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

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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 RMOS-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 thatstudied 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.

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 thatsoil animals and microbes are also involved in signaling processes which 10 contribute to the integrity of agroecosystems and which sustaincrop production (Blouin et al., 2005; 11 Sanon et al., 2009; Endlweber et al., 2011).

12 Soil biotic communitieswere 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 l'Environnement et de la Maîtrise de l'Énergie") urged scientists to develop tools for monitoring soil 16 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 networkwasselected 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).

Earthworms, macroinvertebrates other than earthworms, microarthropods, nematodes, and microbial communities were selected as a set of indicator groups proposed at European level (Bispo et 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 indiceshave 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).

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

Some agricultural practices aim at restoring soil fertility, compensating for the exportation of nutrients through herbage and food crop production. Among fertilizing practices, those increasing soil organic matter content, i.e. the application of manure, compost and organic-rich waste products of animal husbandry such as chicken droppings or pig slurry, are known to improve soil quality and crop yield but also lead touncontrolled N losses (Cox et al., 2001; Antil et al., 2009; Chirinda et al., 2010). Slurry application may thus compensate for the negative effects of agricultural intensity, in particular
 for those species relying on soil organic matter (SOM) for food requirements, i.e. saprophages: this is
 our second hypothesis.

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

8

9 2. Materials and methods

10 2.1. Study sites

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

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

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

1	• Permanent meadows: no ploughing/tillage or only occasional (when sawn), 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.

13 2.2. Sampling procedure

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

Sampling plots for soil biota were chosen as near as possible from those previously used for
soil description and soil physical-chemical analyses (Arrouays et al., 2002), i.e. 5 m northward.
Occasional shifts to another direction (west, south, or east) were necessary in cases of unexpected
impediment. Sampling plot was a 34 x 3 m stretch of land, homogeneous in plant cover and soil
features. This zone was subdivided into elementary sub-plots 1 x 3 m each, identified by stakes of
varying color according to soil biota groups, as already described in more detail by Cluzeau et al.
(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 m^2). Earthworms expelled to the surface by the 5 irritant solution were collected by hand then preserved in 4% formalin dilution. After completion of earthworm extraction, a 0.25 x 0.25 x 0.25 soil block was dug up at the center of each quadrat then 6 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 soils according to ISO 23611-5 (ISO, 2011). Formalin (0.2% dilution) was applied every 10 min on a 16 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.

Sampling and extraction of microarthropods (springtails, mites) were performed according to
ISO 23611-2 (ISO, 2006). Microarthropods were sampled in triplicate with a soil corer, especially
designed for the RMQS-BioDiv program, which was forced into the ground. At the inside of the corer
three 6 cm-diameter PMMA ('Plexiglas') plastic cylinders allowed to separate three depth levels, 0-5
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), functional (life forms: euedaphic, hemiedaphic, epigeic) and demographic level (total abundance of 6 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

Decomposition or Channel Index (DI), measuring environmental stability, resource availability and
 bacterial activity, respectively (Ferris et al., 2001), and Nematode Damage Index (IP), measuring the
 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 (crumby 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

Data were analyzed separately for each group by Redundancy Analysis (RDA), a multivariate
regression method, using biotic variables (Appendix 2) as explained variables and 'environmental'
variables (land use, practices, geology, year, and geographic position) as explanatory variables
(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).

Biological variables responding the best to agricultural practices were used to build a composite indicator, which allowed scoring land uses and practices of the studied region according to 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*

Permutation tests showed that earthworm communities were significantly affected by land use and agricultural practices upon discarding the effects of geology, year and latitude/longitude (Pseudo-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 $crops \rightarrow crops$ in rotation \rightarrow meadows in rotation \rightarrow permanent meadows. Plant cover increased, 5 while depth of tillage, fertilization (whether mineral or organic) and pesticide use decreased along this gradient of decreasing intensity of agricultural use. The second canonical factor (14% of explained 6 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.

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

21

22 *3.2. Macroinvertebrates other than earthworms*

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

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

Like anecic earthworms, densities of other macroinvertebrates declined in crops, whether permanent or in rotation, compared with permanent meadows (Table 1). Although not dominant in numbers among macroinvertebrates, saprophages shared thisgeneral trend. Total densities of macrofauna of crops (permanent and in rotation) increased in the presence of slurry, but this increase 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 the positive side, i.e. maximizing microarthropod densities) being opposed to permanent meadows and 26

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 according to plant cover, abundance of oribatid mites being associated with increased plant cover on 6 the negative side of F2. Slurry application did not exhibit any clear trend in microarthropod 7 8 community parameters.

With the exception of *Lepidocyrtus lignorum* and *Sphaeridia pumilis*, all epigeic springtail
species followed the general trend displayed by F2, i.e. they increased in density with intensification
of agriculture. Epigeic springtails were five times more abundant in permanent crops than in
permanent meadows (Table 1), while oribatid mites displayed an opposite (although not significant)
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 categorydid not respond to land use. Land uses were not discriminated when r-selected (c-p-1) and K-selected (c-p-2-3-4) groups of bacterivorous nematodes were analyzed 6 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 and agricultural practices upon discarding the effects of geology, year and latitude/longitude (Pseudo-12 F = 0.36, P < 0.01). The first canonical factor F1 (65% of the explained variance) corresponded to a 13 gradient of increasing microbial biomass (whether expressed per unit soil or carbon weight) according 14 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

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

The second canonical factors of partial RDAs corresponded to slurry application for earthworms, macrofauna other than earthworms and nematodes. These three factors were positively correlated (Table 3), at a higher level of significance between nematodes and earthworms or macrofauna than between earthworms and macrofauna: endogeic earthworms, saprophagous macrofauna and bacterivorous nematodes reacted positively and in a coordinated manner to slurry 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, endogeic abundance was positively correlated with the abundance of phytophages ($r_s = 0.37$; P < 15 0.001). No correlation was found between endogeic abundance and microarthropod, nematode or 16 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 abundance of the epigeic springtail *Isotomurus* gr. *palustris* ($r_s = -0.38$; P < 0.001). In the nematode 24 25 community the abundance of macrofauna was negatively correlated with the Decomposition Index (CI) ($r_s = -0.35$; P < 0.01). The abundance of macrofauna other than earthworms was positively 26

2

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

3 The abundance of saprophagous macrofauna other than earthworms was positively correlated with the abundance and biomass of epigeic earthworms ($r_s = 0.37$; P < 0.01in both cases). Within the 4 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 biomass, either calculated per unit soil mass or per unit carbon ($r_s = 0.35$ and 0.37, respectively; P < 15 0.01 and 0.001, respectively), and with the abundance of denitrifiers (narG) ($r_s = 0.34$; P < 0.01). 16 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 < 0.001

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. palustrisand 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.

