Mesofauna as effective indicators of soil quality differences in the agricultural systems of central Cuba

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Abstract[1]

Soil mesofauna play an essential role in soil functioning. However, in studies on the impact of agricultural management on soil quality, the overall abundance of soil mesofauna and specific groups thereof has not been widely used as an indicator in developing countries. Here, we used soil mesofauna as a soil quality indicator compared to more traditional soil chemical, physical, and microbial indicators, in a comparison of the impact of three diverse agricultural management systems in Central Cuba: state (CSt), conventional private (CPr), and organic private (OPr) farms. We sampled the top 20 cm of soil of 30 fields from 12 farms and 1 natural reference site (NR) and analysed a number of soil chemical, physical, and microbial soil parameters as well as mesofauna (Acari and Collembola, further subdivided into Mesostigmata–Prostigmata–Oribatida–Astigmata and Isotomidae–Entomobryidae, respectively). Differences in soil properties between agricultural fields and natural soil were observed (especially in the multivariate analysis), but no significant differences were observed between agricultural systems, probably due to a lack of differences in soil organic carbon (SOC) content. The mesofauna differed strongly between the NR and the two conventional management practices (CSt and CPr), both in total numbers and in group numbers for most groups and in both rainy and dry seasons, whereas there were almost no significant differences between NR and OPr. Principal component analysis based on mesofauna clearly distinguished NR from all farming systems and OPr from CSt and CPr. Differences in soil mesofauna were mainly attributed to the use of synthetic pesticides. We conclude that in this context, without

[1] Abbreviations: conventional state farm, CSt; conventional private farm, CPr; organic private farm, OPr; natural reference site, NR; soil organic carbon, SOC; soil organic matter, SOM; biological soil quality, BSQ; total organic carbon, TOC; microbial biomass carbon, MBC; dehydrogenase activity, DHA; β-glucosidase, BGA; β-glucosaminidase, BGAA; phospholipid fatty acids, PLFAs; fatty acid methyl esters, FAMEs; arbuscular mycorrhizal fungi, AMF; bacteria:fungi ratio, B:F; generalised linear mixed models, GLMMs

clear differences in SOC content between agricultural fields, mesofauna is a superior soil quality indicator. Our results indicate that simple counts of total abundance are as useful as counts of specific mesofauna groups irrespective of the sampling period (dry or wet season).

Keywords: Soil quality indicators; soil mesofauna; Cuba; organic private farms; conventional private farms; state farms.

1. Introduction

Soil provides essential ecosystem services, such as soil organic matter (SOM) decomposition, C sequestration, and nutrient cycling, through the actions of the extremely diverse organisms inhabiting it (Wardle et al., 2004; Bardgett and Van der Putten, 2014). Soil mesofauna are thought to play essential roles in providing these ecosystem functions and maintaining soil quality (Barrios, 2007). Specifically, Collembola (springtails) and Acari (mites), together representing the largest proportion of soil mesofauna, have been shown to promote litter decomposition and nutrient cycling directly by feeding on plant residues and indirectly through interactions with soil microbes (Teuben and Verhoef, 1992; Chamberlain et al., 2006; Neher and Barbercheck, 2019). Agricultural intensification through the use of chemical fertilisers (Su et al., 2015; Cao et al., 2011), pesticides (Roy et al., 2009) and tillage activities (Heisler and Kaiser, 1995) have been reported to negatively influence the activities and diversity of mesofauna and lead to the deterioration of soil quality (Postma-Blaauw et al., 2010). A recent study showed that land-use intensification outweighs the impact of climate change in reducing the functional diversity of Collembola (Yin et al., 2020). In contrast, sustainable agricultural practices, such as conservation tillage (van Capelle et al., 2012) and organic amendment usage (Sánchez-Moreno et al., 2018) have been shown to increase the abundance and activities of soil microbes and soil fauna, thus enhancing soil quality.

Two primary approaches have been applied to monitor and evaluate the effects of agricultural intensification and management practices on soil quality. The first approach is a general soil quality assessment that uses a minimum set of selected physical, chemical, and biological parameters to monitor soil quality. This approach is widely used in countries where national soil-quality monitoring programmes have been established (Schipper and Sparling, 2000; Bünemann et al., 2018). In these minimum datasets,

biological parameters are often limited to microbial and biochemical parameters, such as microbial biomass C, respiration, and enzymes, but exclude soil fauna, particularly mesofauna (Schipper and Sparling, 2000; Filip, 2002; Idowu et al., 2008).

The second approach, which focuses on soil biological quality assessment, primarily uses biological parameters but does not consider chemical and/or physical parameters (Parisi et al., 2005; Ritz et al., 2009; Pulleman et al., 2012; Yan et al., 2012). In the past two decades, mesofauna have been increasingly included in environmental monitoring and assessments of forest (Nsengimana et al., 2018), urban (Fountain and Hopkin, 2004), and agricultural soils (Rutgers et al., 2009). Soil mesofauna consist almost exclusively of microarthropods, primarily specific groups of Acari and Collembola, which are important consumers of microbial films and fungal hyphae or larger plant detritus and can even influence soil structure in some systems (Rusek, 1998), and with mesostigmatic mites being predators of a wide range of invertebrate fauna (Gulvik, 2007). The increasing application of mesofauna (at a coarse taxonomic level) for biological soil quality assessment is related to a combination of their sensitivity to disturbances (Rüdisser et al., 2015), relationship with soil functions (Culman et al., 2010), and relatively lower cost of assessment compared to microbial parameters such as DNA/RNA and phospholipid fatty acid analysis.

Mesofauna have been included in soil quality assessments of agricultural fields to a very limited extent (Mantoni et al., 2021) especially in developing countries, and their potential as indicators compared to other physical, chemical, and biological parameters remains poorly understood. Moreover, it remains unclear how the abundance of mesofauna (identified at coarse taxonomic resolution, e.g. order to super family level) performs as a soil quality indicator compared to diversity indices based on detailed taxonomic description, that is, species level, or to simple presence/absence indices. For instance, the

biological soil quality (BSQ) index considers the ecomorphological scores calculated based on the absence or presence of mesofauna without considering their abundance (Parisi et al., 2005), while other studies (e.g. Yan et al., 2012) calculated soil quality indices based on a combination of mesofauna abundance and traits characterised at the species level, which requires highly specialised skills and is significantly time consuming. The agricultural sector in Cuba is characterised by farming systems that strongly differ in terms of land ownership, management practices, and land use. State farms are characterised by conventional farming practices and the intensive use of agricultural inputs, with large field sizes, monocultures, and relatively good access to mechanised tillage and chemical inputs, including the intensive use of pesticides. In contrast, private farms are small, typically use animal traction for land preparation, and have limited or no access to chemical inputs. Within private farms, a distinction can be made between farmers using conventional inputs, including mineral fertilisers and synthetic pesticides, and farmers following organic farming practices. From the input perspective, private conventional farms can be considered an intermediate between state and private organic farms. Such differences in land management, particularly disturbances during soil preparation and synthetic pesticide and mineral fertiliser application, could lead to significant differences in soil quality (Johnsen et al., 2001; Moeskops et al., 2010). Moreover, 43% of agricultural soils in Cuba are affected by different degradation processes and 70% show low SOM content, which, among other factors, confirms decreased soil fertility (Lok, 2016).

