

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

Sandrine S. Salmon, Tom Vittier, Sébastien Barot, Jean-François Ponge,

Farida Ben Assoula, Pauline Lusley

▶ 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

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

2 Responses of Collembola communities to mixtures of wheat varieties: a

3 trait-based approach

- 4 Sandrine Salmon^{a1}, Tom Vittier^a, Sébastien Barot^b, Jean-François Ponge^a, Farida Ben
- 5 Assoula^a, Pauline Lusley^{c,d} and the Wheatamix consortium
- 6 ^aMuséum National d'Histoire Naturelle, Département Adaptations du Vivant, CNRS UMR
- 7 7179 MECADEV, 4 avenue du Petit Château, 91800 Brunoy, France
- 8 ^bIEES-Paris (CNRS, UPMC, IRD, INRA, UPEC), UPMC, 4 place Jussieu, 75252 Paris Cedex
- 9 *05, France*
- 10 ^cINRA UMR ECOSYS, AgroParisTech, Université Paris-Saclay, 78850 Thiverval-Grignon,
- 11 France
- ¹² ^dUniLaSalle, Campus de Rouen, 3 rue du Tronquet, BP 76130 Mont Saint Aignan, France
- 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

¹Corresponding author.

E-mail address: <u>sandrine.salmon@mnhn.fr</u> (Sandrine Salmon)

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

43 *Keywords:* crop management practices; genetic diversity; arthropod communities; wheat

44 variety mixture; functional diversity; plant functional traits

45 **1. Introduction**

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

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

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

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

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

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).

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

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

In the present study, we assessed whether the number of wheat varieties (genetic diversity), the number of functional groups (functional diversity), the composition of functional groups and wheat traits influence 1) the species richness and abundance of Collembola, and (2) species and trait assemblages of Collembola. The focus on functional traits of communities (e.g. plants), in addition to species, is an approach which allows addressing directly the functions fulfilled by organisms both at species and community levels
(Vandewalle et al., 2010). Several studies showed that functional traits of Collembola allow
better predicting environmental effects on soil collembolan communities than species do
(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

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

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

Functional group c2 comprised wheat varieties with short root lengths, high rate of NO_3^{-1} 143 absorption, high relative growth rate and low sensitivity to fungal diseases. The c3 functional 144 group was composed of varieties characterized by their slow growth but elevated 145 aggressiveness regarding plant-plant competition, and with high rate of NH₄⁺ absorption 146 capacity. Finally, the c4 functional group contained varieties with high specific root lengths, 147 low relative growth rate and low rate of NO_3^{-1} absorption capacity (Dubs et al. 2018a). Sixteen 148 149 varieties have been selected to be used in the experiment, in order to maximize the overall functional diversity: for each cluster four varieties have been chosen avoiding varieties too far 150 from the center of the cluster (thus varieties not representative of the cluster) and avoiding 151 152 varieties that are too similar within the cluster. These 16 varieties were used to create 72 combinations of varieties encompassing three levels of diversity: 24, 28, and 20 mixtures 153 combining 2, 4 and 8 varieties, respectively (Dubs et al., 2018a). The number of functional 154 155 groups also varied in each of the three levels of variety mixtures: some mixtures were functionally "homogeneous" (a single functional group) while other were heterogeneous (two 156 157 or more functional groups). Thus, these mixtures have been implemented for experimental purpose, to be able to compare mixtures with different number of varieties and different levels 158 of functional diversity. These mixtures were clearly not designed because of their particular 159 160 relevance for farmers. The list of varieties, mixtures and their distribution over the 104 plots are detailed in Dubs et al. (2018a). The 72 mixtures have been seeded into 72 plots and the 16 161 varieties have also been seeded alone, in duplicate, providing a total of 104 10.5 m x 8.0 m 162 plots encompassing 4 levels of variety mixtures (1, 2, 4 and 8 varieties each). 163

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

were used except for seed coating, the same for all varieties for which CELEST (2 1 t^{-1} -168 Fludioxonil 25 g l^{-1}) and SIGNAM (0.6 kg g t^{-1} -Cypermethryne 300 g l^{-1}) were used. One 169 spraying of two herbicides (Archipel®, 50% Iodosulfuron and 50% Mesosulfuron; Harmony 170 Extra®, 66 % thifensulfuron-methyl and 33% tribenuron-methyle) was performed on March 171 14, 2015. 160 kg N ha⁻¹was used as compared to the estimated optimal amount of 180 kg N 172 ha⁻¹. The fertilizer (ammonium-nitrate) was spread as follows: 40 kg N ha⁻¹ on March 5, 2015, 173 80 kg N ha⁻¹on April 16, 2015, 40 kg N ha⁻¹on May 11, 2015. All plots were harvested 174 175 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

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

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

198 2.3. Statistical analysis

Abundances of collembolan species in the three samples taken in each plot werepooled for the calculation of abundance and species richness per plot.

