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1 Impact of crop genetic diversity on a litter consumer

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8 Abstract

9 Belowground communities, and especially earthworms, provide numerous services in 10 agroecosystems. In the current context of crop genetic erosion, this study aims at assessing the 11 effect of wheat cultivar diversity on earthworm growth and survival. Our laboratory 12 experiment was divided into two periods: (1) the "feeding period" (4 months), simulating 13 conditions in autumn with cool temperatures and high food availability, and (2) the "non-14 feeding period" (1 month) simulating conditions in winter with cold temperatures and low 15 food availability because litter had already been consumed without replacement. The aerial biomass of mixtures of wheat cultivars was used as food for earthworms and their growth was 16 17 measured twice during the feeding period and once during the non-feeding period. We found 18 two major effects on earthworm growth. Increasing the cultivar number (i) increased juvenile 19 earthworm growth and earthworm survival and (ii) decreased adult earthworm growth. A 20 consistent positive effect of nitrogen concentration of the biomass was found on growth and 21 this effect was independent of biodiversity effects. This study suggests that the loss of litter

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intraspecific genetic diversity has an impact on earthworm populations, probably through mechanisms linked to the variance in edibility or the balanced diet hypotheses. While they remain to be tested in the field, these results suggest that the current losses of crop genetic diversity could potentially impact processes at the community or ecosystem level through a decrease in food quality.

Keywords: balanced diet hypothesis; cultivar mixture; earthworms; genetic diversity; mixed
diet hypothesis; sustainable agriculture

29 Introduction

It is now well documented that species richness, mostly through functional diversity, strongly 30 31 influences ecosystem functioning (Isbell et al., 2011; Cardinale et al., 2012). While most 32 studies focus on species richness, recent studies are showing that genetic diversity within 33 species can also influence species interactions and ecosystem processes (Hughes et al., 2008; 34 Cook-Patton et al., 2011; Prieto et al., 2015) through variations in ecologically important traits 35 within the species (Mcgill et al., 2006). Due to the fact that phenotypic diversity can be as high within species as among species (Bangert et al., 2005), it would not be surprising if 36 37 interspecific diversity and intraspecific diversity had the same type of ecological 38 consequences. Some recent results are in fact pointing in that direction (Creissen et al., 2013; 39 Schöb et al., 2015), even if underlying mechanisms have not yet been fully documented for 40 intraspecific genetic diversity.

The effect of horizontal biodiversity, i.e. within a trophic group, on adjacent trophic levels is, however, less known and more complicated to study (Duffy et al., 2007). Prey diversity, has been shown to influence ecosystem functioning through various mechanisms reviewed by Duffy et al. (2007). According to the balanced diet hypothesis, a more diverse resource assemblage leads to the consumption of more diverse nutritional resources, which

improves the growth of the consumer (DeMott, 1998; Pfisterer et al., 2003). On the other 46 47 hand, according to the variance in edibility hypothesis, a more diverse range of resources 48 likely contains resources resistant to consumption or at least less valuable in terms of nutrient 49 content, which could decrease consumer growth (Leibold, 1989). These two mechanisms are 50 not incompatible and can operate simultaneously. The balanced diet hypothesis relies on the 51 fact that animals have particular food requirements, called "intake target", for different 52 nutrients such as proteins or carbohydrates (Senior et al., 2015). It has been shown that 53 animals more easily reach their intake target with a diet composed of more than one type of 54 food, i.e. a mixed diet (DeMott, 1998; Simpson et al., 2004; Senior et al., 2015). However, 55 these experiments only manipulated species richness and not genetic intraspecific diversity. 56 Our goal is thus to test whether genetic diversity within a plant species can impact its 57 consumer through mechanisms linked to the balanced diet and variance in edibility 58 hypotheses.

59 The intensification of agriculture has reduced crop biodiversity at different scales during the 20th century (FAO, 2010). In particular, genetically homogeneous crop cultivars 60 61 have been selected and usually a single cultivar is planted within each field. However, more 62 and more results are showing that mixing crop cultivars could be beneficial through an 63 increase in production and a decrease in its temporal variability (Kiær et al., 2009; Barot et 64 al., 2017). Among the identified mechanisms, a decrease in the sensitivity of crops to 65 pathogens and parasites (Zhu et al., 2000) or to climate change (Tilman & Downing, 1994) 66 seems to be particularly important. However, mixing crop cultivars could also promote the 67 activity of beneficial organisms such as earthworms through the improvement of 68 belowground-aboveground interactions (Postma-Blaauw et al., 2010). The influence of within 69 field plant diversity loss on earthworm abundance and diversity is not yet fully demonstrated (Spehn et al., 2000; Laossi et al., 2008). Anecic earthworms in agricultural fields mostly feed 70

