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► **To cite this version:**

Pierre Chassé, Céline Pelosi, Jean-Christophe Lata, Sébastien Barot. Impact of crop genetic diversity on a litter consumer. *Basic and Applied Ecology*, 2019, 36, pp.1-11. 10.1016/j.baae.2019.02.002 . hal-02273148

HAL Id: hal-02273148

<https://hal.science/hal-02273148>

Submitted on 28 Aug 2019

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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
16 biomass of mixtures of wheat cultivars was used as food for earthworms and their growth was
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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22 intraspecific genetic diversity has an impact on earthworm populations, probably through
23 mechanisms linked to the variance in edibility or the balanced diet hypotheses. While they
24 remain to be tested in the field, these results suggest that the current losses of crop genetic
25 diversity could potentially impact processes at the community or ecosystem level through a
26 decrease in food quality.

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

29 **Introduction**

30 It is now well documented that species richness, mostly through functional diversity, strongly
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
36 high within species as among species (Bangert et al., 2005), it would not be surprising if
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.

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

46 improves the growth of the consumer (DeMott, 1998; Pfisterer et al., 2003). On the other
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
60 during the 20th century (FAO, 2010). In particular, genetically homogeneous crop cultivars
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
70 (Spehn et al., 2000; Laossi et al., 2008). Anecic earthworms in agricultural fields mostly feed

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
74 environment. If the balanced diet hypothesis applies to earthworms, genetic crop diversity
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,
131 manganese, phosphorus, potassium, sodium and zinc concentrations were measured by dry
132 mineralization and spectrometry (radial ICP-AES, Varian Vista RL).

133 *Earthworm growth experiment*

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

138 *L. terrestris* were obtained from a commercial supplier (<http://appats-michel.fr/>). They
139 were patted dry, weighed and classified into juveniles or adults based on the presence of a
140 clitellum. 88 juveniles and 224 adults (average fresh weight $2.34\text{g} \pm 0.14\text{ g}$ for juveniles and
141 $4.25\text{ g} \pm 0.11\text{ g}$ for adults) were used in the experiment. Each container (10 cm inner diameter,
142 15 cm height) was filled with 775 g of soil. The soil moisture was adjusted to 80% of the soil
143 water holding capacity during the whole experiment (by weighing the pots every week). A
144 single earthworm was placed in each container. The containers were covered with perforated

145 lids to prevent earthworm escape. Each earthworm was fed with the litter of a single
146 experimental plot, i.e. a single mixture of wheat cultivar. The 16 treatments with litters
147 obtained from one cultivar were replicated 6 times, one time with a juvenile and five times
148 with an adult. The 72 treatments with litters combining more than one cultivar i.e. mixtures of
149 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.

168 *Calculation of earthworm growth rate*

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

171
$$\text{IGR} = \ln(W_t/W_i)/\Delta t,$$

172 where W_t (g) is the earthworm mass in February for the feeding period and in March for the
173 non-feeding period and W_i (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 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*

206 By February, all juveniles were adults so that during the non-feeding period all earthworms
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
209 “juveniles” and “adults” in our statistical analyses. On average in all treatments, the biomass
210 of juveniles increased by 309% ($\pm 8\%$) with a mean IGR of $1.1 \cdot 10^{-2} \text{ day}^{-1}$ ($\pm 0.6 \cdot 10^{-3} \text{ day}^{-1}$) in
211 the feeding period. During the non-feeding period, juveniles lost 1% ($\pm 1\%$) of their weight.
212 The biomass of adults increased by 168% ($\pm 4\%$) with a mean IGR of $5.1 \cdot 10^{-3} \text{ day}^{-1}$ ($\pm 0.2 \cdot 10^{-3}$
213 day^{-1}) in the feeding period. During the non-feeding period, adults lost 6% ($\pm 1\%$) of their
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

216 adults during the non-feeding period. However, in February, young adults had a lower weight
217 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
222 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
224 been provided during the previous months on earthworm growth.

225 *Influence of cultivar functional diversity on earthworm growth*

226 During the feeding period, there was no general effect of cultivar functional diversity on
227 earthworm growth (Table 2). During the non-feeding period, earthworms lost significantly
228 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

239 functional group 3 during the feeding period (Table 3, Fig. 3). This suggested that the
240 negative effect of cultivar number on adult earthworm growth was due to the presence of
241 wheat from functional group 3 when the number of cultivars increases. During the non-
242 feeding period, the effect of functional group 3 was the opposite: earthworms that had eaten
243 litter from functional group 3 during the feeding period lost less weight than the others (Table
244 3).