We conducted a representative sampling of soils in these different agricultural systems in central Cuba and hypothesised that soil quality would decrease in the order of private organic farms > private conventional farms > state farms. Given the assumed sensitivity of soil mesofauna to agricultural management practices and soil disturbances, we

hypothesised that this would be reflected in the differences in the abundance and community composition of microarthropods (representing the bulk of the soil mesofauna), which could be a sensitive indicator of soil quality changes resulting from differences in agricultural management systems. More specifically, we hypothesised that the abundance of Collembola and Acari would be higher in less disturbed private organic systems compared to conventional private and state farming systems and that differences in mesofauna abundance can be used as a soil quality indicator for agricultural ecosystems in the study area. To contextualise these differences between agricultural systems, we also evaluated a natural 'reference' ecosystem. We aimed to compare the indicator value of these mesofauna communities for soil quality in the tested agroecosystems with other chemical, physical, and microbial parameters commonly used as soil quality indicators.

2. Materials and methods

2.1. Research setting and soil sampling

We studied diverse agricultural management systems in the vicinity of the city of Santa Clara, Villa Clara Province, located in central Cuba. Given that inherent soil properties (mainly mineralogy and texture) may also strongly influence biological activities, only farms/fields with brown calcareous soil, classified as Orthic–Calcareous Cambisol (World Reference Base, 2015) were selected.

We selected 12 farms to represent the prevailing farming systems in Cuba: five private farms under organic management, five private farms under conventional management, and two state farms under conventional management that grow mixed crops. The typical size range of Cuban private farms is 15–25 ha and 500–2000 ha for state farms that grow mixed crops. Farm management was classified as organic if organic fertilisers were used and synthetic pesticides were avoided. In this sense, organic management should not be

understood as a certified organic system but rather as a type of management that is similar to extant certified systems. Under conventional management, farmers used intensive tillage and synthetic fertilisers and pesticides. These practices were more intensive in state farms than in private conventional farms, which is mainly related to the difference in accessibility of synthetic inputs.

We selected 2–3 fields in each private farm and 4 fields in each state farm, with a total of 11 fields in private organic farms (OPr), 10 fields in private conventional farms (CPr), and 8 fields in state farms (CSt). A natural ecosystem reference (NR) consisting of a secondary forest was included (Table S1) to provide estimates of biological parameters in relatively undisturbed ecosystems. Because the soil texture of one of the organic fields deviated significantly from that of the other fields (and given the overriding effect of soil texture on soil biological properties), this field was excluded from further analysis, resulting in 29 selected fields.

Each field (including the NR) was divided into four equally sized rectangular subplots, and composite soil samples were collected to a depth of 20 cm from each subplot. The composite samples per subplot were composed of 10 individual samples evenly distributed over each subplot. The soil samples were homogenised, air-dried, and analysed for physical (texture), chemical (pH-KCl, P-Olsen, and soil organic carbon (SOC)), and microbiological (microbial biomass carbon, phospholipid fatty acids, β-glucosidase, β-glucosaminidase, and dehydrogenase activities) properties. For the extraction of mesofauna (Acari and Collembola), soil samples were taken from all fields and subplots during both the dry (November 2015) and rainy (July 2017) seasons and transferred to the laboratory where they were kept fresh at room temperature (25 ± 2 °C) for 12 h before extraction was initiated. The soil bulk density was determined by taking

five undisturbed soil samples per field using steel rings with a radius of 3.5 cm and height of 6.0 cm for a soil volume of 230.9 cm^3.

2.2. Physical and chemical soil properties analysis

The soil texture was determined using the combined sieve and pipette method (Gee and Bauder, 1986). Bulk density was determined by taking the weight of the oven-dried soil and the known volume of the sample (Campbell, 1994). The pH–KCl was measured in slurries of 1 M KCl using a soil:KCl ratio of 1:2.5 (weight:volume). The SOC content was determined using the solid sample module of a total organic carbon (TOC) analyser (TOC-V CPN, Shimadzu Corporation, Kyoto, Japan). Available phosphorus (P) was extracted using the Olsen method, and the extract was analysed for inorganic P using a Cary 50 UV-Visible spectrophotometer (Varian Inc., Palo Alto, USA).

2.3. Soil microbial analysis

To reactivate soil microbial activity in the air-dried soil, following Moeskops et al. (2010), 100 g of soil from each replicate was filled into PVC tubes (diameter: 0.034 m; height: 0.068 m), and demineralised water was added to a moisture content equivalent to 50% water-filled pore space (soil filled at a bulk density of 1.23 Mg m^{-3}). The soil was incubated at room temperature (20.3 ± 1.0 °C) for one week, after which soil microbial parameters were analysed.

2.3.1. Microbial biomass carbon (MBC)

MBC was determined using the fumigation–extraction method as described by Vance et al. (1989). The fumigated and non-fumigated soil samples were extracted with 0.5 M K_2SO_4 (1:2 w:v) after shaking for one hour and stored at −20 °C until analysis with a total

199 organic carbon (TOC) analyser (TOC-V CPN, Shimadzu Corporation, Kyoto, Japan).
200 MBC was calculated as the difference in TOC between the fumigated and non-fumigated
201 soils and using an extraction efficiency or k_{EC} value of 0.45 (Joergensen, 1996).
202
203 2.3.2. Enzyme activities
204 Enzyme activity was determined according to procedures reported in detail in our
205 previous studies (Moeskops et al., 2010; Gebremikael et al., 2015). Dehydrogenase
206 activity (DHA) was determined in triplicate from 5 g of moist soil using
207 triphenyltetrazolium chloride as a substrate. The activities of β-glucosidase (BGA) and
208 β-glucosaminidase (BGAA) were determined in triplicate from 1 g of soil using *p*-
209 nitrophenyl-β-D-glucoside and p-nitrophenyl-N-acetyl-β-D-glucosaminide as substrates,
210 respectively.
211
212 2.3.3. Phospholipid fatty acids (PLFA) analysis
213 The microbial community structure was assessed by analysing PLFAs in the soil using a
214 modified method derived from Bligh and Dyer (1959) as described by Moeskops et al.
215 (2010, 2012). Briefly, lipids were extracted from 4 g of freeze-dried soil with phosphate
216 buffer (pH 7.0), chloroform, and methanol, and phospholipids were separated from the
217 lipid extracts via solid phase extraction using silica columns and transformed into methyl
218 esters (FAMEs). Finally, individual FAMEs were identified and quantified by gas
219 chromatography–mass spectrometry (GC–MS) on a Thermo Focus GC system combined
220 with a Thermo DSQ quadrupole MS (Interscience BVBA, Louvain-la-Neuve, Belgium)
221 in electron ionisation mode.
222 For gram-positive bacteria, the sum of iC15:0, aC15:0, iC16:0, iC17:0, and aC17:0 was
223 used. The fatty acids C16:1ω7c, C18:1ω7c, and cyC17:0 were considered typical of gram-

224 negative bacteria. The sum of 10MeC16:0 and 10MeC18:0 is regarded as a reliable
225 indicator of Actinomycetes. The total bacterial community was assumed to be represented
226 by the sum of the marker PLFAs for gram-positive and -negative bacteria and C:15,
227 C17:0, and cyC19:0ω11,12c. The fatty acid C18:2ω6,9c was used as a signature fatty acid
228 for fungi, and C16:1ω5c was used as the signature fatty acid for arbuscular mycorrhizal
229 fungi (AMF). Bacteria:fungi (B:F) ratios were calculated by dividing the respective sum
230 of marker fatty acids (Moeskops et al., 2010).
231
232 *2.4. Mesofauna assessment*
233 Dedicated sampling was performed for mesofauna assessment at two time points (once
234 during the rainy season and once during the dry season) on the same subplots where
235 samples for other soil properties had been taken. Sampling was performed by taking 10
236 subsamples per plot using a wide auger (7 cm diameter) to the same depth of 20 cm. The
237 samples were bulked into one composite sample and transferred immediately to the
238 laboratory. The soil was homogenised, and a 300 g subsample was taken and instantly
239 transferred to Berlese–Tullgren funnels for Acari and Collembola extraction, as described
240 by Socarrás and Robaina (2011). The funnels were placed under separate electric bulbs
241 (40 W), driving individuals downwards through the soil, which were eventually collected
242 in a beaker containing 70% alcohol. After four days, the beakers were removed, and the
243 number of individuals was counted and subsequently determined under a binocular
244 biological microscope (NOVEL) using the appropriate keys, namely Krantz and Walter
245 (2009) for Acari and Díaz (2004) for Collembola. Acari were classified to the highest
246 taxonomic level only, that is, the order Mesostigmata (superorder Parasitiformes) and
247 three groups within the superorder Acariformes: the order Prostigmata, the order
248 Oribatida, and the cohort Astigmata (within the order Oribatida). Within the Collembola

class, we identified two important groups, namely the families Isotomidae and Entomobryidae. Collectively, these groups constitute the largest share of soil mesofauna and are assumed to play important direct and indirect roles in soil functioning.

