Plant community composition determines the strength of top-down control in a soil food web motif

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Top-down control of prey by predators are magnified in productive ecosystems due to higher sustenance of prey communities. In soil micro-arthropod food webs, plant communities regulate the availability of basal resources like soil microbial biomass. Mixed plant communities are often associated with higher microbial biomass than monocultures. Therefore, top-down control is expected to be higher in soil food webs of mixed plant communities. Moreover, higher predator densities can increase the suppression of prey, which can induce interactive effects between predator densities and plant community composition on prey populations. Here, we tested the effects of predator density (predatory mites) on prey populations (Collembola) in monoculture and mixed plant communities. We hypothesized that top-down control would increase with predator density but only in the mixed plant community. Our results revealed two contrasting patterns of top-down control: stronger top-down control of prey communities in the mixed plant community, but weaker top-down control in plant monocultures in high predator density treatments. As expected, higher microbial community biomass in the mixed plant community sustained sufficiently high prey populations to support high predator density. Our results highlight the roles of plant community composition and predator densities in regulating top-down control of prey in soil food webs.

Trophic interactions in food webs are observed as a combination of top-down and bottom-up control among consumers and their resources that principally regulate population dynamics in ecosystems1,2. In tri-trophic interactions, either stronger top-down control (predator-induced control) or stronger bottom-up control (plant-induced control) of herbivore/detritivore populations have commonly been observed3,4. Moreover, recent studies have revealed that variations in plant community composition with respective changes in the basal resource regulate top-down control in ecological communities5,6. Plant communities with a high number of species produce higher plant biomass providing sufficient energy to support greater communities of herbivores and detritivores, which cascade to higher densities of predators6,7, with a subsequent increase in top-down effects5. These findings of a productivity-driven proportional increase in the strength of trophic interactions at higher trophic levels agree with the classical Oksanen et al. (1981)8 hypothesis that predicts increased top-down control of prey by predators at high productivity (higher resource availability for prey). However, it is unclear how the relative importance of top-down and bottom-up control may change in ecosystems, which are experiencing shifts in plant community composition9 as well as declines in densities of predators10. Taken together, these two factors could potentially interact in complex ways and change the relative importance of top-down and bottom-up forces in influencing ecosystem processes. Here, we chose an experimental approach manipulating top-down forces in systems differing in productivity and illustrate that top-down control in a soil food web motif are contingent upon plant community composition.

In soil food webs, bottom-up forces through litter quantity and quality and microbial community biomass together with soil physio-chemical characteristics influence the strength of top-down control11. In the microarthropod sub-web of soil food webs, the main food source of prey communities like Collembola is soil microbial biomass12. At higher microbial biomass, many Collembola species are expected to thrive, which may simultaneously increase the density of their predators, such as predatory mites13. With an increase in prey density, both per capita and net prey suppression by predators get saturated14. However, saturation of predation also depends on the predator density, which co-determines prey suppression in combination with prey density15,16. For instance, at high predator density, antagonistic predator-predator interactions, such as interference and can-
nibalism, may reduce the ability of predators to suppress prey. However, the magnitude of predator interference may decrease when the prey population is high and heterogeneously distributed.

Plant communities fuel soil food webs via litter and dead root inputs, together with rhizodeposits that plant roots release into soil during plant growth. These organic inputs collectively represent the key resource for microbial community biomass in soil. However, several studies have shown variations among plant community compositions and among plant species in fueling soil microbial biomass and related food webs. Plant mixtures with functionally different species were shown to enhance microbial biomass in soil. Furthermore, certain plant functional groups are associated with higher microbial biomass due to their positive association with N-fixing bacterial species (legumes) or due to high root biomass (grasses). Functionally different plant groups also create heterogeneous environments in soil that may favour predators in suppressing prey.

