



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

Nathan Garcia, Laurent Folcher, Luc Biju-Duval, Agathe Maupetit, Benoit Ricci, Eric Grenier

► To cite this version:

Nathan Garcia, Laurent Folcher, Luc Biju-Duval, Agathe Maupetit, Benoit Ricci, et al.. Impact of agricultural practices and environmental variables on plant-parasitic nematode communities in fields at a landscape scale. *Nematology*, 2018, 20 (3), pp.211-233. 10.1163/15685411-00003136 . hal-02625400

HAL Id: hal-02625400

<https://hal.inrae.fr/hal-02625400>

Submitted on 22 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Nathan GARCIA^{a, b, *}, Laurent FOLCHER^a, Luc BIJU-DUVAL^c, Agathe MAUPETIT^d,
Benoit RICCI^c, Eric GRENIER^b

^a ANSES, Plant Health Laboratory – Nematology Unit, Domaine de la Motte au Vicomte - BP
35327 - 35653 Le Rheu Cédex - France

^b IGEPP, Agrocampus-Ouest, INRA, Rennes 1 University, Domaine de la Motte au Vicomte -
BP 35327 - 35653 Le Rheu Cédex - France

^c Agroecology, AgroSup Dijon, INRA, Bourgogne Franche-Comté University, 17 rue Sully -
BP 86510 - 21065 Dijon Cédex France

^d Rennes 1 University, Bretagne-Loire University, CS 74205, 35042 Rennes Cédex, France

* Corresponding author: Nathan Garcia: natgarcia.pro@gmail.com

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

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

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

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

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

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

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

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

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

Material and methods

SAMPLING AND CHARACTERISTICS OF THE STUDIED AREA

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

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

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

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

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

NEMATODE EXTRACTION AND IDENTIFICATION

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

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

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

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

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

Results

PLANT-PARASITIC NEMATODE COMMUNITIES

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

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

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

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

VARIABLE SELECTION

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

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

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

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

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

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

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

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

Discussion

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

SAMPLING PROCESS AND COMPOSITION OF THE COMMUNITIES

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

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

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

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

VARIABLE SELECTION

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

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

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

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

EFFECTS OF PESTICIDE USES

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

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

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

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

Conclusion

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

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

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

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

Acknowledgments

This work was funded by the Plant Health and Environment Department of INRA and is part of a PhD project founded by the Brittany region and ANSES. The studies on the Fénay study area were coordinated by Sandrine Petit and Jean-Philippe Guillemin. We would like to thank Alain Buisson, Magali Esquibet, Didier Fouville, Catherine Porte, Elsa Rulliat and Corinne Sarniguet for their technical support during sampling, nematode extraction and identification. We would also like to thank Laura Royer who worked on the 2013 data during her internship. Lastly, we wish to thank the farmers who allowed us to conduct sampling in their fields.

References

428 Alenda, C., Montarry, J. & Grenier, E. (2014). Human influence on the dispersal and genetic
 429 structure of French *Globodera tabacum* populations. *Infection, Genetics and Evolution* 27,
 430 309–317. doi:10.1016/j.meegid.2014.07.027
 431 Altieri, M.A. (1999). The ecological role of biodiversity in agroecosystems. *Agriculture,*
 432 *Ecosystems & Environment* 74, 19–31. doi:10.1016/S0167-8809(99)00028-6
 433 Andersen, P.K., Borgan, O., Gill, R.D. & Keiding, N. (1997). *Statistical models based on*
 434 *counting processes*. Springer series in statistics. Springer, New York.
 435 Barton, K. (2016). MuMIn: multi-model inference. R package version 1.15.6.
 436 <https://CRAN.R-project.org/package=MumIn>.
 437 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models
 438 using lme4. *Journal of Statistical Software* 67(1), 1-48. doi:10.18637/jss.v067.i01.
 439 Bongers, T. (1990). The maturity index: an ecological measure of environmental disturbance
 440 based on nematode species composition. *Oecologia* 83, 14–19. doi:10.1007/BF00324627
 441 Bongers, T. & Ferris, H. (1999). Nematode community structure as a bioindicator in
 442 environmental monitoring. *Trends in Ecology & Evolution* 14, 224–228.
 443 doi:10.1016/S0169-5347(98)01583-3
 444 Bünemann, E.K., Schwenke, G.D. & Zwieter, L.V. (2006). Impact of agricultural inputs on
 445 soil organisms—a review. *Soil Research* 44, 379–406. doi:10.1071/SR05125
 446 Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a*
 447 *practical information-theoretic approach*. Springer, New York.
 448 Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J.H., Schondube, J.E., de Freitas, S.M. &
 449 Fahrig, L. (2015). Impact of landscape composition and configuration on forest specialist
 450 and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biological*
 451 *Conservation* 184, 117–126. doi:10.1016/j.biocon.2015.01.014

452 Cibois, P. (1997). Les pièges de l'analyse des correspondances. *Histoire & Mesure* 12(3/4)
 453 299–320.

454 Cibois, P. (1986). L'analyse des correspondances : l'indispensable retour aux données.
 455 *Histoire & Mesure* 1, 239–247. doi:10.3406/hism.1986.1540

456 Decraemer, W. & Hunt, D.J. (2006). Structure and Classification. In Perry, R.N. & Moens, M.
 457 (eds) *Plant Nematology* 3-32. CABI, Wallingford, UK. doi:10.1079/9781845930561.0003

