

Shared community history strengthens plant diversity effects on belowground multitrophic functioning

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Abstract

The relationship of plant diversity and several ecosystem functions strengthens over time. This suggests that the restructuring of biotic interactions in the process of a community's assembly and the associated changes in function differ between species-rich and species-poor communities. An important component of these changes is the feedback between plant and soil community history. In this study, we examined the interactive effects of plant richness and community history on the trophic functions of the soil fauna community. We hypothesized that experimental removal of either soil or plant community history would diminish the positive effects of plant richness on the multitrophic functions of the soil food-web, compared to mature communities. We tested this hypothesis in a long-term grassland biodiversity experiment by comparing plots across three treatments (without plant history, without plant and soil history, controls with ~20 years of plot specific community history). We found that the relationship between plant richness and belowground multitrophic functionality is indeed stronger in communities with shared plant and soil community history. Our findings indicate that anthropogenic disturbance can impact the functioning of the soil community through the loss of plant species but also by preventing feedbacks that develop in the process of community assembly.

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(JExIS; <https://jexis.idiv.de>). The code necessary to reproduce the calculations of fluxes, the analyses and figures is available on Github (https://github.com/amynang/DBEF_soil_foodwebs) and will be archived in Zenodo.

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Abstract

The relationship of plant diversity and several ecosystem functions strengthens over time. This suggests that the restructuring of biotic interactions in the process of a community's assembly and the associated changes in function differ between species-rich and species-poor communities. An important component of these changes is the feedback between plant and soil community history. In this study, we examined the interactive effects of plant richness and community history on the trophic functions of the soil fauna community. We hypothesized that experimental removal of either soil or plant community history would diminish the positive effects of plant richness on the multitrophic functions of the soil food-web, compared to mature communities. We tested this hypothesis in a long-term grassland biodiversity experiment by comparing plots across three treatments (without plant history, without plant and soil history, controls with ~20 years of plot specific community history). We found that the relationship between plant richness and belowground multitrophic functionality is indeed stronger in communities with shared plant and soil community history. Our findings indicate that anthropogenic disturbance can impact the functioning of the soil community through the loss of plant species but also by preventing feedbacks that develop in the process of community assembly.

Introduction

Changes in biodiversity due to anthropogenic pressure have motivated ecological research to focus on the relationship between biodiversity and ecosystem functioning (BEF) and its relevance for the provision of ecosystem services (Isbell et al. 2017). A plethora of empirical (Tilman et al. 1997, Hector 1999, Cardinale et al. 2011) and theoretical studies (Loreau 1998,

Maureaud et al. 2020, Albert et al. 2022) has demonstrated that this relationship is generally positive, across different systems (Huang et al. 2018), for several ecosystem functions above- as well as belowground, indicating that loss of biodiversity would be detrimental to the functioning of ecosystems. There is also mounting evidence that BEF relationships strengthen over time (Reich et al. 2012, Huang et al. 2018), which motivated our study addressing which processes during community assembly could be responsible for this change (Eisenhauer et al. 2019).

The functioning of an ecological community is driven by the biotic interactions of its constituent species (Randall and Smith 2019). These interactions change over time, through a combination of plastic adaptations and species turnover processes in response to competition or environmental variability (Agrawal 2001, O’Sullivan et al. 2021, Bauer et al. 2022). The restructuring of biotic interactions therefore shapes the community’s history which influences the level of functioning at different points in time. In that light, diversity can be seen as a crucial context dependency, in the sense that, to understand how functioning will change over time, we need to consider whether the community in question is species-poor or species-rich.

Plant species have been shown to shift their traits to facilitate coexistence despite competition (Zuppinge-Dingley et al. 2014). This process of niche differentiation among populations in species-rich plant communities increases complementarity, whereas the potential for this would be reduced in species-poor communities and not feasible for monocultures. Therefore, plastic or inter-generational changes of plant niches during the plant community history can be responsible for the steepening of the diversity - productivity relationship (Amyntas et al. 2023). This in turn should enhance soil ecosystem functioning through increased resource input (root biomass, exudates, litter) (Hooper et al. 2000, Eisenhauer et al. 2013, Eisenhauer et al. 2017).

However, plant niche partitioning was also shown to depend on soil community composition that may co-determine eco-evolutionary processes (Zuppinger-Dingley et al. 2015). During assembly, the soil community experiences shifts in species composition, in a turnover process that tends to replace pioneer species (quick colonizers, opportunistic, with a broad niche spectrum) with K-strategists that are more competitive and efficient in using resources (Cesarz et al. 2015).

Overall, community assembly should lead to a composition of species that are well adapted to the environment and each other. This process also implies a restructuring of trophic interactions in the soil food web, which can be highly dependent on the diversity of the underlying plant community (Eisenhauer et al. 2012). High plant diversity offers a variety of niches for the soil fauna, creating the circumstances that would foster a soil community that can maintain higher levels of functioning such as decomposition, herbivory but also control of herbivory by predators (Barnes et al. 2020).

Taken together, the functioning of soil food-webs should be maximized in plant-rich communities with plant history as well as soil community history. While there is evidence of a positive effect of plant diversity on trophic functions in aboveground food-webs (Buzhdygan et al. 2020, Barnes et al. 2020) this relationship is less clear for belowground food-webs (Buzhdygan et al. 2020). Moreover, the interactive effects of plant diversity and community history on the functioning of the soil fauna community remain untested so far. This leads us to the following questions: (a) how does soil community history change the biodiversity ecosystem functioning relationship, and (b) how does plant community history change this relationship? We addressed these questions in a large-scale experiment, manipulating plant coexistence history and soil community history, to examine their effects on the functioning of the soil fauna community. We used energy flux in the soil food-web as a proxy of different trophic functions of the soil

fauna community (Barnes et al. 2018). More specifically, we hypothesize that (H1) plant richness increases the overall functioning of the soil fauna across communities with plot specific soil and plant history. (H2) This relationship is weakened by the absence of soil or plant history. (H3) Consistent with what has been observed above-ground (Barnes et al. 2020), the restructuring of trophic interactions over time leads to increased herbivore control at higher richness and reduced herbivory pressure on plants.

Methods

Experimental field site

The Jena Experiment was established in 2002 in the floodplain of the river Saale (Thuringia, Germany, 50°55′ N, 11°35′ E; 130m above sea level) (Roscher et al. 2004). It is a long-term biodiversity ecosystem functioning experiment, consisting of 80 grassland plots with maintained plant species richness. Across the plots, sown species richness doubles from 1 to 16 species (each level of richness is replicated 16 times except for 1- and 16-species plots that are replicated 14 times). Additionally, there are four plots sown with all 60 species which comprise the whole species pool of the experiment. Plots are arranged in four blocks. Experimental species richness is maintained by weeding three times per year. Plots are mown twice a year, consistent with typical management practice in Central European extensively-used grasslands.

The ΔBEF experiment

In 2016 a split-plot design was established in each plot of the Jena Experiment (details in Vogel et al. (2019)). One subplot is the control, with plot-specific soil community and plant community history and the other two are treatments with a cumulative removal of community history: a subplot with soil history but without plant history (i.e. it was resown, with the same plant species

as done in 2002) and a subplot with neither soil nor plant history (i.e soil was excavated to a depth of 30 cm, replaced with soil from an arable field and resown with the same plant species).

Sampling and data collection

The sampling campaign took place between June 14 and 24 2021, shortly after the first plant biomass harvest and at peak biological activity. From each subplot, we extracted one soil core of 20 cm Ø, one soil core of 5 cm Ø, and four cores of 2 cm Ø. The sampled depth was 10 cm for all cores.

For each subplot, we pooled the 2 cm Ø cores and then sieved the soil to break large aggregates and removed seeds and roots. To assess nematode species composition and density, we extracted nematodes from ~25 g of the sieved soil, using a modified Baermann-Funnel method (Cesarz et al. 2019). We then counted the extracted individuals and randomly identified up to 100 individuals from each sample to genus or family level. The density of nematodes per m^2 was estimated based on the number of individuals per g of dry soil and the g of dry soil per cm^3 (i.e., we calculated the number of individuals of each nematode taxon in a volume of $100 \cdot 100 \cdot 10$ cm). The taxon composition of the identified sub-sample was then extrapolated to the estimated density of nematodes per m^2 .