2.5. Data processing

All statistical analyses were performed using R 4.1.2 (R Core Team, 2021). Negative binomial generalised linear mixed models (GLMMs) were constructed to analyse the count data of mesofauna by using the *glmmTMB* function in the glmmTMB package (Brooks et al., 2017), Tweedie GLMMs (Astigmata and Oribatida in the rainy season) were used when necessary, and zero-inflated negative binomial GLMMs (Prostigmata in the rainy season) were used in cases where the model fit was poor even with Tweedie GLMMs. Soil characteristics and PLFAs data were modelled by linear mixed models (LMMs) via the function *lmer* from package lme4 (Bates et al., 2015), and transformation (log, root square, or square) was performed to achieve normality and homoscedasticity of residuals when necessary. Current farming systems/land use was used as a fixed factor with four levels (conventional state farms, conventional private farms, organic private farms, and NR), and farms/sites and fields were selected as random intercepts to account for the two levels of nesting according to our sampling design (four subplots in each field and fields within each farm). The normality and homogeneity of residuals of all constructed models were inspected using a simulation-based approach in the DHARMa package (Hartig, 2020) and *check_heteroscedasticity* in the package performance (Lüdecke et al., 2021). The significance of the fixed factor in all models (except for the zero-inflated negative binomial mixed models) was retrieved using the *anova* function from the lmerTest package (Kuznetsova et al, 2017) and function *Anova()* from the package car (Fox & Weisberg, 2019) for LMMs and GLMMs, respectively. Pairwise

comparisons between significant fixed factors were performed using the function *emmeans* from the emmeans package (Lenth, 2022), and the false discovery rate method was used for p-value adjustment. The 95% confidence intervals of marginal effects (conditioned on fixed effects) were extracted using the emmeans function and back-transformed if needed. For zero-inflated negative binomial mixed models, 95% confidence intervals of the marginal effect (conditioned on the fixed effects and the zero-inflation component) were extracted using *ggemmeans* from the ggeffects package (Lüdecke, 2018), but without post-hoc pairwise comparisons. The R-squared values of all models were calculated using the *r2_nakagawa* function in the package performance. Principal component analysis (PCA) was conducted on data aggregated to the field level for i) combined soil physical, chemical, and microbiological parameters; ii) PLFAs; iii) mesofauna in the rainy season; and iv) mesofauna in the dry season separately using the *prcomp* function in the stats package to evaluate the indicator value (under the assumption of soil quality differences among the farming systems) of soil mesofauna as compared to the indicator value of soil chemical, physical, and bulk microbiological characteristics, and PLFA. Additionally, pairwise permutational multivariate analysis of variance (PERMANOVA) tests were performed to evaluate differences in i) combined soil physical, chemical, and microbiological parameters; ii) PLFA; iii) mesofauna in the rainy season; and iv) mesofauna in the dry season between CSt, CPr, and OPr by the *pairwise.adonis* function (9999 permutations) from the pairwiseAdonis package (Martinez, 2020) on the scaled data at the farm/site level. P-values for multiple comparisons were adjusted using the false discovery rate method after performing the PERMANOVA.

3. Results

3.1. Soil physical and chemical properties

All soils were classified as clay according to the USDA textural triangle. The CSt and CPr had a significantly lower ($p<0.05$) SOC content than the natural system (difference of 1.30 and 1.10%, respectively), whereas the OPr did not differ significantly from the conventional farms or from the NR (Fig. 1A). There were no significant differences in available phosphorus (P-Olsen), bulk density, or pH between the systems (Fig. 1B-D).

3.2. Soil microbial biomass and enzyme activity

NR tended to have a higher MBC than all other farming systems, but this difference was not significant (Fig. 2A). There were no significant differences in BGA, but DHA was significantly higher in NR than in CPr and OPr (all $p<0.05$), whereas BGAA was significantly higher in NR than in all three farming systems (all $p<0.05$) (Fig. 2B-D). The only significant difference between the farming systems was in DHA, which was significantly lower in CPr than in CSt and OPr ($p<0.05$).

3.3. Soil microbial community composition

Similar to MBC, no significant differences were found among farming systems in terms of total or marker PLFAs for individual microbial groups (Fig. 3). In contrast to MBC, NR had significantly higher total and marker PLFAs and individual microbial groups compared to all farming systems ($p <0.001$), except for actinomycetes (no significant differences) and fungal biomarkers (significant difference with CPr only). There were no significant differences in the B:F ratio.

3.4. Mesofauna numbers and community composition

The abundance of mesofauna (individual groups and total) was consistently much higher during the rainy season than during the dry season. The total abundance of Acari,

Collembola, and total mesofauna (Acari and Collembola) in both conventional farming systems (CPr and CSt) was significantly lower ($P<0.001$) than in OPr by 50–70% and NR by 59–88% in both seasons (with the exception of no significant difference in total Acari between CPr and NR in the dry season) (Fig. 4A-C), but the significance of these differences was larger in the rainy season than in the dry season.

For these situations, contrasts could be calculated (i.e. not for the Prostigmata in the rainy season), and the abundances of individual groups (orders and cohort) of Acari were significantly lower in CSt and CPr than in OPr, and also significantly lower than in NR for Astigmata and Oribatida in the dry season (Fig. 5). There were more pronounced significant differences in the abundance of the two families of Collembola in both the dry and rainy seasons: the CSt and CPr differed (highly) significantly from both NR and OPr both in the dry and rainy seasons, excluding Entomobryidae in CSt in the dry season. There were no significant differences between CSt and CPr for any individual mesofauna groups, and only a significant difference between OPr and NR in Entomobryidae and Oribatida abundance in the rainy season and Isotomidae in dry season.

The contributors to Acari and Collembola abundance were consistently dominated by Oribatida and Isotomidae, respectively, both in the rainy and dry seasons, while Prostigmata and Mesostigmata were equally represented, and Astigmata was limited to only a few percent (Supplementary Fig. S1). Season had no impact on the relative distribution of the taxonomic groups of either Acari or Collembola.

3.5. Multivariate analysis including soil chemical, physical, and biological parameters

All PCAs (based on combined soil physical, chemical, and microbiological parameters based on PLFA and mesofauna in the rainy and dry seasons: Fig. 6A-D, respectively) clearly separated the agricultural systems from the natural reference. The PCAs based on

the combined soil physical, chemical, and microbiological parameters did not separate the farming systems, and PCA based on PLFAs did so even less. Consequently, from the pairwise PERMANOVA, there were no significant differences between the farming systems for combined general soil parameters ($p>0.05$) or PLFA ($p=1$) (Table 1). In contrast, the PCA based on the mesofauna clearly separated the CSt and CPr from the OPr in both the rainy and dry seasons, reflected in the significant or marginally significant differences in pairwise PERMANOVA p-values ($p< 0.05$ for CPr vs OPr and $p< 0.1$ for CSt vs OPr in both the rainy and dry seasons), whereas CSt and CPr overlapped in these PCAs, without significant differences in PERMANOVA p values. The PCA based on soil mesofauna clearly separated OPr and NR from CPr and CSt, mainly along PC1 in both seasons, with all mesofauna groups having relatively equal loadings on this PC.

