

Shared community history strengthens plant diversity effects on belowground multitrophic functioning

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August 17, 2023

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.

1 **Journal name:** Ecology
2 **Manuscript type:** Article
3 **Manuscript title: Plant diversity effects on belowground multitrophic functioning strengthen**
4 **with time**

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20 **Open research statement:** The data will be made available online in the Jena Experiment database

21 (JExIS; <https://jexis.idiv.de>). The code necessary to reproduce the calculations of fluxes, the analyses and

22 figures is available on Github (https://github.com/amynang/DBEF_soil_foodwebs) and will be archived in

23 Zenodo.

24 **Keywords: a minimum of six and a maximum of 12 key words alphabetically**

25 belowground, community assembly, detritivory, food web, herbivory, predation, soil fauna

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33 suggests that the restructuring of biotic interactions in the process of a community's assembly
34 and the associated changes in function differ between species-rich and species-poor
35 communities. An important component of these changes is the feedback between plant and soil
36 community history. In this study, we examined the interactive effects of plant richness and
37 community history on the trophic functions of the soil fauna community. We hypothesized that
38 experimental removal of either soil or plant community history would diminish the positive
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40 communities. We tested this hypothesis in a long-term grassland biodiversity experiment by
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42 controls with ~20 years of plot specific community history). We found that the relationship
43 between plant richness and belowground multitrophic functionality is indeed stronger in
44 communities with shared plant and soil community history. Our findings indicate that
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46 plant species but also by preventing feedbacks that develop in the process of community
47 assembly.

48 **Introduction**

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

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

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

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

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

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

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

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

104 **Methods**

105 **Experimental field site**

106 The Jena Experiment was established in 2002 in the floodplain of the river Saale (Thuringia,
107 Germany, 50°55′ N, 11°35′ E; 130m above sea level) (Roscher et al. 2004). It is a long-term
108 biodiversity ecosystem functioning experiment, consisting of 80 grassland plots with maintained
109 plant species richness. Across the plots, sown species richness doubles from 1 to 16 species
110 (each level of richness is replicated 16 times except for 1- and 16-species plots that are replicated
111 14 times). Additionally, there are four plots sown with all 60 species which comprise the whole
112 species pool of the experiment. Plots are arranged in four blocks. Experimental species richness
113 is maintained by weeding three times per year. Plots are mown twice a year, consistent with
114 typical management practice in Central European extensively-used grasslands.

115 **The Δ BEF experiment**

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

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

122 **Sampling and data collection**

123 The sampling campaign took place between June 14 and 24 2021, shortly after the first plant
124 biomass harvest and at peak biological activity. From each subplot, we extracted one soil core of
125 20 cm Ø, one soil core of 5 cm Ø, and four cores of 2 cm Ø. The sampled depth was 10 cm for
126 all cores.

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

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

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

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

154 **Calculation of energy flux**

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

164 **Population level metabolic losses**

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

177 **The trophic interaction matrix**

178 We used information on the trophic relationships of the different soil fauna groups (as reviewed
179 in Potapov et al. (2022)) as well as traits that influence the strength of these interactions (Potapov
180 2022), combined with our data of the biomass and body mass distribution of the different taxa, to
181 estimate energy fluxes in the soil food-web (Barnes et al. 2018; Jochum et al. 2021; Potapov
182 2022). For the feeding type and body-mass distributions of the different nematode taxa we relied
183 on (Mulder and Vonk 2011) and Nemaplex (Ferris 1999). Collembola were grouped to
184 functional leagues according to Potapov et al. (2016).

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

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

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

219 **Community level energy flux**

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

225 **Below-ground herbivory pressure**

226 We calculated herbivory pressure as the sum of outflux of energy from plants to their consumers
227 (including omnivores) per mg of root biomass. Root biomass data were available for a 0-5 cm
228 depth across all experimental units (data for 5-10 cm were only available for the control
229 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

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

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

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

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

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

278 **Results**

279 **Community level energy flux**

280 Plant richness had a clear positive effect on community level flux, in control communities with
281 plant and soil history (mean slope [90% HPD] = 0.11 [0.08, 0.14], Fig. 2a). As expected, this
282 relationship was shallower in the case of the treatment communities lacking aspects of shared
283 history (with soil but not plant history: 0.06 [0.025, 0.09]; without soil or plant history: 0.04
284 [0.01, 0.08]). In both cases, the difference between the slope in control and that in treatment
285 communities was clear (-0.05 [-0.095, -0.01] and -0.07 [-0.115, -0.02], respectively, Fig. 2a).