245 *Influence of nutrient concentrations on earthworm growth*

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

251 We also analyzed the influence of the wheat cultivar number, wheat functional
252 diversity and the presence of particular functional groups on the two influential nutrients.
253 There was no significant effect on nitrogen concentrations (result of linear models). There
254 was a decrease in magnesium concentration with wheat cultivar (regression, $P=0.001$) number
255 and wheat functional diversity (regression, $P=0.005$). Moreover, there was less magnesium in
256 mixtures containing cultivars from the functional group 3 (ANOVA result, $P<0.001$, decrease
257 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

263 regression, $P=0.0428$, Fig. 4). We did not find any significant effect of cultivar functional
264 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.

283 During the feeding period, juveniles behaved differently from adults since their growth
284 increased with the number of cultivars. This result could be explained by the balanced diet
285 hypothesis. This hypothesis is based on the fact that a more diverse resource assemblage leads
286 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.

310 In our experiment, it is likely that the variance in edibility hypothesis occurred in both
311 adults 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
324 balanced diet effect on juvenile earthworm growth cannot be explained by the mineral
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).

335 We did not find any effect of an increase of functional diversity on earthworm growth.
336 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*

347 For technical reasons, the non-feeding period simulating winter only lasted one month but we
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*

366 The mortality rate after December was similar or lower than in other earthworm laboratory
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

411 assessed for other earthworm and soil fauna species and other crop types. Moreover, our
412 results also depend on potential interactions between specific wheat cultivars and earthworm
413 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.

416 **Acknowledgments**

417 The wheat biomass was produced by the experimental unit of INRA Versailles directed by C.
418 Montagnier in an experiment coordinated by S. Saint-Jean, D. Tropée and P. Lusley and
419 involving all the WHEATAMIX Consortium (www.inra.fr/Wheatamix). We thank M. Mendez
420 from the Alysés analytical platform who has done the N analyses. We thank the INRA
421 USRAVE laboratory for the other elemental analyses. This work was supported by the
422 WHEATAMIX project, financed by the French National Research Agency (ANR-13-AGRO-
423 0008).

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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561 economics spectrum. *Nature* 428, 821–827.

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
570 juveniles (Juv).

	FP			NFP		
	DF	F	P	DF	F	P
A	1	517.00	<0.001	1	17.0	<0.001
N	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
		<i>Ad: - ; Juv: +</i>				
Total	248			247		
		R² = 0.68			R² = 0.07	

571

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).

	FP			NFP			
	DF	F	P	DF	F	P	
A	1	494.00	<0.001	1	17.0	<0.001	
N	1	4.09	0.044 (+)	1	4.3	0.040 (-)	
Mg	1	5.30	0.022 (+)			NS	
F	1	0.11	NS	1	7.0	0.008 (+)	
A×F	1	3.15	<i>0.077</i>			NS	
	<i>Ad: - ; Juv: No effect</i>						
Total	248			247			
		R² = 0.67			R² = 0.09		

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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≠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	P	F	P	F	P
A	515.0	<0.001	511.0	<0.001	17.0	<0.001
N	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 effect ; Juv: +		Ad: No effect ; Juv: +			
Total DF	248		248		247	
R²	0.68		0.68		0.09	

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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 $y = 0.00027 x + 0.01$ (juveniles, $P = 0.02$) and $y = -0.0001 x +$
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 $y = 0.00055 x - 0.00273$ ($P = 0.001$). 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 $= 0.00032 x + 0.01$ (juveniles, $P = 0.02$) and $y = -0.00008 x + 0.00531$ (adults, $P = 0.15$). The
616 confidence intervals (95%) of the regression fits are represented by the grey area.

