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1 **Functional collembolan assemblages induce different plant responses in *Lolium perenne***

2

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18

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20

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24 discussions.

25

26 **Abstract**

27

28 Background and aims

29 Interactions between functional groups of soil fauna and plants are poorly explored although they drive
30 functional processes such as nutrient availability and therefore plant performance. Here, we investigated
31 the separated and combined effects of two collembolan functional groups on soil properties and growth of
32 *Lolium perenne*, a typical grass species from temperate grasslands.

33

34 Methods

35 Under microcosm conditions, we established four treatments based on the presence and combination of two
36 collembolan functional groups: 1) control without Collembola; 2) epedaphic species; 3) euedaphic species;
37 4) epedaphic+euedaphic species. After five months of experiment, we measured the effect of those
38 treatments on both nutritional and morphological variables of *L. perenne* and on soil properties.

39

40 Results

41 Collembolan presence stimulated plant performance. Individuals of *L. perenne* growing with euedaphic
42 species presented higher numbers of leaves and nutrient contents compared with individuals growing with
43 epedaphic species. Further, the combination of both collembolan functional groups enhanced plant
44 performance and soil nutrient availability, demonstrating that a functionally diversified soil fauna
45 assemblage cause overyielding of ecological processes.

46

47 Conclusion

48 Our results provide evidences of complementarity interactions between different functional groups of soil
49 fauna causing overyielding of primary production.

50

51 **Keywords**

52 Functional complementarity; facilitation, plant performance; springtails; soil fauna; biotic interaction

53

54 **Introduction**

55

56 It is acknowledged that soil decomposers at the basis of “brown food webs” play an important role
57 in regulating different ecosystem functionalities, i.e. organic matter decomposition, nutrient cycling, carbon
58 storage, and net primary production (Eisenhauer et al. 2018). Although soil microbes have a direct effect
59 on nutrient mineralization by degrading complex organic compounds such as cellulose and lignin, their
60 composition, structure and activity are often influenced by the presence of animal decomposers such as
61 Collembola and earthworms (Cragg and Bardgett 2001; Ngosong et al. 2004; Eisenhauer et al. 2010;
62 Coulibaly et al. 2019). By feeding on organic residues at different decomposition stages (Endlweber et al.
63 2009; Chahartaghi et al. 2005) and/or a wide range of soil microbes (Tordoff et al. 2008; Lenoir et al. 2006),
64 soil animal decomposer activity may translate to plant performance by influencing the rates of

65 mineralization and nutrient availability for plants (Scheu et al. 1999; Bardgett and Chan 1999; Partsch et
66 al. 2006; Hedde et al. 2010; Eisenhauer et al. 2011, 2018; Forey et al. 2015).

67 Results of several experiments have reported that plants growing with decomposers present higher
68 shoot biomass and foliar nutrient content due to the enhanced soil fertility and nutrient uptake (Partsch et
69 al. 2006; Schütz et al. 2008; Wagg et al. 2014; Forey et al. 2015). In parallel, complementary works reported
70 that the level of diversity and functional dissimilarity within a given assemblage of soil animal decomposers
71 might determine the magnitude of ecological processes (Heemsbergen et al. 2004; Eisenhauer et al. 2011).
72 For instance, Partsch et al. (2006) noticed that root biomass decreased in the presence of either Collembola
73 or earthworms but increased when both organisms were present. Likewise, using three different
74 collembolan species (each of them belonging to a different functional group), Eisenhauer et al. (2011)
75 observed that shoot and root biomasses were significantly higher in forb communities containing three
76 collembolan species than in those containing one or two species. In this last case, despite the authors were
77 not able to decipher the effect of species identity from the effect of functional group, they suggested that
78 the positive effect of collembolan richness on plant growth was due to complementary interaction among
79 the three species or functional groups. Complementarity occurs when the presence of some species improve
80 resource availability or environmental conditions for other species, also called facilitation (Schmid et al.
81 2008; Hedde et al. 2010; Guenay et al. 2013), or when species share resources, resulting in niche
82 partitioning (Finke and Snyder 2008; Hooper et al. 2005; Brady et al. 2002). Therefore, complementarity
83 is thought to be the primary mechanism that may account for positive patterns through greater efficiency
84 in resource use, leading to the phenomenon of overyielding (Hector et al. 2002; Loreau et al. 2002), that
85 represents an increase of ecosystem productivity (Isbell et al., 2015; Clark et al., 2012; Díaz and Cabido,
86 2001; Loreau and Hector, 2001). Overyielding has been widely demonstrated within plant communities
87 through manipulation of their diversity in experiments focusing on plant productivity (Schmid et al. 2008;
88 Gross et al. 2007; Hector et al. 2002) or litter decomposition efficiency (Gartner and Cardon 2004; Santonja
89 et al. 2015). But, to our knowledge, the effects of different functional groups of soil organisms alone or in
90 combination upon soil functioning and plant growth are still largely unexplored. This is especially true
91 regarding the community effects, as most of the studies previously described were done at the species level
92 (i.e. one species per functional group). By focusing on soil Collembola, one of the major decomposer
93 groups in the soil, strongly interacting with the microbial component (Coulibaly et al. 2019), we wanted to
94 address this gap of knowledge by using a natural community approach (i.e. working with natural
95 assemblages of several species).