286 **Individual trophic functions**

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

291 The effect of plant richness on predation was clearly positive across control and treatment
292 communities (with soil and plant history: 0.12 [0.07, 0.17]; with soil but not plant history: 0.06
293 [0.005, 0.11]; without soil or plant history: 0.075 [0.02, 0.13], fig.2c). The slope of the
294 relationship in the case of soil but no plant history was shallowest and clearly different from that

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

298 The effect of plant richness on detritivory was clearly positive across control and treatment
299 communities (with soil and plant history: 0.16 [0.12, 0.21]; with soil but not plant history: 0.13
300 [0.08, 0.17]; without soil or plant history 0.10 [0.05, 0.145], fig.2d). The slope was steeper across
301 communities with soil and plant history but this difference was only clear when compared to
302 communities without soil or plant history (-0.06 [-0.12, -0.005]). The effect of plant richness on
303 microbivory was also positive (with soil and plant history: 0.14 [0.10, 0.17]; with soil but not
304 plant history: 0.11 [0.07, 0.15]; without soil or plant history 0.07 [0.03, 0.11], fig.2e). Once
305 again, the slope was steeper across communities with soil and plant history compared to the two
306 treatments but this difference was only clear when compared to communities without soil or
307 plant history (-0.07 [-0.12, -0.02]).

308 **Herbivory pressure on plants and control of herbivory by predation**

309 Plant-rich communities experienced reduced herbivory pressure (with soil and plant history: -
310 0.18 [-0.25, -0.11]; with soil but not plant history: -0.13 [-0.20, -0.06]; without soil or plant
311 history -0.18 [-0.27, -0.10], fig.3a). There were no clear differences in slope between control and
312 treatments for any pairwise combination. In a sensitivity analysis, this negative relationship
313 between herbivory pressure and plant species richness was robust to increasing root
314 measurement depth (Fig. S6). Finally, the relationship of herbivory control by predators with
315 plant richness was positive or negative but always unclear across control and treatment
316 communities (with soil and plant history: 0.05 [-0.07, 0.16]; with soil but not plant history: -0.01
317 [-0.14, 0.12]; without soil or plant history: 0.11 [-0.01, 0.23]).

318 **Discussion**

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

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

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

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

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

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

386 Our findings indicate that the effects of biodiversity on belowground ecosystem functioning are
387 dependent on the shared history of producers and consumers in the community, supporting the
388 idea that a combination of niche differentiation with turnover processes are reshaping this
389 relationship over time. This suggests that BEF relationships are context dependent, varying not
390 only across space (Thompson et al. 2018), but also in time. In natural ecosystems, the trajectory
391 of community change over time will likely be influenced by factors that determine the potential
392 for plant niche differentiation but also those regulating animal community assembly, such as
393 latitudinal or environmental gradients of regional species richness or landscape characteristics
394 that affect accessibility through dispersal (Ye and Wang 2023). Therefore, to understand how
395 BEF relationships develop over time, future research should traverse the temporal and spatial
396 dimension, examining how meta-community processes shape local dynamics (Amarasekare
397 2008).

398 **Acknowledgements**

399 We thank everyone involved in the maintenance of the field site of the Jena Experiment,
400 particularly the gardeners, technicians, and student helpers. We are grateful to David Schulz,
401 Felix Zeh and Carla Silvar for their assistance in the field and lab, Anja Zeuner and Carla
402 Klusmann for sample processing and Susanne Böning-Klein and Chiara Epifanio for soil fauna
403 sorting. Angelos Amyntas was supported by the Jena Experiment Research Unit, funded by the
404 German Research Foundation (DFG, BR 2315/23-1, FOR 5000).

405 **Conflict of Interest Statement:** The authors declare that they have no conflicts of interest.