The abundance of bacterivorous nematodes was not correlated with any parameters of the macrofauna community (earthworms included). In the microarthropod community it was positively correlated with the abundance of gamasid mites, a predatory group ($r_s = 0.42$; P < 0.001), and that of *Isotomiella minor*, an endogeic springtail ($r_s = 0.35$; P < 0.01). Within the nematode community, after discarding trivial results, the abundance of bacterivorous nematodes was positively correlated with the Nematode Channel Ratio (NCR) and the Decomposition Index (CI) ($r_s = 0.42$ and 0.39, respectively; P < 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 macrofauna, whether total or restricted to saprophages ($r_s = 0.41$ and 0.35, respectively; P < 0.001 and 23 24 < 0.01, respectively). In the microarthropod community, it was negatively correlated with the abundance of the epigeic springtail *Isotomurus* gr. *palustris* ($r_s = -0.39$; P < 0.001) and positively with 25 that of the epigeic springtail Sphaeridia pumilis ($r_s = 0.41$; P < 0.001). In the nematode community, 26 27 microbial biomass per unit soil weight was positively correlated with total nematode abundance and

1taxonomic richness ($r_s = 0.37$ and 0.38, respectively; P < 0.01 and < 0.001, respectively), with the</th>2abundance of phytophagous and omnivorous nematodes ($r_s = 0.39$ and 0.43, respectively; P < 0.001 in</td>3both cases), with the Maturity Index (MI), the Maturity Index without phytoparasites and the4Bacterivore Maturity Index (BaMI) ($r_s = 0.45$, 0.46 and 0.41, respectively; P < 0.0001, < 0.0001 and</td>50.001, respectively) and was negatively correlated with the Enrichment Index (EI) ($r_s = -0.38$; P <</td>60.001).

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 8 biotic groups: anecic earthworms, endogeic earthworms, macrofauna other than earthworms 10 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.

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

1 **4. Discussion**

2

4.1. Groups which responded negatively to agricultural intensity

We showed that a variety of animal and microbial groups were negatively affected by the intensity of agriculture, from permanent meadows to permanent crops, while meadows and crops in 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 poolsto 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 biomassand 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 saprophagousor 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 the Netherlands by Postma-Blaauw et al. (2010, 2012), who showed that bigger-sized animals were 6 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 explain the observed negative response of soil biota to agricultural intensity (Ingham et al., 1985; 15 Alphei et al., 1996; Bonkowski et al., 2000), although we did not provide data about it, except 16 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 reportedby 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.

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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 underintensive agriculture (supported by our results, see Fig. 2), a reason invoked 11 to explain the rapid recovery of epigeic springtail populationsafter 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.

The increase of mesofaunal richness, diversity and evenness, observed along our gradient of agricultural intensity, contrasts with the decrease of species richness observed in macrofauna. This might indicate either opposite trends in microarthropods (to the exception of oribatid mites, see Fig. 3) and macroinvertebrates in their response to agricultural intensity, or negative interactions between 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 agricultural intensity than by negative interactions. Published studies where microarthropods and 6 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; Guttiérrez-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 impactson 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

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

Direct and indirect effects of land use and agricultural practices on soil biota were synthesized in a composite biotic indicator, which was used to compare farming systems of French Brittany by aggregate rank scores. We showed that the intensity of agriculture, from permanent meadows to permanent crop fields, passing by rotation fields in intermediary position, exerted unfavorable effectson soil biota, and this for a variety of reasons, which all tend to impoverish and simplify soil trophic networks: decrease of plant cover, decrease in microbial biomass and SOM content, increase in 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 meadows (Postma-Blaauw et al., 2012), and (ii)soil biodiversity of agroecosystemsmay recover 16 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.

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

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

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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. Upperscript letters indicate significant differences among means.

	Permanent meadow	Meadow in rotation	Crop in rotation	Permanent crop	1	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 macroacroarthropods 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	

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

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.

Table 3. Covariation between 3 subsets ofthe biological database. Pearson correlationcoefficients between second canonicalfactors of partial RDAs. Significance levels:*, ***, **** = P < 0.05, 0.001, 0.0001,respectively.

		Earthworms	Macrofauna
	Macrofauna	0.21*	
1	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.



2 Fig. 1



- 2 Fig. 2

F2 (15%) Epigeic springtails Manure Crop in rotation Mesofaunal richness Mesofaunal diversity Mesofaunal evenness **Total springtails** Mineral fertilization Permanent crop Pesticides Depth of tillage Total mesofauna Total acaridid mites Droppings **Total actinedid mites** Litter amount Euedaphic springtails Hemiedaphic springtails Meadow in rotation F1 (21%) Total gamasid mites Slurry Compost Direct drilling Total mites Total oribatid mites Plant cover Permanent meadow