96 Collembolan species are differentiated according to their vertical distribution, food preference and
97 bio-demographic strategies (i.e. r or K strategy) (Chauvat et al. 2014; Chahartaghi et al. 2005; Petersen
98 2002; Hopkin 1997), which enable different functional roles in the ecosystem. Epedaphic species are
99 surface dweller dominated by strongly pigmented species with large body size and biomass, well-developed
100 eyes and appendages (i.e. furca, antennae, legs). They have a high metabolic activity and consume highly
101 palatable food substrates like pollen or algae (Petersen 2002). According to Rusek (1998), epedaphic
102 species tend to stimulate microbial colonization of fresh litter, speeding up decomposition rates, but with
103 the risk of nutrients immobilization in the microbial loop. Furthermore, Coulibaly et al. (2019) showed that
104 epedaphic Collembola mainly relates to Gram-positive bacteria. In contrast, the euedaphic group is

105 dominated by species with small body size and biomass, colorless and with reduced appendages. Those are
106 deep-living species that consume low-quality food and have a low metabolic activity. Unlike epedaphic
107 species, several euedaphic species were shown to increase mineralization processes into the soil and to
108 affect root nutrient uptake by regulating microbial activity within the rhizosphere (Petersen, 2002). They
109 rather stimulate Gram-negative bacteria (Coulibaly et al. 2019). Finally, the hemiedaphic group includes
110 species sharing intermediate characteristics. In this work, we aim to evaluate the effects of natural
111 assemblages of epedaphic and euedaphic Collembola, alone or in combination, on plant and soil
112 compartments. We addressed the following hypotheses: i) collembolan presence stimulates plant
113 performance through an increase in nutrient mineralization and nutrient availability; ii) euedaphic
114 Collembola have a more positive effect on plants compared with the epedaphic group because they are
115 directly linked to increases in soil nutrient mineralization by stimulating microbial activity in the
116 rhizosphere; iii) complementarity interaction through niche partitioning takes place between epedaphic and
117 euedaphic Collembola due to their functional dissimilarity, resulting in a higher plant productivity (i.e.
118 overyielding).

119

120 **Material and methods**

121

122 Experimental set-up

123 The experiment was carried out under microcosm conditions using soil and Collembola collected
124 at a depth of 0-10 cm from a native grassland site located on Yvetot (49°37'04.00''N, 0°45'18.76''E),
125 Lycée Agricole d'Enseignement Général et Technique Agricole d'Yvetot (Seine-Maritime, Haute-
126 Normandie), France. The soil was classified as Neoluvisol-Luvisol (French Classification; INRA 1998),
127 characterized by a pH water of 6.1 and a particle-size distribution of 200 g sand, 650 g silt and 150 g clay
128 per kg.

129 The microcosms were constructed by filling plastic flowerpots of 250 mL with 150 g of substrate
130 that consisted of a mixture of defaunated soil (sieved through a 5 mm mesh) with one centimeter of sand at
131 the bottom for drainage. The soil was defaunated by autoclaving (twice at 105 °C for 15 min every 48 h).
132 After the autoclaving, the soil was dried at 105 °C, sieved at 2 mm and then placed above the sand.

133 We used a microbial suspension (fresh soil + physiological solution - 0.85% NaCl in the
134 proportion of 4:1) to adjust all microcosms to 70% water holding capacity and to re-establish the microbial
135 community. Fifteen days after microbial inoculation, a single seedling of *Lolium perenne* (L.), a typical
136 and dominant forage grass species from temperate grasslands, was transplanted into each microcosm and
137 then we inoculated Collembola.

138 In this study, we focused our attention on two highly contrasted Collembola functional groups:
139 epedaphic (Ep) and euedaphic (Eu) species. Collembolan communities of each functional group were taken
140 from soil monoliths which were extracted using a Berlese-Tullgren funnel during 7 days. Epedaphic species
141 were extracted from litter layer and soil surface (0 to 1 cm depth) and euedaphic species were obtained
142 from soil subsurface (4 to 6 cm depth). To collect living collembola, we used the same protocol as described
143 in Coulibaly et al. (2019). We placed pots filled with moist plaster under the funnels. Once extracted,
144 inoculation of Collembola into the microcosms to establish the different treatments was done with help of

145 homemade pooters. To control inoculation of the right functional group (epedaphic or euedaphic) into the
146 right treatment, Collembola were sorted out under binocular before being transferred with the pooters.
147 Under the binocular, we used three morphological criteria to distinguish the two functional groups, namely
148 pigmentation, ocelli, and jump organ: the furca. Individuals were considered as euedaphic if they were not
149 pigmented, had no ocelli and no furca observable at the binocular. Individuals strongly pigmented, with a
150 large patch of ocelli and a long furca were categorized into epedaphic species. Individuals that did not share
151 these criteria were left out. Based on this protocol, we worked at community level since we extracted an
152 entire community from soil for each group and we established four treatments: C (control without
153 Collembola); Ep (only epedaphic species); Eu (only euedaphic species); and Ep + Eu (both collembolan
154 functional groups). Fifteen replicates per treatment were considered for a total of 60 microcosms. For more
155 details, see Coulibaly et al. (2019). Empty cylinders of 6 cm diameter and of 6 cm height that fitted on top
156 of the soil (one cylinder per microcosm) were used to avoid escape of collembolan species.

157 Before beginning of the experiment, collembolan assemblages were characterized in each
158 treatment (Supplementary Table S1). Dominant species in the epedaphic community were *Isotomorus*
159 *prasinus*, *Lepidocyrtus cyaneus* and *Desoria violacea*. The euedaphic community was mainly composed
160 by *Isotomiella minor*, *Cryptopygus sp.*, *Mesophorura yosii*, and *Protaphorura armata*.

161 After collembolan inoculation, microcosms were incubated during 5 months in climate-controlled
162 chambers with a constant 20 °C temperature, a 16 h: 8 h light: dark photoperiod, and a light intensity of
163 5000 lux. Microcosms were watered with demineralized water every 3rd day to compensate for
164 evapotranspiration and soil moisture was adjusted by weighing the microcosms. At the end of the
165 experiment, functional assemblages of collembolan communities were maintained (Supplementary Table
166 S1).

167 168 *Measurement of ecological processes*

169 Collectively, all variables related to plant and soil were interpreted as measurements of ecological
170 processes such as organic matter decomposition, nutrient mineralization, soil nutrient turnover and
171 consequently plant growth and primary production.