We performed generalized linear models (GLM) to determine whether the abundance 201 202 and species richness of Collembola were influenced by the number of wheat varieties, wheat functional diversity (number of functional groups), functional group composition (c1, c2, c3, 203 or c4) and mean of wheat functional traits in variety mixtures. Given the high number of 204 205 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 diseases. At least some collembolan species are known to live and feed on roots (Thimm and 207 208 Larink, 1995), depend on plant cover (Heiniger et al., 2015) and feed on fungi, including pathogenic fungi (Friberg et al., 2005; Jorgensen et al., 2005; Ponge, 1988). Wheat trait 209 measures and soil features were then standardized (thus discarding spurious effects of various 210 units). Spearman correlation coefficients were calculated between wheat traits, soil features 211 and geographical coordinates in order to eliminate correlated explanatory variables (Table 212 213 S3). As coarse silt was highly correlated with other particle size fractions and with geographical coordinates according to a textural gradient, the latter two sets of variables were 214 215 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 coarse silt and remove geographical coordinates. The set of soil features selected for further
analyses was coarse silt, soil pH, soil water content and C/N ratio. Correlation coefficients
also allowed to select the set of wheat traits used in further analyses (Table 1).

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

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

241 "Zeroinflation" (tests if there are more zeros than expected). In order to fulfil all model242 assumptions (especially dispersion), collembolan abundances were log-transformed.

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

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

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

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

wheat diversity and of the two other types of wheat traits. RDAs were followed by MonteCarlo 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*

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

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

314

.

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

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

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

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

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

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

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

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

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

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

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

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

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

We observed that the composition of the functional groups of wheat and some traits influence the species richness and abundance of Collembola. Collembolan species richness 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).

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

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

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

499 Wheat traits related to the sensitivity to fungal diseases and to characteristics of aerial (plant cover) and root parts impacted significantly, although weakly, the distribution of 500 501 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 especially to septoria leaf blotch, were the only trait the effect of which remains significant 504 505 after deleting the effect of all other variables. Among species associated to wheat varieties sensitive to septoria leaf blotch, Parisotoma notabilis, Sminthurinus elegans and 506 Megalothorax incertus group are known to feed on fungi (Addison et al., 2003; Gillet and 507

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

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

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

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

increase collembolan species richness by providing more habitat and food. Moreover, our 558 study suggests that keeping in mixture some wheat varieties with a lower resistance to fungal 559 diseases (e.g. by selecting other traits related to higher yield) could be compensated by the 560 561 consumption of fungal pathogens by Collembola (Sabatini et al., 2000), which would contribute to increase collembolan species richness. This greater effect of the composition of 562 wheat varieties could explain why our results, contrast with those of a previous study (Chateil 563 et al., 2013), which showed that wheat genetic diversity increased the species richness of 564 several groups of invertebrates, including Collembola. In fact, the field experiment of Chateil 565 et al. (2013) encompassed a low number of wheat varieties, and the varieties added in the 566 567 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 features, especially particle size, impacted more strongly Collembola than wheat composition 572 573 or diversity. Our study suggests that, at least in conventional agroecosystems, other factors such as soil features, but also perhaps the surrounding landscape or agricultural practices 574 contribute more to structuring collembolan communities than intraspecific diversity. Studying 575 the effect of the diversity of wheat varieties using the same experimental method (high 576 577 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 the impact of intraspecific diversity and composition of plants on soil invertebrate 579 580 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

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

589 **References**

- Abrams, P., 1983. The theory of limiting similarity. Annu. Rev. Ecol. Syst. 14, 359-376.
- Axelsen, J.A., Kristensen, K.T., 2000. Collembola and mites in plots fertilised with different
 types of green manure. Pedobiologia 44, 556-566.
- Barot, S., Allard, V., Cantarel, A., Enjalbert, J., Gauffreteau, A., Goldringer, I., Lata, J.C., Le
 Roux, X., Niboyet, A., Porcher, E., 2017a. Designing mixtures of varieties for
 multifunctional agriculture with the help of ecology. A review. Agronomy for
 Sustainable Development 37.
- Barot, S., Ye, L., Abbadie, L., Blouin, M., Frascaria-Lacoste, N., 2017b. Ecosystem services
 must tackle anthropized ecosystems andecological engineering. Ecological
 Engineering 99, 486-495.
- Bengtsson, J., Ahnstrom, J., Weibull, A.C., 2005. The effects of organic agriculture on
 biodiversity and abundance: a meta-analysis. Journal of Applied Ecology 42, 261-269.
- Bonnin, I., Bonneuil, C., Goffaux, R., Montalent, P., Goldringer, I., 2014. Explaining the
 decrease in the genetic diversity of wheat in France over the 20th century. Agriculture
 Ecosystems & Environment 195, 183-192.
- Borg, J., Kiaer, L.P., Lecarpentier, C., Goldringer, I., Gauffreteau, A., Saint-Jean, S., Barot,
 S., Enjalbert, J., 2018. Unfolding the potential of wheat cultivar mixtures: A metaanalysis perspective and identification of knowledge gaps. Field Crops Research 221,
 298-313.
- Bretfeld, G., 1999. Synopses on Palaearctic Collembola. Volume 2. Symphypleona.
 Abhandlungen und Berichte des Naturkundemuseums Goerlitz 71, 1-318.
- Castagneyrol, B., Jactel, H., 2012. Unraveling plant-animal diversity relationships: a meta regression analysis. Ecology 93, 2115-2124.
- Chateil, C., Goldringer, I., Tarallo, L., Kerbiriou, C., Le Viol, I., Ponge, J.F., Salmon, S.,
 Gachet, S., Porcher, E., 2013. Crop genetic diversity benefits farmland biodiversity in
 cultivated fields. Agriculture Ecosystems & Environment 171, 25-32.
- Clements, R.O., Murray, P.J., Sturdy, R.G., 1991. The impact of 20 years' absence of
 earthworms and three levels of N fertilizer on a grassland soil environment.
 Agriculture, Ecosystems & Environment 36, 75-85.
- Cluzeau, D., Guernion, M., Chaussod, R., Martin-Laurent, F., Villenave, C., Cortet, J., RuizCamacho, N., Pernin, C., Mateille, T., Philippot, L., Bellido, A., Rougé, L., Arrouays,
 D., Bispo, A., Pérès, G., 2012. Integration of biodiversity in soil quality monitoring:
 Baselines for microbial and soil fauna parameters for different land-use types.
 European Journal of Soil Biology 49, 63-72.
- Cortet, J., Ronce, D., Poinsot-Balaguer, N., Beaufreton, C., Chabert, A., Viaux, P., de
 Fonseca, J.P.C., 2002. Impacts of different agricultural practices on the biodiversity of
 microarthropod communities in arable crop systems. European Journal of Soil Biology
 38, 239-244.
- Crawford, K.M., Crutsinger, G.M., Sanders, N.J., 2007. Host-plant genotypic diversity
 mediates the distribution of an ecosystem engineer. Ecology 88, 2114-2120.
- Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C., Sanders, N.J., 2006.
 Plant genotypic diversity predicts community structure and governs an ecosystem
 process. Science 313, 966-968.
- de Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Bracht
 Jørgensen, H., Brady, M.V., Christensen, S., de Ruiter, P.C., d'Hertefeldt, T., Frouz,
 J., Hedlund, K., Hemerik, L., Hol, W.H.G., Hotes, S., Mortimer, S.R., Setälä, H.,
 Sgardelis, S.P., Uteseny, K., van der Putten, W.H., Wolters, V., Bardgett, R.D., 2013.
- Sgardelis, S.P., Uteseny, K., van der Putten, W.H., Wolters, V., Bardgett, R.D., 2013
 Soil food web properties explain ecosystem services across European land use