Macrofauna were extracted by heat from the 20 cm Ø cores (Kempson et al. 1963), while mesofauna were extracted from the 5 cm Ø cores (Macfadyen 1961). To extract soil mesofauna, we split the 10 cm soil core into 5 cm cores, to increase extraction efficiency. The animals extracted were stored in 65% ethanol. Mesofauna were sorted to Acari, Collembola, Protura, Pauropoda and Symphyla, and subsequently Acari and Collembola were identified to order and family level, respectively. Macrofauna were identified to order level. To calculate the density of

macrofauna and mesofauna taxa, we extrapolated from the number of individuals found within the surface sampled by the respective core to the number of individuals per m^2 . The loss of vials during processing resulted in lack of information for Acari and Collembola in 7 out of 240 subplots. We used multiple imputation of missing data as implemented by the *mice* package (Buuren and Groothuis-Oudshoorn 2011) to impute the density of the different Acari and Collembola groups in the samples that lacked this information. This resulted in 100 versions of the subplot by taxon dataframe, capturing uncertainty for the imputed values. This approach allowed us to estimate energy fluxes for all 240 subplots.

Our study captures a considerable portion of the soil fauna community, with all its trophic functions well represented (by herbivores, predators, primary and secondary decomposers). We will subsequently refer to the soil fauna community, acknowledging that we are dealing with a representative and consistent subset of it.

Calculation of energy flux

We calculated energy flux for each of the 240 soil food-webs in the Jena Experiment using the *fluxweb* package (Gauzens 2018; Gauzens et al. 2019). Details on the concept and application of this framework can be found in Barnes et al. (2018) and Jochum et al. (2021). Briefly, the energy that flows across every link in a food-web is inferred by considering energetic losses of each node due to metabolism and consumption. That is, under a steady-state assumption, every node (population) is compensating its losses by absorbing energy from its resources. Due to assimilation inefficiencies, a surplus of energy is required to compensate for a given amount of lost energy. Fluxes are calculated from the top to the bottom of the food-web, so the energy that flows out of a trophic level is enough to support all the levels above it.

Population level metabolic losses

Resting metabolic rate is a power-law function of body mass (Ehnes et al. 2011). To estimate the body mass distribution of the different taxa, we aimed to measure the length (and width in the case of macrofauna) of up to 10 individuals per taxon per subplot. As the large number of samples made it infeasible to do this for all subplots, we did so selectively for up to 24 samples spanning the plant richness gradient. We then used published taxon-specific relationships of length (and width) to mass (Mercer et al. 2001; Sohlström et al. 2018) to calculate the body-mass of each measured individual. By pooling information across samples, we determined the body-mass distribution characteristic of each taxon, expressed by its mean and standard deviation. To estimate population level metabolic losses per m^2 , we first drew N samples from a lognormal distribution based on the calculated mean and sd, where N is the number of individuals/ m^2 of a given taxon. We then calculated metabolic losses as a function of body-mass (based on Ehnes et al. (2011)) for the N body-masses and summed them up to population level losses.

The trophic interaction matrix

We used information on the trophic relationships of the different soil fauna groups (as reviewed in Potapov et al. (2022)) as well as traits that influence the strength of these interactions (Potapov 2022), combined with our data of the biomass and body mass distribution of the different taxa, to estimate energy fluxes in the soil food-web (Barnes et al. 2018; Jochum et al. 2021; Potapov 2022). For the feeding type and body-mass distributions of the different nematode taxa we relied on (Mulder and Vonk 2011) and Nemaplex (Ferris 1999). Collembola were grouped to functional leagues according to Potapov et al. (2016).

We started by constructing a square matrix m expressing trophic relationships among all trophic groups observed in the entire experiment, as well as four basal resources (roots, detritus, bacteria and fungi). When taxon i is consumed by taxon j , m_{ij} has a non-zero value. Initial values were chosen to reflect broad preferences of the different trophic groups (Potapov et al. 2022). For example, Diplopoda are primarily detritivores that also consume microbes. This can be expressed as an expected diet composition of 75% detritus and 12.5% each for fungi and bacteria. In the case of predatory interactions, to begin with, we used values reflecting equal preference among potential prey. Once this preliminary matrix was complete (Table S1), we used additional information such as predator-prey body-mass ratios (Brose et al. 2006) as well as prey attributes such as agility or the possession of physical or chemical defenses and finally, the probability of encounter between individuals of different taxa given their similarity in vertical stratification, to refine the expected interaction strength among taxa (following Potapov 2022). At this stage, the matrix expressed the expected affinity for different resources.

This matrix was subsequently split into 240 subplot-specific matrices, containing only the basal resources and the taxa found in each subplot. Then, trophic interactions were further modified by the relative availability of different prey taxa (based on relative biomass). Therefore, the elements of each column in the resulting matrices expressed the expected diet composition of each consumer j . The matrix elements are a composite of probability of encounter, probability of a predator of certain size to subdue prey of a certain size or with certain physical or chemical attributes. Accordingly, to account for the inherently probabilistic nature of these interactions, we treated the elements in each matrix column as the component probabilities of a Dirichlet distribution. We generated 1000 versions of each subplot-specific matrix; in each version, the elements of each column were one sample from a Dirichlet distribution whose component

probabilities was the vector of the original elements, multiplied by a constant. In practice, this meant that zero elements remained zero and non-zero elements were approximately normally distributed around the expected value, while column sums were constrained to 1. Therefore, a consumer's diet was, on average, the expected diet but with some variation around this expectation. The amount of variation depends on the constant (higher values result in less variation). We tested the sensitivity of our energy flux estimates and any subsequent inferences by choosing different levels of the constant (Fig. S2). Combining the 1000 matrices with the multiple imputation described above, our modified application of this framework accounts for the uncertainty of trophic interactions as well as uncertainty for the missing data. Due to the probabilistic nature of our interaction matrix, the estimated energy fluxes were also distributions rather than single values.

Community level energy flux

We calculated the total energy flux in the soil fauna community by summing the energy of all individual links in each food-web. This quantity is a proxy of the composite multitrophic functioning of the soil fauna community. We additionally calculated the sum of energy flux of links that correspond to distinct trophic functions, namely herbivory, predation, detritivory as well as microbivory.

Below-ground herbivory pressure

We calculated herbivory pressure as the sum of outflux of energy from plants to their consumers (including omnivores) per mg of root biomass. Root biomass data were available for a 0-5 cm depth across all experimental units (data for 5-10 cm were only available for the control subplots) while energy fluxes were based on animals sampled at a 0-10 cm depth. We have

230 conducted a sensitivity analysis to test the influence of excluding the 5-10 cm layer in control
231 subplots.

232 **Control of herbivory**

233 In the absence of omnivores, control of herbivory through predation can be quantified as the ratio
234 of outfluxes from herbivores to their consumers over the influxes to herbivores (outfluxes from
235 plants to herbivores times assimilation efficiency). Given the steady state assumption, this
236 quantity is a fraction, expressing how much of the energy that is absorbed by herbivores is taken
237 away from them through consumption. Omnivores complicate this calculation, as their outfluxes
238 are partly relevant for herbivory control but only to the extent that omnivores rely on plants. To
239 incorporate omnivores in the calculation of herbivory control, the numerator was instead the sum
240 of outfluxes from plant consumers after those had been weighted by each consumer's proportion
241 of energy uptake that comes from plants (1 for herbivores, <1 for omnivores). The denominator
242 was the sum of energy influxes from plants to plant consumers.

