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► **To cite this version:**

Sandrine S. Salmon, Tom Vittier, Sébastien Barot, Jean-François Ponge, Farida Ben Assoula, et al.. Responses of Collembola communities to mixtures of wheat varieties: a trait-based approach. *Pedobiologia*, 2021, 87-88, pp.150755. 10.1016/j.pedobi.2021.150755 . hal-03315374

HAL Id: hal-03315374

<https://hal.science/hal-03315374>

Submitted on 5 Aug 2021

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1 Ref.: Ms. No. PEDOBI-D-20-00086

2 **Responses of Collembola communities to mixtures of wheat varieties: a**
3 **trait-based approach**

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13

14 **Highlights**

15 Mixtures of wheat varieties did not increase abundance and richness of Collembola

16 Wheat traits explained 13% of species assemblages of Collembola

17 Wheat traits explained 11% of trait assemblages of Collembola

18 Wheat sensitivity to fungal diseases explained 4.7% of trait assemblages of Collembola

19 Soil features explained 10.8% of species assemblages of Collembola

20 **ABSTRACT**

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21 The genetic diversity of cultivated crops has decreased continuously since the beginning of
22 the 20th century, because of the gradual replacement of genetically heterogeneous traditional
23 varieties by new genetically homogenous varieties, grown in monospecific stands. The
24 resulting agro-ecosystems are now considered as unsustainable. Increasing within-field
25 genetic crop diversity by using a mixture of varieties could increase the sustainability of these
26 agro-ecosystems. This could also potentially increase non-crop biodiversity. In the present
27 study we used an experimental approach to test whether the number of wheat varieties
28 (genetic diversity), the number of functional groups (functional diversity), the composition of
29 functional groups and wheat traits influence (1) species richness and abundance of
30 Collembola, and (2) species and trait assemblages of Collembola. A total of 104 plots were
31 seeded with either monocultures or mixtures of 2, 4 and 8 wheat varieties. Soil cores were
32 collected in each plot to extract Collembola and measure soil features. The number of wheat
33 varieties and the functional wheat diversity did not influence the abundance and species
34 richness of Collembola. The sensitivity of wheat to septoria leaf blotch was positively related
35 to the abundance and species richness of Collembola, while specific root length was
36 positively related to collembolan species richness. Wheat traits related to sensitivity to fungal
37 diseases, (more especially septoria leaf blotch) and characteristics of aerial parts and roots
38 impacted collembolan species and trait assemblages, but these effects were weak. Soil
39 features, especially the proportion of coarse silt, were also influential. Our study did not show
40 a favorable impact of wheat genetic diversity on soil Collembola, which might result from
41 their low abundance. Nevertheless, it suggests correlations between some variety traits and
42 the species richness and abundance of Collembola.

43 *Keywords:* crop management practices; genetic diversity; arthropod communities; wheat
44 variety mixture; functional diversity; plant functional traits

45 **1. Introduction**

46 Most current cropping systems are based on the use of a small number of species,
47 usually grown in monospecific stands (Litrice et al., 2015). Within-field genetic diversity has
48 decreased since the beginning of the 20th century through the gradual replacement of
49 genetically-heterogeneous traditional varieties with genetically-homogeneous varieties, often
50 selected for higher yield or higher resistance to certain diseases (Bonnin et al., 2014).
51 However, it is increasingly accepted that this mode of production is fragile and unsustainable:
52 genetically poor farming systems can resist pests and maintain high yields only through the
53 use of chemical inputs (e.g. nitrogen and phosphorus mineral fertilizers), and through the
54 intensive use of pesticides that tend to decrease non-crop biodiversity (Tooker and Frank,
55 2012). A profound questioning of the modes of agricultural production thus became
56 necessary. Favoring inter- and intraspecific crop diversity could be a promising alternative as
57 part of sustainable agriculture (Barot et al., 2017a; Crutsinger et al., 2006; Loeuille et al.,
58 2013).

59 Many studies showed that increasing plant species richness improved ecosystem
60 functioning, e.g. increased nutrient retention or biomass production and stabilization of crop
61 production (Prieto et al., 2015; Tooker and Frank, 2012). Plant diversity also increases the
62 resistance of ecosystem productivity to climate extremes, which is an advantage in the context
63 of global change (Isbell et al., 2015). Functional crop diversity (i.e. diversity of crop
64 characteristics or traits) can even provide more ecosystem services than species richness per
65 se, such as increases in yield or aboveground biomass nitrogen (Finney and Kaye, 2017).
66 These favorable effects of biodiversity are partly explained by functional complementarity
67 attributed to niche partitioning (Loreau and Hector, 2001). Another mechanism may explain
68 the positive effect of crop diversity on ecosystem functions: the “sampling effect” (Barot et
69 al., 2017a), i.e. the natural selection of species within a diverse community (compared to a

70 community poorer in species), increases the likelihood of communities to host productive
71 species in given local conditions (soil properties, climate...). For instance, Prieto et al (2015)
72 showed that multispecies assemblages of plants were more productive than monocultures
73 when subjected to drought, and that the number of genotypes per species present increased the
74 temporal stability of production under both drought and non-drought conditions. This led us
75 to hypothesize that mixing crop varieties would lead to the same positive effects as increased
76 species diversity, and through the same mechanisms (Barot et al., 2017b; Borg et al., 2018;
77 Prieto et al., 2015).

78 Biodiversity in one trophic group may also impact biodiversity in other trophic groups
79 through vertical, i.e. inter-trophic levels effects (Duffy et al., 2007). For example, the
80 diversity of arthropods often increases with plant species richness (Castagneyrol and Jactel,
81 2012). Plant species richness and plant functional diversity have also often been shown to
82 benefit growth, density and diversity of soil organisms (Eisenhauer et al., 2011; Milcu et al.,
83 2006), presumably by improving quality or diversity of belowground resources. Nevertheless,
84 a number of studies showed no strong, or controversial, effects of plant diversity per se on soil
85 fauna (Wardle et al. 2003, Milcu et al. 2006, Korboulewsky et al. 2016), which highlights the
86 lack of consistency in results so far obtained.

87 Intraspecific genetic diversity could lead to the same types of effect. For example the
88 positive impact of plant genetic diversity (variety mixtures) on the diversity of arthropods has
89 been shown in forests (Tovar-Sánchez et al., 2015) and agricultural crop systems (Crutsinger
90 et al., 2006; McArt et al., 2012). It is hypothesized that, by increasing crop genetic and
91 phenotypic diversity, the number of available resources increases, which in turn has a positive
92 impact on the diversity of fauna (Abrams, 1983). Besides providing various food resources,
93 mixtures of crop varieties could also provide different micro-habitats that can similarly shape
94 richer arthropod communities. Moreover, experiments on variety mixtures have shown that

95 intraspecific diversity can increase the abundance of natural enemies of insect pests and thus
96 could be used as a plant disease management technique (Chateil et al., 2013; Zhu et al., 2000).

97 Collembola are an arthropod group known to be impacted by plant community
98 composition and diversity (Chateil et al., 2013; Eisenhauer et al., 2011). They are among the
99 most widespread and abundant groups of terrestrial arthropods and they impact ecosystem
100 functioning by their high number (Hopkin, 1997). One of the main roles of Collembola is the
101 regulation and dispersal of decomposer microorganisms (fungi and bacteria) which are
102 responsible for the recycling of nutrients taken up by plants (de Vries et al., 2013). By
103 consuming plant fungal pathogens, Collembola can limit fungal diseases (Meyer-Wolfarth et
104 al., 2017; Schrader et al., 2013). By regulating the activity and dispersal of mycorrhizal fungi,
105 they can also they can also either promote or reduce the uptake of nutrients by cultivated
106 plants (Warnock et al., 1982; Ngosong et al., 2014) or regulate the architecture of some plants
107 (Endlweber and Scheu, 2007).

108 A previous study showed that wheat genetic diversity benefited collembolan species
109 richness in cultivated fields (Chateil et al., 2013). However, this study did not test for a
110 possible effect of the identity/quality of varieties which could interact with the effect of
111 genetic diversity. Other studies suggested that the quality of resources (e.g. litter) that enter
112 belowground ecosystems, depending on plant identity, had more impact on the composition or
113 biomass of soil fauna than plant diversity (Milcu et al., 2006; Viketoft and Sohlenius, 2011).

114 In the present study, we assessed whether the number of wheat varieties (genetic
115 diversity), the number of functional groups (functional diversity), the composition of
116 functional groups and wheat traits influence 1) the species richness and abundance of
117 Collembola, and (2) species and trait assemblages of Collembola. The focus on functional
118 traits of communities (e.g. plants), in addition to species, is an approach which allows

119 addressing directly the functions fulfilled by organisms both at species and community levels
120 (Vandewalle et al., 2010). Several studies showed that functional traits of Collembola allow
121 better predicting environmental effects on soil collembolan communities than species do
122 (Bokhorst et al., 2012; Salmon et al., 2014; Vanhee et al., 2017).

123 **2. Material and methods**

124 *2.1. Study site, wheat varieties and experimental design*

125 Our field experiment took place in an experimental research station in Versailles,
126 France. Winter wheat *Triticum aestivum* was chosen because it is the main cereal crop of the
127 region, and also because it displays a wide array of phenotypic variation among varieties. The
128 experiment has been fully described in Dubs et al. (2018a).

129 We have followed the general approach of biodiversity-ecosystem functioning
130 experiment as implemented in the Jena experiments (Weisser 2017) and thoughts on the
131 implementation of functional diversity in such experiments (Ebeling 2014). Twenty-seven
132 functional traits (above- and belowground morphological, phenological and physiological
133 traits) have been measured in 57 varieties that have been chosen to be representative of the
134 diversity of varieties cultivated in the Parisian basin. Hence they include both local landraces
135 and modern elite varieties (Dubs et al., 2018a). Wheat traits were measured in the field and in
136 greenhouses by different teams of the Wheatamix consortium in 2014 (i.e. before our
137 experiment), except traits related to diseases that come from Arvalis and databases of two
138 laboratories (see Table 2 of Dubs et al., 2018a). Using a hierarchical clustering method
139 (Ward method), these varieties have been classified on the base of 27 functional traits (yield,
140 earliness, Specific Leaf Area, specific root length, root absorption capacity of nitrate and
141 ammonium...) into 4 functional groups thereafter named c1, c2, c3, c4 clusters. Wheat
142 varieties of the c1 functional group were characterized by high sensitivity to fungal diseases.

143 Functional group c2 comprised wheat varieties with short root lengths, high rate of NO_3^-
144 absorption, high relative growth rate and low sensitivity to fungal diseases. The c3 functional
145 group was composed of varieties characterized by their slow growth but elevated
146 aggressiveness regarding plant-plant competition, and with high rate of NH_4^+ absorption
147 capacity. Finally, the c4 functional group contained varieties with high specific root lengths,
148 low relative growth rate and low rate of NO_3^- absorption capacity (Dubs et al. 2018a). Sixteen
149 varieties have been selected to be used in the experiment, in order to maximize the overall
150 functional diversity: for each cluster four varieties have been chosen avoiding varieties too far
151 from the center of the cluster (thus varieties not representative of the cluster) and avoiding
152 varieties that are too similar within the cluster. These 16 varieties were used to create 72
153 combinations of varieties encompassing three levels of diversity: 24, 28, and 20 mixtures
154 combining 2, 4 and 8 varieties, respectively (Dubs et al., 2018a). The number of functional
155 groups also varied in each of the three levels of variety mixtures: some mixtures were
156 functionally “homogeneous” (a single functional group) while other were heterogeneous (two
157 or more functional groups). Thus, these mixtures have been implemented for experimental
158 purpose, to be able to compare mixtures with different number of varieties and different levels
159 of functional diversity. These mixtures were clearly not designed because of their particular
160 relevance for farmers. The list of varieties, mixtures and their distribution over the 104 plots
161 are detailed in Dubs et al. (2018a). The 72 mixtures have been seeded into 72 plots and the 16
162 varieties have also been seeded alone, in duplicate, providing a total of 104 10.5 m x 8.0 m
163 plots encompassing 4 levels of variety mixtures (1, 2, 4 and 8 varieties each).

164 Varieties were seeded in November 2014 after ploughing. After sowing, the mixtures
165 of seeds from the different varieties we controlled for the spatial homogeneity of germination,
166 which shows that all varieties germinated. The crop was grown with a target yield of 60
167 quintal ha^{-1} (75 = French average national wheat yield in 2015). No insecticide and fungicide

168 were used except for seed coating, the same for all varieties for which CELEST (2 l t⁻¹–
169 Fludioxonil 25 g l⁻¹) and SIGNAM (0.6 kg g t⁻¹–Cypermethryne 300 g l⁻¹) were used. One
170 spraying of two herbicides (Archipel®, 50% Iodosulfuron and 50% Mesosulfuron; Harmony
171 Extra®, 66 % thifensulfuron-methyl and 33% tribenuron-methyle) was performed on March
172 14, 2015. 160 kg N ha⁻¹ was used as compared to the estimated optimal amount of 180 kg N
173 ha⁻¹. The fertilizer (ammonium-nitrate) was spread as follows: 40 kg N ha⁻¹ on March 5, 2015,
174 80 kg N ha⁻¹ on April 16, 2015, 40 kg N ha⁻¹ on May 11, 2015. All plots were harvested
175 between the last week of July and the first week of August 2015.
176 After harvest, wheat crop residues were left in the field until last soil faunal sampling (from
177 which springtails were extracted), in November.

