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Impact of agricultural practices and environmental variables on plant-parasitic nematode communities in fields at a landscape scale

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17 **Summary** - Agricultural practices shaping plant-parasitic nematode (PPN) assembly are still
18 unclear, and this limits our understanding of the anthropic disturbances impact on the
19 resilience of PPN communities and the emergence of agronomic problems. Here the
20 abundance and diversity of PPN in France's oilseed rape production area was determined by
21 sampling 72 fields over 2 consecutive years. We identified and counted PPN taxa and
22 collected anthropic and environmental variables for the past 5 years. PPN were assigned to
23 seven genera and one family including PPN that have not been identified until genus level.
24 Using multiple correspondence analyses, we selected the main variables and tested their effect
25 on the abundance of each taxon with mixed generalized linear models. We emphasize that at
26 the landscape scale investigated, crop rotations were no longer a major factor impacting the
27 PPN communities. However, we observed that tillage and pesticides had a significant impact
28 on several taxa.

29

30 **Keywords** - Community ecology; agricultural practices; multiple correspondence analysis;
31 model averaging

32

33 Nematodes are ubiquitous soil fauna that can be either plant-parasitic nematodes (PPN),
34 bacterial or fungal feeders, or omnivores. Because of their trophic ecologies, nematodes play
35 a role in nutrient recycling by feeding on plant tissue and microorganisms. PPN can have a
36 significant impact on yields and leading to economic issues (Nicol *et al.*, 2011; Jones *et al.*,
37 2013). According to Decraemer and Hunt (2006), at least 4100 species of PPN have been
38 described and the impact of many of them is still unknown.

39 Several studies have dealt with nematode communities, but many of them focus on their
40 role as bioindicators of soil quality. Indeed, various indices, such as the maturity index and
41 the plant-parasitic index (Bongers, 1990; Bongers and Ferris, 1999) (see Yeates (2003) for a
42 nematode index review) have been created to characterise nematode communities based on
43 the relative proportion of various trophic groups. These indices make it possible to evaluate
44 the impact of soil characteristics or management practices on nematode communities. For
45 example, Ugarte *et al.* (2013) show that community indices vary during the growing season
46 for different types of agriculture (from conventional to organic), depending, among other
47 things, on N availability and the presence/absence of tillage.

48 However, even though these indices highlight soil health and provide an overall
49 description of nematode communities, they do not allow for a precise evaluation of the
50 community structure or variations among communities of a single trophic group. The life
51 cycle of PPN is highly susceptible to climatic and host variations. Thus, their communities are
52 influenced by habitat heterogeneity and changes that influence their food sources or
53 environment, including agricultural management practices (Freckman and Ettema, 1993;
54 Villenave *et al.*, 2013). In agroecosystems, changes in PPN communities have received the
55 most attention because of the economic impact of these parasites on crop plants (Gomes *et al.*,
56 2003; Palomares-Rius *et al.*, 2015; Pokharel *et al.*, 2015). Only a few studies have focused on
57 the impact of environmental factors on the structure of PPN communities. Mateille *et al.*

58 (2014) showed that PPN communities vary among coastal foredunes due to sand texture and
59 mineral and carbonate concentrations. Similar results were found by Palomares-Rius *et al.*
60 (2015) who showed that olive variety and soil texture were the main factors shaping the
61 composition of PPN communities in olive orchards in Spain.

62 In agricultural studies, authors often examine a single crop or simple rotations involving a
63 maximum of two or three crops (Li *et al.*, 2015; Palomares-Rius *et al.*, 2015). Similarly,
64 authors often focus on the effect of a specific management practice, such as tillage, or on just
65 a few soil parameters (Parmelee and Alston, 1986; Porazinska *et al.*, 1999; Zhang *et al.*,
66 2015), but rarely on the combination of several management practices and several
67 environmental factors. The agricultural practices shaping the abundance and assembly of PPN
68 are still unclear, and this limits our understanding of the impact of anthropic disturbances on
69 the resilience of PPN communities and the emergence of agronomic problems. As PPN can
70 survive in numerous small patches in the soil environment, spatial sampling is a major key for
71 assessing PPN communities. However, results from spatial sampling alone neglect temporal
72 effects. It is therefore valuable to consider these two types of sampling in order to provide an
73 accurate view of the PPN community. It is worth noting that as far as we know, rare
74 investigations have been conducted at the landscape scale (Schomaker and Been, 1999; King
75 and Taberna, 2013) even though this scale is relevant since it can integrate high variability in
76 terms of soil types and climates. Moreover, it is also the scale of human activity, which
77 includes land use and agricultural practices.

78 In this study, we analysed the relationships between PPN communities and both the
79 physico-chemical properties of the soil and agricultural practices. To this end, we studied an
80 agroecosystem in the east of France composed of 72 fields representing 16 farmers for two
81 successive years. For each of these fields, five-year rotations, agricultural management
82 practices (number and type of tillage, use of pesticides, use of herbicides, sowing date) and

83 the physico-chemical proprieties of the soil (soil texture, N, C, organic matter, pH) were
84 collected, offering an opportunity to study the relative influence of soil properties and land
85 management practices in shaping PPN communities at a landscape scale. The following
86 questions have been addressed: are PPN heterogeneously distributed at this spatial scale?
87 Were the PPN communities stable for two successive years? Which variables and land
88 management practices characterise each plant-parasitic genus at this scale?

89

90 **Material and methods**

91

92 SAMPLING AND CHARACTERISTICS OF THE STUDIED AREA

93

94 This study was conducted near Dijon, in eastern France (47°14'N 5°03'E). This
95 geographical area (approximately 1400 ha) is defined as a temperate region with warm
96 summers (Peel *et al.*, 2007).

97 Mean monthly temperatures and rainfall data were collected from October 2012 to
98 September 2014.

99 Seventy-two fields, ranging from 0.46 ha to 28.65 ha and representing 16 different farmers,
100 were sampled in September 2013 and 2014 shortly after harvest time. For each fields and each
101 years since 2010, informations about cultivation practices including crop rotations from 2010
102 to 2014, the type and number of soil operations (deep or superficial tillage) and the type and
103 number of applications of plant protection products (herbicides on the one hand and
104 fungicides, insecticides and molluscicides grouped together under the category of non-
105 herbicides on the other hand), were collected from farmers. No nematicide was used since
106 2010 in any of the fields. The physico-chemical properties of the soil, including pH, organic

107 carbon, total nitrogen and soil texture, were obtained in September 2011 for each sampled
108 field as described by Dequiedt *et al.* (2011).

109 Seven sample points were considered alongside the longest diagonal of each field. Two
110 soil cores (depth of 30 cm using a manual auger (diameter 2.5 cm)) were taken at each of the
111 seven points and separated into two plastic bags (the seven points were pooled into the two
112 plastic bags), resulting, per field, in two bags, each containing about 1.5 kg of soil. One bag
113 was used for cyst extraction and identification and the other bag was used for free living PPN
114 extraction and identification. The GPS coordinates were recorded at each point in 2013 in
115 order to repeat the same samplings process in 2014.

116

117 NEMATODE EXTRACTION AND IDENTIFICATION

118

119 PPN communities were extracted from 400g of soil, according to the EPPO bulletin (2013)
120 protocol, using an Oostenbrink elutriator (MEKU) followed by centrifugal flotation. All PPN
121 families and genera from each extract were identified and counted using a binocular magnifier
122 based on the expertise of the National Reference Laboratory (NRL). In order to standardise
123 the counts, individuals were counted after a dilution step (depending on the density of
124 nematodes in the extracts), in 5mL of the dilution.

125 Cyst nematode communities were extracted from 600g of soil using two sieves fitted
126 together (800µm for the upper one and 250µm for the lower one). Then, cysts were manually
127 isolated, identified and counted from the total extract obtained on the 250µm sieve using a
128 binocular magnifier based on the expertise of the NRL. Cyst numbers were converted in
129 juvenile numbers based on the mean egg cyst content observed for the extracted cysts.

130

131 STATISTICAL ANALYSIS

132

133 Statistical analyses were conducted with R software (R Core Team, 2016). Mean monthly
134 temperatures from October 2012 to September 2013, and from October 2013 to September
135 2014, were compared using Student's t-test. Rainfall data for the same periods were compared
136 with the Wilcoxon (non-parametric) test.

137 Student's t-test was also used to assess differences, between 2013 and 2014, in the
138 abundance of each PPN taxon and the Shannon-Weaver diversity index (Shannon and
139 Weaver, 1949).

140 In order to explain the distribution of the various genera observed regarding the anthropic
141 and environmental variables considered for our study, we used the following statistical
142 strategy. Firstly, we carried out Multiple Correspondence Analysis (MCA) to select the main
143 contributing variables without any *a priori* knowledge (Burnham and Anderson, 2002;
144 Grueber *et al.*, 2011). Secondly, we used a model averaging approach (Burnham and
145 Anderson, 2002; Grueber *et al.*, 2011) to assess the influence of the previously selected
146 variables on the abundance of each PPN taxon.

147 The MCAs were performed using the FactoMineR package (Le *et al.*, 2008) (see Table 1
148 for the corresponding codes and Table S1 for the detail of limits and values of each variable).
149 We performed several MCAs for the PPN communities sampled in 2013 and 2014. In order to
150 assess whether past farming practices had an impact on the current abundance of PPN
151 communities, we considered the agricultural practices of the sampling year and the sum of the
152 different practices over previous growing periods (in 2013 and over the 2012-2013, 2011-
153 2013 and 2010-2013 periods for the 2013 sampling; in 2014 and over the 2013-2014, 2012-
154 2014, 2011-2014 and 2010-2014 periods for the 2014 sampling). PPN abundances were
155 considered as supplementary variables and thus did not contribute to the construction of the
156 factorial axis. Furthermore, only the modalities of variables whose absolute contributions

157 were more than twice the mean absolute contribution were represented (Cibois, 1986, 1997).
158 For the model averaging approach, we only used variables showing opposite modalities
159 considering the two factorial axes in at least two different maps.