458 Dequiedt, S., Saby, N.P.A., Lelievre, M., Jolivet, C., Thioulouse, J., Toutain, B., Arrouays,
 459 D., Bispo, A., Lemanceau, P. & Ranjard, L. (2011). Biogeographical patterns of soil
 460 molecular microbial biomass as influenced by soil characteristics and management. *Global*
 461 *Ecology and Biogeography* 20, 641–652. doi:10.1111/j.1466-8238.2010.00628.x

462 EPPO bulletin (2013). PM 7/119 Nematode extraction. *EPPO Bulletin* 43, 471–495.
 463 doi:10.1111/epp.12077

464 Franzluebbers, A.J. (2002). Soil organic matter stratification ratio as an indicator of soil
 465 quality. *Soil and Tillage Research* 66, 95–106. doi:10.1016/S0167-1987(02)00018-1

466 Freckman, D.W. & Ettema, C.H. (1993). Assessing nematode communities in agroecosystems
 467 of varying human intervention. *Agriculture, Ecosystems & Environment* 45, 239–261.
 468 doi:10.1016/0167-8809(93)90074-Y

469 Galipaud, M., Gillingham, M.A.F., David, M. & Dechaume-Moncharmont, F.-X. (2014).
 470 Ecologists overestimate the importance of predictor variables in model averaging: a plea
 471 for cautious interpretations. *Methods in Ecology and Evolution* 5, 983–991.
 472 doi:10.1111/2041-210X.12251

473 Gomes, G.S., Huang, S.P. & Cares, J.E. (2003). Nematode community, trophic structure and
 474 population fluctuation in soybean fields. *Fitopatologia Brasileira* 28, 258–266.
 475 doi:10.1590/S0100-41582003000300006

476 Goodell, P. & Ferris, H. (1980). Plant-parasitic nematode distributions in an alfalfa field.
 477 *Journal of Nematology* 12, 136–141.

478 Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011). Multimodel inference in
 479 ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology* 24, 699–
 480 711. doi:10.1111/j.1420-9101.2010.02210.x

481 Hendrix, P.F., Parmelee, R.W., Crossley, D.A., Coleman, D.C., Odum, E.P. & Groffman,
 482 P.M. (1986). Detritus food webs in conventional and no-tillage agroecosystems.
 483 *BioScience* 36, 374–380. doi:10.2307/1310259

484 Jibrin, M.O., Lawal, H.M. & Chindo, P.S. (2014). Influence of cover crops and tillage
 485 systems on nematode populations in a maize-cover crop intercrop. *Archives of*
 486 *Phytopathology and Plant Protection* 47, 703–710. doi:10.1080/03235408.2013.819654

487 Jones, J.T., Haegeman, A., Danchin, E.G.J., Gaur, H.S., Helder, J., Jones, M.G.K., Kikuchi,
 488 T., Manzanilla-López, R., Palomares-Rius, J.E., Wesemael, W.M.L., *et al.* (2013). Top 10
 489 plant-parasitic nematodes in molecular plant pathology. *Molecular Plant Pathology* 14,
 490 946–961. doi:10.1111/mpp.12057

491 Kerry, B.R. (2000). Rhizosphere interactions and the exploitation of microbial agents for the
 492 biological control of plant-parasitic nematodes. *Annual Review of Phytopathology* 38, 423–
 493 441.

494 King, B.A. & Taberna, J.P. (2013). Site-specific management of *Meloidogyne chitwoodi* in
 495 Idaho potatoes using 1,3-dichloropropene; approach, experiences, and economics. *Journal*
 496 *of Nematology* 45, 202–213.

497 Lankinen, A., Smith, H.G., Andersson, S. & Madjidian, J.A. (2016). Selection on pollen and
 498 pistil traits during pollen competition is affected by both sexual conflict and mixed mating
 499 in a self-compatible herb. *American Journal of Botany* 103, 541–552.
 500 doi:10.3732/ajb.1500148

501 Le, S., Josse, J. & Husson, .F. (2008). FactoMineR: an R package for multivariate analysis.
502 *Journal of Statistical Software* 25(1), 1-18. 10.18637/jss.v025.i01

503 Li, X., Ding, C., Liu, J., Zhang, T. & Wang, X. (2015). Evident response of the soil nematode
504 community to consecutive peanut monoculturing. *Agronomy Journal* 107, 195.
505 doi:10.2134/agronj14.0257

506 Mateille, T., Tavoillot, J., Martiny, B. & Fargette, M. (2014). Importance of soil
507 characteristics for plant-parasitic nematode communities in European coastal foredunes.
508 *European Journal of Soil Biology* 64, 53–60. doi:10.1016/j.ejsobi.2014.08.002

509 McSorley, R. & Gallaher, R.N. (1993). Effect of crop rotation and tillage on nematode
510 densities in tropical corn. *Journal of Nematology* 25, 814–819.

511 Minton, N.A. (1986). Impact of conservation tillage on nematode populations. *Journal of*
512 *Nematology* 18, 135.

513 Nicol, J.M., Turner, S.J., Coyne, D.L., Nijs, L. den, Hockland, S. & Maafi, Z.T. (2011).
514 Current nematode threats to world agriculture, in: Jones, J., Gheysen, G. & Fenoll, C.
515 *Genomics and Molecular Genetics of Plant-Nematode Interactions*. Springer Netherlands,
516 pp. 21–43.