172 At the end of the experiment (5 months), shoot traits were measured on all plant individuals. The
173 total numbers of replicates per treatment changed during the experiment, since some plant individuals were
174 lost. Thus, the number of replicates (n) per treatment was: Control (n = 13), Ep (n = 11), Eu (n = 11), and
175 Ep+Eu (n = 12). Root traits were only measured on five randomly selected individuals per treatment (n =
176 5) in order to leave intact soil replicates for further soil measurements. Number of leaves and maximum
177 height were determined before harvest on all *L. perenne* individuals. Subsequently, plants were harvested
178 and carefully washed to measure different morphological and chemical variables. Shoot was cut at the soil
179 surface and was dried at 65 °C for 48 h to obtain shoot dry biomass. Fresh root volume was measured using
180 a graduated cylinder and then roots were dried at 65 °C for 48 h to obtain root dry biomass. Each shoot
181 sample was powdered in order to measure carbon (C) and nitrogen (N) content by gas chromatography
182 using a CHN pyrolysis micro-analyzer (Flash 2000 Series, CHNS/O Analyser Thermo Scientific, France)
183 and phosphorus (P) and sulphur (S) content using an atomic absorption spectrophotometer (AAS, ICE 3000
184 SERIES, Thermo Scientific, China).

185 Soil chemical variables were quantified on six randomly selected samples per treatment (n = 6).
186 The soil was sieved through a 2 mm mesh to remove large roots and stored at 4 °C until further processing.
187 Dissolved organic carbon and mineral nitrogen (N-NO₃⁻ and N-NH₄⁺) were extracted using 0.25 M K₂SO₄.
188 For that, 20 g of sieved soil (2 mm) were shaken for 1 h in a solution of a 0.25 M K₂SO₄, and then filtered
189 through a Whatman 42 filter. Concentrations of dissolved organic carbon were measured by gas
190 chromatography using a Thermo scientific Flash 2000 CHN S/O analyzer. Concentrations of N-NO₃⁻ and
191 N-NH₄⁺ were determined colorimetrically (Sequential analyser Gallery, Thermo scientific).

192 A HCl- HNO₃ digestion procedure followed by an analysis of the digested solution using atomic
193 absorption spectrophotometry (AAS, ICE 3000 SERIES, Thermo Scientific, China) was employed to
194 determine total phosphorus (P) and sulfur (S) concentrations in soil samples. Soil pH in water (pH_{H2O}) was
195 determined following ISO 10390.

196

197 *Data analyses*

198 The effects of collembolan treatments on plant and soil variables were evaluated by analysis of
199 variance (ANOVA) with permutation tests. *P*-values were determined using 10,000 permutations
200 (Anderson 2001). Tests were chosen since data are non-parametric and do not assume normally distributed
201 errors. Post-hoc *t*-statistic tests are used to allow pairwise comparisons between all pairs of treatments
202 (Anderson, 2001). To explore the interaction between Ep and Eu treatments, we first performed two-way
203 ANOVAs with epedaphic or euedaphic Collembola as two independent factors. Then, to identify if
204 complementarity interaction occurs between Ep and Eu on ecological processes, we firstly calculated a
205 Relative Effect Index (REI) on the different measured soil and plant variables: $REI = (X_T - X_C) / X_C$, where
206 X_T corresponds to the value of a treatment including collembolan species (i.e. Ep, Eu, or Ep+Eu treatments),
207 and X_C corresponds to the mean value of the control treatment (i.e. without Collembola). Then, we
208 compared the REI values observed in the treatment including the two collembolan functional groups (i.e.
209 Ep+Eu) with expected values based on the two treatments Ep and Eu. This Combined Functional Group
210 Effect (CFGE) was calculated according to the formula: Observed REI – Expected REI, where the
211 Observed REI value corresponds to the REI of the combined treatment (Ep + Eu), while Expected REI
212 corresponds to the additive value of REI for Ep and Eu. This CFGE could be additive (no significant
213 difference between observed and expected values), synergistic (higher observed than expected values)
214 causing overyielding, or antagonistic (lower observed than expected values) causing underyielding effects
215 on plant and soil properties. Based on literature, additive effects will indicate niche partitioning, most
216 probably for spatial resources; positive effects indicate facilitative interactions for resource use, while
217 negative effects will indicate competitive interactions for resource use (Loreau and Hector 2001; Hedde et
218 al. 2010). We performed two sample-paired tests (*t* test) to compare expected REI (sum of single functional
219 groups) and observed REI (Ep+Eu) for each response variable of soil and plant. All statistical analyses and
220 permutation tests were performed using the statistical software PAST v.3.25, available at
221 <https://folk.uio.no/ohammer/past/> (Hammer et al. 2001).

222

223 **Results**

224

225 *Soil variables*

226 The presence of Collembola led to significant changes for five out of six measured soil variables
227 (Table 1). All nutrients were more concentrated in Ep+Eu than in control treatment. The Eu treatment had
228 intermediate values for P and S, and lower values than Ep+Eu treatment for both NO_3^- and NH_4^+ . The Ep
229 treatment was similar to the control for NO_3^- , NH_4^+ and P. The pH showed a different pattern, being higher
230 in control than in Ep with the two other treatments having intermediate values. Finally, for all soil variables,
231 no significant difference was detected between Ep and Eu treatments.

232

233 *Nutritional plant performance*

234 Foliar nutrient contents of *L. perenne* were strongly affected by collembolan presence, whatever
235 the assemblages (Table 2; Fig. 1A). Comparatively to the control, foliar C content was significantly lower
236 in Ep+Eu treatment (-4.8%). Maximum foliar C was observed for the Eu treatment. Nitrogen and S showed
237 an increased concentration when increasing the complexity of collembolan assemblage (control < Ep or Eu
238 < Ep+Eu). Indeed, the presence of Ep, Eu and Ep+Ep species increased respectively by 36%, 32% and 67%
239 the N content in leaves compared with the control treatment. Foliar S content was around 2.2-fold higher
240 in Ep+Eu than in control treatment. Similarly, C:N and C:S ratios were 1.7 and 2.4-fold lower in Ep+Eu
241 than in control treatment, respectively. Only C and S content in leaves were different between the treatments
242 with a single collembolan functional group, with higher values in Eu than in Ep treatments.