- systems. Proceedings of the National Academy of Sciences of the United States ofAmerica 110, 14296-14301.
- bubs, X. Le Roux, V. Allard, B. Andrieu, S. Barot, A. Cantarel, C. de Vallavielle-Pope, A.,
 Gauffreteau, I.G., C. Montagnier, T. Pommier, E. Porcher, S. Saint-Jean, J. Borg, S.,
 Bourdet-Massein, D.C., A. Duclouet, E. Forst, N. Galic, L. Gerard, M. Hugoni, A.
- Hure, A., Larue, J.-C.L., C. Lecarpentier, M. Leconte, E. Le Saux, I. Le Viol, P.
- L'hote, P. Lusley, M., Mouchet, A.N., j, R. Perronne, E. Pichot, S. Pin, S. Salmon, D.
 Tropée, A. Vergnes, I, T. Vidal, Enjalbert, J., 2018a. An experimental design to test
 the effect of wheat variety mixtures on biodiversity and ecosystem services. HAL Id:
- 647 hal-01843564.
- Dubs, F., Vergnes, A., Mirlicourtois, E., Le Viol, I., Kerbiriou, C., Goulnik, J., Belghali, S.,
 Bentze, L., Barot, S., Porcher, E., 2018b. Positive effects of wheat variety mixtures on
 aboveground arthropods are weak and variable. Basic and Applied Ecology.
- Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thebault, E., Loreau, M., 2007. The
 functional role of biodiversity in ecosystems: incorporating trophic complexity.
 Ecology Letters 10, 522-538.
- Ebeling, A., S. Pompe, J. Baade, N. Eisenhauer, H. Hillebrand, R. Proulx, C. Roscher, B.
 Schmid, C. Wirth, and W. W. Weisser. 2014. A trait-based experimental approach to
 understand the mechanisms underlying biodiversity–ecosystem functioning
 relationships. Basic and Applied Ecology 15, 229-240.
- Eerpina, R., Boiteau, G., Lynch, D.H., 2017. Collembola diet switching in the presence of
 maize roots varies with species. Canadian Journal of Soil Science 97, 171-177.
- Eisenhauer, N., Milcu, A., Sabais, A.C.W., Bessler, H., Brenner, J., Engels, C., Klarner, B.,
 Maraun, M., Partsch, S., Roscher, C., Schonert, F., Temperton, V.M., Thomisch, K.,
 Weigelt, A., Weisser, W.W., Scheu, S., 2011. Plant Diversity Surpasses Plant
 Functional Groups and Plant Productivity as Driver of Soil Biota in the Long Term.
 PLoS ONE 6.
- Endlweber, K., Ruess, L., Scheu, S., 2009. Collembola switch diet in presence of plant roots
 thereby functioning as herbivores. Soil Biology & Biochemistry 41, 1151-1154.
- Endlweber, K., Scheu, S., 2007. Interactions between mycorrhizal fungi and Collembola:
 effects on root structure of competing plant species. Biology and Fertility of Soils 43,
 741-749.
- Finney, D.M., Kaye, J.P., 2017. Functional diversity in cover crop polycultures increases
 multifunctionality of an agricultural system. Journal of Applied Ecology 54, 509-517.
- Frampton, G.K., Van den Brink, P.J., Wratten, S.D., 2001. Diel activity patterns in an arable
 collembolan community. Applied Soil Ecology 17, 63-80.
- Fratello, B., Bertolani, R., Sabatini, M.A., Mola, L., Rassu, M.A., 1985. Effects of atrazine on
 soil microarthropods in experimental maize fields. Pedobiologia 28, 161-168.
- Friberg, H., Lagerlöf, J., Rämert, B., 2005. Influence of soil fauna on fungal plant pathogens
 in agricultural and horticultural systems. Biocontrol Science and Technology 15, 641658.
- Grossi, J.L., Brun, J.J., 1997. Effect of climate and plant succession on lumbricid populations
 in the French Alps. Soil Biology and Biochemistry 29, 329-333.
- Håkansson, I., Lipiec, J., 2000. A review of the usefulness of relative bulk density values in
 studies of soil structure and compaction. Soil and Tillage Research 53, 71-85.
- 683 Heiniger, C., Barot, S., Ponge, J.F., Salmon, S., Meriguet, J., Carmignac, D., Suillerot, M.,
- 684Dubs, F., 2015. Collembolan preferences for soil and microclimate in forest and685pasture communities. Soil Biology & Biochemistry 86, 181-192.

