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

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Highlights

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

Wheat traits explained 13% of species assemblages of Collembola

Wheat traits explained 11% of trait assemblages of Collembola

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

Soil features explained 10.8% of species assemblages of Collembola

ABSTRACT

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The genetic diversity of cultivated crops has decreased continuously since the beginning of the 20th century, because of the gradual replacement of genetically heterogeneous traditional varieties by new genetically homogenous varieties, grown in monospecific stands. The resulting agro-ecosystems are now considered as unsustainable. Increasing within-field genetic crop diversity by using a mixture of varieties could increase the sustainability of these agro-ecosystems. This could also potentially increase non-crop biodiversity. In the present study we used an experimental approach to test 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) species richness and abundance of Collembola, and (2) species and trait assemblages of Collembola. A total of 104 plots were seeded with either monocultures or mixtures of 2, 4 and 8 wheat varieties. Soil cores were collected in each plot to extract Collembola and measure soil features. The number of wheat 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 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 diseases, (more especially septoria leaf blotch) and characteristics of aerial parts and roots impacted collembolan species and trait assemblages, but these effects were weak. Soil features, especially the proportion of coarse silt, were also influential. Our study did not show a favorable impact of wheat genetic diversity on soil Collembola, which might result from their low abundance. Nevertheless, it suggests correlations between some variety traits and the species richness and abundance of Collembola.

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

1. Introduction

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

Many studies showed that increasing plant species richness improved ecosystem functioning, e.g. increased nutrient retention or biomass production and stabilization of crop production (Prieto et al., 2015; Tooker and Frank, 2012). Plant diversity also increases the resistance of ecosystem productivity to climate extremes, which is an advantage in the context of global change (Isbell et al., 2015). Functional crop diversity (i.e. diversity of crop characteristics or traits) can even provide more ecosystem services than species richness per 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 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 al., 2017a), i.e. the natural selection of species within a diverse community (compared to a

community poorer in species), increases the likelihood of communities to host productive 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 when subjected to drought, and that the number of genotypes per species present increased the temporal stability of production under both drought and non-drought conditions. This led us to hypothesize that mixing crop varieties would lead to the same positive effects as increased species diversity, and through the same mechanisms (Barot et al., 2017b; Borg et al., 2018; Prieto et al., 2015).

Biodiversity in one trophic group may also impact biodiversity in other trophic groups through vertical, i.e. inter-trophic levels effects (Duffy et al., 2007). For example, the diversity of arthropods often increases with plant species richness (Castagneyrol and Jactel, 2012). Plant species richness and plant functional diversity have also often been shown to benefit growth, density and diversity of soil organisms (Eisenhauer et al., 2011; Milcu et al., 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 fauna (Wardle et al. 2003, Milcu et al. 2006, Korboulewsky et al. 2016), which highlights the lack of consistency in results so far obtained.

Intraspecific genetic diversity could lead to the same types of effect. For example the positive impact of plant genetic diversity (variety mixtures) on the diversity of arthropods has been shown in forests (Tovar-Sánchez et al., 2015) and agricultural crop systems (Crutsinger 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 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 richer arthropod communities. Moreover, experiments on variety mixtures have shown that

intraspecific diversity can increase the abundance of natural enemies of insect pests and thus 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 composition and diversity (Chateil et al., 2013; Eisenhauer et al., 2011). They are among the most widespread and abundant groups of terrestrial arthropods and they impact ecosystem functioning by their high number (Hopkin, 1997). One of the main roles of Collembola is the 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 consuming plant fungal pathogens, Collembola can limit fungal diseases (Meyer-Wolfarth et al., 2017; Schrader et al., 2013). By regulating the activity and dispersal of mycorrhizal fungi, 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 (Endlweber and Scheu, 2007).

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).