517 Okada, H. & Harada, H. (2007). Effects of tillage and fertilizer on nematode communities in a
518 Japanese soybean field. *Applied Soil Ecology* 35, 582–598.
519 doi:10.1016/j.apsoil.2006.09.008

520 Palomares-Rius, J.E., Castillo, P., Montes-Borrego, M., Navas-Cortés, J.A. & Landa, B.B.
521 (2015). Soil properties and olive cultivar determine the structure and diversity of plant-
522 parasitic nematode communities infesting olive orchards soils in southern Spain. *PLoS*
523 *ONE* 10, e0116890. doi:10.1371/journal.pone.0116890

524 Parmelee, R.W. & Alston, D.G. (1986). Nematode trophic structure in conventional and no-
525 tillage agroecosystems. *Journal of Nematology* 18, 403–407.

526 Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007). Updated world map of the Köppen-
 527 Geiger climate classification. *Hydrology and Earth System Sciences Discussions* 4, 439–
 528 473.

529 Poeydebat, C., Tixier, P., Chabrier, C., de Bellaire, L. de L., Vargas, R., Daribo, M.-O. &
 530 Carval, D. (2017). Does plant richness alter multitrophic soil food web and promote plant-
 531 parasitic nematode regulation in banana agroecosystems? *Applied Soil Ecology* 117, 137–
 532 146. doi:10.1016/j.apsoil.2017.04.017

533 Pokharel, R., Marahatta, S.P., Handoo, Z.A. & Chitwood, D.J. (2015). Nematode community
 534 structures in different deciduous tree fruits and grape in Colorado, USA and impact of
 535 organic peach and apple production practices. *European Journal of Soil Biology* 67, 59–68.
 536 doi:10.1016/j.ejsobi.2015.02.003

537 Ponge, J.-F., Pérès, G., Guernion, M., Ruiz-Camacho, N., Cortet, J., Pernin, C., Villenave, C.,
 538 Chaussod, R., Martin-Laurent, F., Bispo, A. *et al.* (2013). The impact of agricultural
 539 practices on soil biota: A regional study. *Soil Biology and Biochemistry* 67, 271–284.
 540 doi:10.1016/j.soilbio.2013.08.026

541 Porazinska, D.L., Duncan, L.W., McSorley, R. & Graham, J.H. (1999). Nematode
 542 communities as indicators of status and processes of a soil ecosystem influenced by
 543 agricultural management practices. *Applied Soil Ecology* 13, 69–86. doi:10.1016/S0929-
 544 1393(99)00018-9

545 Quist, C.W., Schrama, M., de Haan, J.J., Smant, G., Bakker, J., van der Putten, W.H. &
 546 Helder, J. (2016). Organic farming practices result in compositional shifts in nematode
 547 communities that exceed crop-related changes. *Applied Soil Ecology* 98, 254–260.
 548 doi:10.1016/j.apsoil.2015.10.022

549 R Core Team (2016). R: A language and environment for statistical computing. *R Foundation*
 550 *for Statistical Computing*, Vienna, Austria. URL <https://www.R-project.org/>.

551 Rahman, L., Chan, K.Y. & Heenan, D.P. (2007). Impact of tillage, stubble management and
552 crop rotation on nematode populations in a long-term field experiment. *Soil and Tillage*
553 *Research* 95, 110–119. doi:10.1016/j.still.2006.11.008

554 Renčo, M., Čerevková, A., Homolová, Z. & Gömöryová, E. (2015). Long-term effects on soil
555 nematode community structure in spruce forests of removing or not removing fallen trees
556 after a windstorm. *Forest Ecology and Management* 356, 243–252.
557 doi:10.1016/j.foreco.2015.07.008

558 Rodriguez-Kabana, R. & Curl, E.A. (1980). Nontarget effects of pesticides on soilborne
559 pathogens and disease. *Annual Review of Phytopathology* 18, 311–332.
560 doi:10.1146/annurev.py.18.090180.001523

561 Schomaker, C.H. & Been, T.H. (1999). A model for infestation foci of potato cyst nematodes
562 *Globodera rostochiensis* and *G. pallida*. *Phytopathology* 89, 583–590.
563 doi:10.1094/PHYTO.1999.89.7.583

564 Shannon, C. & Weaver, W. (1949). *The mathematical theory of information*. University of
565 Illinois Press.

566 Siddiqui, Z.A. & Mahmood, I. (1996). Biological control of plant-parasitic nematodes by
567 fungi: A review. *Bioresource Technology* 58, 229–239. doi:10.1016/S0960-
568 8524(96)00122-8

569 Smiley, R.W., Machado, S., Gourlie, J.A., Pritchett, L.C., Yan, G. & Jacobsen, E.E. (2013).
570 Effects of crop rotations and tillage on *Pratylenchus* spp. in the semiarid Pacific Northwest
571 United States. *Plant Disease* 97, 537–546.

572 Stirling, G.R., Halpin, N.V., Bell, M.J. & Moody, P.W. (2011). Impact of tillage and residues
573 from rotation crops on the nematode community in soil and surface mulch during the
574 following sugarcane crop. *International Sugar Journal* 113, 56–64.