- Heisler, C., Kaiser, E.-A., 1995. Influence of agricultural traffic and crop management on
 collembola and microbial biomass in arable soil. Biology and Fertility of Soils 19,
 159-165.
- Hopkin, S.P., 1997. Biology of the Springtails (Insecta: Collembola). Oxford University Press
 Oxford.
- Hopkin, S.P., 2007. A Key to the Springtails (Collembola) of Britain and Ireland. Field
 Studies Council (AIDGAP Project). 245pp. pp.
- Imhoff, S., Pires da Silva, A., Ghiberto, P., Tormena, C., Pilatti , M., Libardi, P., 2016.
 Physical Quality Indicators and Mechanical Behavior of Agricultural Soils of
 Argentina. PLoS ONE 11, e0153827.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer,
 T.M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J.N., Guo, Q.,
 Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T.,
- 699 Mori, A.S., Naeem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C.,
- Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., van der Putten,
 W.H., van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., Eisenhauer, N., 2015.
- Biodiversity increases the resistance of ecosystem productivity to climate extremes.
 Nature advance online publication.
- Jeanneret, P., Schupbach, B., Luka, H., 2003. Quantifying the impact of landscape and habitat
 features on biodiversity in cultivated landscapes. Agriculture Ecosystems &
 Environment 98, 311-320.
- Johnson, M.T.J., Lajeunesse, M.J., Agrawal, A.A., 2006. Additive and interactive effects of
 plant genotypic diversity on arthropod communities and plant fitness. Ecology Letters
 9, 24-34.
- Joimel, S., Schwartz, C., Hedde, M., Kiyota, S., Krogh, P.H., Nahmani, J., Pérès, G., Vergnes,
 A., Cortet, J., 2017. Urban and industrial land uses have a higher soil biological
 quality than expected from physicochemical quality. Science of the Total Environment
 584-585, 614-621.
- Jones, T.S., Allan, E., Harri, S.A., Krauss, J., Muller, C.B., van Veen, F.J.F., 2011. Effects of
 genetic diversity of grass on insect species diversity at higher trophic levels are not
 due to cascading diversity effects. Oikos 120, 1031-1036.
- Jorgensen, H.B., Johansson, T., Canback, B., Hedlund, K., Tunlid, A., 2005. Selective
 foraging of fungi by collembolans in soil. Biology Letters 1, 243-246.
- Lagerlof, J., Andren, O., 1991. ABUNDANCE AND ACTIVITY OF COLLEMBOLA,
 PROTURA AND DIPLURA (INSECTA, APTERYGOTA) IN 4 CROPPING
 SYSTEMS. Pedobiologia 35, 337-350.
- Legendre, P., Legendre, L., 1998. Numerical Ecology. Second english edition. Elsevier,
 Amsterdam, 853 pp.
- Litrico, I., Goldringer, I., Enjalbert, J., 2015. Plus-value de la diversité génétique intra parcelle pour la stabilité de la production et autres services écosystémiques.
 Innovations Agronomiques 43, 7-18.
- Loeuille, N., Barot, S., Georgelin, E., Kylafis, G., Lavigne, C., 2013. Eco-Evolutionary
 Dynamics of Agricultural Networks: Implications for Sustainable Management, In:
 Woodward, G., Bohan, D.A. (Eds.), Advances in Ecological Research, Vol 49:
 Ecological Networks in an Agricultural World. Elsevier Academic Press Inc, San
 Diego, pp. 339-435.
- Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity
 experiments. Nature 412, 72-76.