2 Fig. 3

3



2 Fig. 4



2 Fig. 5

1	
T	

ppendix 1. Explanatory variables used in Redundancy Analysis.																								
Sites	312	362	363	364	365	366	368	418	420	421	422	423	424	425	428	430	431	432	480	481	482	483	484	485
Practices	<u>_</u>	~		0					<u>_</u>		0						^				^			0
Meadow in rotation	1	0	0	0	0	0	0 1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Crop in rotation	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Crop field	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1
Mineral fertilization	1	1	1	1	1	1	1 1	0	1	0	1	0	1	1	1	0	0	1	0	0	1	0	0	1
Manure Dislobishos share	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	1
Pigronicken slurry Comport	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Chicken droppings	õ	0	0	0	ő	0	0	0	0	0	ő	õ	õ	0	0	õ	ő	õ	0	0	0	õ	0	0
Direct drilling	0	0	0	ō	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Depth of tillage	2	2	2	2	0	0	0	0	2	0	1	2	0	1	1	2	2	0	1	2	1	2	0	1
Pesticides	1	0	1	1	0	1	0	0	0	0	1	0	1	1	1	0	1	0	1	0	1	1	1	1
Plant cover (%)	100.0	1.3	10.7	3.0	100.0	99.0	96.7	100.0	100.0	100.0	20.0	69.3	95.0	32.0	100.0	70.0	1.3	100.0	93.0	100.0	96.7	98.3	100.0	45.0
Litter	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Geology																								
Granite	1	1	0	0	1	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0
loam	0	0	1	1	1	1	1	n	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Micaschist	0	0	0	ò	o l	0	0	1	0	0	o l	0	0	0	0	0	1	1	0	0	0	0	0	0
Medium schist	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1
Gneiss	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Soft schist	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Schist-sandstone	0	0	0	0	0	0	0	n	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colluvial and alluvial deposits	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rocky terrace	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brown soil	1	1	0	0	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	0	0	1	0	1
Other soils	0	0	1	1	0	1	0	n	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Year	2006	2007	2007	2007	2006	2007	2007	2006	2007	2007	2007	2007	2007	2006	2006	2007	2007	2006	2007	2007	2006	2007	2006	2007
Position (Lambert coordinates)													10000			0.0000		070004				101005		107050
Longitude (m)	2442168	2427210	2428006	2428029	2428012	2427045	2427061	2410400	2412060	2412000	2411100	2411508	2411704	2412011	214983	24/022	262462	2/9381	2205010	2206140	2206050	134695	150913	2205000
	- /10100	- 1414 19	- 40000	-7410/32	-10010	- 161 - 143	- 160 1001	/10-00	- /12000	- ******	-711 (22	-711300	-711/24	et real 11	-712000	-716300	_110-03	- 10/24		-320140	-3300/30			-393330
Sites	488	489	490	491	493	494	496	539	540	541	542	543	544	545	546	547	548	550	552	553	554	597	598	599
Practices	·	0		0		^	0		<u>_</u>	0	0	0	0	0	0	0		0	0	0	^		0	0
r emahent meadow Meadow in rotation	0	0	1	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	1	1	0	0	0
Crop in rotation	1	ŏ	0	ŏ	ŏ	ĭ	ŏ	D	0	0	ŏ	ŏ	ò	ŏ	1	ò	ŏ	ŏ	0	0	0	1	ŏ	ŏ
Crop field	0	1	0	1	0	0	1	D	0	0	1	1	0	1	0	0	1	1	0	0	0	0	1	1
Mineral fertilization	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Manure	1	0	1	1	0	0	1	1	0	1	0	1	1	0	1	1	0	1	0	1	0	0	1	1
Pigronicken slurry	U	U	U O	1	U O	U	0	u D	0	U O	1	U O	1	1	U O	1	1	1	1	U O	U	1	U	0
CompOSt Chicken dranningr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Direct drilling	õ	ŏ	ŏ	ŏ	ŏ	ŏ	0	Ď	1	ŏ	1	ŏ	ŏ	ŏ	ŏ	ŏ	ŏ	ŏ	1	ŏ	ŏ	ŏ	ŏ	ŏ
Depth of tillage	1	2	2	2	0	2	2	0	0	1	o l	2	2	2	2	0	1	2	ò	1	1	1	1	1
Pesticides	1	1	1	1	0	0	0	1	0	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1
Plant cover (%)	30.3	40.0	100.0	18.3	91.7	18.3	43.3	75.0	90.0	100.0	31.0	50.0	90.7	90.0	31.7	90.0	46.7	76.7	100.0	95.7	95.0	8.3	100.0	50.0
Litter	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Granite	1	0	0	1	1	0	1 1	n	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Sand	0	0	0	0		0	0	0	0	0	ő	õ	õ	õ	0	õ	ő	õ	0	0	0	õ	0	0
Loam	0	0	0	0	0	0	i)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Micaschist	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Medium schist	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Soft schist	0	1	1	0	0	0	0	n	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0
Hard sandstone	0	ò	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Schist-sandstone	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Colluvial and alluvial deposits	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rocky terrace	0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brown leached soil	0	0	0	0	0	0	1 1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Other soils	0	0	1	0	0	0	0 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-
Year	2007	2007	2006	2006	2007	2007	2007	2007	2007	2007	2007	2007	2006	2007	2007	2006	2007	2007	0007	2006	0007		~	0
						2001	2007	2007	2007	2007	2007							2007	2007	2000	2007	2007	2007	2007
Position (Lambert coordinates)									2007	2007	1000		100070			0000.00		2007	2007	2000	2007	2007	2007	2007
