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► To cite this version:

Jean-François Ponge, Guénola Pérès, Muriel Guernion, Nuria Ruiz-Camacho, Jérôme Cortet, et al.. The impact of agricultural practices on soil biota: a regional study. *Soil Biology and Biochemistry*, 2013, 67, pp.271-284. 10.1016/j.soilbio.2013.08.026 . hal-00869859

HAL Id: hal-00869859

<https://hal.science/hal-00869859>

Submitted on 4 Oct 2013

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1 **The impact of agricultural practices on soil biota: a regional study**

2 **Jean-François Ponge^{a,*}, Guénola Pérès^b, Muriel Guernion^b, Nuria Ruiz-Camacho^c, Jérôme**
 3 **Cortet^{d,**}, Céline Pernin^{d,***}, Cécile Villenave^{e,****}, Rémi Chaussod^f, Fabrice Martin-Laurent^f,**
 4 **Antonio Bispo^g, Daniel Cluzeau^b**

5 ^a*Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-Château, 91800 Brunoy,*
 6 *France*

7 ^b*Université de Rennes I, CNRS UMR 6553 'EcoBio', OSUR, Station Biologique de Paimpont, 35380*
 8 *Paimpont, France*

9 ^c*Institut pour la Recherche et le Développement, UMR 7618 'Bioemco', Centre France-Nord, 32*
 10 *avenue Henri-Varagnat, 93143 Bondy Cedex, France*

11 ^d*Université de Lorraine, Laboratoire Sols et Environnement, INRA UMR 1120, 2 avenue de la Forêt de*
 12 *Haye, 54518 Vandœuvre-lès-Nancy Cedex, France*

13 ^e*Institut pour la Recherche et le Développement, UMR ECO&SOLS, 2 place Viala, 34060 Montpellier*
 14 *Cedex 2, France*

15 ^f*Institut National de la Recherche Agronomique, UMR 1347 'Agroécologie', 17 rue Sully, 21065*
 16 *Dijon Cedex, France*

17 ^g*Agence de l'Environnement et de la Maîtrise de l'Énergie, Centre d'Angers, 20, avenue du Grésillé,*
 18 *BP 90406, 49004 Angers Cedex 1, France*

19

20 **Keywords:** agricultural intensity; soil quality index; earthworms; macrofauna; microarthropods;

*Corresponding author. Tel.: +33 (0) 678930133; fax: +33 (0) 160465719. E-mail address: ponge@mnhn.fr (J.F. Ponge).

**Present address: Université Paul Valéry, UMR 5175, CEFE, Route de Mende, 34000 Montpellier, France

***Present address: Université de Lille I, Laboratoire Génie Civil & Géo-Environnement, EA 4515, 59655 Villeneuve d'Ascq Cedex, France

****Present address: ELISOL Environnement, Campus de la Gaillarde, 2 place Viala, 34060 Montpellier Cedex 2, France

1 nematodes; microbial biomass

2

3 ABSTRACT

4 A gradient of agricultural intensification (from permanent meadows to permanent crops, with rotation
5 crop and meadows as intermediary steps) was studied in the course of the RMQS-Biodiv program,
6 covering a regular grid of 109 sites spread over the whole area of French Brittany. Soil biota
7 (earthworms, other macrofauna, microarthropods, nematodes, microorganisms) were sampled
8 according to a standardized procedure, together with visual assessment of a Humus Index. We
9 hypothesized that soil animal and microbial communities were increasingly disturbed along this
10 gradient, resulting in decreasing species richness and decreasing abundance of most sensitive species
11 groups. We also hypothesized that the application of organic matter could compensate for the negative
12 effects of agricultural intensity by increasing the abundance of fauna relying directly on soil organic
13 matter for their food requirements, i.e. saprophagous invertebrates. We show that studied animal and
14 microbial groups, with the exception of epigeic springtails, are negatively affected by the intensity of
15 agriculture, meadows and crops in rotation exhibiting features similar to their permanent counterparts.
16 The latter result was interpreted as a rapid adaptation of soil biotic communities to periodic changes in
17 land use provided the agricultural landscape remains stable. The application of pig and chicken slurry,
18 of current practice in the study region, alone or in complement to mineral fertilization, proves to be
19 favorable to saprophagous macrofauna and bacterivorous nematodes. A composite biotic index is
20 proposed to synthesize our results, based on a selection of animals groups which responded the most
21 to agricultural intensification or organic matter application: anecic earthworms, endogeic earthworms,
22 macrofauna other than earthworms (macroarthropods and mollusks), saprophagous macrofauna other
23 than earthworms (macroarthropods and mollusks), epigeic springtails, phytoparasitic nematodes,
24 bacterivorous nematodes and microbial biomass. This composite index allowed scoring land uses and
25 agricultural practices on the base of simple morphological traits of soil animals without identification
26 at species level.

1

2 **1. Introduction**

3 Soil biota are a major component of agroecosystems, playing a decisive role in ecosystem
4 services such as, among many others, nutrient capture and cycling (Carpenter et al., 2007; Van der
5 Heijden et al., 2008; Murray et al., 2009), building and control of soil organic matter (SOM) or soil
6 physical structure (Wolters, 2000; Jégou et al., 2001; Jouquet et al., 2006), and vegetation dynamics
7 (De Deyn et al., 2003; Mitschunas et al., 2006; Forey et al., 2011), with synergistic effects on crop
8 production (Ingham et al., 1985; Eisenhauer et al., 2010). Studies on plant-soil feedbacks mediated by
9 soil biota showed that soil animals and microbes are also involved in signaling processes which
10 contribute to the integrity of agroecosystems and which sustain crop production (Blouin et al., 2005;
11 Sanon et al., 2009; Endlweber et al., 2011).

12 Soil biotic communities were included in soil quality monitoring programs in Europe, an
13 initiative stimulated by adoption of the Thematic Strategy for Soil Protection by the European Union
14 (EC, 2006), and sets of biological indicators of soil quality were proposed, based on national programs
15 (Black et al., 2003; Rutgers et al., 2009; Keith et al., 2012). In France, the ADEME (“Agence de
16 l’Environnement et de la Maîtrise de l’Énergie”) urged scientists to develop tools for monitoring soil
17 quality from a biological point of view and initiated and financially supported the RMQS-BioDiv
18 program in French Brittany, a western peninsula mostly covered with agricultural land. The national
19 RMQS (“Réseau de Mesures de la Qualité des Sols”) network (2200 sites, distant of 16 km) is devoted
20 to the monitoring of physical-chemical properties of soils (Arrouays et al., 2002; Saby et al., 2011) but
21 with future prospects in soil microbiology (Ranjard et al., 2010). The French Brittany part of this
22 network was selected for the assessment of soil biotic communities and the search for a biotic index of
23 soil quality in agricultural land (Cluzeau et al., 2009; Cluzeau et al., 2012; Villenave et al., 2013).

24 Earthworms, macroinvertebrates other than earthworms, microarthropods, nematodes, and
25 microbial communities were selected as a set of indicator groups proposed at European level (Bispo et
26 al., 2009). All of them are known for their sensitivity to disturbances associated to agriculture, among

1 others tillage (Cortet et al., 2002b; Krogh et al., 2007; Lagomarsino et al., 2009), fertilizer
2 addition (Cole et al., 2005; Van der Wal et al., 2009), pesticide treatment (Frampton, 1997; Rebecchi et
3 al., 2000; Cortet et al., 2002a), disappearance or simplification of ground cover (Filser, 1995;
4 Loranger–Merciris et al., 2006), soil compaction (Cluzeau et al., 1992; Heisler and Kaiser, 1995), and
5 heavy metal contamination (Bruce et al., 1999; Hedde et al., 2012).

6 Apart from species richness and diversity/evenness indices, widely used at community level,
7 some indices based on species traits directly relevant to disturbance levels were identified for
8 nematodes, such as the Maturity Index (Ettema and Bongers, 1993). Similar indices have been
9 proposed for some other invertebrate groups (Parisi et al., 2005) and for the whole faunal community
10 (Yan et al., 2012). Direct extraction of DNA and other standardized microbiological methods also
11 allow estimating parameters of soil biological (mainly microbial) activity (Harris, 2003; Petric et al.,
12 2011). To the study of these taxonomic groups was added a Humus Index, derived from the
13 assessment of biological activity through the identification of humus forms in forest soils (Ponge and
14 Chevalier, 2006), specially adapted to agricultural soils on the base of previous results on the influence
15 of farming systems on soil structure (Topoliantz et al., 2000).

16 Meadows, meadows in rotation, crop fields in rotation and permanent crop fields can be
17 considered as forming a gradient of increasing intensity of agricultural practices (Burel et al., 1998;
18 Stoate et al., 2001; Decaëns et al., 2008). Our first hypothesis is that increasing disturbance in soil
19 animal and microbial communities can be observed along this gradient, which could be revealed by
20 decreasing species richness and decreasing abundance of more sensitive species groups (Eggleton et
21 al., 2005; Osler and Murphy, 2005).

22 Some agricultural practices aim at restoring soil fertility, compensating for the exportation of
23 nutrients through herbage and food crop production. Among fertilizing practices, those increasing soil
24 organic matter content, i.e. the application of manure, compost and organic-rich waste products of
25 animal husbandry such as chicken droppings or pig slurry, are known to improve soil quality and crop
26 yield but also lead to uncontrolled N losses (Cox et al., 2001; Antil et al., 2009; Chirinda et al., 2010).

1 Slurry application may thus compensate for the negative effects of agricultural intensity, in particular
2 for those species relying on soil organic matter (SOM) for food requirements, i.e. saprophages: this is
3 our second hypothesis.

4 Spatiotemporal influences on the distribution of soil biota (Winkler and Kampichler, 2000;
5 Decaëns, 2010; Jangid et al., 2011), as well as the effects of geology and related soil features (Kováč,
6 1994; Popovici and Ciobanu, 2000; Fierer and Jackson, 2006) will be taken into account in our
7 regional scale census of the impact of agricultural practices on soil biotic communities.

8

9 **2. Materials and methods**

10 *2.1. Study sites*

11 A total of 109 sites, distant of 16 km on a regular grid, among which 99 in agricultural land
12 (53 crop fields, 46 meadows), were selected for the present study. All these sites pertain to the national
13 RMQS network. They were characterized by geographical position, parent rock and soil type, land use
14 and farming system (Appendix 1). The climate is typically Atlantic but there is a west-east gradient of
15 increasing seasonal contrast and a north-south gradient of increasing temperature and decreasing
16 rainfall due to mainland effect and Gulf Stream influence, respectively. In French Brittany, most
17 frequent geological substrates are hard rocks such as granite and hard sandstone.

18 At the time of sampling (2006 and 2007) crop fields were mostly permanent (42 among 53,
19 i.e. 79%), while half of the meadows (23 among 46) were included in rotations with crops (Appendix
20 1). Mineral fertilization was widely used in the studied region (84 sites among 99), alone (20 sites) or
21 more often combined with cattle manure (32 sites), pig and chicken slurry (19 sites) or both (11 sites).