- McArt, S.H., Cook-Patton, S.C., Thaler, J.S., 2012. Relationships between arthropod richness,
 evenness, and diversity are altered by complementarity among plant genotypes.
 Oecologia 168, 1013-1021.
- Mehl, F., 1996. Frassaktivitat von Collembolen (Isotomina thermophila, Heteromurus nitidus, Folsomia candida) an drei verschiedenen, bodenburtigen, phytopathogenen
 Schadpilzen der Gattung Fusarium (F. subglutinans, F. graminearum, F. oxysporum).
 Pflanzenschutzberichte 56, 1-23.
- Meyer-Wolfarth, F., Schrader, S., Oldenburg, E., Weinert, J., Brunotte, J., 2017.
 Collembolans and soil nematodes as biological regulators of the plant pathogen
 Fusarium culmorum. Journal of Plant Diseases and Protection 124, 493-498.
- Milcu, A., Partsch, S., Langel, R., Scheu, S., 2006. The response of decomposers
 (earthworms, springtails and microorganisms) to variations in species and functional
 group diversity of plants. Oikos 112, 513-524.
- Ngosong, C., Gabriel, E., Ruess, L., 2014. Collembola grazing on arbuscular mycorrhiza
 fungi modulates nutrient allocation in plants. Pedobiologia 57, 171-179.
- Nuutinen, V., 1992. Earthworm community response to tillage and residue management on
 different soil types in southern finland. Soil & Tillage Research 23, 221-239.
- Ponge, J.-F., Charpentié, M.-J., 1981. Etude des relations microflore-microfaune : expériences
 sur Pseudosinella alba (Packard), Collembole mycophage. Revue d'Ecologie et
 Biologie du Sol 18, 291-303.
- Ponge, J.-F., Gillet, S., Dubs, F., Fedoroff, E., Haese, H., Sousa, J.P., Lavelle, P., 2003.
 Collembolan communities as bioindicators of land use intensification. Soil Biology and Biochemistry 35, 813-826.
- Ponge, J.F., 1988. Ecological study of a forest humus by observing a small volume III. The F 1 layer from a moder humus under pinus-sylvestris. Pedobiologia 31, 1-64.
- Potapow, M., 2001. Synopses on Palaearctic Collembola. Volume 3. Isotomidae, 1-603 pp.
- 760 Prieto, I., Violle, C., Barre, P., Durand, J.-L., Ghesquiere, M., Litrico, I., 2015.
- Complementary effects of species and genetic diversity on productivity and stability ofsown grasslands. Nature Plants 1.
- Querner, P., Bruckner, A., 2010. Combining pitfall traps and soil samples to collect
 Collembola for site scale biodiversity assessments. Applied Soil Ecology 45, 293-297.
- Rebecchi, L., Sabatini, M.A., Cappi, C., Grazioso, P., Vicari, A., Dinelli, G., Bertolani, R.,
 2000. Effects of a sulfonylurea herbicide on soil microarthropods. Biology and
 Fertility of Soils 30, 312-317.
- Ricotta, C., Moretti, M., 2011. CWM and Rao's quadratic diversity: a unified framework for
 functional ecology. Oecologia 167, 181-188.
- Salamon, J.A., Schaefer, M., Alphei, J., Schmid, B., Scheu, S., 2004. Effects of plant diversity
 on Collembola in an experimental grassland ecosystem. Oikos 106, 51-60.
- Salmon, S., Ponge, J.F., Gachet, S., Deharveng, L., Lefebvre, N., Delabrosse, F., 2014.
 Linking species, traits and habitat characteristics of Collembola at European scale.
 Soil Biology & Biochemistry 75, 73-85.
- Santonja, M., Aupic-Samain, A., Forey, E., Chauvat, M., 2018. Increasing temperature and
 decreasing specific leaf area amplify centipede predation impact on Collembola.
 European Journal of Soil Biology 89, 9-13.
- Schrader, S., Lingnau, M., 1997. Influence of soil tillage and soil compaction on microarthropods in agricultural land. Pedobiologia 41, 202-209.
- Schrader, S., Wolfarth, F., Oldenburg, E., 2013. Biological Control of Soil-borne
 Phytopathogenic Fungi and their Mycotoxins by Soil Fauna A review. Bulletin of
 University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca Agriculture
 70, 291-298.

- Sousa, J.P., da Gama, M.M., Pinto, P., Keating, A., Calhoa, F., Lemos, M., Castro, C., Luz,
 T., Leitao, P., Dias, S., 2004. Effects of land-use on Collembola diversity patterns in a
 Mediterranean landscape. Pedobiologia 48, 609-622.
- Tenenhaus, M., 1998. La Régression PLS, Théorie et Pratique. . Editions Technips, Paris, 254
 pp.
- Ter Braak, C., J. F., 1986. Canonical Correspondence Analysis: A New Eigenvector
 Technique for Multivariate Direct Gradient Analysis. Ecology 67, 1167-1179.
- Thibaud, J.-M., Schulz, H.-J., da Gama Assalino, M.M., 2004. Synopses on Palaearctic
 Collembola Hypogastruridae. Abhandlungen und Berichte des Naturkundemuseums
 Goerlitz 75, 1-287.
- Thimm, T., Larink, O., 1995. Grazing preferences of some Collembola for endomycorrhizal
 fungi. Biology and Fertility of Soils 19, 266-268.
- Tooker, J.F., Frank, S.D., 2012. Genotypically diverse cultivar mixtures for insect pest
 management and increased crop yields. Journal of Applied Ecology 49, 974-985.
- Tsiafouli, M.A., Thebault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H.,
 Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L.,
 Jorgensen, H.B., Christensen, S., D' Hertefeldt, T., Hotes, S., Hol, W.H.G., Frouz, J.,
 Liiri, M., Mortimer, S.R., Setala, H., Tzanopoulos, J., Uteseny, K., Pizl, V., Stary, J.,
 Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across
- 802 woners, v., Hedunid, K., 2013. Intensive agriculture reduces son biodrivers 803 Europe. Global Change Biology 21, 973-985.
- Viketoft, M., Sohlenius, B., 2011. Soil nematode populations in a grassland plant diversity
 experiment run for seven years. Applied Soil Ecology 48, 174-184.
- Weisser, W. W., C. Roscher, S. T. Meyer, A. Ebeling, G. Luo, E. Allan, H. Beßler, R. L.
 Barnard, N. Buchmann, F. Buscot, C. Engels, C. Fischer, M. Fischer, A. Gessler, G.
 Gleixner, S. Halle, A. Hildebrandt, H. Hillebrand, H. de Kroon, M. Lange, S. Leimer,
 X. Le Roux, A. Milcu, L. Mommer, P. A. Niklaus, Y. Oelmann, R. Proulx, J. Roy, C.
 Scherber, M. Scherer-Lorenzen, S. Scheu, T. Tscharntke, M. Wachendorf, C. Wagg,
 A. Weigelt, W. Wilcke, C. Wirth, E.-D. Schulze, B. Schmid, and N. Eisenhauer. 2017.
 Biodiversity effects on ecosystem functioning in a 15-year grassland experiment:
- Patterns, mechanisms, and open questions. Basic and Applied Ecology 23, 1-73.
- Warnock, A. J., Flitter, A. H., Usher, M. B., 1982. The influence of a springtail *Folsomia candida* (Insecta, Collembola) on the mycorrhizal association of leek *Allium porrum*and the vesicular-arbuscular mycorrhizal endophyte *Glomus fasciculatus*. New
 Phytologist 90, 285-292.
- Zhu, Y.Y., Chen, H.R., Fan, J.H., Wang, Y.Y., Li, Y., Chen, J.B., Fan, J.X., Yang, S.S., Hu,
 L.P., Leung, H., Mew, T.W., Teng, P.S., Wang, Z.H., Mundt, C.C., 2000. Genetic
 diversity and disease control in rice. Nature 406, 718-722.
- 821
- 822