2. Material and methods

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 experiment as implemented in the Jena experiments (Weisser 2017) and thoughts on the implementation of functional diversity in such experiments (Ebeling 2014). Twenty-seven functional traits (above- and belowground morphological, phenological and physiological traits) have been measured in 57 varieties that have been chosen to be representative of the 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 greenhouses by different teams of the Wheatamix consortium in 2014 (i.e. before our experiment), except traits related to diseases that come from Arvalis and databases of two laboratories (see Table 2 of Dubs et al., 2018a). Using a hierarchical clustering method (Ward method), these varieties have been classified on the base of 27 functional traits (yield, earliness, Specific Leaf Area, specific root length, root absorption capacity of nitrate and ammonium...) into 4 functional groups thereafter named c1, c2, c3, c4 clusters. Wheat varieties of the c1 functional group were characterized by high sensitivity to fungal diseases.

Functional group c2 comprised wheat varieties with short root lengths, high rate of NO_3^- absorption, high relative growth rate and low sensitivity to fungal diseases. The c3 functional group was composed of varieties characterized by their slow growth but elevated aggressiveness regarding plant-plant competition, and with high rate of NH_4^+ absorption capacity. Finally, the c4 functional group contained varieties with high specific root lengths, low relative growth rate and low rate of NO_3^- absorption capacity (Dubs et al. 2018a). Sixteen 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 from the center of the cluster (thus varieties not representative of the cluster) and avoiding 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 combining 2, 4 and 8 varieties, respectively (Dubs et al., 2018a). The number of functional 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 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 of functional diversity. These mixtures were clearly not designed because of their particular 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 varieties have also been seeded alone, in duplicate, providing a total of 104 10.5 m x 8.0 m plots encompassing 4 levels of variety mixtures (1, 2, 4 and 8 varieties each).

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 l t^{-1} –Fludioxonil 25 g l^{-1}) and SIGNAM (0.6 kg g t^{-1} –Cypermethryne 300 g l^{-1}) were used. One spraying of two herbicides (Archipel®, 50% Iodosulfuron and 50% Mesosulfuron; Harmony Extra®, 66 % thifensulfuron-methyl and 33% tribenuron-methyle) was performed on March 14, 2015. 160 kg N ha^{-1} was used as compared to the estimated optimal amount of 180 kg N ha^{-1} . The fertilizer (ammonium-nitrate) was spread as follows: 40 kg N ha^{-1} on March 5, 2015, 80 kg N ha^{-1} on April 16, 2015, 40 kg N ha^{-1} on May 11, 2015. All plots were harvested between the last week of July and the first week of August 2015.

After harvest, wheat crop residues were left in the field until last soil faunal sampling (from which springtails were extracted), in November.

2.2. Collembola sampling

Collembola were sampled in March (one core sample taken in the center of each plot) and November 2015 (two core samples taken in the center of each half plot) in the 104 plots. The three samples taken in each plot at two sampling dates allowed better accounting spatial and temporal plot heterogeneity. Each core sample was 5 cm in diameter and 15 cm deep, leading to a total sampled area of 59 cm^2 per plot. Collembola were extracted during ten days by the Berlese method (Edwards and Fletcher, 1971). The three samples of Collembola were pooled together for each plot because the density of Collembola in one sample was relatively low. They were then sorted, mounted, cleared in chloral-lactophenol and identified to species level under a light microscope ($400\times$ magnification) according to Hopkin (2007), Potapow (2001), Thibaud et al. (2004) and Bretfeld (1999). Other samples were taken in the same plots 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 in March 2015. Another soil core (8 cm diameter, 15cm depth, litter excluded) was taken in

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).

2.3. Statistical analysis

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

We performed generalized linear models (GLM) to determine whether the abundance 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, or c4) and mean of wheat functional traits in variety mixtures. Given the high number of wheat traits available, we first made an a priori selection according to their potential impact 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 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 measures and soil features were then standardized (thus discarding spurious effects of various units). Spearman correlation coefficients were calculated between wheat traits, soil features and geographical coordinates in order to eliminate correlated explanatory variables (Table 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 discarded from further analyses. As the impact of soil texture on soil fauna is well known, 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 information about wheat diversity, they were analysed separately, like wheat traits and the 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 composition of wheat functional groups (c1, c2, c3 and c4), and soil features, on species richness and abundance of Collembola, respectively. This model allowed to share the part of diversity and that of composition of functional groups (varying according to traits displayed in 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 diversity), the set of wheat traits and soil features, on species richness and abundance of 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 to soil variation.

