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Intraspecific niche partitioning in macrodetritivores enhances mixed leaf litter decomposition

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Abstract

1. In biodiversity and ecosystem functioning research, the consideration of intraspecific trait variation and multiple trophic levels – both largely overlooked so far – has been proposed as a promising step towards a consensus about causal relationships and mechanisms.
2. Soil invertebrates contribute crucially to leaf litter decomposition and thus to the functioning of one of the most diverse ecosystem components on Earth. On the one hand, a positive effect of leaf litter diversity on decomposition was shown by several studies. On the other hand, at the interspecific level, differences in body size and feeding traits of consumers influence this process by interacting with leaf litter traits that define decomposability, such as nutrient content and physical properties. It is also known that the feeding niche of consumers can vary during their ontogeny as it depends on individual body size, metabolism and physiology. However, whether and how intraspecific trait variation of macrodetritivores contributes through niche partitioning to the positive effect of litter combinations on decomposition was never investigated.
3. Here we tested experimentally the effect of intraspecific body size differences in the common terrestrial isopod species *Oniscus asellus* on the decomposition of the two co-occurring litter species *Acer platanoides* and *Betula pendula*. We hypothesized complementary resource use by two distinct isopod body size classes, leading to decreased competition and higher overall litter decomposition.
4. In a full factorial design with all possible combinations of litter species and isopod body size classes, litter mixtures enhanced decomposition beyond the additive effect of each single species, especially in isopod mixed-body size treatments. Our results suggest an interaction between litter and consumer diversity driving intraspecific

feeding niche partitioning. Although the focus on a single detritivore species does not allow for generalizations, our results should stimulate the investigation of the mechanisms of biotic interactions among individual organisms.

Keywords: body size, complementarity, decomposition, functional diversity, intraspecific trait variation, Isopoda, ontogeny, soil biota

Introduction

It has been long recognized that biodiversity can have a positive influence on ecosystem processes. However, relationships observed in a variety of systems are far from being consistent (see review by Cardinale et al., 2012) and a deep understanding of the driving mechanisms is still lacking. For this reason, a broadening of perspectives and new approaches in biodiversity and ecosystem functioning (BEF) research have been called for, such as the explicit inclusion of food web structure (e.g. Reiss, Bridle, Montoya, & Woodward, 2009; Seibold, Cadotte, MacIvor, Thorn, & Müller, 2018), the adoption of trait-based approaches (McGill, Enquist, Weiher, & Westoby, 2006) and the consideration of different levels of biological organization, especially intraspecific trait variation (Violle et al., 2012).

In community ecology the focus has mainly been on interspecific trait variability, largely based on mean field theory, which suggests that mean trait values capture the majority of species and community dynamics (MacArthur & Levins, 1967). In the last decade, the legitimacy of this view has been strongly challenged by both theoretical work (e.g. Violle et al., 2012; De Laender et al., 2014; Barabás & D'Andrea, 2016) and empirical studies that quantify the relative contribution to trait variation of the intra- and interspecific components (Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Siefert et al., 2015; Volf et al., 2016; Chalmandrier et al., 2017; Bonfanti et al., 2018; Rhoades, Best, & Stachowicz, 2018). These

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studies showed that intraspecific trait variation can be comparable or even larger than interspecific trait variation, and trait differences among conspecific individuals can have community-wide consequences. Still, intraspecific trait variation was largely overlooked in BEF research (Bolnick et al., 2011; but see Raffard et al., 2017; Des Roches, 2018; Fontana, Thomas, Moldoveanu, Spaak, & Pomati, 2018; Raffard, Santoul, Cucherousset, & Blanchet, 2019), whilst functional traits of individuals determine their fitness in changing environments (McGill et al., 2006; Violle et al., 2007) and finally the effects of species on ecosystem processes (e.g. Bolnick et al., 2003; Violle et al., 2012). This is particularly relevant when considering biological interactions, which are by definition realized at the individual level. We urgently need to incorporate explicitly intraspecific variation (e.g. due to ontogeny, sexual dimorphism, genetic differences or phenotypic plasticity) into BEF research to link the traits of primary producers to those of consumers, and thus afford a food web perspective.

In soil food webs, litter decomposition is a key process that sustains biogeochemical cycles across ecosystems, and contributes crucially to the functioning of soils and their service delivery (Bardgett & van der Putten, 2014; Wagg, Bender, Widmer, & van der Heijden, 2014). Nevertheless, linking soil biodiversity to ecosystem processes is far from being a trivial task (Wall, Bardgett, & Kelly, 2010; Eisenhauer et al., 2017). Attempts to gain mechanistic understanding of litter decomposition should take into account the complex trait-mediated interactions between litter species and soil fauna communities, namely the co-occurrence of bottom-up and top-down effects (Hättenschwiler & Gasser, 2005). Leaf litter species traits can influence decomposition through a variety of mechanisms (Hättenschwiler, Tiunov, & Scheu, 2005; Gessner et al., 2010), which result in non-additive effects (i.e., the observed decomposition of a litter mixture deviates from expectations derived by summing decomposition rates of litter monocultures). For example, a positive effect of leaf litter species combinations on decomposition can be driven by interspecific differences in litter

quality (determined by traits such as physical and structural properties, and the concentration of nutrients and secondary metabolites), which cause the preferential consumption of one litter species when the consumer has the possibility to choose among many (e.g.