243 Foliar P content was higher in the presence of Collembola than in their absence, and this whatever
244 the treatment. Similarly, the C:P ratio was higher in presence than in absence of Collembola.

245

246 *Plant performance*

247 Except for plant height, all other morphological traits were affected by collembolan treatments
248 (Fig.1). Overall, plants growing with Eu and Ep+Eu had 47% and 68% more leaves than in control
249 treatment, while shoot biomass in Ep+Eu was about twice higher than in both control and Ep treatments.
250 In contrast, root biomass was significantly higher in the absence of Collembola and decreased in Ep or Eu
251 treatments to reach a minimum in the Ep+Eu treatment. As a consequence, the shoot: root (S:R) ratio (Fig.
252 1L) also strongly decreased in the presence of Collembola.

253

254 *Interaction between collembolan functional groups*

255 Results of two-way ANOVAs showed that the interaction between Ep and Eu (Ep x Eu) was
256 significant for several plant variables (Foliar N, P, S content and plant height) and for soil ammonium
257 concentration (Fig. 1 and Table 1). Furthermore, the Collembola Functional Group Effect index was
258 statistically significant for 6 out of 9 variables tested (Table 2; Fig. 2), being consistent with previous results
259 of the two-way ANOVAs. Observed Ep+Eu REI was significantly higher than the expected Ep+Eu REI for
260 foliar N (+ 40.4 %), foliar S (+ 38.7 %), plant height (+ 600 %) and soil N-NH_4^+ (+ 310 %). Conversely,
261 the observed Ep+Eu REI was significantly lower than the expected Ep+Eu REI for foliar P (-48.5 %) and
262 root biomass (-56.6%).

263

264

265 **Discussion**

266

267 Our results show that plant growth can be driven by the presence and composition of collembolan
268 communities. In accordance with past observations (Scheu et al. 1999; Bardgett and Chan 1999; Cragg and
269 Bardgett 2001; Forey et al. 2015) and our first hypothesis, the presence of Collembola in soil has a positive
270 effect on plant morphological variables (i.e. number of leaves and shoot and root biomasses) and foliar
271 nutrient contents. Although the presence of Collembola may affect plant performance in different ways (i.e.
272 pathogen control or facilitation of plant-microbial assemblages), previous studies have shown that their
273 main ecological role seems to increase nutrient availability for plants through stimulating mineralization
274 processes (Gange 2000; Schütz et al. 2008; Eisenhauer et al. 2011; Forey et al. 2015). For instance, Scheu
275 et al. (1999) and Bardgett and Chan (1999) showed that the presence of Collembola increases soil N
276 mineralization. Likewise, Cragg and Bardgett (2001) reported a positive effect of collembolan species on
277 soil processes such as litter degradation and N mineralization. Our finding appears to confirm this
278 assumption, since we found higher concentrations of nutrients such as N in soil and plant in presence than
279 in absence of Collembola.

280 Besides increase in nutrient availability, presence of Collembola can also enhance plant nutrient
281 uptake by modifying the distribution of nutrients in the rhizosphere (Teuben 1991; Lussenhop 1992),
282 increasing the formation of nutrient-rich patches and changing root morphological variables. As a
283 consequence, plants tend to invest less in their roots when a soil is nutrient-rich (Hodge 2004, 2009;
284 Endlweber et al. 2009). Those assumptions can explain the higher foliar nutrient contents and the lower
285 root biomass observed in *L. perenne* growing with Collembola in the present study. Similar effects on root
286 variables of collembolan presence were also previously documented (Partsch et al. 2006; Endlweber et al.
287 2009; Eisenhauer et al. 2011). Lambers et al. (2006) reported that P acquisition could be increased by root
288 traits like root proliferation or increased length of root hairs, enhancing allocation to shallow soil horizons,
289 and mycorrhizal symbiosis. Although we only evaluated root biomass, we suggest that collembolan
290 presence can modify root traits, for example by consuming vesicular-arbuscular mycorrhiza (VAM) hyphae
291 which might negatively affect P uptake by roots, although this has not been conclusively demonstrated yet.

292 Previous studies have highlighted that soil processes and plant growth are strongly dependent on
293 functional dissimilarity among soil fauna species (Heemsbergen et al. 2004; Eisenhauer et al. 2011). In the
294 present study, we expected that euedaphic and epedaphic communities differently influence plant
295 performance due to their different functional traits (Supplementary Table S1) and their different interactions
296 with soil microbes (Coulibaly et al. 2019). However, except for the number of *L. perenne* leaves, no
297 statistical difference was observed between both treatments, rejecting our second hypothesis: euedaphic
298 Collembola have not a more positive effect on plant growth than epedaphic species. Thus, different
299 functional groups of a same taxon (in this case, Collembola) might similarly affect plant growth, which
300 may reveal functional redundancy or a similar importance of both groups for plants. Surprisingly, the role
301 played by these two collembolan functional groups on plant performance was little studied until now.
302 Eisenhauer et al. (2011) approached this by evaluating the effects of three collembolan species, each
303 belonging to a distinct functional group. They found that functional group effects depended on plant
304 functional group identity. Furthermore, it is well known that within the same functional group, species

305 could differ regarding their functional traits and then their functions (Winck et al. 2017; Pey et al. 2014;
306 Fonseca and Ganade 2001), altogether making predictions difficult. Determining and measuring effect traits
307 of Collembola might partly solve the potential generalization of these results. However, we noted that
308 euedaphic group tended to have a more positive effect on *L. perenne* performance compared with the
309 epedaphic functional group, supporting the idea that euedaphic Collembola strongly interact with microbial
310 communities in the rhizosphere, thereby increasing soil nutrients availability by stimulating microbial
311 activity and mineralization (Petersen 2002).