243 **Statistical analysis**

244 We examined whether the relationship between plant species richness and the energy flows of
245 interest (community level, herbivory pressure and control, detritivory and microbivory) differs
246 depending on absence versus presence of history. To get a better understanding of any effects on
247 the fluxes of interest, we conducted additional analyses with overall predation and overall
248 herbivory as a response. Our models had the general formula

249 $response.mean/mi(response.sd) \sim 1 + richness*history + (1 + history/block/plot).$

250 The left-hand side of the formula indicates that the response consists of distributions rather than
251 single values, defined by the mean and the standard deviation of the energy flux across the 1000

versions of each food-web. This distribution reflects the uncertainty for the real value. We therefore employ an analytical approach that is used to account for measurement error (McElreath 2020; Bürkner 2021) to incorporate the varying flux uncertainty that was produced by diet composition uncertainty (Figs. S2-S3). After an initial modeling attempt, posterior predictive checks showed that linear models failed to reproduce the right skewed distribution of observed values. We therefore log-transformed fluxes before calculating the mean and sd across the 1000 versions. The exception to this was herbivory control which, as a continuous proportion, was modeled with a Beta distribution.

The right-hand side of the formula indicates that we are estimating the coefficients for the intercept and slope of the average relationship between response and plant species richness for the control subplots, and the coefficients for the difference in intercept and slope between each treatment and control, while ensuring that treatment differences are estimated within each plot rather than across plots. Plots themselves are nested within blocks. Plant species richness was log-transformed (base 2), centered and scaled.

We fitted models in Stan via the *brms* package (Bürkner 2018), using default priors and four MCMC chains with at least 4000 iterations each (with the first half used for warm-up). We evaluated our models with posterior predictive checks, visual inspection of chain mixing, as well as Rhat values (not exceeding 1.01).

We report mean estimates and 90% highest posterior density intervals (HPD) of slopes and their contrasts, extracted using the *emmeans* package (Lenth 2023). We note the sign of a relationship and use the exclusion of zero from the interval to evaluate whether a relationship is statistically clear or not (Dushoff et al. 2019).

Finally, we examined the sensitivity of our results on assuming different levels of diet uncertainty by repeating our analyses for 3 levels of uncertainty as well as without uncertainty (results reported in the main text are for intermediate uncertainty). We found that the coefficients of our models were robust to increasing diet uncertainty (fig. S4).

Results

Community level energy flux

Plant richness had a clear positive effect on community level flux, in control communities with plant and soil history (mean slope [90% HPD] = 0.11 [0.08, 0.14], Fig. 2a). As expected, this relationship was shallower in the case of the treatment communities lacking aspects of shared history (with soil but not plant history: 0.06 [0.025, 0.09]; without soil or plant history: 0.04 [0.01, 0.08]). In both cases, the difference between the slope in control and that in treatment communities was clear (-0.05 [-0.095, -0.01] and -0.07 [-0.115, -0.02], respectively, Fig. 2a).

Individual trophic functions

Plant richness had a weakly positive but clear effect on herbivory in communities with soil and plant history (0.06 [0.02, 0.10], Fig.2b). This relationship was weakly positive or negative but very unclear for the two history treatments (with soil but not plant history: 0.02 [-0.02, 0.06]; without soil or plant history: -0.01 [-0.06, 0.03], Fig. 2b).

The effect of plant richness on predation was clearly positive across control and treatment communities (with soil and plant history: 0.12 [0.07, 0.17]; with soil but not plant history: 0.06 [0.005, 0.11]; without soil or plant history: 0.075 [0.02, 0.13], fig.2c). The slope of the relationship in the case of soil but no plant history was shallowest and clearly different from that

of control communities (-0.06 [-0.13, -0.001]), while the relationship across communities without soil or plant history was intermediate and not clearly different from either control or the other treatment (-0.05 [-0.11, 0.02] and 0.02 [-0.05, 0.08]).

The effect of plant richness on detritivory was clearly positive across control and treatment communities (with soil and plant history: 0.16 [0.12, 0.21]; with soil but not plant history: 0.13 [0.08, 0.17]; without soil or plant history 0.10 [0.05, 0.145], fig.2d). The slope was steeper across communities with soil and plant history but this difference was only clear when compared to communities without soil or plant history (-0.06 [-0.12, -0.005]). The effect of plant richness on microbivory was also positive (with soil and plant history: 0.14 [0.10, 0.17]; with soil but not plant history: 0.11 [0.07, 0.15]; without soil or plant history 0.07 [0.03, 0.11], fig.2e). Once again, the slope was steeper across communities with soil and plant history compared to the two treatments but this difference was only clear when compared to communities without soil or plant history (-0.07 [-0.12, -0.02]).

Herbivory pressure on plants and control of herbivory by predation

Plant-rich communities experienced reduced herbivory pressure (with soil and plant history: -0.18 [-0.25, -0.11]; with soil but not plant history: -0.13 [-0.20, -0.06]; without soil or plant history -0.18 [-0.27, -0.10], fig.3a). There were no clear differences in slope between control and treatments for any pairwise combination. In a sensitivity analysis, this negative relationship between herbivory pressure and plant species richness was robust to increasing root measurement depth (Fig. S6). Finally, the relationship of herbivory control by predators with plant richness was positive or negative but always unclear across control and treatment communities (with soil and plant history: 0.05 [-0.07, 0.16]; with soil but not plant history: -0.01 [-0.14, 0.12]; without soil or plant history: 0.11 [-0.01, 0.23]).

Discussion

In our study manipulating plant species richness across treatments of soil and plant community history, we found that plant rich communities support higher levels of multitrophic functioning of the soil fauna community. Moreover, we found that this diversity-function relationship was generally weaker in communities without shared plant community history with only minor additional effects of non-shared soil community history. Together, these results imply that the steepening of the diversity functioning relationship is mainly driven by processes depending on shared plant community history.

Here we provide experimental evidence of a positive effect of plant richness on the functioning of the soil fauna food-web. Previous studies have demonstrated that plant diversity has a positive effect on the abundance and diversity of the invertebrate community, below as well as above ground (Scherber et al. 2010, Milcu et al. 2013, Ebeling et al. 2018), suggesting consequent changes on their ecosystem functioning. Subsequent research has corroborated the relationship between diversity and invertebrate food-web functioning above ground (Buzhdygan et al. 2020, Barnes et al. 2020). However, evidence of a link between plant diversity and soil fauna functions has remained elusive (Buzhdygan et al. 2020). A particular challenge of the below-ground component of an ecosystem is that, with the exception of detritivory (Birkhofer et al. 2011), the feeding activity of soil fauna is difficult to assess directly. The calculation of energy flux in a food-web provides a way to circumvent this limitation. Our findings show that indeed the soil fauna community multitrophic functioning, estimated by the overall energy that flows across links in the soil food-web, increases with increasing plant richness. When considering trophic functions separately, we found that this relationship is stronger for the brown food-web (detritivory, microbivory) and predation, while the effect of plant richness on herbivory was

weaker and context dependent. Our approach of applying energy-flux calculations to belowground food webs has thus demonstrated that plant diversity has a positive effect on functioning, despite some variation across different ecosystem functions.

The evidence of a positive effect of plant richness on invertebrate communities and their functioning, comes from data that were collected some years after the establishment of an experiment (Scherber et al. 2010, Milcu et al. 2013, Ebeling et al. 2018, Buzhdygan et al. 2020, Barnes et al. 2020), or in unmanipulated ecosystems (Birkhofer et al. 2011). In other words, these relationships have generally been observed in established communities with a shared history among producers and consumers. At the same time, longitudinal data of other ecosystem functions, such as primary productivity (Reich et al. 2012, Huang et al. 2018) or soil microbial activity (Eisenhauer et al. 2010), have shown that BEF relationships may be absent or weak in the early stages of a community's development and emerge or become stronger later on. This has led to our hypothesis that disrupting the biotic interactions that have been formed during a community's history by experimentally removing components of this history, would diminish the positive effect of plant diversity on soil fauna community functioning. Our results largely support this hypothesis; the relationship of community level energy flux was clearly stronger across control communities with both soil and plant community history, compared to either of the two history removal treatments. The removal of plant history is seemingly enough to diminish the overall BEF relationship as the two treatments had a similar pattern. Although the difference to the two treatments was not always clear, the slope of the diversity-function relationship was consistently steeper among control communities, regardless of the specific trophic function considered. In the case of trophic functions of the brown food-web, the most pronounced difference of control communities was with communities with neither soil nor plant

history, which exhibited the shallowest BEF relationships. These findings indicate that biotic changes that take place in communities over time are responsible for the strengthening of BEF relationships belowground.