Position (Lambert coordinates) Longitude (m)	214887	230981	246938	263038	295081	311011	342978	103054	118737	134749	150821	166134	182976	198894	214911	230840	247012	278985	311000	326967	2007 342788 2379902	2007 86947 2363983	2007 103085 2363462	2007 118666 2363930
Position (Lambert coordinates) Longitude (m) Latitude (m)	214887 2396007	230981 2396040	246938 2396057	263038 2395978	295081 2396026	311011 2396020	342978 2396020	103054 2379400	118737 2379430	134749 2380080	150821 2380018	166134 2380650	182976 2380055	198894 2380060	214911 2380188	230840 2379989	247012 2380018	278985 2379996	2007 311000 2379992	326967 2380045	2007 342788 2379902	2007 86947 2363983	2007 103085 2363462	2007 118666 2363920
Position (Lambert coordinates) Longitude (m) Latitude (m)	214887 2396007	230981 2396040	246938 2396057	263038 2395978	295081 2396026	311011 2396020	342978 2396020	103054 2379400	118737 2379430	134749 2380080	150821 2380018	166134 2380650	182976 2380055	198894 2380060	214911 2380188	230840 2379989	247012 2380018	278985 2379996	311000 2379992	326967 2380045	2007 342788 2379902	2007 86947 2363983	2007 103085 2363462	0 2007 118666 2363920
Position (Lambert coordinates) Longitude (m) Latitude (m) Sites	214887 2396007 601	230981 2396040 602	246938 2396057 604	263038 2395978 605	295081 2396026 606	311011 2396020 607	342978 2396020	103054 2379400 609	118737 2379430 610	134749 2380080 612	150821 2380018 656	166134 2380650 657	182976 2380055 658	198894 2380060 659	214911 2380188 660	230840 2379989 661	247012 2380018 662	278985 2379996 663	2007 311000 2379992 665	326967 2380045 666	2007 342788 2379902 667	2007 86947 2363983 668	2007 103085 2363462 669	0 2007 118666 2363920 670
Position (Lambert coordinates) Longitude (m) Latitude (m) Sites Practices Paractors	214887 2396007 601	230981 2396040 602	246938 2396057 604	263038 2395978 605	295081 2396026 606	311011 2396020 607	342978 2396020 : 608 :	103054 2379400 609	118737 2379430 610	134749 2380080 612	150821 2380018 656	166134 2380650 657	182976 2380055 658	198894 2380060 659	214911 2380188 660	230840 2379989 661	247012 2380018 662	278985 2379996 663	311000 2379992 665	326967 2380045 666	342788 2379902 667	2007 86947 2363983 668	2007 103085 2363462 669	0 2007 118666 2363920 670
Position (Lambert coordinates) Longitude (m) Latitude (m) Sites Practices Permanent meadow Meadow in rotation	214887 2396007 601 0	230981 2396040 602 1 0	246938 2396057 604 0	263038 2395978 605 0	295081 2396026 606 1 0	311011 2396020 607 0	342978 2396020 : 608 0	103054 2379400 609 1	118737 2379430 610 0	134749 2380080 612 0	150821 2380018 656 0	166134 2380650 657 0 0	182976 2380055 658 0	198894 2380060 659 0	214911 2380188 660 0	230840 2379989 661 1 0	247012 2380018 662 0	278985 2379996 663 0	2007 311000 2379992 665 0 0	326967 2380045 666 0	342788 2379902 667 0	2007 86947 2363983 668 1 0	2007 103085 2363462 669 0	0 2007 118666 2363920 670 0
Position (Lambert coordinates) Longitude (m) Latitude (m) Sites Practices Permanent meadow Meadow in rotation Copi in rotation	214887 2396007 601 0 0 0	230981 2396040 602 1 0 0	246938 2396057 604 0 0 0	263038 2395978 605 0 1 0	295081 2396026 606 1 0 0	311011 2396020 607 0 1 0	342978 2396020 608 0 0	103054 2379400 609 1 0	118737 2379430 610 0 0 0	134749 2380080 612 0 0 0	150821 2380018 656 0 1 0	166134 2380650 657 0 0 0	182976 2380055 658 0 0 1	198894 2380060 659 0 1 0	214911 2380188 660 0 0 1	230840 2379989 661 1 0 0	247012 2380018 662 0 0 0	278985 2379996 663 0 0 0	2007 311000 2379992 665 0 0 0	326967 2380045 666 0 1 0	342788 2379902 667 0 0 0	2007 86947 2363983 668 1 0 0	2007 103085 2363462 669 0 0 0	0 2007 118666 2363920 670 0 0 0
Position (Lambert coordinates) Longitude (m) Latitude (m) Sites Practices Permanent meadow Meadow in rotation Crop in rotation Crop field	214887 2396007 601 0 0 0 1	230981 2396040 602 1 0 0 0	246938 2396057 604 0 0 0 1	263038 2395978 605 0 1 0 0	295081 2396026 606 1 0 0 0	311011 2396020 607 0 1 0 0	342978 2396020 : 608 0 0 0 1	103054 2379400 609 1 0 0 0	118737 2379430 610 0 0 0 1	134749 2380080 612 0 0 0 1	150821 2380018 656 0 1 0 0	166134 2380650 657 0 0 0 1	182976 2380055 658 0 0 1 0	198894 2380060 659 0 1 0 0 0	214911 2380188 660 0 0 1 0	230840 2379989 661 1 0 0 0	247012 2380018 662 0 0 0 1	278985 2379996 663 0 0 0 1	2007 311000 2379992 665 0 0 0 0 1	326967 2380045 6665 0 1 0 0	342788 2379902 667 0 0 0 1	2007 86947 2363983 668 1 0 0 0	2007 103085 2363462 669 0 0 0 1	0 2007 118666 2363920 670 0 0 0 1
Position (Lambert coordinates) Longitude (m) Latitude (m) Sites Permanent meadow Meadow in rotation Crop in rotation Crop field Mineral fertilization	214887 2396007 601 0 0 0 1 1	230981 2396040 602 1 0 0 0 1	246938 2396057 604 0 0 0 1 1	263038 2396978 605 0 1 0 0 1	295081 2396026 606 1 0 0 0	311011 2396020 607 0 1 0 0 1	342978 2396020 : 608 0 0 0 1 1	103054 2379400 609 1 0 0 0	118737 2379430 610 0 0 0 1 1	134749 2380080 612 0 0 0 1 1	150821 2380018 656 0 1 0 0	166134 2380650 657 0 0 0 1 1	182976 2380055 658 0 0 1 0 1	198894 2380060 659 0 1 0 0 0	214911 2380188 660 0 0 1 0 1	230840 2379989 661 1 0 0 0 0	247012 2380018 662 0 0 0 1 0	278985 2379996 663 0 0 0 1 1	311000 2379992 665 0 0 0 1 1	326967 2380045 6666 0 1 0 0 1	342788 2379902 667 0 0 0 1 1	2007 86947 2363983 668 1 0 0 0 0	2007 103085 2363462 669 0 0 0 1	0 2007 118666 2363920 670 0 0 0 1 1