160 In accordance with the Grueber *et al.* (2011) appendix, we performed model averaging
161 using Poisson Generalized Linear Mixed Model (GLMM) (Andersen *et al.*, 1997). We
162 implemented fields surface as random effect because the sampling protocol described
163 previously was similar for all fields regardless the surface. We use the corrected Akaike
164 information criterion (AICc). We first built a global model with the lme4 package (Bates *et*
165 *al.*, 2015), implementing all the explanatory variables selected using MCA. We then
166 performed model averaging with the MuMIn package (Barton 2016) to rank all the sub-
167 models. We only selected as the best models those having a $\Delta AICc < 2$, where $\Delta AICc$ is the
168 difference between the AICc of each sub-model and the AICc of the first best model
169 (Burnham and Anderson, 2002; Grueber *et al.*, 2011). The procedure estimated an average
170 weight for each explanatory variable based on the number of appearances in the selected
171 models. For the interpretation, we mainly focused on the 95% confidence interval (95% CI) of
172 the estimates and the sum of weights (SW) of each explanatory variable, to highlight the
173 major variables (Galipaud *et al.*, 2014). Variables with a confidence interval including zero
174 were considered to have no effect (Grueber *et al.*, 2011).

175

176 **Results**

177

178 PLANT-PARASITIC NEMATODE COMMUNITIES

179

180 Among the 72 fields, all PPN genera found were morphologically identified and counted
181 (Table 2): *Helicotylenchus*, *Pratylenchus*, *Heterodera*, *Macrotrophurus*, *Paratylenchus*,

182 *Criconemoides* and *Trichodorus*. Furthermore, Telotylenchidae other than *Macrotrophurus*
183 were counted but not identified to the genus level. The *Helicotylenchus* genus was the most
184 abundant genus each year (mean per field: 248.60 ± 15.91 indiv./100g wet soil for 2013 and
185 202.06 ± 18.68 indiv./100g wet soil for 2014) (Table 2). On the other hand, *Trichodorus* was
186 the least abundant genus (1.38 ± 1.05 indiv./100g wet soil for 2013 and 0.71 ± 0.38
187 indiv./100g wet soil for 2014) (Table 2). *Helicotylenchus*, *Pratylenchus* and Telotylenchidae
188 were clearly dominant (found in 100% of the fields in 2013 and respectively in 100%, 97%
189 and 97% of the fields in 2014, Table 2), whereas the others were identified in few fields and
190 were usually less abundant.

191 A comparison of the Shannon-Weaver index values showed that the diversity of PPN
192 communities changed significantly between 2013 and 2014 ($t=2.63$, $df=71$, $P=0.010$) (Table
193 2). However, Student's t-test shows significant differences, between 2013 and 2014 only for
194 the abundances of *Helicotylenchus*, *Pratylenchus* and *Paratylenchus* (respectively $t=3.17$,
195 $df=71$ and $P=0.002$; $t=4.75$, $df=71$ and $P<10^{-4}$; $t=3.17$, $df=71$ and $P=0.002$) (Table 2). There
196 were no differences between the mean monthly temperatures and rainfalls (calculated over a
197 year before the sampling dates) of the two sampling years ($t = -0.479$, $df = 11$, $P=0.637$ and
198 $Tw = 83$, $df = 11$, $P=0.551$ respectively).

199 The significant differences between the 2013 and 2014 communities and the lack of
200 climate differences between the two years suggest a strong impact of the previous year's
201 practices on the PPN communities. This is why we analysed the communities from 2013 and
202 2014 separately for the rest of the study.

203

204 VARIABLE SELECTION

205

206 In order to assess the impact of anthropic and environmental variables on the PPN
207 communities, we used MCA to select major variables without *a priori* knowledge to test their
208 influence in the models of the model averaging approach.

209 Seven variables were implemented in these analyses (Tillage, SupW, Herbi, NHerbi, Silt,
210 pH and Crops) (Table 1) and as PPN abundances were considered as supplementary variables,
211 they did not contribute to the construction of the axes. Depending on the time-period
212 considered, agricultural practices and environmental variables accounted for 10.7% to 13.9%
213 of the variability of the dataset on the first axis and for 9.5% to 12.1% on the second axis. On
214 average, taking into account all the factorial maps, the first two axes absorbed about 22.5% of
215 the variance.

216 The four factorial maps built for the PPN sampled in 2013 (Fig. 1 and Fig. S1 to Fig. S4)
217 showed opposite modalities for the following variables: Tillage (Fig. S1 and Fig. S4), SupW
218 (Fig. 1 and Fig. S3), Herbi and NHerbi (Fig. 1 and Fig. S1 to Fig. S4). These four variables
219 were therefore considered for testing in the model averaging approach. For the PPN sampled
220 in 2014, except SupW, the three same variables were considered based on the five factorial
221 maps built (Fig. 2 and Fig. S5 to Fig. S9): Tillage (Fig. 2 and Fig. S5 to Fig. S9), Herbi and
222 NHerbi (Fig. 2 and Fig. S5 to Fig. S9).

223

224 MODEL SELECTION AND EFFECT OF ANTHROPIC VARIABLES ON THE 225 ABUNDANCE OF PLANT-PARASITIC NEMATODES

226

227 GLMM were implemented with the previously selected variables and using fields surface
228 as random effect. Concerning the nematodes sampled in 2013, 16 first-order models,
229 implemented for each taxon and year of a given cultivation practice with the four selected
230 explanatory variables, were ranked. The SW and 95% CI were calculated for the explanatory

231 variables present in the subset of models with a $\Delta AICc < 2$, but only the explanatory variables
232 with an SW=1 are represented in Table 3. Indeed, the majority of the 95% CIs included zero,
233 indicating that the effect of the explanatory variables was uncertain. However, each time the
234 SW=1, the 95% CI did not include zero, indicating that the explanatory variable could be
235 considered as significant to explain the abundance of the taxon (for instance, for
236 *Pratylenchus*, 95% CIs for NHerbi 2013 and 2012-13 were respectively 0.007 to 0.143 and
237 0.014 to 0.102, and 95% CIs for Tillage 2011-13 and 2010-13 were respectively -0.476 to -
238 0.070 and -0.339 to -0.037 (see full results in Table S2)).

239 In a few cases, explanatory variables had an SW > 0.8 (2013 Tillage for *Pratylenchus*
240 (SW=0.84) and 2011-2013 Tillage for *Macrotrophurus* (SW=0.82)). This threshold is
241 sometimes considered as a rule of thumb to highlight the effect of an explanatory variable on
242 a variable but Galipaud *et al.* (2014) demonstrated that this rule is not always accurate.
243 Furthermore, the 95% CI included zero in all such cases (-1.027 to 0.153, -1.894 to 0.350 and
244 -0.061 to 0.005 respectively).

245 Concerning the nematodes sampled in 2014, for each taxon and year of a given cultivation
246 practice, 8 first-order models, implemented with the three selected explanatory variables,
247 were ranked. The SW and 95% CI were calculated for the explanatory variables present in the
248 subset of models with a $\Delta AICc < 2$, but only the explanatory variables with an SW=1 are
249 represented in Table 4. As for the results of 2013, the majority of the 95% CIs included zero,
250 indicating that the effect of the explanatory variables was uncertain. However, as for 2013,
251 each time the SW=1, the 95% CI did not include zero (for instance, for *Helicotylenchus*, the
252 95% CI for Herbi 2014 was 0.014 to 0.143 (see full results in Table S3)). Unlike the results
253 for 2013, none of the explanatory variables had an SW > 0.8.

254

255 **Discussion**

256

257 Oilseed rape cultivated areas have increased nearly five-fold in France over the last 40
258 years. Oilseed rape has high nitrogen needs and is now found frequently in field crop rotations
259 in France, sometimes even in very short rotations. This study was the first nematode
260 community analysis conducted in arable fields where oilseed rape was the main crop. It was
261 also the first PPN community analysis conducted at a geographic scale that allowed for the
262 simultaneous integration of the effects of different years, soil types, and land uses and
263 agricultural practices. Our results showed significant spatial and temporal variations in PPN
264 abundance at this newly investigated scale. Statistical analyses allowed us to highlight the
265 impact of soil operations, and more precisely tillage, as well as the use of plant protection
266 products (*i.e.* herbicides and non-herbicide products), but not of crop rotation or soil type,
267 contrary to what we might have expected.

268

269 SAMPLING PROCESS AND COMPOSITION OF THE COMMUNITIES

270

271 The sampling protocol was the same over the 72 fields of the study and was conducted
272 irrespective of the whole surface of each field. This may have led to some bias for an
273 exhaustive description of the nematode biodiversity in the largest fields as rare genera may
274 have not been sampled. We also choose to make composite samples made from a limited
275 number of individual soil cores but still representing a total weight of soil of at least 1.5 Kg,
276 as it can be found in other studies (Poeydebat *et al.*, 2017). This protocol was considered as
277 the best trade-off between technical effort and accuracy for the community characterization
278 considering the number of fields investigated and our wish to survey the same sampling
279 points to minimize inter annual sampling bias. Furthermore, in regards to the damages on
280 crops or pests management, rare species were considered as marginal.

281 The PPN communities in the investigated area contained eight taxa; this is quite similar to
282 what is commonly found in other anthropic ecosystems (Freckman and Ettema, 1993; Zheng
283 *et al.*, 2012; Zhang *et al.*, 2015; Quist *et al.*, 2016) but lower than what has been found in
284 natural ecosystems (Mateille *et al.*, 2014; Renčo *et al.*, 2015). As sampling was performed at
285 the same period for two successive years, but not at different periods during the growing
286 season, we cannot exclude the possibility that we missed some endoparasitic taxa which
287 would have been in root remains or weed roots rather than in soil or that endoparasitic
288 nematodes abundance have been underestimated. But this is unlikely, since we sampled fields
289 shortly after harvest time (*i.e.* without crops or with very recent seedling) and also since we
290 were able to identify *Pratylenchus* (a migratory endoparasitic nematode) and juveniles of
291 *Heterodera* (a sedentary endoparasitic nematode).

292 Prevalence revealed that in our study, PPN were not always distributed homogeneously
293 throughout the landscape. Indeed, only three out of the eight taxa were found in more than
294 90% of the fields over the two years of sampling. This seems consistent with previous
295 findings in the literature about nematodes living in patches (Goodell and Ferris, 1980),
296 probably because of a low capacity for active dispersion (Wallace, 1968) and passive
297 dispersion due to agricultural management (Alenda *et al.*, 2014).

298 Even though the identified taxa were the same in 2013 and 2014, the Shannon-Weaver
299 index and the abundance of several of these taxa showed significant variation between the two
300 years of sampling. This confirms previous findings in the literature showing that PPN are
301 organisms that respond quickly to changes in their environment (Bongers, 1990; Yeates and
302 Bongers, 1999). As the two years of sampling were not significantly different in terms of
303 monthly mean temperature and rainfall, it was interesting to investigate the impact of other
304 environmental and anthropic variables, in order to ascertain the major variables in variation of
305 PPN abundance.