178

179 2.2. *Collembola* sampling

180 Collembola were sampled in March (one core sample taken in the center of each plot)
181 and November 2015 (two core samples taken in the center of each half plot) in the 104 plots.
182 The three samples taken in each plot at two sampling dates allowed better accounting spatial
183 and temporal plot heterogeneity. Each core sample was 5 cm in diameter and 15 cm deep,
184 leading to a total sampled area of 59 cm² per plot. Collembola were extracted during ten days
185 by the Berlese method (Edwards and Fletcher, 1971). The three samples of Collembola were
186 pooled together for each plot because the density of Collembola in one sample was relatively
187 low. They were then sorted, mounted, cleared in chloral-lactophenol and identified to species
188 level under a light microscope (400× magnification) according to Hopkin (2007), Potapow
189 (2001), Thibaud et al. (2004) and Bretfeld (1999). Other samples were taken in the same plots
190 to measure soil features. A soil core (5 cm diameter, 15 cm depth) was taken in the center of
191 each plot to measure soil water content (dry/wet weight) and pH_{water} according to ISO 10390
192 in March 2015. Another soil core (8 cm diameter, 15cm depth, litter excluded) was taken in

193 the center of each plot in October 2015 to measure particle size distribution (clay, fine silt,
194 coarse silt, fine sand, coarse sand) according to NF X 31-107, total concentration in nitrogen
195 according to ISO 13878, total concentration in organic carbon and organic matter by dry
196 combustion according to ISO 10694, and the C/N ratio. Soil analyses were performed at the
197 INRA Laboratory for Soil Analysis (Arras, France).

198 *2.3. Statistical analysis*

199 Abundances of collembolan species in the three samples taken in each plot were
200 pooled for the calculation of abundance and species richness per plot.

201 We performed generalized linear models (GLM) to determine whether the abundance
202 and species richness of Collembola were influenced by the number of wheat varieties, wheat
203 functional diversity (number of functional groups), functional group composition (c1, c2, c3,
204 or c4) and mean of wheat functional traits in variety mixtures. Given the high number of
205 wheat traits available, we first made an a priori selection according to their potential impact
206 on Collembola. We selected traits related to root system, plant cover, and sensitivity to fungal
207 diseases. At least some collembolan species are known to live and feed on roots (Thimm and
208 Larink, 1995), depend on plant cover (Heiniger et al., 2015) and feed on fungi, including
209 pathogenic fungi (Friberg et al., 2005; Jorgensen et al., 2005; Ponge, 1988). Wheat trait
210 measures and soil features were then standardized (thus discarding spurious effects of various
211 units). Spearman correlation coefficients were calculated between wheat traits, soil features
212 and geographical coordinates in order to eliminate correlated explanatory variables (Table
213 S3). As coarse silt was highly correlated with other particle size fractions and with
214 geographical coordinates according to a textural gradient, the latter two sets of variables were
215 discarded from further analyses. As the impact of soil texture on soil fauna is well known,
216 especially in conventional agroecosystems (Grossi and Brun, 1997) we preferred to keep

217 coarse silt and remove geographical coordinates. The set of soil features selected for further
218 analyses was coarse silt, soil pH, soil water content and C/N ratio. Correlation coefficients
219 also allowed to select the set of wheat traits used in further analyses (Table 1).

220 As the number of varieties and the number of functional groups bring redundant
221 information about wheat diversity, they were analysed separately, like wheat traits and the
222 composition of functional groups (groups of varieties associated according to their traits). We
223 thus performed a first model to test the effect of wheat diversity (number of varieties), the
224 composition of wheat functional groups (c1, c2, c3 and c4), and soil features, on species
225 richness and abundance of Collembola, respectively. This model allowed to share the part of
226 diversity and that of composition of functional groups (varying according to traits displayed in
227 each functional group) in the effect of wheat on Collembola communities (Spehn et al. 2005).
228 In the same way, we then analysed the effect of the number of functional groups (functional
229 diversity), the set of wheat traits and soil features, on species richness and abundance of
230 Collembola. Soil features were included in models, because the potential effect of variety
231 mixtures on collembolan communities could be blurred or biased in the absence of reference
232 to soil variation.

233 We then selected final models step by step, by keeping variables that significantly
234 contributed to models and by using AIC (Spehn et al. 2005, Bolker et al. 2009). All models
235 were diagnosed with the “DHARMA” package (Hartig, 2020) for R software: “Uniformity”
236 (tests if the global distribution of residuals is in line with predicted values with a
237 Kolmogorov-Smirnov test and a QQ-plot), “Outliers” (tests if there are more simulation
238 outliers than expected), “Dispersion” (tests if the simulated dispersion is equal to the observed
239 dispersion), “Quantiles” (fits a quantile regression or residuals against a predictor (predicted
240 value by default), and tests if that predictor conforms to the expected quantile),

241 “Zeroinflation” (tests if there are more zeros than expected). In order to fulfil all model
242 assumptions (especially dispersion), collembolan abundances were log-transformed.

243 At last we performed Analyses of Deviance (Type II Wald chi-square tests) on final
244 models, with the “Anova” function of the “car” R package. Full models and codes are detailed
245 in Tables S3 to S7).

246 Canonical correspondence analysis (CCA; Ter Braak (1986) followed by Monte Carlo
247 permutation tests (999 permutations) was used to assess whether wheat variety traits, variety
248 number, functional group number, functional group composition and soil features constrained
249 collembolan species assemblages. This technique was particularly appropriate to our data
250 because it addresses the large number of zeros which characterizes community compositional
251 data (Legendre and Legendre, 1998) and does not try to display all variation in the data, but
252 only the part that can be explained by the constraints. Species represented by only one
253 individual in one sample were deleted from CCA analyses. Two first CCAs were performed
254 following the same logic and using the same explanatory variables as for GLM, i.e. one with
255 the number of wheat varieties, the composition of wheat functional groups (c1, c2, c3, c4) and
256 soil features (soil water content, pH_{water}, coarse silt, and C/N ratio), the other CCA with the
257 number of wheat functional groups, wheat traits (see Table 1) and soil features. Soil features
258 were included in all analyses to separate the variation of collembolan species distribution due
259 to soil features from that due to wheat related variables. This also limited misinterpretations in
260 the case of interactions between soil features and wheat related variables. Soil features and
261 wheat traits were standardized prior to CCA. Then, partial CCAs (pCCA) were performed
262 from each of the two first CCAs, to disentangle the effects of wheat diversity (number of
263 variety or number of functional groups), wheat composition (functional group composition or
264 traits) and soil features, on the composition of collembolan communities. Prior to partial
265 CCAs, two partial least square regressions (CCA-PLSs; Tenenhaus, 1998) were performed

266 using the same variables as for the two first CCAs, in order to classify explanatory variables
267 according to their contribution to the distribution of species. Variables contributing most to
268 species distribution (with the highest Variable Importance in the Projection, VIP) were
269 included in three partial CCAs and their effect was displayed in three graphics (Figs. 3a, b, c).

270 Two redundancy analyses (RDA; Legendre and Legendre, 1998) were performed,
271 following the same procedure and using the same explanatory variables as for GLM and
272 CCA, to measure the effects of 1) variety number, functional group composition and soil
273 features, and 2) functional group number, wheat variety traits (Table 1), and soil features, on
274 community-weighted mean traits (CWM) of Collembola. RDA was chosen because CWMs
275 are continuous variables. CWM traits have been widely used in ecological research for
276 summarizing different facets of functional composition and shifts in mean trait values within
277 communities due to environmental selection for some functional traits (Ricotta and Moretti,
278 2011). Collembolan traits were extracted from the Coltrait database (Salmon et al., 2014),
279 then the CWM of each trait was calculated using “species x traits” and “plots x species
280 abundance” matrices (Ricotta and Moretti, 2011). RDA is a direct gradient ordination method
281 that constrains the position of response variables, here collembolan CWMs, by a set of
282 environmental factors, here wheat related variables and soil features (Legendre and Legendre,
283 1998). Using RDA to analyze the impact of diverse environmental variables on the
284 distribution of CWMs is a common practice in trait-based approaches in ecology (Vandewalle
285 et al., 2010). As for pCCAs, partial RDAs (pRDA) were performed to disentangle the effects
286 of wheat diversity (variety or functional group number), wheat composition (functional group
287 composition or traits) and soil features on collembolan CWMs. Then, further partial RDAs
288 were performed to assess the relative importance of traits related to either sensitivity to fungal
289 diseases, crop canopy cover or root characteristics, after removing the effects of soil features,

290 wheat diversity and of the two other types of wheat traits. RDAs were followed by Monte
291 Carlo permutation tests (999 permutations).

292 GLMs were performed with R software (version 3.6.3, 2020), using the “glmmTMB”
293 package (Brooks et al 2017) for GLM construction, the DHARMA package for diagnostics of
294 models (Hartig, 2020). Analyses of Deviance on final models were performed with the “car”
295 package (Fox, Weisberg, 2019). CWMs were calculated with the FD package (Laliberté et al.,
296 2014) of R. CCA and RDA were performed with XLSTAT (v2013.3.05, Addinsoft, 2021).

297

298 **3. Results**

299 *3.1. Effect of wheat varieties on abundance and species richness of Collembola*

300 A total of 1,594 individuals were found. The abundance of Collembola in the three
301 pooled samples varied from 10 ± 0.53 individuals ($1,698 \text{ ind.m}^{-2}$) in plots with two varieties
302 to 25 ± 3.25 individuals ($4,246 \text{ ind.m}^{-2}$) in plots with eight varieties (mean \pm standard error),
303 but the difference was not significant (Fig. 1a, Table S5). Collembolan species richness per
304 plot did not vary with the number of wheat varieties, averaging four species per plot (Fig. 1b,
305 Table S4). First, models showed that variety number and functional group number did not
306 influence the species richness and abundance of Collembola (S4 and S5, Fig.1). Two wheat
307 traits, Specific Root Length and sensitivity to septoria leaf blotch, and the c1 functional group
308 positively increased the species richness of Collembola but to a lesser extent than the coarse
309 silt content (Table 2, Figs. 2b, c, S2, S3b). The sensitivity to Septoria leaf blotch also
310 significantly increased the abundance of Collembola but its effect was twice less than that of
311 coarse silt content (Tables 2, S7, Figs. 2a, S3a). A negative effect of the c2 functional group

312 on collembolan abundance was also detected by the first models but this effect was no longer
313 significant (or only marginally significant) in the final model (Tables 2, S6).

314 .

315 *3.2. Effect of wheat varieties on species assemblages of Collembola*

316 The CCA with wheat variety number, wheat functional group composition (c1, c2, c3,
317 c4) and soil features (soil water content, pH_{water}, coarse silt, and C/N) showed that these
318 variables significantly (p-value: 0.011) explained 23.3% of the variation of species
319 distribution. Partial CCAs testing the effect of variety number and functional group
320 composition after removing the effect of soil features showed that variety number and
321 functional group composition significantly explained 9.4% (p-value: 0.010) of the
322 collembolan species distribution. When variety number (1.1%, p-value 0.60) and functional
323 group composition (6.6%, p-value: 0.13) were tested separately, their effect was not
324 significant. The effect of soil features after removing the effect the variety number and
325 functional group composition accounted for 8.7% (p-value: 0.006) of the collembolan species
326 distribution.

327 The CCA with functional group number, wheat traits (Table 1) and soil features as
328 explanatory variables showed that these variables significantly explained 27% (p-value: 0.04)
329 of the variation of collembolan species distribution. Partial CCAs testing the effect of
330 functional group number and wheat traits after removing the effect of soil features showed
331 that functional group number and wheat traits significantly explained 14.5% (p-value: 0.01) of
332 the collembolan species distribution. When the functional group number and wheat traits were
333 tested separately, wheat traits significantly explained 13.1% (p-value 0.016) of collembolan
334 species distribution, while the effect of functional group number was not significant (1.173%,

335 p-value: 0.659). The effect of soil features after removing the effect of wheat traits and
336 functional group number accounted for 10.8% (p-value < 0.0001).

337 The first CCA-PLS classified the variety number, functional group composition and
338 soil features as follow: nbvar > Co-silt > C_N > pH > c2-0 > c2-1 > Water > c3-0 > c3-1 >
339 c1-0 > c1-1 > c4-0 > 4-1. The second CCA-PLS classified functional group number, wheat
340 traits and soil features as follows: GAIT1 > Co-silt > Septo > pH > C_N > SRR > GAIT6 >
341 nbclu > YR > Water > SRL > RD. In order to facilitate the interpretation of CCA graphs by
342 limiting the effect of interacting factors, we performed three CCAs with the most influential
343 variables given by the two CCA-PLSs: a first one with the number of wheat varieties and the
344 c2 functional group (Fig. 3a), the second one with the three traits most contributing to
345 Collembola species distribution (GAIT1, Septo, SRR, Fig. 3b) and the third CCA with the
346 three most contributing soil features (Co-silt, pH, C/N, Fig. 3c). Figure 3a shows that species
347 positively influenced by the number of wheat varieties were *Proisotoma minuta*, *Seira*
348 *domestica*, *Entomobrya lanuginosa* and *Folsomides parvulus*. *P. minima* and *Folsomia*
349 *candida* were more abundant in the c2 wheat functional group, while *Desoria tigrina*,
350 *Isotomurus palustris* and *Megalothorax gr. incertus* were less abundant or absent from plots
351 with the c2 functional group. Figure 3b shows that *D. tigrina*, *Seira domestica* and *Willowsia*
352 *platani* were positively influenced by plant cover (GAIT1). *Isotomurus palustris*,
353 *Sminthurinus elegans*, *Sminthurides signatus*, *Parisotoma notabilis* and *Megalothorax gr.*
354 *incertus* were positively impacted by the shoot/root ratio and/or the sensitivity to septoria. At
355 last, Figure 3c shows that *F. parvulus*, *S. signatus*, *Sminthurinus aureus*, and *P. minima* were
356 negatively impacted by coarse silt, contrary to *P. minuta*, *F. candida*, and *Megalothorax*
357 *minimus* which were more frequent or abundant in plots with a higher level of coarse-silt.
358 Higher soil pH was favorable to *Heteromurus nitidus* and *I. palustris* and the C/N ratio
359 positively influenced the distribution of *D. tigrina* and *S. domestica*.