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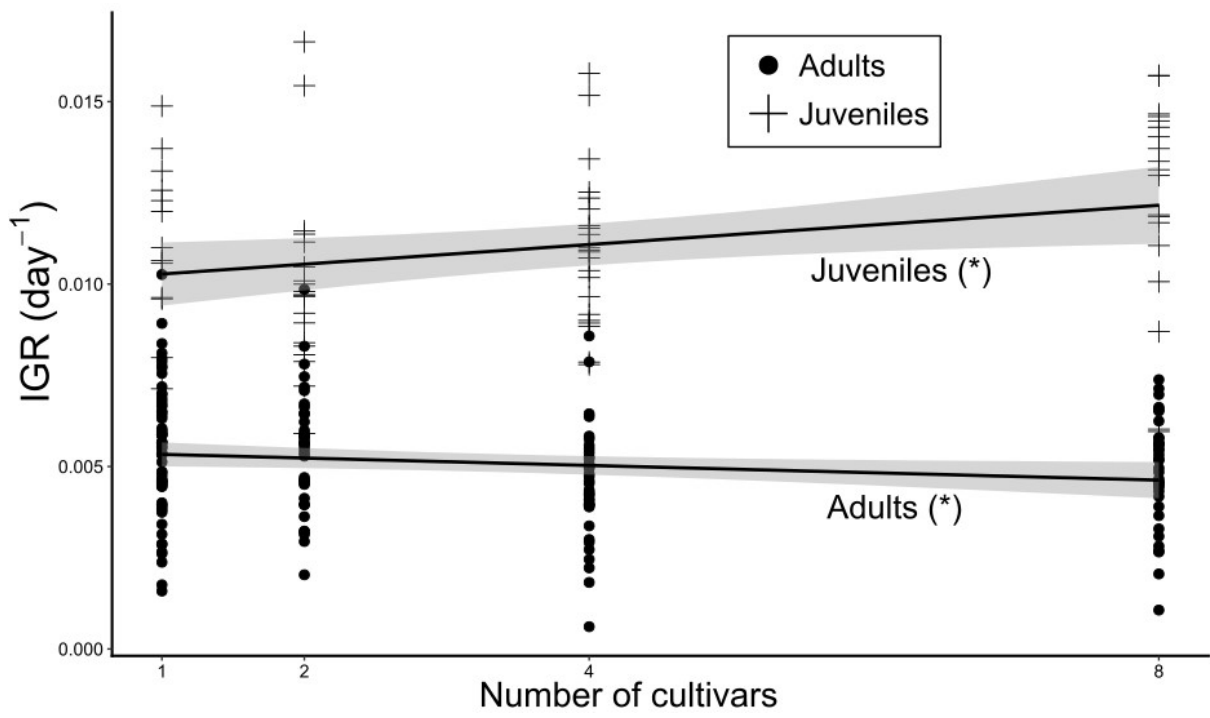
618 Fig. 4. Logistic regression between the mortality probability and the number of cultivars.
619 Mortality probability is indicated in the graph for each number of cultivars. $P(D/N=1) =$
620 0.247 , $P(D/N=2) = 0.225$, $P(D/N=4) = 0.186$, $P(D/N=8) = 0.124$. N , number of cultivars;
621 $P(D/i)$, the probability of mortality if there are i cultivars. Probabilities are indicated by “o”.
622 P -value = 0.043. Confidence interval (95%) of the regression fit is represented by the grey
623 area.

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626 Fig. 1

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631 Fig. 2

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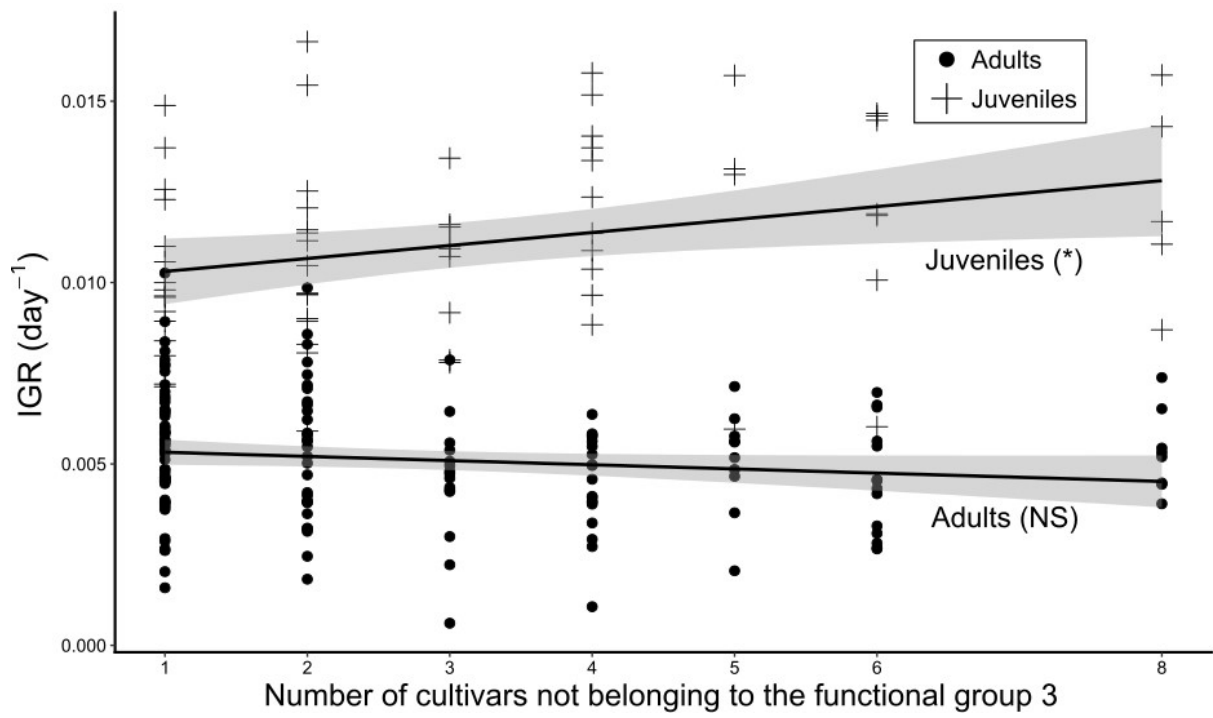


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635 Fig. 3

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651 Fig. 4

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