We also considered the effect of plant diversity on herbivory pressure on plants, as well as herbivory control through predation. The relationship of these functions to plant diversity has been examined in above-ground food-webs of well established communities. In such mature communities, control of herbivory was shown to increase with plant richness, while herbivory pressure had the opposite relationship with plant richness, indicating a top-down mechanism (Barnes et al. 2020). Here, we hypothesized this mechanism to be emerging through the restructuring of trophic interactions over time. Contrary to our expectations, we did not find clear evidence of herbivory control increasing with richness regardless of community history. At the same time, herbivory pressure was indeed reduced with increasing plant richness, with no clear effects of community history on the strength of this relationship. This reduction of pressure seems to emerge from weakly increasing or unchanging herbivory, combined with a clear increase of root biomass with increasing plant richness (Fig. S5). We therefore suggest the presence of an alternative mechanism for the multitrophic reduction of herbivory pressure: we have seen that the functioning of the brown food-web, which is instrumental for nutrient availability (Wardle et al. 2004, Wurst 2013), is positively influenced by plant richness. This relationship can in turn enhance plant productivity in plant-rich communities, leading to the observed net reduction of herbivory pressure. Therefore, different multitrophic mechanisms can be important for promoting plant productivity, depending on whether we consider the above or below-ground component of an ecosystem.

Our findings indicate that the effects of biodiversity on belowground ecosystem functioning are dependent on the shared history of producers and consumers in the community, supporting the idea that a combination of niche differentiation with turnover processes are reshaping this relationship over time. This suggests that BEF relationships are context dependent, varying not only across space (Thompson et al. 2018), but also in time. In natural ecosystems, the trajectory of community change over time will likely be influenced by factors that determine the potential for plant niche differentiation but also those regulating animal community assembly, such as latitudinal or environmental gradients of regional species richness or landscape characteristics that affect accessibility through dispersal (Ye and Wang 2023). Therefore, to understand how BEF relationships develop over time, future research should traverse the temporal and spatial dimension, examining how meta-community processes shape local dynamics (Amarasekare 2008).

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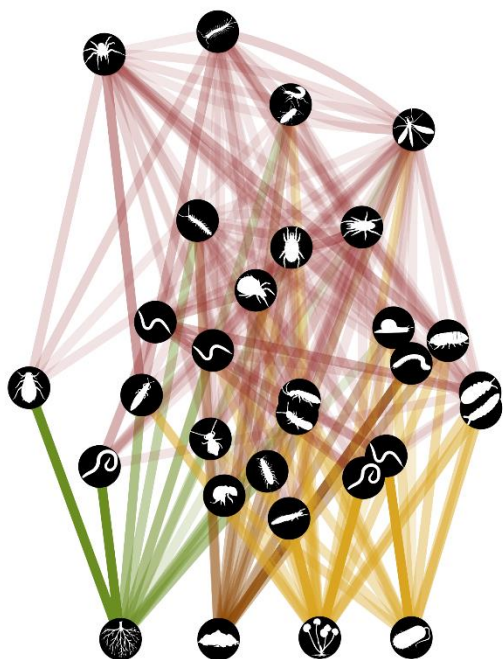
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Figure 1 The meta food-web of the soil fauna community, depicting predatory (red), herbivorous (green), detritivorous (brown) and microbivorous (yellow) interactions of the taxa listed in Table S2.

Figure 2 The relationship between plant richness and summed energy flux for different combinations of plant and soil community history. (a) Total energy flux, (b) herbivory fluxes, (c) predation, (d) detritivory and (e) microbivory. Lines show mean estimates for the average richness-flux relationship bound by 90% uncertainty intervals. Dashed lines indicate relationships whose slope is not clearly different from zero.

Figure 3 The relationship between plant richness and (a) herbivory pressure on plants and (b) control of herbivory through predation. Lines show mean estimates for the average richness-function relationship bound by 90% uncertainty intervals. Dashed lines indicate relationships whose slope is not clearly different from zero.



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588 **Figure1**

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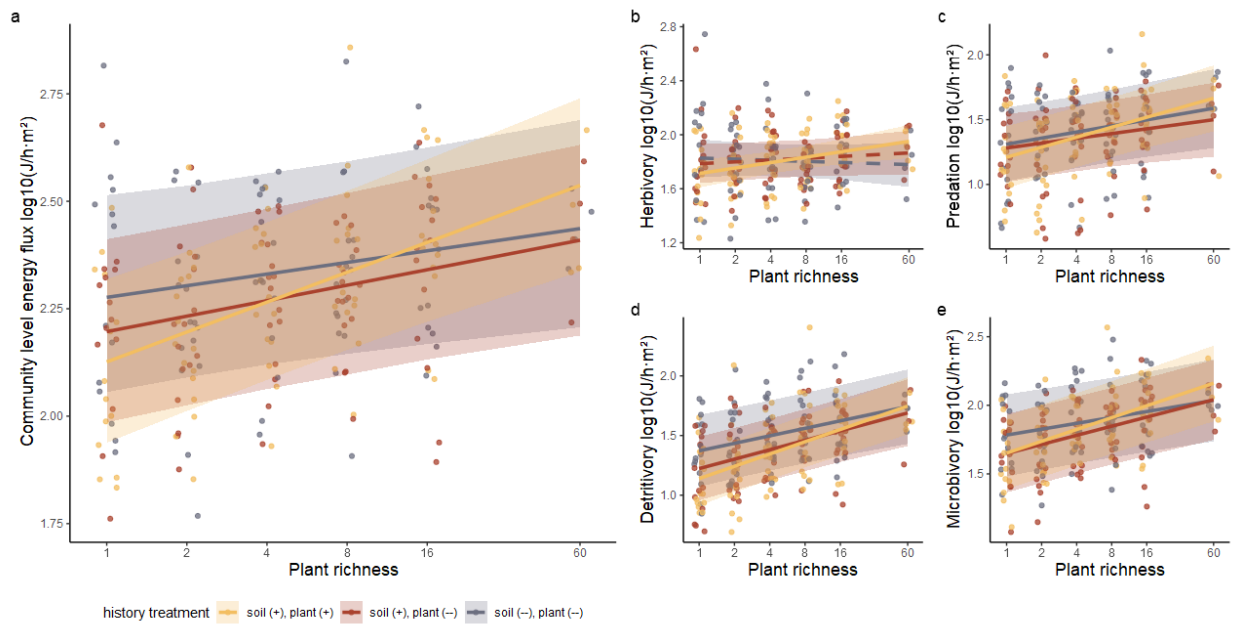
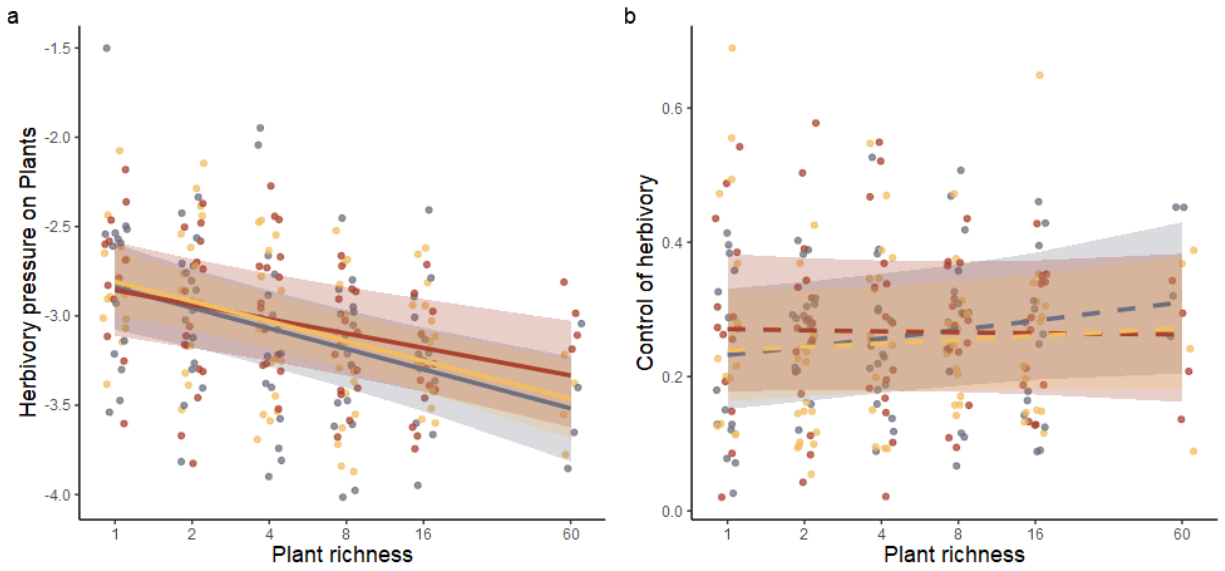