306

307 VARIABLE SELECTION

308

309 The use of multiple correspondence analyses was for us a way of avoiding the *a priori*
310 selection of variables to implement in the models. Indeed, several publications implement
311 variables based on strong ecological knowledge of the organisms they are dealing with
312 (Grueber *et al.*, 2011; Carrara *et al.*, 2015; Lankinen *et al.*, 2016). Here we chose the MCA
313 approach, which better suited our incomplete knowledge of the biology of some of the
314 identified taxa and the wide biological diversity of the identified taxa. The MCA approach
315 allowed us to choose the major variables that should be tested with the model averaging
316 approach. Surprisingly, crop rotation was not retained on our factorial maps, even though it is
317 a variable highlighted in several previous studies (Freckman and Ettema, 1993; Ponge *et al.*,
318 2013; Zhang *et al.*, 2015; Zhong *et al.*, 2016). In our case, the non-selection of this variable
319 following MCA analysis may have been due to the area investigated in this study. Indeed, the
320 Fenay region is geographically limited (about 1400Ha) and crop rotations were quite similar
321 in all of the fields over at least the last six years rotations : 65 out of 72 fields harboured only
322 cereal/Brassicacea (oilseed rape or mustard) and the others had only one other crop for one
323 year over the studied period. The absence of both crop rotation and environmental variables
324 on the majority of the factorial maps proves that our decision to use MCA instead of *a priori*
325 ecological knowledge was sound. In fact, after summarising all the factorial maps, it appeared
326 that at the landscape scale investigated, only anthropic practices such as soil operations and
327 the use of pesticides impacted the PPN communities and required further investigation
328 through the model averaging procedure.

329

330 EFFECTS OF SOIL OPERATIONS

331

332 Among the four variables selected by the MCA analysis and implemented in the model
333 averaging approach (*i.e.* Tillage, SupW, Herbi and NHerbi), the amount of superficial tillage
334 was never selected as a major explanatory variable at the end of the model averaging
335 procedures. It is possible that the impact of the other variables was stronger and hindered the
336 potential effect of superficial tillage. Indeed, tillage may have a stronger impact on several
337 PPN because it disturbs the ground on a deeper level than superficial tillage (Minton, 1986).

338 In contrast, tillage is a practice that was selected several times as a major variable
339 impacting the abundance of PPN taxa. It seems obvious that tillage impacts both ectoparasites
340 (*i.e. Macrotrophurus*) and endoparasites because it occurs when there is no crop in place and
341 thus when endoparasites are also present in the soil. In this study, we usually found that tillage
342 had a negative impact but this cannot be generalised as we also found that it sometimes had a
343 positive impact.

344 It had already been demonstrated that tillage has a strong impact on the soil food web
345 (Hendrix *et al.*, 1986; Zhong *et al.*, 2016) which could affect some of the PPN taxa by
346 modifying the availability of weed roots. Here we highlighted the negative impact on
347 *Pratylenchus* and *Macrotrophurus*, in line with the findings of Smiley *et al.* (2013). In
348 contrast with superficial tillage, tillage modifies the soil more deeply (Altieri, 1999;
349 Franzluebbers, 2002), which could have a significant impact on their abundance (Rahman *et*
350 *al.*, 2007).

351 However, it should be noted that tillage had a positive impact on *Paratylenchus* and this
352 effect seemed to be consistent in both the 2013 and 2014 samplings (although it was stronger
353 in the 2014 sampling). This result seems to conflict with the above hypothesis, but there are
354 other examples in the literature reporting similar effects of tillage on PPN (Stirling *et al.*,
355 2011; Palomares-Rius *et al.*, 2015). It is possible that this genus is less susceptible to

356 disturbance, perhaps because of its small size. Also, as tillage decreases the abundance of the
357 other PPN taxa, it allows *Paratylenchus* to replace them and increase in the soil.

358 The impact of tillage can vary depending on many other parameters. For example, in our
359 study we found that tillage had a negative impact on *Pratylenchus* whereas McSorley and
360 Gallaher (1993) found that tillage increased *Pratylenchus* abundance. These differences can
361 be explained by a difference in soil properties, *i.e.* mainly slit soils in our case, while it was
362 mainly sand soils in Gallaher's (1993) study. Furthermore, the impact of interactions between
363 variables has not been analysed here to avoid implementing too many terms in the models
364 (Burnham and Anderson, 2002; Grueber *et al.*, 2011). Interactions have, however, sometimes
365 proven to affect the abundances of PPN (Okada and Harada, 2007; Jibrin *et al.*, 2014) and it
366 might be interesting to develop this hypothesis in future studies.

367

368 EFFECTS OF PESTICIDE USES

369

370 Since no nematicide was used in the sampled fields, pesticides were divided into two
371 groups, herbicides and non-herbicides, and both were selected as major explanatory variables
372 at the end of the model averaging approach for several nematode taxa.

373 Non-herbicide products had a positive impact on the abundance of only two PPN genera
374 (*i.e.* *Pratylenchus* and *Paratylenchus*). Among these products, fungicides are used most often.
375 These products can sometimes reduce PPN directly (Van der Putten and Van der Stoel, 1998).
376 However, fungicides can also increase PPN (Rodriguez-Kabana and Curl, 1980), for example
377 by stimulating hatching of eggs.

378 It is known that some fungi are natural enemies of nematodes and more precisely of PPN
379 (Siddiqui and Mahmood, 1996; Kerry, 2000). Thus, it is possible that by eliminating enemies
380 such as predators and parasites, fungicides have enabled PPN to increase in the soil.

381 Only the 2014 herbicide uses seemed to impact PPN abundance, even though the number
382 of uses was not significantly different in 2013 and 2014 (data not shown). It was the only
383 variable that seemed to positively impact *Helicotylenchus* while herbicides usually have no or
384 little effect on soil microorganisms directly (Bünemann *et al.*, 2006). The effect of herbicides
385 on PPN has been poorly studied to our knowledge, making this variable an interesting avenue
386 for future research. In this study, it was not possible to collect information about inter-season
387 cover crops or weed communities. Thus, discussing the impact of herbicides would be
388 speculative, as we do not know the potential host plants of the identified PPN and further
389 investigations will need to be developed.

390

391 **Conclusion**

392

393 We showed that at the landscape scale, which was investigated in this study and which
394 corresponds to the scale of human activities at which land use and agricultural practices are
395 integrated, crop rotation was no longer the main factor impacting PPN communities as it can
396 be observed at field scale. In contrast, and in agreement with the literature, soil operations,
397 and more precisely tillage, had a major impact on PPN. This was obviously because tillage
398 modifies the interactions between soil organisms, as well as food availability and habitat.
399 However, the effect (*i.e.* positive or negative) can hardly be generalised, as we found both
400 positive and negative impacts depending on the nematode taxon. It would be interesting to
401 push forward these findings in order to develop hypotheses on the interactions between tillage
402 and other variables such as soil properties and plant protection products.

403 Pesticides also seemed to play a key role in variations in PPN abundance in crops, but their
404 effects here were unclear and the literature seems to lack information about their effects on

405 PPN. Further investigations are therefore needed on this topic to develop the hypotheses
406 expressed in this article.

407 This study was a first step towards understanding the impact of farming practices and
408 environmental conditions on PPN communities found in crop fields. It was conducted in a
409 limited area, which explains the homogeneous climatic and soil conditions as well as the
410 similarity of the crop rotations among the fields. To push the analyses further, it is now
411 necessary to compare these results with communities from other sampling operations,
412 especially in other agricultural environments, including other crop rotations and other climatic
413 conditions.

414

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416

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425

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Table 1. Considered variables and corresponding codes used in the figures of this article and the supplementary material

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Codes	Type	Description
Tillage / NoTillage	Quantitative	Presence or absence of tillage for the period considered
SupW	Quantitative	Number of superficial tillage for the period considered
Herbi	Quantitative	Number of applications of herbicide products for the period considered
NHerbi	Quantitative	Number of applications of non-herbicide products (fungicides, insecticides or molluscicides) for the period considered
Silt	Quantitative	Percentage of silt in the soil, ranging from 39.1 % to 85.8 %
pH	Quantitative	pH ranging from 4.83 to 8.40
Surface	Quantitative	Field surface ranging from 0.46Ha to 28.65Ha
Crops	Qualitative	Crop rotation: mainly cereals (wheat and barley), mainly <i>Brassicacea</i> (oilseed rape and mustard) or mainly other land uses

Table 2. Abundance comparison of the PPN communities found in 2013 and 2014

	Mean \pm Standard error (indiv./100g of wet soil)		Mean abundance comparison 2013-2014				Prevalence (%)	
	2013	2014	t	df	p-value	significance	2013	2014
<i>Helicotylenchus</i>	248.60 \pm 15.91	202.06 \pm 18.68	3.17	71	0.002	**	100	100
<i>Pratylenchus</i>	93.40 \pm 8.38	57.28 \pm 5.37	4.75	71	<10 ⁻⁴	***	100	97
<i>Heterodera</i>	20.20 \pm 8.08	40.70 \pm 17.67	-1.41	71	0.163		19	18
<i>Macrotrophurus</i>	6.58 \pm 2.00	3.29 \pm 1.22	1.59	71	0.117		35	23
<i>Paratylenchus</i>	72.37 \pm 13.07	43.31 \pm 7.30	3.17	71	0.002	**	89	84
<i>Criconemoïdes</i>	7.44 \pm 3.32	8.72 \pm 5.09	-0.49	71	0.623		36	19
<i>Trichodorus</i>	1.38 \pm 1.05	0.71 \pm 0.38	0.89	71	0.379		15	6
Other Telotylenchidae	144.92 \pm 15.12	138.01 \pm 13.73	0.44	71	0.661		100	97
Shannon-Weaver Index	0.50 \pm 0.01	0.47 \pm 0.01	2.63	71	0.01	*		

* < 0.05 ; ** < 0.005 ; *** < 0.001

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Table 3. Results of models selections for 2013 samplings. Only the explicative variables with a SW=1 are presented in the equations preceded by the estimate value. See full results in supplementary material (Table S2).