71 on litter composed of crop residues that are relatively poor in terms of nutrient compare to 72 forest litter for instance. Yet, it is likely that earthworms could not reach their intake target for 73 an optimal growth through this single genetically poor food resource available in this environment. If the balanced diet hypothesis applies to earthworms, genetic crop diversity 74 75 erosion could affect earthworm growth and survival leading to a decrease in their activities 76 and in the ecosystem services they provide. This is an important issue because: (1) 77 Decomposers and especially earthworms provide many services to agriculture (Bertrand et al., 78 2015). Earthworms are known to contribute to physical, chemical and biological soil 79 properties. Anecic earthworms accelerate the decomposition of plant litter and enhance water 80 infiltration. (2) Current intensive agriculture has often deleterious effects on soil macrofauna 81 (Birkhofer et al., 2008; Postma-Blaauw et al., 2010) and decrease earthworm abundance and 82 diversity (Postma-Blaauw et al., 2010) through widespread practices such as tillage (Pelosi et 83 al., 2009) and pesticides (Pelosi et al., 2014).

84 It is now well recognized that our current agricultural model based on the use of huge 85 amounts of inputs and a few selected cultivars is not sustainable (Tilman et al., 2002; Foley et 86 al., 2011). In order to maintain yields while developing a more sustainable agriculture, it is 87 necessary to develop new alternative agricultural practices. The results of agroecological or 88 ecological engineering experiments suggest that increasing biodiversity in agrosystems to 89 mimic natural ecosystems could be a way to benefit from the services provided by 90 biodiversity and consequently lower the use of chemical inputs (Malézieux, 2011). In this line 91 of thought, this study aims at investigating the influence of mixtures of wheat cultivars on the 92 growth and the survival of an anecic earthworm, Lumbricus terrestris. This species was 93 selected for its crucial role in the decomposer communities of agricultural and forest 94 ecosystems in temperate zones. Because food diversity could affect juvenile and adult 95 earthworms differently, the aerial biomass of a field experiment was harvested and used as

96 food for earthworms at both the juvenile and adult life stage in a laboratory experiment. We 97 assessed the effect of intraspecific genetic diversity of wheat cultivars and the effect of their 98 functional diversity. We tested the general hypothesis that a high level of intraspecific 99 diversity and functional diversity leads to high litter quality, providing more diverse nutrients 100 to earthworms and consequently leading to higher growth and survival rates. This would 101 support the balance diet hypothesis for earthworms. On the contrary, a negative effect of 102 diversity would support the variance in edibility hypothesis.

103 Materials and methods

104 Wheat cultivars

105 The present experiment is based on a field experiment in small plots that is fully described 106 elsewhere (Dubs et al., 2018). Wheat, Triticum aestivum, was used in the experiment. 107 Twenty-four functional traits (See Appendix A: Table 1) were measured for 58 different 108 cultivars. These cultivars were classified using their functional traits in a hierarchical cluster 109 analysis, using Ward method into 4 "functional groups" (See Appendix A: Table 2). Four 110 cultivars were selected from each of the 4 functional groups (16 cultivars in total). These 16 111 cultivars were chosen according to seed availability and in order to maximize the overall 112 functional diversity, making sure that the clustering in four groups remained robust when the 113 clustering process was applied to the 16 cultivars (Dubs et al., 2018). Among these cultivars, 114 9 were modern winter cultivars, selected to have high yields, 5 cultivars were old landraces, 115 locally selected by farmers, and 2 cultivars were selected within an INRA MAGIC 116 population, i.e. a highly recombinant and multi-parental population (60 parents: see Thepot et 117 al. 2015 for more details). From these 16 different cultivars, 72 different combinations of 118 wheat cultivars were created. Among these mixtures, 24, 28 and 20 mixtures respectively 119 combined 2, 4 and 8 cultivars. Cultivars were selected in the mixtures in order to create, for

120 each level of cultivar diversity, homogeneous mixtures with low functional diversity (28 and 121 30 mixtures combined cultivars from only one or two functional groups respectively) and 122 heterogeneous mixtures with high functional diversity (16 and 14 mixtures combined cultivars 123 from three and four functional groups respectively) (See Appendix A: Table 3). The 16 plots 124 with a single cultivar and the 72 plots with mixtures of cultivars were sown in Versailles 125 (48°48'26"N 2°05'13"E) on November 2014. Earthworms were fed with 88 different litters 126 coming from the aerial biomass of the 88 wheat mixtures harvested in May 2015. The 127 aboveground biomass was dried (30 °C for 3 days) and cut (3 min in a blender) into small 128 pieces (from 0.1 cm to 1 cm long). 129 The nitrogen concentration of each litter was measured on a sub-sample using an 130 elemental analyzer (Flash HT, Thermo Scientific). The calcium, copper, iron, magnesium,

manganese, phosphorus, potassium, sodium and zinc concentrations were measured by dry
mineralization and spectrometry (radial ICP-AES, Varian Vista RL).