Figure 2



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599 **Figure 3**

Table S1. The initial interaction matrix, before considering traits, reflecting what the different taxa feed on, as reviewed in Potapov et al. (2022). Unless more detailed information was available, omnivores were assumed to feed equally from different resource channels (eg. roots, detritus, animal prey). Values shown here have been rounded to 2 significant digits

	Bacterivore.nematodes	Fungivore.nematodes	Herbivore.nematodes	Omnivore.nematodes	Predator.nematodes	Edaphic.Entomobryomorpha	Edaphic.Neelipleona	Edaphic.Poduromorpha	Epigeic.Entomobryomorpha	Epigeic.Poduromorpha	Epigeic.Symphyleona	Mesostigmata	Oribatida	Pauropoda	Prostigmata	Protura	Symphyla	Araneae	Chilopoda	Coleoptera	Diplopoda	Gastropoda	Hemiptera	Isopoda	Thysanoptera	Diptera.larvae
roots	0	0	1	0.25	0	0.33	0.33	0	0.25	0	0.25	0	0	0.33	0.25	0	0.33	0	0	0.25	0	0.1	1	0	0.5	0.1
detritus	0	0	0	0	0	0	0	0	0.25	0	0.25	0	0.25	0.33	0.25	0.1	0.33	0	0	0.25	0.75	0.3	0	0.33	0	0.3
bacteria	1	0	0	0.25	0	0.33	0.33	0.5	0.25	0.33	0.25	0	0.25	0	0	0	0	0	0	0	0.13	0.3	0	0.33	0	0
fungi	0	1	0	0.25	0	0.33	0.33	0.5	0.25	0.33	0.25	0	0.25	0.33	0.25	0.9	0	0	0	0.25	0.13	0.3	0	0.33	0.5	0.3
Bacterivore.nematodes	0	0	0	0.05	0.2	0	0	0	0	0.07	0	0.06	0.05	0	0.01	0	0.02	0	0	0	0	0	0	0	0	0.01
Fungivore.nematodes	0	0	0	0.05	0.2	0	0	0	0	0.07	0	0.06	0.05	0	0.01	0	0.02	0	0	0	0	0	0	0	0	0.01
Herbivore.nematodes	0	0	0	0.05	0.2	0	0	0	0	0.07	0	0.06	0.05	0	0.01	0	0.02	0	0	0	0	0	0	0	0	0.01
Omnivore.nematodes	0	0	0	0.05	0.2	0	0	0	0	0.07	0	0.06	0.05	0	0.01	0	0.02	0	0	0	0	0	0	0	0	0.01
Predator.nematodes	0	0	0	0.05	0.2	0	0	0	0	0.07	0	0.06	0.05	0	0.01	0	0.02	0	0	0	0	0	0	0	0	0.01
Edaphic.Entomobryomorpha	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Edaphic.Neelipleona	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Edaphic.Poduromorpha	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Epigeic.Entomobryomorpha	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Epigeic.Poduromorpha	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Epigeic.Symphyleona	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Mesostigmata	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Oribatida	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Pauropoda	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Prostigmata	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Protura	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Symphyla	0	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0.01	0	0.02	0.05	0.05	0.01	0	0	0	0	0	0.01
Araneae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0	0	0	0	0	0	0.01
Chilopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0.01
Coleoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.01	0	0	0	0	0	0.01
Diplopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.01	0	0	0	0	0	0.01
Gastropoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.01	0	0	0	0	0	0.01
Hemiptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.01	0	0	0	0	0	0.01
Isopoda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.01	0	0	0	0	0	0.01
Thysanoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.01	0	0	0	0	0	0.01
Diptera.larvae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.01	0	0	0	0	0	0.01

Table S2. The attributes of taxa that co-determine the relative strengths in the interaction matrix. “above”, “epi”, “hemi”, “eu” refer to the vertical stratification of a group. All attributes except body mass were taken from Potapov (2022)

taxon	Avg Mass (mg)	SD Mass	Agility	PhysicalProtection	Metabolites	above	epi	hemi	eu
Bacterivore nematodes	0.000197	0.002474	1	1	1	0	0	1	1
Fungivore nematodes	0.000133	0.000415	1	1	1	0	0	1	1
Herbivore nematodes	0.000157	0.000864	1	1	1	0	0	1	1
Omnivore nematodes	0.000649	0.016282	1	1	1	0	0	1	1
Predator nematodes	0.003057	0.004190	1	1	1	0	0	1	1
Edaphic Entomobryomorpha	0.018402	0.026293	0.7	1	1	0	0	1	0.5
Edaphic Neelipleona	0.001299	0.000682	0.7	1	1	0	0	1	0.5
Edaphic Poduromorpha	0.008425	0.00718	0.7	1	1	0	0	1	0.5
Epigeic Entomobryomorpha	0.032618	0.019112	0.7	1	1	0.5	1	0.5	0
Epigeic Poduromorpha	0.015901	0.014885	0.7	1	1	0.5	1	0.5	0
Epigeic Symphypleona	0.002524	0.002563	0.7	1	1	0.5	1	0.5	0
Mesostigmata	0.005589	0.008244	1	0.7	1	0	0	1	0.5
Oribatida	0.012428	0.012256	1	0.4	0.7	0	0	1	0.5
Paupoda	0.010055	0.006513	1	1	1	0	0	1	1
Prostigmata	0.002877	0.004196	1	0.7	1	0	0.5	1	0.5
Protura	0.012832	0.006904	1	1	1	0	0	1	1
Symphyla	0.115804	0.091635	1	1	0.4	0	0	1	1
Araneae	1.672674	4.982685	1	1	1	0.5	1	0.5	0
Chilopoda	2.95958	3.617553	1	1	1	0	0.5	1	0.5
Coleoptera	1.788838	2.929927	1	0.4	0.4	1	1	1	1
Diplopoda	4.970418	8.525162	1	0.4	0.7	0	1	1	0.5
Gastropoda	29.07547	51.57957	1	0.4	0.4	0.5	1	1	0.5
Hemiptera	0.804769	1.868784	0.7	0.7	0.7	0.5	1	0.5	0.5
Isopoda	16.31278	6.293062	1	0.4	1	0	1	0.5	0
Thysanoptera	0.13635	0.165533	1	1	1	0	1	0	0
Diptera larvae	0.249	0.0578	1	1	1	1	1	1	0

The use of body-mass information is described in Figure S1. The vectors Agility, PhysicalProtection and Metabolites down-weight the probability of an interaction with a given prey, in the presence of the relevant attribute. The vertical stratification vectors were used to construct a Bray-Curtis dissimilarity matrix, which reflects the probability of encounter between taxa based on their vertical stratification.