4. Discussion

4.1. Soil chemical, physical, and microbiological properties

We used a set of simple but commonly used soil chemical and physical parameters in combination with bulk (MBC, enzyme activities) and more specific (PLFA) microbiological parameters to characterise (differences between) these farming systems. One of the main pitfalls of analysing soil quality is the confounding effects of land management with the effects of inherent soil properties, mainly soil texture and mineralogy. It is well known that soil texture has an overriding effect on nearly all other soil properties, including SOC (e.g. Johannes et al., 2017) and biological properties (e.g. Candinas et al., 2002), and strong differences in texture usually mask potential management effects. Therefore, we effectively selected a wide range of fields with similar soil parent material and soil texture as selection criteria (and excluded one field with a deviating texture) to minimise such confounding effects.

Despite the relatively long period for which these management systems were in place at different locations (5–20 years, Table S1), differences in the chemical and physical soil parameters were relatively small, with a tendency for higher P-Olsen in the CPr. Despite significantly different management approaches, with little or no organic inputs, and intensive and deep tillage in the CSt, the SOC content did not differ significantly between the three farming systems. SOC content is probably the most widely used soil quality indicator, given its very strong influence on and resultant correlation with many other soil parameters, including biological parameters. The lack of significant differences in SOC in this study seems to indicate a relatively limited potential for discrimination between systems based on standard soil parameters. The natural system, not surprisingly, stood out in that respect, with approximately double the SOC content as the CSt, which was also reflected in soil microbiological properties.

Soil MBC and enzyme activities are regularly used as indicators of soil quality. Here, we selected the activities of a group of intracellular enzymes (DHA) and two extracellular enzymes (BGA and BGAA), all of which are highly relevant to C and/or N cycling in soils. DHA measured in soil enzymology represents the cumulative activities of many microbial dehydrogenases involved in the oxidation of a multitude of organic molecules during microbial respiration (Prosser et al., 2011). BGA and BGAA are important enzymes in the hydrolytic degradation of major macromolecular compounds in soil (cellulose and chitin) and bacterial cell wall polysaccharides, thus playing key roles in C and N mineralisation in soils (Piotrowska-Długosz, 2020). Contrary to our expectations, the conventionally managed fields did not have significantly lower MBC or enzyme activities than those in organically managed fields (with the exception of lower DHA in CPr compared to CSt and OPr). Previous research has proposed DHA as a sensitive indicator of differences in soil quality, with extreme differences between organic and

399 conventional intensive horticulture in the tropics (Moeskops et al., 2010), and we do not
400 have a clear explanation regarding the difference in our results other than the absence of
401 significant differences in SOC content. The lack of significant differences in SOC
402 between farming systems may explain the lack of clear and consistent differences in bulk
403 microbial properties between these systems. The higher DHA and BGAA and the
404 tendency for higher MBC in the NR are likely to a large extent also related to the much
405 higher SOC content in NR.
406 The total PLFA followed the same pattern as the MBC (but the differences were
407 significant) and was 2.5–3 times higher in the NR than in the farming systems, confirming
408 the value of total PLFAs as a measure of (active) microbial biomass (e.g. Rinklebe and
409 Langer, 2010). The PLFA biomarkers of the individual microbial groups were also
410 significantly higher in the NR than in the farming systems, with the exception of
411 actinomycetes and fungi. Biomarker PLFA analysis revealed no significant differences in
412 the microbial community composition between farming systems (not in total PLFA or in
413 PLFA of individual groups). There is consensus in the scientific literature that tillage
414 negatively affects AMF abundance in soils (e.g. Sharma-Poudyal et al., 2017). However,
415 there were no differences in the PLFA marker for AMF, despite differences in tillage
416 intensity between OPr, CPr, and CSt (which was most intensive in CSt).
417 Another potentially important factor influencing soil quality is the management and land-
418 use history of the fields, which could partially override or mitigate the effects of current
419 management. However, in this study, the impact of historic management, which was
420 recorded in detail (Table S1), must have been limited. First, the management system for
421 each area was already in place for at least 5 years, with most locations having been
422 maintained under the same system for over 15 years. Although this may not be long
423 enough to completely rule out the effects of land use history (Gajda et al., 2016; Le

Provost et al., 2019), we expect that such effects would be limited. More importantly, the management history was diverse in both OPr and CPr fields (with Marabou infestation being similar to forest cover), and differences in historic land use were no longer reflected in a significant difference in SOC content between the two systems. Moreover, the variability between fields within the individual systems for most parameters analysed here was small, further indicating that potential land use history effects had largely disappeared.

The PCA results based on the combination of soil chemical, physical, and bulk microbiological parameters (Fig. 6A) as well as PLFA (Fig. 6B) and PERMANOVA results broadly confirmed the above findings, showing a very clear separation of all farming systems from the NR, but no separation amongst the farming systems.

4.2. Mesofauna as an indicator of soil quality

Microarthropods have frequently been used as indicators of diversity and habitat quality for ecosystem monitoring (Gerlach et al., 2013) and have even been included in national monitoring programmes of soil quality (George et al., 2017). However, they have been used much less frequently than traditional soil chemical, physical, and microbiological parameters to compare the effect of specific agricultural management on soil quality within a given soil type and climate. In contrast to the physical, chemical, and microbial parameters, the number of microarthropods differed significantly between the OPr and CPr and CSt fields. In addition, the number of microarthropods differed significantly between NR, CPr, and CSt, but the differences with OPr were no longer significant with one exception. Despite the much lower microarthropod abundance in the dry season than in the rainy season, significant differences between the agricultural systems (and NR) were observed equally clearly in the dry and rainy seasons.

The possible reasons for the very clear separation of farming systems (CPr and CSt versus OPr) were not immediately clear in our analysis and are explored further here. Although the OPr fields were not certified as organic, they adhered to the principles of organic agriculture. The sole use of mineral fertilisers in CPr is mainly due to the large labour requirements for collecting, preparing, and adding organic materials and composts to soil. Previous research has indicated that organically managed fields exhibit greater arthropod abundance and diversity than in conventionally managed fields (e.g. Berry et al., 1996; Hole et al., 2005; Pimentel et al., 2005). Clearly, SOC content is not a possible explanation for these differences, given that SOC was not significantly different in the farming systems. One of the management differences between these systems is the higher tillage intensity and absence of conservation tillage practices in CSt and CPr compared to OPr. It has been widely observed that tillage negatively impacts soil-dwelling (micro)arthropods, especially Acari, by changing the soil pore structure and habitable pore space, increasing the exposure of soil organisms to desiccation, and negatively affecting access to food sources (Menta et al., 2020). Given that the differences in tillage were not extreme (OPr fields were tilled), tillage could explain differences in mesofauna to a small extent at best. Given that crop rotations were not very different in CPr and OPr, the most important factors controlling the microarthropod abundance must have been the inputs of agrochemicals, which are used intensively in CPr and CSt, and are not used at all in OPr and NR. Insecticides logically have been shown to have strong negative effects on soil microarthropods. In conventional fields, a diversity of insecticides was routinely applied, and for example Pamminger et al. (2022) reported strong negative effects of methamidophos on both Acari and Collembola abundance in soil. However, based on an extensive literature review, Gunstone et al. (2021) demonstrated that herbicides and

fungicides also negatively affect the abundance and activity of Acari and Collembola, albeit to a lesser extent than insecticides.