575 Ugarte, C.M., Zaborski, E.R. & Wander, M.M. (2013). Nematode indicators as integrative
 576 measures of soil condition in organic cropping systems. *Soil Biology and Biochemistry* 64,
 577 103–113. doi:10.1016/j.soilbio.2013.03.035
 578 Van der Putten, W.H. & Van der Stoep, C.D. (1998). Plant-parasitic nematodes and spatio-
 579 temporal variation in natural vegetation. *Applied Soil Ecology* 10, 253–262.
 580 doi:10.1016/S0929-1393(98)00124-3
 581 Villenave, C., Jimenez, A., Guernion, M., Pérès, G., Cluzea, D., Mateille, T., Martiny, B.,
 582 Fargette, M. & Tavoillot, J. (2013). Nematodes for soil quality monitoring: results from the
 583 RMQS BioDiv programme. *Open Journal of Soil Science* 3, 30–45.
 584 doi:10.4236/ojss.2013.31005
 585 Wallace, H.R. (1968). The dynamics of nematode movement. *Annual Review of*
 586 *Phytopathology* 6, 91–114. doi:10.1146/annurev.py.06.090168.000515
 587 Yeates, G.W. (2003). Nematodes as soil indicators: functional and biodiversity aspects.
 588 *Biology and Fertility of Soils* 37, 199–210. doi:10.1007/s00374-003-0586-5
 589 Yeates, G.W. & Bongers, T. (1999). Nematode diversity in agroecosystems. *Agriculture,*
 590 *Ecosystems & Environment* 74, 113–135. doi:10.1016/S0167-8809(99)00033-X
 591 Zhang, Z., Zhang, X., Zhao, J., Zhang, X. & Liang, W. (2015). Tillage and rotation effects on
 592 community composition and metabolic footprints of soil nematodes in a black soil.
 593 *European Journal of Soil Biology* 66, 40–48. doi:10.1016/j.ejsobi.2014.11.006
 594 Zheng, G.D., Shi, L.B., Wu, H.Y. & Peng, D.L. (2012). Nematode communities in continuous
 595 tomato-cropping field soil infested by root-knot nematodes. *Acta Agriculturae*
 596 *Scandinavica, Section B — Soil & Plant Science* 62, 216–223.
 597 doi:10.1080/09064710.2011.598545

598 Zhong, S., Zeng, H. & Jin, Z. (2016). Response of soil nematode community composition and
599 diversity to different crop rotations and tillage in the tropics. *Applied Soil Ecology* 107,
600 134–143. doi:10.1016/j.apsoil.2016.05.013
601

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

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

607

608

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

609
610

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

611

612

613

614

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

615

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>Criconemoïdes</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	-	-	-	-	-	-

616

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

617

618

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

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

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

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

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

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

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

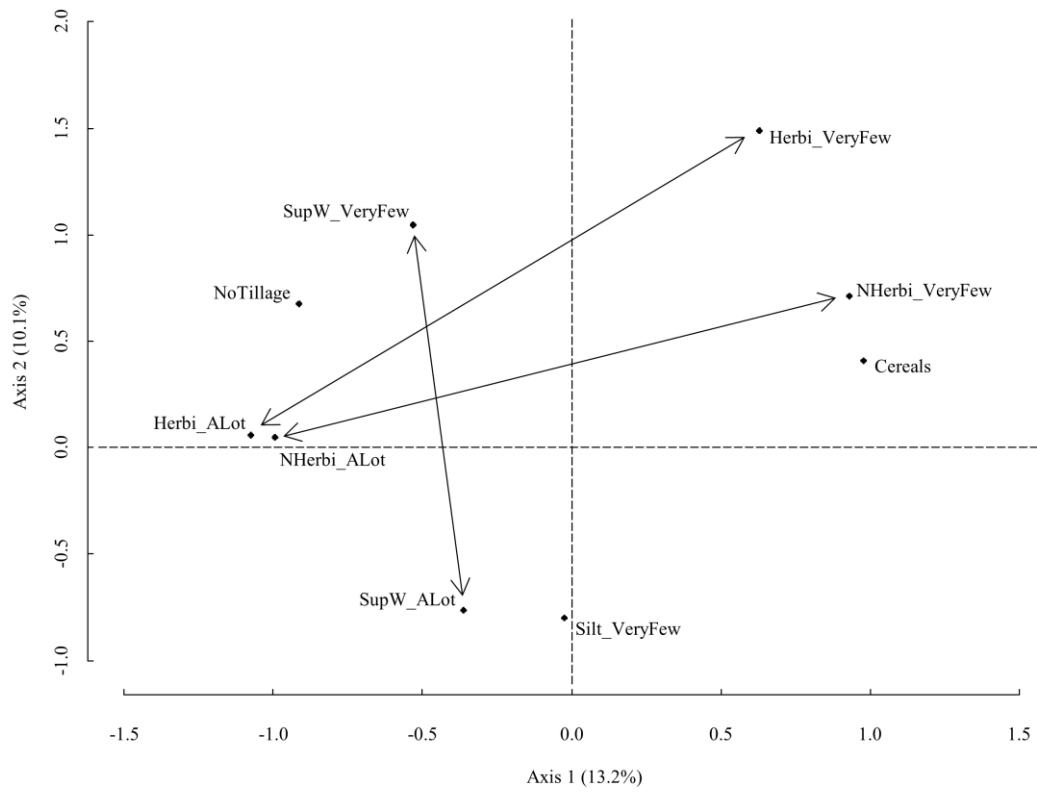
Fig. S5. Projection of the modalities of environmental and anthropic variables from 2014 using MCA (see Table 1 for abbreviation meanings and Table S1 for classes limits and values). The absolute contribution threshold to show the modalities of variables was 6.67. The 2014 PPN modalities of abundance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