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

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

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

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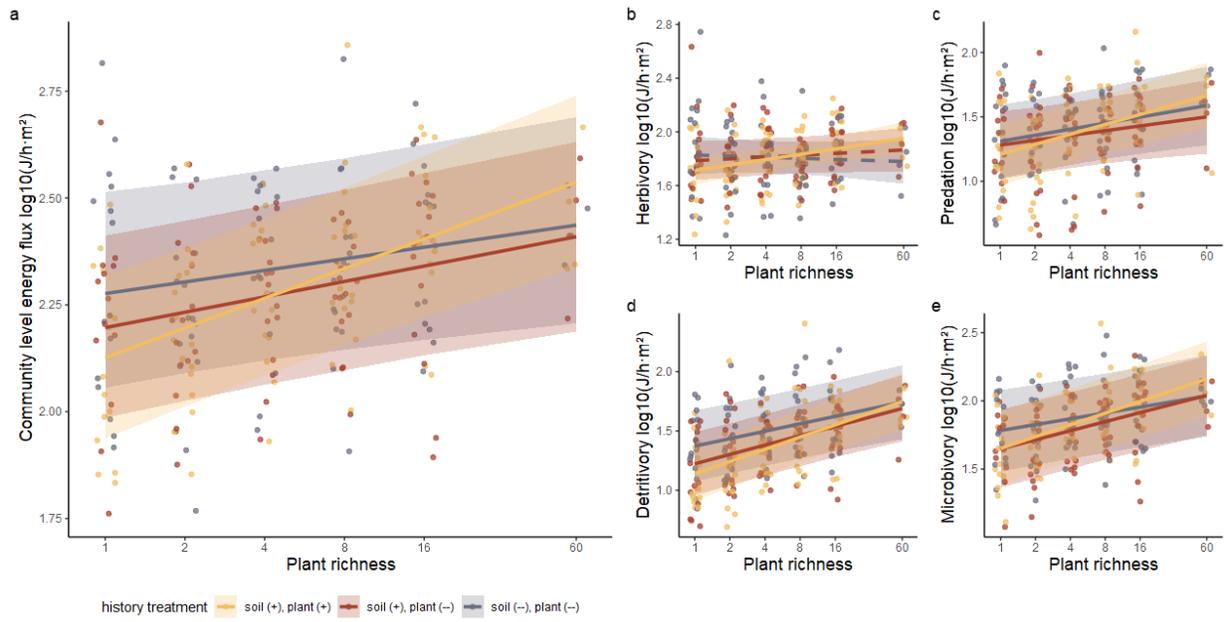
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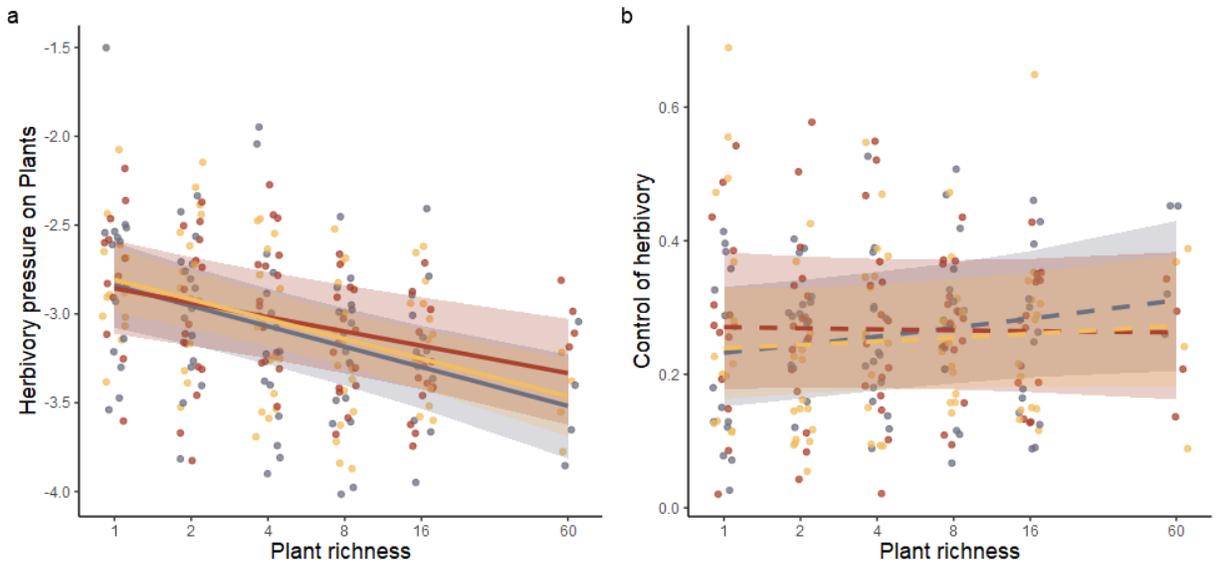
593 **Figure 2**

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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	0.13	0.3	0	0.33	0	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	0.05	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.