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 were diagnosed with the “DHARMA” package (Hartig, 2020) for R software: “Uniformity” (tests if the global distribution of residuals is in line with predicted values with a Kolmogorov-Smirnov test and a QQ-plot), “Outliers” (tests if there are more simulation outliers than expected), “Dispersion” (tests if the simulated dispersion is equal to the observed 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),

“Zeroinflation” (tests if there are more zeros than expected). In order to fulfil all model 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 permutation tests (999 permutations) was used to assess whether wheat variety traits, variety number, functional group number, functional group composition and soil features constrained collembolan species assemblages. This technique was particularly appropriate to our data because it addresses the large number of zeros which characterizes community compositional data (Legendre and Legendre, 1998) and does not try to display all variation in the data, but 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 following the same logic and using the same explanatory variables as for GLM, i.e. one with the number of wheat varieties, the composition of wheat functional groups (c1, c2, c3, c4) and soil features (soil water content, pH_{water}, coarse silt, and C/N ratio), the other CCA with the 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 to soil features from that due to wheat related variables. This also limited misinterpretations in the case of interactions between soil features and wheat related variables. Soil features and 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 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 CCAs, two partial least square regressions (CCA-PLSs; Tenenhaus, 1998) were performed

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, following the same procedure and using the same explanatory variables as for GLM and CCA, to measure the effects of 1) variety number, functional group composition and soil features, and 2) functional group number, wheat variety traits (Table 1), and soil features, on community-weighted mean traits (CWM) of Collembola. RDA was chosen because CWMs are continuous variables. CWM traits have been widely used in ecological research for summarizing different facets of functional composition and shifts in mean trait values within 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), 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 that constrains the position of response variables, here collembolan CWMs, by a set of environmental factors, here wheat related variables and soil features (Legendre and Legendre, 1998). Using RDA to analyze the impact of diverse environmental variables on the distribution of CWMs is a common practice in trait-based approaches in ecology (Vandewalle et al., 2010). As for pCCAs, partial RDAs (pRDA) were performed to disentangle the effects of wheat diversity (variety or functional group number), wheat composition (functional group 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 diseases, crop canopy cover or root characteristics, after removing the effects of soil features,

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

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

3. Results

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 pooled samples varied from 10 ± 0.53 individuals ($1,698 \text{ ind.m}^{-2}$) in plots with two varieties to 25 ± 3.25 individuals ($4,246 \text{ ind.m}^{-2}$) in plots with eight varieties (mean $\pm$ standard error), but the difference was not significant (Fig. 1a, Table S5). Collembolan species richness per plot did not vary with the number of wheat varieties, averaging four species per plot (Fig. 1b, Table S4). First, models showed that variety number and functional group number did not influence the species richness and abundance of Collembola (S4 and S5, Fig.1). Two wheat traits, Specific Root Length and sensitivity to septoria leaf blotch, and the c1 functional group 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 significantly increased the abundance of Collembola but its effect was twice less than that of coarse silt content (Tables 2, S7, Figs. 2a, S3a). A negative effect of the c2 functional group

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

3.2. Effect of wheat varieties on species assemblages of Collembola

The CCA with wheat variety number, wheat functional group composition (c1, c2, c3, c4) and soil features (soil water content, pH_{water}, coarse silt, and C/N) showed that these variables significantly (p-value: 0.011) explained 23.3% of the variation of species 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 functional group composition significantly explained 9.4% (p-value: 0.010) of the collembolan species distribution. When variety number (1.1%, p-value 0.60) and functional group composition (6.6%, p-value: 0.13) were tested separately, their effect was not 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 distribution.

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

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

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

The RDA testing the effect of wheat variety number, functional group composition and soil features showed that these variables together significantly explained 14.1% of the variation of collembolan trait distribution (p-value: 0.004). Partial RDAs testing the effect of variety number after removing the effects of soil features and functional group composition showed no significant effect on collembolan trait distribution (0.45%, p-value: 0.78). The effect of functional group composition after removing that of soil features and variety number 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 composition had no significant effect. The effect of soil features after removing the effect the variety number and functional group composition accounted for 9.7% (p-value:0.004) of the variation in collembolan trait distribution.