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

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

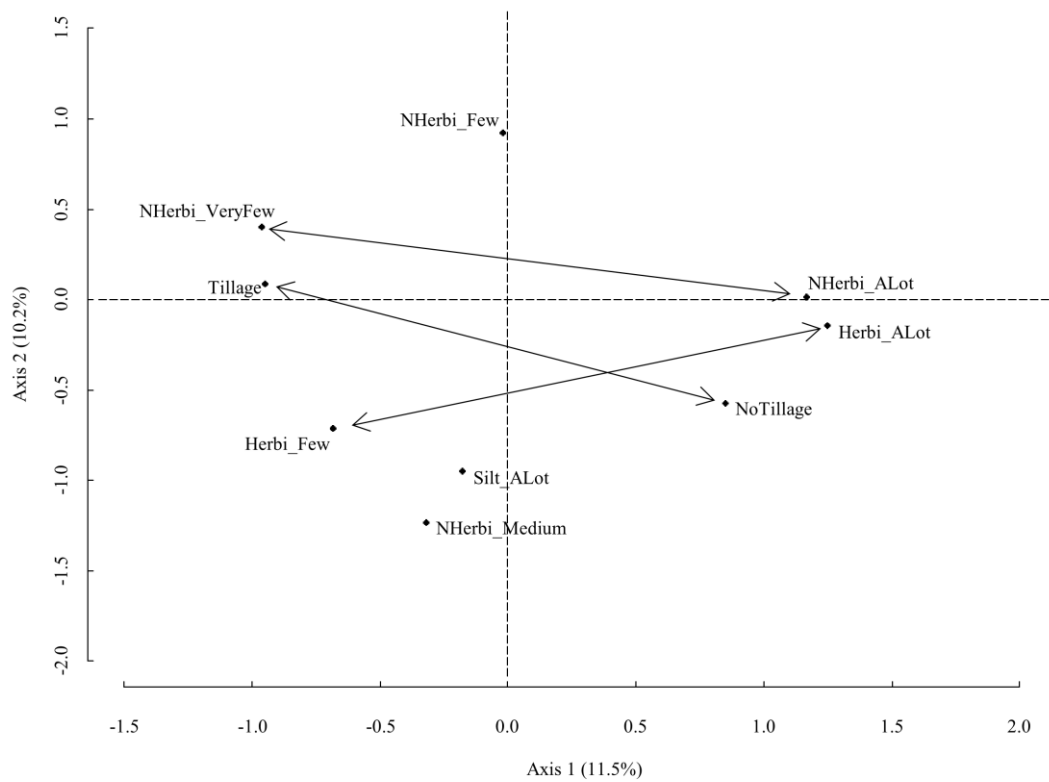
Fig. S8. Projection of the modalities of environmental and anthropic variables summed over the 2011-2014 period using MCA (see Table 1 for abbreviation meanings and Table S1 for classes limits and values). The absolute contribution threshold to show the modalities of variables was 6.67. The 2014 PPN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