Hättenschwiler, Tiunov, & Scheu, 2005). This so-called selection effect also depends on the identity of the consumer considered (Heemsbergen et al., 2004; Hättenschwiler & Gasser, 2005), as confirmed by results from different macrodetritivore taxa (Vos et al., 2011).

Besides the selection effect, complementary effects have also been described, in which enhanced decomposition of a litter mixture is determined by the advantages of a balanced diet or by complementary resource use between microbes and macrodetritivores (Vos et al., 2013). The same authors suggested that additional consideration of macrodetritivore trait diversity might contribute to explain a greater positive effect of leaf litter trait variation (see also Heemsbergen et al., 2004; but see Bílá et al., 2014). This was already shown for two soil macrofauna classes (Diplopoda and Gastropoda), whose very distinct traits led to complementary consumption of leaf litter mixtures (De Oliveira, Hättenschwiler, & Handa, 2010).

On the contrary, the consequences of arguably smaller trait differences, such as those among individuals of the same consumer species, were not experimentally tested for their interaction with litter diversity effects so far. Animal trait-based ecology suffers from a lack of mechanistic understanding behind the link between traits and ecosystem functioning (Didham, Leather, & Basset, 2016), which hampers predictive multi-trophic BEF research (but see e.g. Coulis et al., 2015; Schleuning, Fründ, & García, 2015; Schmitz, Buchkowski, Burghardt, & Donihue, 2015; Muñoz, Schaefer, Böhning-Gaese, & Schleuning, 2017).

Interestingly, in herbivores and detritivores, intraspecific trait differences can drive variation in consumption rates among individuals of a population, as experimental approaches have shown (Raffard et al., 2017; Rhoades, Best, & Stachowicz, 2018; Rota, Jabiol, Chauvet, &

Lecerf, 2018). However, none of these studies investigated how trait variation can determine niche partitioning within a single consumer species, and whether the resulting resource use complementarity (due to decreased competition) enhances mixed litter decomposition.

During its ontogeny a given consumer species might occupy distinct niches (e.g. Polis, 1984; Clegg, Ali, & Beckerman, 2018; Start, 2018), defined by stage-specific feeding modes due to differences in body size (Werner & Gilliam, 1984). This ontogenetic niche shift reflects changes in energetic requirements, metabolism and physiology, and can result in preferences for different leaf parts (Vilisics, Szekeres, & Hornung, 2012), or litter traits or microenvironmental conditions, which depend on litter species combinations (Hättenschwiler, Tiunov, & Scheu, 2005).

Here we tested experimentally whether intraspecific body size differences in the common terrestrial isopod species *Oniscus asellus* Linnaeus, 1758 (*Oniscus* hereafter) affect the decomposition of the two co-occurring litter species *Acer platanoides* (Norway maple, *Acer* hereafter) and *Betula pendula* (Silver birch, *Betula* hereafter). Isopods, as significant part of soil macrofauna in most terrestrial ecosystems, throughout their life cycle play an important role in litter decomposition (Hättenschwiler, Tiunov, & Scheu, 2005; David, 2014). By testing all compositions of litter species (*Acer* and *Betula* alone, as well as mixed) and *Oniscus* body size classes (large and small alone, as well as mixed) in a full factorial design, we aimed at elucidating how intraspecific body size variation of the consumers mediates the effect of litter species composition on litter mass loss. *Acer* and *Betula* have different traits (e.g. C to N ratio, magnesium and calcium content, physical resistance to consumption by macrodetritivores), which result in a slightly higher decomposition rate (= litter quality) in *Betula* (Cornelissen, 1996; Finerty et al., 2016). A combination of *Oniscus* body size classes could be expected to enhance the positive, non-additive effect of litter diversity on consumption, thanks to intraspecific feeding niche partitioning.

In this study, we tested the following specific hypotheses and related expectations:

- 1) Leaf litter mixtures can enhance decomposition independent of consumer identity and species composition, due to selection and/or complementarity effects driven by trait differences among litter species. Therefore, we expect positive non-additive effects of the two litter species (*Acer* and *Betula*) on total litter mass lost in all treatments of our experiment.
- 2) If the above pattern is enhanced by intraspecific feeding niche partitioning of the consumer, the positive effect of a litter mixture on overall decomposition is expected to be highest when the variation in consumer traits is maximized. Therefore, we expect the greatest positive difference between observed and expected total leaf litter mass loss (*Acer* + *Betula*) in the mixed-body size treatment of the consumer, assuming that body size relates to feeding traits and strategies in *Oniscus* (Werner & Gilliam, 1984; Vilisics, Szekeres, & Hornung, 2012).