133 Earthworm growth experiment

The soil used in the experiment was collected from the 0-30 cm soil layer of a wheat cultivated field. For technical reasons this was another field than the one used to grow the mixtures of cultivars. It was a sandy-loam soil made of 53% sand, 34% silt, 11% clay, and with 2.8% of organic matter. The soil was air-dried and manually homogenized.

L. terrestris were obtained from a commercial supplier (http://appats-michel.fr/). They were patted dry, weighed and classified into juveniles or adults based on the presence of a clitellum. 88 juveniles and 224 adults (average fresh weight $2.34g \pm 0.14$ g for juveniles and $4.25 \text{ g} \pm 0.11$ g for adults) were used in the experiment. Each container (10 cm inner diameter, 15 cm height) was filled with 775 g of soil. The soil moisture was adjusted to 80% of the soil water holding capacity during the whole experiment (by weighing the pots every week). A single earthworm was placed in each container. The containers were covered with perforated lids to prevent earthworm escape. Each earthworm was fed with the litter of a single
experimental plot, i.e. a single mixture of wheat cultivar. The 16 treatments with litters
obtained from one cultivar were replicated 6 times, one time with a juvenile and five times
with an adult. The 72 treatments with litters combining more than one cultivar i.e. mixtures of
cultivars, were replicated 3 times, one time with a juvenile and two times with an adult.

150 The experiment was divided into two periods to simulate local field conditions in 151 cereal cultivation. The first one, simulating the autumn period, started in October 2015 and 152 ended in February 2016. During this period called "feeding period", all containers were kept 153 at 15 °C and fed with 10 g of wheat litter by month (20 g of litter was added twice at the 154 surface of the soil in October and December 2015). Earthworms were removed for weighing 155 in February 2016 after little more than 3 months of experiment. Each earthworm was patted 156 dry, weighed without voiding gut content (to avoid stress) and returned in its container. The 157 second period, simulating winter and called "non-feeding period", occurred between February 158 and March 2016. Earthworms were kept at 8 °C without any new food supply. They were 159 weighed in March 2016 using the method described above. Earthworm survival was assessed 160 in December, in February and in March. During autumn, a significant quantity of litter is 161 available at the soil surface (at least before tillage in agricultural systems) and earthworms are 162 active. On the contrary, during winter, there is almost no litter available, temperature falls and 163 earthworms are less active. The second period, between February and March, gave us 164 information about a potential "carryover effect" (O'Connor et al., 2014), i.e. the capability of 165 earthworms to survive and grow throughout winter depending on their previous feeding 166 conditions. This experiment thus aims to study the influence of food genetic diversity on 167 growth but also on the capability of earthworms to survive during winter.

We used the instantaneous growth rate (IGR, d⁻¹) (Daniel et al., 1996; Whalen & Parmelee,
170 1999), and calculated as,

171 IGR = $\ln(Wt/Wi)/\Delta t$,

172 where Wt (g) is the earthworm mass in February for the feeding period and in March for the 173 non-feeding period and Wi (g) the mass in October for the feeding period and the mass in 174 February for the non-feeding period. Δt was measured in days and represented the time 175 interval for the studied growth interval.

176 Statistical analyses

177 We used linear models to determine whether earthworm growth was influenced by the 178 mineral nutrient concentrations, the wheat cultivar number (WCN), wheat functional diversity 179 (as assessed by the number of cultivar functional groups in the mixtures of cultivars, F) and 180 the presence of each functional group (the effect of one particular functional group). The 181 number of cultivars and the number of functional groups within a mixture are not independent 182 because the number of functional groups cannot be higher than the number of cultivars and 183 conversely that mixtures of 8 cultivars have at least 2 functional groups. This is why we used 184 two different ANCOVA models to the test the effect on earthworm growth of the 185 developmental stage (juvenile or adult, A), the effect of the wheat cultivar number or wheat 186 functional group, and the interaction between the two. We used an ANOVA model to test the 187 effect on earthworm growth of the developmental stage, the effect of the presence of each 188 functional group in the mixture and the interaction between the two. We considered the wheat 189 cultivar number and the wheat functional diversity as continuous variables to increase the 190 power of the tests and because we expected linear effects of diversity and tested their 191 interactions with the development stage. We first used linear mixed effect models, using the

192 composition of the cultivar mixture as a random effect, but as this random effect was never 193 significant, we used standard models with only fixed effects. Homoscedasticity and normality 194 of model residuals were tested to ensure the robustness of the results. Dead earthworms were 195 removed from growth analyses. The influences of cultivar number, cultivar functional 196 diversity and the presence of particular functional groups in the mixture on earthworm death 197 were analyzed by logistic regressions (glm procedure using a logit link function with a 198 binomial error) in three separate models to avoid any problem of dependence between tested 199 factors. In these three models assessing the effect of wheat cultivar number, wheat functional 200 diversity and the presence of particular functional groups in the mixture on earthworm 201 growth, we also tested the effect of nutrient concentrations. Non-significant nutrients were 202 removed manually from the final model. We used R software version 3.1.2 for all statistical 203 analyses (R Development Core Team, 2008).

