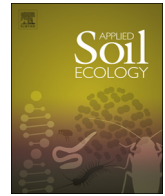




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Macro-detritivore identity and biomass along with moisture availability control forest leaf litter breakdown in a field experiment

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ABSTRACT

Forests are structurally rich ecosystems with strong spatial variation in microclimate. Local temperature and soil moisture are important drivers of leaf litter breakdown, a key ecosystem process vital for forest functioning. Additionally, detritivore species composition and activity are equally dependent on microclimate, rendering changes in microclimate key to understand leaf litter breakdown. We investigated the interaction between microclimatic variables (i.e. temperature and moisture) and different combinations of macro-detritivores (a drought sensitive i.e. *Oniscus asellus* vs. a drought tolerant species i.e. *Glomeris marginata*) on litter breakdown of easily decomposable (high quality) *Acer* litter and decomposition resistant (low quality) *Quercus* litter in a full factorial microcosm field experiment in a temperate forest in Belgium. We hypothesize litter breakdown to be faster for high quality litter and macro-detritivore biomass and dependent on macro-detritivore identity, mediated by forest microclimate e.g. faster with higher soil moisture and warmer temperatures.

We found high quality litter breakdown to be reduced by decreasing moisture availability, while it was not affected by temperature. There was no effect of moisture and temperature on litter breakdown of low quality litter. The effect of detritivore biomass on the breakdown of *Quercus* litter depended on detritivore identity: elevated millipede biomass increased *Quercus* litter breakdown, which was not the case for woodlice. There was a positive effect of macro-detritivore biomass but no effect of macro-detritivore identity on leaf litter breakdown of high quality litter. In addition, the relative consumption rates were equal between the drought sensitive (woodlouse) and the drought tolerant (millipede) species for high quality litter, but different for low quality litter. The woodlouse species was more efficient in the breakdown of low quality litter compared to our tested millipede species. Relative consumption rate was not influenced by the moisture or temperature treatments. Combining both detritivore taxa in a single microcosm had additive (non-synergistic) effects on litter breakdown, indicating that they are not complementary in their resource use. We conclude that mainly differences in moisture availability in forest ecosystems are important for litter breakdown and that detritivore identity is critical for the breakdown of especially low quality litter.

1. Introduction

Temperature and moisture determine global patterns in the breakdown of terrestrial leaf litter, with higher temperatures and moisture availability generally enhancing its fragmentation (Prescott, 2010). Similar variation in temperature and moisture can, however, be found at much smaller scales. For instance in forests, strong microclimatic gradients can be observed in relation to edge effects and other horizontal gradients in forest structure (Arx et al., 2013; Chen et al., 1999; Delgado et al., 2007; Gehlhausen et al., 2000; Loescher et al., 2014).

This microclimatic variation is regarded as one of the main drivers of understory plant community composition (De Frenne et al., 2015; Normann et al., 2016). In parallel, the same drivers cause a strong shift in decomposer community composition (De Smedt et al., 2016; Remy et al., 2018; Riutta et al., 2012) which depend on air and soil moisture and environmental temperature (Dias et al., 2013; Dixie et al., 2015; Meyer and Eisenbeis, 1985). Microclimatic effects on litter breakdown have recently been addressed (Prescott, 2010), however, the interaction of the microclimate with the decomposer community is poorly studied (cf. David and Handa, 2010; Prescott, 2010; Sariyildiz, 2008).

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Investigating whether changes in forest microclimate regimes moderate leaf litter breakdown by decomposers is essential to understand the integral role that microclimate plays in ecosystem functioning, and especially nutrient cycling.

Macro-detritivores are key components of the decomposer community because they increase breakdown by transforming leaf litter to a more readily accessible form for soil micro-organisms (such as micro-fauna, fungi and bacteria) (Bradford et al., 2002; Hättenschwiler et al., 2005). Macro-detritivore abundance, identity and diversity can strongly influence breakdown (Hättenschwiler et al., 2005; Vos et al., 2011). Macro-detritivore distribution in forests is highly species-specific, possibly resulting in contrasting decomposition rates in forest ecosystems (De Smedt et al., 2016, 2018a). Macro-decomposers similarly prefer feeding on dead plant material, synergies between macro-detritivores have been reported in lab experiments (e.g. Collison et al., 2013; De Oliveira et al., 2010; Zimmer et al., 2005). Synergistic effects are positive non-additive effects, meaning that the litter decomposition rate by the different species together is faster than the sum of the decomposition rates by the individual species. In general, macro-detritivore species loss may jeopardize litter breakdown (Handa et al., 2014; Huhta et al., 1998) indicating the importance of complementarity between different groups in the decomposition process. This complementarity is expected to be caused by different feeding strategies of macro-detritivores or different nutritional requirements (Bardgett and Chan, 1999; Zimmer et al., 2005).

Woodlice (Malacostraca, Isopoda, Oniscidea) and millipedes (Diplopoda) are dominant litter dwelling macro-detritivores in temperate regions (comprising about 30% of the macro-fauna individuals per square meter of forest soil) (Jeffery et al., 2010). Despite their taxonomic dissimilarity, woodlice and millipedes share similar ecological niches within the leaf litter and the upper soil layers of forests, in contrast to e.g. earthworms which are dominant soil dwellers (David and Handa, 2010). Being ecologically similar, millipedes and woodlice show contrasting responses to environmental gradients, predicted by the among (De Smedt et al., 2016) and within (De Smedt et al., 2018a) taxa differences in species desiccation resistance, with drought resistant species dominating in the drier and warmer microsites (De Smedt et al., 2018a). Therefore, we can expect an interaction between species identity and leaf litter breakdown with drought tolerant species performing better under higher temperatures and lower humidity compared to drought sensitive ones.