Materials and methods

Litter collection and preparation

To maximize the probability of detecting non-additive effects of small- and large-sized *Oniscus* on litter decomposition, we avoided pairs of litter species with a large difference in palatability and decomposability, which would probably have caused a much higher consumption of one litter species independent of *Oniscus* body size classes' composition. Therefore, we selected two common and co-occurring tree species, i.e. *Acer* and *Betula*, which show moderate differences in decomposition rates determined by traits affecting resource quality for decomposers (Cornelissen, 1996; Finerty et al., 2016). Freshly fallen leaves at time of leaf abscission without any visible sign of herbivory consumption, fungal attack or diseases were collected. In order to minimize leaf trait variation within species we

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focused litter collection on a few healthy trees in a restricted area of the Canton of Zurich, Switzerland (*Acer*: 47°14'N / 8°31'E in October 2016; *Betula*: 47°22'N / 8°27'E in November 2016). Leaves were collected in paper bags and dried in a stove set at 40 °C, subsequently put in sealed plastic bags after air was removed manually, and stored in a dark aerated room. Note that during the experiment leaf litter was dried several times (see below for details). While temperature was always set at 40 °C, the duration of the drying process was adapted to initial water content and litter quantity to assure complete water removal (according to previous experience), and was always >14 h. Prior to the experiment (September 2017), leaves' size and shape were standardized by cutting them with a metal hole punch in round pieces of 2 cm diameter.

Animal collection and sorting

Ten and nine days before experiment start, *Oniscus* was collected in a deciduous forest in the city of Zurich, Switzerland (47°24'N / 8°31'E). Animals were stored under experimental conditions (85% relative humidity; daily fluctuating temperature, day 20 °C and night 15 °C; 12:12 h light-dark cycle, 8 am / 8 pm) in plastic boxes (20.0 cm length; 9.5 cm width; 9.0 cm height) with a moist bottom layer of plaster of Paris. Individuals were sorted by eye into two distinct body size classes, which were defined in the attempt of maximizing differences between large and small animals given size distributions observed in field samples collected prior to the experiment (e.g. Supporting Information Fig. S1). Body size was defined as fresh body mass, which is easy to measure on living *Oniscus* and showed a strong positive correlation with body length (Supporting Information Fig. S1). By discarding the intermediate body sizes, we made sure fresh body mass of small (range = 10.7-45.6 mg; mean = 29.5 mg; median = 30.0 mg) and large *Oniscus* (range = 53.7-146.3 mg; mean = 80.7 mg; median = 78.0 mg) showed a non-overlapping distribution at the beginning of the experiment,

with large animals being more than double as heavy as small ones on average (Supporting Information Fig. S2). *Oniscus* with a developed marsupium (a brood pouch with eggs or embryos) were excluded, because they would probably deviate from the fresh body mass to length relationship (Supporting Information Fig. S1) and to assure a constant number of animals per microcosm throughout the whole experiment.

Microcosm setting

Each microcosm was composed of a transparent Perspex ring (6.3 cm diameter; 3.0 cm height), closed at the bottom with a moist layer of plaster of Paris (approx. 0.8 cm thickness) and closed on the top with a lid with a central round mesh (2.0 cm diameter; 200 μm mesh size) for gas exchange. All microcosms were put in plastic trays (Fig. 1) on a moist layer of plaster of Paris (approx. 3.0 cm thickness), which allowed to keep the leaf litter in the microcosms moist without disturbance by watering the trays only (from there the water was also equally sucked by capillary action into the plaster of Paris of each microcosm).

Experimental design

We tested litter decomposition of three *Oniscus* body size combinations (large only: 79.4 mg mean fresh body mass; small only: 29.3 mg; large and small mixed: 55.1 mg) on three litter species combinations (*Acer* only, *Betula* only, a mixture of both). This resulted in nine treatments, with 10 replicates each (total = 90 microcosms). Each microcosm contained four animals (all large, all small, or two large and two small). In addition, 30 control microcosms with litter only were included (= 3 litter species combinations x 10 replicates) to measure litter decomposition by microbes.

The experiment was conducted in a climate chamber with the same conditions as above. In order to assure *ad libitum* food, and so avoid the influence of food limitation on observed patterns, the experiment was carried on for three weeks until approximately 50% litter mass loss in the microcosms with the fastest decomposition. Although we did not expect environmental conditions to vary much among microcosms, we subdivided them into two blocks (= trays), each one containing five replicates of each treatment in varying position (Fig. 1A). Control microcosms were grouped in an additional block (Fig. 1B).