204 Results

205 General description of the results

By February, all juveniles were adults so that during the non-feeding period all earthworms 206 207 were adults. However, the growth difference between young adults and adults was still 208 significant during the October-February and the February-March periods so that we compared "juveniles" and "adults" in our statistical analyses. On average in all treatments, the biomass 209 of iuveniles increased by 309% (\pm 8%) with a mean IGR of 1.1 10⁻² day⁻¹ (\pm 0.6 10⁻³ day⁻¹) in 210 211 the feeding period. During the non-feeding period, juveniles lost $1\% (\pm 1\%)$ of their weight. The biomass of adults increased by 168% (\pm 4%) with a mean IGR of 5.1 10⁻³ day⁻¹ (\pm 0.2 10⁻ 212 ³ day⁻¹) in the feeding period. During the non-feeding period, adults lost 6% (\pm 1%) of their 213 214 weight. These results illustrate the effect of the developmental stage (Tables 1 and 2): 215 juveniles thus grew faster than adults during the feeding period and lost less weight than

adults during the non-feeding period. However, in February, young adults had a lower weight than adults (result of t-test, $t_{148}=2.58$, P=0.01).

218 Influence of wheat cultivar number on earthworm growth

219 During the feeding period, no general effect of wheat cultivar number on earthworm growth

220 was found but a significant interaction between development stage and wheat cultivar number

221 occurred (Table 1). During the feeding period, juvenile growth significantly increased and

adult growth significantly decreased with the number of cultivars (Fig. 1). During the non-

223 feeding period, there was no significant effect of the cultivar number in feed mixtures that had

been provided during the previous months on earthworm growth.

225 Influence of cultivar functional diversity on earthworm growth

During the feeding period, there was no general effect of cultivar functional diversity on
earthworm growth (Table 2). During the non-feeding period, earthworms lost significantly
less weight with an increasing functional diversity (Table 2, Fig. 2).

229 Influence of the presence of particular functional groups

230 Among the four functional groups, only one functional group had a significant influence on 231 earthworm growth. Earthworms that ate wheat litter from functional group 3 gained less 232 weight than the others (regression, P < 0.01). When the mineral nutrient concentrations were 233 added to the models, earthworm growth was no longer affected by cultivars from the 234 functional group 3 but was positively affected by magnesium concentration (Table 3). When 235 the negative effect of the functional group 3 was removed from the analyses, the growth of 236 adult earthworms did not decrease anymore with increasing number of wheat cultivars or 237 increasing wheat functional diversity (Table 3, Fig. 3). The growth of juvenile earthworms 238 even increased significantly with an increasing number of wheat cultivars not belonging to the functional group 3 during the feeding period (Table 3, Fig. 3). This suggested that the
negative effect of cultivar number on adult earthworm growth was due to the presence of
wheat from functional group 3 when the number of cultivars increases. During the nonfeeding period, the effect of functional group 3 was the opposite: earthworms that had eaten
litter from functional group 3 during the feeding period lost less weight than the others (Table
3).

245 Influence of nutrient concentrations on earthworm growth

Only nitrogen and magnesium had significant effects on earthworm growth (Tables 1 and 2).
Nitrogen had a positive effect during the feeding periods and a negative effect during the nonfeeding period. Magnesium had a positive effect during the feeding period. We found no
interactions between the development stage and the different nutrient concentrations
(statistical details not shown).

We also analyzed the influence of the wheat cultivar number, wheat functional diversity and the presence of particular functional groups on the two influential nutrients. There was no significant effect on nitrogen concentrations (result of linear models). There was a decrease in magnesium concentration with wheat cultivar (regression, P=0.001) number and wheat functional diversity (regression, P=0.005). Moreover, there was less magnesium in mixtures containing cultivars from the functional group 3 (ANOVA result, P<0.001, decrease in Mg content of 10% for mixtures with the functional group 3).

