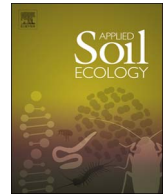




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Short communication

Aboveground macrodetritivores and belowground soil processes: Insights on species redundancy

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ABSTRACT

Quantifying the level of overlap between species-specific effects in a given process – i. e. their functional redundancy – remains a central issue in predicting the shape of diversity-productivity or diversity-stability relationships. We compared the indirect effects of six aboveground macro-detrivores on two belowground processes, cellulose decay and nutrient mineralization, in single-species microcosms ($n = 5$) containing standardized substratum, mixed litter, and four individuals of detritivores. In all microcosms, there was an overall increase in phosphate and decrease in nitrate and ammonium over four weeks. Cellulose decay was $\approx 30\%$. Compared to fauna-free controls, there were a few noticeable fauna effects: decay was higher in microcosms with *Armadillidium vulgare* and *Porcellio scaber*, nitrate immobilization was lower in *Cylindroiulus caeruleocinctus* microcosms, and ammonium immobilization was lower in *A. vulgare* and *P. scaber* microcosms. The multivariate effects were idiosyncratic and related to a high intraspecific variation. Contrary to our expectations, the most noticeable difference was between *P. scaber* and *Trachelipus rathkii*. Our results point to redundancy due to high intraspecific variation. It is postulated that, if redundancy arises from high intraspecific variation, upon the loss of species, large population sizes of remaining species from the same functional group might explain positive effects of redundancy on ecosystem resilience.

1. Introduction

There is increasing evidence that biodiversity enhances ecosystem functioning – the rate, level or temporal dynamics of one or more ecosystem processes (*sensu* Tilman, 2001) – and/or the stability of these processes upon environmental changes (Naeem et al., 1995; Yachi and Loreau, 1999; Hooper et al., 2012). Most explanations for such relationship can be grouped into two mechanisms. One is the “rivet hypothesis”, which assumes that species are unique in their contribution to ecosystem functioning, therefore more diverse communities contain a range of species that can use the entire resource spectrum (Naeem, 1998; Tilman, 2001). The other explanation is the “sampling effect”, which states that with increasing diversity within a trophic level it becomes more likely that a species with superior ability in using the resources will be present. This is derived from the “redundant species hypothesis” (Lawton, 1994), which proposed that a minimum diversity is necessary to maintain a given ecosystem process, and assumes that most species are redundant. Redundancy, therefore, is an important community feature, especially in the context of resistance and resilience, and lies at the core of the discussion of diversity-productivity

and diversity-stability relationships (Lawton, 1994; Bengtsson, 1998; Naeem, 1998). Besides the differences between the mechanisms above, both emphasize that diversity effects on ecosystem functioning depend on the role that each species performs (Zimmer et al., 2005), and that it is necessary to know “what do species do in ecosystems” (Lawton, 1994). Thus, the practical approach to address these questions involves measuring species-specific effects on processes of interest.

Aboveground macro-detrivores ingest litter, and shelter, burrow, and deposit feces in the uppermost soil layer, thus connecting the aboveground and belowground compartments mechanically and chemically (Lavelle et al., 1995; Zimmer, 2002). They affect belowground processes directly – through the mechanical fragmentation, digestion of decaying leaf litter and egestion of feces – and indirectly, by mediating microbial activity. Direct effects are consequences of their feeding rates and preferences, and have been studied extensively (Zimmer, 2002; Hedde et al., 2007; Quadros and Araujo, 2008; Boelter et al., 2009; David, 2014; Quadros et al., 2014). The indirect effects arrive from their interaction with microorganisms, as proposed by the “Sleeping Beauty Paradox” (Lavelle et al., 1995), which translates as microorganisms being dormant until the soil fauna “awakes” them, acting as

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“Prince Charming”. As the soil microbiota is enzymatically capable of decaying virtually all substrates but has limited mobility, microorganisms need the soil fauna to transport them to new resources (Lavelle et al., 1995). The indirect effects of isopods and diplopods on belowground processes have been addressed less frequently than direct effects. However, it is known, that their activity influences microbial activity. For instance, there are changes in microbial respiration rates (Kaneko 1999; Heemsbergen et al., 2004; Zimmer et al., 2005; Špaldoňová and Frouz, 2014) and production of extracellular enzymes (Jia et al., 2015) when detritivores are present.