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

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

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

Table 3. Names and codes of Collembola specie										
Species name	Code									
Desoria tigrina	Destig									
Deuterosminthurus sp.	Deutersp									
Entomobrya lanuginosa	Entlan									
Entomobrya sp. cf multifasciata	Entmul									
Entomobryoides purpurascens	Entpur									
Entomobrya sp.	Entsp									
Folsomia candida	Folcan									
Folsomides parvulus	Folpar									
Heteromurus nitidus	Hetnit									
Isotomurus antennalis	Isoant									
Isotomurus palustris	Isopal									
Lepidocyrtus cyaneus	Lepcya									
Lepidocyrtus lanuginosus	Leplan									
Lepidocyrtus lignorum	Leplig									
Megalothorax group incertus	Meginc									
Megalothorax group minimus	Megmin									
Mesaphorura sp.	Messp									
Neotullbergia ramicuspis	Neoram									
Parisotoma notabilis	Parnot									
Proisotoma minima	Promini									
Proisotoma minuta	Prominu									
Pseudosinella alba	Psealb									
Seira domestica	Seidom									
Sminthurinus aureus	Smiaur									
Sminthurides signatus	Smisig									
Sminthurinus group aureus	Smigraur									

Sminthurinus elegans

Smiele

Wilpla

Willowsia platani

838

839

- **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)

848 Figure captions

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

856

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

862

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

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.
879	
880	
881	
882	
883	
884	





911





- 916 917





936 Figure 3b







947	Supplementary material
948	
949	
950	
951	
952	
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

		Α		В		С		D		Е		F		G			
1,76 m																	
10,50 m		107A 107B		69		11		71		12		85		5			
1,76 m																	
10,50 m		15		25		79		65		83		105		31			
1,76 m																	
10,50 m	N 3m	51		117		63		29		55		14		27			
1,76 m	4 KUH												_		_		
10,50 m	e avec combi	109	TWN	81	TWN	77	TWN	49	TWN	33	ale GRANDVA	115	ale GRANDVA	1	ale GRANDVA		
1,76 m	²) semé		GRAND		GRANE		GRAND		GRANE		= Tritica		= Tritica		= Tritic		
10,50 m	VAL (250 griftin	6	ure = Trificale	16	ure = Trificale	35	ure = Trificale	2	ure = Triticale	19	Bordum	21	Bordure	75	Bordure		
1,76 m	BRAND		Bord		Bord		Bord		Bord								
10,50 m	re = Trificale (57		119		53		17		9		41		з			
1,76 m	Bordu																
10,50 m		7		39		113		23		73	_	37		8			
1,76 m																	
10,50 m		13		4		61		87		47		10		45			
1,76 m																	
10,50 m		43		59		111		67		110		91		82			
1,76 m																	
10,50 m		64		40		80		104		46		114		93			
1,76 m																	
10,50 m		102		98		26		52		34	N 3m	78	N 3m	28	IN 3m		
1,76 M	Ę		E		Ę		Ę		Ę		né KUH		né KUH		iné KUH		
10,50 m	mbiné KUHN 3	60	mbiné KUHN 3	62	mbiné KUHN 3	97	mbiné KUHN 3	99	mbiné KUHN 3	74	e avec combi	106	le avec combi	90	ée avec comb		
	avec co		avec co		avec co		avec co		avec co		mes (ru		n ³) sem		n2) sem		
10,50 m	rfm2) semée	118	rfm2) semée	22	rtm2) semée	54	rtm2) semée	88	rfm2) semée	48	VAL (250 grh	30	VAL (250 grh	72	VAL (250 grh		
	L (250 g		L (250 g		L (250 g		L (250 g		L (250 g		GRAND		GRAND		GRAND		
10,50 m	RANDVA		RANDVA		RANDVA		RANDVA		RANDVA		Trificale		Trificale		Triticale		
1,76 m	ticale G	68	ticale G	56	ficale G	32	ácale G	101	ticale G	24	= euro	76	= emp	66	= empio		
10,50 m	Bordure = Tri	108	Bordure = Tri	86	Bordure = Tri	95	Bordure = Tri	44	Bordure = Tri	70	Bo	89	8	38	ă		
1,76 m																	
10,50 m		18		103		42		112A 112B		50		36		94			
1,76 m																	
10,50 m		116		92		100		20		84		95		58			
1,76 m																	