Position (Lambert coordinates) Longitus (m) Latitude (m) Sites Practices Practices Practices Practices Practices Practices Copi In datation Copi In datation Copi In datation Copi In datation Mineau I estimation Mineau I estimation	214887 2396007 601 0 0 0 1 1 1	230981 2396040 602 1 0 0 0 0 1 0	246938 2396057 604 0 0 0 1 1 1 0	263038 2395978 605 0 1 0 0 1 1	295081 2396026 606 1 0 0 0 1 0	311011 2396020 607 0 1 0 0 1 0 0	342978 2396020 608 0 0 1 1	103054 2379400 609 1 0 0 0 1	2007 118737 2379430 610 0 0 0 0 1 1 1 1	2007 134749 2380080 612 0 0 0 1 1 1 1	150821 2380018 656 0 1 0 0 1 1 1	166134 2380650 657 0 0 0 1 1 1 0	182976 2380055 658 0 0 1 0 1 1 0	198894 2380060 659 0 1 0 0 1 1 0 0	214911 2380188 660 0 0 1 1 0 1 1 2	230840 2379989 661 1 0 0 0 1 1 2	247012 2380018 662 0 0 0 1 0 1 0	278985 2379996 663 0 0 0 1 1 1 0	2007 311000 2379992 665 0 0 0 1 1 1 0	326967 2380045 666 0 1 0 0 1 0 0	342788 2379902 667 0 0 0 1 1 1	2007 206947 2363983 668 1 0 0 0 0 0 0 0 0 0	2007 103085 2363462 669 0 0 0 1 1 1 0	0 2007 118666 2363920 670 0 0 0 1 1 1 0
Position (Lambert coordinates) Longhula (m) Latitude (m) Sites Practices Perament meadow Meadow in rotation Ocep Ind Casion Ocep Ind Casion Meanow Meanow Interaction Pipcihicken starry Compost	214887 2396007 601 0 0 0 1 1 1 1 1 0 0	230981 2396040 602 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0	246938 2396057 604 0 0 0 1 1 1 0 0 0 0 0	263038 2395978 605 0 1 0 0 1 1 1 0 0	295081 2396026 606 1 0 0 0 1 0 1 0 0	311011 2396020 607 0 1 0 0 1 0 0 1 0 0 1 0 0	342978 2396020 608 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	103054 2379400 609 1 0 0 0 1 0 1 0 0 1 0 0	2007 118737 2379430 610 0 0 0 0 1 1 1 1 0 0	2007 134749 2380080 612 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	150821 2380018 656 0 1 0 0 1 1 1 0 0 0 0	166134 2380650 657 0 0 0 1 1 1 0 0 0	182976 2380055 658 0 0 1 0 1 1 1 0 0 0	198894 2380060 659 0 1 0 0 1 1 0 0 0 0	214911 2380188 660 0 0 1 1 0 1 1 0 0 0	230840 2379989 661 1 0 0 0 1 1 1 0 0 0	247012 2380018 662 0 0 0 0 1 0 1 0 0 0 0 0	278985 2379996 663 0 0 1 1 1 0 1 0	2007 311000 2379992 665 0 0 0 1 1 1 0 0 1 0 0	326967 2380045 666 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 342788 2379902 667 0 0 0 1 1 1 1 1 0 0 0	2007 86947 2363983 668 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 103085 2363462 669 0 0 0 0 1 1 1 0 1 0	0 2007 118666 2363920 670 0 0 0 1 1 1 0 1 0 0
Position (Lambert coordinates) Longitude (m) Latitude (m) Sites Permanent meadow Meadow in rotation Crop in rotation Crop intertia Mineral Institution Mineral Institution Pojrichken atry Compost Christen droppings	214887 2396007 601 0 0 0 1 1 1 1 1 0 0 0	230981 2396040 602 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	246938 2396057 604 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	263038 2396978 605 0 1 0 0 1 1 1 1 0 0 0	295081 2396026 606 1 0 0 0 1 1 0 1 0 0 1 0 0 0	311011 2396020 607 0 1 0 0 1 0 0 1 0 0 1 0 0 0	342978 2396020 : 608 : 0 : 0 : 1 : 1 : 0	103054 2379400 609 1 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0	118737 2379430 610 0 0 0 1 1 1 1 1 1 0 0 0	134749 2380080 612 0 0 0 1 1 1 1 1 0 0 0 0	150821 2380018 656 0 1 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0	166134 2380650 657 0 0 0 0 1 1 1 0 0 0 0 0 0 0	182976 2380055 658 0 0 1 1 1 1 0 0 0 0 0	198894 2380060 659 0 1 0 0 1 1 1 0 0 0 0 0 0	214911 2380188 660 0 0 1 1 0 1 1 0 0 0 0 0 0	230840 2379989 661 1 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0	247012 2380018 662 0 0 0 0 1 1 0 1 0 0 0 0 0 0	278985 2379996 663 0 0 0 1 1 1 0 1 0 0 0 0 0 0 0	2007 311000 2379992 665 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 0	326967 2380045 6666 0 1 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0	2007 342788 2379902 667 0 0 0 1 1 1 1 1 0 0 0 0	2007 86947 2363983 668 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 103085 2363462 669 0 0 0 0 1 1 0 1 0 0 1 0 0	0 2007 118666 2363920 670 0 0 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