Taxon	Estimate of the significant variables
<i>Pratylenchus</i> =	0.075 Non-herbicide ₂₀₁₃
	0.056 Non-herbicide ₂₀₁₂₋₂₀₁₃
	-0.273 Tillage ₂₀₁₁₋₂₀₁₃
	-0.188 Tillage ₂₀₁₀₋₂₀₁₃
<i>Macrotrophurus</i> =	-2.682 Tillage ₂₀₁₃
	-1.949 Tillage ₂₀₁₂₋₂₀₁₃
	-0.835 Tillage ₂₀₁₀₋₂₀₁₃
<i>Paratylenchus</i> =	0.559 Tillage ₂₀₁₁₋₂₀₁₃

Indices under each explicative variable indicate the year or period for which the explicative variable is significant

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Table 4. Results of models selections for 2014 samplings. Only the explicative variables with a SW=1 are presented in the equations preceded by the estimate value. See full results in supplementary material (Table S3).

Taxon	Estimate of the significant variables
<i>Helicotylenchus</i> =	0.079 Herbicide ₂₀₁₄
<i>Paratylenchus</i> =	1.290 Tillage ₂₀₁₄ 1.020 Tillage ₂₀₁₃₋₂₀₁₄ + 0.068 Non-herbicide ₂₀₁₃₋₂₀₁₄ 0.683 Tillage ₂₀₁₂₋₂₀₁₄ + 0.058 Non-herbicide ₂₀₁₂₋₂₀₁₄ 0.478 Tillage ₂₀₁₁₋₂₀₁₄ 0.342 Tillage ₂₀₁₀₋₂₀₁₄

Indices under each explicative variable indicate the year or period for which the explicative variable is significant

Table S1. Limits and values used to code each MCA variables among the year periods. Limits were determine mainly based on quartiles of each variables when four classes were possible, or based on the presence/absence in order to obtain classes of variables as balanced as possible

Codes	Year period	Limits and values
Tillage / NoTillage	2013	Tillage = 1 ; NoTillage = 0
	2012-2013	Tillage = 1 ; NoTillage = 0
	2011-2013	NoTillage = 0 ; Few = 1 ; Alot >1
	2010-2013	NoTillage = 0 ; Few = 1 ; Medium = 2 ; Alot >2
	2014	Tillage = 1 ; NoTillage = 0
	2013-2014	NoTillage = 0 ; Few = 1 ; Alot >1
	2012-2014	Few = 1 ; Medium = 2 ; Alot >2
	2011-2014	NoTillage = 0 ; Few <3 ; Medium <4 ; Alot >4
2010-2014	NoTillage = 0 ; Few <3 ; Medium <5 ; Alot >5	
SupW	2013	VeryFew <2 ; Medium <3 ; Alot >3
	2012-2013	VeryFew <4 ; Few <5 ; Medium <6 ; Alot >6
	2011-2013	VeryFew <6 ; Few <8 ; Medium <9 ; Alot >9
	2010-2013	VeryFew <7 ; Few <10 ; Medium <11 ; Alot >11
	2014	VeryFew <2 ; Few <3 ; Medium <4 ; Alot >4
	2013-2014	VeryFew <3 ; Few <5 ; Medium <6 ; Alot >6
	2012-2014	VeryFew <6 ; Few <7 ; Medium <9 ; Alot >9
	2011-2014	VeryFew <7 ; Few <10 ; Medium <12 ; Alot >12
2010-2014	VeryFew <9 ; Few <12 ; Medium <14 ; Alot >14	
Herbi	2013	VeryFew <3 ; Few <4 ; Medium <6 ; Alot >6
	2012-2013	VeryFew <4 ; Few <6 ; Medium <10 ; Alot >10
	2011-2013	VeryFew <8 ; Few <10 ; Medium <13 ; Alot >13
	2010-2013	VeryFew <10 ; Few <13 ; Medium <17 ; Alot >17
	2014	VeryFew <3 ; Few <4 ; Medium <5 ; Alot >5
	2013-2014	VeryFew <5 ; Few <7 ; Medium <9 ; Alot >9
	2012-2014	VeryFew <7 ; Few <10 ; Medium <16 ; Alot >16
	2011-2014	VeryFew <10 ; Few <13 ; Medium <18 ; Alot >18
2010-2014	VeryFew <13 ; Few <17 ; Medium <23 ; Alot >23	
NHerbi	2013	VeryFew <5 ; Few <7 ; Medium <9 ; Alot >9
	2012-2013	VeryFew <8 ; Few <12 ; Medium <15 ; Alot >15
	2011-2013	VeryFew <13 ; Few <17 ; Medium <20 ; Alot >20
	2010-2013	VeryFew <17 ; Few <22 ; Medium <25 ; Alot >25
	2014	VeryFew <4 ; Few <5 ; Medium <6 ; Alot >6
	2013-2014	VeryFew <9 ; Few <11 ; Medium <15 ; Alot >15
	2012-2014	VeryFew <13 ; Few <16 ; Medium <20 ; Alot >20
	2011-2014	VeryFew <18 ; Few <21 ; Medium <27 ; Alot >27
2010-2014	VeryFew <22 ; Few <26 ; Medium <31 ; Alot >31	

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Table S1. (Continued)

Codes	Year period	Limits and values
Silt	-	VeryFew <49.58 ; Few <55.75 ; Medium <63.58 ; Alot >63.58
pH	-	Acid < 7.157 ; Acid/Neutral < 7.945 ; Neutral/Basic < 8.148 ; Basic > 8.148
Crops	2013	Wheat ; Barley ; Oilseed
	2012-2013	Brassicacea: at least 1 oilseed or mustard ; Cereals : no oilseed or mustard
	2011-2013	Brassicacea: at least 1 oilseed or mustard ; Cereals : no oilseed or mustard
	2010-2013	Brassicacea: at least 2 oilseed or mustard ; Cereals < 2 oilseed or mustard
	2014	Wheat ; Barley ; Oilseed ; Other
	2013-2014	Brassicacea: at least 1 oilseed or mustard ; Cereals : no oilseed or mustard
	2012-2014	Brassicacea: at least 1 oilseed or mustard ; Cereals : no oilseed or mustard
	2011-2014	Brassicacea: at least 2 oilseed or mustard ; Cereals < 2 oilseed or mustard
	2010-2014	Brassicacea: at least 2 oilseed or mustard ; Cereals < 2 oilseed or mustard

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Table S2. Results of models selections for 2013 samplings

	Variable	Cultural practices 2013			Cultural practices 2012-2013			Cultural practices 2011-2013			Cultural practices 2010-2013		
		Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW
<i>Helicotylenchus</i>	(Intercept)	5.336	5.121, 5.550		5.374	5.074, 5.674		5.391	4.969, 5.812		5.427	5.046, 5.809	
	Tillage	-0.026	-0.191, 0.140	0.20	-0.027	-0.151, 0.098	0.24	-0.007	-0.061, 0.047	0.14	-0.013	-0.075, 0.050	0.24
	Superficial tillage	-	-	-	-0.004	-0.040, 0.031	0.15	-0.010	-0.056, 0.036	0.29	-0.007	-0.040, 0.027	0.24
	Herbicides	0.005	-0.022, 0.033	0.24	0.002	-0.012, 0.017	0.18	0.003	-0.013, 0.020	0.28	0.001	-0.009, 0.011	0.15
	Non-herbicides	0.001	-0.010, 0.012	0.15	0.001	-0.007, 0.008	0.13	0.001	-0.006, 0.008	0.12	-	-	-
<i>Pratylenchus</i>	(Intercept)	3.937	3.420, 4.454		3.668	3.140, 4.196		3.940	3.098, 4.781		3.992	3.102, 4.882	
	Tillage	-0.437	-1.027, 0.153	0.84	-0.055	-0.276, 0.166	0.36	-0.273	-0.476, -0.070	1.00	-0.188	-0.339, 0.037	1.00
	Superficial tillage	0.050	-0.129, 0.229	0.36	-	-	-	0.040	-0.058, 0.139	0.54	0.013	-0.041, 0.066	0.35
	Herbicides	-0.060	-0.164, 0.044	0.71	-0.021	-0.081, 0.039	0.48	-0.037	-0.107, 0.033	0.66	-0.028	-0.096, 0.039	0.55
	Non-herbicides	0.075	0.007, 0.143	1.00	0.056	0.014, 0.102	1.00	0.044	-0.002, 0.090	1.00	0.039	-0.003, 0.081	1.00
<i>Macrotrophurus</i>	(Intercept)	-2.285	-5.024, 0.453		-2.095	-5.397, 1.208		-2.497	-6.635, 1.642		-1.367	-5.061, 2.327	
	Tillage	-2.682	-5.224, -0.139	1.00	-1.949	-3.381, -0.516	1.00	-0.772	-1.894, 0.350	0.82	-0.835	-1.580, -0.090	1.00
	Superficial tillage	0.233	-0.663, 1.135	0.31	0.299	-0.346, 0.943	0.61	0.029	-0.203, 0.260	0.16	-	-	-
	Herbicides	0.016	-0.140, 0.173	0.15	-	-	-	0.047	-0.117, 0.212	0.34	0.023	-0.107, 0.153	0.26
	Non-herbicides	0.012	-0.094, 0.118	0.16	-	-	-	0.007	-0.060, 0.072	0.14	0.007	-0.059, 0.072	0.20
<i>Paratylenchus</i>	(Intercept)	2.872	2.045, 3.700		2.280	0.695, 3.864		1.792	0.210, 3.373		2.371	0.382, 4.360	
	Tillage	0.463	-0.602, 1.528	0.59	0.462	-0.289, 1.212	0.78	0.559	0.174, 0.944	1.00	0.216	-0.169, 0.601	0.73
	Superficial tillage	0.017	-0.155, 0.189	0.12	-	-	-	-0.095	-0.292, 0.103	0.57	-0.030	-0.160, 0.101	0.27
	Herbicides	0.007	-0.055, 0.069	0.14	0.014	-0.054, 0.082	0.21	0.043	-0.068, 0.154	0.50	0.006	-0.039, 0.052	0.11
	Non-herbicides	0.004	-0.035, 0.043	0.13	0.024	-0.045, 0.095	0.38	0.040	-0.038, 0.117	0.60	0.023	-0.039, 0.085	0.49
<i>Criconemoides</i>	(Intercept)	-2.024	-4.588, 0.541		-1.014	-4.278, 2.251		-1.707	-5.082, 1.668		-2.219	-5.215, 0.777	
	Tillage	0.768	-1.584, 3.120	0.42	0.605	-0.891, 2.100	0.51	0.106	-0.447, 0.660	0.29	0.063	-0.306, 0.433	0.21
	Superficial tillage	-0.206	-1.039, 0.628	0.35	-0.425	-1.133, 0.282	0.77	-0.121	-0.533, 0.291	0.39	-0.036	-0.255, 0.184	0.21
	Herbicides	-0.182	-0.656, 0.292	0.53	-	-	-	-0.008	-0.081, 0.065	0.14	-0.008	-0.082, 0.067	0.16
	Non-herbicides	0.076	-0.199, 0.351	0.32	0.010	-0.063, 0.083	0.16	-	-	-	-	-	-