258 Influence of wheat cultivar number on earthworm mortality

259 Forty-one adults and 13 juveniles died during the October-December period. Between

260 December and February, only 3% of the 258 remaining earthworms died: 8 adults and 1

261 juvenile. During the non-feeding period, only one juvenile died. Overall, over the feeding and

262 non-feeding period, earthworm survival increased with the number of cultivars (logistic

regression, P=0.0428, Fig. 4). We did not find any significant effect of cultivar functional
diversity or nutrient concentrations on earthworm mortality (statistical details not shown).

265 **Discussion**

266 *Effect of cultivar mixtures during the Feeding period*

267 During the feeding period, adult growth decreased with the number and the functional 268 diversity of cultivars. This decrease could be explained by the variance in edibility hypothesis. 269 This hypothesis is based on the fact that a more diverse range of resources likely contains 270 resources resistant to consumption or at least less valuable in terms of nutrient content 271 (Leibold, 1989). In our experiment, increasing the number of cultivars in mixtures increased 272 the likelihood to have a cultivar from functional group 3, which has a negative effect on adult 273 earthworm growth. To support the hypothesis that cultivars from functional group 3 triggered 274 the negative effect of the increasing number of cultivars on adult earthworm growth, we 275 analyzed the effect of an increase in the number of cultivars not belonging to the functional 276 group 3. Since no relationship between adult growth and the number of cultivars not 277 belonging to the functional group 3 has been found, this suggests that the decrease in adult 278 earthworm growth can only be explained by the presence of cultivars from the functional 279 group 3. Our results on nutrient concentration suggest that the negative effect of the functional 280 group 3 is due to the lower magnesium concentration of the cultivars belonging to this 281 functional group. We indeed found that the magnesium content of the wheat biomass had a 282 positive effect on earthworm growth during the feeding period.

During the feeding period, juveniles behaved differently from adults since their growth increased with the number of cultivars. This result could be explained by the balanced diet hypothesis. This hypothesis is based on the fact that a more diverse resource assemblage leads to the consumption of more diverse nutritional resources, which improves the growth of the

287 consumer (DeMott, 1998; Pfisterer et al., 2003). Increasing the number of cultivars would 288 lead to a better diet because cultivar diversity (apart from functional group 3) provides a more 289 diverse range of nutrients for juvenile earthworms. To our knowledge, this is the first time 290 intraspecific genetic diversity is shown to lead to the balanced diet or the variance in edibility 291 hypothesis. Most of the experiments on the links between diet and animal growth and 292 performance addressed the influence of interspecific resource diversity (DeMott, 1998; 293 Pfisterer et al., 2003; Lefcheck et al., 2013). Most of them found positive effects of mixtures 294 on the performance of consumers. DeMott (1998) suggested for instance that a diet composed 295 of different prey species can be beneficial for its consumer. In this case, the different kinds of 296 nutrients brought by each of the two prey species were complementary and increased 297 consumer growth. A few studies observed negative effects of mixed diet on periphyton and 298 amphibian biomass (Stoler & Relyea, 2011). Swan and Palmer (2006) documented an overall 299 negative effect of interspecific litter diversity on detritivore growth. These opposite results 300 may be related to the breadth of the diet of the consumer. Because some species have high 301 requirements for particular nutrients, specialist consumers can be negatively impacted by a 302 mixed diet because of the lower concentration of the food they particularly need. Generalist 303 consumers likely have the opposite response. Earthworms are detritivores and *L. terrestris* 304 feed on a wide range of organic materials and are considered generalist feeders (Curry & 305 Schmidt, 2007). Our results support the idea that a more diverse intraspecific mix diet could 306 provide a more diverse range of nutrients leading to a positive influence on generalist feeders. 307 Overall, we hypothesize that depending on the consumer needs and the composition of its 308 diet, either the balanced diet or the variance in edibility mechanisms, which have opposite 309 consequences, are more influential.

In our experiment, it is likely that the variance in edibility hypothesis occurred in bothadults and juveniles and the balanced diet hypothesis for juveniles only. There is already