22 Permanent meadows, meadows in rotation, crops in rotation and permanent crops formed a
23 gradient of agricultural intensity according to increasing use of ploughing, fertilizer and pesticide
24 application:

- 1 • Permanent meadows: no ploughing/tillage or only occasional (when sown), no or only
2 occasional pesticide application, no fertilizers or varied organic and/or mineral fertilizers,
3 permanent plant cover
- 4 • Meadows in rotation: same as above but alternating with crops
- 5 • Crops in rotation: same as below but alternating with meadows
- 6 • Permanent crops: ploughing/tillage each year (one to three/four times per year), various levels
7 and types of pesticide and fertilizer use, seasonal plant cover

8 Given the complexity of measuring the impact of pesticides, which may vary in quantity and
9 variety, frequency of application, and ecotoxicity (Sattler et al., 2007), we decided for the present
10 study to note only whether pesticides were used or not, without trying to separate them into categories
11 nor defining any scale of intensity of pesticide use.

12

13 *2.2. Sampling procedure*

14 Sampling took place in 2006 (30 sites) and 2007 (69 sites). With the exception of non-
15 earthworm macroinvertebrates, sampling was done by the same team, previously trained to the
16 different sampling methods in use. Sampling campaigns took place between 15 February and 25 April,
17 the most favorable period in French Brittany agricultural land. Site descriptors were coded and
18 recorded in the DONESOL database (Jolivet et al., 2006a, b).

19 Sampling plots for soil biota were chosen as near as possible from those previously used for
20 soil description and soil physical-chemical analyses (Arrouays et al., 2002), i.e. 5 m northward.
21 Occasional shifts to another direction (west, south, or east) were necessary in cases of unexpected
22 impediment. Sampling plot was a 34 x 3 m stretch of land, homogeneous in plant cover and soil
23 features. This zone was subdivided into elementary sub-plots 1 x 3 m each, identified by stakes of
24 varying color according to soil biota groups, as already described in more detail by Cluzeau et al.
25 (2012).

1 Earthworms were sampled in triplicate according to the method devised by Bouché (1972),
2 which was adapted to agricultural context by Cluzeau et al. (1999, 2003). Ten liters of formalin (37%
3 formaldehyde solution) at 0.25, 0.25 and 0.4% dilution were watered every 15 min over each
4 elementary 1 x 1 m quadrat (total surface sampled 3 m²). Earthworms expelled to the surface by the
5 irritant solution were collected by hand then preserved in 4% formalin dilution. After completion of
6 earthworm extraction, a 0.25 x 0.25 x 0.25 soil block was dug up at the center of each quadrat then
7 spread on a plastic sheet, to be sorted by hand for remaining earthworms. Identification was done at
8 species level in the laboratory according to a key (Cluzeau, unpublished, available upon request),
9 based on Bouché (1972). For the present study, the three replicates were compounded in each site.
10 Earthworm species were characterized by abundance and biomass (fresh weight in formalin solution).
11 They were grouped into 'ecological' categories (epigeic, anecic, endogeic) according to Bouché
12 (1972). Earthworm taxonomic (species) richness, diversity (Shannon H') and evenness were calculated
13 on the compound sample (Appendix 2).

14 Other macroinvertebrates were sampled in six replicates according to the TSBF (Tropical Soil
15 Biology and Fertility) method (Lavelle, 1988; Anderson and Ingram, 1993), modified for temperate
16 soils according to ISO 23611-5 (ISO, 2011). Formalin (0.2% dilution) was applied every 10 min on a
17 25 x 25 cm area during half an hour. All macroinvertebrates expelled by the irritant solution (except
18 earthworms) were collected with forceps and preserved in 4% formalin dilution. A block of soil 15 cm
19 deep was then dug up to be sorted for all macroinvertebrates visible to the naked eye (except
20 earthworms), which were added to early collected animals. Identification was done at family or above
21 level (Appendix 2). Taxonomic groups were classified in phytophages, saprophages and predators.
22 Macrofauna richness was calculated on one compound sample per site.

23 Sampling and extraction of microarthropods (springtails, mites) were performed according to
24 ISO 23611-2 (ISO, 2006). Microarthropods were sampled in triplicate with a soil corer, especially
25 designed for the RMQS-BioDiv program, which was forced into the ground. At the inside of the corer
26 three 6 cm-diameter PMMA ('Plexiglas') plastic cylinders allowed to separate three depth levels, 0-5
27 cm, 5-10 cm and 10-15 cm, which were sent separately to the laboratory for extraction.

1 Microarthropods were extracted in the plastic cylinders according to the high gradient method (Block,
2 1966). After extraction, dry samples were sent to another laboratory for the assessment of the Humus
3 Index, as explained below. Springtails (Collembola) were identified to species level while mites
4 (Acari) were classified in Oribatida, Actinedida, Acaridida and Gamasida (suborder level).
5 Microarthropod communities were characterized at taxonomic (taxa, richness, diversity, evenness),
6 functional (life forms: euedaphic, hemiedaphic, epigeic) and demographic level (total abundance of
7 springtails and mites and abundance of mite suborders). The three depth levels and the three replicates
8 were pooled in the present study.

9 Nematodes were sampled, extracted and identified using ISO 23611-4 (ISO, 2007). For each
10 site, a single sample was composited from 32 samples collected from the surface soil layer (0–15 cm).
11 The nematodes were extracted from approximately 300 g wet soil by elutriation, followed by an active
12 passage through a cotton wool filter for 48 hours; they were then counted using a binocular
13 microscope. The composition of the soil nematofauna was determined after fixation in a
14 formaldehyde-glycerol mixture and transfer to mass slides. On average, 200 nematodes per mass slide
15 were identified to family or genus level at 400 X magnification. Genera were grouped in families or
16 sub-families for the present study (Appendix 2). Nematode communities were characterized at
17 taxonomic (taxa, richness, diversity, evenness), functional (sixtrophic groups or functional guilds,
18 nematological indices) and global demographic level (total abundance of nematodes, total abundance
19 of free-living and parasite nematodes). Several indices were used to characterize nematode
20 communities from a functional point of view. The Maturity Index (MI) is based on the successional
21 replacement of colonizers and persisters (corresponding to r- and K-selected life-history strategies)
22 along a c-p scale varying from 1 to 5 (Bongers, 1990; Bongers and Bongers, 1998). MI values increase
23 along successional gradients but this index also measures the level of disturbance of the environment,
24 lower values indicating disturbed environments. It was also calculated separately for free-living, plant-
25 parasitic (PPI), bacterial-feeding and fungal-feeding nematodes (Appendix 2). Other functional
26 indicators were used in the present study: Nematode Channel Ratio (NCR), measuring the relative
27 abundance of bacterial-feeders (Yeates, 2003), Structure Index (SI), Enrichment Index (EI) and

1 Decomposition or Channel Index (DI), measuring environmental stability, resource availability and
2 bacterial activity, respectively (Ferris et al., 2001), and Nematode Damage Index (IP), measuring the
3 impact of nematode pathogens (Dirzo and Domínguez, 1995).

4 Microbial biomass was measured on an aliquot of a compound sample by the fumigation-
5 extraction method (Chaussod et al., 1988), according to ISO 14240-2 (ISO, 1997). DNA was extracted
6 from the soil according to ISO 11063 (ISO, 2012). The proportion of bacterial DNA was calculated by
7 measuring the number of copies of 16S ribosomal DNA (Martin-Laurent et al., 2001). Bacterial
8 functional groups involved in denitrification and degradation of phenolic compounds (involved in the
9 degradation of mineral fertilizers and pesticides, respectively) were estimated by the number of copies
10 of narG and PcaH genes, respectively. The contribution of these two groups to the total bacterial
11 community was estimated by dividing narG and PcaH by 16S, respectively.

12 The Humus Index, formerly designed for forest soils (Ponge et al., 2002), was used here as an
13 index of annelid activity, based on previous studies of soil biogenic structures in agricultural soils
14 (Topoliantz et al., 2000). It was visually estimated on soil structure of the dry soil according to a scale
15 varying from 1 (crumbly structure, due to earthworm activity) to 3 (compact structure, due to the
16 absence of any visible annelid activity). The intermediate value, 2, corresponds to a spongy structure
17 typical of enchytraeid activity (Topoliantz et al., 2000). For each depth level Humus Index values were
18 averaged among the three replicate samples taken for the extraction of microarthropod fauna. Only
19 mean Humus Index (averaged among the three depth levels 0–5 cm, 5–10 cm and 10–15 cm) and
20 surface Humus Index (0–5 cm) were kept for the present analysis.

21

22 *2.3. Data analysis and statistical treatment*

23 Data were analyzed separately for each group by Redundancy Analysis (RDA), a multivariate
24 regression method, using biotic variables (Appendix 2) as explained variables and ‘environmental’
25 variables (land use, practices, geology, year, and geographic position) as explanatory variables
26 (Appendix 1). For the sake of analysis data about agricultural practices were simplified, with

1 12dummy (presence/absence) variables for land use, fertilizer and pesticide application, direct drilling
2 and litter, one ordinal variable for depth of tillage and one continuous variable for plant cover.
3 Multiple practices (fertilizers, pesticides, etc.) could be combined for the same site by allowing several
4 variables to take 1 as value. Significance of the co-variation between biotic and ‘environmental’
5 variables was tested by Monte-Carlo permutation using 500 runs. Partial RDA was used to analyze
6 graphically the influence of land use and agricultural practices upon discarding confounding effects of
7 geology, year and xy position. Most prominent effects depicted by partial RDA were further tested by
8 Mann-Whitney and Kruskal-Wallis non-parametric tests, the latter followed by multiple comparisons
9 among means (two-sided Dunn tests).

10 Co-variation between the five partial RDAs was tested by calculating the product-moment
11 (Pearson) coefficient of correlation between site scores along canonical factors of the different
12 analyses. We also calculated coefficients of correlation (Spearman) between all biological variables
13 and those biological variables which responded the best to agricultural practices according to RDAs,
14 using Bonferroni correction for significance level (0.003 in place of 0.05) given the high number of
15 variables to be compared (234).

16 Biological variables responding the best to agricultural practices were used to build a
17 composite indicator, which allowed scoring land uses and practices of the studied region according to
18 soil biological variables, following the method by Bert et al. (2012).