Table S2. (Continued)

	Variable	Cultural practices 2013			Cultural practices 2012-2013			Cultural practices 2011-2013			Cultural practices 2010-2013		
		Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW
<i>Trichodorus</i>	(Intercept)	-5.925	-9.285, -2.565		-5.672	-8.758, -2.586		-5.938	-8.916, -2.960		-5.973	-8.997, -2.948	
	Tillage	0.197	-1.232, 1.626	0.19	-	-	-	0.067	-0.551, 0.686	0.27	0.071	-0.442, 0.585	0.28
	Superficial tillage	0.081	-0.579, 0.742	0.19	-	-	-	-	-	-	-	-	-
	Herbicides	-0.024	-0.266, 0.218	0.18	-0.020	-0.184, 0.143	0.28	-	-	-	-	-	-
	Non-herbicides	-	-	-	-	-	-	-	-	-	-	-	-
<i>Heterodera</i>	(Intercept)	-7.476	-10.903, -4.050		-7.486	-11.582, -3.390		-8.341	-13.547, -3.135		-7.738	-13.381, -2.094	
	Tillage	0.181	-1.419, 1.781	0.16	-	-	-	-	-	-	-	-	-
	Superficial tillage	0.054	-0.625, 0.733	0.15	0.057	-0.427, 0.541	0.19	0.117	-0.489, 0.722	0.32	0.063	-0.359, 0.485	0.21
	Herbicides	-0.022	-0.305, 0.260	0.15	-0.015	-0.187, 0.158	0.17	-	-	-	-0.011	-0.155, 0.132	0.17
	Non-herbicides	-0.016	-0.196, 0.164	0.15	-0.014	-0.152, 0.123	0.18	-	-	-	-0.009	-0.107, 0.089	0.17
Other Telotylenchidae	(Intercept)	4.633	4.286, 4.980		4.754	4.306, 5.201		4.832	4.223, 5.441		5.066	4.248, 5.884	
	Tillage	-0.022	-0.222, 0.178	0.17	-0.059	-0.284, 0.165	0.36	-0.015	-0.112, 0.081	0.21	-0.006	-0.063, 0.052	0.15
	Superficial tillage	-0.012	-0.102, 0.0081	0.17	-0.006	-0.055, 0.044	0.15	-0.024	-0.107, 0.058	0.38	-0.044	-0.124, 0.037	0.72
	Herbicides	-	-	-	-0.004	-0.030, 0.021	0.27	-	-	-	-0.002	-0.017, 0.013	0.16
	Non-herbicides	0.004	-0.019, 0.028	0.23	-	-	-	-	-	-	-	-	-

- indicates that variable were not present in the top 2AICc models

Table S3. Results of models selections for 2014 samplings

	Variable	Cultural practices 2014			Cultural practices 2013-2014			Cultural practices 2012-2014			Cultural practices 2011-2014			Cultural practices 2010-2014		
		Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW
<i>Helicotylenchus</i>	(Intercept)	4.644	4.231, 5.057		4.769	4.352, 5.185		4.721	4.258, 5.184		4.763	4.256, 5.270		4.744	4.171, 5.316	
	Tillage	0.061	-0.235, 0.357	0.28	-	-	-	-	-	-	-	-	-	-	-	-
	Herbicides	0.079	0.014, 0.143	1.00	0.020	-0.023, 0.062	0.60	0.011	-0.020, 0.042	0.50	0.011	-0.017, 0.040	0.49	0.009	-0.017, 0.036	0.43
	Non-herbicides	0.004	-0.028, 0.036	0.21	0.007	-0.020, 0.035	0.39	0.009	-0.017, 0.035	0.50	0.004	-0.013, 0.020	0.23	0.004	-0.013, 0.020	0.27
<i>Pratylenchus</i>	(Intercept)	3.658	3.157, 4.159		3.294	2.705, 3.883		3.323	2.692, 3.954		3.430	2.641, 4.219		3.452	2.649, 4.256	
	Tillage	-0.152	-0.639, 0.335	0.44	-	-	-	-	-	-	-0.020	-0.126, 0.087	0.28	-0.015	-0.098, 0.067	0.21
	Herbicides	-	-	-	-0.011	-0.056, 0.033	0.34	-0.005	-0.033, 0.023	0.23	-0.004	-0.028, 0.021	0.16	-0.004	-0.031, 0.022	0.17
	Non-herbicides	0.012	-0.043, 0.067	0.33	0.035	-0.016, 0.086	0.81	0.021	-0.018, 0.060	0.71	0.014	-0.022, 0.049	0.55	0.011	-0.022, 0.044	0.47
<i>Macrotrophurus</i>	(Intercept)	-4.518	-7.907, -1.129		-4.099	-7.282, -0.916		-3.810	-7.769, 0.084		-4.472	-7.979, -0.965		-4.418	-8.324, -0.512	
	Tillage	-0.128	-1.307, 1.052	0.17	-0.247	-1.252, 0.758	0.35	-0.238	-1.097, 0.621	0.40	-0.075	-0.506, 0.356	0.21	-0.096	-0.536, 0.343	0.25
	Herbicides	0.020	-0.182, 0.223	0.17	0.125	-0.118, 0.368	0.62	0.084	-0.135, 0.304	0.56	0.055	-0.119, 0.229	0.43	0.057	-0.124, 0.239	0.43
	Non-herbicides	-0.067	-0.426, 0.292	0.25	-0.038	-0.208, 0.131	0.27	-0.032	-0.176, 0.111	0.25	-0.010	-0.092, 0.072	0.14	-0.012	-0.098, 0.074	0.14
<i>Paratylenchus</i>	(Intercept)	1.952	1.230, 2.675		0.978	-0.292, 2.184		0.738	-0.597, 2.009		0.709	-0.732, 2.151		1.134	-0.702, 2.970	
	Tillage	1.290	0.529, 2.052	1.00	1.020	0.526, 1.536	1.00	0.683	0.348, 1.031	1.00	0.478	0.224, 0.732	1.00	0.342	0.127, 0.557	1.00
	Herbicides	-	-	-	-	-	-	-	-	-	0.017	-0.042, 0.076	0.44	-	-	-
	Non-herbicides	0.010	-0.056, 0.076	0.29	0.068	0.004, 0.133	1.00	0.058	0.010, 0.106	1.00	0.039	-0.021, 0.098	0.78	0.030	-0.023, 0.083	0.69
<i>Criconemoides</i>	(Intercept)	-6.310	-9.217, -4.101		-6.389	-9.291, -4.205		-6.498	-9.171, -3.824		-6.493	-9.166, -3.820		-6.541	-9.278, -3.804	
	Tillage	-	-	-	-	-	-	0.075	-0.595, 0.745	0.27	0.053	-0.447, 0.553	0.27	0.064	-0.387, 0.515	0.29
	Herbicides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Non-herbicides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table S3. (Continued)

	Variable	Cultural practices 2014			Cultural practices 2013-2014			Cultural practices 2012-2014			Cultural practices 2011-2014			Cultural practices 2010-2014		
		Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW	Estimate	95% CI	SW
<i>Trichodorus</i>	(Intercept)	-9.029	-18.384, -5.802	-	-8.441	-14.423, -2.459	-	-8.250	-14.571, -1.929	-	-8.348	-14.644, -2.052	-	-8.282	-14.773, -1.791	-
	Tillage	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Herbicides	-	-	-	-0.096	-0.867, 0.675	0.29	-0.086	-0.687, 0.515	0.30	-0.055	-0.469, 0.358	0.29	-0.048	-0.392, 0.296	0.29
	Non-herbicides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Heterodera</i>	(Intercept)	-7.644	-11.468, -3.819	-	-7.904	-11.455, -4.354	-	-7.798	-11.206, -4.390	-	-7.860	-11.391, -5.672	-	-7.860	-11.391, -5.672	-
	Tillage	0.231	-2.021, 2.483	0.21	0.203	-1.153, 1.559	0.24	0.069	-0.685, 0.823	0.21	-	-	-	-	-	-
	Herbicides	-0.089	-0.780, 0.602	0.24	-0.021	-0.261, 0.219	0.21	-0.015	-0.177, 0.147	0.21	-	-	-	-	-	-
	Non-herbicides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Other Telotylenchidae	(Intercept)	4.450	4.032, 4.868	-	4.448	4.029, 4.868	-	4.521	4.269, 4.767	-	4.473	4.023, 4.924	-	4.521	4.269, 4.767	-
	Tillage	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Herbicides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Non-herbicides	0.019	-0.047, 0.085	0.41	0.006	-0.021, 0.033	0.34	-	-	-	0.002	-0.014, 0.019	0.28	-	-	-

- indicates that variable were not present in the top 2AICc models

621 **Fig. 1.** Projection of the modalities of environmental and anthropic variables summed over the
622 2012-2013 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
623 classes limits and values). Arrows highlight opposite modalities from a same variable. The
624 absolute contribution threshold to show the modalities of variables was 7.14. See also
625 supplementary material Fig. S2 for the visual display of the 2013 PPN abundance as
626 supplementary variables on this map.

627

628 **Fig. 2.** Projection of the modalities of environmental and anthropic variables summed over the
629 2013-2014 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
630 classes limits and values). Arrows highlight opposite modalities from a same variable. The
631 absolute contribution threshold to show the modalities of variables was 6.90. See also
632 supplementary material Fig. S6 for the visual display of 2014 PPN abundance as
633 supplementary variables on this map.

634

635 **Fig. S1.** Projection of the modalities of environmental and anthropic variables from 2013
636 using MCA (see Table 1 for abbreviation meanings and Table S1 for classes limits and
637 values). The absolute contribution threshold to show the modalities of variables was 7.14. The
638 2013 PPN modalities of abundance were considered as supplementary variables within the
639 analysis.

640

641 **Fig. S2.** Projection of the modalities of environmental and anthropic variables summed over
642 the 2012-2013 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
643 classes limits and values). The absolute contribution threshold to show the modalities of
644 variables was 7.14. The 2013 PPN modalities of abundance were considered as
645 supplementary variables within the analysis.

646

647 **Fig. S3.** Projection of the modalities of environmental and anthropic variables summed over
648 the 2011-2013 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
649 classes limits and values). The absolute contribution threshold to show the modalities of
650 variables was 6.90. The 2013 PPN modalities of abundance were considered as
651 supplementary variables within the analysis.