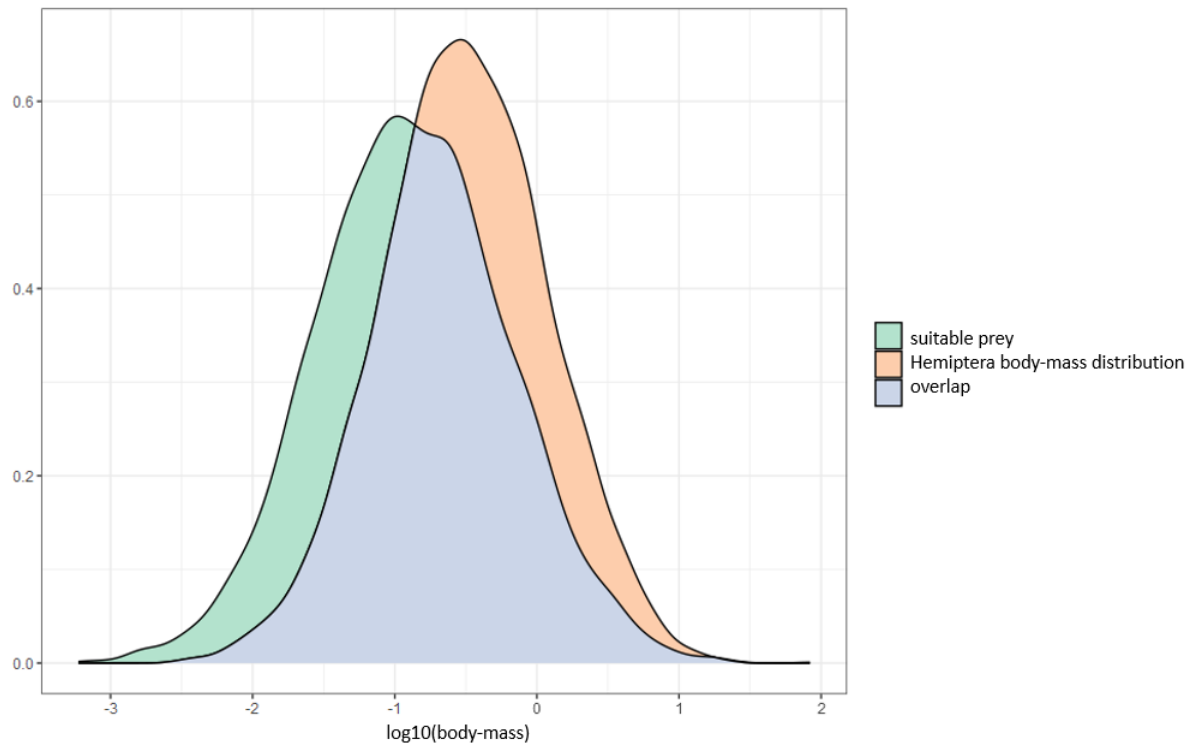


Figure S1 Schematic representation of the calculation of the probability of a predator consuming certain prey taxa based on body-mass, using Araneae and Hemiptera as an example. Suitable prey body-mass distribution was derived from the predator body-mass distribution assuming PPMR = $3.98 (10^{0.6})$. The overlap of the body-mass distribution of a potential prey taxon with the suitable prey distribution determines the probability of consuming that prey taxon.

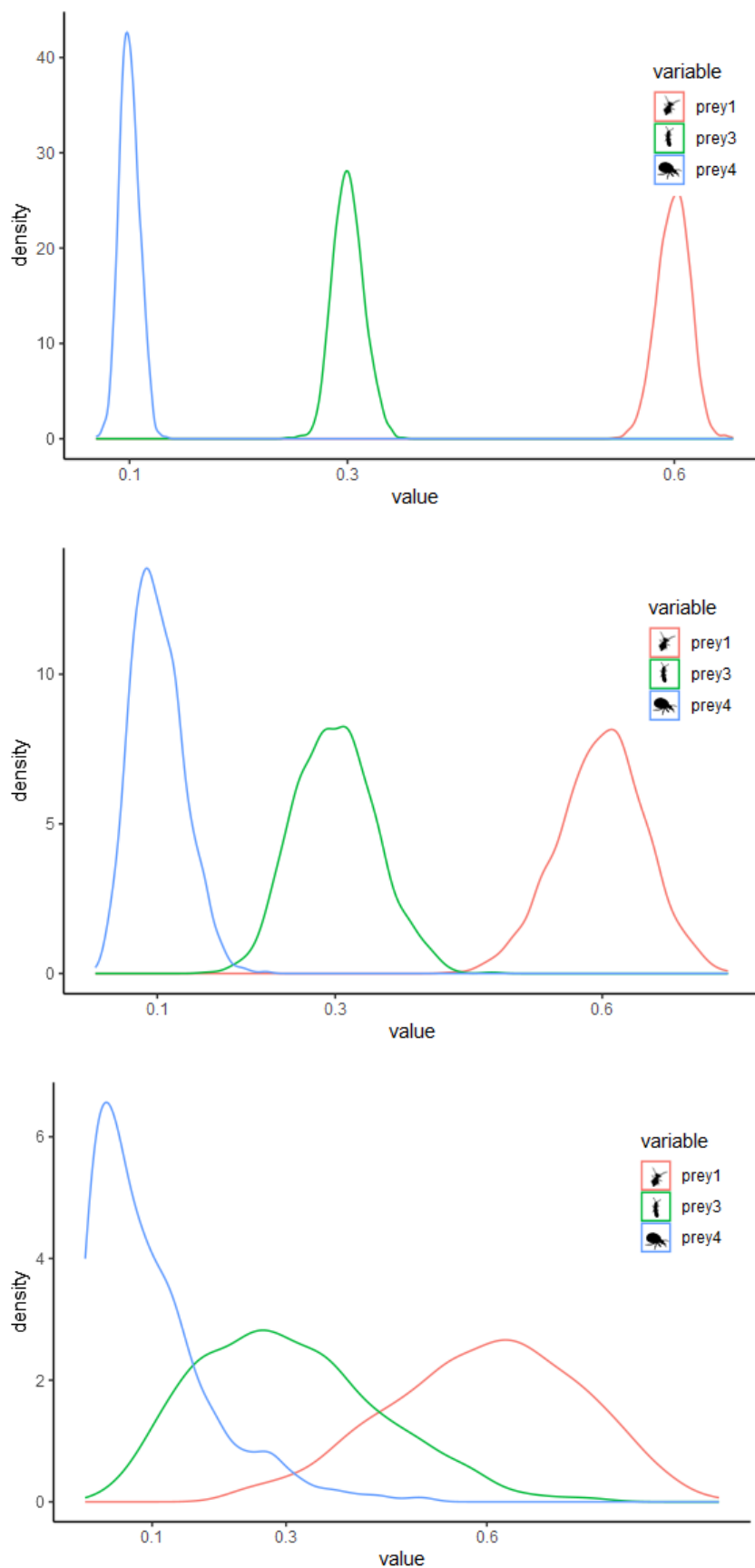


Figure S2 Example of low (top), intermediate (middle) and high (bottom) consumer diet uncertainty, for a hypothetical consumer with an expected diet composition of (0.1, 0.3, 0.6) of three prey taxa.