968

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

ts (se	e Table	S1 and	S2 for a	abbrevia	ations of	species a	and trait	t names)	
bheB	Scal	Pigm	BodyL	Ocel	FurcaL	AntL	PAO	Tricho	Pso
							Ves		
	0	1	2.1	8	4	1.35	1	0	0
	0	1	0.75	8	4	1.87	0	1	0

1	Table S1: Values of	Collembola traits (see Table S1	and S2 for abbre	viations of species	s and trait names)
---	---------------------	---------------------	--------------	------------------	---------------------	--------------------

	Repro Sex	Repro Part	СуІВ	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	Ері
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	Ері
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	Ері
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	Ері
Smidsig	1	0	0	1	0	1	0.3	8	4	1.57	0	1	0	0.49	0	Ері
Smigraur	1	0	0	1	0	1	0.85	8	4	1.2	0	1	0	0.6	0	Ері
Sminele	1	0	0	1	0	1	0.7	8	4	1.4	0	1	0	0.6	0	Ері
Wilpla	1	0	1	0	1	1	3	8	4	2.64	0	1	0	0.34	1	Ері

4 Table S2: see Excel file

Table S2. Abundances of Collembola species in three pooled samples of 104 plots of the Wheatamix project

53

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	Ν	C/N	Corg	OM	w
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	
Ν	-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	
рН	-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	
с3	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	

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)
Ν	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) Mean Green Area Index in December= ratio of leaf green area to ground
GAIT1	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) Mean of sensitivity to Septoria leaf blotch (mean percentage of sporulating
Septoria	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)

```
Mod1 <- glmmTMB (RS ~ nbvar+ c1+ c2+ c3+c4+Co-silt+C_N+eau+pH, data= datanorm, family = gaussian)
15
     > summary(Mod1)
16
      Family: gaussian (identity)
17
18
     Formula:
     RS \sim nbvar + c1 + c2 + c3 + c4 + Co-silt + C_N + water + pH
19
20
     Data: datanorm
21
                          logLik deviance df.resid
22
          AIC
                    BIC
23
        408.7
                  437.8
                          -193.3
                                     386.7
                                                  93
24
25
26
27
28
     Dispersion estimate for gaussian family (sigma^2): 2.41
     Conditional model:
29
                  Estimate Std. Error z value Pr(>|z|)
30
31
     (Intercept)
                 3.69880
                              0.32645
                                       11.330 < 2e-16
                                                         ***
     nbvar
                  -0.05125
                              0.08364
                                        -0.613 0.540057
32
33
34
     c1
                   0.90900
                              0.34351
                                         2.646 0.008140 **
     c2
                  -0.29404
                              0.33605
                                        -0.875 0.381587
     с3
                  -0.06463
                              0.33780
                                        -0.191 \ 0.848278
35
36
                   0.66819
                               0.33888
                                         1.972 0.048635 *
     c4
     Co-silt
                      0.60274
                                  0.17530
                                             3.438 0.000585 ***
37
                   0.09837
                              0.15733
                                         0.625 0.531815
     CN
38
                                 0.16650 -0.573 0.566479
                    -0.09545
     water
39
     рΗ
                   0.02284
                              0.16640
                                         0.137 0.890812
40
     Mod1 <- glmmTMB (RS~Co-silt+c1, data= datanorm, family = gaussian)</pre>
41
42
     > summary(Mod1)
43
     Family: gaussian ( identity )
44
45
                        RS \sim Co-silt + c1
     Formula:
46
     Data: datanorm
47
```

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

- 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
- of Collembola (full model followed by final model, followed by Analysis of Deviance Table; intermediate model indicated that no
- 78 interaction was significant)

```
Mod1 <- glmmTMB (RS ~ nbclu+SRR+SRL+RD+GAIT1+GAIT6+YR+Septo+Co-silt+C_N+eau+pH, data= datanorm, family = gaussian)
 80
     > summary(Mod1)
 81
 82
       Family: gaussian (identity)
 83
      Formula:
 84
      RS ~ nbclu + SRR + SRL + RD + GAIT1 + GAIT6 + YR + Septo + Co-silt +
 85
86
          C_N +water+ pH
      Data: datanorm
 87
 88
           AIC
                          logLik deviance df.resid
                    BIC
 89
                  446.3
                          -190.7
                                     381.3
         409.3
                                                 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)
                               0.31809
                                        11.612 < 2e-16
                  3.69358
 97
                   0.22052
                               0.14068
                                         1.568 0.116989
      nbclu
 98
      SRR
                  -0.09037
                               0.19944
                                        -0.453 0.650474
 99
                               0.18780
                   0.47410
      SRL
                                         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
                  -0.04138
                               0.26335
                                        -0.157 0.875141
      YR
104
      Septo
                   0.53499
                               0.22318
                                         2.397 0.016526 *
105
      Co-silt
                      0.63010
                                  0.17474
                                            3.606 0.000311 ***
                   0.15544
                               0.15797
106
      C_N
                                         0.984 0.325123
107
      water
                    -0.16827
                                 0.16276 -1.034 0.301219
```