Animal acclimation

The microcosms used for *Oniscus* acclimation were identical to the ones used for the experiment. To inoculate the dried leaf litter with a natural microbial community and thus facilitate consumption by *Oniscus* (Zimmer, 2006), fifteen days before experiment start a microbial wash was made by collecting 750 mL partially degraded litter in a mixed deciduous forest close to the Swiss Federal Research Institute WSL (47°21'N / 8°27'E). This litter was mixed with 1.5 L tap water, shaken overnight in a 2 L bottle (150 rpm, VWR Microplate Shaker) and left 7 hours to extract microbes. The liquid fraction was then sieved in two successive steps (250 and 50- μ m metal mesh, respectively), kept hereafter in the climate chamber under experimental conditions and shaken manually from time to time to avoid anoxia. Fourteen days before experiment start, microcosms were filled with leaf litter leftovers resulting from cutting round pieces for the experiment (as described above), according to treatment (*Acer* only, *Betula* only, or a mixture of both litters in approx. equal proportion). The layer of plaster of Paris in the tray was saturated with water (and kept saturated during the following days by adding water when necessary), and each microcosm was sprayed with a standardized dose of microbial wash (approx. 2.5 mL, which was enough to reach a leaf litter water content of about 50% according to pre-tests). The same microbial

treatment was applied a second time ten days before experiment start. The day after, *Oniscus* collected in the field were transferred into microcosms, selecting individuals of similar body size within each category (small or large, single-size treatments), while maximizing body size variation in mixed-size treatments (Supporting Information Fig. S3). After seven days of acclimation following Moretti et al. (2017), leaf litter and faeces were carefully removed with a brush from the microcosms and *Oniscus* were starved for two days (under identical conditions, except for the absence of food), to make sure that they would have empty guts at the start of the experiment. The same acclimation and starving procedure as described above (but with a mixture of the two litter species only) was applied to several spare animals (divided by size class in separate boxes). During the acclimation phase, it was necessary to substitute 15 dead *Oniscus* (eight small- and seven large-sized out of a total of 360 specimens).

Experiment preparation

The leaf litter disks were dried to remove the small amount of water that accumulated since their preparation. Immediately after that, leaf litter portions were weighted using a precision balance accurate to 0.01 mg (Mettler Toledo AE 240), and added to the microcosms (including control microcosms) according to their treatment (three days before experiment start). A total amount of approx. 500 mg leaf litter (range = 472-548 mg) was put in each microcosm, aiming at an equal proportion of the two species in mixed litter treatments (range = 237-275 mg each). To facilitate the identification of the two species in mixed litter treatments at the end of the experiment, leaf disks were horizontally separated in all microcosms for consistency (where both species were present, *Acer* left side and *Betula* right side of the microcosm). A standardized dose of microbial wash (approx. 2.5 mL) was also

sprayed twice to each microcosm, to increase leaf water content and allow the colonization by microbes during three days before adding *Oniscus* (following e.g. Bílá et al., 2014).

Experiment and final measurements

All acclimated *Oniscus* were weighted using a precision balance accurate to 0.01 mg (Mettler Toledo AX205 DeltaRange) and then transferred into the microcosms (official start of the experiment). During the experiment, water was poured into the trays every 2-3 days to make sure the layer of plaster of Paris in the microcosms was constantly moist. As a consequence, leaf litter showed a gradient of decreasing moisture content from bottom to top of the litter layers, allowing individual *Oniscus* to find their preferred microenvironment. Every 1-2 days we checked each microcosm for dead *Oniscus* and noted dates and times when we found any.

To minimize disturbance and leaf litter movements, the search was kept as short as possible and dead animals were not removed from the microcosms. The experiment was stopped after 21 days, i.e. when approximately half of the litter was lost in the treatment with highest decomposition. All *Oniscus* were separated from leaf litter and weighted again. Remaining leaf litter was dried and fragments were then separated according to litter species using a binocular. During litter separation, *Oniscus* faeces and extensive fungal mycelium were carefully removed. Leaf fragments were dried again and immediately weighted.

Statistical analyses

Oniscus mortality during the experiment was very low (5%; 18 dead individuals out of 360), affecting 16 out of 90 microcosms. We decided to completely exclude from further analyses the microcosms with dead individuals. This decision was made because of the low number of microcosms affected, and to avoid an estimation of partial contributions to decomposition

that would have introduced uncertainties and confounding factors (e.g. unbalanced design, possible cannibalism, nutrient addition from dead animals).

Leaf litter relative consumption rate in presence of *Oniscus* (RCR) was defined by litter mass loss for each microcosm and leaf litter species separately using the following formula:

$$RCR = (ML [mg] - \text{mean } ML \text{ microbial controls } [mg]) / (\text{time } [d] * \text{Oniscus mass} [mg]) \quad [1]$$

where *ML* is leaf litter dry mass loss, and *Oniscus mass* is the sum of four individuals' fresh body masses (averaged between the start and the end of the experiment).