In this research, we expect predator density (top-down force) and plant community-induced variations in soil microbial biomass (bottom-up force) to interactively affect prey populations. Higher densities of predators can increase the suppression of prey; however, only when the prey has sufficient amounts of resources to exploit, which would depend on plant community composition. Therefore, we hypothesize that the strength of top-down control will increase with predator density in the mixed plant community, but will decline with predator density in monoculture plant communities. We test our hypotheses in a soil micro-arthropod predator-prey system with Collembola as prey species and predatory mites as predators. This soil food web motif was studied in different plant communities, consisting of a mixed plant community with three plant functional groups (grass, herb, and legume) together and the respective monocultures.

Results
We found no significant main effects of predator density (GLMM, F = 0.09, P = 0.55) and plant community composition (GLMM, F = 1.31, P = 0.63) on Collembola density. However, and in line with our expectation, we found a significant interaction effect of predator density and plant community composition on total Collembola density (GLMM, F = 4.18, P = 0.02). In treatments with high predator densities, total Collembola densities decreased in the mixed plant community, while they increased in monoculture plant communities (Figure 2a). The interactive effect of predator density and plant community composition on total Collembola density was driven by the response of Proisotoma minuta - the smallest body-sized prey species in our experiment (GLMM, F = 5.62, P = 0.01; Figure 2b). Folsomia candida showed a similar response, but the interaction effect was not significant (GLMM, F = 2.40, P = 0.12; Figure 2c). By contrast, S. curviseta showed no response to the interaction between predator density and plant community composition (GLMM, F = 0.008 and P = 0.9; Figure 2d). Further, we also found no interactive effects of predator density and plant monocultures on Collembola species (Proisotoma: F = 0.10, P = 0.90; Folsomia: F = 0.32, P = 0.72; Sinella: F = 0.16, P = 0.84) (Supplementary Figure S1).

In line with our expectations, soil microbial biomass C was significantly higher in the mixed plant community compared to monoculture plant communities (+30%; LMM, F = 8.13, P < 0.01; Figure 3a), but did not vary significantly among the different monocultures (LMM, F = 2.12, p = 0.11, Supplementary Figure S2). Predator density had no significant effect on soil microbial biomass C (LMM, F = 0.05, P = 0.82). In addition, we found a marginally significant interactive effect of plant community composition and predator density on soil microbial biomass C (LMM, F = 2.92, P = 0.08). Microbial biomass C increased in the mixed plant community compared to the soil at the start of the experiment (+7%), whereas it decreased in monoculture plant communities (−17%).

Results from quantile regression showed that at the higher quantile (0.90) of total Collembola density, soil microbial biomass and Collembola density were positively associated (Figure 3b). On the contrary, at lower quantiles, soil microbial biomass and Collembola density showed a negative relation (Figure 3b). The non-parametric quantile regression tests revealed significant associations between soil microbial biomass and Collembola density at quantiles 0.90 (P = 0.04), 0.75 (P < 0.01), and 0.50 (P < 0.001), whereas associations were not significant at quantiles 0.25 (P = 0.13) and 0.10 (P = 0.52).

Discussion
Our results show two contrasting patterns of top-down control of prey populations based on experimentally varied predator density and plant community composition. Top-down control of Collembola increased (i.e., decrease in Collembola density) at high predator density in the mixed plant community, but not in monoculture plant communities, which agrees with our hypothesis. We speculate that the contrasting predator density effects on suppression of Collembola populations were partly due to effects mediated by plant community on soil microbial community biomass.

Microbial biomass was significantly higher in the mixed plant community than in monoculture plant communities (Figure 3a). Moreover, the positive association of higher Collembola population density and higher microbial community biomass indicates that the higher availability of microbial biomass supported higher Collembola population densities (Figure 3b). Although correlative, this relation provides some evidence that the higher sustenance of the prey community was possible only when the basal resource level was high. Hence, due to favourable conditions (higher microbial biomass) for
Collembola population in the soil of the mixed plant community, only a higher predator density was able to exert top-down control, but not the low predator density treatment.

Our results support the hypothesis of increased trophic control of prey by predators as productivity increases\(^8,29\). Furthermore, our results show interactive effects of predator density and productivity co-determining changes in prey populations. This is also in accordance to studies showing interactive effects of top-down and bottom-up forces in regulating food web structure\(^30,31\). Although, most of these previous studies demonstrated the influence of a top-down force by manipulating the presence/absence of predators, our results show that differences in predator density can alter food web structure depending on the availability of the basal resources.