рН

```
0.01884 0.16422 0.115 0.908689
```

110

```
Mod1 <- glmmTMB (RS ~ SRL + Septo + Co-silt, data= datanorm, family = gaussian)
111
112
     summary(Mod1)
113
114
     Family: gaussian ( identity )
115
     Formula:
                       RS ~ SRL + Septo + Co-silt
116
     Data: datanorm
117
118
                   BIC logLik deviance df.resid
          AIC
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
                   0.3197
     SRL
                              0.1582
                                      2.021 0.04331 *
128
                              0.1589 2.811 0.00493 **
     Septo
                   0.4467
129
     Co-silt
                      0.7034
                                 0.1566 4.492 7.06e-06 ***
130
131
     library(car)
132
     Anova(Mod1)
     Analysis of Deviance Table (Type II Wald chisquare tests)
133
134
135
     Response: RS
             Chisq Df Pr(>Chisq)
136
            4.0832 1 0.043311 *
137
     SRL
     Septo 7.9036 1
                      0.004934 **
138
     Limg 20.1757 1 7.065e-06 ***
139
140
```

- 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
- indicated that no interaction was significant)

```
Mod1 <- qlmmTMB (LogAb~ nbvar+ c1+ c2+ c3+c4+Co-silt+C_N+water+pH, data= datanorm, family = gaussian)
146
      summary(Mod1)
147
      Family: gaussian (identity)
148
149
      Formula:
      LogAb \sim nbvar + c1 + c2 + c3 + c4 + Co-silt + C_N + water + pH
150
151
      Data: datanorm
152
                           logLik deviance df.resid
153
           AIC
                    BIC
154
          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:
160
                  Estimate Std. Error z value Pr(>|z|)
161
      (Intercept)
                  1.02129
                               0.06655
                                        15.347
                                                 < 2e-16
                                                         ***
162
                   0.01233
                               0.01705
                                         0.723
                                                 0.4696
      nbvar
163
      c1
                   0.05521
                               0.07003
                                         0.788
                                                  0.4304
164
      c2
                  -0.13935
                               0.06851
                                        -2.034
                                                  0.0419 *
165
      с3
                  -0.07537
                               0.06886
                                        -1.094
                                                  0.2738
166
      c4
                   0.02859
                               0.06908
                                         0.414
                                                  0.6790
167
      Co-silt
                       0.14121
                                  0.03574
                                             3.951 7.77e-05 ***
168
                   0.03117
                               0.03207
                                         0.972
      C_N
                                                  0.3312
                     0.02246
169
                                 0.03394
                                           0.662
                                                    0.5083
      Water
170
                   0.01312
                               0.03392
                                         0.387
                                                  0.6989
      рН
171
172
173
174
      Mod1 <- glmmTMB (LogAb~ Co-silt+c2, data= datanorm, family = gaussian)
175
      > summary(Mod1)
       Family: gaussian (identity)
176
                         LoqAb \sim Co-silt + c2
177
      Formula:
```

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

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)

```
Mod1 <- glmmTMB (LogAb~ nbclu+SRR+SRL+RD+GAIT1+GAIT6+YR+Septo+Co-silt+C_N+eau+pH, data= datanorm, family = gaussian)
208
209
      > summary(Mod1)
210
       Family: gaussian (identity)
211
      Formula:
212
      LogAb ~ nbclu + SRR + SRL + RD + GAIT1 + GAIT6 + YR + Septo +
          Co-silt + C_N +water+ pH
213
214
      Data: datanorm
215
216
           AIC
                     BIC
                           logLik deviance df.resid
217
                            -24.4
          76.7
                   113.7
                                       48.7
                                                  90
218
219
220
      Dispersion estimate for gaussian family (sigma^2): 0.0935
221
222
223
      Conditional model:
                    Estimate Std. Error z value Pr(>|z|)
224
225
226
                                         15.907
      (Intercept)
                   1.022507
                               0.064282
                                                  < 2e-16 ***
      nbclu
                   -0.012473
                               0.028429
                                          -0.439
                                                  0.66084
                                          -0.395
      SRR
                   -0.015933
                               0.040304
                                                  0.69260
227
                   0.033206
                               0.037951
                                           0.875
                                                  0.38159
      SRL
228
      RD
                   0.012039
                               0.043987
                                           0.274
                                                  0.78432
229
      GAIT1
                   0.008373
                               0.042122
                                           0.199
                                                  0.84244
230
                   -0.005605
                                          -0.141
      GAIT6
                               0.039711
                                                  0.88775
231
      YR
                   -0.068785
                               0.053220
                                          -1.292
                                                  0.19620
232
                   0.132573
                                           2.939 0.00329 **
      Septo
                               0.045102
233
                                              4.323 1.54e-05 ***
      Co-silt
                       0.152664
                                  0.035312
234
                   0.037322
                               0.031923
                                           1.169 0.24235
      C_N
235
      water
                      0.017596
                                 0.032892
                                             0.535 0.59268
236
                   0.005600
                               0.033188
                                           0.169 0.86600
      рН
237
238
239
240
241
242
```

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