Position (Lambert coordinates) Longhula (m) Latitude (m) Sites Practices Peractores Peractores Peractores Peractores Composition Composition Pipelinician starry Composition Christen droppings	214887 2396007 601 0 0 0 1 1 1 1 1 1 0 0 0 0	230981 2396040 602 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	246938 2396057 604 0 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0	263038 2396978 605 0 1 0 0 1 1 1 1 1 0 0 0 0	295081 2396026 606 1 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 0	311011 2396020 607 0 1 0 1 0 1 0 1 0 0 1 0 0 0 0 0 0 0 0	342978 3342978 2396020 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	103054 2379400 609 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0	118737 2379430 610 0 0 0 1 1 1 1 1 1 0 0 0 0	134749 2380080 612 0 0 0 1 1 1 1 1 0 0 0 0 0	150821 2380018 656 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0	166134 2380650 657 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	182976 2380055 658 0 0 1 1 0 1 1 0 0 0 0 0 0 0	198894 2380060 659 0 1 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0	214911 2380188 660 0 1 1 0 1 1 0 0 0 0 0 0 0 0	230840 2379989 661 1 0 0 0 1 1 1 0 0 0 0 1 1	247012 2380018 662 0 0 0 0 1 1 0 1 0 0 0 0 0 0	278985 2379996 663 0 0 0 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0	2007 311000 2379992 665 0 0 0 1 1 1 0 1 0 1 1 0 0 1	326967 2380045 6666 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0	342788 2379902 667 0 0 0 1 1 1 1 1 0 0 0 0 0	2007 86947 2363983 668 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 103085 2363462 669 0 0 0 0 1 1 1 0 1 0 1 1 0 1 1 0 1	0 2007 118666 2363920 670 0 0 0 0 1 1 1 0 0 1 1 0 0 0 0 0 0 0 0
Pedison (Lambert coordinates) Lambdude (m) State State Persators Meadow in retation Orop in retation Orop in retation Orop ind Mead Ministration Mead Ministration Mead Ministration Oropotot Orichen dropping Direct drilling	214887 2396007 601 0 0 0 1 1 1 1 1 0 0 0 1 1	230981 2396040 602 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	246938 2396057 604 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0	263038 2395978 605 0 1 1 0 0 1 1 1 0 0 0 1 1	295081 2396026 606 1 0 0 1 0 1 0 0 1 0 0 0 0 0 0 0 0	311011 2396020 0 1 0 0 1 0 0 1 0 0 1 0 0 1 0 0 1 1 0 0 0 1	342978 2396020 : 608 : 0 0 0 0 1 1 1 0 0 0 0 0 1 1 0 0 0 0 1 0 0 0 0	103054 2379400 509 1 1 0 0 1 1 0 0 1 1 0 0 1	2007 118737 2379430 610 0 0 0 0 1 1 1 1 1 1 1 0 0 0 0 1 1	134749 2380080 612 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0	150821 2380018 656 0 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1	166134 2380650 657 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 1	182976 2380055 658 0 0 1 1 0 1 1 0 0 0 1 1	198894 2380060 659 0 1 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1	214911 2380188 660 0 0 1 1 0 0 1 1 0 0 0 0 0 1	230840 2379989 661 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0	247012 2380018 662 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	278985 2379996 663 0 0 0 0 1 1 1 0 0 1 1 0 0 0 1 1	2007 311000 2379992 6665 0 0 0 1 1 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0	326967 2380045 6666 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0	2007 342788 2379902 6657 0 0 0 0 1 1 1 1 0 0 0 0 0 0 0 2 2	2007 86947 2363983 668 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 100085 2363462 0 0 0 0 1 1 1 0 0 1 0 0 1 1 0 0	0 2007 118666 2263920 0 0 0 0 1 1 1 0 0 0 0 1 1
Pediton (Lambert coordinates) Lambde (m) Steen Steen Persaneer meadow Meadow in relation Meadow in re	214887 2396007 601 0 0 0 1 1 1 1 1 0 0 0 0 1 1 1 0 0 0 0 1 0	230981 2396040 602 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	246938 2396057 604 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0	263038 2396978 0 1 0 0 1 1 1 0 0 0 1 1 1 0 0 0 1 1 1 1 0 0 0 1 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 1 0 0 1 1 1 0 0 1	295081 2396026 606 1 0 0 0 1 1 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 0 0 0 0 1 2 0 0 0 0	311011 2396020 607 0 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1 1 2 3 2 0	342978 2396020 608 0 0 0 1 1 0 0 0 0 0 0 1 1 0 0 0 0 0 0	103054 2379400 509 1 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 0	118737 2379430 610 0 0 0 0 1 1 1 1 1 0 0 0 0 1 1 1 1	134749 2380080 612 0 0 0 1 1 1 1 0 0 0 0 0 2 0 0 0 0 2 2 0 0	150821 2390018 656 0 1 0 0 1 1 0 0 0 0 0 1 1 0 0 0 0 1 0	166134 2380650 657 0 0 0 0 1 1 1 0 0 0 0 0 1 1 1 1 0 0 0 0	182976 2380055 658 0 0 1 1 1 0 0 0 0 0 1 1 1 1 0 0 0 0 1 1 1 1 2 0 0 0 0	198894 2380060 659 0 1 0 0 1 1 1 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0	214911 2380188 660 0 0 1 1 1 1 0 0 0 0 0 0 0 0 1 0 0 0 0	230840 2379989 661 1 0 0 0 1 1 1 0 0 0 1 1 0 0 0 0 1 0	247012 2380018 662 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 2 0 0	278985 2379996 663 0 0 0 0 1 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 2 2	2007 311000 2379992 665 0 0 0 0 1 1 0 0 1 1 0 0 0 1 1 0 0 0 0	326967 2380045 666 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 342788 2379902 667 0 0 0 1 1 1 1 1 0 0 0 0 2 0 0 0 2 2 0 0	2007 86947 2363983 668 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 103085 2363462 669 0 0 0 1 1 0 0 1 0 0 1 0 0 1 0 0 1 0 0 2 7 7	0 2007 118666 2363920 670 0 0 0 1 1 1 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 8 0 0 0 0