312 Despite the potential functional redundancy between epedaphic and euedaphic Collembola
313 revealed by the weak differences observed in terms of plant response to the presence of each functional
314 group, the presence of both life-forms clearly showed significant interactions calling for functional
315 complementarity (i.e. niche partitioning or facilitation; Hooper et al. 2005). Although our study did not
316 evaluate the outcome of the interactions between collembolan species or functional groups on their own
317 fitness, the overyielding observed in soil nutrients, foliar nutrients and in leaf numbers in the treatment
318 including the two functional groups could be interpreted as a result of those interactions. We observed that
319 the number of leaves and shoot biomass appear to be related to niche partitioning, while foliar nutrient
320 content (N and S) would result from facilitative interactions. Contrary to our results that did not reveal
321 antagonisms between collembolan functional groups, Cragg and Bardgett (2001) found that an increase in
322 collembolan species could reduce ecological processes in the soil due to competitive interaction among
323 species. Furthermore, Eisenhauer et al. (2011) also showed that adding two collembolan species with
324 similar functional traits could negatively affect plant performances due to strong competition between these
325 species. We cannot exclude, and this is highly possible, that interspecific competitive interactions may have
326 existed in our study. But those interactions have not prevailed between functional groups. This highlights
327 the need when dealing with biotic interactions to consider as far as possible complex assemblages. The
328 nature and magnitude of biotic interactions are fluctuating according to the biotic and abiotic environment
329 (Bertness and Callaway 1994; Dangles et al. 2013; O'Brien et al. 2018).

330 The positive effect on plants and soil processes (i.e. overyielding) observed in the treatment
331 combining both collembolan functional groups are supported by the study of Heemsbergen et al. (2004), as
332 they found a positive linear response of leaf litter decomposition process to an increase in decomposer
333 functional dissimilarity. Previous studies suggesting a distinct resource use and occupation of soil habitat
334 between these two collembolan functional groups can explain our findings (Gisin 1943; Petersen 2002;
335 Berg et al. 2004; Chahartaghi et al. 2005; Coulibaly et al. 2019). The overyielding effects observed in *L.*
336 *perenne* foliar nutrients appear to be related to an increase in mineralization processes leading to an increase
337 in nutrient availability and plant uptake. Similar results were reported by Eisenhauer et al. (2011), with an
338 increase in collembolan species and functional richness leading to higher C and N mineralization and then
339 increased leaf N content and shoot biomass of forbs. However, in a study focusing on the soil microbial
340 compartment and associated functions, Coulibaly et al. (2019) pointed to a virtual lack of complementarity
341 between epedaphic and euedaphic Collembola. Several studies have recently highlighted the role of signal
342 molecules as an important feature of direct interactions between plants and free-living soil organisms, e.g.
343 earthworms (Puga-Freitas and Blouin 2015). We could hypothesize that such direct interactions may exist
344 between Collembola and plants. Finally, although not documented in the literature, we cannot exclude that

345 the presence of epedaphic Collembola may favor or facilitate euedaphic ones by fostering nutrient release
346 aboveground that could stimulate belowground microbial communities in the soil and thus provide more
347 resources for euedaphic Collembola.

348

349 **Conclusion**

350

351 We clearly demonstrated that a soil fauna group (here Collembola) might drive soil fertility and
352 plant performances of a grass species (*Lolium perenne*) and that the magnitude and direction of these effects
353 are strongly dependent on functional species assemblages. This experiment also highlights the importance
354 of a diverse functional soil assemblage that might drive overyielding of ecological processes (among which
355 plant productivity of an economically important forage species).

356 Experiments on ecosystem overyielding traditionally only manipulate specific and functional
357 diversity of plants. Through our experimental approach, we demonstrated that manipulating soil functional
358 assemblages at a local scale was experimentally possible, and was highly relevant for understanding
359 synergistic effects on plant productivity. Thus, soil organism diversity-mediated interactions are essential
360 for enhancing plant productivity and maximizing ecosystem processes and thus subsequent services. We
361 strongly recommend developing such experimental methodology for different soil fauna group
362 assemblages. Nevertheless, we recommend manipulating natural assemblages, considering the natural
363 dissimilarity among species into every group regarding their functional traits. Lastly, our experiment also
364 suggests positive interactions between collembolan functional groups. This experiment was not designed
365 to study the nature of these interactions (competition vs. facilitation or complementarity), but similarly to
366 plant-plant interaction theoretical models, we encourage to test direct and indirect positive interactions
367 between Collembola and to test the importance of the environment on the intensity of these interactions.

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498 Table 1. Effects of collembolan functional group combination on soil parameters: Dissolved Organic Carbon (DOC), Nitrate (NO₃), Ammonium (NH₄⁺), Phosphorus (P)
 499 Sulphur (S) and pH after 5 months of experimentation. Control: without Collembola; Eu: euedaphic Collembola; Ep: epedaphic Collembola; Ep + Eu: combined functional
 500 groups. Means ± SD.

Factor	DOC	NO ₃ ⁻	NH ₄ ⁺	P	S	pH
Treatments	One-Way ANOVA					
Control	54.09 ± 15.12	2.26 ± 0.07 b	1.49 ± 0.59 b	0.94 ± 0.05 b	0.29 ± 0.01 c	6.25 ± 0.21 a
Ep	65.08 ± 16.78	3.74 ± 2.09 ab	2.17 ± 0.16 b	0.98 ± 0.08 b	0.33 ± 0.01 b	5.92 ± 0.18 b
Eu	58.36 ± 14.47	2.53 ± 0.27 b	1.79 ± 0.48 b	1 ± 0.06 ab	0.35 ± 0.04 ab	6.06 ± 0.21 ab
Ep + Eu	73.95 ± 25.24	5.64 ± 1.7 a	9.21 ± 3.12 a	1.11 ± 0.06 a	0.37 ± 0.02 a	5.98 ± 0.15 ab
F	1.38	5.94	28.64	5.83	12.9	3.57
P value	0.277	0.006	<0.001	0.008	<0.001	0.033
Ep x Eu	Two-Way ANOVA					
F	0.1	0.98	21	-2.27	-1.69	2.71
P value	0.7559	0.17	0.0002	0.5213	0.9982	0.1161