In contrast to the results in the mixed plant community, interference among predatory mites at high predator density may have increased in monoculture plant communities due to low Collembola density causing a weak top-down control (Figure 2a). Interference among predatory mite individuals are argued to be low at sufficiently abundant prey populations due to their ability of dispersing into prey clusters\(^18\). This could cause a higher suppression of prey, as in the case of high density predator treatments in the mixed plant community in this study.

Mixed plant communities in combination with different functional groups including legumes and grasses have been shown to increase Collembola densities, likely due to elevated microbial biomass in soil\(^26,33\). Due to higher production of fine roots and an associated increase in rhizodeposition, mixed plant communities potentially provide favourable microhabitat conditions in soil for microbial growth\(^26,34\).

To overcome predation pressure, prey communities may show compensatory population growth via faster regeneration\(^35\). In order to do so, Collembola species are expected to increase their grazing activity on microbial communities\(^36\). Increased Collembola grazing potentially can decrease microbial biomass; however, our finding suggest that this was not the case, at least in the mixed plant community. It is important to note though that our study design did not allow us to test how Collembola grazing pressure could have affected microbial biomass (Supplementary Figure S3). Some studies have reported that Collembola grazing could essentially influence soil microbial biomass\(^36,37\); however, less is known about how such grazing effects could occur in the context of different plant communities\(^38\). Our results also show that realized predator density was higher in the mixed plant community independent of predator density treatments at the final harvest supporting the notion that plant species mixtures support higher predator densities than monocultures\(^5,6\) (Supplementary Figure S4).

The significant suppression of only *P. minuta* by predators among the three studied Collembola species indicates a combination of strong and weak trophic interactions in our study depending on Collembola species identity (Figure 2b). A plausible reason for strong suppression of *P. minuta* could be their relatively small body size, which may cause higher foraging advantages, such as reduced handling time, for predators compared to the large-sized prey such as *S. curviseta*\(^39\). Interestingly, when changes in Collembola density from the start of the experiment to the final harvest were compared, *P. minuta* density also increased more than the other two Collembola species (see differences in Y-axis scales in Figure 2b, c, and d). This further indicates compensatory population growth in *P. minuta*.

**Figure 2** | (a) Total Collembola densities, (b) densities of *Proisotoma minuta*, (c) densities of *Folsomia candida*, and (d) densities of *Sinella curviseta* at the end of the experiment as affected by experimental predator densities (indicated by predator: prey ratio) and plant community composition. The black solid lines show significant relationships, whereas dotted lines indicate non-significant relationships.
which could occur in prey communities when exposed to high predation pressure\textsuperscript{35,40}. Species undergoing faster regeneration like \textit{P. minuta}\textsuperscript{41} often show compensatory patterns and are therefore superior at exploiting available resources\textsuperscript{42}. At high predator density, an increase in prey density would lead to a higher probability of predator-prey encounters, which could have contributed to the observed suppression of \textit{P. minuta} in the resource-rich environment of the mixed plant community.

Spatial and resource heterogeneity in soil have been shown to be higher in diverse plant communities than in monocultures\textsuperscript{43}. We observed consistent patterns of soil microbial biomass and prey population among monocultures of the three plant functional groups at different predator density treatments (Supplementary Figure S1), which is inconsistent with studies that have reported stronger plant identity effects on the trophic structure of soil food webs due to plant species-specific soil environments\textsuperscript{44}. The plant species that we used have different root architectures and biomass\textsuperscript{45}, and variations in plant-derived organic inputs in the mixed plant community\textsuperscript{25} may have created a more heterogeneous environment\textsuperscript{46} in soil promoting prey suppression by predators. Such heterogeneous environments will enhance the clustering of Collembola species in resource-rich patches (higher microbial biomass) that in general would favour predation by predatory mites\textsuperscript{18}. However, as we were unable to show such direct links in the present study, the proposed relationship between resource heterogeneity and predator-prey interactions in soil merits further exploration.