360 *3.3. Effect of wheat varieties on trait assemblages of Collembola*

361 The RDA testing the effect of wheat variety number, functional group composition
362 and soil features showed that these variables together significantly explained 14.1% of the
363 variation of collembolan trait distribution (p-value: 0.004). Partial RDAs testing the effect of
364 variety number after removing the effects of soil features and functional group composition
365 showed no significant effect on collembolan trait distribution (0.45%, p-value: 0.78). The
366 effect of functional group composition after removing that of soil features and variety number
367 on collembolan trait distribution was not significant (5.1 %, p-value:0.17). Even when tested
368 together after removing the effect of soil features, variety number and functional group
369 composition had no significant effect. The effect of soil features after removing the effect the
370 variety number and functional group composition accounted for 9.7% (p-value:0.004) of the
371 variation in collembolan trait distribution.

372 The RDA with wheat functional group number, wheat traits (Table 1) and soil features
373 showed that these variables significantly explained 19.2% (p-value: 0.004) of the variation of
374 collembolan trait distribution. Partial RDAs testing the effect of functional group number and
375 wheat traits after removing the effect of soil features showed that they significantly explained
376 10.9% (p-value: 0.004) of collembolan trait distribution. When functional group number and
377 wheat traits were tested separately, wheat traits significantly explained 10.85% (p-value
378 0.015) of collembolan trait distribution, while the effect of functional group number was not
379 significant (0.08%, p-value: 0.999). The effect of soil features after removing the effect of
380 wheat traits and functional group number accounted for 8.8% (p-value: 0.002) (Fig. 4a).
381 Further partial RDAs were achieved to disentangle the effect of three types of wheat traits
382 linked to: 1) roots (SRL, SRR, RD), 2) plant cover (Green Area Index: GAI), 3) sensitivity to
383 fungal diseases (Septo, YR). These partial RDAs were performed after removing the effect of
384 soil features, functional group number and the two other types of wheat traits than that tested.

385 Traits linked to the root system (2.8%, p-value: 0.45) and plant cover (2.25 %, p-value: 0.29)
386 had no significant effects on the distribution of collembolan traits, respectively. The
387 sensitivity to fungal diseases (septoriose and yellow rust) significantly explained 4.7% (p-
388 value: 0.018) of collembolan trait distribution (Fig. 4a).

389 Partial RDAs assessing the effects of the sensitivity to fungal diseases on the
390 distribution of collembolan traits (Fig. 4a) showed that the sensitivity to septoria leaf blotch
391 (Septo) was associated to Collembola with pigmented and spherical body, long furcula,
392 presence of trichobothria, high ocelli number and living in superficial soil layers. Axis 2
393 separated collembolan traits according to sensitive and insensitive varieties to yellow rust.
394 Collembola associated to the sensitivity to yellow rust were pigmented, with high ocelli
395 number, pseudocelli, sexual reproduction and not specialized for a soil layer depth (NS).

396 The RDA assessing the effects of soil features (Fig.4b) (after removing variety number
397 and functional group composition) showed that they explained 9.7% ($p = 0.004$) of the
398 variation in the distribution of collembolan traits. Axis 1 separated soils with a high content of
399 coarse silt on the positive side from soils with a low content of coarse silt and thus more clay
400 on the negative side. Axis 2 separated soils with a neutral pH from soils that were richer in
401 organic matter (C/N) and wetter (Water). Plots with more coarse silt accommodated species
402 living only deeply in the soil (Eda), or in upper soil layers (Hemieda), and species living in
403 both deep and superficial soil layers (Eda-Hemieda) while soils with less coarse silt and thus
404 more clay accommodated epigeic species, living above the soil surface (Epi) or species
405 without preference regarding soil layers (NS). Morphological traits supported this
406 interpretation: characteristics of epigeic species such as spherical body, higher number of
407 visual organs (Ocel), long legs (LegL), long furcula (FurcaL), presence of trichobothria
408 (Tricho) and pigmentation (Pigm) of the body were associated with soils displaying less
409 coarse silt and therefore more clay. Species with cylindrical body occurred more frequently in

410 soils with high coarse silt content. The number of Collembola that did not have a preference
411 for soil depth (NS) was higher in average in wetter soils with a high C/N ratio.

412 **4. Discussion**

413 *4.1. Effect of wheat varieties on the abundance and species richness of Collembola*

414 The number of wheat varieties and wheat functional groups (functional wheat
415 diversity) did not impact the abundance and species richness of Collembola, contrary to our
416 expectation (Hypothesis 1). This result is not due to the short duration of our study since
417 Aström and Bengtsson (2011) observed no dispersal limitation of Collembola over distances
418 as far as 3 meters in 10 weeks. Our results support the conclusions of several studies showing
419 little effects of plant species or functional group richness on soil biota, including Collembola
420 (Wardle et al. 2003, Salamon et al., 2004, Milcu et al. 2006, Korboulewsky et al. 2016). The
421 weakness of the effect of wheat genetic diversity is supported by the results of Dubs et al.
422 (2018b) for aboveground arthropods on the same experimental parcels. Nevertheless, plant
423 genetic and functional diversities have been shown to increase the density and/ or the
424 diversity of many groups of invertebrates (Crawford et al., 2007; Crutsinger et al., 2006;
425 Johnson et al., 2006; Jones et al., 2011). Moreover, Chateil et al. (2013) observed that
426 mixtures of wheat varieties increased the species richness of Collembola compared to a single
427 wheat variety. However, in Chateil et al. (2013) the respective effects of diversity and
428 composition of wheat varieties could not really be disentangled. In fact, the observed increase
429 in collembolan species richness could have resulted from the identity of wheat varieties that
430 had been added to the single variety (used as a control) when creating variety mixtures.

431 Discrepancies among the effects of plant diversity observed in different studies on
432 species richness of Collembola suggest that these effects are weak and/or are blurred by
433 interactive factors. The effect of crop diversity could depend on other factors such as

434 agricultural practices (e.g. conventional vs. organic farming), surrounding landscape
435 (Bengtsson et al., 2005; Jeanneret et al., 2003) and soil features (Heiniger et al., 2015). The
436 favorable impact of coarse silt (its content being inversely proportional to clay content) on the
437 abundance and species richness of Collembola is likely due to the fact that coarse silt (in
438 comparison to clay) reduces soil compaction. Indeed, soil compaction often increases with
439 soil tillage in conventionally cultivated crops where earthworms are scarce (Clements et al.,
440 1991; Imhoff et al., 2016; Nuutinen, 1992). By limiting soil compaction (Håkansson and
441 Lipiec, 2000), known to decrease the abundance of Collembola (Schrader and Lingnau,
442 1997), a more silty texture could favor a higher abundance and species richness of
443 Collembola. Regarding agricultural practices, our field experiment was conducted in an
444 experimental agricultural research center so that our plots had a long history of conventional
445 use of tillage and pesticides, which can have reduced collembolan biodiversity at start of the
446 experiment (Cortet et al., 2002; Tsiafouli et al., 2015), limiting the response of this
447 microarthropod group to mixtures of varieties, contrary to the field experiment by Chateil et
448 al. (2013), which was under organic farming. This hypothesis is corroborated by the
449 particularly low abundances of Collembola in our field experiment. Although collembolan
450 abundances were within the range found by Cluzeau et al. (2012) and Joimel et al. (2017) in
451 arable lands, they were in average twice to three times lower than in other conventional crop
452 systems in Europe (Cluzeau et al., 2012; Heisler and Kaiser, 1995; Lagerlof and Andren,
453 1991). The mean local species richness was also relatively low in all plots and was at the
454 lowest level of the range of species richness observed by Cluzeau et al. (2012) for the same
455 sample size.

456 We observed that the composition of the functional groups of wheat and some traits
457 influence the species richness and abundance of Collembola. Collembolan species richness
458 increased in plots with varieties of the c1 functional group, which was characterized by a high

459 sensitivity to fungal diseases. This effect was supported by the significant impact of two
460 wheat traits: sensitivity to septoria leaf blotch, which was related to increase in both
461 abundance and species richness of Collembola, and specific root length, related to increase in
462 their species richness. However, these effects were weak, and generally twice less as the
463 effect of soil particle size (coarse silt).

464 Although weak, the effect of wheat composition was higher than that of wheat
465 diversity in our field experiment. Other studies on collembolan populations showed that the
466 effect of plant functional groups was stronger than the effect of plant diversity per se (Milcu
467 et al., 2006; Salamon et al., 2004). However, these studies dealt with functional groups of
468 various plant species and it is the first time that this effect could be demonstrated with groups
469 of plant varieties. Our results suggest that specific root length could contribute to increase
470 collembolan species richness by increasing food resources for soil-dwelling species: the
471 higher the specific root length, the thinner the roots and the shorter their lifespan (Eissenstat et
472 al., 2000). Some collembolan species are known to feed on roots (Thimm and Larink, 1995).
473 Moreover some Collembola, assumed to be mainly decomposers, switch their diet in the
474 presence of plant roots, especially fine roots, and may obtain carbon and nitrogen almost
475 exclusively from plant roots (Eerpina et al., 2017; Endlweber et al., 2009). In the same way,
476 an increase in the sensitivity of wheat varieties to septoria leaf blotch, may increase food
477 resources for fungal-feeding collembolan species (Friberg et al., 2005; Jorgensen et al., 2005;
478 Ponge, 1988). The biomass of fungi and fungal-invaded area of wheat available to Collembola
479 should increase in the more fungal-sensitive wheat varieties.

480 *4.2. Effect of wheat on species and trait assemblages of Collembola*

481 Most of the species collected in our study are frequently observed in agricultural
482 crops, e.g. *Entomobrya multifasciata*, *Folsomides parvulus*, *Heteromurus nitidus*, *Isotomurus*

483 *palustris*, *Lepidocyrtus cyaneus*, *L. lanuginosus*, *Megalothorax minimus*, *Neotullbergia*
484 *ramiscuspis*, *Parisotoma notabilis*, *Proisotoma minuta*, *Pseudosinella alba*, *Sminthurinus*
485 *aureus*, *Sminthurinus elegans* (Axelsen and Kristensen, 2000; Frampton et al., 2001; Fratello
486 et al., 1985; Ponge et al., 2003; Querner and Bruckner, 2010; Rebecchi et al., 2000; Sousa et
487 al., 2004).

488 The number of wheat varieties, the number of functional groups and functional group
489 composition (c1, c2, c3 or c4) did not have any effects on collembolan species and trait
490 assemblages when tested alone. The effect of variety number and functional group
491 composition (especially c2, including varieties with low sensitivity to septoria leaf blotch)
492 together was significant but weak as it explained 9.4% of the collembolan species distribution.
493 The contribution of functional group composition to explain the distribution of collembolan
494 species and traits was weak but about six times higher (about 6%) than that of variety number.
495 As for the variety number, the effect of the functional diversity (functional group number)
496 alone was extremely weak (about 1%) and not significant. Wheat traits contributed the most
497 to explain the distribution of collembolan species and traits but only about 13% and 11%,
498 respectively.

499 Wheat traits related to the sensitivity to fungal diseases and to characteristics of aerial
500 (plant cover) and root parts impacted significantly, although weakly, the distribution of
501 collembolan species and traits. Wheat traits related to aerial parts (plant cover) and root
502 characteristics contributed to explain the distribution of collembolan traits but their effects
503 were not significant when analysed separately. The sensitivity to fungal diseases, and more
504 especially to septoria leaf blotch, were the only trait the effect of which remains significant
505 after deleting the effect of all other variables. Among species associated to wheat varieties
506 sensitive to septoria leaf blotch, *Parisotoma notabilis*, *Sminthurinus elegans* and
507 *Megalothorax incertus group* are known to feed on fungi (Addison et al., 2003; Gillet and

508 Ponge, 2005). Other species found in our study, e.g. *Pseudosinella alba*, *Folsomia candida*,
509 also known to feed on fungi, including pathogenic species (Mehl, 1996; Meyer-Wolfarth et
510 al., 2017; Ponge and Charpentié, 1981; Ponge, 1988), were not really linked to the sensitivity
511 of wheat varieties to septoria leaf blotch in our graphics. This discrepancy may be explained
512 by the selective attraction of Collembola to fungi (Jorgensen et al., 2005), while the above
513 cited experimental studies concerned fungal pathogens other than *Mycosphaerella*
514 *graminicola* (septoria leaf blotch). *Isotomurus palustris*, another species associated to the
515 sensitivity to septoria leaf blotch, was also less abundant in plots with wheat varieties less
516 sensitive to septoria (c2 functional group), corroborating the influence of this wheat trait.
517 Wheat varieties with both increased sensitivity to fungal diseases and high canopy cover,
518 including high shoot-root ratios, favored logically Collembola living aboveground with
519 morphological traits adapted to aerial life, e.g. with pigmented and spherical body, long
520 furcula and high ocelli number (Salmon et al., 2014). Furthermore, the effect of canopy cover
521 had been observed to impact collembolan populations, the abundance of which decreased
522 indirectly with specific leaf area of oak leaves (Santonja et al., 2018). This is exemplified in
523 our study by *Willowsia platani*, an epigeic species that was positively influenced by plant
524 cover and is known to search for protection against light and dryness (usually under bark of
525 trees or lichen) (Gisin, 1960).