The RDA with wheat functional group number, wheat traits (Table 1) and soil features showed that these variables significantly explained 19.2% (p-value: 0.004) of the variation of collembolan trait distribution. Partial RDAs testing the effect of functional group number and wheat traits after removing the effect of soil features showed that they significantly explained 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 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 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 linked to: 1) roots (SRL, SRR, RD), 2) plant cover (Green Area Index: GAI), 3) sensitivity to 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.

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% (p-value: 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).

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 variation in the distribution of collembolan traits. Axis 1 separated soils with a high content of coarse silt on the positive side from soils with a low content of coarse silt and thus more clay on the negative side. Axis 2 separated soils with a neutral pH from soils that were richer in 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 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 without preference regarding soil layers (NS). Morphological traits supported this interpretation: characteristics of epigeic species such as spherical body, higher number of 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 coarse silt and therefore more clay. Species with cylindrical body occurred more frequently in

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

4. Discussion

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

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 expectation (Hypothesis 1). This result is not due to the short duration of our study since 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 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 weakness of the effect of wheat genetic diversity is supported by the results of Dubs et al. (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 diversity of many groups of invertebrates (Crawford et al., 2007; Crutsinger et al., 2006; 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 wheat variety. However, in Chateil et al. (2013) the respective effects of diversity and composition of wheat varieties could not really be disentangled. In fact, the observed increase in collembolan species richness could have resulted from the identity of wheat varieties that 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 (Bengtsson et al., 2005; Jeanneret et al., 2003) and soil features (Heiniger et al., 2015). The favorable impact of coarse silt (its content being inversely proportional to clay content) on the 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 soil tillage in conventionally cultivated crops where earthworms are scarce (Clements et al., 1991; Imhoff et al., 2016; Nuutinen, 1992). By limiting soil compaction (Håkansson and Lipiec, 2000), known to decrease the abundance of Collembola (Schrader and Lingnau, 1997), a more silty texture could favor a higher abundance and species richness of Collembola. Regarding agricultural practices, our field experiment was conducted in an experimental agricultural research center so that our plots had a long history of conventional use of tillage and pesticides, which can have reduced collembolan biodiversity at start of the 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 al. (2013), which was under organic farming. This hypothesis is corroborated by the particularly low abundances of Collembola in our field experiment. Although collembolan abundances were within the range found by Cluzeau et al. (2012) and Joimel et al. (2017) in arable lands, they were in average twice to three times lower than in other conventional crop systems in Europe (Cluzeau et al., 2012; Heisler and Kaiser, 1995; Lagerlof and Andren, 1991). The mean local species richness was also relatively low in all plots and was at the lowest level of the range of species richness observed by Cluzeau et al. (2012) for the same sample size.

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

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

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

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

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

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

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

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

Ponge, 2005). Other species found in our study, e.g. *Pseudosinella alba*, *Folsomia candida*, also known to feed on fungi, including pathogenic species (Mehl, 1996; Meyer-Wolfarth et al., 2017; Ponge and Charpentié, 1981; Ponge, 1988), were not really linked to the sensitivity 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 cited experimental studies concerned fungal pathogens other than *Mycosphaerella graminicola* (septoria leaf blotch). *Isotomurus palustris*, another species associated to the 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. Wheat varieties with both increased sensitivity to fungal diseases and high canopy cover, including high shoot-root ratios, favored logically Collembola living aboveground with morphological traits adapted to aerial life, e.g. with pigmented and spherical body, long 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 indirectly with specific leaf area of oak leaves (Santonja et al., 2018). This is exemplified in 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 trees or lichen) (Gisin, 1960).

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 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 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 thus more clayish and compact). This finding corroborates the role of coarse silt suggested above (section 4.1), i.e. attenuating soil compaction and allowing more euedaphic Collembola 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 aureus* and *aureus* group, *Lepidocyrtus cyaneus*) were probably more abundant than euedaphic species because of the reduction in the number and size of soil pores (Schrader and Lingnau, 1997).

