) with a pH ($CaCl_2$) of 5.01 ± 0.07 and soil moisture (November) of 26.7 ± 0.7% of soil fresh weight. Soil carbon (C) and N concentrations are 2.22 ± 0.05% and 0.14 ± 0.003%, respectively, with a $\delta^{15}N$ signature of 0.49 ± 0.24‰. The soil was taken from the upper 10 cm homogenized by passing through a 10 mm screen and defaunated by three freeze-thaw cycles switching between −30 °C and +20 °C every 72 h.

Two year old beech saplings (*F. sylvatica*) were obtained from a local forestry nursery (Billen Forst GmbH, Bösinghausen, Göttingen). Five trees were cut into roots and shoots, dried at 105 °C for 72 h, milled to powder and analyzed for concentration of C, N and ^{15}N stable isotope signature. Initial concentration of C was 43.61 ± 1.49% and 48.15 ± 0.72%, initial concentration of N was 1.12 ± 0.03% and 0.76 ± 0.15% and initial δ ^{15}N signature was 2.45 ± 0.42‰ and 1.69 ± 0.95‰ for roots and shoots, respectively.

To obtain ^{15}N labeled leaf litter, young beech trees were grown in PVC containers in a climate controlled greenhouse and watered with ^{15}N labeled ammonium ($^{15}NH_4^+$ 99 atom% ^{15}N; Campro Scientific, Berlin, Germany) over a period of two years. Senescent leaf litter was collected, air dried and stored at room temperature until set up of the experiment. C and N concentrations of the litter were 47.10 ± 0.80% and 1.09 ± 0.04%, respectively, with a C-to-N ratio of 43.22 and δ ^{15}N signature of 2888.7 ± 791.3‰.

2.2. Earthworms and Collembola

Individuals of the “soil-associated” earthworm species