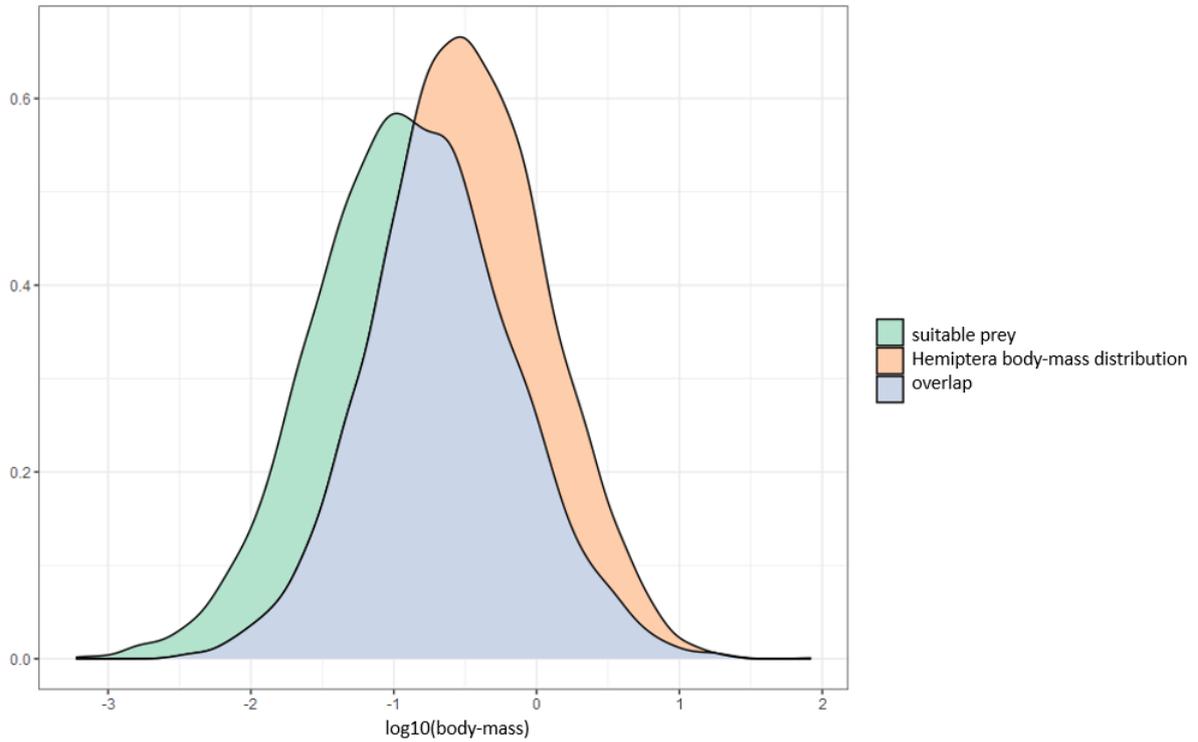


Figure S1 Schematic representation of the calculation of the probability of a predator consuming certain prey taxa based on body-mass, using Araneae and Hemiptera as an example. Suitable prey body-mass distribution was derived from the predator body-mass distribution assuming PPMR = 3.98 ($10^{0.6}$).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