19 All calculations were performed with XLSTAT (Addinsoft[®], Paris, France).

20

21 **3. Results**

22 *3.1. Earthworms*

23 Permutation tests showed that earthworm communities were significantly affected by land use
24 and agricultural practices upon discarding the effects of geology, year and latitude/longitude (Pseudo-
25 $F = 0.6$; $P < 0.0001$). Figure 1 shows graphically which and how composite variables describing the

1 earthworm community were influenced by land use and agricultural practices. The first canonical
2 factor (32% of explained variance) displayed a gradient of increasing anecic abundance and biomass,
3 earthworm species richness and earthworm biomass, corresponding to a land use gradient: permanent
4 crops → crops in rotation → meadows in rotation → permanent meadows. Plant cover increased,
5 while depth of tillage, fertilization (whether mineral or organic) and pesticide use decreased along this
6 gradient of decreasing intensity of agricultural use. The second canonical factor (14% of explained
7 variance) displayed a gradient of increasing endogeic abundance and biomass, total earthworm
8 abundance, and decreasing earthworm diversity and evenness, according to a gradient of increasing
9 use of pig slurry.

10 Scores of earthworm species along the first two canonical factors (not shown, available upon
11 request) were in accordance with composite variables. All anecic species increased in abundance along
12 the gradient of decreasing intensity of agricultural use represented by the first canonical factor. The
13 second canonical factor corresponded mainly to the endogeic *Nicodrilus caliginosus caliginosus*
14 *typica*, the most abundant and widely represented earthworm species in the studied agricultural crops.

15 Anecic and endogeic abundances were selected to test the effects of land use and slurry
16 application (Table 1). Crop fields (whether permanent or in rotation) exhibited a smaller anecic
17 population size than meadows (whether permanent or in rotation). In crop fields, endogeic abundance
18 was doubled by slurry application. Anecic earthworms did not respond significantly to slurry
19 application, although their density was increased. Endogeic earthworms did not respond significantly
20 to agricultural intensification, although they were more abundant in meadows.

21

22 3.2. Macroinvertebrates other than earthworms

23 Permutation tests showed that macroinvertebrate communities were significantly affected by
24 land use and agricultural practices upon discarding the effects of geology, year and latitude/longitude
25 (Pseudo-F = 0.68, $P < 0.05$). Partial RDA shows graphically (Fig. 2) that abundance of macro-
26 invertebrates, whether total or distributed in guilds (predators, phytophages, saprophages) and

1 taxonomic richness increased when the intensification of agriculture decreased (same gradient as for
2 earthworms) and plant cover increased accordingly (Factor F1, 34% of explained variance). The
3 second canonical factor (14% of explained variance) displayed a positive relationship between slurry
4 application and saprophage abundance. Direct drilling was also shown graphically to be positively
5 correlated with saprophage abundance, but this practice was poorly represented in the studied region
6 (9 sites, compared to 19 sites for slurry application), making conclusions for direct drilling less sure
7 than for slurry application.

8 With the exception of millipedes (Iulidae, Polydesmidae, Glomeridae), all soil macroarthropod
9 and mollusk (slugs and snails) taxa responded negatively to increased intensification of agriculture
10 (F1). Tipulid larvae were dominant in abundance among the saprophagous macroarthropod and
11 mollusk taxa which responded positively to slurry application (F2).

12 Like anecic earthworms, densities of other macroinvertebrates declined in crops, whether
13 permanent or in rotation, compared with permanent meadows (Table 1). Although not dominant in
14 numbers among macroinvertebrates, saprophages shared this general trend. Total densities of
15 macrofauna of crops (permanent and in rotation) increased in the presence of slurry, but this increase
16 was even more prominent in saprophages.

17

18 *3.3. Microarthropods*

19 Permutation tests showed that microarthropod communities were significantly affected by land
20 use and agricultural practices upon discarding the effects of geology, year and latitude/longitude
21 (Pseudo-F = 1, $P < 0.0001$). The first canonical factor (F1, 21% of total variance) represented a
22 gradient of increasing abundance of total mesofauna as well as of its two main component groups,
23 mites and springtails (Fig. 3). With the exception of epigeic springtails, all microarthropod groups
24 increased in abundance (although not in richness, diversity and evenness) along F1. The first canonical
25 factor did not display a gradient of decreasing intensification of agriculture, meadows in rotation (on
26 the positive side, i.e. maximizing microarthropod densities) being opposed to permanent meadows and

1 crops in rotation on the negative side of F1. The contrast between crops and meadows, associated with
2 a corresponding increase in plant cover, was represented by the second canonical factor F2, crops
3 (permanent and in rotation) maximizing densities of epigeic springtails as well mesofaunal richness,
4 diversity and evenness, opposite to permanent meadows, meadows in rotation being in intermediary
5 position. The second canonical factor expressed also a contrast between mites and springtails
6 according to plant cover, abundance of oribatid mites being associated with increased plant cover on
7 the negative side of F2. Slurry application did not exhibit any clear trend in microarthropod
8 community parameters.

9 With the exception of *Lepidocyrtus lignorum* and *Sphaeridia pumilis*, all epigeic springtail
10 species followed the general trend displayed by F2, i.e. they increased in density with intensification
11 of agriculture. Epigeic springtails were five times more abundant in permanent crops than in
12 permanent meadows (Table 1), while oribatid mites displayed an opposite (although not significant)
13 pattern (data not shown).

14

15 3.4. Nematodes

16 Permutation tests showed that nematode communities were significantly affected by land use
17 and agricultural practices upon discarding the effects of geology, year and latitude/longitude (pseudo-F
18 = 1.1, $P < 0.0001$). According to the first canonical factor F1 (35% of explained variance), the gradient
19 of decreasing intensification of agriculture from permanent crops to permanent meadows maximized
20 the number of phytoparasites, the total abundance of nematodes, the Maturity Index MI, and
21 minimized the Enrichment Index EI and the Decomposition or Channel Index DI (Fig. 4). As for
22 earthworms and other macrofauna, the second canonical factor corresponded to slurry application.
23 When analyzed graphically, this practice tended to maximize the Decomposition or Channel Index DI,
24 the Nematode Channel Ratio NCR, the density of pioneer bacterivores (c-p 1 group), and more
25 generally free-living nematodes, and minimized the Bacterivore Maturity Index.

1 The abundance of phytoparasites decreased regularly along the gradient of intensification of
2 agriculture, being divided by three in permanent crops compared to permanent meadows (Fig. 8a,
3 Table 1), while phytoparasites did not respond to slurry application (Table 1). There was a significant
4 (although not very pronounced) increase in the abundance of bacterivores in the presence of slurry
5 application, while this feeding category did not respond to land use. Land uses were not discriminated
6 when r-selected (c-p-1) and K-selected (c-p-2-3-4) groups of bacterivorous nematodes were analyzed
7 separately (data not shown), although c-p-2-3-4 bacterivores seemed to react negatively to increased
8 intensification of agriculture, as suggested by Figure 4.

9 10 *3.5. Microbial communities*

11 Permutation tests showed that microbial communities were significantly affected by land use
12 and agricultural practices upon discarding the effects of geology, year and latitude/longitude (Pseudo-
13 $F = 0.36$, $P < 0.01$). The first canonical factor F1 (65% of the explained variance) corresponded to a
14 gradient of increasing microbial biomass (whether expressed per unit soil or carbon weight) according
15 to decreasing intensification of agriculture (Fig. 5). The second canonical factor F2 (19% of explained
16 variance) did not exhibit any clear environmental trend, neither in land use nor in agricultural
17 practices, and could not be interpreted with accuracy: the position of narG/16S and PcaH/16S far from
18 the origin along F2 indicated that there was a gradient among the study sites in the contribution of
19 denitrifiers and protocatechuate degraders to the bacterial community, which could not be explained
20 by agricultural practices.

21 There was a good agreement between microbial biomass and the level of intensification of
22 agriculture: microbial biomass decreased regularly along the gradient permanent meadows →
23 meadows in rotation → crops in rotation → permanent crops, while not responding to slurry
24 application (Table 1). The second canonical axis corresponded to variable proportions of bacterial
25 functional groups but without any marked links with agricultural practices.

1 3.6. *Humus Index*

2 Permutation tests showed that the Humus Index was not significantly affected by land use and
3 agricultural practices upon discarding the effects of geology, year and latitude/longitude (Pseudo-F =
4 0.024, $P = 0.35$), thus the null hypothesis was accepted. Examination by total RDA of subsets of the
5 ‘environmental’ matrix revealed a significant geologic signal (Pseudo-F = 0.44, $P < 0.01$), a marginally
6 significant geographic signal (Pseudo-F = 0.06, $P = 0.058$) and a nil year signal (Pseudo-F = 0.002, P
7 = 0.84).

8

9 3.7. *Co-variation between biotic components*

10 Based on results of separate multivariate analyses the first canonical factor was selected as
11 corresponding to the gradient of agricultural intensity for earthworms, macrofauna other than
12 earthworms, nematodes and microbes, while the same gradient was represented by the second
13 canonical factor for microarthropods. Table 2 shows that the ordination of agricultural sites co-varied
14 at a high level of significance ($P < 0.0001$) in the separate analyses performed on different animal and
15 microbial groups. In absolute value the product-moment correlation coefficient varied from 0.41
16 (macrofauna other than earthworms versus microarthropods) to 0.86 (earthworms versus microbes).
17 Negative values (for microarthropods) indicate that the gradient from meadows to crop fields was
18 inverted compared to the four other groups. Mesofaunal richness, diversity, and evenness were on the
19 positive side of F2 (Fig. 3), i.e. favored by agricultural intensity (crop fields), while the contrary was
20 shown for earthworms (Fig. 1) and macrofauna other than earthworms (Fig. 2).

21 The second canonical factors of partial RDAs corresponded to slurry application for
22 earthworms, macrofauna other than earthworms and nematodes. These three factors were positively
23 correlated (Table 3), at a higher level of significance between nematodes and earthworms or
24 macrofauna than between earthworms and macrofauna: endogeic earthworms, saprophagous
25 macrofauna and bacterivorous nematodes reacted positively and in a coordinated manner to slurry
26 application.

1 Anecic abundance was positively correlated with earthworm abundance, biomass, species
 2 richness and diversity ($r_s = 0.57, 0.84, 0.55$ and 0.51 , respectively; $P < 0.0001$), anecic biomass ($r_s =$
 3 0.89 , $P < 0.0001$), epigeic abundance and biomass ($r_s = 0.37$ and 0.40 , respectively; $P < 0.001$ in both
 4 cases) and endogeic biomass ($r_s = 0.39$; $P < 0.001$). In the macrofauna community anecic abundance
 5 was positively correlated with the abundance of saprophagous tipulid larvae ($r_s = 0.40$, $P < 0.001$). In
 6 the microarthropod community anecic abundance was negatively correlated with the abundance of
 7 epigeic springtails and that of the epigeic *Isotomurus gr. palustris* ($r_s = -0.38$ and -0.34 , respectively; P
 8 < 0.001 and 0.01 , respectively). In the nematode community anecic abundance was positively
 9 correlated with the Plant Parasite Index (PPI), the abundance of phytoparasites ($r_s = 0.36$ and 0.44 ,
 10 respectively; $P < 0.001$ and 0.0001 , respectively), and the abundance of the phytoparasitic
 11 Meloidogynae ($r_s = 0.44$, $P < 0.0001$). No significant correlation was found with microbial parameters.