In general, at high predator density, prey suppression can increase for a short duration when prey population growth is constrained by a lack of the basal resource\textsuperscript{47}. It is important to note that when resource availability limits prey population growth, predator density would decline due to starvation-induced mortality. This could be one reason for weak effects of initial predator densities on the realized predator densities compared to differences between the mixed and monoculture plant communities (Supplementary Figure S4). In low productive systems (monoculture plant communities), high predator density might have suppressed Collembola population initially, but as the experiment progressed, prey suppression may have decreased as Collembola population did not thrive as much as in the mixed plant community, consequently leading to the decline in predator densities. Multiple harvests or developing procedures to temporally track population dynamics\textsuperscript{48} in such experiments can provide further insights into density effects of predators on prey suppression as influenced by resource availability.

Prey suppression by predators in ecosystems contribute to many ecosystem functions, such as nutrient cycling\textsuperscript{49}. Predators are the most vulnerable trophic group to the effects of disturbances, such as land fragmentation and climate warming\textsuperscript{10,50}. A decline in predator density can detrimentally affect ecosystem processes through trophic cascades\textsuperscript{49}. Utilizing a soil food web motif, our study shows that the top-down control of prey depends on the availability of the basal resource as well as on the density of predators. We argue that such interactive effects of predator density (top-down force) and productivity or resource availability mediated via the plant community (bottom-up force) play a crucial role in structuring food webs. Since both top-down and bottom-up factors determining food web structure are subjected to acute and chronic anthropogenic perturbations, our study highlights that such interactions are crucial to understand and predict changes in food web structure and concomitant ecosystem functions.
Plant communities. Mixed and monoculture plant communities were established in the defaunated soils, which had been incubated with grass litter for 2 weeks. The mixed plant community included *Trifolium pratense (legume)*, *Poa pratensis* (grass), and *Rumex acetosa* (herb), and monoculture plant communities consisted of those three plant species alone in the microcosms. These plant species have been shown to vary in their root traits such as root depth and are part of plant species pool of the Jena Experiment. We used these plant species (obtained from Schneckenprofi GmbH, Blaufelden-Raboldshausen, Germany) were sown separately in the same defaunated soil and transplanted into the microcosms after six weeks of germination (seedlings were chosen with similar heights of about 5–8 cm). Three plant individuals from one species were planted into monoculture microcosms (establishing three different monoculture treatments), whereas one individual per plant species was planted to construct a mixed plant community. To give plant communities sufficient time to establish in the microcosms, Collembola were added only after 20 days from the plant transplantations into the microcosms.

Soil microarthropod community. The prey community consisted of three *Collembola* species (*Priapulus minutula, Folosoma candida*, and *Sinella curviseta*), which were added to the microcosms in equal densities (details below). Families of these species (*P. minutula*; Isotomidae, *F. candida*, and *S. curviseta*; Entomobryidae) are reported in the soil of the Jena Experiment\(^3\), while the used species are easy to culture. Besides, plant-derived carbon inputs in soil are often positively correlated to microbial biomass \(C\) and predation density \(g \times C\) (we used as a proxy of resource availability for Collembola in soil). We tested if soil microbial biomass \(C\) was influenced by plant community composition and predation density treatments. For this, we used linear mixed effect models (LMM) with blocks as the random effect. We also tested whether plant monocultures and predation densities affected Collembola density (GLMM for count data, negative binomial error) and microbial biomass \(C\) (LMM for biomass data). We correlated microbial biomass \(C\) with Collembola density using quantile regression due to over-dispersion\(^4\) of Collembola data. We used quantile regression at quantiles 0.10, 0.25, 0.50, 0.75, and 0.90. Quantile regression incorporates the unequal variances of the response variables and is useful to consider the possibility of multiple slopes for minimum to maximum responses\(^5\). All statistical analyses were carried out in R statistical software version 2.15.2 (R Development Core Team, 2012).

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Author contributions
M.P.T. and N.E. designed the experiment. M.P.T. performed the experiment and analyzed the data. M.P.T. wrote the first draft of the manuscript, and N.E. contributed to the revisions.

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