312 evidence showing that food requirements are changing during an individual's life 313 (Raubenheimer et al., 2007; Simpson & Raubenheimer, 2012). For instance, Dussutour and 314 Simpson (2009) showed that ants, depending on their developmental stage, need a protein-315 rich diet or a carbohydrate-rich diet in order to maximize their performance (survival and 316 production of larvae). The major difference between juvenile and adult earthworms is the 317 presence of the reproductive organs. It has been shown that juveniles use food resources for 318 the formation of sexual organs rather than their growth (Daniel et al., 1996). We could assume 319 that juvenile earthworms that ate a more diverse range of nutrients (e.g. amino acids) were 320 able to save energy – that they would otherwise have had to use to metabolize them – and 321 allocated it both to the formation of their sexual organs and their growth. The nutrient intake 322 target would be lower for adults than juveniles and could be reached with only one cultivar in 323 adults, which would explain why there was no balanced diet effect in adults. However, the balanced diet effect on juvenile earthworm growth cannot be explained by the mineral 324 325 nutrients we measured. The only effects of nutrients on earthworm growth during the feeding 326 period were the positive effect of nitrogen and magnesium concentrations (see Table 1 and 327 Table 2) but there was no relationship between nitrogen and wheat cultivar number and a 328 negative relationship between magnesium and wheat cultivar number. In this case, no nutrient 329 can explain the positive effect of cultivar numbers on earthworm growth. This suggests that 330 another undocumented feature of wheat biomass was involved. We tried to assess the effect of 331 other wheat functional traits measured on the 16 wheat cultivars but results remained difficult 332 to interpret (See Appendix B). The positive effect of nitrogen concentration on earthworm 333 growth during the feeding period is consistent with previous experiments on earthworms 334 (Schonholzer et al. 1998; Eisenhauer et al. 2010).

We did not find any effect of an increase of functional diversity on earthworm growth.This result suggests that our approximation of functional diversity, i.e. the number of

337 functional groups in the litter, does not reflect a diversity affecting earthworm growth. 338 Cultivars were classified using plant functioning and growth strategy traits (Wright et al., 339 2004). They might not be fully relevant to predict interactions with other trophic groups. 340 However, it cannot be excluded that the positive effect of the number of cultivars is caused by 341 a specific group of cultivars that has not been identified but whose likelihood of presence 342 would increase with the number of cultivars. The use of traits more closely linked to litter 343 quality and its nutritive value could help us to interpret our results and support either the 344 variance in edibility or the balanced diet effect. In any case, whatever the underlying 345 mechanism, we have demonstrated a trophic impact of intraspecific genetic diversity.

346 Effects of functional diversity during the non-feeding period

For technical reasons, the non-feeding period simulating winter only lasted one month but we 347 348 can assume that the effect would have been amplified if the period had lasted longer. During 349 the non-feeding period, earthworm growth increased with litter functional diversity. This 350 result is consistent with the balanced diet hypothesis predicting that a mixed diet is beneficial. 351 Moreover, we also found a positive effect of cultivars from functional group 3. Earthworms 352 that ate cultivars from functional group 3 or litter composed of cultivars with a more diverse 353 functional diversity during the feeding period lost less weight during the non-feeding period. 354 Shipitalo et al. (1988) showed that L. terrestris ingested more slowly low-quality food than 355 high-quality food. One explanation would then be that cultivars from functional group 3, 356 providing a low-quality food (low magnesium concentration), were ingested more slowly than 357 cultivar mixtures not containing wheat from this function group. Consequently, food 358 containing cultivars from functional group 3 remained more available for earthworms during 359 the non-feeding period, allowing them to lose less weight. This would also explain the 360 negative influence of nitrogen concentration on earthworm growth during the non-feeding 361 period. The low nitrogen concentration of particular cultivars would have decreased their

362 consumption rate during the feeding period and these low-quality cultivars (low nitrogen
363 concentration) could still have been available during the non-feeding period for earthworms,
364 allowing them to lose less weight.

365 Influence of the cultivar number on earthworm mortality

The mortality rate after December was similar or lower than in other earthworm laboratory 366 367 studies despite the rather small size of the vials used in the present study (Daniel et al., 1996; 368 Milcu et al., 2006). The higher mortality between October and December is probably due to 369 the fact that earthworms came from a commercial supplier and had to adjust to the laboratory 370 conditions. The positive effect of the number of cultivars on earthworm survival during the 371 whole experiment was mainly due to the high mortality rate between October and December 372 and suggests that the adaptation to the laboratory environment was facilitated by a more 373 diverse food. This result on mortality is consistent with our results on earthworm growth 374 supporting the balanced diet hypothesis. However, it remains difficult to determine whether 375 this effect is driven by the balanced diet hypothesis, i.e. the positive influence of the 376 interactions between cultivars, or the variance in edibility hypothesis, i.e. the positive 377 influence of a particular cultivar or functional group that we did not identify. Such effects of 378 interspecific food diversity on mortality have already been documented (Lefcheck et al., 379 2013). It has been shown for two bug species that larval survival was higher when they fed on 380 several plants (Di Giulio & Edwards, 2003). Insect species likely depend on a specific 381 nutrient balance, including amino acids, water content, minerals and trace elements that 382 cannot be provided by a single-species diet but by the complementarity effect of a mixed diet. 383 In our case, none of the studied mineral nutrients had an effect on earthworm mortality. 384 However, other unmeasured characteristics of the biomass could explain the positive effect of 385 the number of cultivars on earthworm survival.