12 Endogeic abundance was positively correlated with earthworm abundance and biomass ($r_s =$
 13 0.89 and 0.55 , respectively; $P < 0.0001$ in both cases), endogeic biomass ($r_s = 0.91$; $P < 0.0001$) and
 14 abundance of the anecic *Lumbricus terrestris* ($r_s = 0.37$; $P < 0.001$). In the macrofauna community,
 15 endogeic abundance was positively correlated with the abundance of phytophages ($r_s = 0.37$; $P <$
 16 0.001). No correlation was found between endogeic abundance and microarthropod, nematode or
 17 microbial parameters.

18 The abundance of macrofauna other than earthworms was positively correlated with
 19 earthworm species richness ($r_s = 0.37$; $P < 0.01$) and with the abundance and biomass of epigeic
 20 earthworms ($r_s = 0.41$ and 0.43 , respectively; $P < 0.001$ in both cases). In the macrofauna community,
 21 if we discard trivial relationships with groups included in its calculation, the abundance of macrofauna
 22 was positively correlated with macrofaunal taxonomic richness ($r_s = 0.57$; $P < 0.0001$). In the
 23 microarthropod community, the abundance of macrofauna was negatively correlated with the
 24 abundance of the epigeic springtail *Isotomurus gr. palustris* ($r_s = -0.38$; $P < 0.001$). In the nematode
 25 community the abundance of macrofauna was negatively correlated with the Decomposition Index
 26 (CI) ($r_s = -0.35$; $P < 0.01$). The abundance of macrofauna other than earthworms was positively

1 correlated with microbial biomass, either calculated per unit soil mass or per unit carbon ($r_s = 0.41$ and
2 0.43 , respectively; $P < 0.001$ in both cases).

3 The abundance of saprophagous macrofauna other than earthworms was positively correlated
4 with the abundance and biomass of epigeic earthworms ($r_s = 0.37$; $P < 0.01$ in both cases). Within the
5 macrofauna community it was positively correlated with phytophagous, predator and, as expected,
6 total abundance of macrofauna ($r_s = 0.42, 0.49$ and 0.63 , respectively; $P < 0.001$ and < 0.0001 in the
7 two latter cases). The abundance of saprophagous macrofauna was also positively correlated with
8 macrofaunal taxonomic richness ($r_s = 0.69$; $P < 0.0001$). In the microarthropod community it was
9 negatively correlated with the abundance of the epigeic springtail *Isotomurus gr. palustris* ($r_s = -0.42$;
10 $P < 0.001$). In the nematode community the abundance of saprophagous macrofauna was positively
11 correlated with the Maturity Index (MI), the Maturity Index without phytoparasites and the
12 Bacterivore Maturity Index (BaMI) ($r_s = 0.37, 0.37$ and 0.35 , respectively; $P < 0.01$ in all cases), and
13 was negatively correlated with the Enrichment Index (EI) ($r_s = -0.37$; $P < 0.001$). In the microbial
14 community the abundance of saprophagous macrofauna was positively correlated with microbial
15 biomass, either calculated per unit soil mass or per unit carbon ($r_s = 0.35$ and 0.37 , respectively; $P <$
16 0.01 and 0.001 , respectively), and with the abundance of denitrifiers (*narG*) ($r_s = 0.34$; $P < 0.01$).

17 The abundance of epigeic springtails was negatively correlated with earthworm species
18 richness and diversity ($r_s = 0.38$ and 0.34 , respectively; $P < 0.001$ and 0.01 , respectively) and with the
19 abundance of anecic earthworms ($r_s = 0.34$; $P < 0.01$). In the macrofauna community, it was negatively
20 correlated with macrofaunal taxonomic richness and abundance of phytophages ($r_s = -0.38$ and -0.39 ,
21 respectively; $P < 0.001$ in both cases) and with the abundance of ants and woodlice ($r_s = -0.41$; $P <$
22 0.001 in both cases). Within the microarthropod community, the abundance of epigeic springtails was
23 positively correlated with total springtail abundance ($r_s = 0.53$; $P < 0.0001$), and total mesofaunal
24 abundance, taxonomic richness and diversity ($r_s = 0.44, 0.49$ and 0.37 , respectively; $P < 0.0001, <$
25 0.0001 and 0.01 , respectively). In the microbial community it was negatively correlated with the
26 microbial biomass per unit carbon ($r_s = -0.38$; $P < 0.001$). No significant correlation was observed with
27 nematode parameters.

1 The abundance of phytoparasitic nematodes was positively correlated with earthworm biomass
 2 and species richness ($r_s = 0.38$ and 0.35 , respectively; $P < 0.001$ and 0.01 , respectively) and with
 3 anecic biomass ($r_s = 0.36$; $P < 0.01$). In the microarthropod community it was negatively correlated
 4 with the abundance of the epigeic springtail *Isotomurus* gr. *palustris* and that of the endogeic springtail
 5 *Mesaphorura hylophila* ($r_s = -0.39$ and -0.37 , respectively; $P < 0.001$ and < 0.01 , respectively). Within
 6 the nematode community, if we discard trivial relationships with members of this trophic group, the
 7 abundance of phytoparasites was positively correlated with the Maturity Index with (MI) or without
 8 phytoparasites ($r_s = 0.52$ and 0.50 , respectively; $P < 0.0001$ in both cases), with the Bacterivore
 9 Maturity Index (BaMI) ($r_s = 0.46$; $P < 0.0001$), and negatively with the Enrichment Index (EI) ($r_s = -$
 10 0.41 ; $P < 0.001$). The abundance of phytoparasitic nematodes (per unit soil weight, as for all nematode
 11 parameters) was positively correlated with the microbial biomass per unit soil weight ($r_s = 0.39$; $P <$
 12 0.001). No significant correlation was observed with macrofaunal parameters.

13 The abundance of bacterivorous nematodes was not correlated with any parameters of the
 14 macrofauna community (earthworms included). In the microarthropod community it was positively
 15 correlated with the abundance of gamasid mites, a predatory group ($r_s = 0.42$; $P < 0.001$), and that of
 16 *Isotomiella minor*, an endogeic springtail ($r_s = 0.35$; $P < 0.01$). Within the nematode community, after
 17 discarding trivial results, the abundance of bacterivorous nematodes was positively correlated with the
 18 Nematode Channel Ratio (NCR) and the Decomposition Index (CI) ($r_s = 0.42$ and 0.39 , respectively; P
 19 < 0.001 in both cases). No correlation was observed with any microbial parameters.

20 The microbial biomass per unit soil weight was positively correlated with earthworm biomass
 21 and taxonomic richness ($r_s = 0.41$ and 0.38 , respectively; $P < 0.001$ in both cases) and with anecic
 22 biomass ($r_s = 0.34$; $P < 0.01$). It was also positively correlated with the abundance of non-earthworm
 23 macrofauna, whether total or restricted to saprophages ($r_s = 0.41$ and 0.35 , respectively; $P < 0.001$ and
 24 < 0.01 , respectively). In the microarthropod community, it was negatively correlated with the
 25 abundance of the epigeic springtail *Isotomurus* gr. *palustris* ($r_s = -0.39$; $P < 0.001$) and positively with
 26 that of the epigeic springtail *Sphaeridia pumilis* ($r_s = 0.41$; $P < 0.001$). In the nematode community,
 27 microbial biomass per unit soil weight was positively correlated with total nematode abundance and

1 taxonomic richness ($r_s = 0.37$ and 0.38 , respectively; $P < 0.01$ and < 0.001 , respectively), with the
2 abundance of phytophagous and omnivorous nematodes ($r_s = 0.39$ and 0.43 , respectively; $P < 0.001$ in
3 both cases), with the Maturity Index (MI), the Maturity Index without phytoparasites and the
4 Bacterivore Maturity Index (BaMI) ($r_s = 0.45$, 0.46 and 0.41 , respectively; $P < 0.0001$, < 0.0001 and
5 0.001 , respectively) and was negatively correlated with the Enrichment Index (EI) ($r_s = -0.38$; $P <$
6 0.001).

7

8 *3.8. A composite biotic indicator of agroecosystems for French Brittany*

9 Results presented in Table 1 allow ranking agricultural usages from 1 to 4 taking into account
10 8 biotic groups: anecic earthworms, endogeic earthworms, macrofauna other than earthworms
11 (macroarthropods and mollusks), saprophagous macrofauna (macroarthropods and mollusks), epigeic
12 springtails, phytoparasitic nematodes, bacterivorous nematodes, and microbial biomass. Some groups
13 responded significantly to land use type (permanent meadows, meadows in rotation, crops in rotation,
14 permanent crops), others to slurry application, a fertilizing practice widely used in the studied region.
15 These ranks were averaged per column, giving a rank score to each land use type and to each
16 agricultural practice from French Brittany. Here only slurry application was addressed among
17 agricultural practices, since most studied groups exhibited a clear slurry application signal in
18 Redundancy Analysis. Note that according to this method of calculation the lower the rank score, the
19 higher the biotic improvement, and that no statistical testing of the observed differences is possible.

20 According to this composite biotic indicator, the gradient of intensity of agriculture exhibited
21 an array of scores ranging from 1.8 for permanent meadows (the 'best' land use from the point of view
22 of selected soil biota) to 3.1 for permanent crops. The increase from permanent meadows (1.8) to
23 meadows in rotation (2.1) was weak, as was the increase from crops in rotation (3.0) to permanent
24 crops (3.1). The impact of slurry (1.4 for slurry against 1.6 for no slurry) was weak.

25

1 **4. Discussion**

2 *4.1. Groups which responded negatively to agricultural intensity*

3 We showed that a variety of animal and microbial groups were negatively affected by the
4 intensity of agriculture, from permanent meadows to permanent crops, while meadows and crops in
5 rotation exhibited intermediary features, thereby supporting our first hypothesis.

6 The 56% decrease in microbial biomass observed along our gradient of agricultural intensity
7 (Table 1), a decrease often reported in a wide range of agroecosystems (Fließbach et al., 2007;
8 Lagomarsino et al., 2009; Jangid et al., 2011), has been mainly explained by a decrease in soil organic
9 matter: more plant biomass is exported through crop yields, vegetation covers the ground over a
10 shorter period and tillage decreases SOM pools to a greater extent in crop fields when compared to
11 meadows (Duxbury et al., 1989; Lagomarsino et al., 2009). Complementary data on our study sites
12 (Appendix 3) showed that organic carbon and total nitrogen decreased by 28 and 25%, respectively,
13 and plant cover was divided by two from permanent meadows to permanent crops. A clear positive
14 relationship between microbial biomass and SOM content has been established in agricultural soils by
15 Insam and Domsch (1988) and has been widely reported since then (Nair and Ngouajio, 2012).