We determined both the overall abundance and distribution of the major groups of Acari and Collembola. Oribatids are the characteristic soil Acari and, by far, the most abundant group in these soils. Strikingly, neither agricultural management nor season had an impact on the relative distribution of the taxonomic groups of either Acari or Collembola. In particular, the Oribatids would be sensitive to the effects of tillage (Crossley et al. 1992), whereas Prostigmata have better tolerance against stress factors (Bedano et al., 2005), but we found no evidence for this in our fields. The impacts of disturbances on Collembola research results are less clear, with some studies (e.g. Filser et al. 2002) reporting higher Collembola abundances in intensive high-input systems compared to low-input systems. Here, Collembola and Acari were affected to the same extent by agricultural management; therefore, there would be no preference for either group in the assessment of agricultural management effects.

5. Conclusions

Despite the pronounced differences in management in the agricultural systems analysed, we found no significant differences in soil quality indicators based on chemical, physical, and microbiological properties but very consistent differences in soil microarthropod community characteristics between these systems, which supported our hypothesis. The management systems could be differentiated equally well based on total microarthropod numbers than on microarthropod community composition, and this was the case in both the rainy and dry seasons. This suggests that microarthropods are very sensitive indicators of soil quality in the agricultural setting analysed here, superior to soil microbiological properties, and that simple counting seems to be sufficient for such soil quality analysis,

eliminating the need for in-depth analysis techniques such as determining mesofauna community composition.

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710

Figure captions

Fig. 1: Chemical and physical soil properties in the three farming systems and natural reference area: (A) SOC, (B) P-Olsen, (C) bulk density, and (D) pH. Bullets represent the marginal means of the three farming systems and the natural reference; error bars represent the 95% confidence interval of the means.

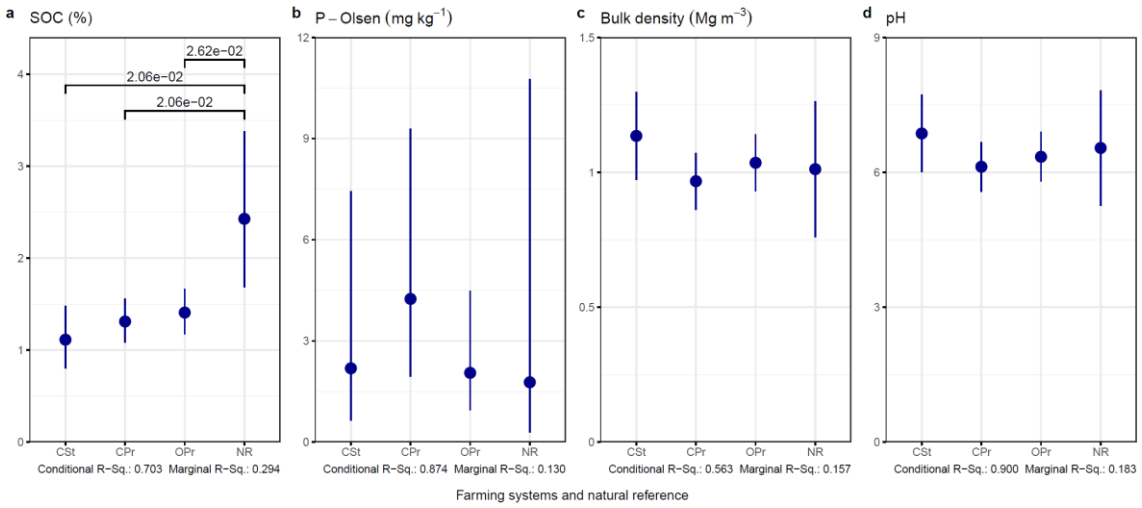
Fig. 2. Soil microbial biomass carbon (MBC) (A) and enzymatic activities of dehydrogenase (DHA) (B), β-glucosidase (BGA) (C) and β-glucosaminidase (BGAA) (D) in the three farming systems and natural reference. Bullets represent the marginal means of the three farming systems and natural reference; error bars represent the 95% confidence interval of the means. Bars indicate significant differences, with p-values above the bars.

Fig. 3. Total PLFA and microbial biomarker concentrations (nmol g^{-1} dry soil) and B:F (bacteria:fungi) ratio in the different farming systems and natural reference. Bullets represent the marginal means of the three farming systems and the natural reference; error bars represent the 95% confidence interval of the means. Bars indicate significant differences, with p-values above the bars.

Fig. 4. Abundance of total mesofauna (A), Acari (B), and Collembola (C) in soil in the three farming systems and the natural reference in the rainy and dry seasons. Bullets represent the marginal means of the three farming systems and the natural reference; error bars represent the 95% confidence interval of the means. Bars indicate significant differences, with p-values above the bars.

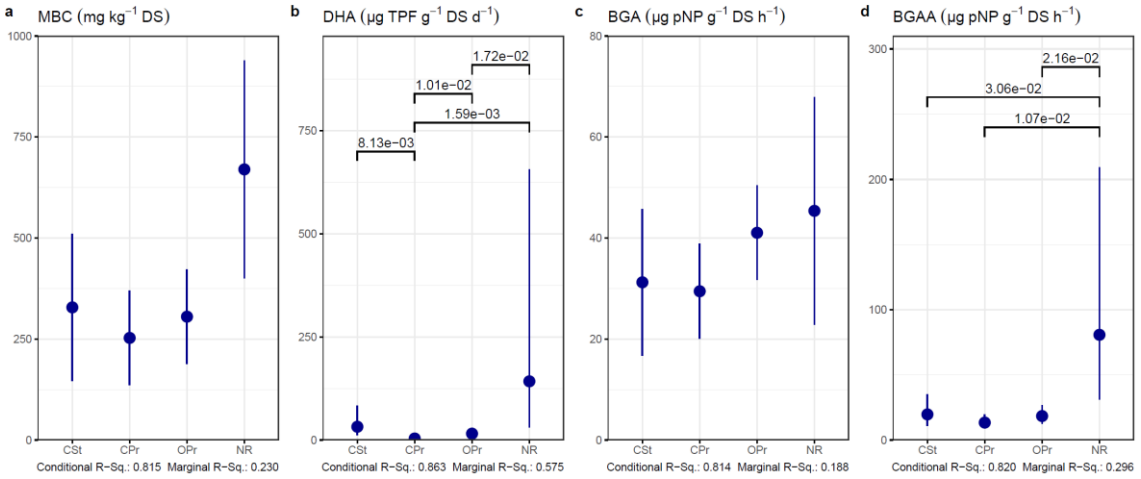
Fig. 5. Individual numbers of the Acari: (A) Astigmata, (B) Prostigmata, (C) Oribatida, (D) Mesostigmata, and Collembola: (E) Entomobryidae and (F) Isotomidae in soil in the three farming systems and the natural reference in the rainy and dry seasons. Bullets represent the marginal means of the three farming systems and the natural reference; error bars represent the 95% confidence interval of the means. Bars indicate significant differences, with p-values above the bars.

Fig. 6. Principal component analysis (PCA) biplot of sampled fields based on soil chemical, physical, and bulk microbiological characteristics (A), PLFA (B), and mesofauna community from rainy (C) and dry seasons (D).