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



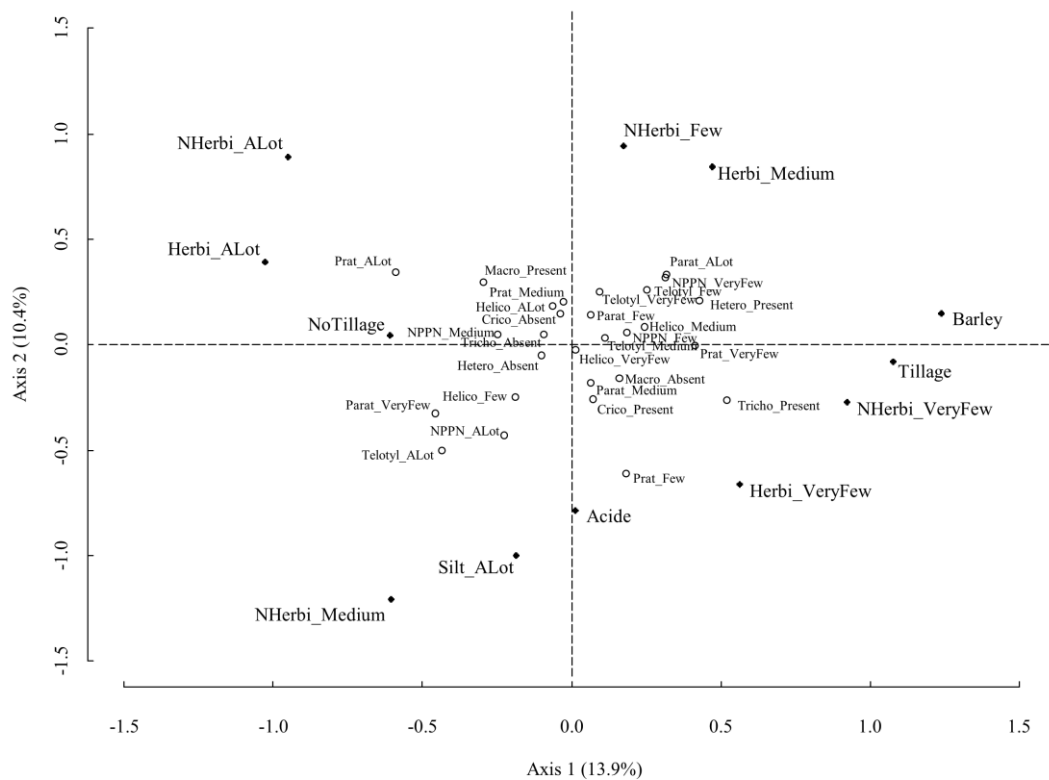
689

690 Figure 1



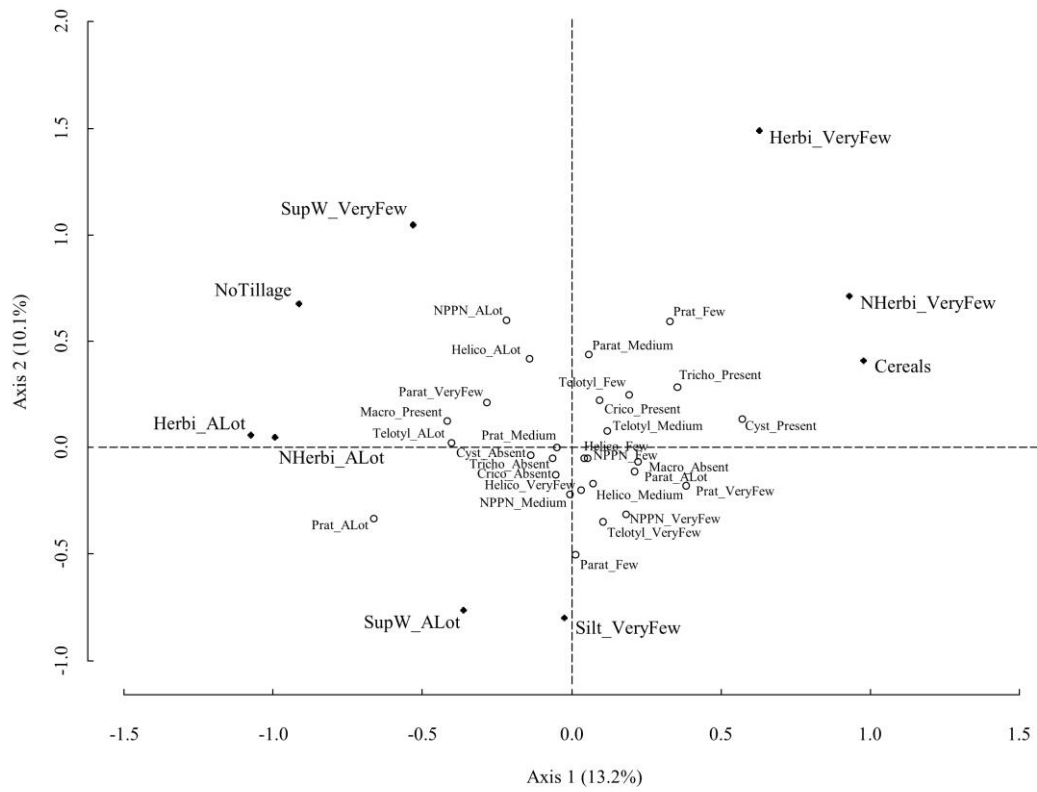
691

692 Figure 2