16 By being at the base of soil trophic networks, microbial biomass controls the development of
17 all organisms ingesting it directly or indirectly, i.e. saprophages (including microbivores) and, by chain
18 reaction, predators (Ponsard et al., 2000). However, microbial biomass is in turn controlled by the
19 activity of soil engineers (earthworms in our temperate context) and litter animal decomposers
20 (millipedes, woodlice, tipulid larvae, etc.) which are involved in mutual relationships with microbial
21 communities (Lavelle et al., 2006; Ponge, 2013). This was reflected in the positive relationships
22 between microbial biomass and biomass and taxonomic richness of earthworms, abundance of
23 macrofauna other than earthworms, abundance and taxonomic richness of nematodes. Decreases in
24 densities and species richness of macroinvertebrates, whether saprophagous or predatory, have been
25 noted along intensification gradients (Eggleton et al., 2005; Postma–Blaauw et al., 2010, 2012). We
26 also showed that macroinvertebrates were severely affected by agricultural intensity, while

1 bacterivorous nematodes (the dominant trophic group of nematodes) were not affected at all (Table 1).
2 Co-variation analyses on our data showed that microbial biomass was positively correlated with the
3 abundance of phytophagous and omnivorous nematodes, but not with that of bacterivorous nematodes,
4 and was positively correlated with several nematological indices indicating maturation of the
5 community to the expense of pioneer bacterivores. This result could be compared with a study done in
6 the Netherlands by Postma–Blaauw et al. (2010, 2012), who showed that bigger-sized animals were
7 more affected by agricultural intensity than smaller-sized animals. They attributed this difference to
8 the impact of mechanical disturbance on bigger-sized animals, which adds another mechanism to the
9 disturbance caused by shortage in microbial biomass. Negative effects of plant species rarefaction on
10 soil microbial communities have been also experimentally demonstrated (Loranger–Merciris et al.,
11 2006), as well as the sensitivity of microbial biomass to pesticide use (Harden et al., 1993) and
12 agricultural traffic (Heisler and Kaiser, 1995).

13 Other factors, such as the development of root systems, involved in mutualisms with soil
14 microbial and animal communities (Heil, 2011; Ponge, 2013), should also be taken into account to
15 explain the observed negative response of soil biota to agricultural intensity (Ingham et al., 1985;
16 Alpehi et al., 1996; Bonkowski et al., 2000), although we did not provide data about it, except
17 indirectly through the plant cover, which was divided by two from meadows to crop fields (Appendix
18 3), and the abundance of phytoparasite nematodes, which was divided by three along the same
19 gradient (Table 1). Root biomass is known to be higher and more stable over seasons in perennial
20 compared to annual crops (Zan et al., 2001), which may explain, together with the current use of
21 nematicides in annual crops, the pattern we observed in phytoparasitic nematodes, a result already
22 reported by Yeates and Bird (1994), but not retrieved in the experiment by Postma–Blaauw et al.
23 (2010). As for other results of co-variation analyses, it should be noted that the positive relationship
24 observed along our gradient of agricultural intensity between the abundance of anecics and that of
25 phytoparasites (and associated nematological indices) was probably due to common trends in
26 requirements of these animals more than to positive direct or indirect interactions between them.

1 4.2. Groups which responded positively to agricultural intensity

2 The case of epigeic springtails should be considered apart, since these animals are living at the
3 soil surface and on low vegetation (Frampton et al., 2001) and thus do not respond to the same
4 constraints as soil-dwelling biota, even though collected in the same core samples. Epigeic springtails
5 are very mobile animals (Frampton et al., 2001) which are able to find refuges within or in the vicinity
6 of agricultural fields and may recolonize after the field has been disturbed by agricultural traffic or
7 spraying (Mebes and Filser, 1997; Alvarez et al., 1997, 2000). However, this does not explain why they
8 were comparatively disfavored in meadows, in particular in permanent meadows, compared to annual
9 crops (Filser et al., 2002). Possible reasons are the lower density level of surface predators such as
10 carabids and spiders under intensive agriculture (supported by our results, see Fig. 2), a reason invoked
11 to explain the rapid recovery of epigeic springtail populations after insecticide application (Duffield
12 and Aebischer, 1994), and the detrimental effects of grazing pressure (Dombos, 2001; Petersen et al.,
13 2004). Co-variation analyses did not throw any light on possible relationships between epigeic
14 springtails and their predators, to the exception of a negative relationship with ants. It must be noticed
15 that the observed decrease in the abundance of epigeic springtails in permanent meadows, compared to
16 permanent and rotation crops, conflicts at first sight with results obtained in Germany (86 sites) by
17 Chauvat et al. (2007), who showed that the abundance of springtails increased from permanent crop
18 fields to meadows and increased then decreased according to the age of meadows. However,
19 examination of their data (Table 2 in Chauvat et al., 2007) showed that the two most common epigeic
20 species of crop fields (*Isotoma viridis*, *Lepidocyrtus lanuginosus*), which made the bulk of their
21 epigeic group, were more abundant in permanent crop fields than in old meadows (> 40 years),
22 thereby explaining apparent disagreement between our results and theirs.

23 The increase of mesofaunal richness, diversity and evenness, observed along our gradient of
24 agricultural intensity, contrasts with the decrease of species richness observed in macrofauna. This
25 might indicate either opposite trends in microarthropods (to the exception of oribatid mites, see Fig. 3)
26 and macroinvertebrates in their response to agricultural intensity, or negative interactions between
27 organisms of various sizes. It should be noted that the latter pattern could be revealed only by

1 comparing samples within sites, or by discarding site effects, which was not possible with our data,
 2 since microarthropods, macroinvertebrates and microbial communities were not studied on the same
 3 samples. The pattern observed with epigeic springtail species, in particular *Isotomurus gr. palustris*,
 4 which displayed negative relationships with the abundance of macroinvertebrates, whether
 5 saprophagous, predatory or phytophagous, is probably explained more by opposite trends according to
 6 agricultural intensity than by negative interactions. Published studies where microarthropods and
 7 macroinvertebrates were sampled together rather indicate positive interactions between Collembola
 8 (and their mesostigmatid mite predators) and earthworms (Marinissen and Bok, 1988; Hamilton and
 9 Sillman, 1989; Loranger et al., 1998, Maraun et al., 1999), explained by direct favorable trophic
 10 influences (Salmon, 2004; Monroy et al., 2011; Gutiérrez-López et al., 2011) and ecosystem
 11 engineering (Marinissen and Bok, 1988; Hamilton and Sillman, 1989; Maraun et al., 1999;
 12 Eisenhauer, 2010). In the present study we did not find such a positive relationship but, as mentioned
 13 above, only within-site comparisons should be acceptable in this context.

14

15 *4.3. Groups which did not respond to agricultural intensity*

16 Endogeic earthworms did not respond to agricultural intensity while anecic earthworms did:
 17 they decreased in density, but not significantly and not to the same extent as anecic worms. This can be
 18 explained by the higher sensitivity of anecic earthworms to conventional cropping systems (Lamandé
 19 et al., 2003; Krogh et al., 2007; Pelosi et al., 2009), due to differential impact on this ecological
 20 category of agricultural traffic (Pižl, 1992), ploughing (Edwards and Lofty, 1975; Wyss and
 21 Glasstetter, 1992) and pesticide use (Wright, 1977), although some studies did not conclude to any
 22 detrimental effect of deep tillage on anecics in maize crops (Debeljak et al., 2007). This result
 23 contradicts common tenets about life-history strategies in lumbricid worms (Satchell, 1980), since K-
 24 selected endogeic worms seem to be better adapted to disturbance than r-selected anecic worms.

25 The case of bacterivorous nematodes (in particular the c-p-1 r-selected guild) is less easy to
 26 explain, because they should be directly affected by the dramatic decrease in microbial biomass which

1 was observed along the studied gradient of agricultural intensification (Freckman, 1988). However, we
2 did not register any correlation between the abundance of bacterivorous nematodes and any of the
3 studied microbial parameters, nor with macrofaunal parameters. A weaker response of bacterivorous
4 nematodes compared to bigger-sized saprophages has been also reported by Postma–Blaauw et al.
5 (2010, 2012).

6 The Humus Index (Ponge et al., 2002; Ponge and Chevalier, 2006) can be ruled out as a means
7 to assess the impact of agricultural intensification on soil biota, given its too high sensitivity to
8 geology. In particular, the dominance of sand-size fractions may impede to adequately record fine
9 spongy structures created by enchytraeid worms when compared to compact soils deprived of biogenic
10 structures (Topoliantz et al., 2000).

11

12 *4.4. Responses of soil biota to slurry application*

13 Slurry application elicited a positive response of some biota, in particular endogeic
14 earthworms, bacterivorous nematodes and macrofauna relying on SOM, i.e. saprophages, supporting
15 our second hypothesis. Above all, the richness of chicken and pig slurry in easily degraded or directly
16 assimilated nitrogenous and carbonaceous compounds must be thought responsible for the observed
17 effects (Jensen et al., 2000). Endogeic earthworms are favored by easily degradable and nitrogen-rich
18 organic matter (Zajonc, 1975; Tiunov and Scheu, 2004; Van Eekeren et al., 2009), while bacterivorous
19 nematodes are favored by labile compounds in slurry (De Goede et al., 2003; Van Eekeren et al.,
20 2009). The case of other macrofauna (saprophagous or predatory) is less easy to explain, although they
21 may benefit from the presence of coarse organic matter in applied slurries (Sasada et al., 2011).
22 Other indirect effects can be suspected, too, such as the ingestion of nematodes (Hyvönen et al., 1994;
23 Monroy et al., 2008).

24

25 *4.5. The composite biotic indicator*

1 Direct and indirect effects of land use and agricultural practices on soil biota were synthesized
2 in a composite biotic indicator, which was used to compare farming systems of French Brittany by
3 aggregate rank scores. We showed that the intensity of agriculture, from permanent meadows to
4 permanent crop fields, passing by rotation fields in intermediary position, exerted unfavorable
5 effectson soil biota, and this for a variety of reasons, which all tend to impoverish and simplify soil
6 trophic networks: decrease of plant cover, decrease in microbial biomass and SOM content, increase in
7 intensity and frequency of mechanical disturbance, and pesticide use (Duxbury et al., 1989).

8 The observed similarity in composite rank scores between permanent land uses and those
9 included in rotationsis worth of notice. It seems to indicate that in the studied region soil communities
10 (*i*) adapt rapidly to changes in land use in agricultural land, at least at the level of broad taxonomic
11 groups, and (*ii*) are not favored by rotation itself. This contradicts, at least at first sight, studies
12 showing that soil animal communities lag behind rapid shifts in plant communities observed after land
13 use change from forest to agricultural land, and the reverse (Kardol et al., 2005; Ponge et al., 2006).
14 This might indicate that (*i*) meadows and crop fields do not differ to a so great extent, crop fields
15 being, at least from the point of view of soil biota, nothing else than an impoverished variant of
16 meadows (Postma–Blaauw et al., 2012), and (*ii*)soil biodiversity of agroecosystemsmay recover
17 rapidly once main stress factors (lack of plant cover and soil organic matter, pesticide use, mechanical
18 disturbance) are definitively or temporarily alleviated (Postma–Blaauw et al., 2010). However, it must
19 be noticed that Postma–Blaauw et al. (2012) showed that rapid recovery of invertebrate communities
20 after conversion of cropland to grassland did not occur in predatory mites and enchytraeids.