526 However, we have to acknowledge that the effect of wheat traits on Collembola
527 communities was very weak. The fact that wheat traits had been measured one year before our
528 field experiment and on different sites, or come from literature, may explain at least partly the
529 weakness of the relationships observed. In fact, a measure of each wheat trait in each plot
530 probably could have better clarified their effect on Collembola communities. The weak effect
531 of wheat traits may also be explained by the low abundances of Collembola in our field
532 experiment, as discussed above.

533 Soil features explained about 10% of the variation in collembolan species and trait
534 assemblages. Among soil features, coarse silt had the strongest impact on Collembola species
535 and trait distribution. Species living belowground were more abundant in plots with a higher
536 content in coarse silt while species living aboveground (with long appendices, pigmentation
537 and air-sensitive bristles) were more abundant in plots with lower content in coarse silt (and
538 thus more clayish and compact). This finding corroborates the role of coarse silt suggested
539 above (section 4.1), i.e. attenuating soil compaction and allowing more euedaphic Collembola
540 to live belowground, while in soils with less coarse silt (and thus more clayish and compact)
541 epigeic species (here *Sminthurides signatus*, *Entomobrya* cf. *multifasciata*, *Sminthurinus*
542 *aureus* and *aureus* group, *Lepidocyrtus cyaneus*) were probably more abundant than
543 euedaphic species because of the reduction in the number and size of soil pores (Schrader and
544 Lingnau, 1997).

545 The increase in wheat diversity did not foster collembolan species diversity,
546 corroborating some previous studies failing to show an effect of plant diversity on soil fauna
547 communities. This may be due to the fact that (1) wheat varieties most suitable to Collembola
548 were underrepresented, (2) the overall low collembolan diversity in the experimental plots
549 prevented an increase in local species richness with wheat diversity, and (3) soil features,
550 especially particle size distribution (texture), impacted collembolan distribution despite our
551 efforts (seedling randomization) to take this natural effect in account in our experimental
552 design. Moreover, our results show that the composition of plant populations, including
553 functional composition, has a greater impact (although low) than intraspecific plant diversity
554 on collembolan communities. They showed significant although weak effects of the
555 composition of wheat functional groups that likely provide more resources and/or a larger
556 niche volume (more roots and more fungal pathogens) suitable to Collembola. This suggests
557 that mixtures with wheat varieties having a higher specific root length could be chosen to

558 increase collembolan species richness by providing more habitat and food. Moreover, our
559 study suggests that keeping in mixture some wheat varieties with a lower resistance to fungal
560 diseases (e.g. by selecting other traits related to higher yield) could be compensated by the
561 consumption of fungal pathogens by Collembola (Sabatini et al., 2000), which would
562 contribute to increase collembolan species richness. This greater effect of the composition of
563 wheat varieties could explain why our results, contrast with those of a previous study (Chateil
564 et al., 2013), which showed that wheat genetic diversity increased the species richness of
565 several groups of invertebrates, including Collembola. In fact, the field experiment of Chateil
566 et al. (2013) encompassed a low number of wheat varieties, and the varieties added in the
567 higher level of diversity were probably all beneficial to Collembola.

568

569 **5. Conclusions**

570 Our study showed no effect of genetic wheat diversity on Collembola communities
571 and weak although significant effects of wheat variety composition and traits. In fact, soil
572 features, especially particle size, impacted more strongly Collembola than wheat composition
573 or diversity. Our study suggests that, at least in conventional agroecosystems, other factors
574 such as soil features, but also perhaps the surrounding landscape or agricultural practices
575 contribute more to structuring collembolan communities than intraspecific diversity. Studying
576 the effect of the diversity of wheat varieties using the same experimental method (high
577 number of varieties and four levels of diversity, respectively) but in crops grown in organic
578 farming, and with more homogenous soil features (if possible), could allow better assessing
579 the impact of intraspecific diversity and composition of plants on soil invertebrate
580 communities. A measure of each functional wheat trait during the experiment would also
581 allow to directly assess potential impacts of wheat traits on Collembola.

582 **Acknowledgements**

583 This work was supported by the ANR WHEATAMIX project, grant ANR-13-AGRO-
584 0008 of the French National Research Agency. The authors thank all the persons who were
585 involved in the management of the field experiment, and particularly Dr. Jérôme Enjalbert,
586 Dr. Sébastien Saint-Jean, and Christophe Montagnier. The authors gratefully thank Pr.
587 Emmanuelle Porcher for constructive comments and recommendations which helped to
588 improve quality of the paper.

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825 **Table 1.** Wheat trait in mixtures of varieties and their codes used in our statistical analyses.

Trait code	Wheat trait in mixtures of varieties
SRL	Mean specific root length (m.g^{-1})
SRR	Mean shoot/root ratio
RD	Mean root diameter (mm)
GAIT1	Mean Green Area Index in December = ratio of leaf green area to ground area
YR	Mean sensitivity to yellow rust (mean percentage of sporulating area)
Septo	Mean sensitivity to septoria leaf blotch (mean percentage of sporulating area)
GAIT6	Mean of Green Area Index in April = ratio of leaf green area to ground area

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828 **Table 2.** Analysis of Deviance Table (Type II Wald chisquare tests) (Chisquare, P-value) from final
829 models with abundance and species richness of Collembola as response variables respectively, soil
830 features+ variety number+ functional group composition or soil features+ functional group number+
831 wheat traits , as explanatory variables. Only explanatory variables showing a significant effect were
832 kept in the final model (See Tables S4 to S7 for details). See Table 1 for wheat trait codes; Co-silt: the
833 amount of coarse silt; C1, C2: C1 and C2 functional groups of wheat.

	Final model	Explanatory variables	Degrees of freedom	Chisquare	P-value
Species richness	C1+Co-silt	Co-silt	1	16.4311	5.045e-05
		C1	1	7.9275	0.004869
	SRL+Septo+Co-silt	SRL	1	4.0832	0.043311
		Septo	1	7.9036	0.004934
		Co-silt	1	20.1757	7.065e-06
Abundance	C2+Co-silt	Co-silt	1	17.1698	3.418e-05
		C2	1	3.2121	0.07309
	Septo+Co-silt	Septo	1	9.7172	0.001826
		Co-silt	1	20.1981	6.982e-06

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837 **Table 3.** Names and codes of Collembola species

Species name	Code
<i>Desoria tigrina</i>	Destig
<i>Deuterosminthurus sp.</i>	Deutersp
<i>Entomobrya lanuginosa</i>	Entlan
<i>Entomobrya sp. cf multifasciata</i>	Entmul
<i>Entomobryoides purpurascens</i>	Entpur
<i>Entomobrya sp.</i>	Entsp
<i>Folsomia candida</i>	Folcan
<i>Folsomides parvulus</i>	Folpar
<i>Heteromurus nitidus</i>	Hetnit
<i>Isotomurus antennalis</i>	Isoant
<i>Isotomurus palustris</i>	Isopal
<i>Lepidocyrtus cyaneus</i>	Lepcya
<i>Lepidocyrtus lanuginosus</i>	Leplan
<i>Lepidocyrtus lignorum</i>	Leplig
<i>Megalothorax group incertus</i>	Meginc
<i>Megalothorax group minimus</i>	Megmin
<i>Mesaphorura sp.</i>	Messp
<i>Neotullbergia ramicuspis</i>	Neoram
<i>Parisotoma notabilis</i>	Parnot
<i>Proisotoma minima</i>	Promini
<i>Proisotoma minuta</i>	Prominu
<i>Pseudosinella alba</i>	Psealb
<i>Seira domestica</i>	Seidom
<i>Sminthurinus aureus</i>	Smiaur
<i>Sminthurides signatus</i>	Smisig
<i>Sminthurinus group aureus</i>	Smigraur

<i>Sminthurinus elegans</i>	Smiele
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<i>Willowsia platani</i>	Wilpla
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842 **Table 4.** Names and codes of Collembola traits. Micro-habitats (Epi, Eda, Hemi-Eda) were attributed
843 from micro-habitats where species are usually collected (they are not life forms deduced from
844 morphological traits, see Salmon et al. 2014)

Trait code	Trait name
ReproPart	Parthenogenetic reproduction
ReproSex	Sexual reproduction
SpheB	Spherical body
CylB	Cylindrical body
BodyL	Body length
FurcaL	Furcula length
LegL	Leg length
AntL	Antenna length (wearing sensory organ)
Ocel	Number of ocelli (visual organ)
PAOVes	Max number of PAO vesicles (sensory organ)
Tricho	Trichobothria (sensory organ)
Scal	Scales (protective feature)
Pigm	Pigmentation (UV protection)
Psoc	Pseudocelli (defense against predators)
Epi	Micro-habitat Epigeic (above soil surface)
Eda	Micro-habitat Edaphic (soil)
Hemieda	Micro-habitat Hemiedaphic (litter)
Hemi-Eda	Micro-habitat Hemiedaphic & Edaphic (litter and soil)
NS	No specialisation for micro-habitat (depth)

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Figure captions

849 **Fig. 1.** Box-plots of log-transformed abundance (a, decimal logarithm of the number of
850 individuals in 3 pooled samples) and species richness (b, number of species in 3
851 pooled samples) of Collembola for each number of wheat varieties (varnb): 1, 2, 4 and
852 8 varieties per plot. Upper, lower and median bands of boxes, crosses and dots
853 represent first and third quartiles, median, average, minimum and maximum values,
854 respectively. The ends of whiskers are calculated using 1.5 times the interquartile
855 space (distance between 1st and 3rd quartiles).

856

857 **Fig. 2.** Abundance (a, decimal logarithm of the number of individuals in 3 pooled samples)
858 and species richness (b, number of species in 3 pooled samples) of Collembola as a
859 function of the standardized mean sensitivity to septoria (a, b, percentage of leaf area
860 covered by septoria), and specific root length (c) of wheat in each plot. Each dot
861 represents one plot.

862

863 **Fig. 3.** Canonical correspondence analysis (CCA) showing the distribution and assemblage of
864 species (active variables) constrained by the number of wheat variety (nbvar) and the
865 presence of the c2 functional group (5a), three wheat traits (5b) and three soil features
866 (5c) along the first two canonical axes F1 and F2. Explicative variables (c2 functional
867 group, nbvar, Septo, GAIT1, Septo, Co-silt, pH, C_N) were the variables that
868 impacted the most the collembolan assemblages as shown by the CCA PLS. Co-silt:
869 Coarse silt ; C/N: soil carbon to nitrogen ratio, pH: soil pH. See Table 1 for wheat trait
870 abbreviations and Table 3 for Collembola species name abbreviations

871 **Fig. 4.** Redundancy analysis (RDA) showing the distribution and assembly of community
872 weighted-mean (CWM) collembolan functional traits (active variables) constrained by
873 two wheat traits (a) and four soil features (b) along canonical axes F1 and F2. Septo:
874 sensitivity to Septoria; YR: sensitivity to Yellow rust ; Co-silt: Coarse silt; C/N: soil
875 carbon to nitrogen ratio; pH: soil pH; Water: soil water content. See Table1 for wheat
876 trait abbreviations. See Table 4 for collembolan trait abbreviations, Table S1 for
877 collembolan trait values and Salmon et al. (2014) for more details about collembolan
878 traits.