The increase in wheat diversity did not foster collembolan species diversity, corroborating some previous studies failing to show an effect of plant diversity on soil fauna 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 prevented an increase in local species richness with wheat diversity, and (3) soil features, especially particle size distribution (texture), impacted collembolan distribution despite our efforts (seedling randomization) to take this natural effect in account in our experimental design. Moreover, our results show that the composition of plant populations, including functional composition, has a greater impact (although low) than intraspecific plant diversity 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 niche volume (more roots and more fungal pathogens) suitable to Collembola. This suggests 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 study suggests that keeping in mixture some wheat varieties with a lower resistance to fungal diseases (e.g. by selecting other traits related to higher yield) could be compensated by the 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 wheat varieties could explain why our results, contrast with those of a previous study (Chateil et al., 2013), which showed that wheat genetic diversity increased the species richness of several groups of invertebrates, including Collembola. In fact, the field experiment of Chateil et al. (2013) encompassed a low number of wheat varieties, and the varieties added in the higher level of diversity were probably all beneficial to Collembola.

5. Conclusions

Our study showed no effect of genetic wheat diversity on Collembola communities 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 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 contribute more to structuring collembolan communities than intraspecific diversity. Studying the effect of the diversity of wheat varieties using the same experimental method (high number of varieties and four levels of diversity, respectively) but in crops grown in organic 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 communities. A measure of each functional wheat trait during the experiment would also allow to directly assess potential impacts of wheat traits on Collembola.

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

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

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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.

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

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

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

<i>Sminthurinus elegans</i>	Smiele
<i>Willowsia platani</i>	Wilpla

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

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

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848 **Figure captions**

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

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

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

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

Figure 1

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923 Figure 3a

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Figure 3c

Figure 4a

Figure 4b

Supplementary material

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

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

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

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

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

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 μm) in soil. Each dot represents one plot.

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

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

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

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

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7 Table S3: Spearman correlation coefficients between explanatory variables

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

10

variable codes

variable name and unity

xDD

geographical coordinate x

yDD

geographical coordinate y

pH

soil pH

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

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

```

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

```

```

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

```

```

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

```

75

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

79

```

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

```

```

108 pH          0.01884    0.16422    0.115 0.908689
109
110

```

```

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

```

```

113
114 Family: gaussian  ( identity )
115 Formula:          RS ~ SRL + Septo + Co-silt
116 Data: datanorm
117
118      AIC      BIC   logLik deviance df.resid
119  400.6    413.8   -195.3    390.6        99
120
121
122 Dispersion estimate for gaussian family (sigma^2):  2.5
123
124 Conditional model:
125      Estimate Std. Error z value Pr(>|z|)
126 (Intercept)  4.1346      0.1552  26.645 < 2e-16 ***
127 SRL          0.3197      0.1582   2.021  0.04331 *
128 Septo        0.4467      0.1589   2.811  0.00493 **
129 Co-silt      0.7034      0.1566   4.492  7.06e-06 ***
130

```

```

131 library(car)
132 Anova(Mod1)
133 Analysis of Deviance Table (Type II wald chisquare tests)
134
135 Response: RS
136      Chisq Df Pr(>Chisq)
137 SRL    4.0832 1  0.043311 *
138 Septo  7.9036 1  0.004934 **
139 Limg  20.1757 1  7.065e-06 ***
140

```

```

141

```

142

143 Table S6: Results of glm on the effect of the variety number (nbvar), composition of wheat variety assemblies (C1..) and soil parameters on the
 144 Log of Collembola abundance (full model followed by final model, followed by Analysis of Deviance Table; intermediate model
 145 indicated that no interaction was significant)

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

147 `summary(Mod1)`

148 Family: gaussian (identity)

149 Formula:

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

151 Data: datanorm

152

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

155

156

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

158

159 Conditional model:

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

171

172

173

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

175 `> summary(Mod1)`

176 Family: gaussian (identity)

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

```

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

```

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

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

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

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

218
 219
 220 Dispersion estimate for gaussian family (sigma^2): 0.0935
 221

222 Conditional model:

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

237
 238
 239
 240
 241
 242


```

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

```