Pedistion (Lambert coordinates) Lambude (m) Sites Practices nanadrov Meadowin natadron Carge Indi Practices nanadrov Meadowin natadron Carge Indi Anatowin Pilothokan slumy Concenting Decke dings Decke dings Dec	214887 2396007 601 0 0 0 1 1 1 1 1 0 0 0 0 1 1 0 0 0 0	230981 2396040 602 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	246938 2396057 604 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	263038 2395978 605 0 1 0 0 1 1 1 1 1 0 0 0 0 1 1 1 88.3 0	295081 2396026 606 1 0 0 0 1 0 0 1 0 0 1 0 0 0 1 96.0 0	311011 239607 0 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1 83.3 0	342978 2396020 608 0 0 0 1 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0	103054 2379400 509 1 0 0 0 1 0 0 1 0 0 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 0 0 1 1 0 0 0 0 1 2 7 9 400 2 7 9 40 2 7 9 40 2 7 9 40 2 7 9 40 2 7 9 40 2 7 9 40 2 7 9 9 10 10 10 10 10 10 10 10 10 10 10 10 10	2007 118737 2379430 610 0 0 0 0 1 1 1 1 0 0 0 0 1 1 1 1 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	134749 2380080 612 0 0 1 1 1 1 0 0 0 0 2 0 0 0 0 0 0 0 0	150821 2380018 6556 0 1 1 0 0 1 1 1 0 0 0 0 0 0 1 1 0	166134 2380650 657 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	182976 2380055 0 0 1 1 0 1 1 0 0 0 0 0 0 1 1 1 97.0 0	198894 2380060 659 0 1 1 0 0 0 1 1 0 0 0 0 0 1 1 1 90.0 0	214911 2380188 660 0 1 1 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 1 0 0 1 8	230840 2379989 661 1 0 0 0 1 1 0 0 0 1 0 0 0 1 0 0 0 0	247012 2380018 662 0 0 0 1 1 0 1 0 0 0 0 0 2 0 0 0 45.0 0	278985 2379996 663 0 0 0 1 1 0 0 1 0 0 0 1 1 0 0 0 1 1 0 0 3.3 1	2007 311000 2379992 6655 0 0 0 1 1 0 0 1 1 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	326967 2390045 666 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 342788 2379902 6667 0 0 0 1 1 1 1 0 0 0 0 0 2 2 0 66.0 0 0	2007 86947 2363983 6658 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 103085 2363462 669 0 0 0 0 1 1 0 1 0 1 0 0 1 0 77.7 1	0 0 118666 2263920 670 0 0 0 0 1 1 0 0 1 1 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0
Pedison (Lambert coordinates) Lambde (m) Lambde (m) Sites Persaneer meadow Meadow in retainon Meadow	214887 2396007 601 0 0 0 1 1 1 1 1 0 0 0 0 1 0 85.0 0	230981 2396040 602 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	246938 2396057 604 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 2 0 0 0 2 1 1	263038 2395978 0 0 1 0 0 1 1 1 0 0 0 1 1 1 88.3 0	295081 2396026 1 0 0 0 1 0 0 0 1 0 0 0 0 1 96.0 0 0	311011 2396020 607 0 1 0 0 1 0 0 1 0 0 0 1 1 83.3 0	342978 2396020 608 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	103054 2379400 509 1 0 0 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 1 0 0 1	118737 2379430 610 0 0 0 0 1 1 1 1 1 1 0 0 0 0 1 1 50.0 0 0	134749 134749 2380080 612 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0	150821 2380018 656 0 1 0 0 1 1 0 0 0 0 0 0 0 0 0 1 0 95.0 0	166134 2380650 657 0 0 0 0 1 1 0 0 0 0 0 0 1 1 1 40.0 0 0	182976 2380065 0 0 1 0 1 1 0 0 0 0 0 1 1 97.0 0	198894 2380060 659 0 1 0 0 1 1 0 0 0 0 1 1 90.0 0 0	214911 2380188 660 0 1 1 0 1 1 0 0 0 0 1 0 0 0 49.7 0	230840 2379989 661 1 0 0 0 1 1 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 0 1 0	247012 2380018 662 0 0 0 1 1 0 0 0 0 0 2 0 0 45.0 0	278985 2379996 663 0 0 0 0 1 1 1 0 0 1 1 0 0 0 0 1 1 0 0 3.3 1	2007 311000 2379992 665 0 0 0 0 0 1 1 1 0 0 1 1 0 0 0 5 5.0 0 0 65.0 0 0	326967 2390045 666 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 342788 2379902 667 0 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0	2007 86947 2363983 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 103085 2363462 669 0 0 0 1 1 0 0 1 1 0 0 1 1 0 0 777.7 1	0 2007 118666 2363920 670 0 0 0 1 1 0 0 1 1 0 0 1 0 0 0 1 1 0 0 0 0 0 1 1 0
Pediation (Lambort coordinates) Lambude (m) Sites Practices nanow Meadow in rotation Corp Indiation Corp India Corp Indiation Corport Pipchoken stury Contront data Death of Italiga Pediations for the Death of Italiga Pediations (%) Death of Italiga Pediations (%) Death of Italiga Pediations (%) Death of Italiga Pediations (%) Death of Italiga	214887 2396007 601 0 0 0 1 1 1 1 0 0 0 0 1 1 0 0 0 0 0	230981 2396040 602 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 1 0 0 0 1 1 1 0 0 0 1	246938 2396057 604 0 0 0 0 1 1 1 0 0 0 0 0 0 0 0 0 2 0 0 0 0	263038 2396978 2005 0 1 0 0 1 1 1 1 0 0 0 1 1 1 1 88.3 0 0 0	295081 2996026 606 1 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0	311011 2396020 607 0 1 1 0 0 1 1 0 0 1 1 0 0 0 1 1 1 8.3.3 0 0	342978 2396020 608 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	103054 2379400 509 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 0 1 1 0 0 0 0 1 1 0 0 0 1 2 0 1 1 1 0 1 1 1 1	118737 2379430 610 0 0 0 0 1 1 1 1 1 0 0 0 0 1 1 0	134749 238000 612 0 0 0 0 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0	150621 2380018 6556 0 1 1 0 0 1 1 1 0 0 0 1 1 1 0 0 0 0 1 1 0	166134 2380650 657 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 1 1 40.0 0 0 1	182976 2380055 658 0 0 1 1 0 1 1 1 0 0 0 0 1 1 97.0 0 1	198994 2390060 659 0 1 0 0 1 1 0 0 0 1 1 1 0 0 0 0 1 1 1 90.0 0 0 1	214911 2380188 660 0 0 1 1 0 0 1 1 0 0 0 0 1 0 0 0 0 1 0	230840 2379989 661 1 0 0 0 1 1 0 0 0 0 0 1 1 0 0 0 0 0	247012 2380018 662 0 0 0 1 1 0 0 0 0 0 2 0 0 0 2 0 0 0 1	278985 2379996 663 0 0 0 0 1 1 1 0 0 0 1 1 0 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 1 1 0 0 0 0 0 1 1 0	2007 311000 2379992 665 0 0 0 1 1 1 0 0 1 1 0 0 1 1 0 0 0 0 0	326967 2280045 6665 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 342788 2379902 667 0 0 0 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0	2007 86947 2363983 6668 1 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 103085 2363462 669 0 0 0 0 1 1 0 1 0 1 0 1 0 1 0 1 0 1 0 1 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0	2007 118666 2363920 670 0 0 0 0 0 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0