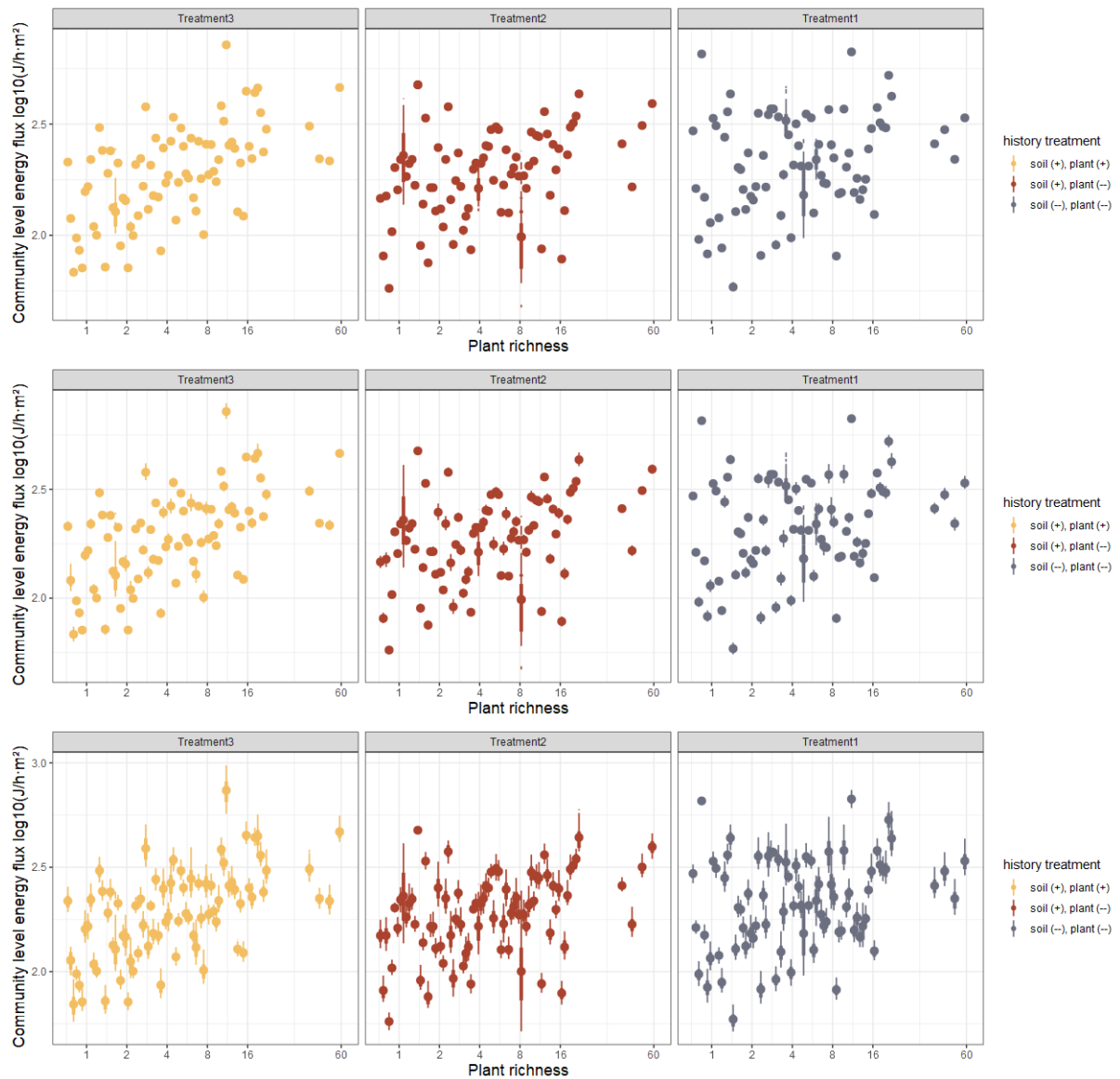


Figure S3 The effect of low (top), intermediate (middle) and high (bottom) consumer diet uncertainty on community level energy flux. The color scheme is the same as in the main figures. For a given level of diet uncertainty, some food-webs are more sensitive (variable) than others.

Food-webs exhibited varying sensitivity to diet uncertainty, in terms of the resulting flux uncertainty (Figure S3). However, incorporating diet uncertainty had negligible effects on model estimates (Figure S4). This indicates that the extent of flux uncertainty is not associated with variables of interest, but rather is randomly distributed in food-webs across the range of the dependent and the independent variables.

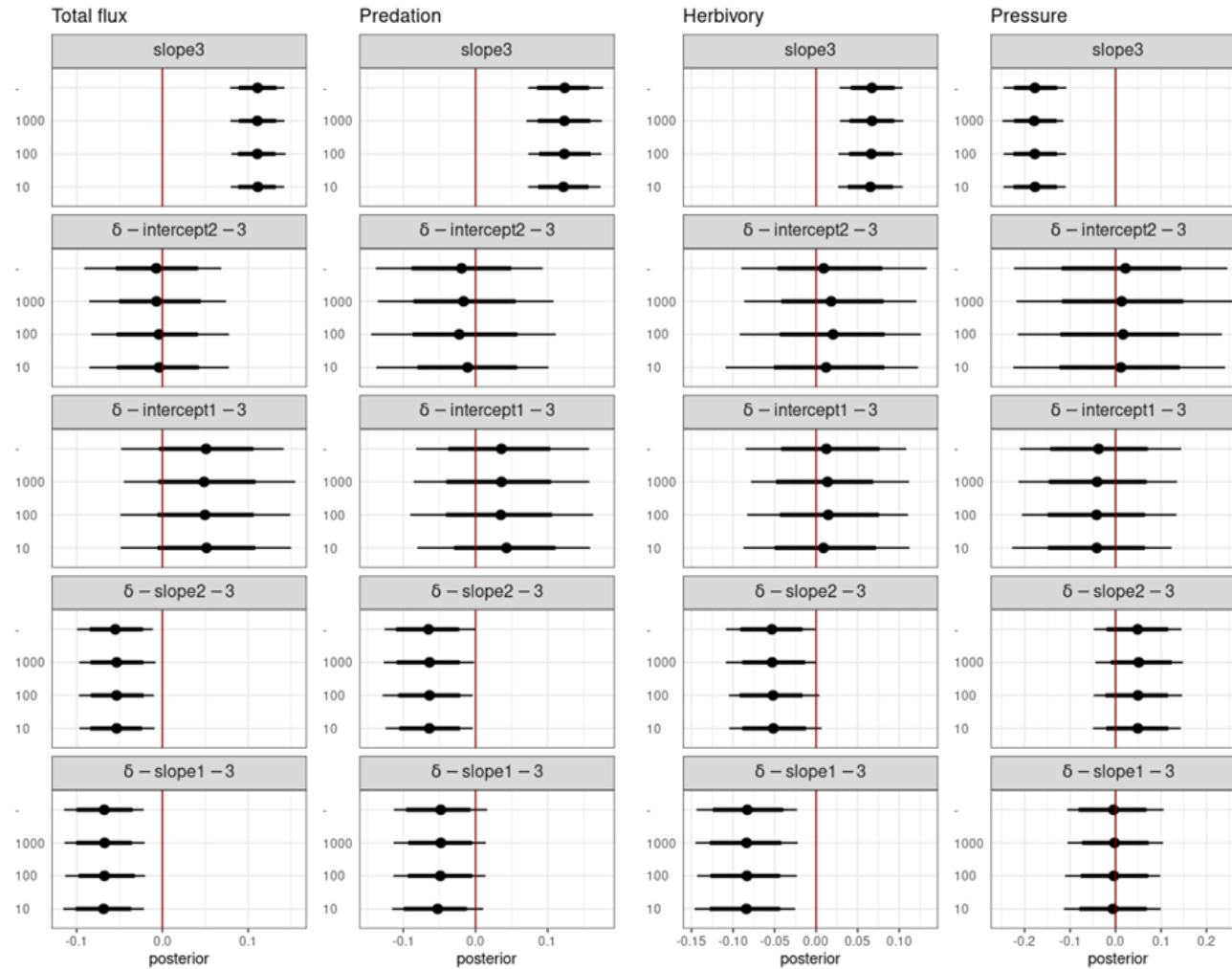


Figure S4 Model coefficients excluding diet uncertainty (-) and at low (1000), intermediate (100) and high (10) uncertainty. Each column corresponds to a model. Despite the effects of diet uncertainty on energy fluxes as shown in Figure S3, model coefficients remained practically unchanged. Points are mean estimates bound by 90% credible intervals.