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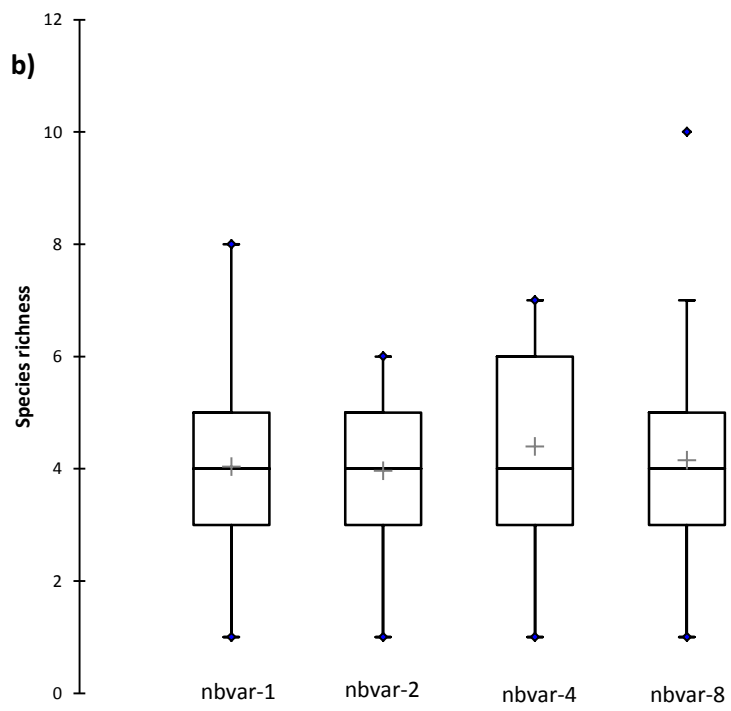
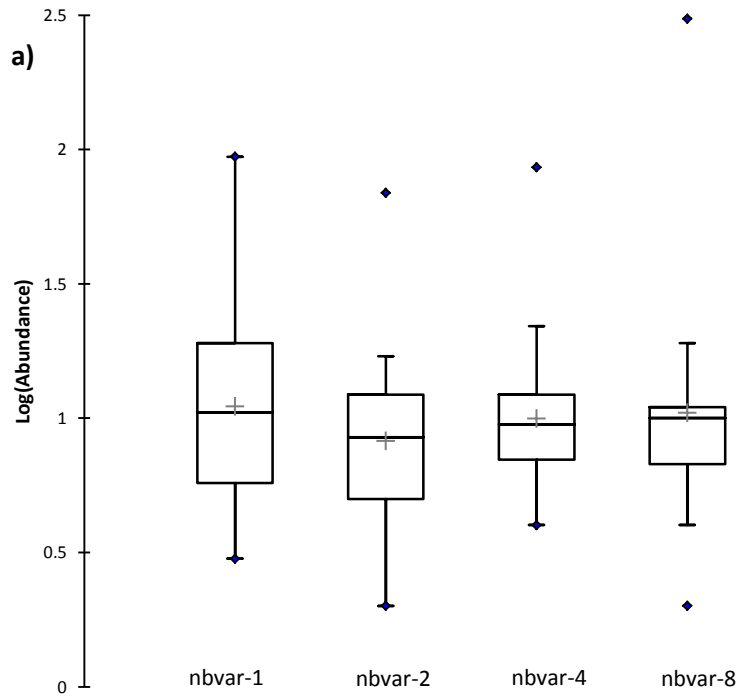
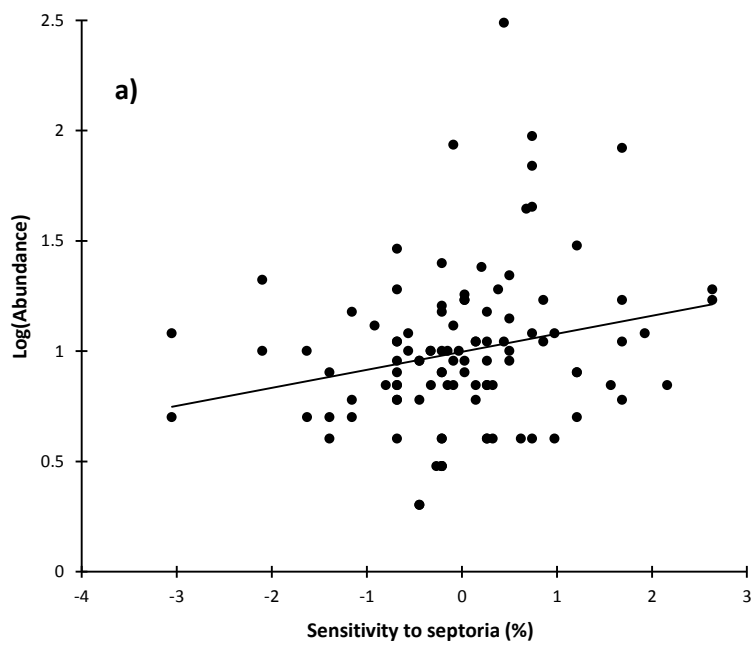
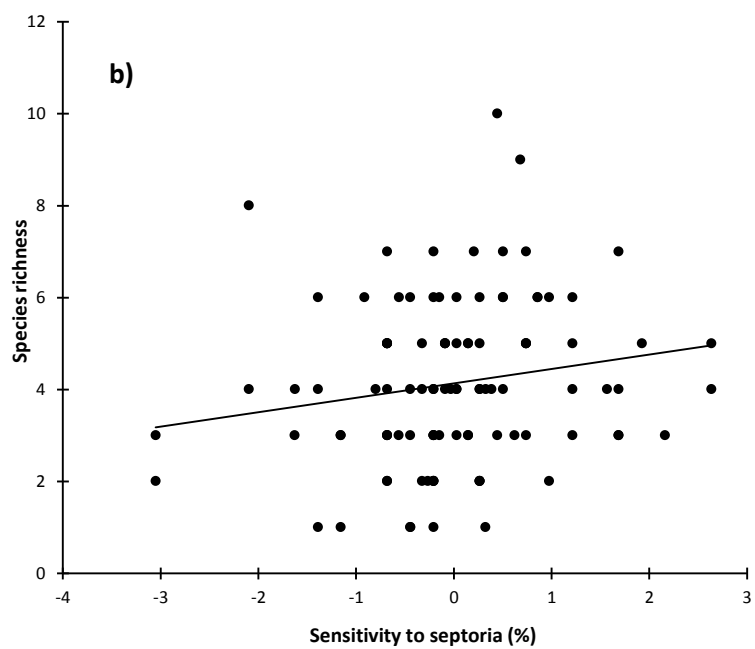


Figure 1

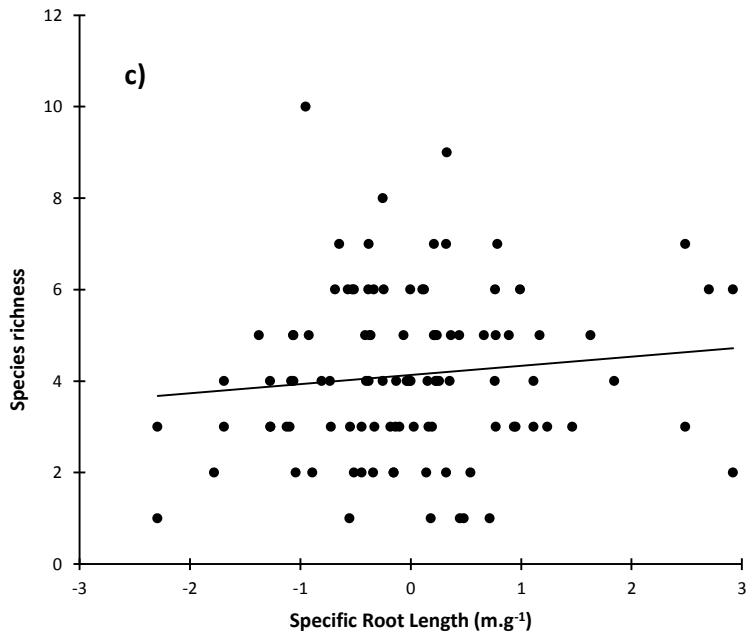
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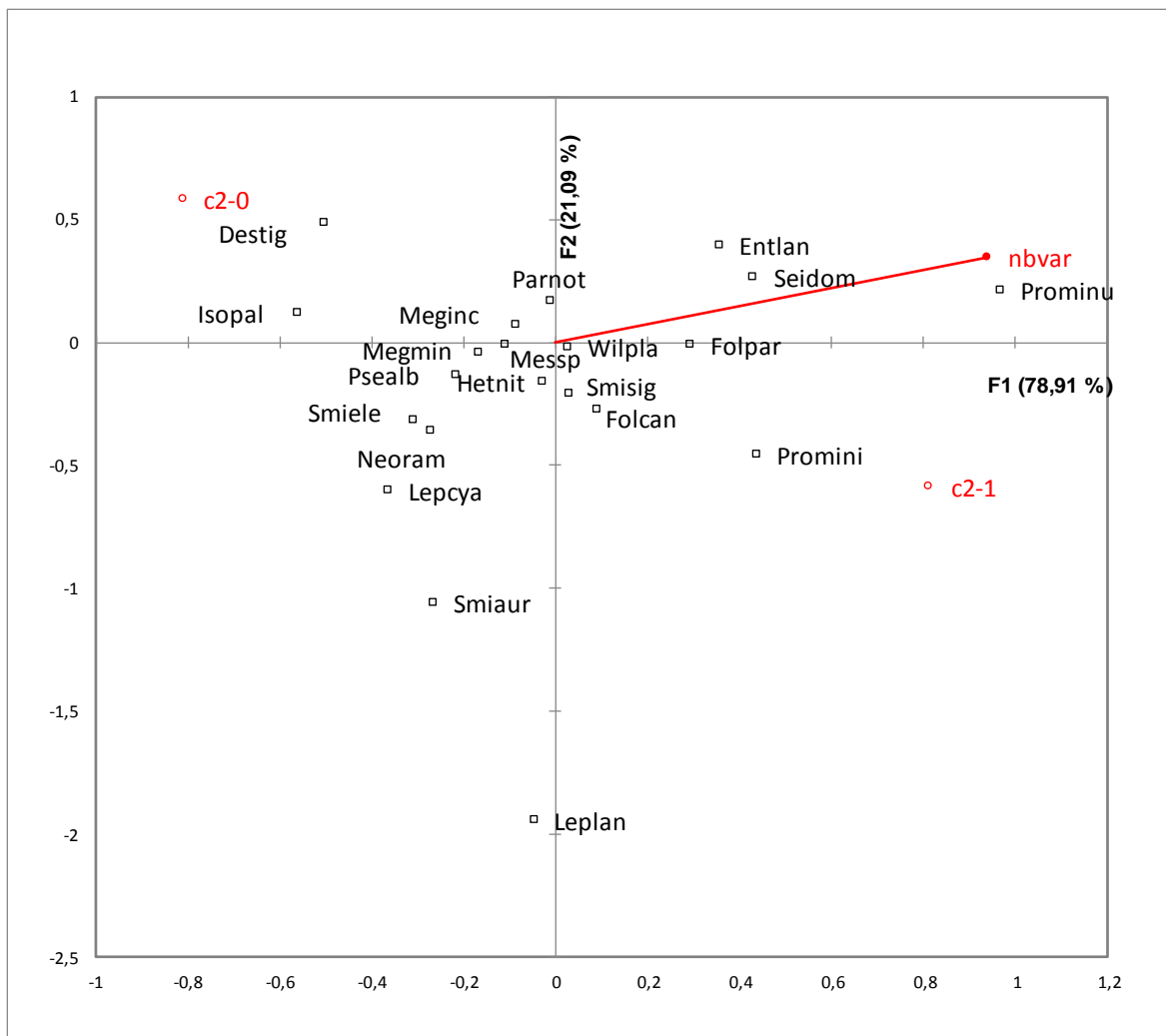
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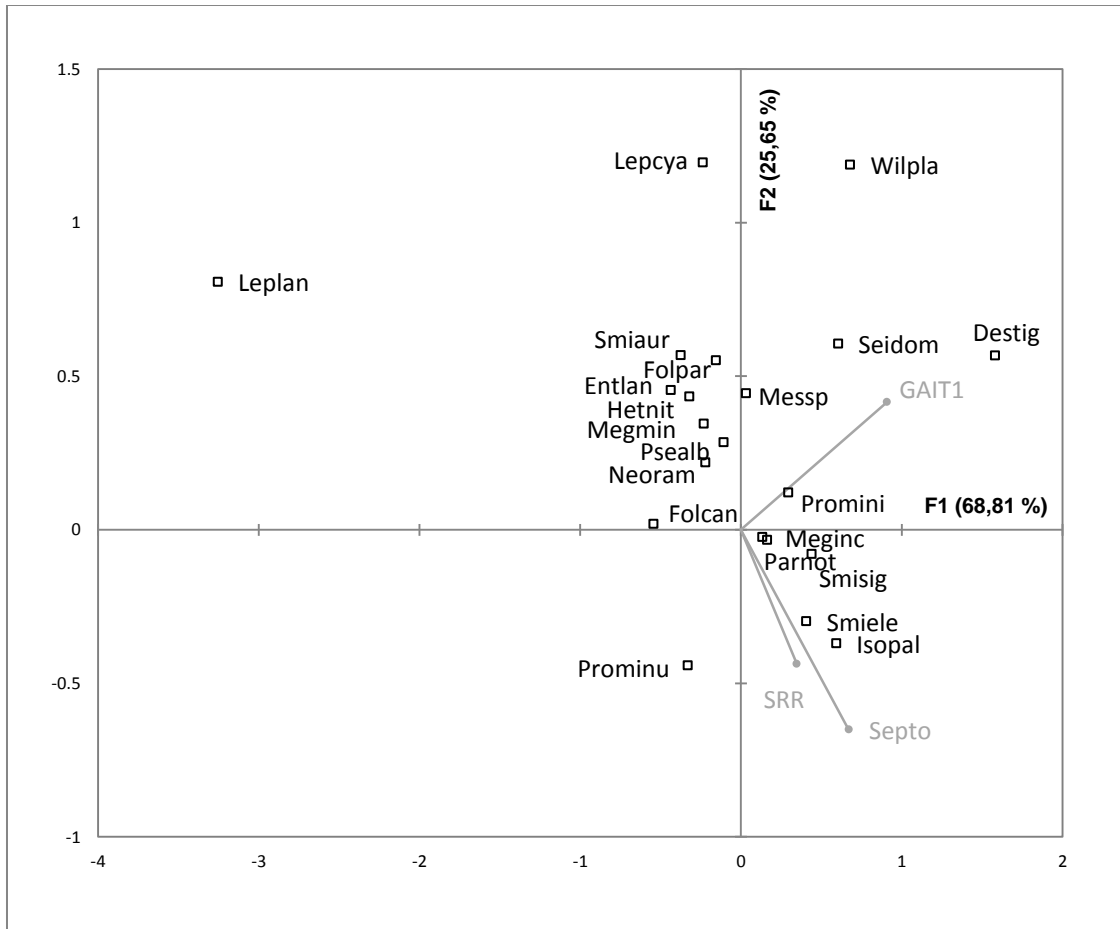
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923 Figure 3a