21 We must now question the generality of the proposed composite biotic indicator of agricultural
22 soil quality. First, it is based on a regional study, thus over a restricted array of climate, geologic and
23 historical conditions, such as that found in French Brittany. Second, the proposed selection of faunal
24 and microbial variables (Table 1) may differ according to the purpose of biotic indication: clearly it
25 does not apply to the assessment of soil health in industrial, urban or forest soils. Admittedly, it should
26 be tested in other regions of prevailing agriculture, since it applies only to agroecosystems.

1 Other soil fauna indices of soil quality, based either on the presence/absence (Parisi et al.,
2 2005) or on the abundance of species (Cortet et al., 2002b; Ruiz et al., 2011; Yan et al., 2012) have
3 been proposed and were tested on various agricultural sites. Both Parisi' and Yan' indices weight the
4 species by their functional traits, as does the Maturity Index for nematodes. However, all these indices
5 are based on complete identification at species level of a large array of taxonomic groups, a time-
6 consuming step, while our composite biotic index did not necessitate so a fine resolution, most
7 indicator groups listed in Table 1 being easy to record without resorting to specialists. Other indices
8 are similarly based on wide taxonomic groups, easy to identify, but they include also variables
9 describing the physical and chemical state of the soil (roughly speaking, soil fertility). The best
10 example is the GISQ multifactorial indicator of soil quality proposed by Velasquez et al. (2007), based
11 on a set of 5 sub-indicators further combined in a single general indicator of soil quality. One of the
12 sub-indicators is devoted to macrofauna and could be used independently of the others. Another biotic
13 indicator, BISK, reaching a level of model complexity and universality similar to GISQ, has been
14 proposed within the Netherlands Monitoring Network (Rutgers et al., 2009). Here too, soil
15 characteristics are incorporated into the composite indicator, in particular heavy metals and pesticides,
16 which evidently have a prominent importance in the impact of agricultural practices on soil organisms.
17 However we suspect that incorporating in BISK some soil characteristics which are directly under the
18 influence of human practices will increase artificially the chance to find statistically significant
19 impacts of human activities on soil quality. This is the reason why we suggest to consider only biota
20 (and preferably a limited array of easily identifiable organisms or bulk biological variables such as
21 microbial biomass) in a composite indicator of soil 'health' and to detect community changes after
22 discarding the influence of factors not directly influenced by human activities. Given the
23 abovementioned limits of our composite indicator, we consider it as a mean to synthesize our results in
24 a regional context. This does not preclude any endeavor towards building a universal index of soil
25 quality which includes soil biota, a wish shared since a long-time by the community of soil biologists.

26

27 **Acknowledgements**

1 Many people, owners, farmers, students, and technicians, were involved in the selection and disposal
2 of sites, of sampling material, sampling process, transport and identification. They are collectively
3 acknowledged. Without their help, nothing would have been made possible. The authors acknowledge
4 the “Agence de l’Environnement et de la Maîtrise de l’Énergie” (ADEME) for incitation and financial
5 support, and Laurence Rougé for conception of the RMQS-Biodiv database and fruitful interaction
6 with the participants.

7

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Table 1. Mean values of selected indicator variables according to land use (meadows and crop fields, permanent or in rotation) and slurry application (in permanent crop fields), and bulk comparisons by rank scores (see text). Confidence levels are indicated for Kruskal-Wallis test (for land use) and Mann-Whitney tests (for slurry application): NS = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; **** = $P < 0.0001$. Uppercase letters indicate significant differences among means.

	Permanent meadow	Meadow in rotation	Crop in rotation	Permanent crop		Slurry	No slurry	
Anecic earthworms (ind.m ⁻²)	64.5±13.5 ^a	58.4±12.2 ^{ab}	22.0±6.6 ^b	28.3±4.4 ^b	***	41.2±8.7	25.3±4.6	NS
Endogeic earthworms (ind.m ⁻²)	229±58	211±28	134±25	167±23	NS	230±42 ^a	124±16 ^b	**
Total macroarthropods and mollusks (ind.m ⁻²)	349±51 ^a	312±66 ^{ab}	130±20 ^b	173±22 ^b	****	232±45 ^a	137±19 ^b	*
Saprophagous macroarthropods and mollusks (ind.m ⁻²)	69.6±22.7 ^a	67.4±17.4 ^{ab}	23.8±7.6 ^b	24.6±6.7 ^b	***	40.5±13.6 ^a	15.7±3.5 ^b	*
Epigeic springtails (ind.m ⁻²)	810±240 ^b	3520±1130 ^{ab}	5540±2370 ^a	4100±890 ^a	*	2480±800	5150±1340	NS
Phytoparasitic nematodes (ind.g ⁻¹ dry soil)	1560±240 ^a	1050±200 ^a	620±90 ^{ab}	490±60 ^b	***	470±90	500±80	NS
Bacterivorous nematodes (ind.g ⁻¹ dry soil)	574±88	621±82	687±155	588±52	NS	669±70 ^a	578±69 ^b	*
Microbial biomass (mg C.kg ⁻¹)	553±45 ^a	385±27 ^{ab}	269±29 ^{bc}	243±11 ^c	****	369±75	460±72	NS
Rank score	1.8	2.1	3.0	3.1		1.4	1.6	

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Table 2. Covariation between the 5 subsets of the biological database. Pearson correlation coefficients between first canonical factors of partial RDAs (second canonical factor for microarthropods). All coefficients significant at $P < 0.0001$.

	Earthworms	Macrofauna	Microarthropods	Nematodes
Macrofauna	0.58			
Microarthropods	-0.76	-0.41		
Nematodes	0.83	0.71	-0.73	
1 Microbes	0.86	0.83	-0.63	0.83

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Table 3. Covariation between 3 subsets of the biological database. Pearson correlation coefficients between second canonical factors of partial RDAs. Significance levels: *, ***, **** = $P < 0.05$, 0.001 , 0.0001 , respectively.

	Earthworms	Macrofauna
1	Macrofauna 0.21*	
2	Nematodes 0.37***	0.47****

1 **Figure Captions**

2 **Fig. 1.** Partial redundancy analysis (partial RDA), with earthworm data (listed in Appendix 2) as
3 explained variables and environmental data (listed in Appendix 1) as explanatory variables:
4 year, geology and latitude/longitude effects were excluded. Earthworm community variables
5 (species density variables not shown) and agricultural practices are projected in the plane of
6 the first two canonical factors.

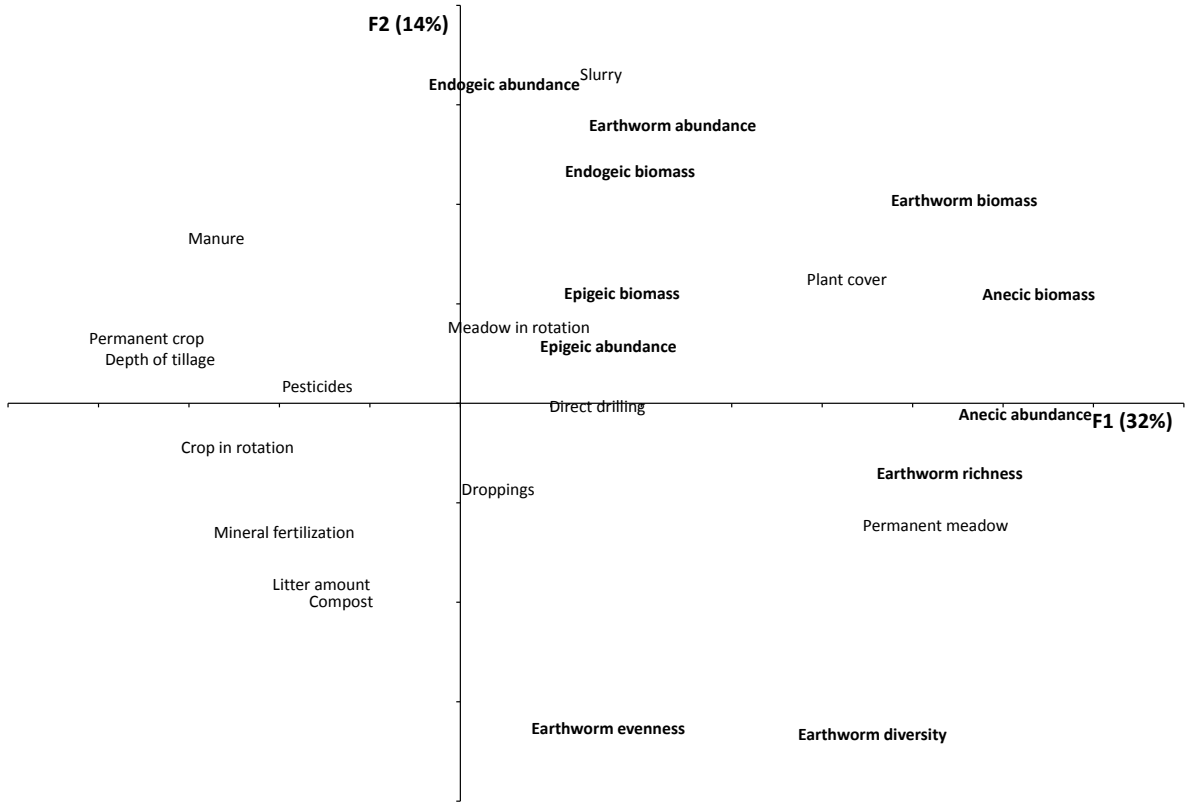
7 **Fig. 2.**As Fig. 1 for macrofauna (macroarthropods and mollusks).

8 **Fig. 3.**As Fig. 1 for microarthropods.

9 **Fig. 4.**As Fig. 1 for nematodes.

10 **Fig. 5.**As Fig. 1 for microbial data.