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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)	Arrhopalites sp.	Achromodoridae	Microbial biomass (mg C.kg-1)	Mean Humus Index
Dendrobaena octaedra	Coleoptera Elateridae (larvae)	Bourletiella hortensis	Alaimidae	Microbial biomass (% total C)	Surface Humus Index
Dendrobaena pygmea cognettii	Coleoptera Staphylinidae (adults)	Brachystomella parvula	Anatonchidae	ADNr 16S	
Dendrobaena rubida rubida	Coleoptera Curculionidae (adults)	Ceratophysella denticulata	Anguinidae	Denitrifiers (narG)	
Eisenia eiseni	Coleoptera Curculioinidae (larvae)	Cryptopygus bipunctatus	Aphelenchidae	narG/16S	
Eiseniella tetraedra	Coleoptera Coccinellidae (adults)	Cryptopygus thermophilus	Aphelenchoididae	Protocatechuate degraders (PcaH)	
Lumbricus castaneus	Coleoptera Chrysomelidae (adults)	Desoria sp.	Aporcelaimidae	PcaH/16S	
Lumbricus centralis	Coleoptera Cantharidae (larvae)	Entomobrya sp.	Bastianiidae		
Lumbricus festivus	Coleoptera Carabidae (adults)	Folsomia candida	Belondiridae		
Lumbricus friendi	Coleoptera Carabidae (larvae)	Folsomia fimetaria	Belonolaiminae		
Lumbricus rubellus castanoides	Coleoptera Scarabaeidae (adults)	Folsomia quadrioculata	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	Diphterophoridae		
Nicodrilus caliginosus meridionalis	Hymenoptera Formicidae (aduits)	Heteromurus major	Diplogasteridae		
Nicodrilus caliginosus tuberculata	Hymenoptera miscellaneous (nymphs)	Heteromurus nitidus	Diplopeltidae		
Nicodrilus glardi	Hemiptera Aphidoidea (adults)	Hypogastrura sp.	Discolalmidae		
Nicodrilus longus longus	Hemiptera Heteroptera (adults)	isotoma sp.	Dorylaimoidea		
Nicodrilus nocturnus	Hemiptera miscellaenous (adults)	Isotomodes productus	Heteroderidae		
Octolasium cyaneum	Dermaptera	Isotomodes trisetosus	Hopiolaimidae		
Earthwarm biamage	Lepidoptera (larvae)		Leptonamidae		
Earnworm biomass	Diptora Tipulidae (Israe)	Isotomurus antennalis	Leptononidae		
Anecic abundance	Diptera lipulidae (larvae)	isotomurus gr. paiustris	Longidoridae		
Endogeic abundance	Diptera miscellaneous (larvae)	Lepidocitus cyaneus	Meloloogynae		
Epigeic abundance	Diptera (pupae)	Lepidocyrtus lanuginosus	Monhysteridae		
Anecic biomass	Orthoptera (adults)	Lepidocyrtus lignorum	Nononchidae		
Endogeic biomass	Diplopoda lulidae	Megalothorax minimus	Neodiplogasteridae / Monhysteridae		
Epigeic biomass	Dipiopoda Polydesmidae	Mesaphorura sp.	Nordildae		
Earthworm taxonomic richness	Dipiopoda Giomeridae	Mesaphorura fiorae	Nygolalmidae		
Earthworm diversity	Diplopoda miscellaenous	Mesaphorura hylophila	Odontolaimidae		
Earthworm evenness	Chilopoda Lithobiomorpha	Mesaphorura Italica	Odontopnaryngidae		
	Chilopoda Geophilomorpha	Mesaphorura krausbaueri	Osstellidae		
	Chilopoda Scolopendromorpha	Mesaphorura macrochaeta	Panagrolaimidae		
	Araneae Inomisidae	Mesaphorura sylvatica	Paratylenchidae		
	Araneae miscellaneous	Micranurida sensillata	Plectidae		
	Opiliones	Monobella grassei	Pratylenchidae		
	Pseudoscorpionida	Mucrosomia garretti	Prismatolaimidae		
	Isopoda	Mucrosomia garretti	Qudsianematidae		
	Gastropoda Arionidae	Orchesella sp.	Rhabditidae		
	Gastropoda Agriolimacidae	Paratulibergia callipygos	Rhabdolaimidae		
	Gastropoda miscellaneous (slugs)	Parisotoma notabilis	Steinernematidae		
	Gastropoda miscellaneous (snalis)	Proisotoma admantima	Telotylenchidae		
	Macrotauna abundance	Proisotoma minima	Teratocephalidae		
	Macrotauna richness	Proisotoma minuta	Thomenematidae		
	Phytophage abundance	Protaphorura armata	Inchodoridae		
	Saprophage abundance	Protaphorura subuliginata	Inpylidae		
	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)		
		Xenyliodes armatus	Bacterivores c-p 2-3-4 (Ba234)		
		Iotal mesotauna	Bacterivores		
		rotal springtails	Fungivores		
		⊏pigeic springtails	Omnivores		
		Hemiedaphic springtails	Carnivorês		
		Euedaphic springtails	Plant-teeders		
		rotal mites	Root-nair feeders		
		Total oribatid mites	rotal nematodes		
		Total gamasid mites	Free nematodes		
		Total actinedid mites	rinytoparasites		
		I Utal acaridid mites	Nematode taxonomic richness		
		Meesternel diamity	Nemalode diversity		
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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; **** =

	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)