Having the “Sleeping Beauty Paradox” in mind, it can be hypothesized that detritivores differing in morphology and behavior (e.g. activity level, digging/burrowing habits, temperature and moisture preferences, etc.) interact with different microbial communities resulting in species-specific effects on belowground processes. Here we tested this hypothesis comparing the species-specific effects of five woodlouse and one diplopod species. We measured four belowground properties as indicators of two soil processes: cellulose decay and nutrient immobilization/mineralization, asking (I) whether these species affect these processes, and (II) whether there are any multivariate species-specific effects, i.e. the effect of each species on the four properties altogether. The species were *Armadillidium vulgare* Latreille, 1804 (Armadillidiidae), *Porcellio scaber* Latreille, 1804 (Porcellionidae), *Cylisticus convexus* (de Geer, 1778) (Cylisticidae), *Oniscus asellus* Linnaeus, 1758 (Oniscidae), *Trachelipus rathkii* (Brandt, 1833) (Trachelipodidae), and *Cylindroiulus caeruleocinctus* (Wood, 1864) (Julidae). These species are commonly found in lowland deciduous forests and widely distributed in Europe (de Jong et al., 2014), and differ in morphological and behavioral traits. *O. asellus*, *P. scaber* and *T. rathkii* are clinger isopods, but *O. asellus* has less tolerance to desiccation and prefers moister habitats; *A. vulgare* and *C. convexus* are rollers (*sensu* Schmalfuss, 1984), and like to burrow in the topsoil. We expected more pronounced differences, i.e. less redundancy, between roller and clingers, and between isopods and the diplopod.

2. Material and methods

Isopods and diplopods were captured in the surroundings of Salzburg, Austria, in summer 2012, and kept in laboratory stocks with mixed litter at 15°C. Transparent boxes (1.5 L) were used as microcosms. They were filled with 140 g of standardized substratum ED73 (Einheitserde GmbH, Germany), 4 g of leaf litter and a cotton pad (shelter). According to the manufacturer’s description, ED73 is an organic peat-based substratum, with 40–50% organic matter, 300 mg L⁻¹ P₂O₅ (approx. 87.5 mg kg⁻¹ dry weight, considering a calculated density of 3.43 kg dry weight per L), 1% available N, 30% organic C, C:N ratio of 45. The substratum was sieved through a 6.3 mm mesh, air-dried and mixed thoroughly, before being added to the boxes. Upon starting the experiment, ≈ 20 g of this substratum was frozen and kept at -20 °C for subsequent analyses (see below). Substratum moisture was adjusted to 50% with distilled water. The leaf litter was composed by 1 g of *Fagus sylvatica*, 1 g of *Acer pseudoplatanus* and 2 g of *Tilia cordata*. This set of leaves combined the least preferred (*F. sylvatica* and *A. pseudoplatanus*) with the preferred food (*T. cordata*) (pers. obs.). All leaf litter was collected in Salzburg, from the ground, after litterfall in 2012, air-dried for one week and stored in mesh bags. Prior weighing and distributing it into the microcosms, the litter was placed on a plastic bag, crushed into smaller pieces and mixed. Mixing the substratum, and the litter, before distributing them in the microcosms intended to spread microbial spores and propagules, homogenizing the initial conditions as much as possible. Each microcosm had four individuals, and there were five replicates per species and five fauna-free controls.

As a proxy of microbial activity, we measured belowground cellulose decay with a modification of the cotton-strip assay (Gestel et al., 2003). Pieces of 4 cm² of 99% cellulose paper (Whatman®) were cut,

dried (60 °C for 24 h) and weighed. Each piece had initially ≈ 70 mg dry weight. Then, using tweezers, they were inserted vertically in the microcosm substratum at 1 cm depth (one piece per microcosm), and covered.