386 Consequences for agricultural systems and ecosystems

387 The effect of crop genetic erosion on belowground communities has so far hardly been 388 investigated. For instance, there is evidence suggesting that reducing plant species richness 389 reduces earthworm species abundance in particular cases (Spehn et al., 2000). The underlying 390 mechanism would be the reduction of primary production, which decreases the resources 391 available to earthworms. Our results suggest that crop genetic erosion, besides its impact on 392 crop production (Kiær et al., 2009; Borg et al., 2018), decreases earthworm growth and 393 increases their mortality through the quality of the provided food. The decrease in earthworm 394 abundance in cropping systems could thus be amplified by the intra-field reduction in crop 395 genetic diversity. Since, the importance of services provided by earthworms to agriculture has 396 been widely demonstrated (Bertrand et al., 2015), mixing cultivars could be a way to support 397 earthworm populations and increase the services they provide. However, because the effects 398 of cultivar mixtures on earthworm growth and mortality that we have documented in 399 controlled conditions are rather small, field trials and modeling would be required to better 400 assess the real and long term influence of these effects on earthworm populations in cropping 401 systems.

402 However, to increase earthworm abundances using mixtures of cultivars it would first 403 be necessary to determine the cultivar functional traits affecting earthworms in order to 404 choose the right cultivars to be mixed. Indeed, as we saw with cultivars from functional group 405 3, mixing cultivars could have deleterious effects on earthworm growth. Moreover, the impact 406 of crop genetic diversity we have detected on earthworms could also impact the whole soil 407 biodiversity because a high proportion of soil organisms are decomposers that feed on litter. 408 Hence, mixing cultivars could also affect the whole micro food-webs through the quality of 409 the litter provided by mixtures. However, before using our results to improve agricultural 410 practices, our results should be tested in field experiments and their robustness should be

assessed for other earthworm and soil fauna species and other crop types. Moreover, our
results also depend on potential interactions between specific wheat cultivars and earthworm
genotypes and we did not control for these genotypes. Earthworm genetic diversity is likely

- 414 higher in agricultural fields and could influence the impact of the genetic diversity of their
- 415 food.

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- 424 Appendix A. Supplementary data
- 425 Supplementary data associated with this article can be found, in the online version, at
- 426 XXXXX.

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562	Table 1. Results of two linear models analyzing earthworm growth (IGR) as a function of the
563	developmental stage (A), mineral nutrient concentrations (N: nitrogen, Mg: magnesium),
564	wheat cultivar number (WCN) and their interactions during the two periods: FP for the
565	feeding period and NFP for non-feeding period. The non-significant variables and
566	interactions are removed from the models (e.g. other mineral nutrient concentrations). The
567	negative effect "(-)" or the positive effect "(+)" of the variables are indicated in the P column
568	for each period. In case of significant interaction between the maturity stage and the cultivar
569	number the effect (+ or -) of cultivar number is indicated separately for adults (Ad) and

	FP				NFP		
	DF	F	Р	DF	F	Р	
А	1	517.00	<0.001	1	17.0	<0.001	
Ν	1	4.28	0.040 (+)	1	4.2	0.040 (-)	
Mg	1	5.55	0.020 (+)			NS	
WCN	1	1.59	NS			NS	
A×WCN	1	13.20	<0.001			NS	
	-	Ad: - ; Juv: +	-				
Total	248			247			
		R ² =	0.68		$\mathbf{R}^2 =$	0.07	

570 juveniles (Juv).

572	Table 2. Results of a linear model analyzing earthworm growth (IGR) as a function of the
573	developmental stage (A), mineral nutrient concentrations (N: nitrogen, Mg: magnesium),
574	wheat functional diversity (F, number of functional groups in the mixtures of cultivars) and
575	their interactions during the two periods: FP for the feeding period and NFP for non-feeding
576	period. The non-significant variables and interactions are removed from the models (e.g.
577	other mineral nutrient concentrations). The negative effect "(-)" or the positive effect "(+)" of
578	the variables are indicated in the P column for each period. In case of significant interaction
579	between the maturity stage and the cultivar number the effect (+ or -) of cultivar number is
580	indicated separately for adults (Ad) and juveniles (Juv).