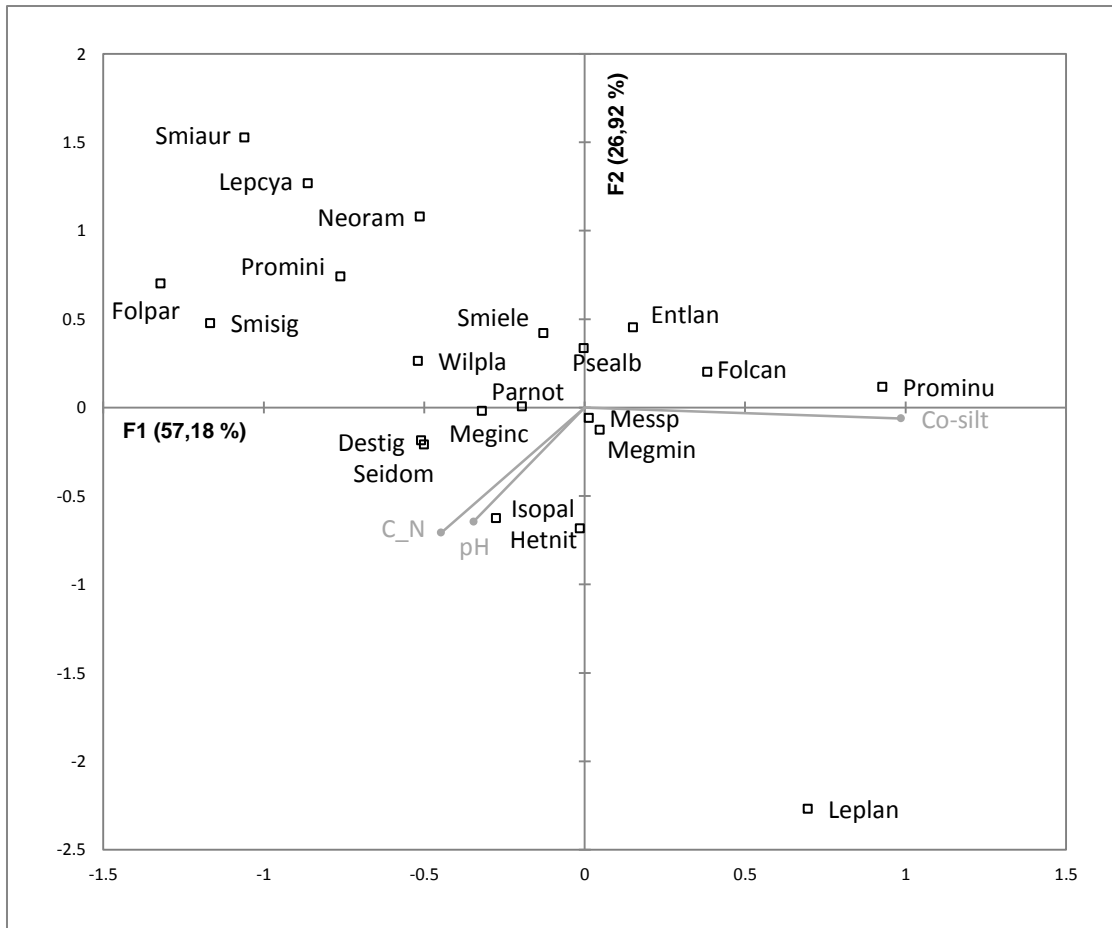
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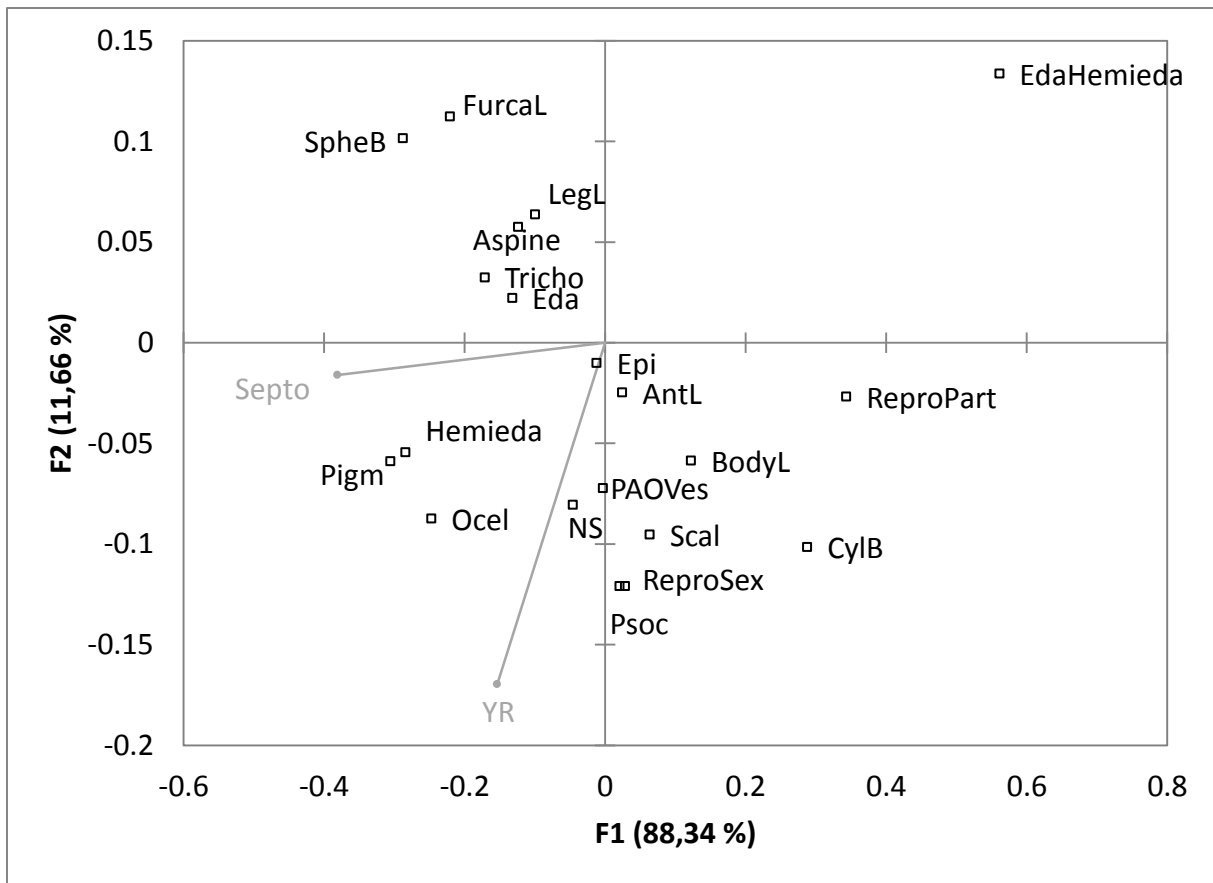
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936 Figure 3b



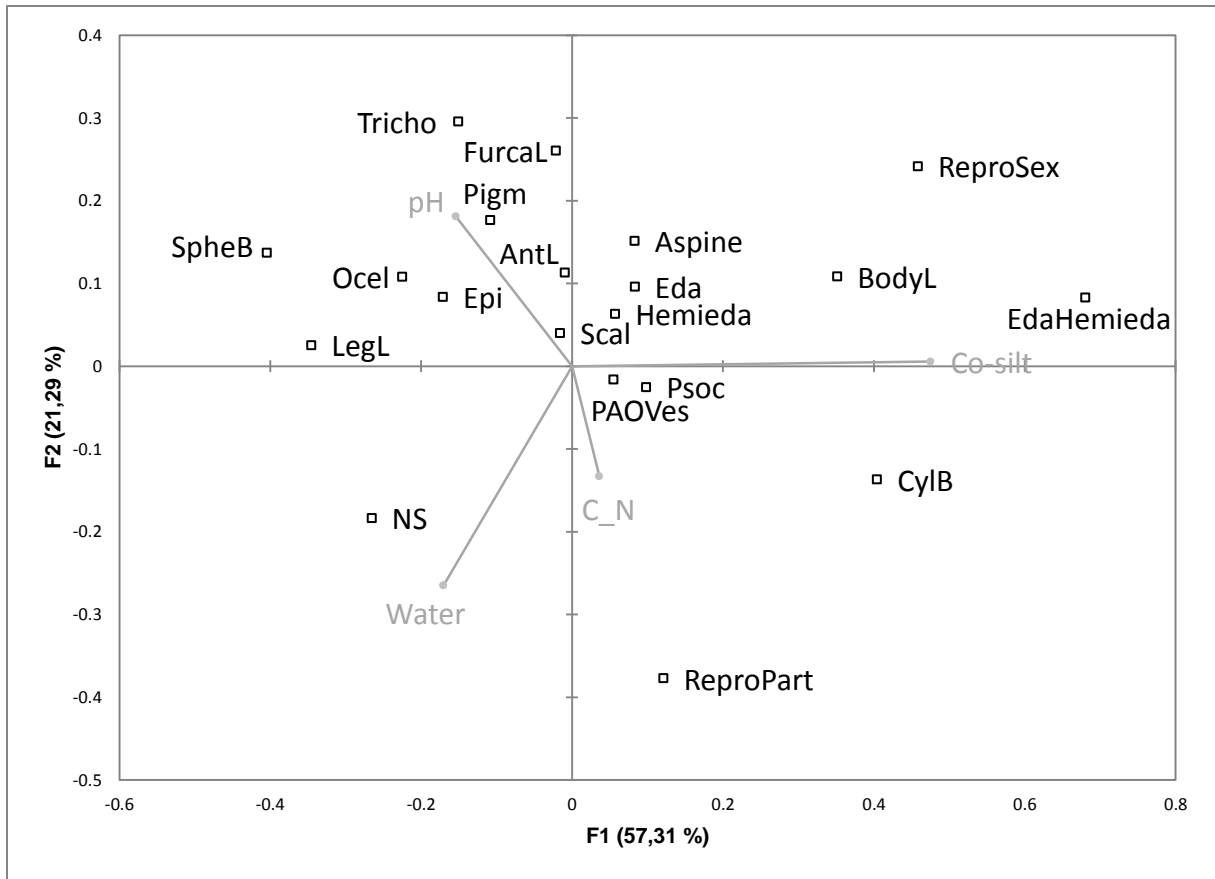
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Figure 3c



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Figure 4a



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Supplementary material

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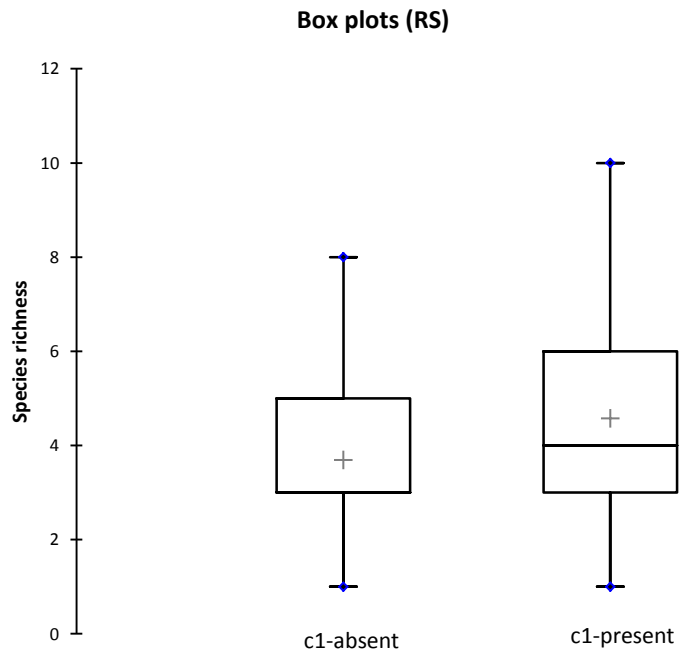
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953 Figure S1 : Part of the experimental design of randomized plots in the Wheatamix project.

954 Orange : pure (1 variety) ; Pink :2 varieties ; Green :4 varieties, Yellow : 8 varieties ;

955 Red : commercial varieties, not taken into account in the present study. Grey bands : Triticale

	A	B	C	D	E	F	G
1,76 m							
10,50 m	107A 107B						
1,76 m		69	11	71	12	85	6
10,50 m							
1,76 m	15	25	79	65	63	105	31
10,50 m							
1,76 m	51	117	63	29	55	14	27
10,50 m							
1,76 m	109	81	77	49	33	115	1
10,50 m							
1,76 m	6	16	35	2	19	21	75
10,50 m							
1,76 m	57	119	53	17	9	41	3
10,50 m							
1,76 m	7	39	113	23	73	37	8
10,50 m							
1,76 m	13	4	61	87	47	10	45
10,50 m							
1,76 m	43	59	111	67	110	91	82
10,50 m							
1,76 m	64	40	80	104	46	114	93
10,50 m							
1,76 m	102	98	26	52	34	78	28
10,50 m							
1,76 m	60	62	97	99	74	106	90
10,50 m							
1,76 m	118	22	54	88	48	30	72
10,50 m							
1,76 m	68	56	32	101	24	76	66
10,50 m							
1,76 m	108	86	96	44	70	89	38
10,50 m							
1,76 m	18	103	42	112A 112B	50	36	94
10,50 m							
1,76 m	116	92	100	20	84	95	58



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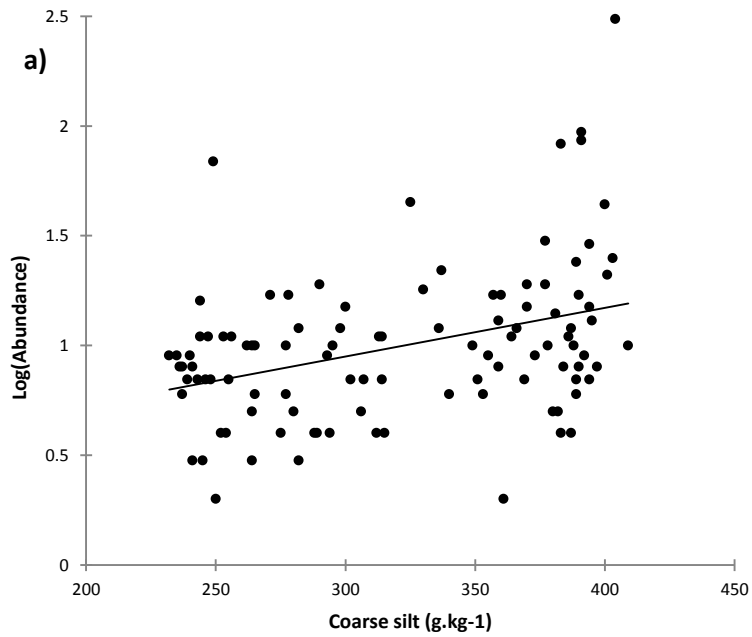
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960 **Fig. S2.** Box-plots of species richness (number of species in 3 pooled samples) of Collembola,
961 comparing plots without (c1-absent) and with (c1-present) the c1 functional group. See
962 Figure 1 for the meaning of boxes, whiskers, crosses and dots.