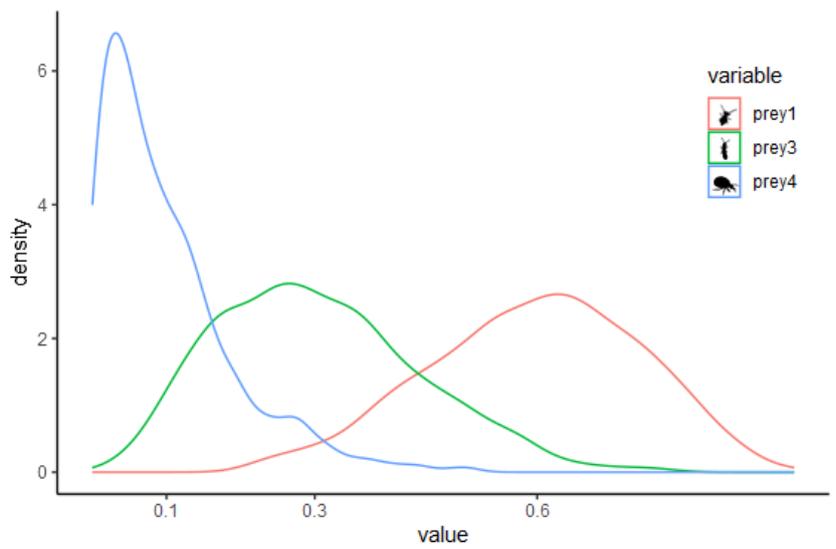
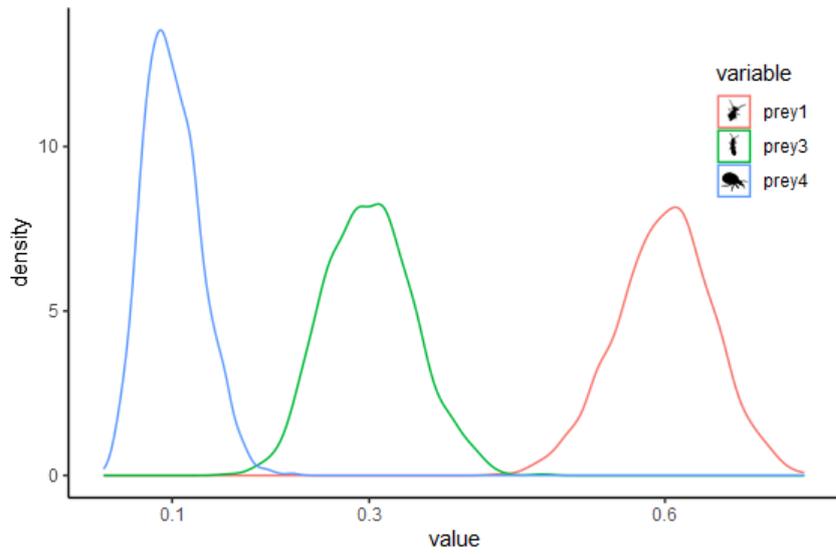
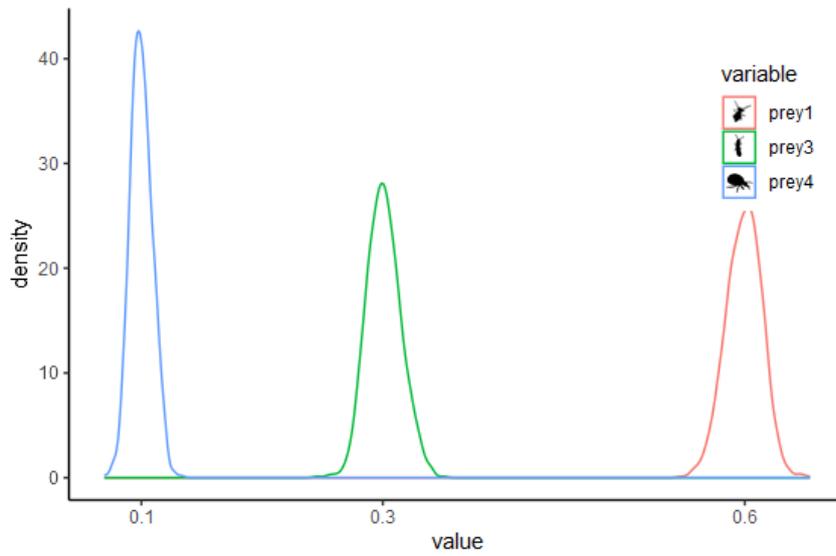


Figure S2 Example of low (top), intermediate (middle) and high (bottom) consumer diet uncertainty, for a hypothetical consumer with an expected diet composition of (0.1, 0.3, 0.6) of three prey taxa.