DF F P DF F P 1 494.00 <0.001 1 17.0 <0.001 1 4.09 0.044 (+) 1 4.3 0.040 (-) fg 1 5.30 0.022 (+) NS 1 0.11 NS 1 7.0 0.008 (+) ×F 1 3.15 0.077 NS NS $Ad: - ; Juv: No effect$ 247 NS $R^2 = 0.67$ $R^2 = 0.09$			F	Р	NFP		
1 494.00 <0.001 1 17.0 <0.001 1 4.09 0.044 (+) 1 4.3 0.040 (-) 1g 1 5.30 0.022 (+) NS 1 0.11 NS 1 7.0 0.008 (+) ×F 1 3.15 0.077 NS $Ad: - ; Juv: No effect$ 247 R ² = 0.67 R ² = 0.09		DF	F	Р	DF	F	Р
1 4.09 0.044 (+) 1 4.3 0.040 (-) 1g 1 5.30 0.022 (+) NS 1 0.11 NS 1 7.0 0.008 (+) ×F 1 3.15 0.077 NS $Ad: - ; Juv: No effect$ 247 R ² = 0.67 R ² = 0.09	А	1	494.00	<0.001	1	17.0	<0.001
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×F 1 3.15 0.077 NS Ad: -; Juv: No effect otal 248 247 $\mathbf{R}^2 = 0.67$ $\mathbf{R}^2 = 0.09$	F	1	0.11	NS	1	7.0	0.008 (+)
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otal 248 247 $\mathbf{R}^2 = 0.67$ $\mathbf{R}^2 = 0.09$		Ad.	: - ; Juv: No e	ffect			
$R^2 = 0.67$ $R^2 = 0.09$	Total	248			247		
K 0.07			$R^2 = 0.67$		$R^2 = 0.09$		• 0.09

590	Table 3. Results of a linear model analyzing earthworm growth (IGR) as a function of the
591	developmental stage (A), mineral nutrient concentrations (N: nitrogen, Fe: iron, Mg:
592	magnesium), the presence of cultivars belonging to particular functional groups (functional
593	groups from C1 to C4, C: functional group), the number of cultivars not belonging to the third
594	functional group (N \neq C3) and their interactions during the two periods: FP for the feeding
595	period with the effect of magnesium and FP (Mg-) for the feeding period without the effect of
596	magnesium in the model, and NFP for the non-feeding period. Non-significant variables
597	(especially the presence of cultivars from functional group 1, 2, 4 and other mineral nutrient
598	concentrations) have been removed manually for the final model. The negative effect "(-)" or
599	the positive effect "(+)" of the variables are indicated in the P column for each period. In case
600	of significant interaction between the maturity stage and the cultivar number the effect (+ or -)
601	of cultivar number is indicated separately for adults (Juv) and juveniles (Ad).

	FP		FP (Mg-)		NFP	
	F	Р	F	Р	F	Р
А	515.0	<0.001	511.0	<0.001	17.0	<0.001
Ν	4.3	0.040 (+)	4.2	0.040 (+)	4.3	0.040 (-)
Mg	5.5	0.020 (+)	-	-		NS
C3	2.3	NS	5.6	0.018 (-)	5.7	0.020 (+)
WCN≠C3	2.1	NS	1.3	NS		NS
A×WCN≠C3	10.0	0.002	9.9	0.002		NS
	Ad: No e	effect ; Juv: +	Ad: No	effect ; Juv: +		
Total DF 248		248			247	
R ²	0.68		0.68			0.09

603	Fig. 1. Covariance analysis of earthworm growth as a function of the number of cultivars and
604	earthworm stage, i.e. juvenile vs. adult during the feeding period. The trend lines are
605	represented by the equations $y = 0.00027 \text{ x} + 0.01$ (juveniles, $P = 0.02$) and $y = -0.0001 \text{ x} + 0.01 \text{ (juveniles, } P = 0.02)$
606	0.00544 (adults, $P = 0.03$). The confidence intervals (95%) of the regression fits are
607	represented by the grey area.
608	
609	Fig. 2. Effect of wheat functional diversity on earthworm growth during the non-feeding
610	period. The trend line is represented by the equation $y = 0.00055 \text{ x} - 0.00273 \text{ (P} = 0.001)$. The
611	confidence interval (95%) of the regression fit is represented by the grey area.
612	
613	Fig. 3. Effect of the number of wheat cultivars not belonging to the functional group 3 on
614	earthworm growth, depending on their age. The trend lines are represented by the equations y
615	= $0.00032 \text{ x} + 0.01$ (juveniles, P = 0.02) and y = $-0.00008 \text{ x} + 0.00531$ (adults, P = 0.15). The
616	confidence intervals (95%) of the regression fits are represented by the grey area.
617	
618	Fig. 4. Logistic regression between the mortality probability and the number of cultivars.
619	Mortality probability is indicated in the graph for each number of cultivars. $P(D/N=1) =$
620	0.247, $P(D/N=2) = 0.225$, $P(D/N=4) = 0.186$, $P(D/N=8) = 0.124$. N, number of cultivars;
621	$P(D/i)$, the probability of mortality if there are i cultivars. Probabilities are indicated by " \circ ".
622	P-value = 0.043 . Confidence interval (95%) of the regression fit is represented by the grey
623	area.
624	

626 Fig. 1















651 Fig. 4