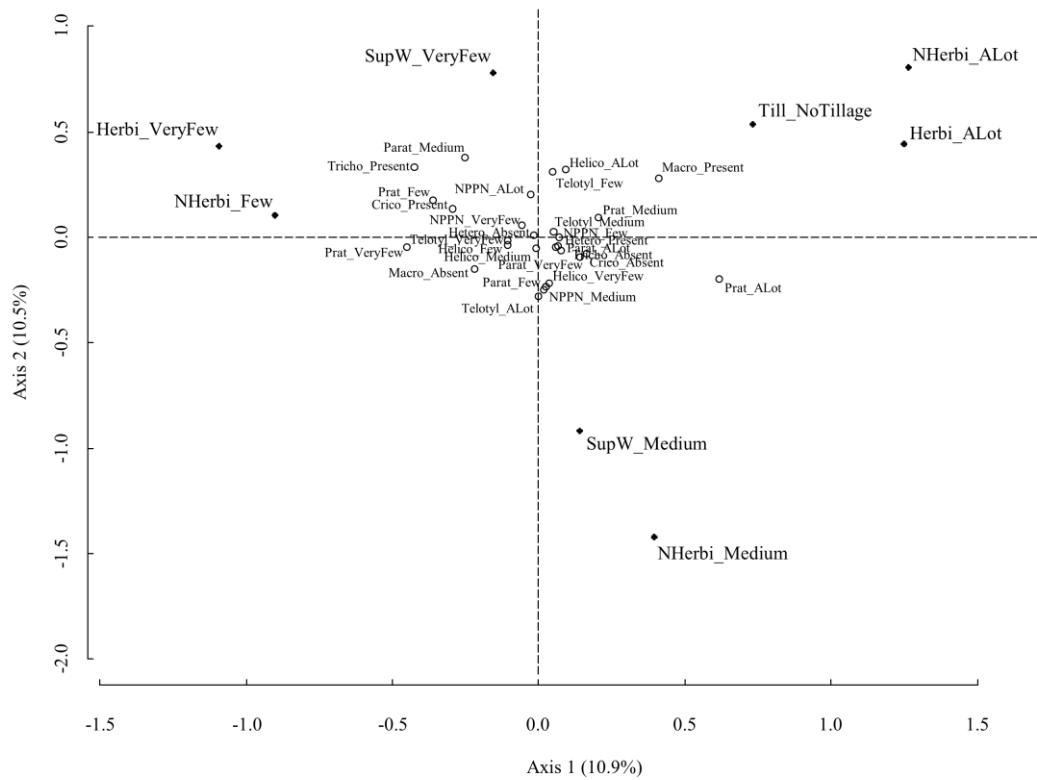
693

694 Figure S1



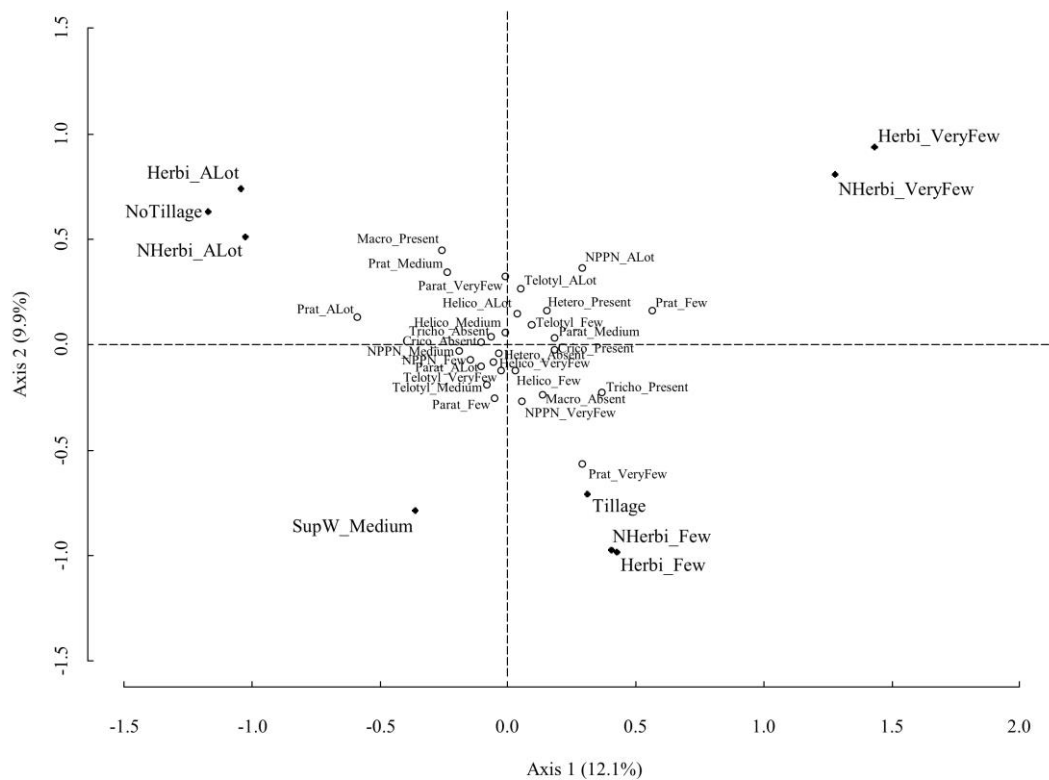
695

696 Figure S2



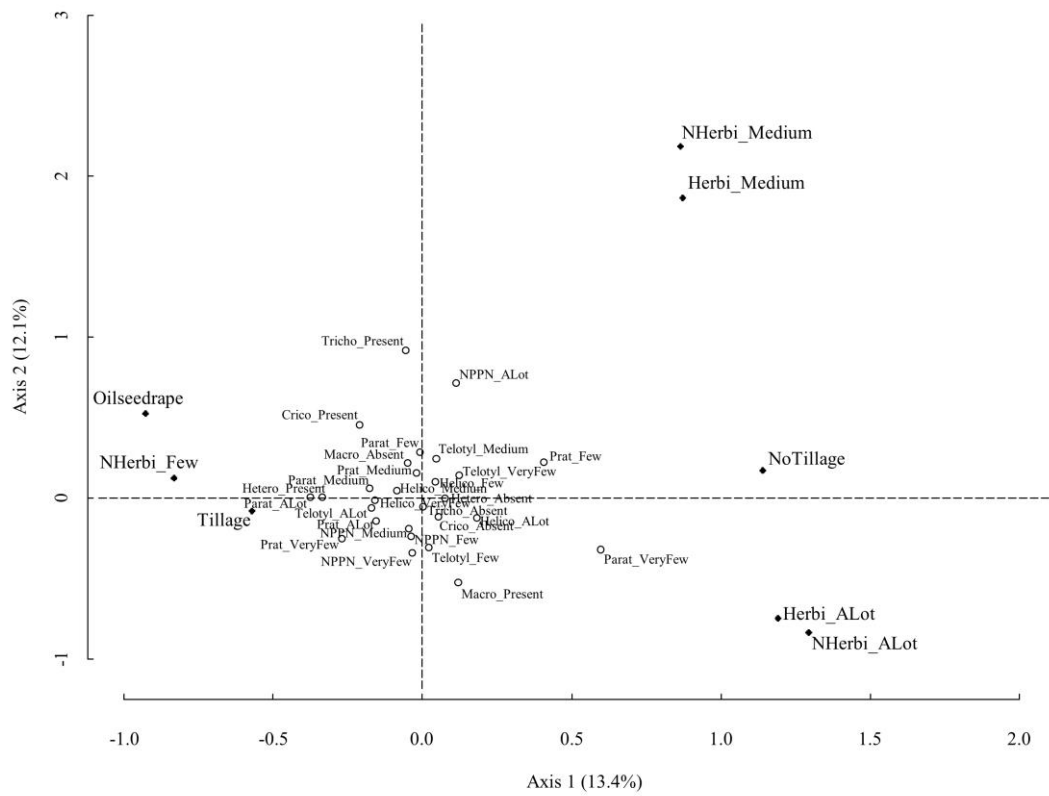
697