652

653 **Fig. S4.** Projection of the modalities of environmental and anthropic variables summed over
654 the 2010-2013 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
655 classes limits and values). The absolute contribution threshold to show the modalities of
656 variables was 6.67. The 2013 PPN modalities of abundance were considered as
657 supplementary variables within the analysis.

658

659 **Fig. S5.** Projection of the modalities of environmental and anthropic variables from 2014
660 using MCA (see Table 1 for abbreviation meanings and Table S1 for classes limits and
661 values). The absolute contribution threshold to show the modalities of variables was 6.67. The
662 2014 PPN modalities of abundance were considered as supplementary variables within the
663 analysis.

664

665 **Fig. S6.** Projection of the modalities of environmental and anthropic variables summed over
666 the 2013-2014 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
667 classes limits and values). The absolute contribution threshold to show the modalities of
668 variables was 6.90. The 2014 PPN modalities of abundance were considered as
669 supplementary variables within the analysis.

670

671 **Fig. S7.** Projection of the modalities of environmental and anthropic variables summed over
672 the 2012-2014 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
673 classes limits and values). The absolute contribution threshold to show the modalities of
674 variables was 6.90. The 2014 PPN modalities of abundance were considered as
675 supplementary variables within the analysis.

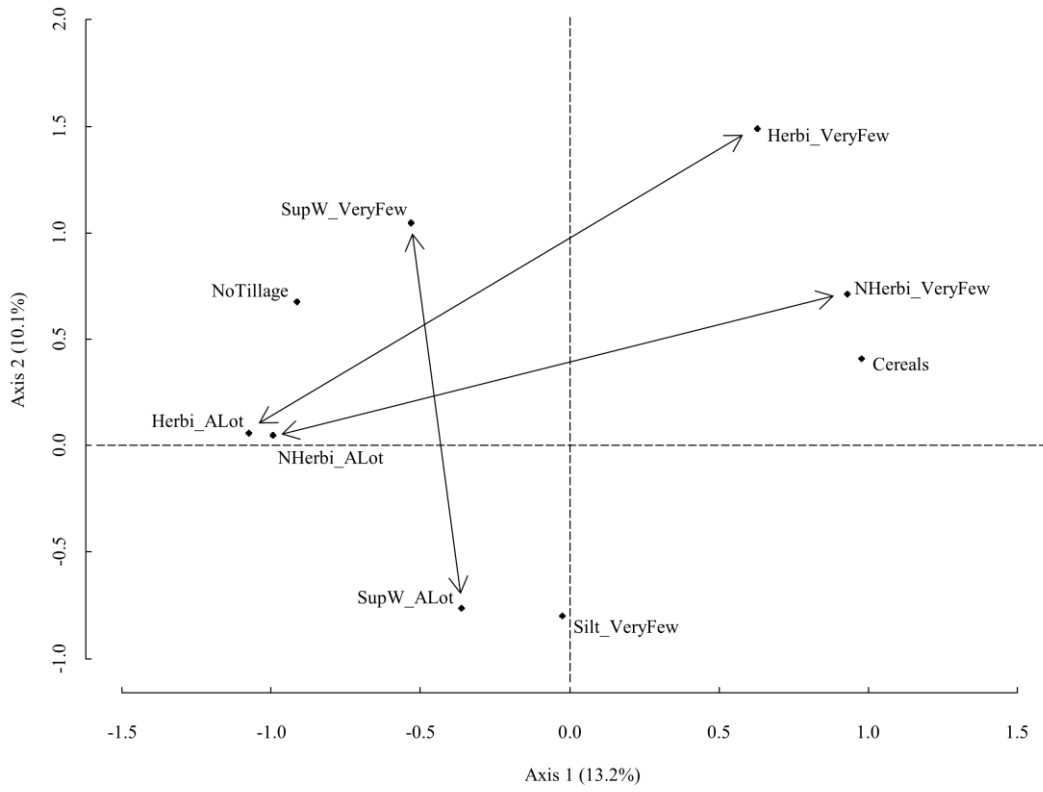
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677 **Fig. S8.** Projection of the modalities of environmental and anthropic variables summed over
678 the 2011-2014 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
679 classes limits and values). The absolute contribution threshold to show the modalities of
680 variables was 6.67. The 2014 PPN modalities of abundance were considered as
681 supplementary variables within the analysis.

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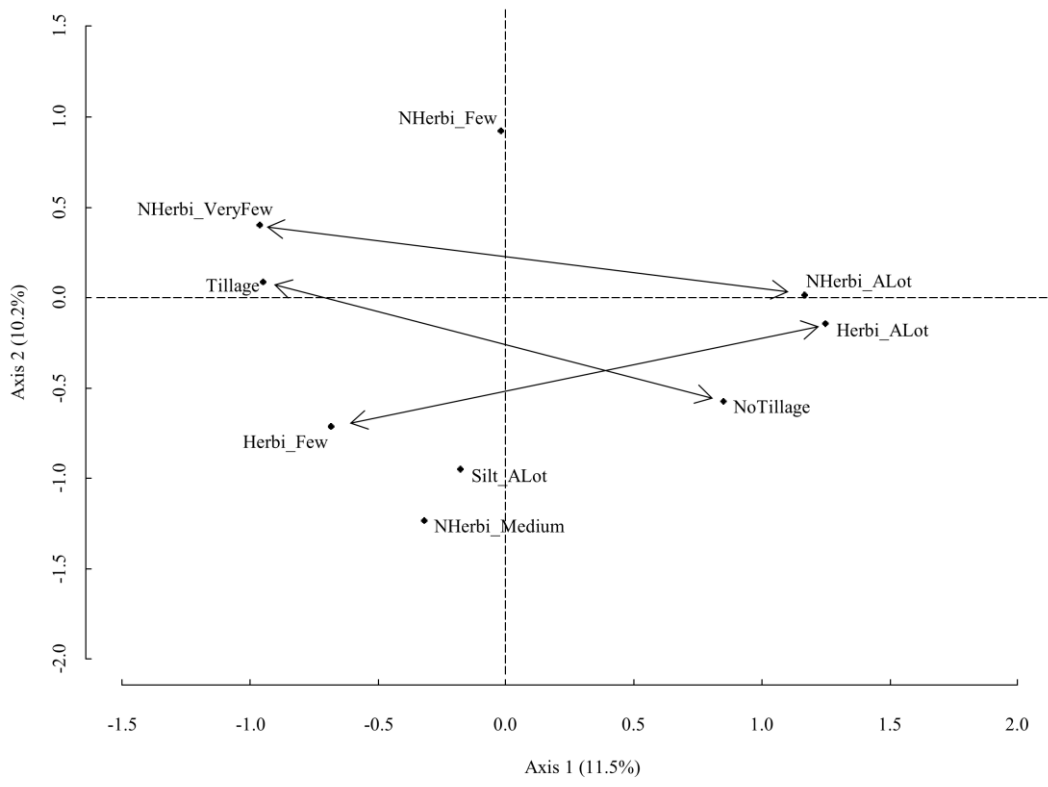
683 **Fig. S9.** Projection of the modalities of environmental and anthropic variables summed over
684 the 2010-2014 period using MCA (see Table 1 for abbreviation meanings and Table S1 for
685 classes limits and values). The absolute contribution threshold to show the modalities of
686 variables was 6.67. The 2014 PPN modalities of abundance were considered as
687 supplementary variables within the analysis.

688



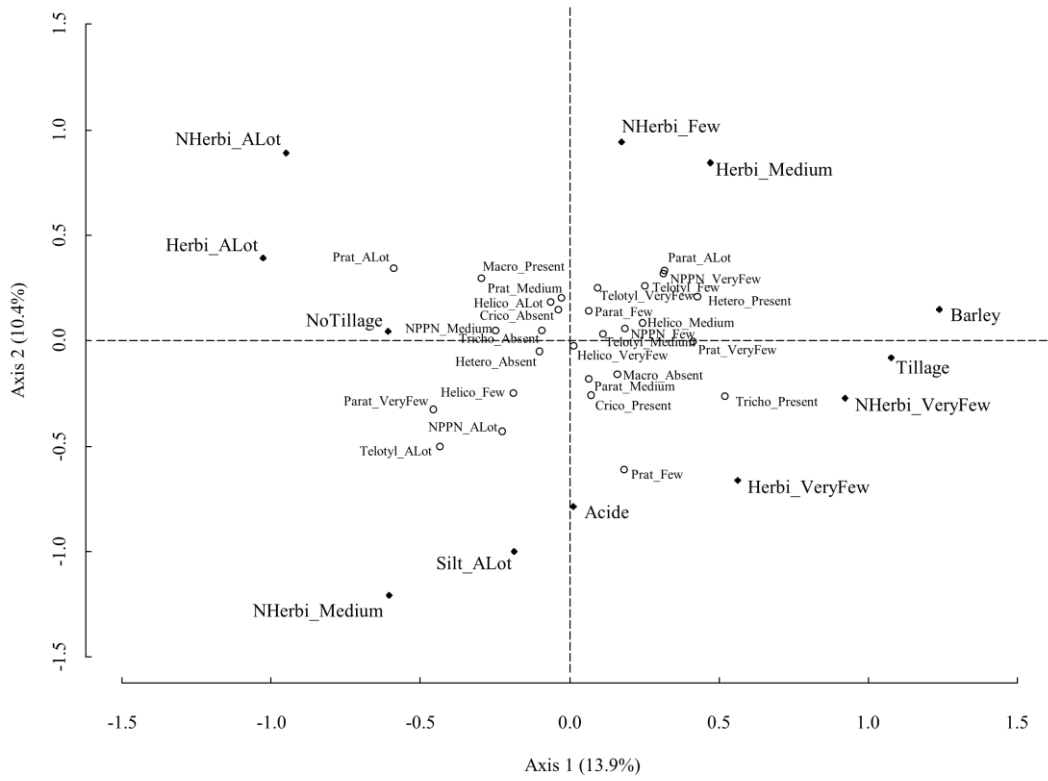
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690 Figure 1