Leaf litter quality is another important driver of litter breakdown. Although, macro-detritivores generally prefer high quality litter (i.e. litter containing a high amount of nitrogen relative to carbon and low concentrations of lignin) (Joly et al., 2015; Zimmer, 2002; Zimmer and Topp, 2000), the relative contribution of different macro-detritivore species to breakdown depends on litter quality. Certain species are more efficient for low or high quality litter compared to other macro-detritivore species (Vos et al., 2011). This could indicate that the effect of environmental variables like moisture availability and temperature on leaf litter breakdown by different assemblies of macro-detritivores might depend on litter quality as well. Additionally, litter quality may also influence complementarity between macro-detritivores (Zimmer et al., 2005).

To study the relative importance of microclimate, detritivore identity and litter quality on litter breakdown dynamics, we designed a full-factorial field experiment in autumn after the dominant litter fall period. We hypothesized that (1) forest leaf litter breakdown depends on macro-detritivore identity, mediated by the forest microclimate. Reduced moisture and increased temperature will more strongly affect consumption by a drought sensitive species than a drought tolerant species. (2) These effects will be more pronounced for high compared to low quality litter, because high quality litter is preferred by macro-detritivores. (3) Synergy (positive additive effects) between woodlice and millipedes for leaf litter breakdown will therefore depend on both microclimate and litter quality.

2. Material and methods

2.1. Study area and experimental set-up

This study was carried out in an ancient, mixed deciduous, temperate forest (39.5 ha), in the northern part of Belgium (Aelmoesene forest, Gontrode). Dominant tree species are *Quercus robur* L., *Fagus sylvatica* L., *Larix kaempferi* Carr., *Fraxinus excelsior* L., and *Acer pseudoplatanus* L. The soil developed in a quaternary layer of sandy loam on a shallow impermeable clay and sand complex of tertiary origin (FAO classification: Gleyic Cambisol). The pH-KCl of the topsoil layer (0–5 cm) averages about 3.53 (Vanhellemont et al., 2014).

We constructed 288 microcosms from PVC pipe (diameter 12 cm, depth 10 cm). The top and bottom were sealed with fiberglass gauze (1 mm × 2 mm mesh size; attached with cable ties to minimize detritivores escaping) to reduce chamber effects and allow for external environmental conditions (e.g., moisture, micro- and meso-fauna) to occur within the microcosms. In each microcosm, we added 10 g of sycamore litter (*Acer pseudoplatanus* L.) and 2 g of oak litter (*Quercus robur* L.). Experimental leaf mass was based on the relative consumption of the different litter species by detritivores in a pilot study. 12 g was the maximum amount of litter that fit in the microcosms without pressing litter together. The choice of the tree species was based on their differences in leaf chemical characteristics (Appendix A). *Acer pseudoplatanus* litter has for example higher Ca-content, lower lignin and lower C/N ratio compared to *Quercus robur* (Hantsch et al., 2014; Reich et al., 2005), therefore, making litter from these two tree species high and low quality food for macro-detritivores in temperate regions (David and Handa, 2010; Gerlach et al., 2014). The tree species will be further referred to by their genus names. We used freshly fallen litter from nearby sites, collected with nets in October 2015 and dried at 26 °C for three days. The experiment was conducted from the end of October 2015 until the end of January 2016.

Four detritivore treatments were applied to the microcosms: woodlouse monocultures (10 individuals; WL), millipede monocultures (10 individuals; MP), mixed cultures (5 woodlice and 5 millipedes; MX) and a control treatment (no woodlice or millipedes; CO) (Fig. 1a). All individuals were adults and pregnant females (with brood pouch) were not used to prevent a sudden increase of juveniles during the experiment. Experimental density of the animals equaled 885 individuals per m², which is rather high for millipedes (Wolters and Ekschmitt, 1997; range 210–700 ind. m²) but within normal ranges for woodlice (Wolters and Ekschmitt, 1997; range 96–1850 ind. m²) in temperate forests. Woodlice and millipedes were weighed together per species and per microcosm before they entered the microcosms to be able to assess macro-detritivore condition (mass loss/gain) after the experiment. We used the woodlouse *Oniscus asellus* L. and the millipede *Glomeris marginata* (Villers), two species that are common in ancient deciduous forests in Western Europe covering the same ecological niche (De Smedt et al., 2018b). However, both species differ strongly in their desiccation tolerance with *G. marginata* able to survive much longer under standardized dry conditions compared to *O. asellus* (Dias et al., 2013; Edney, 1977; pers. comm. M.P. Berg). Animals were collected by hand during mid to late October 2015 around the study area. They were kept up to a maximum of one week in plastic containers with soil and leaf litter collected on site. The leaves in the microcosms were sprayed with a microbial wash before macro-detritivores were added, to restart microbial activity on the leaf litter after drying. The microbial wash was created by soaking the ectorganic horizon of the study site in water for several days. Particles were then filtered out (0.02 mm mesh size of the filter) and the solution was sprayed on the microcosms one day before and at the start of the experiment. This should mimic natural colonization of microbes immediately at the start of the experiment as microbial colonized litter is preferred by detritivores (Zimmer, 2002).

The microcosms were installed on flat forest surface (with one side of fiberglass gauze touching the forest soil) under four different

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