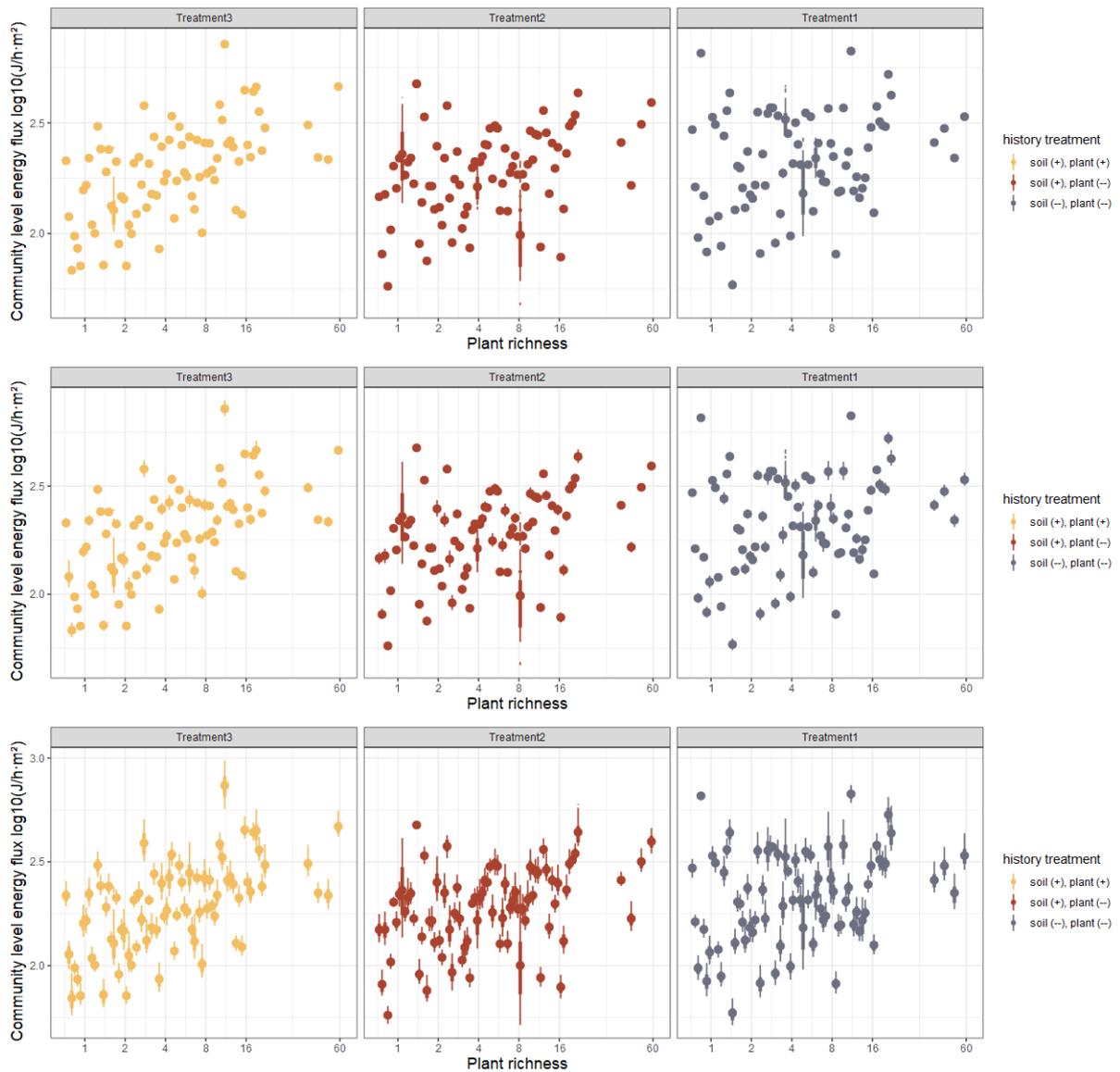


Figure S3 The effect of low (top), intermediate (middle) and high (bottom) consumer diet uncertainty on community level energy flux. The color scheme is the same as in the main figures. For a given level of diet uncertainty, some food-webs are more sensitive (variable) than others.

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.