After four weeks, the leaf litter, animals and cotton pad were removed. All remaining pieces of the cellulose paper were carefully removed with tweezers, washed in a 200 µm mesh, dried and weighed. The substratum was mixed, and a sample of ≈ 20 g was kept for the following analyses. One gram of substratum was weighed and dried to obtain the dry weight, and another 1.5 g (wet weight) of substratum were placed in Falcon tubes with 10 ml of distilled water. These tubes were incubated at 24 °C for 1 h at 150 rpm to extract the water-soluble fraction of nitrate, ammonium and phosphate. Phosphate and ammonium were determined with a photometer, using commercial water test kits (JBL GmbH & Co.KG, Germany). Calibration curves were obtained using solutions of 0–5.5 µg ml⁻¹ NaH₂PO₄ for phosphate, and 0–50 µg ml⁻¹ NH₄NO₃ for ammonium. Nitrate was measured with a nitrate ion-selective electrode (Vernier Software & Technology, LLC). Final concentrations were expressed as µg g⁻¹ substratum (dry weight). The initial concentrations of these nutrients in the substratum, used for comparison, were 282.8 µg g⁻¹ NO₃-N, 19.1 µg g⁻¹ NH₄-N and 50.3 µg g⁻¹ PO₄-P. As there were no roots in the substratum to compete with the microbial communities for nutrients, and no leaching, we assumed that decrease in nutrients was due to immobilization into microbial biomass, while the increase was due to mineralization by microbial metabolism.

We compared the fauna treatments to the fauna-free controls using Cohen’s d effect size (Cohen, 1992) and 95% confidence intervals calculated with the package bootES (Gerlanc and Kirby, 2015) for R (R Core Team, 2017). Question II was approached with multivariate statistics, since we were interested in the multivariate effects, and considering that the belowground properties analyzed here are often correlated. To visualize the multivariate effects, we used a principal component analysis (PCA), after scaling the data to have mean zero and one standard deviation. To test for statistical differences between species we used a multivariate analysis of variance (function manova in R), after a square-root transformation of the data.

3. Results

After four weeks, there was an overall accumulation of phosphate in the substratum and a decrease in nitrate and ammonium (Fig. 1): the fauna-free controls had ≈ 68% of the initial nitrate, ≈ 18% of the initial ammonium and ≈ 123% of the initial phosphate. Cellulose decay was 30% (± 0.4 se.) in the fauna-free controls (0.8 mg d⁻¹) (Fig. 1). We found a few strong effects (Cohen’s d ≥ 0.8, for convention) of some species on the properties studied (Table 1): immobilization of nitrate in *C. caeruleocinctus* microcosms was lower than in the controls, and/or counteracted by the nitrogen present in the species excretion (Fig. 1D), and, in microcosms with *P. scaber* or *A. vulgare*, there was lower ammonium immobilization (Fig. 1C) and higher mass loss (Fig. 1A). However, the only statistically significant effect was of *C. caeruleocinctus* on nitrate (Table 1). Fauna-free controls had, in general, lower variability than microcosms with detritivores (Fig. 1).

As depicted in the PCA (Fig. 2) and in the coefficients of variation (Fig. 1), the species’ effects were variable and largely overlapped, and we could not identify any clear species-specific effect. Only *P. scaber* and *T. rathkii* were apart from each other in the multivariate space (filled shapes in Fig. 2), but the overall MANOVA indicated that these differences were insignificant (Pillai = 0.6762, approx. F = 0.97657). Compared to the controls, *P. scaber* and *T. rathkii* had opposite effects on mass loss, phosphate and nitrate (Table 1). Compared to each other, there was a higher cellulose decay (32% versus 28%), higher P mineralization, and lower ammonium immobilization in *P. scaber* microcosms (Fig. 1).

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