To test whether the combination of two litter species given a certain *Oniscus* body size treatment resulted in additive or non-additive effects, we compared expected vs. observed amount of leaf litter mass loss in microcosms using Welch's t-tests (function *t.test*, R Core Team, 2018). The expected values were calculated by assuming the same *Acer* and *Betula* RCR in a litter mixture as in the corresponding monocultures (we applied the average RCR measured in single-litter treatments). In this case, equal probability of feeding on *Acer* and *Betula* was assumed, that is, expected litter decomposition was calculated by multiplying the species-specific RCR by both the body mass of *Oniscus* and half of the experiment duration (= 10.5 d) (see formula [1]).

To account for the variability in RCR among litter monocultures (in addition to average RCR), we also calculated 95% confidence intervals of expected consumption for single microcosms, and checked if the observed consumption fell within this range. An overlap between observed values and the confidence intervals of expected values would indicate that the total consumption of leaf litter mixtures can be calculated from the consumption of litter monocultures (null hypothesis).

Analyses were carried out using R version 3.5.1 (R Core Team, 2018).

Results

The percentage of decomposed litter at the end of the experiment varied quite a lot among microcosms (range = 7.8-54.0 %, mean = 23.9 %), showing that even in case of the highest decomposition there was no food limitation for *Oniscus*.

The differences between expected and observed leaf litter decomposition in the presence of both *Acer* and *Betula* simultaneously, indicate non-additive effects of the two litter species. In treatments with both large- and small-sized *Oniscus*, the two litter species combined showed the strongest positive effect on total mass loss. Thus, observed total litter decomposition was on average 38% higher than expected, whereas this increase was 22% and 24% in the presence of only large- and small-sized *Oniscus*, respectively (Fig. 2, Table 1). Specifically, in treatments with large-sized *Oniscus* only, mass loss was lower than expected in *Acer*, whereas it was higher for *Betula* (Fig. 2, Table 1). This resulted in higher total leaf litter mass loss than expected (Fig. 2, Table 1). The same general pattern of lower than expected *Acer* but higher than expected *Betula* decomposition was observed also in treatments with small-sized *Oniscus* only (Fig. 2, Table 1). In this case, however, differences were weaker and non-significant.

The consistency of our results is supported by taking into account the variability in relative consumption rate among single replicates, which also showed the predominance of non-additive effects of the two litter species (Supporting Information Fig S4).

Discussion

By explicitly testing for the first time in terrestrial ecosystems the role of consumer intraspecific trait variation in mediating, through niche partitioning, the effects of leaf litter diversity on decomposition, our experiment aimed at elucidating some fundamental

mechanisms in the context of the still lively debate about BEF relationship. Our results demonstrate that intraspecific body size variation in a macrodetritivore species interacts positively with trait differences between two leaf litter species (e.g. nutrient composition and physical properties) to enhance total litter decomposition. This supports our initial hypotheses and suggests the existence of intraspecific feeding niche partitioning among small- and large-sized individuals of *Oniscus*, which was contingent upon the presence of a combination of the two litter species *Acer* and *Betula*. In fact, this resource niche partitioning increased the non-additive effects of the two litter species on decomposition, and was possibly dependent on the possibility for each individual *Oniscus* to select the leaf species that had the best trait matching with consumer's metabolic and biomechanical constraints (Pawar, Dell, & Savage, 2015). Purely behavioural differences between small- and large-sized *Oniscus* might also have contributed to the observed effect. The positive influence of a litter species combination on total mass loss was also present in treatments with a single *Oniscus* body size class. However, in this case the observed effects of litter diversity were less pronounced and apparently only driven by selection effects, i.e. clear shifts towards the leaf litter species with highest quality or most palatable (*Betula*) (Fig. 2, Table 1). In contrast, when small- and large-sized *Oniscus* were present simultaneously in combined litter samples, not only the decomposition of *Betula* increased, but also *Acer* showed the same tendency, or at least its mass loss did not decrease compared to expectations (Fig. 2, Table 1).

We hypothesize that this pattern can be explained by the interaction between leaf litter and consumer traits. For instance, *Betula* litter has a higher quality (that is, higher decomposability) compared to *Acer* which is probably mainly determined by the higher content of calcium and magnesium (Finerty et al., 2016), two fundamental components of isopods' diet and exoskeleton (Nicolai, 1988; Zimmer, 2002; Becker, Ziegler, & Epple, 2005; David & Handa, 2010). In contrast, *Betula* litter has a higher carbon to nitrogen ratio and