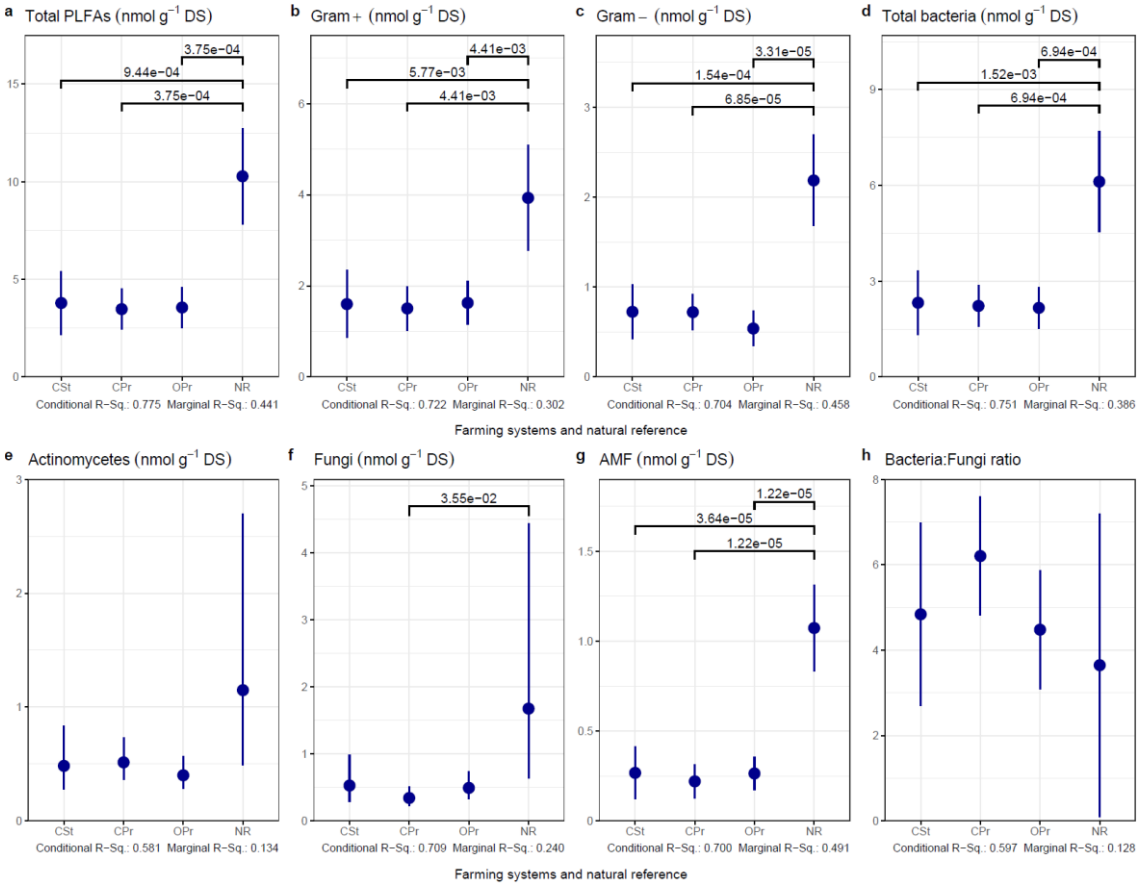

a
SOC (%)
2.62e−02
2.06e−02
2.06e−02
CSt
CPr
OPr
NR
Conditional R−Sq.: 0.703 Marginal R−Sq.: 0.294
b
P – Olsen (mg kg−1)
Conditional R−Sq.: 0.874 Marginal R−Sq.: 0.130
c
Bulk density (Mg m−3)
Conditional R−Sq.: 0.563 Marginal R−Sq.: 0.157
d
pH
Conditional R−Sq.: 0.900 Marginal R−Sq.: 0.183
Farming systems and natural reference

749

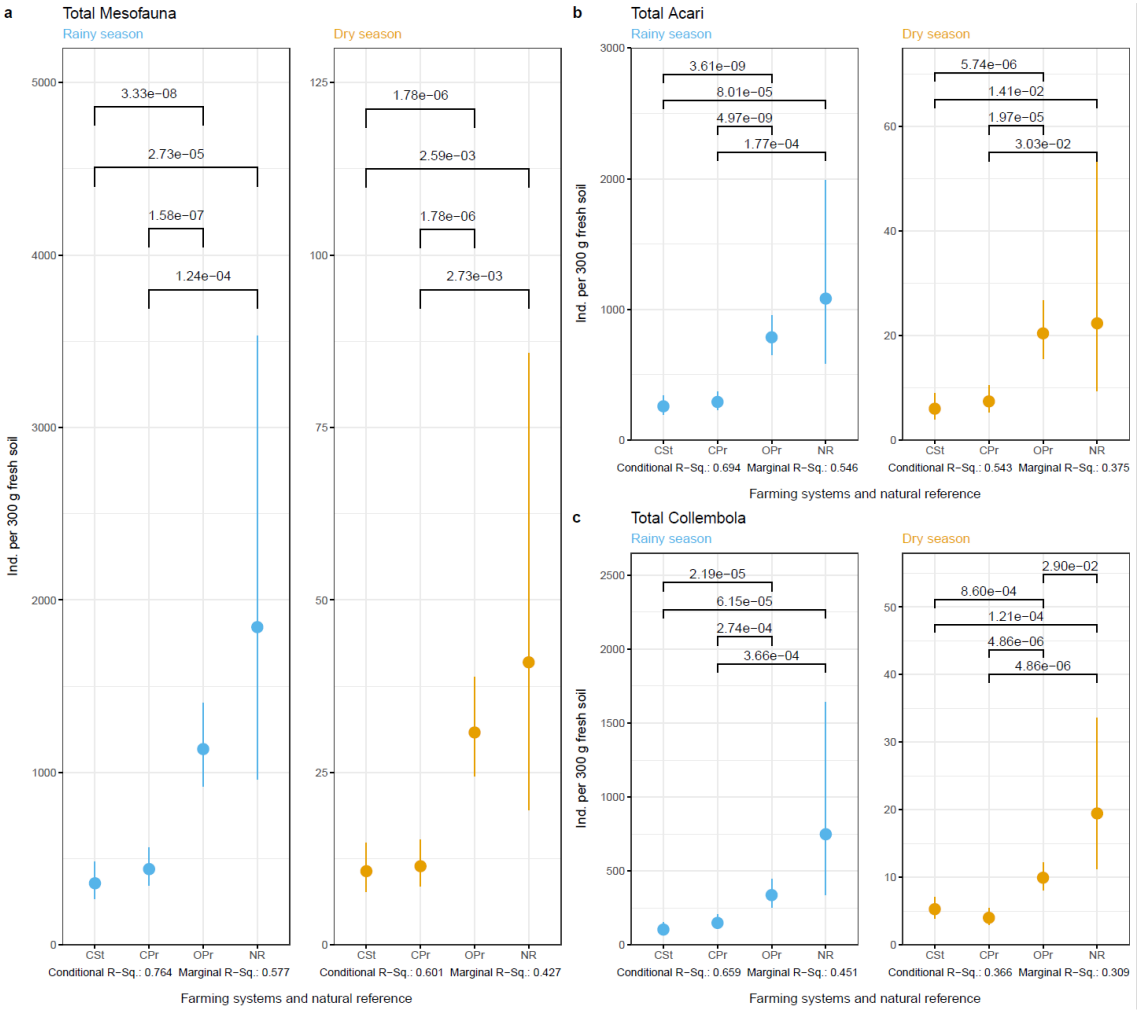
750


a
MBC (mg kg^{-1} DS)
1000
750
500
250
0
CSt
CPr
OPr
NR
Conditional R−Sq.: 0.815 Marginal R−Sq.: 0.230
b
DHA (µg TPF g^{-1} DS d^{-1})
1.72e−02
1.01e−02
1.59e−03
8.13e−03
750
500
250
0
CSt
CPr
OPr
NR
Conditional R−Sq.: 0.863 Marginal R−Sq.: 0.575
c
BGA (µg pNP g^{-1} DS h^{-1})
80
60
40
20
0
CSt
CPr
OPr
NR
Conditional R−Sq.: 0.814 Marginal R−Sq.: 0.188
d
BGAA (µg pNP g^{-1} DS h^{-1})
2.16e−02
3.06e−02
1.07e−02
300
200
100
0
CSt
CPr
OPr
NR
Conditional R−Sq.: 0.820 Marginal R−Sq.: 0.296
Farming systems and natural reference