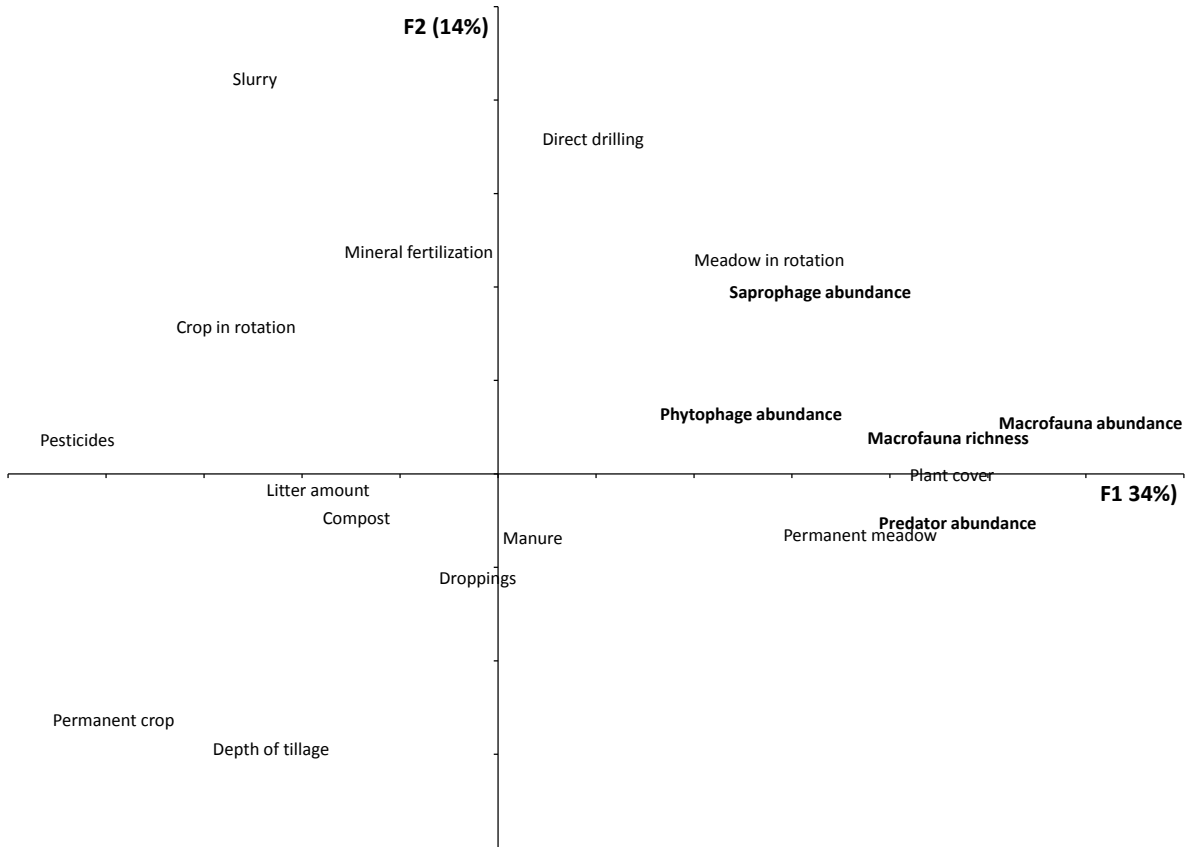
11



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2 Fig. 1

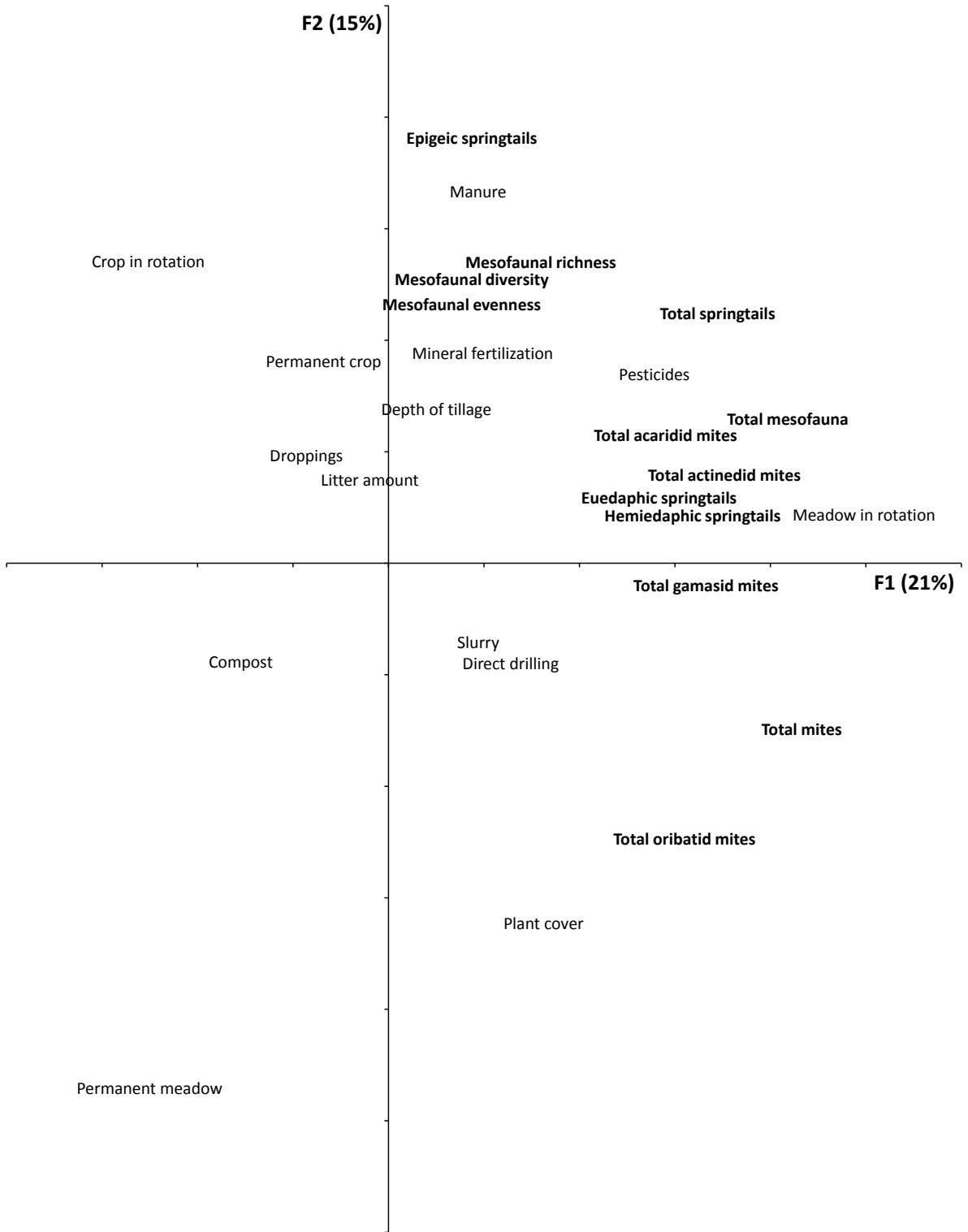
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2 Fig. 2

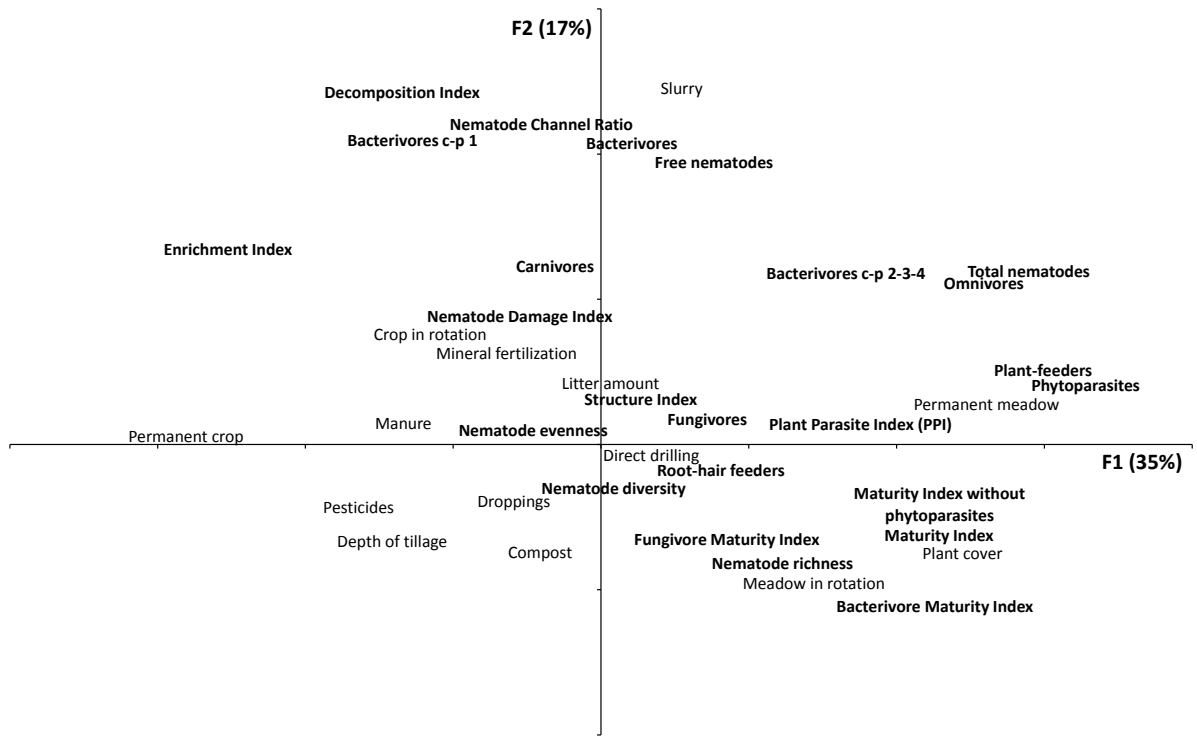
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2 Fig. 3

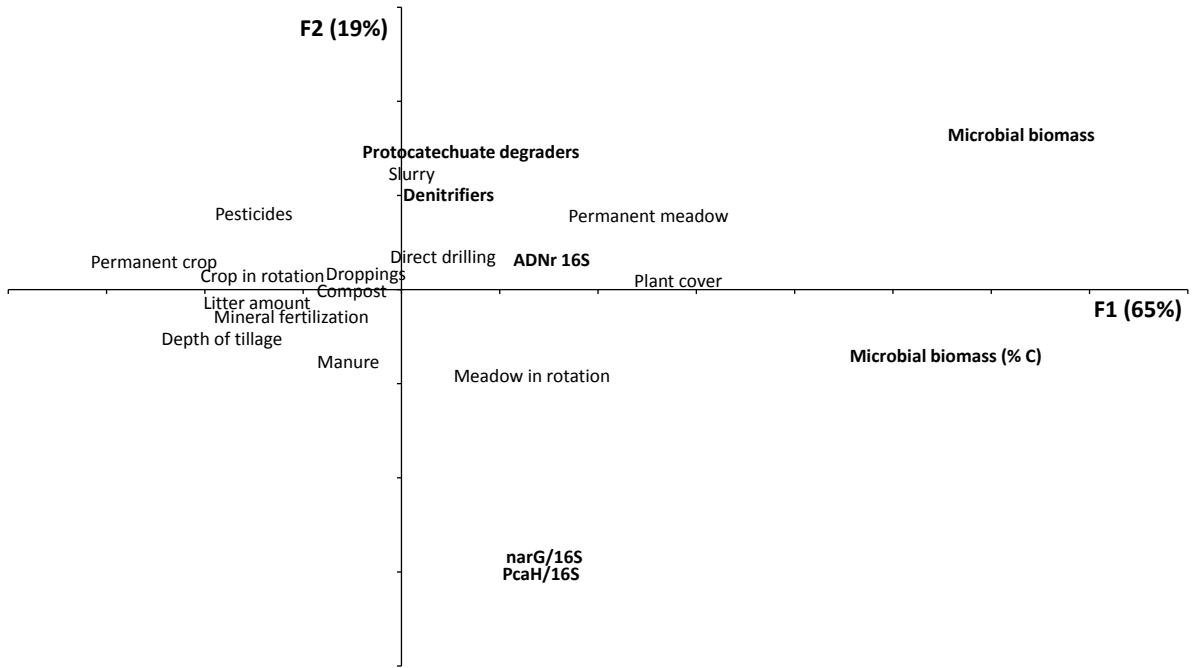
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2 Fig. 4

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2 Fig. 5

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Appendix 2. List of biological variables used in Redundancy Analysis. For animal species, abundances per site were used in the analysis.