tensile strength (Finerty et al., 2016). As a consequence, small-sized *Oniscus* individuals might not be able to produce enough force at the tip of their mandibles to puncture tough *Betula* leaves as efficiently as large-sized individuals, which is consistent with the much smaller increase in *Betula* (respectively decrease in *Acer*) mass loss in small than in large specimens when litter species were combined (Fig. 2, Table 1). In leaf herbivores (i.e. grasshoppers) it has been shown that biomechanical traits such as mandible strength correlate well with plant toughness (Ibanez Lavorel, Puijalón, & Moretti, 2013). Analogously, large-sized *Oniscus* individuals could afford a clearer switch towards *Betula* to fulfill their physiological demand of calcium and magnesium, probably thanks to a higher biting strength. Alternatively, the observed switch towards *Betula* might also be caused by the lower relative consumption rates showed by large-sized *Oniscus* (data not shown); as they consumed less leaf litter per unit body mass and unit time, they needed to spend more time feeding on *Betula*. On the other hand, small-sized *Oniscus* in mixed-size treatments might have profited from the feeding activity of those large-sized *Oniscus* that selected *Betula* (the tougher of the two leaf litter species), possibly by taking advantage of resulting small leaf fragments. A similar mechanism has been proposed for interspecific interactions between litter consumers: the presence of isopods and millipedes facilitate litter consumption by earthworms (Heemsbergen et al., 2004), and the same kind of interspecific facilitation was already shown to be driven by body size differences (Tonin et al., 2018). This hypothesis is also supported by our data, which shows that *Betula* mass loss in mixed-body size microcosms is not intermediate between the two single-size treatments, as one would expect, but much more similar to treatments with large *Oniscus* only (Fig. 2, Table 1). The complementarity between large and small *Oniscus* in the consumption of *Betula* might have in turn favored the feeding activity on *Acer* through transfer of calcium and magnesium (and/or other nutrients) by fungal hyphae or leaching (Hättenschwiler, Tiunov, & Scheu, 2005). Although this

mechanism remains speculative, our results confirm that *Acer* mass loss tended to be higher than expected in mixed-size treatments, while one would have predicted a clear decrease based on single-size patterns (Fig. 2, Table 1). Other indirect effects might also have played a role, such as microbial community changes caused by *Oniscus* activity (e.g. Vos et al., 2011). For example, small and large *Oniscus* could selectively feed on different microbial species or strains, and so modify their competitive interactions and dominance structure, thus increasing microbial activity and/or diversity which in turn lead to a positive effect on decomposition (Gessner et al., 2010).

Previous research has already detected intraspecific differences in macrodetritivore consumption rates, but an experimental investigation of their consequences for population-level niche partitioning and process rates was lacking so far. Vilisics and colleagues (2012) demonstrated that intraspecific body size differences in two common isopod species influence consumption rates of a single litter species, and different size classes also showed distinct patterns of litter degradation. Significant differences in consumption rates among conspecific individuals, driven by a variety of traits, have also been shown in analogous aquatic systems (Raffard et al., 2017; Rota et al., 2018). Interestingly, Reiss and colleagues (2011) specifically tested the effect of intraspecific body size variation in aquatic detritivores on ecosystem functioning. However, the absence of non-additive effects in their study might be due to the use of one single leaf litter species, which decreases the opportunities for intraspecific niche partitioning. Our results built upon this previous knowledge (the differences in consumption rates detected so far among conspecific individuals do not automatically imply complementary resource use), and allowed us to experimentally demonstrate for the first time that intraspecific trait variation matters for small-scale niche partitioning in soil fauna, as it was already shown for primary producers in different systems

(He et al., 2018; Fontana, Thomas, Reyes, & Pomati, 2019), and has consequences for fundamental ecosystem processes.

Our main goal was to provide evidence of the possibility of niche partitioning among individuals of the same species, independent of the reasons why niche partitioning arose. As a consequence, we tried to maximize body size differences being aware that size correlates with many other traits. In our case, ontogeny likely played a major role in determining individual differences. However, since in natural populations generations overlap and different developmental stages coexist at very small spatial scales and compete for the same resources (Paris & Pitelka, 1962; Al-Dabbagh & Block, 1981; AlJetlawi & Nair, 1994), this does not diminish the relevance of our results. The same is true for the fact that total litter decomposition was highest in the presence of large-sized individuals only (Fig. 2), while relative consumption rates were highest in treatments with only small-sized individuals (data not shown), in accordance with previous results (Vilisics, Szekeres, & Hornung, 2012) and the metabolic theory of ecology. However, our *a priori* hypotheses target mechanisms of niche partitioning and thus focus on departures from additivity rather than absolute decomposition rates to assess the effect of both *Oniscus* size classes and litter combinations, and their interaction. Observed mass loss generally showed a higher variability than expected mass loss (Fig. 2). This is not surprising, as we calculated expected values using average relative consumption rates of the litter monocultures, whereas observed values contained sources of variability other than total *Oniscus* mass differences (e.g. individual physiological status).