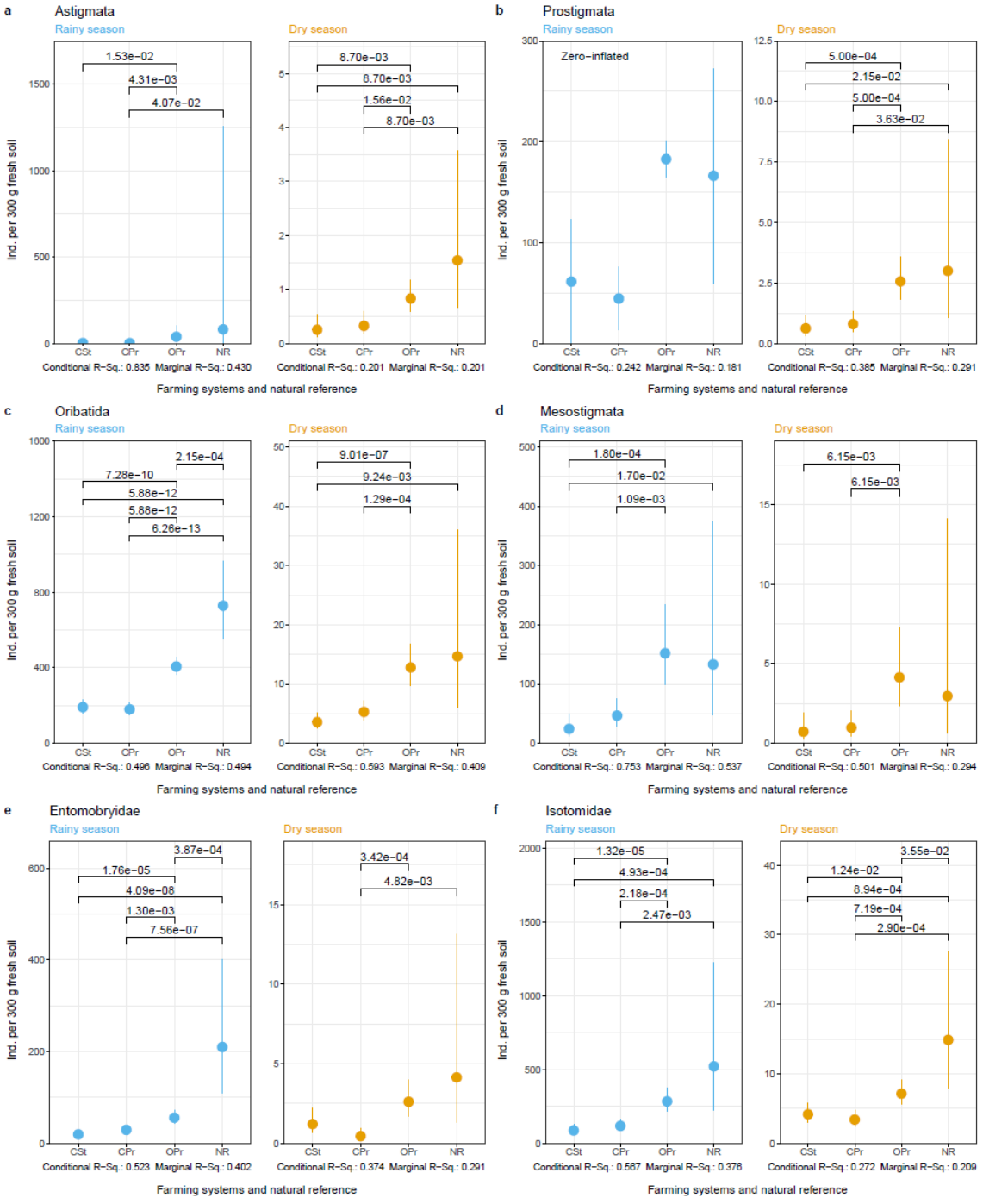
751


a Total PLFAs (nmol g−1 DS)
3.75e−04
9.44e−04
3.75e−04
CSt CPr OPr NR
Conditional R−Sq.: 0.775 Marginal R−Sq.: 0.441
b Gram + (nmol g−1 DS)
4.41e−03
5.77e−03
4.41e−03
CSt CPr OPr NR
Conditional R−Sq.: 0.722 Marginal R−Sq.: 0.302
c Gram − (nmol g−1 DS)
3.31e−05
1.54e−04
6.85e−05
CSt CPr OPr NR
Conditional R−Sq.: 0.704 Marginal R−Sq.: 0.458
d Total bacteria (nmol g−1 DS)
6.94e−04
1.52e−03
6.94e−04
CSt CPr OPr NR
Conditional R−Sq.: 0.751 Marginal R−Sq.: 0.386
Farming systems and natural reference
e Actinomycetes (nmol g−1 DS)
CSt CPr OPr NR
Conditional R−Sq.: 0.581 Marginal R−Sq.: 0.134
f Fungi (nmol g−1 DS)
3.55e−02
CSt CPr OPr NR
Conditional R−Sq.: 0.709 Marginal R−Sq.: 0.240
g AMF (nmol g−1 DS)
1.22e−05
3.64e−05
1.22e−05
CSt CPr OPr NR
Conditional R−Sq.: 0.700 Marginal R−Sq.: 0.491
h Bacteria:Fungi ratio
CSt CPr OPr NR
Conditional R−Sq.: 0.597 Marginal R−Sq.: 0.128
Farming systems and natural reference