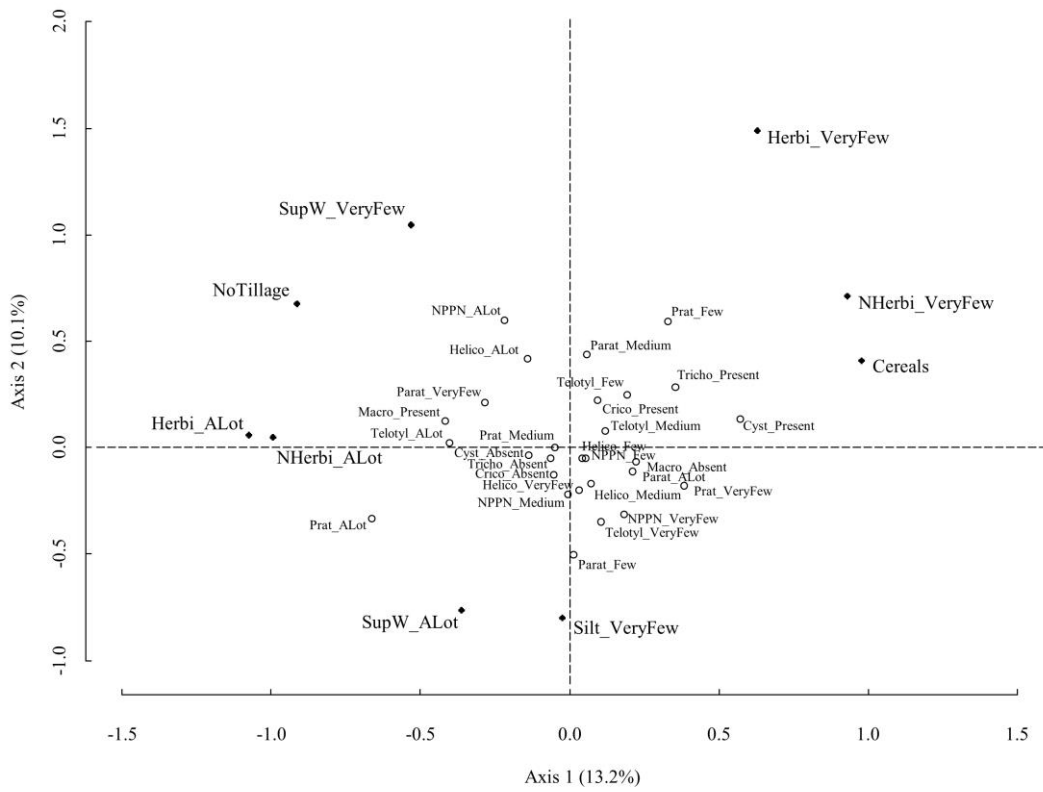
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692 Figure 2



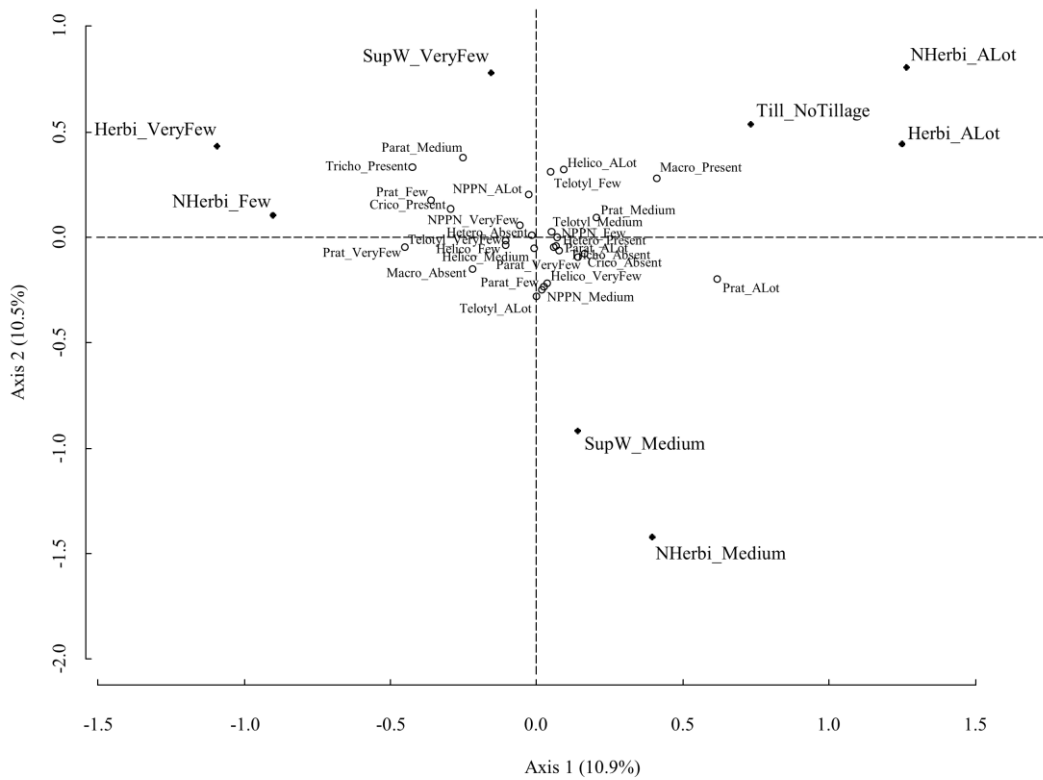
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694 Figure S1



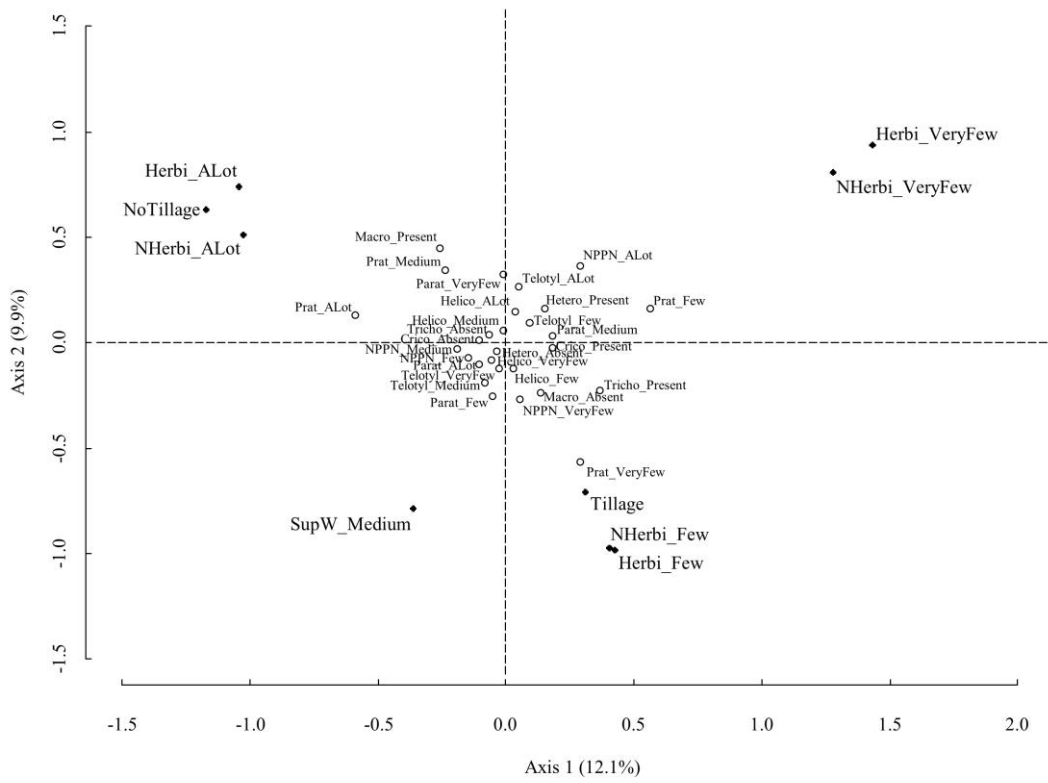
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696 Figure S2



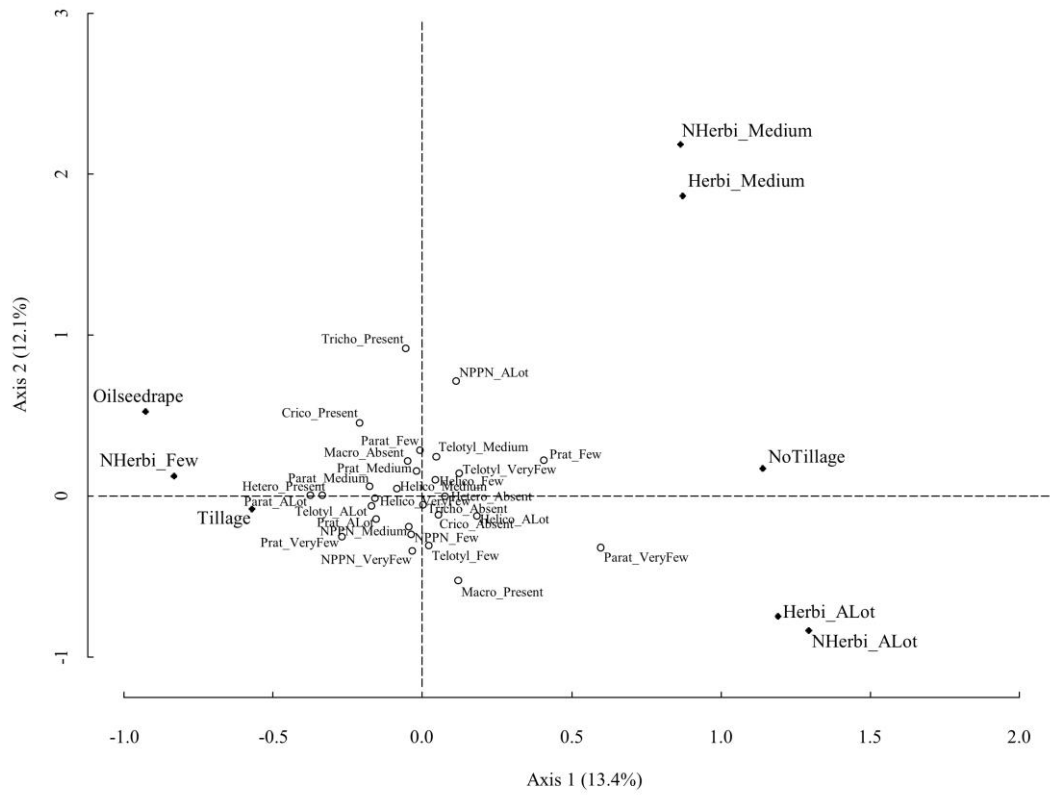
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698 Figure S3