Although the role of litter combinations on ecosystem processes has been investigated quite extensively (e.g. Hättenschwiler, Tiunov, & Scheu, 2005; Handa et al., 2014; Finerty et al., 2016), intraspecific trait diversity of soil macrodetritivores has been largely neglected so far. Our study represents an attempt to unravel the complex interactions regulating the process of

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litter decomposition. We argue that scaling down our focus to the level at which ecological interactions occur – that is between litter and individual consumers – can represent a possible way forward. By demonstrating that intraspecific feeding niche partitioning plays a role in the interactions between food resource and consumer diversity, we suggest here that individual-level trait measurements are a promising way to shed light on some poorly understood aspects of the mechanisms that determine decomposition in natural ecosystems. This calls for an urgent need of standardized individual-level trait measurements, especially of invertebrates (Didham, Edwards, Leather, & Basset, 2013; Moretti et al., 2017; Ellers et al., 2018). We are aware that our focus on a single macrodetritivore species represents a limitation and makes it difficult to generalize our conclusions. Nevertheless, it is noteworthy that intraspecific niche partitioning in *Oniscus* was driven by differences in size, which is an easy-to-measure trait that determines trophic interactions across taxa. Therefore, we consider our results as a first step that should encourage increased efforts in the same direction. Further work is needed to assess to which extent the patterns we observed are general, and including a finer resolution of diversity (e.g. more litter species and size categories, or different traits) might even strengthen our findings. Our results suggest that trait variability can reduce intraspecific competition; especially in case this relationship is non-linear, as it was showed in analogous freshwater systems for the effect of shredding macroinvertebrate density (Little, Fronhofer, & Altermatt, 2018), fine-scale processes, as the ones elucidated in our experiment, might translate into consequences for ecosystem functioning at the landscape level. Beside the possible propagation across spatial scales of the effects described here, it is crucial to consider in BEF research how intraspecific trait variation might have cascading consequences for multiple processes and services (e.g. nutrient cycles, soil fertilization, plant germination, growth and defense), especially under environmental change scenarios.

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Authors' contributions

S.F., M.M., and M.B. conceived the ideas and designed methodology; S.F. collected and analysed the data; S.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

The data analysed in this paper are available in the Zenodo repository at <https://doi.org/10.5281/zenodo.3384279>.

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Table 1. Effects of combining two leaf litter species on litter mass loss, defined as departures from additivity of single-litter relative consumption rates. Results are reported for each *Oniscus* body size composition separately. Summary statistics refer to Welch’s t-tests performed with data reported in Fig. 2. Positive t-values indicate “expected is higher than observed”; vice versa for negative t-values.

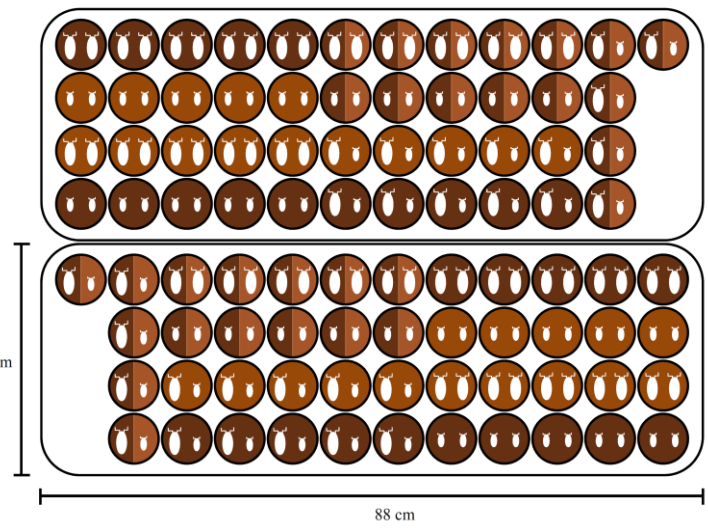
	Expected vs. Observed leaf litter mass loss								
	<i>Acer</i>			<i>Betula</i>			Total (both species)		
	t	n	p	t	n	p	t	n	p
Effect of litter combination									
Large body size	2.105	16	0.071	-4.350	16	0.003	-2.995	16	0.015
Small body size	0.343	14	0.740	-2.193	14	0.058	-1.692	14	0.124
Mixed body sizes	-0.126	20	0.902	-4.077	20	0.002	-3.853	20	0.002

Figure legends

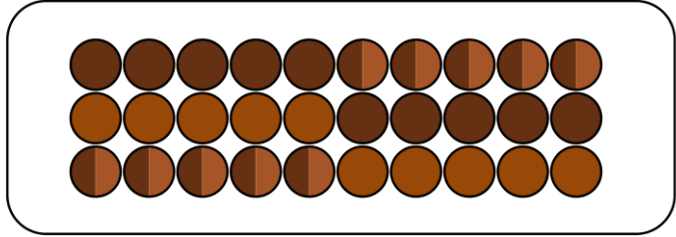
Fig. 1. Experimental setup. (A-B) Dark brown = *Acer* leaf litter disks. Light brown = *Betula* leaf litter disks. A) For simplicity, the proportion of large and small *Oniscus* is reported here depicting only two out of four animals. B) Control microcosms. C) Photo of the experimental microcosms.

Fig. 2. Expected (= additive effect of single-litter species microcosms) vs. observed leaf litter mass loss (mean values \pm SE) in the presence of both litter species *Acer* and *Betula* for any given *Oniscus* body size composition. Welch's t-test significance levels are reported (* $p < 0.1$; * $p < 0.05$; ** $p < 0.01$) where appropriate (see also Table 1).