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503 ¹ The P value in bold indicates a significant effect (P < 0.05) of collembolan life form on the plant variables using analysis of variance (ANOVA One-Way) with permutation
 504 tests. P value was calculated with 9999 permutations. Different letters denote significant differences between means at the 5% level variables according to One-way ANOVA
 505 with the factor “treatment”. Partial results (interactive terms between factors) of Two-way ANOVA (with Ep and Eu as factors) are also given. P value was calculated with
 506 9999 permutations

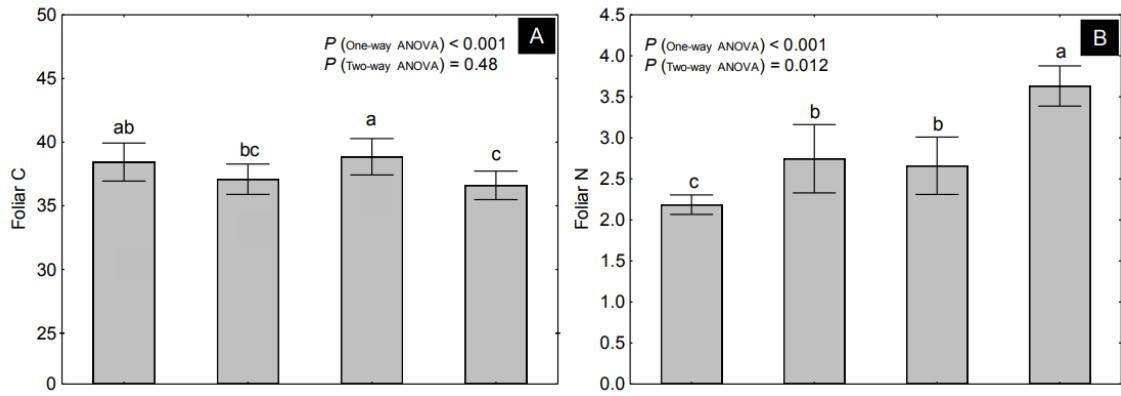
507 Table 2. Complementary effect of Observed and Expected Ep+Eu values for soil and plant variables were
 508 calculated using the Relative Effect Index (REI) and compared with a *t* test. Combined Functional Group
 509 Effect (CFGE) was calculated according to the formula: Observed REI – Expected REI. Null CFGE =
 510 simple additive effect, indicating niche partitioning; positive CFGE = overyielding, and negative CFGE=
 511 underyielding. For more details, see the material and method section. Ep= epedaphic Collembola, Eu=
 512 euedaphic Collembola.

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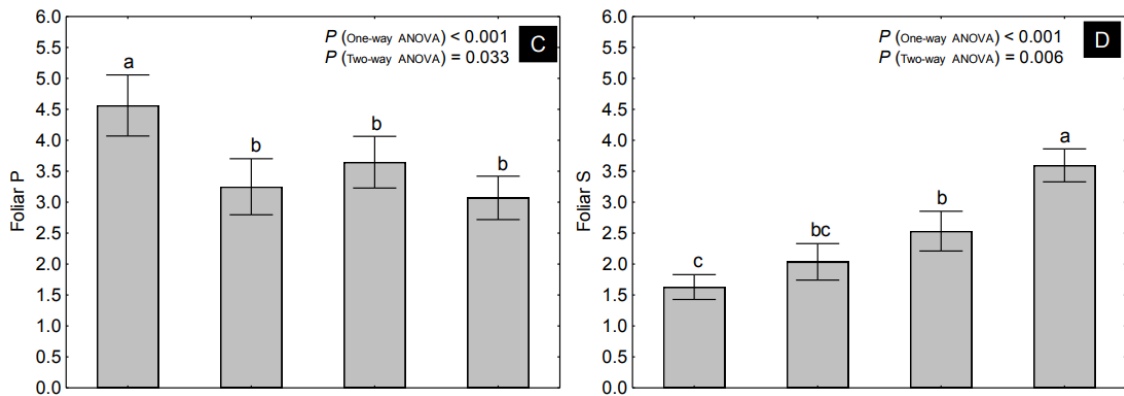
Variables	Observed REI	Expected REI	<i>t</i> test	<i>P</i> value	CFGE
	Ep + Eu	Ep + Eu			
<i>Plant variables</i>					
Foliar C	-0.05	-0.02	1.75	0.101	0
Foliar N	0.66	0.47	-2.41	0.03	+
Foliar P	-0.33	-0.49	-2.67	0.032	-
Foliar S	1.21	0.80	-3.45	0.011	+
Plant height	-0.03	-0.21	-3.07	0.006	+
Number of leaves	0.72	0.56	-1.28	0.228	0
Shoot biomass	1.39	0.50	-1.06	0.33	0
Root biomass	-0.83	-1.30	-8.02	0.009	-
SR ratio	6.06	3.78	-1.87	0.008	+
<i>Soil variables</i>					
N-NO₃⁻	1.50	0.78	-1.29	0.233	0
N-NH₄⁺	5.42	1.32	-3.32	0.011	+
Phosphorus	0.18	0.11	-1.33	0.225	0
Sulfur	0.26	0.30	1.49	0.171	0