Earthworms	Macrofauna other than earthworms	Microarthropods	Nematodes	Microbes	Humus Index
Dendrobaena mammalis	Coleoptera Elateridae (adults)	Arhopalites sp.	Achromodoridae	Microbial biomass (mg C.Kg ⁻¹)	Mean Humus Index
Dendrobaena octaedra	Coleoptera Elateridae (larvae)	Bourletella hortensis	Alaimidae	Microbial biomass (% total C)	Surface Humus Index
Dendrobaena pygmaea cognettii	Coleoptera Staphylinidae (adults)	Brachystomella parvula	Anatonchidae	ADN ¹⁶ S	
Dendrobaena rubida rubida	Coleoptera Curculionidae (adults)	Ceratophysella denticulata	Anguinidae	Denitrifiers (narG)	
Eisenia eiseni	Coleoptera Curculionidae (larvae)	Cryptopygus bipunctatus	Aphelenchidae	narG/16S	
Eiseniella tetraedra	Coleoptera Coccinellidae (adults)	Cryptopygus thermophilus	Aphelenchoididae	Protocatechuate degraders (PcaH)	
Lumbricus castaneus	Coleoptera Chrysomelidae (adults)	Desoria sp.	Aporcainidae	PcaH/16S	
Lumbricus centralis	Coleoptera Cantharidae (larvae)	Entomobrya sp.	Bastianidae		
Lumbricus cystivus	Coleoptera Carabidae (adults)	Folsomia candida	Belonididae		
Lumbricus friendi	Coleoptera Carabidae (larvae)	Folsomia fimetaria	Belonolaiminae		
Lumbricus rubellus castanoides	Coleoptera Scarabaeidae (adults)	Folsomia quadriculata	Cephalobidae		
Lumbricus rubellus rubellus	Coleoptera Scarabaeoidea (larvae)	Folsomia sexoculata	Chromadoridae		
Lumbricus terrestris	Coleoptera miscellaneous (adults)	Folsomia sp.	Criconematidae		
Nicodrilus caliginosus caliginosus trapezoides	Coleoptera miscellaneous (nymphs)	Folsomia thalassophila	Desmodoridae		
Nicodrilus caliginosus caliginosus typica	Coleoptera miscellaneous (larvae)	Friesea mirabilis	Dipterophoridae		
Nicodrilus caliginosus meridionalis	Hymenoptera Formicidae (adults)	Heteromurus major	Diplogasteridae		
Nicodrilus caliginosus tuberculata	Hymenoptera miscellaneous (nymphs)	Heteromurus nitidus	Diplopetidae		
Nicodrilus giardi	Hemiptera Aphidoidea (adults)	Hypogastrura sp.	Discolaimidae		
Nicodrilus longus longus	Hemiptera Heteroptera (adults)	Isotoma sp.	Dorylaimoidea		
Nicodrilus nocturnus	Hemiptera miscellaneus (adults)	Isotomodes productus	Heteroderidae		
Octolasion cyaneum	Dermoptera	Isotomodes trisetosus	Hoplolaimidae		
Earthworm abundance	Lepidoptera (larvae)	Isotomiella minor	Leptolaimidae		
Earthworm biomass	Trichoptera (larvae)	Isotomurus antennalis	Leptonchidae		
Anecic abundance	Diptera Tipulidae (larvae)	Isotomurus gr. palustris	Longidoridae		
Endogeic abundance	Diptera miscellaneous (larvae)	Lepidocyrtus cyaneus	Meloidogynae		
Epigeic abundance	Diptera (pupae)	Lepidocyrtus lanuginosus	Monhysteridae		
Anecic biomass	Orthoptera (adults)	Lepidocyrtus lignorum	Mononchidae		
Endogeic biomass	Diplopoda lulidae	Megalothorax minimus	Neodiplogasteridae / Monhysteridae		
Epigeic biomass	Diplopoda Polydesmidae	Mesaphorura sp.	Nordidae		
Earthworm taxonomic richness	Diplopoda Glomeridae	Mesaphorura florum	Nyglolaimidae		
Earthworm diversity	Diplopoda miscellaneus	Mesaphorura hylophila	Odontolaimidae		
Earthworm evenness	Chilopoda Lithobiomorpha	Mesaphorura italica	Odontopharyngidae		
	Chilopoda Geophilomorpha	Mesaphorura krausbaueri	Ostellidae		
	Chilopoda Scolopendromorpha	Mesaphorura macrochaeta	Panagrolaimidae		
	Araneae Thomisidae	Mesaphorura sylvatica	Paratylenchidae		
	Araneae miscellaneous	Micranurida sensillata	Plectidae		
	Opiliones	Monobella grasselli	Pratylenchidae		
	Pseudoscorpionida	Mucrosomia garretti	Prismatolaimidae		
	Isopoda	Mucrosomia garretti	Quadianematidae		
	Gastropoda Arionidae	Orchesella sp.	Rhabditidae		
	Gastropoda Agriolimacidae	Paratullbergia callipygos	Rhabdolaimidae		
	Gastropoda miscellaneous (slugs)	Parisotoma notabilis	Steinernematidae		
	Gastropoda miscellaneous (snails)	Proisotoma admaritima	Telotylenchidae		
	Macrofauna abundance	Proisotoma minima	Teratocephalidae		
	Macrofauna richness	Proisotoma minuta	Thomenematidae		
	Phytophage abundance	Protaphorura armata	Trichodoridae		
	Saprophage abundance	Protaphorura subuliginata	Tripylidae		
	Predator abundance	Pseudosinella alba	Tylenchidae		
		Pseudosinella immaculata	Maturity Index (MI)		
		Sminthurides malmgreni	Maturity Index without phytoparasites		
		Sminthurides parvulus	Bacterivore Maturity Index (BaMI)		
		Sminthurides sp.	Fungivore Maturity Index (FuMI)		
		Sminthurinus aureus	Nematode Channel Ratio (NCR)		
		Sminthurinus elegans	Plant Parasite Index (PPI)		
		Sminthurinus niger	Enrichment Index (EI)		
		Sminthurus viridis	Structure Index (SI)		
		Sphaeridia pumilis	Nematode Damage Index (IP)		
		Stenaphorura denisi	Decomposition Index (CI)		
		Stenaphorura quadrispina	Bacterivores c-p 1 (Ba1)		
		Xenyllodes armatus	Bacterivores c-p 2-3-4 (Ba234)		
		Total mesofauna	Bacterivores		
		Total springtails	Fungivores		
		Epigeic springtails	Omnivores		
		Hemiedaphic springtails	Carnivores		
		Euedaphic springtails	Plant-feeders		
		Total mites	Root-hair feeders		
		Total oribatid mites	Total nematodes		
		Total gamasid mites	Free nematodes		
		Total actinedid mites	Phytoparasites		
		Total acaridid mites	Nematode taxonomic richness		
		Mesofaunal taxonomic richness	Nematode diversity		
		Mesofaunal diversity	Nematode evenness		
		Mesofaunal evenness			

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Appendix 3. Mean values of physico-chemical variables(*) according to land use (meadows and crop fields, permanent or in rotation) and slurry application (in permanent crop fields). Confidence levels are indicated for Kruskal-Wallis test (for land use) and Mann-Whitney tests (for slurry application): NS = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; **** = $P < 0.0001$. Uppercase letters indicate significant differences among means.

	Permanent meadow	Meadow in rotation	Crop in rotation	Permanent crop		Slurry	No slurry	
	n = 23	n = 23	n = 11	n = 42		n = 15	n = 27	
Sand (‰)	314±28	314±28	340±45	292±24	NS	208±33 ^b	338±30 ^a	***
Silt (‰)	516±27	504±26	478±39	525±21	NS	561±33	505±27	NS
Clay (‰)	169±5	182±9	182±18	183±10	NS	231±21 ^a	157±8 ^b	****
Organic carbon (‰)	30.4±2.0 ^a	25.5±2.0 ^{ab}	30.2±2.5 ^a	22.0±1.6 ^b	***	21.7±1.9	22.3±2.2	NS
Total nitrogen (‰)	2.77±0.15 ^a	2.38±0.18 ^{ab}	2.71±0.20 ^{ab}	2.10±0.12 ^b	**	2.27±0.17	2.00±0.16	NS
C/N	10.9±0.3	10.7±0.2	11.2±0.4	10.3±0.2	NS	9.5±0.2 ^b	10.7±0.3 ^a	**
Water pH	5.65±0.07 ^b	6.13±0.09 ^a	5.93±0.13 ^{ab}	6.01±0.11 ^{ab}	**	5.98±0.10	6.02±0.17	NS
Cation exchange capacity (cmol/kg)	7.19±0.52	7.94±0.44	8.55±0.84	7.04±0.34	NS	7.29±0.39	6.90±0.49	NS
Olsen P (‰)	0.084±0.011 ^b	0.097±0.013 ^{ab}	0.118±0.016 ^{ab}	0.132±0.009 ^a	**	0.121±0.013	0.138±0.012	NS
Plant cover (%)	96.7±1.4 ^a	93.0±1.7 ^a	43.8±8.6 ^b	48.1±4.8 ^b	****	50.3±8.1	46.9±6.0	NS

(*) Data provided by Chambre d'Agriculture du Morbihan (Sylvie Tico), Chambre d'Agriculture des Côtes d'Armor (Jean-Luc Giteau), Chambre d'Agriculture du Finistère (Daniel Hanocq), Chambre d'Agriculture d'Ille-et-Vilaine (Cyril Guérillot), INRA-Orléans, Unité Infosol (Claudy Jolivet & Line Boulonne)