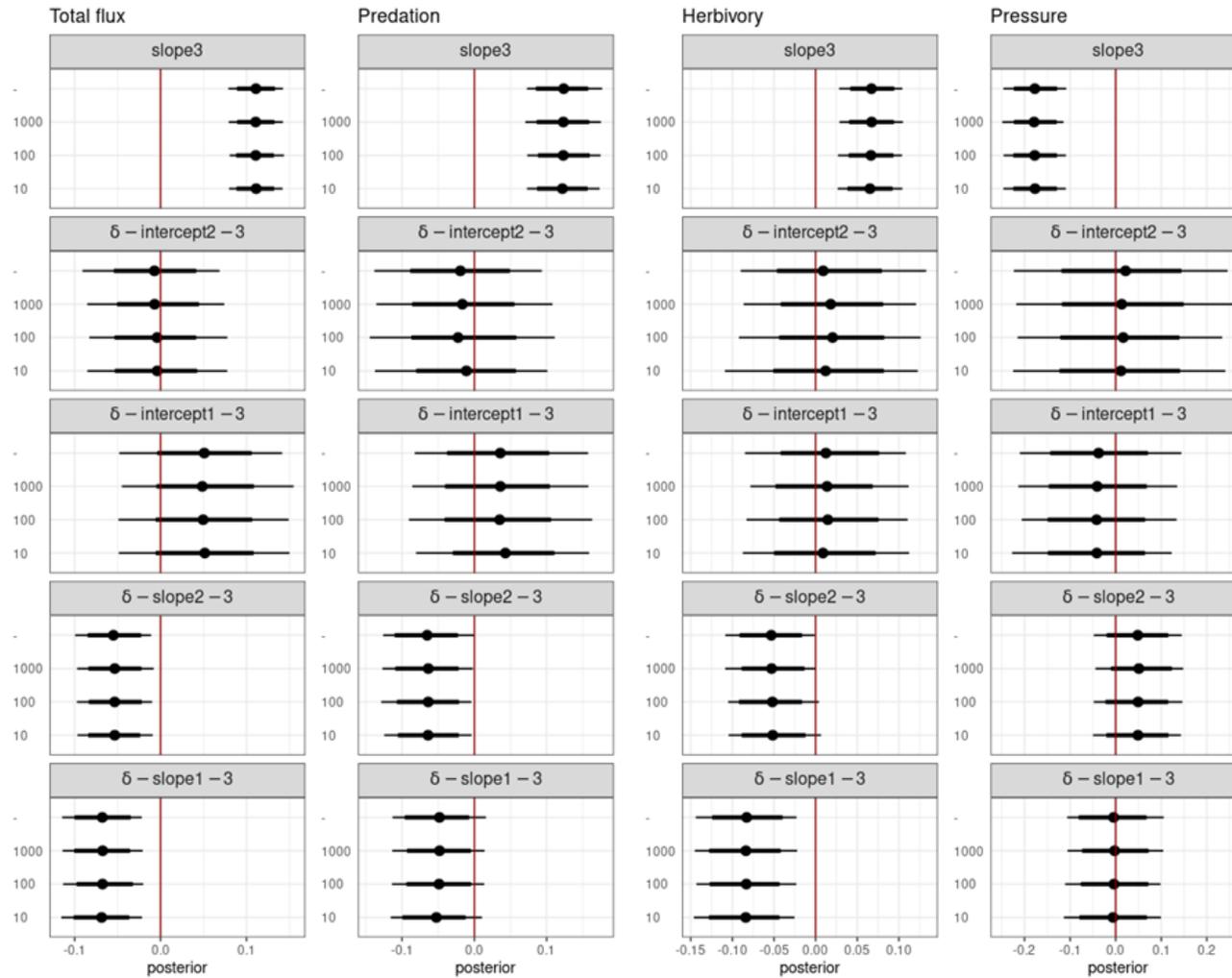


Figure S4 Model coefficients excluding diet uncertainty (-) and at low (1000), intermediate (100) and high (10) uncertainty. Each column corresponds to a model. Despite the effects of diet uncertainty on energy fluxes as shown in Figure S3, model coefficients remained practically unchanged. Points are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

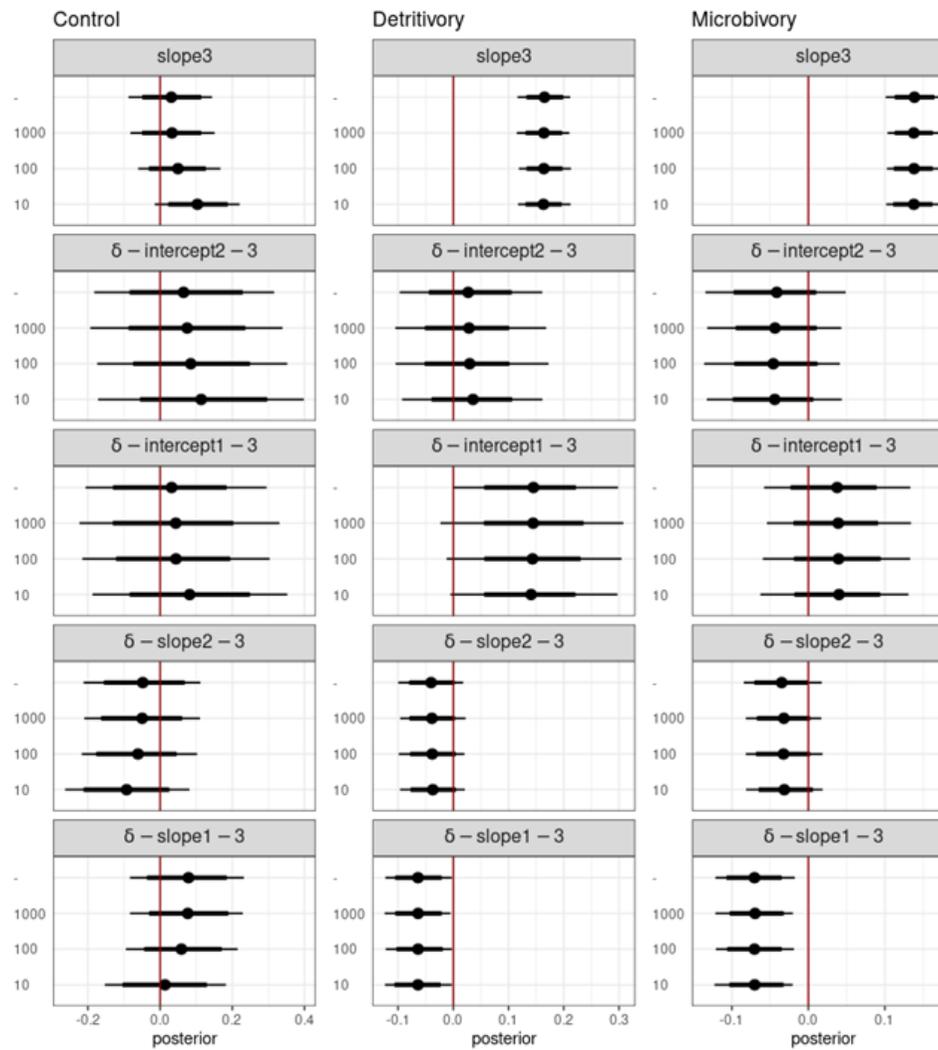


Figure S4 (continued)