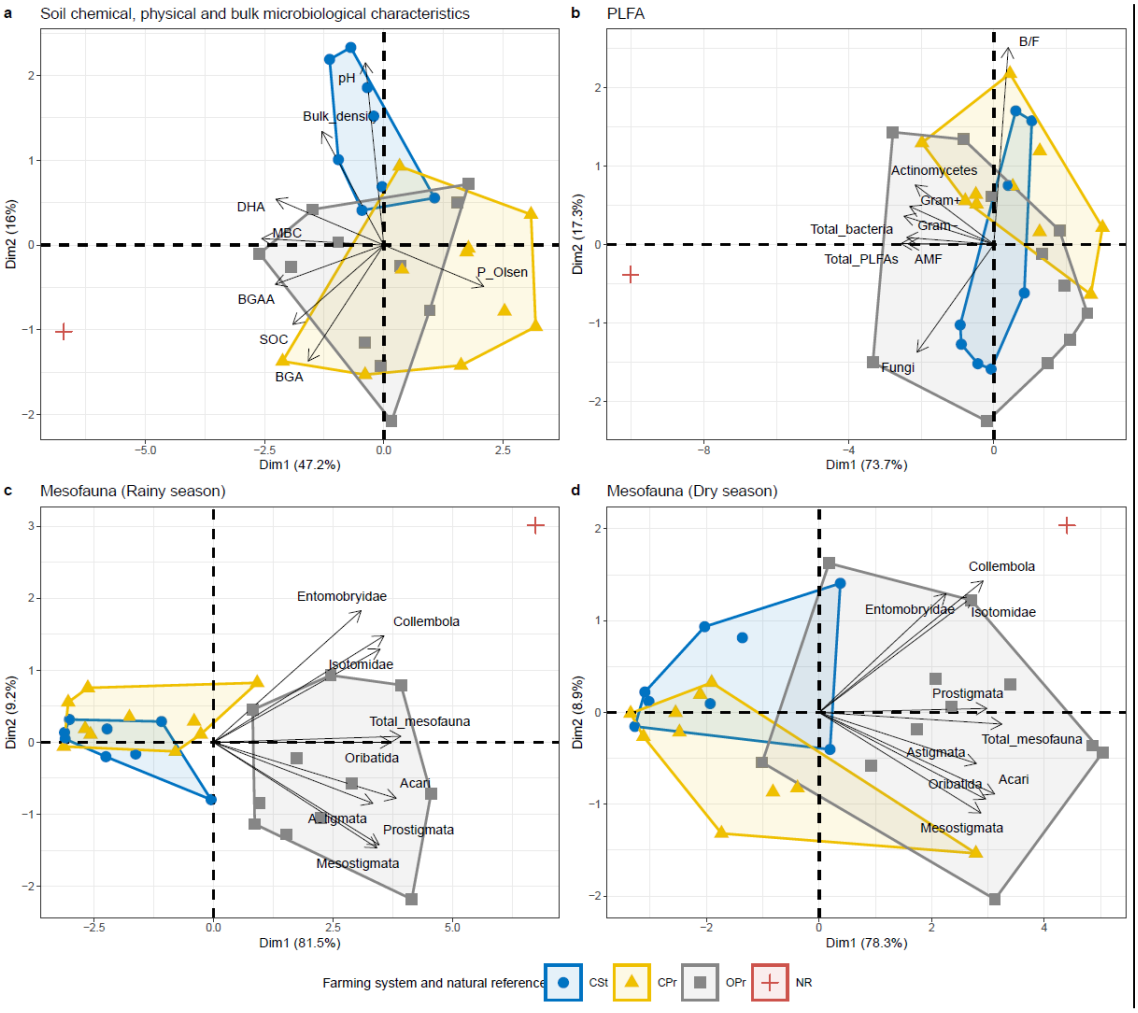
752


a
Total Mesofauna
Rainy season
Dry season
3.33e−08
2.73e−05
1.58e−07
1.24e−04
1.78e−06
2.59e−03
1.78e−06
2.73e−03
Ind. per 300 g fresh soil
CSt
CPr
OPr
NR
Conditional R−Sq.: 0.764 Marginal R−Sq.: 0.577
Conditional R−Sq.: 0.601 Marginal R−Sq.: 0.427
Farming systems and natural reference
b
Total Acari
Rainy season
Dry season
3.61e−09
8.01e−05
4.97e−09
1.77e−04
5.74e−06
1.41e−02
1.97e−05
3.03e−02
Conditional R−Sq.: 0.694 Marginal R−Sq.: 0.546
Conditional R−Sq.: 0.543 Marginal R−Sq.: 0.375
Farming systems and natural reference
c
Total Collembola
Rainy season
Dry season
2.19e−05
6.15e−05
2.74e−04
3.66e−04
2.90e−02
8.60e−04
1.21e−04
4.86e−06
4.86e−06
Conditional R−Sq.: 0.659 Marginal R−Sq.: 0.451
Conditional R−Sq.: 0.366 Marginal R−Sq.: 0.309
Farming systems and natural reference

753


a
Astigmata
Rainy season
Dry season
1.53e−02
4.31e−03
4.07e−02
8.70e−03
8.70e−03
1.56e−02
8.70e−03
Ind. per 300 g fresh soil
CSt CPr OPr NR
Conditional R−Sq.: 0.835 Marginal R−Sq.: 0.430
Conditional R−Sq.: 0.201 Marginal R−Sq.: 0.201
Farming systems and natural reference
b
Prostigmata
Rainy season
Dry season
Zero−inflated
5.00e−04
2.15e−02
5.00e−04
3.63e−02
Conditional R−Sq.: 0.242 Marginal R−Sq.: 0.181
Conditional R−Sq.: 0.385 Marginal R−Sq.: 0.291
Farming systems and natural reference
c
Oribatida
Rainy season
Dry season
2.15e−04
7.28e−10
5.88e−12
5.88e−12
6.26e−13
9.01e−07
9.24e−03
1.29e−04
Conditional R−Sq.: 0.496 Marginal R−Sq.: 0.494
Conditional R−Sq.: 0.593 Marginal R−Sq.: 0.409
Farming systems and natural reference
d
Mesostigmata
Rainy season
Dry season
1.80e−04
1.70e−02
1.09e−03
6.15e−03
6.15e−03
Conditional R−Sq.: 0.753 Marginal R−Sq.: 0.537
Conditional R−Sq.: 0.501 Marginal R−Sq.: 0.294
Farming systems and natural reference
e
Entomobryidae
Rainy season
Dry season
3.87e−04
1.76e−05
4.09e−08
1.30e−03
7.56e−07
3.42e−04
4.82e−03
Conditional R−Sq.: 0.523 Marginal R−Sq.: 0.402
Conditional R−Sq.: 0.374 Marginal R−Sq.: 0.291
Farming systems and natural reference
f
Isotomidae
Rainy season
Dry season
1.32e−05
4.93e−04
2.18e−04
2.47e−03
3.55e−02
1.24e−02
8.94e−04
7.19e−04
2.90e−04
Conditional R−Sq.: 0.567 Marginal R−Sq.: 0.376
Conditional R−Sq.: 0.272 Marginal R−Sq.: 0.209
Farming systems and natural reference

754


a
Soil chemical, physical and bulk microbiological characteristics
pH
Bulk_densi
DHA
MBC
P_Olsen
BGAA
SOC
BGA
Dim2 (16%)
Dim1 (47.2%)
b
PLFA
B/F
Actinomycetes
Gram+
Gram−
Total_bacteria
Total_PLFAs
AMF
Fungi
Dim2 (17.3%)
Dim1 (73.7%)
c
Mesofauna (Rainy season)
Entomobryidae
Collembola
Isotomidae
Total_mesofauna
Oribatida
Acari
Astigmata
Prostigmata
Mesostigmata
Dim2 (9.2%)
Dim1 (81.5%)
d
Mesofauna (Dry season)
Collembola
Entomobryidae
Isotomidae
Prostigmata
Total_mesofauna
Astigmata
Oribatida
Acari
Mesostigmata
Dim2 (8.9%)
Dim1 (78.3%)
Farming system and natural reference
CSt
CPr
OPr
NR

755

Table 1. Result of pairwise PERMANOVA between CSt, CPr snd OPr on 1) soil chemical, physical and bulk microbiological characteristics; 2) PLFA; 3) mesofauna community in rainy season; and 4) mesofauna community in dry season.

pairwise PERMANOVA	df	F	R-sq.	p value
Physical, chemical and bulk microbiological characteristics				
CSt vs CPr	1	2.371	0.322	0.286
CSt vs OPr	1	1.065	0.176	0.429
CPr vs OPr	1	1.512	0.159	0.301
PLFA				
CSt vs CPr	1	0.533	0.096	1
CSt vs OPr	1	0.185	0.036	1
CPr vs OPr	1	1.042	0.115	0.858
Mesofauna community in rainy season				
CSt vs CPr	1	0.477	0.087	0.667
CSt vs OPr	1	16.347	0.766	0.071
CPr vs OPr	1	16.465	0.673	0.023
Mesofauna community in dry season				
CSt vs CPr	1	0.453	0.083	0.619
CSt vs OPr	1	11.503	0.697	0.071
CPr vs OPr	1	13.875	0.634	0.025