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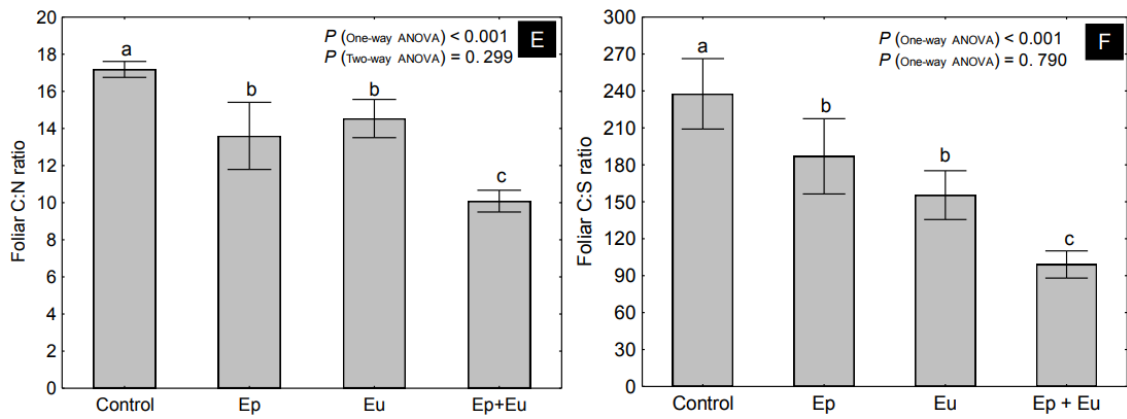
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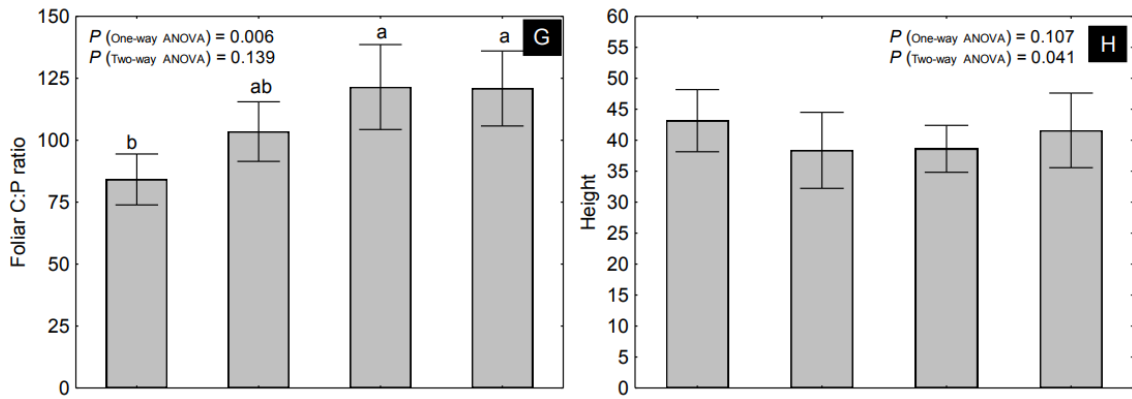


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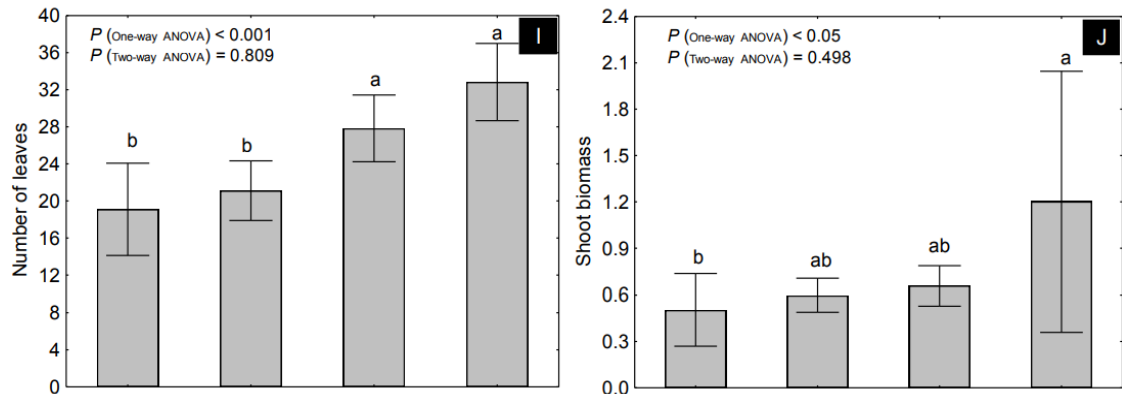