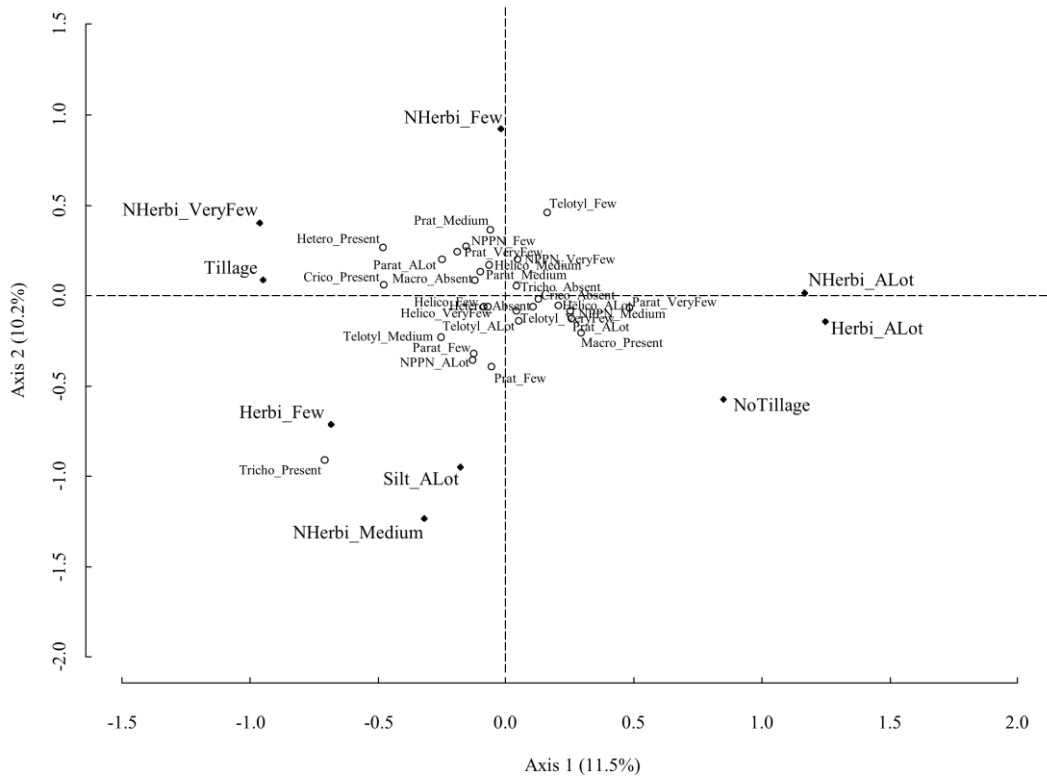
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700 Figure S4



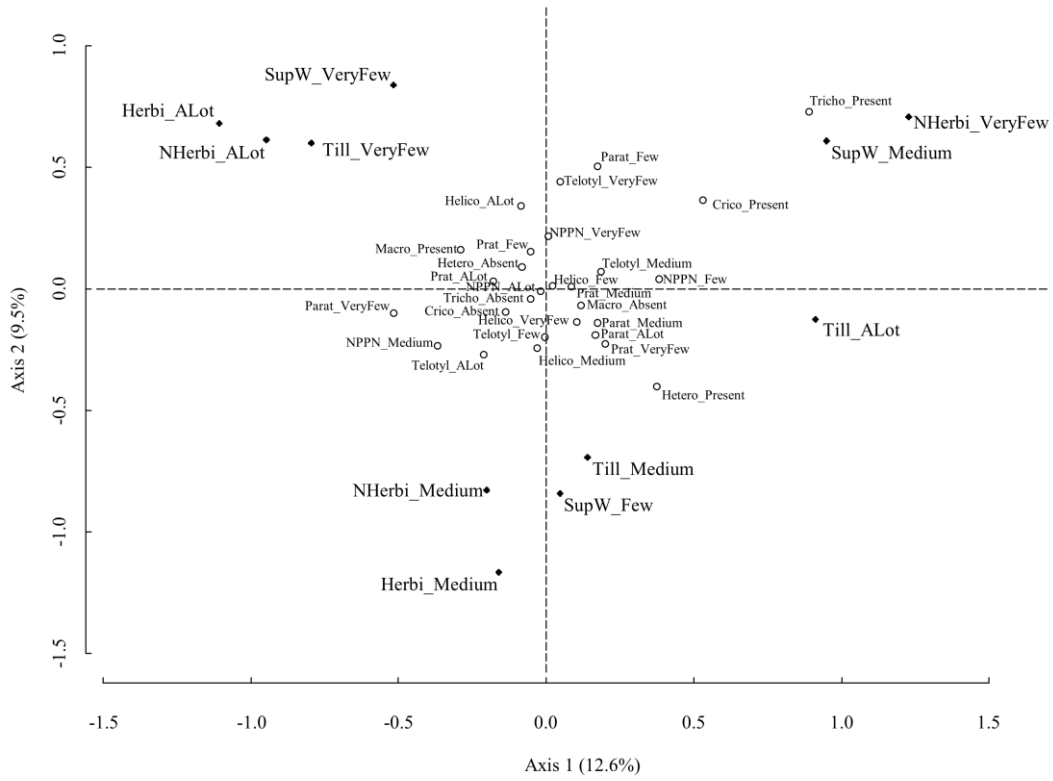
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702 Figure S5



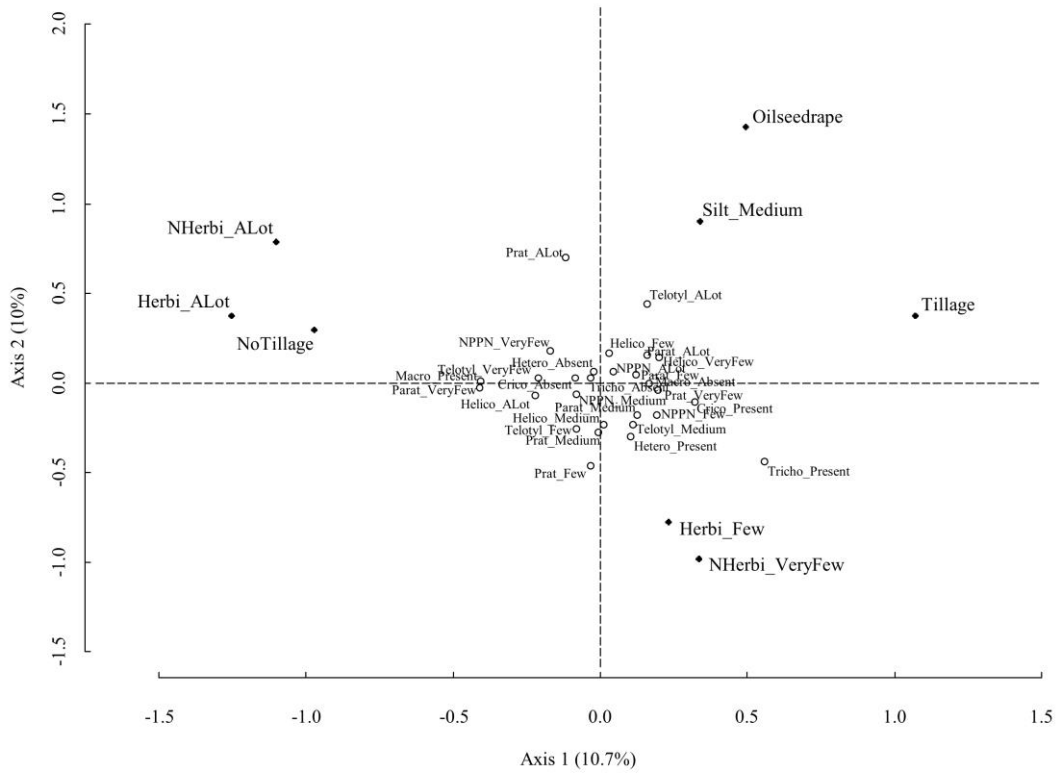
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704 Figure S6



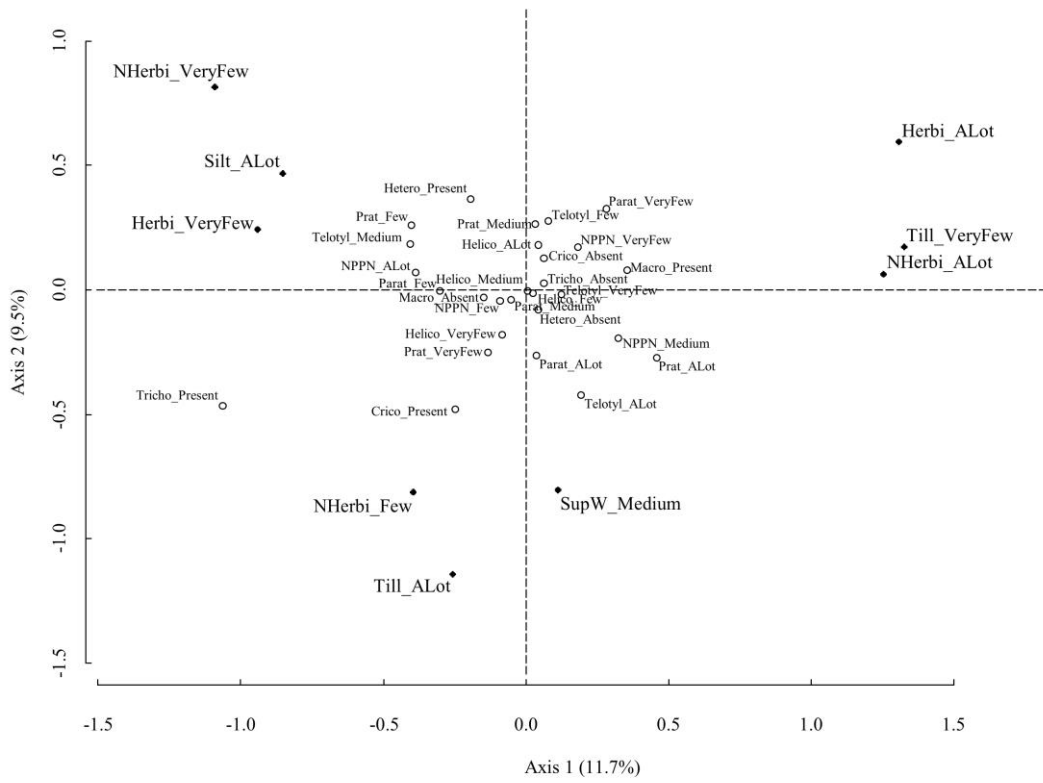
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706 Figure S7



707

708 Figure S8



709

710 Figure S9