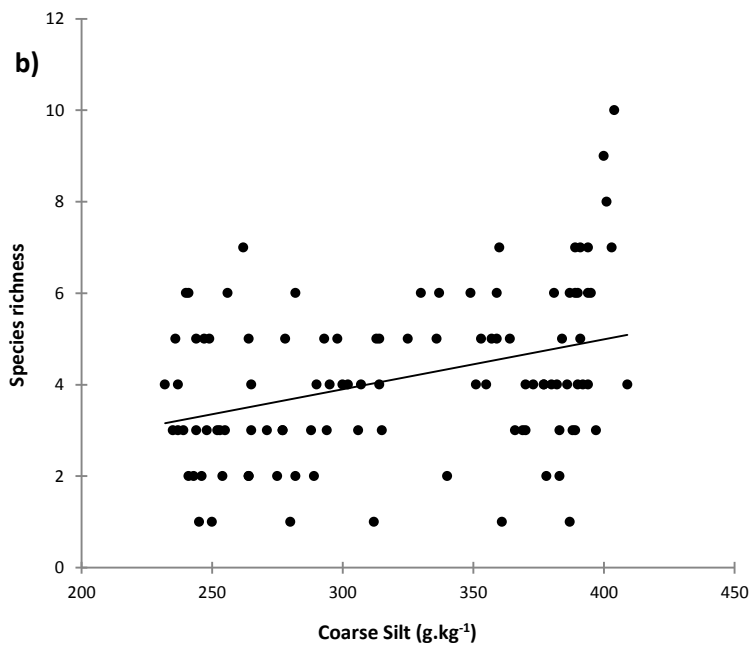
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970 **Figure S3.** Log-transformed abundance (a, decimal logarithm of the number of individuals in
 971 3 pooled samples) and species richness (b, number of species in 3 pooled samples) of
 972 Collembola as a function of the amount of coarse silt (20–50 μm) in soil. Each dot represents
 973 one plot.

1 Table S1: Values of Collembola traits (see Table S1 and S2 for abbreviations of species and trait names)

	Repro Sex	Repro Part	CylB	SpheB	Scal	Pigm	BodyL	Ocel	FurcaL	AntL	PAO Ves	Tricho	Psoc	LegL	Aspine	Micro- Habitat
Destig	1	0	1	0	0	1	2.1	8	4	1.35	1	0	0	0.3	0	NS
Deusp	1	0	1	0	0	1	0.75	8	4	1.87	0	1	0	0.486	0	NS
Entlan	1	0	1	0	0	0	2	8	4	2.337	0	1	0	0.47	0	Epi
Entmul	1	0	1	0	0	1	1.75	8	4	2.407	0	1	0	0.46	0	Epi
Entpur	1	0	1	0	0	1	1.5	8	4	2.35	0	1	0	0.6	0	Epi
Entsp	1	0	1	0	0	0	1.975	8	4	2.7175	0	1	0	0.452	0	Epi
Folcan	1	1	1	0	0	0	1.85	0	3	1.25	1	0	0	0.28	0	Hemi- Eda
Folpar	0	1	1	0	0	0	0.9	2	2	0.9	1	0	0	0.5	0	NS
Hetnit	1	0	1	0	1	1	2.25	2	4	2	0	1	0	0.49	0	Hemi- Eda
Isoant	1	0	1	0	0	1	2.2	8	4	2	1	0	0	0.413	0	Hemieda
Isopal	1	0	1	0	0	1	2.7	8	4	2	1	1	0	0.4	0	NS
Lepcya	1	0	1	0	1	1	1.5	8	4	1.4	0	1	0	0.3925	0	Epi
Leplan	1	0	1	0	1	1	2	8	4	1.6	0	1	0	0.455	0	NS
Leplig	1	0	1	0	1	1	1.8	8	4	1.5	0	1	0	0.48	0	NS
Meginc	0	0	0	1	0	0	0.5	0	4	0.5	0	1	0	0.51	1	Eda
Megmin	0	0	1	0	0	0	0.4	0	4	0.5	0	1	0	0.5	1	Eda

Messsp	1	1	1	0	0	0	0.582	0	0	0	31.8	0	14	0.11	1	Eda
Neoram	1	0	1	0	0	0	1	0	0	0.72	60	0	14	0.14	1	Eda
Parnot	1	1	1	0	0	1	1.2	5	4	0.95	1	0	0	0.34	0	Hemieda
Promini	1	1	1	0	0	0	0.8	5	2	1.05	1	0	0	0.12	0	NS
Prominu	1	0	1	0	0	1	1.2	8	2	0.85	1	0	0	0	0	Epi
Psealb	1	0	1	0	1	0	1.05	2	4	1.8	0	1	0	0.51	0	Eda
Seidom	1	0	1	0	1	0	3	8	4	2.8	0	1	0	0	0	NS
Smiaur	1	0	0	1	0	1	1	8	4	1	0	1	0	0.6	0	Epi
Smidsig	1	0	0	1	0	1	0.3	8	4	1.57	0	1	0	0.49	0	Epi
Smigraur	1	0	0	1	0	1	0.85	8	4	1.2	0	1	0	0.6	0	Epi
Sminele	1	0	0	1	0	1	0.7	8	4	1.4	0	1	0	0.6	0	Epi
Wilpla	1	0	1	0	1	1	3	8	4	2.64	0	1	0	0.34	1	Epi

2

3

4 Table S2: see Excel file
Table S2. Abundances of Collembola species in three pooled samples of 104 plots of the Wheatmix project
nbvar: number of wheat varieties; nbclu: number of clusters (wheat functional groups)
See table 3 for the name of Collembola species

5

6

7 Table S3: Spearman correlation coefficients between explanatory variables

8

9

Variables	nbvar	nbclu	SRR	RDMC	RGR	SRL	RD	GAIT1	GAIT6	Yellow-Rust	Septo	xDD	yDD	Clay	Fi-Silt	Co-Silt	Fi-Sand	Co-Sand	N	C/N	Corg	OM	wa
nbvar	1	0,800	0,180	0,120	-0,055	0,062	0,027	0,018	0,081	0,070	0,026	-0,002	0,031	-0,039	-0,094	-0,051	0,117	0,028	-0,088	0,031	-0,072	-0,076	
nbclu	0,800	1	0,126	0,108	-0,052	0,064	0,023	0,019	0,069	0,066	0,049	-0,045	0,060	-0,075	-0,068	-0,010	0,056	0,023	-0,124	0,079	-0,073	-0,075	
SRR	0,180	0,126	1	0,056	-0,275	0,300	0,333	0,255	0,051	0,004	0,178	-0,201	-0,377	0,315	-0,166	-0,285	0,221	0,265	0,314	-0,166	0,156	0,155	
RDMC	0,120	0,108	0,056	1	0,695	-0,581	0,052	-0,235	0,147	0,111	0,099	0,035	0,066	-0,024	0,081	0,070	-0,142	-0,027	-0,018	0,042	-0,018	-0,021	
RGR	-0,055	-0,052	-0,275	0,695	1	-0,928	0,009	-0,206	0,067	0,277	0,303	0,203	0,078	-0,030	0,014	0,053	-0,129	-0,002	-0,033	0,190	0,063	0,065	
SRL	0,062	0,064	0,300	-0,581	-0,928	1	0,065	0,280	-0,204	-0,228	-0,208	-0,242	-0,045	0,011	0,021	-0,020	0,090	-0,016	-0,012	-0,188	-0,109	-0,110	
RD	0,027	0,023	0,333	0,052	0,009	0,065	1	-0,059	-0,030	0,095	0,450	-0,053	-0,089	0,026	0,017	-0,024	0,033	-0,009	0,058	-0,031	0,052	0,054	
GAIT1	0,018	0,019	0,255	-0,235	-0,206	0,280	-0,059	1	-0,191	0,473	0,262	0,064	-0,131	0,135	-0,277	-0,226	0,291	0,203	0,108	0,005	0,111	0,113	
GAIT6	0,081	0,069	0,051	0,147	0,067	-0,204	-0,030	-0,191	1	-0,450	-0,036	-0,047	-0,048	0,111	-0,033	-0,064	0,014	0,069	0,053	-0,039	0,020	0,018	
Yellow-Rust	0,070	0,066	0,004	0,111	0,277	-0,228	0,095	0,473	-0,450	1	0,486	0,240	0,040	-0,056	-0,117	0,000	0,058	0,015	0,012	0,197	0,155	0,159	
Septo	0,026	0,049	0,178	0,099	0,303	-0,208	0,450	0,262	-0,036	0,486	1	0,040	-0,110	0,101	-0,154	-0,116	0,099	0,135	0,039	0,063	0,100	0,103	
xDD	-0,002	-0,045	-0,201	0,035	0,203	-0,242	-0,053	0,064	-0,047	0,240	0,040	1	-0,097	0,212	-0,278	-0,252	0,224	0,247	0,314	0,710	0,646	0,646	
yDD	0,031	0,060	-0,377	0,066	0,078	-0,045	-0,089	-0,131	-0,048	0,040	-0,110	-0,097	1	-0,845	0,648	0,867	-0,723	-0,793	-0,823	0,134	-0,628	-0,627	
Clay	-0,039	-0,075	0,315	-0,024	-0,030	0,011	0,026	0,135	0,111	-0,056	0,101	0,212	-0,845	1	-0,681	-0,861	0,643	0,799	0,814	-0,027	0,679	0,679	
Fi-Silt	-0,094	-0,068	-0,166	0,081	0,014	0,021	0,017	-0,277	-0,033	-0,117	-0,154	-0,278	0,648	-0,681	1	0,833	-0,895	-0,808	-0,586	-0,112	-0,572	-0,570	
Co-Silt	-0,051	-0,010	-0,285	0,070	0,053	-0,020	-0,024	-0,226	-0,064	0,000	-0,116	-0,252	0,867	-0,861	0,833	1	-0,878	-0,935	-0,785	0,024	-0,659	-0,658	
Fi-Sand	0,117	0,056	0,221	-0,142	-0,129	0,090	0,033	0,291	0,014	0,058	0,099	0,224	-0,723	0,643	-0,895	-0,878	1	0,767	0,634	-0,025	0,535	0,534	
Co-Sand	0,028	0,023	0,265	-0,027	-0,002	-0,016	-0,009	0,203	0,069	0,015	0,135	0,247	-0,793	0,799	-0,808	-0,935	0,767	1	0,714	0,040	0,630	0,628	
N	-0,088	-0,124	0,314	-0,018	-0,033	-0,012	0,058	0,108	0,053	0,012	0,039	0,314	-0,823	0,814	-0,586	-0,785	0,634	0,714	1	-0,032	0,836	0,835	
C/N	0,031	0,079	-0,166	0,042	0,190	-0,188	-0,031	0,005	-0,039	0,197	0,063	0,710	0,134	-0,027	-0,112	0,024	-0,025	0,040	-0,032	1	0,490	0,490	
Corg	-0,072	-0,073	0,156	-0,018	0,063	-0,109	0,052	0,111	0,020	0,155	0,100	0,646	-0,628	0,679	-0,572	-0,659	0,535	0,630	0,836	0,490	1	1,000	
OM	-0,076	-0,075	0,155	-0,021	0,065	-0,110	0,054	0,113	0,018	0,159	0,103	0,646	-0,627	0,679	-0,570	-0,658	0,534	0,628	0,835	0,490	1,000	1	
water	0,090	0,030	0,177	-0,140	-0,206	0,159	-0,057	0,141	-0,013	0,051	-0,011	-0,031	-0,471	0,379	-0,092	-0,317	0,261	0,208	0,527	-0,247	0,335	0,337	
pH	-0,041	-0,057	0,108	-0,056	0,050	-0,069	0,111	0,138	0,045	-0,003	0,071	0,138	-0,201	0,271	-0,447	-0,350	0,409	0,326	0,264	0,039	0,276	0,273	
c1	0,401	0,518	0,053	0,457	0,432	-0,339	0,263	0,065	0,149	0,429	0,532	0,078	0,049	-0,026	-0,033	-0,010	-0,004	0,045	-0,042	0,104	0,043	0,044	
c2	0,401	0,518	-0,018	0,123	0,166	-0,357	-0,123	-0,452	0,185	-0,098	-0,233	-0,018	0,053	-0,071	0,001	0,044	-0,049	-0,010	-0,029	0,045	0,001	-0,002	
c3	0,401	0,518	0,219	0,013	-0,174	0,295	-0,081	0,502	-0,413	0,269	-0,124	0,035	-0,050	0,001	-0,154	-0,113	0,184	0,079	0,072	0,009	0,050	0,050	
c4	0,401	0,518	-0,002	-0,384	-0,522	0,525	-0,012	-0,070	0,212	-0,475	-0,068	-0,243	0,041	-0,080	0,096	0,054	-0,033	-0,055	-0,192	-0,125	-0,247	-0,249	