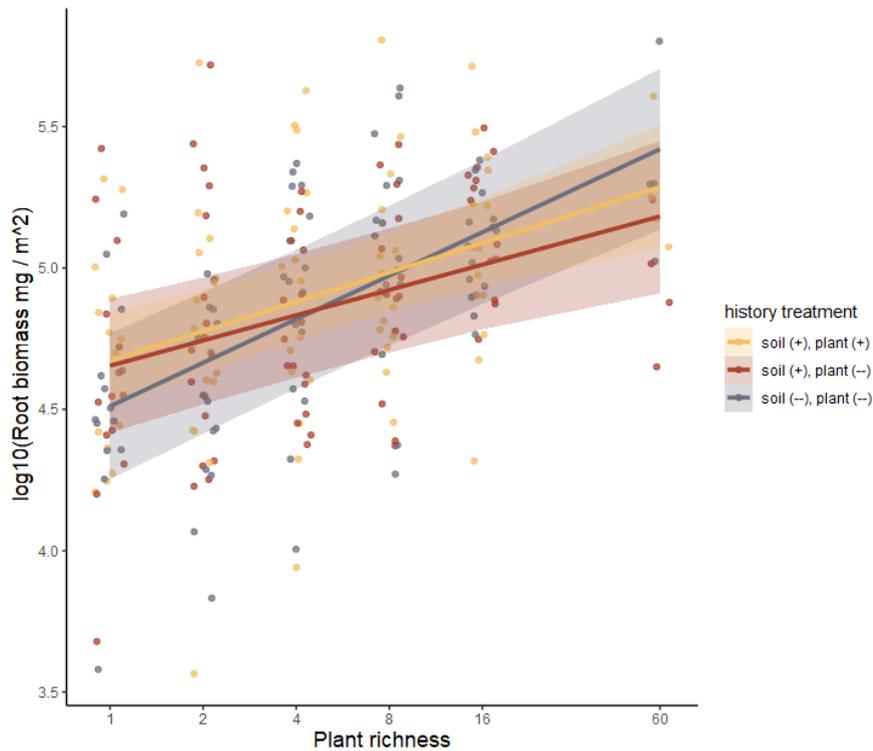


Figure S5 The relationship between plant richness and root biomass in the 0-5 cm depth soil layer. Lines show mean estimates for the average relationship bound by 90% uncertainty intervals.

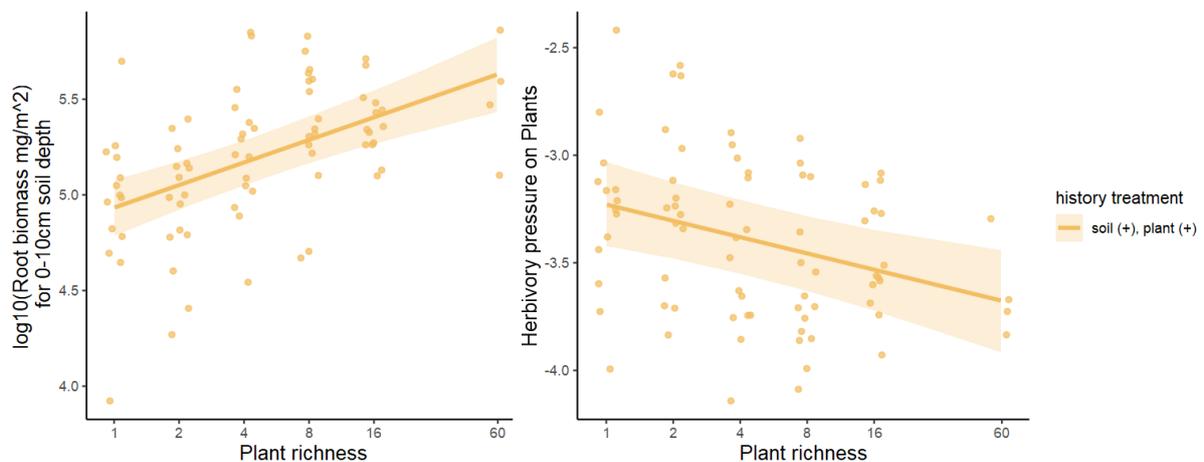


Figure S6 The relationship of plant richness and root biomass in the 0-10 cm depth soil layer in control subplots (left). The relationship between plant richness and herbivory pressure on plants, using the full 0-10 cm depth root biomass (right). Lines show mean estimates for the average relationship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