A



B



C

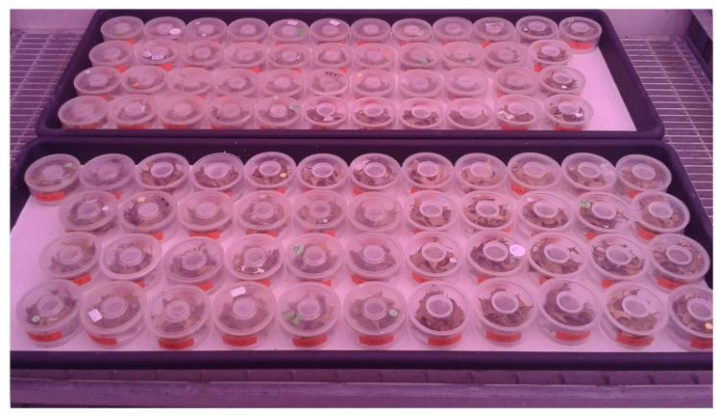


Fig. 1.

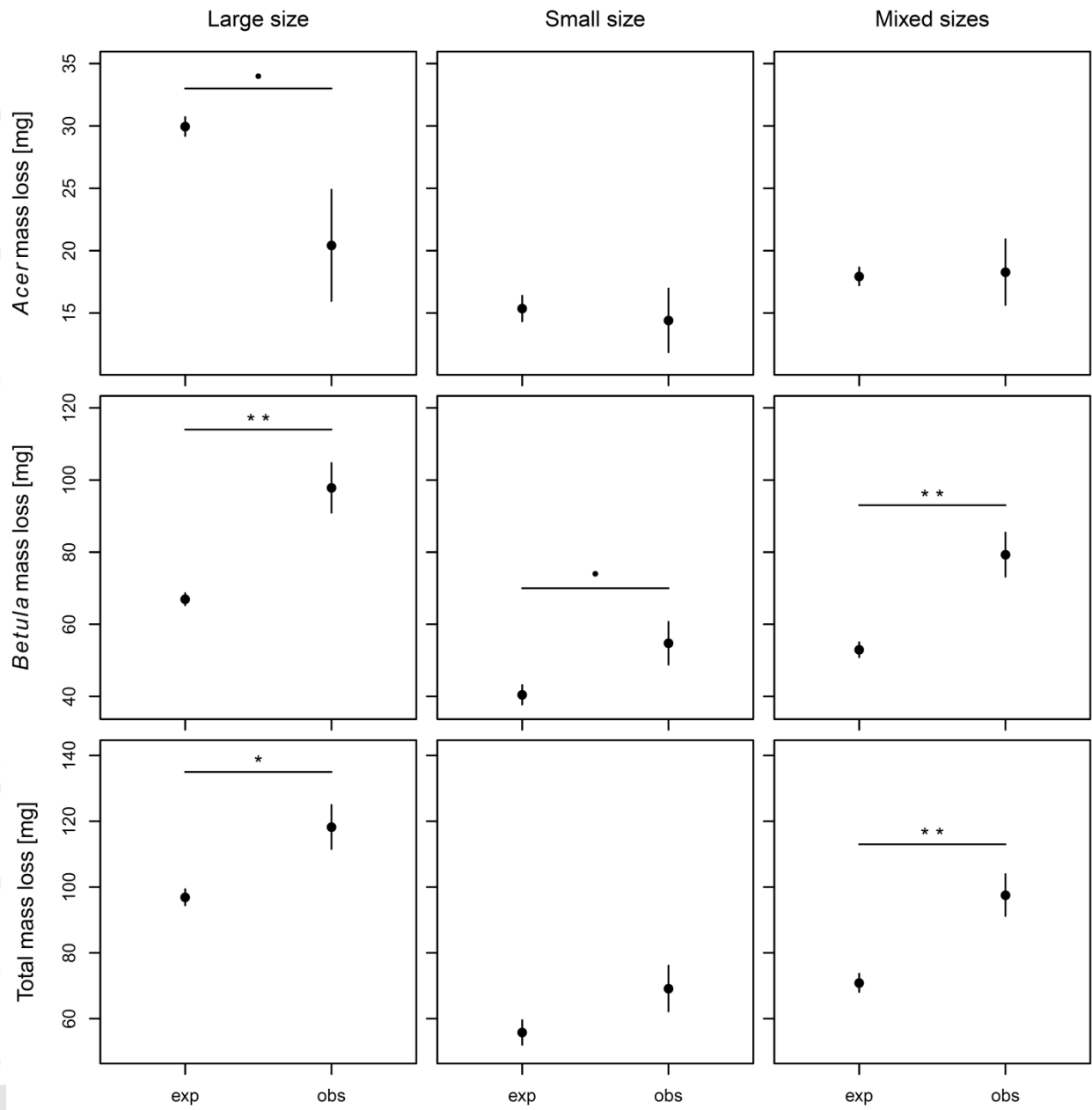


Fig. 2.