10

variable codes variable name and unity

xDD geographical coordinate x

yDD geographical coordinate y

pH soil pH

water	water content in soil cores(g)
Clay	clay (< 2 μm) (g/kg)
Fi-Silt	fine silt (2/20 μm) (g/kg)
Co- Silt	coarse silt (20/50 μm) (g/kg)
Fi- Sand	fine sand (50/200 μm) (g/kg)
Co-Sand	coarse sand (200/2000 μm)
N	Total Nitrogen (g/kg)
C/N	C/N ratio
Corg	Organic Carbon (g/kg)
OM	Organic matter (g/kg)
RDMC	Mean of Root Dry Matter content (mg.g-1)
RGR	Mean of Relative Growth rate (mg.day-1)
SRL	Mean Specific Root Length (m.g-1)
RD	Mean of Root Diameter (mm)
GAIT1	Mean Green Area Index in December= ratio of leaf green area to ground area
GAIT6	Mean of Green Area Index in April= ratio of leaf green area to ground area
Yellow Rust	Mean sensitivity to Yellow Rust (mean percentage of sporulating area)
Septoria	Mean of sensitivity to Septoria leaf blotch (mean percentage of sporulating area)

12 Table S4: Results of glm on the effect of the variety number (nbvar), composition of wheat variety assemblies (C1..) and soil parameters on the
 13 species richness of collembola (full model followed by final model, followed by Analysis of Deviance Table; intermediate model
 14 indicated that no interaction was significant)

```

15 Mod1 <- glmmTMB (RS ~ nbvar+ c1+ c2+ c3+c4+Co-silt+C_N+eau+pH, data= datanorm, family = gaussian)
16 > summary(Mod1)
17 Family: gaussian ( identity )
18 Formula:
19 RS ~ nbvar + c1 + c2 + c3 + c4 + Co-silt + C_N +water+ pH
20 Data: datanorm
21
22      AIC      BIC  logLik deviance df.resid
23  408.7   437.8  -193.3   386.7     93
24
25
26 Dispersion estimate for gaussian family (sigma^2): 2.41
27
28 Conditional model:
29      Estimate Std. Error z value Pr(>|z|)
30 (Intercept)  3.69880    0.32645  11.330 < 2e-16 ***
31 nbvar       -0.05125    0.08364  -0.613 0.540057
32 c1           0.90900    0.34351   2.646 0.008140 **
33 c2          -0.29404    0.33605  -0.875 0.381587
34 c3          -0.06463    0.33780  -0.191 0.848278
35 c4           0.66819    0.33888   1.972 0.048635 *
36 Co-silt      0.60274    0.17530   3.438 0.000585 ***
37 C_N          0.09837    0.15733   0.625 0.531815
38 water       -0.09545    0.16650  -0.573 0.566479
39 pH           0.02284    0.16640   0.137 0.890812
40

```

```

41 Mod1 <- glmmTMB (RS~Co-silt+c1, data= datanorm, family = gaussian)
42 > summary(Mod1)
43
44 Family: gaussian ( identity )
45 Formula:      RS ~ Co-silt + c1
46 Data: datanorm
47

```

```

48      AIC      BIC  logLik deviance df.resid
49  400.7    411.3  -196.4   392.7     100
50
51
52 Dispersion estimate for gaussian family (sigma^2): 2.56
53
54 Conditional model:
55      Estimate Std. Error z value Pr(>|z|)
56 (Intercept)  3.6933    0.2217  16.660 < 2e-16 ***
57 Co-silt      0.6354    0.1568   4.054 5.05e-05 ***
58 c1           0.8827    0.3135   2.816 0.00487 **
59
60
61
62
63
64
65 > library(car)
66 > Anova(Mod1)
67 Analysis of Deviance Table (Type II wald chisquare tests)
68
69 Response: RS
70      Chisq Df Pr(>Chisq)
71 Limg 16.4311  1 5.045e-05 ***
72 c1    7.9275  1 0.004869 **
73
74

```

75

76 Table S5 : Results of glm on the effect of the functional group number of wheat (nbclu), wheat traits and soil parameters on the species richness
 77 of Collembola (full model followed by final model, followed by Analysis of Deviance Table; intermediate model indicated that no
 78 interaction was significant)

79

```

80 Mod1 <- glmmTMB (RS ~ nbclu+SRR+SRL+RD+GAIT1+GAIT6+YR+Septo+Co-silt+C_N+eau+pH, data= datanorm, family = gaussian)
81 > summary(Mod1)
82 Family: gaussian ( identity )
83 Formula:
84 RS ~ nbclu + SRR + SRL + RD + GAIT1 + GAIT6 + YR + Septo + Co-silt +
85 C_N +water+ pH
86 Data: datanorm
87
88      AIC      BIC  logLik deviance df.resid
89  409.3    446.3  -190.7   381.3      90
90
91
92 Dispersion estimate for gaussian family (sigma^2): 2.29
93
94 Conditional model:
95      Estimate Std. Error z value Pr(>|z|)
96 (Intercept)  3.69358    0.31809  11.612 < 2e-16 ***
97 nbclu        0.22052    0.14068   1.568 0.116989
98 SRR         -0.09037    0.19944  -0.453 0.650474
99 SRL          0.47410    0.18780   2.525 0.011584 *
100 RD           0.02947    0.21767   0.135 0.892299
101 GAIT1       -0.21507    0.20844  -1.032 0.302163
102 GAIT6        0.18229    0.19650   0.928 0.353586
103 YR          -0.04138    0.26335  -0.157 0.875141
104 Septo        0.53499    0.22318   2.397 0.016526 *
105 Co-silt      0.63010     0.17474   3.606 0.000311 ***
106 C_N          0.15544    0.15797   0.984 0.325123
107 water       -0.16827     0.16276  -1.034 0.301219

```

```

108 pH          0.01884    0.16422    0.115 0.908689
109
110

```

```

111 Mod1 <- glmTMB (RS ~ SRL + Septo + Co-silt, data= datanorm, family = gaussian)
112 summary(Mod1)

```

```

113
114 Family: gaussian (identity)
115 Formula:          RS ~ SRL + Septo + Co-silt
116 Data: datanorm
117
118      AIC      BIC  logLik deviance df.resid
119  400.6   413.8  -195.3   390.6         99
120
121

```

```

122 Dispersion estimate for gaussian family (sigma^2): 2.5
123

```

```

124 Conditional model:

```

```

125      Estimate Std. Error z value Pr(>|z|)
126 (Intercept)  4.1346      0.1552  26.645 < 2e-16 ***
127 SRL          0.3197      0.1582   2.021 0.04331 *
128 Septo       0.4467      0.1589   2.811 0.00493 **
129 Co-silt     0.7034      0.1566   4.492 7.06e-06 ***
130

```

```

131 library(car)

```

```

132 Anova(Mod1)

```

```

133 Analysis of Deviance Table (Type II wald chisquare tests)
134

```

```

135 Response: RS

```

```

136      Chisq Df Pr(>Chisq)
137 SRL    4.0832 1 0.043311 *
138 Septo  7.9036 1 0.004934 **
139 Limg  20.1757 1 7.065e-06 ***
140

```

```

141

```

142

143 Table S6: Results of glm on the effect of the variety number (nbvar), composition of wheat variety assemblies (C1..) and soil parameters on the

144 Log of Collembola abundance (full model followed by final model, followed by Analysis of Deviance Table; intermediate model

145 indicated that no interaction was significant)

```
146 Mod1 <- glmmTMB (LogAb~ nbvar+ c1+ c2+ c3+c4+Co-silt+C_N+water+pH, data= datanorm, family = gaussian)
```

```
147 summary(Mod1)
```

```
148 Family: gaussian ( identity )
```

```
149 Formula:
```

```
150 LogAb ~ nbvar + c1 + c2 + c3 + c4 + Co-silt + C_N +water+ pH
```

```
151 Data: datanorm
```

152

	AIC	BIC	logLik	deviance	df.resid
	77.9	107.0	-27.9	55.9	93

155

156

```
157 Dispersion estimate for gaussian family (sigma^2): 0.1
```

158

```
159 Conditional model:
```

	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	1.02129	0.06655	15.347	< 2e-16	***
nbvar	0.01233	0.01705	0.723	0.4696	
c1	0.05521	0.07003	0.788	0.4304	
c2	-0.13935	0.06851	-2.034	0.0419	*
c3	-0.07537	0.06886	-1.094	0.2738	
c4	0.02859	0.06908	0.414	0.6790	
Co-silt	0.14121	0.03574	3.951	7.77e-05	***
C_N	0.03117	0.03207	0.972	0.3312	
water	0.02246	0.03394	0.662	0.5083	
pH	0.01312	0.03392	0.387	0.6989	

171

172

173

```
174 Mod1 <- glmmTMB (LogAb~ Co-silt+c2, data= datanorm, family = gaussian)
```

```
175 > summary(Mod1)
```

```
176 Family: gaussian ( identity )
```

```
177 Formula:          LogAb ~ Co-silt + c2
```

```

178 Data: datanorm
179
180      AIC      BIC  logLik deviance df.resid
181    68.4    79.0   -30.2    60.4     100
182
183
184 Dispersion estimate for gaussian family (sigma^2): 0.105
185
186 Conditional model:
187      Estimate Std. Error z value Pr(>|z|)
188 (Intercept)  1.05450    0.04490  23.485 < 2e-16 ***
189 Co-silt      0.13164    0.03177   4.144 3.42e-05 ***
190 c2          -0.11388    0.06354  -1.792  0.0731 .
191
192 Anova\(Mod1\)
193 Analysis of Deviance Table (Type II wald chisquare tests)
194
195 Response: LogAb
196      Chisq Df Pr(>Chisq)
197 Limg 17.1698  1  3.418e-05 ***
198 c2    3.2121  1  0.07309 .
199
200
201
202
203

```

204
 205 Table S7 : Results of glm on the effect of the functional group number of wheat (nbclu), wheat traits and soil parameters on the Log of
 206 Collembola abundance (full model followed by final model, followed by Analysis of Deviance Table; intermediate model indicated that
 207 no interaction was significant)

```
208 Mod1 <- glmTMB (LogAb~ nbclu+SRR+SRL+RD+GAIT1+GAIT6+YR+Septo+Co-silt+C_N+eau+pH, data= datanorm, family = gaussian)
209 > summary(Mod1)
```

```
210 Family: gaussian ( identity )
211 Formula:
212 LogAb ~ nbclu + SRR + SRL + RD + GAIT1 + GAIT6 + YR + Septo +
213 Co-silt + C_N +water+ pH
214 Data: datanorm
```

```
215
216      AIC      BIC  logLik deviance df.resid
217 76.7    113.7   -24.4    48.7      90
```

```
218
219
220 Dispersion estimate for gaussian family (sigma^2): 0.0935
```

```
221 Conditional model:
222      Estimate Std. Error z value Pr(>|z|)
223 (Intercept)  1.022507   0.064282  15.907 < 2e-16 ***
224 nbclu        -0.012473   0.028429  -0.439  0.66084
225 SRR          -0.015933   0.040304  -0.395  0.69260
226 SRL          0.033206   0.037951   0.875  0.38159
227 RD           0.012039   0.043987   0.274  0.78432
228 GAIT1        0.008373   0.042122   0.199  0.84244
229 GAIT6       -0.005605   0.039711  -0.141  0.88775
230 YR          -0.068785   0.053220  -1.292  0.19620
231 Septo        0.132573   0.045102   2.939  0.00329 **
232 Co-silt      0.152664   0.035312   4.323  1.54e-05 ***
233 C_N          0.037322   0.031923   1.169  0.24235
234 water        0.017596   0.032892   0.535  0.59268
235 pH           0.005600   0.033188   0.169  0.86600
```

```
236
237
238
239
240
241
242
```



```

243 Mod1 <- glmmTMB (LogAb~ Septo+Co-silt, data= datanorm, family = gaussian)
244 summary(Mod1)
245 Family: gaussian ( identity )
246 Formula:      LogAb ~ Septo + Co-silt
247 Data: datanorm
248
249      AIC      BIC  logLik deviance df.resid
250  62.3    72.9   -27.2    54.3     100
251
252
253 Dispersion estimate for gaussian family (sigma^2): 0.0987
254
255 Conditional model:
256      Estimate Std. Error z value Pr(>|z|)
257 (Intercept)  0.99756    0.03081  32.38 < 2e-16 ***
258 Septo        0.09661    0.03099   3.12  0.00183 **
259 Co-silt      0.13929    0.03099   4.49  6.98e-06 ***
260
261 library(car)
262 Anova(Mod1)
263 Analysis of Deviance Table (Type II wald chisquare tests)
264
265 Response: LogAb
266      Chisq Df Pr(>Chisq)
267 Septo    9.7172 1  0.001826 **
268 Co-silt 20.1981 1  6.982e-06 ***
269
270
271
272
273

```