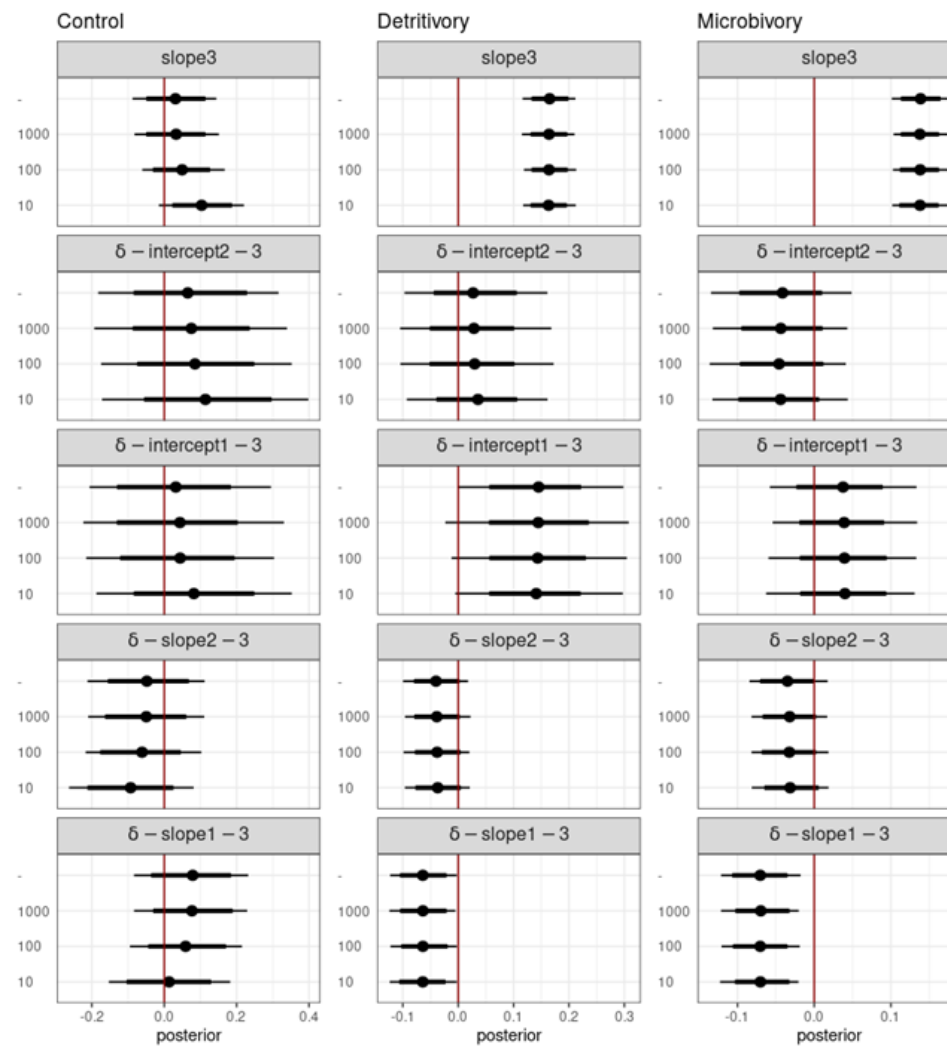


Figure S4 (continued)

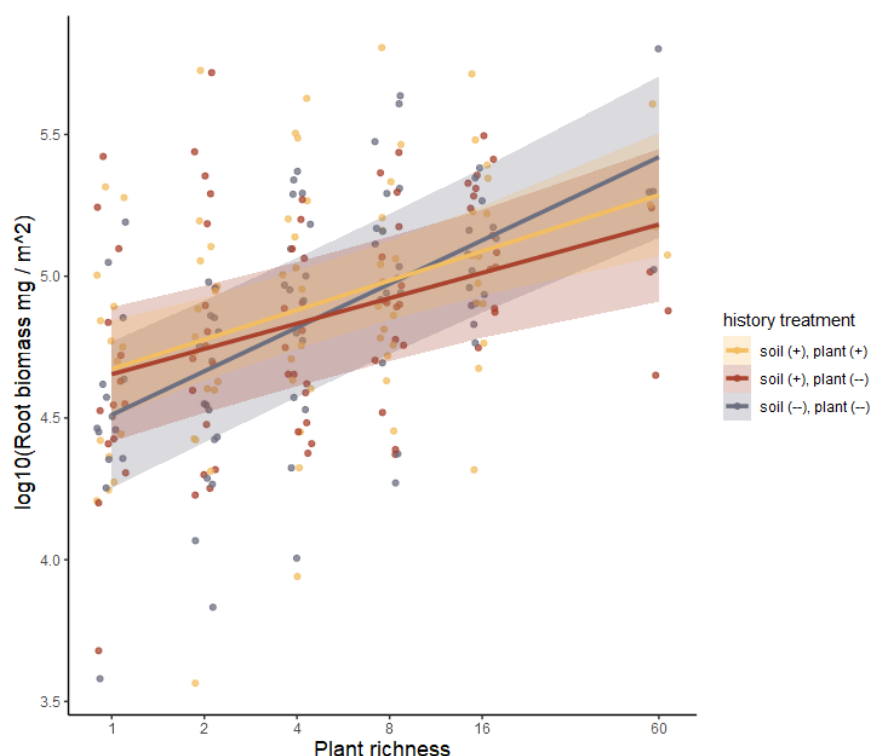


Figure S5 The relationship between plant richness and root biomass in the 0-5 cm depth soil layer. Lines show mean estimates for the average relationship bound by 90% uncertainty intervals.

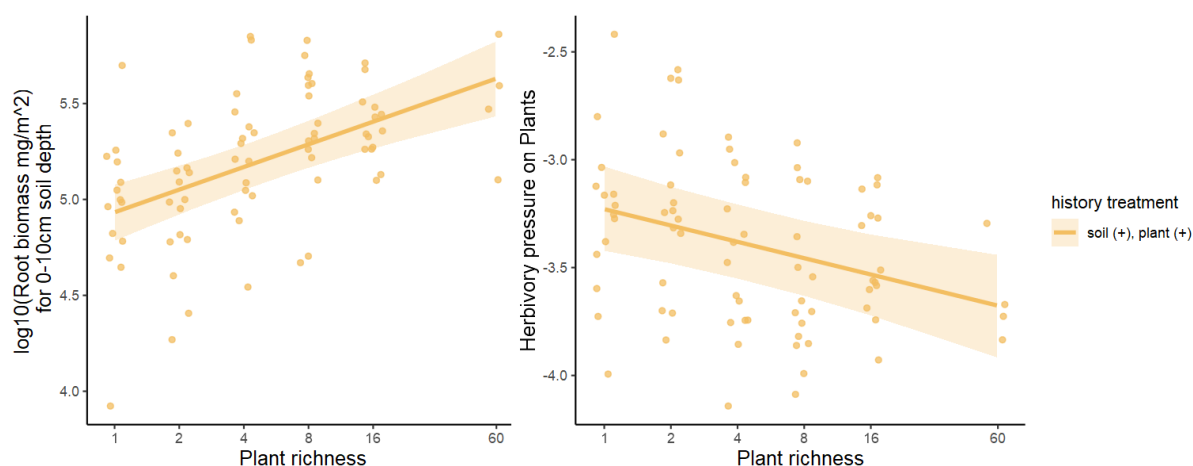


Figure S6 The relationship of plant richness and root biomass in the 0-10 cm depth soil layer in control subplots (left). The relationship between plant richness and herbivory pressure on plants, using the full 0-10 cm depth root biomass (right). Lines show mean estimates for the average relationship bound by 90% uncertainty intervals.

Root biomass in the 0-10 cm depth increased with plant richness in the control plots (Fig. S6, left). The relationship of plant richness and herbivory pressure in control plots is shallower when we incorporate the 0-10 cm root biomass but remains statistically clear (Fig. S6, right; mean slope [90% HPD] = -0.12 [-0.185, -0.05] compared to -0.18 [-0.25, -0.11]).

The mismatch of sampling depth for soil fauna (0-10 cm) and root biomass (0-5 cm) means that, in our main analysis, we are overestimating herbivory pressure in absolute terms. Additionally, communities with plant history may have more root biomass at lower depths compared to communities without plant history. Therefore this overestimation may be more pronounced in our control communities, which in turn might have obscured differences between control and history treatments.