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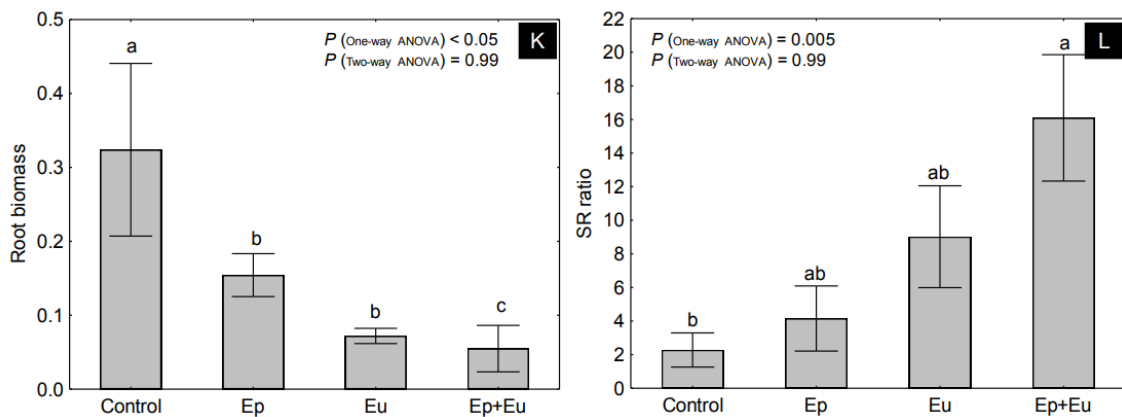
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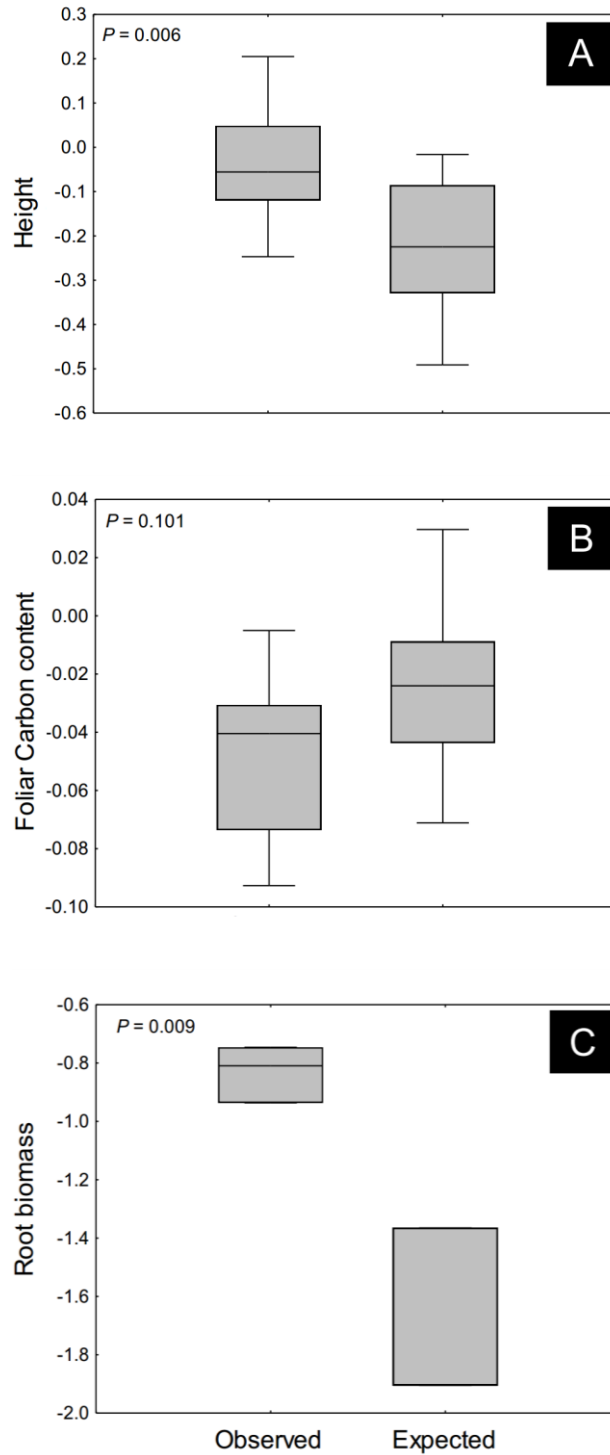


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526 Figure 1. Attributes of *Lolium perenne* according to four different treatments corresponding to the presence
 527 or not of different functional groups of Collembola. Control: without Collembola; Eu: euedaphic
 528 Collembola; Ep: epedaphic Collembola; Ep + Eu: combined functional groups. Error bars show standard
 529 error. Different letters denote significant differences between means at the 5% level variables according to
 530 One-way ANOVA with the factor “treatment”. Partial results (interactive terms between factors) of Two-
 531 way ANOVA (with Ep and Eu as factors) are also given. P value was calculated with 9999 permutations.

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536 Relative Effect Index of height (A), foliar carbon content (B) and root biomass (C) of *Lolium* 536

537 perenne in observed and expected combination of collembolan functional groups (Ep+Eu). Eu: euedaphic

538 Collembola; Ep: epedaphic Collembola; Ep + Eu: Error bars show standard error. P value was calculated

539 with 9999 permutations.

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Supplementary Material

Functional groups of Collembola induce different plant responses in *Lolium perenne*.

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562 Table S1: Assemblages of Collembola at the start and the end of the experiment (i.e. 5 months
 563 later) in 3 different treatments (Ep, Eu and Ep+Eu). Mean (and SD) abundances per species are
 564 given (n = 5). Total mean abundance (SD), mean biomass of C and N content of the Collembola
 565 are given per treatment. EP= epedaphic species, EU= euedaphic species.
 566

Species	START (T=0)			END (T= 5 months)		
	Ep	Eu	Ep+Eu	Ep	Eu	Ep+Eu
<i>Isotomurus prasinus</i>	5.0 (5.0)	0.4 (0.9)	4.4 (3.8)	3.0 (1.4)	0.0 (0)	3 (3.7)
<i>Lepidocyrtus cyaneus</i>	2.8 (1.6)	0.2 (0.4)	1.6 (1.1)	4.2 (3.0)	0.2 (0.5)	3.8 (2.3)
<i>Desoria violacea</i>	1.2 (1.3)	0.0 (0)	0.8 (1.1)	1.8 (0.8)	0.2 (0.5)	1.2 (1.3)
<i>Stenacidia violacea</i>	0.2 (0.4)	0.0 (0)	0.0 (0)	0.6 (0.5)	0.0 (0)	0.4 (0.5)
<i>Cryptopygus thermophilus</i>	0.2 (0.4)	2.2 (1.9)	2.8 (2.6)	0.0 (0)	3.8 (2.6)	3.2 (2.8)
<i>Isotomiella minor</i>	0.0 (0)	7.2 (3.1)	7.0 (3.3)	0.0 (0)	11.4 (5.9)	14.4 (9.8)
<i>Paratullbergia callipygos</i>	0.0 (0)	1.4 (1.3)	2.4 (3.6)	0.0 (0)	1.8 (0.5)	0.4 (0.5)
<i>Protaphorura armata gr</i>	0.0 (0)	1.8 (0.8)	2.2 (1.5)	0.0 (0)	3.4 (3.0)	6.4 (4.2)
<i>Mesophorura yosii</i>	0.0 (0)	6.6 (5.5)	6.0 (4.5)	0.0 (0)	10.0 (7.1)	11.8 (6.0)
<i>Dicyrtoma fusca</i>	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.2 (0.4)
Total abundance	9.4 (6.5)	19.8 (5.1)	27.2 (5.5)	9.6 (1.1)	30.8 (8.1)	44.8 (16.8)
Biomass C (µg C)	195.3	51.4	204.9	143.4	63.6	223.4
Biomass N (µg N)	38.0	10.3	40.3	28.7	12.7	44.7

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