698 Figure S3



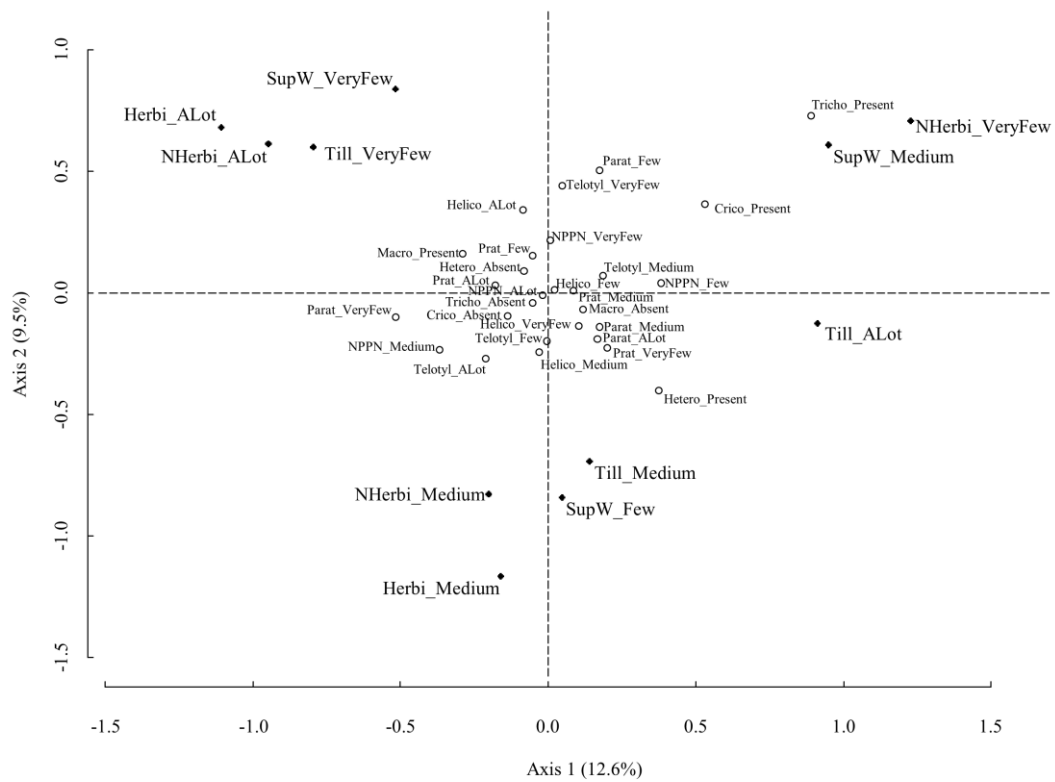
699

700 Figure S4



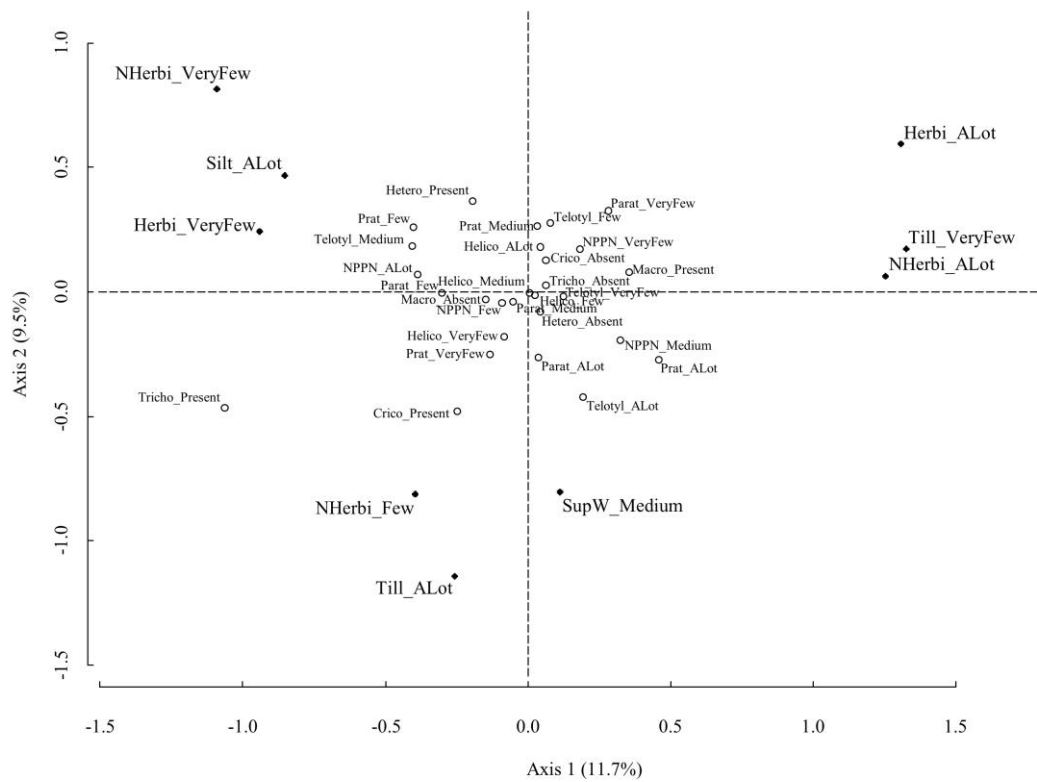
701

702 Figure S5



705

706 Figure S7



709

710 Figure S9