Applied Soil Ecology 164 (2021) 103923

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Abundance, biomass and community composition of soil saprophagous macrofauna in conventional and organic sugarcane fields

Mathieu Coulis

CIRAD, UPR GECO, F-97285 Le Lamentin, Martinique, France

ARTICLE INFO

Keywords:
Diplopod
Earthworm
Isopod
Martinique
Soil biodiversity
Lesser Antilles

ABSTRACT

Tropical island saprophagous invertebrates have received little attention despite their important role in sustaining soil fertility. Soil biodiversity in the agroecosystems of the Lesser Antilles is subject to various anthropic and environmental perturbations; therefore, it is crucial to promote agricultural practices that help preserve it. Here, we investigate the effect of conversion to organic farming in sugarcane production on soil saprophagous invertebrates in a Martinique plantation (Lesser Antilles). The abundance, biomass and diversity of communities were measured in three fields undergoing organic conversion and in two control fields under conventional production. Invertebrates were sampled both by pitfall trapping and Tullgren extraction. The results indicated that abundance was significantly higher in fields undergoing conversion (342 ± 78 ind.m^{-2}) compared to fields under conventional farming (146 ± 34 ind.m^{-2}). The response of the whole community's biomass to organic conversion was not significant, reflecting a contrasting response of each invertebrate taxa: isopod biomass was the most impacted, earthworm biomass was moderately impacted and diplopod biomass was not significantly affected. A total of 25 morphospecies for all taxa were distinguished in this study. However, the diversity did not differ and community composition remained similar under both farming practices. The response of invertebrate abundance and biomass could be either due to the direct toxicity of herbicides intensively used in conventional sugarcane cultivation or to the indirect effects of herbicides modifying micro-habitat parameters (weed biomass, amount of mulch and litter humidity). In conclusion, the study shows that organic farming has a beneficial effect on soil saprophagous invertebrates even after a short period of conversion (between one and two years), which is promising for restoring soil biological processes in the context of agroecological transition.

1. Introduction

Soil biodiversity is essential in sustaining the fertility of tropical soils (Lavelle et al., 2001). Organisms of different functional groups have complementary and synergetic effects on soil functioning (Lavelle, 1996; Wolters and Ekschmitt, 1997). Microorganisms, which are the main decomposers, play an active role in organic matter mineralization, allowing the release of nutrients from crop residues. Thereafter, microbial activity is strongly modulated by soil macrofauna. In a first step, the "litter transformer" (e.g. Diplopoda, Isopoda) fragments coarse organic debris, favoring microbial decomposers by providing them with better access to organic matter. Then earthworms, also called "ecosystem engineers", incorporate fine organic fragments into the mineral horizon of soil. In creating stable organo-mineral aggregates, earthworms help build a reserve of fertility in soil since these aggregates allow the slow, regular liberation of nutrients. These processes are especially important in a tropical context where environmental pressures, such as leaching and erosion, are very high (Lavelle et al., 1992). Therefore, it is crucial to preserve or to allow the regeneration of important soil biodiversity in tropical agroecosystems.

It has long been recognized that pesticides could have a toxic effect on non-target organisms (Hassan et al., 1994). Phytosanitary products are considered a potential threat to soil invertebrates and their excessive use could have important consequences on invertebrate communities, jeopardizing the services they provide (Fox, 1964; Pelosi et al., 2014). Herbicides have long been considered less harmful than insecticides, however their effect on soil organisms is potentially toxic. Studies in controlled conditions have actually demonstrated the toxic effect of several herbicides on soil organisms (Correia and Moreira, 2010; Merlini et al., 2012). However, these tests are often conducted on generalist species from temperate ecosystems. For example, the temperate earthworm *Eiseinia foetida* is often used, while it has been proven to be more resistant than species from tropical areas (De Silva et al., 2010). In addition, these tests are conducted in very controlled conditions and

E-mail address: mathieu.coulis@cirad.fr.

https://doi.org/10.1016/j.apsoil.2021.103923
Received 24 February 2020; Received in revised form 28 January 2021; Accepted 2 February 2021
Available online 18 February 2021

cannot be directly transposed to real situations, underlining the importance of collecting data from the field. In this regard, most studies have investigated the effect of herbicides or organic conversion in temperate regions (Henneron et al., 2015; Paoletti et al., 1995; Pelosi et al., 2014) and there is a real deficit of knowledge on this subject in tropical agroecosystems.

This work aims to fill this deficit through a case study where herbicide use came to an end during the conversion to organic sugarcane production in Martinique. Sugarcane is a major crop worldwide with 26 million hectares cultivated (FAO, 2017). It is a semi-perennial crop having the ability to resprout after harvest. Fields are usually harvested for between five and ten consecutive years before replanting. Sugarcane is generally used for sugar and bio-ethanol production, but in Martinique, it is mainly used to produce top-of-the-range rums for export. There are currently no insect pests that attack sugarcane in Martinique, where the main pest is weeds. For this reason, herbicides are extensively used for weed control.

In this context, the intensive use of herbicides could be an agricultural practice strongly influencing soil invertebrates and especially saprophagous macrofauna which play an important role in providing services related to the sustainability of fertility. In spite of their important role, there is little data on soil invertebrates in soils under sugarcane cultivation and even less is known about the impact of agricultural practices on soil invertebrates. The aim of this work is therefore to (1) contribute to increasing our knowledge on the assemblage of soil saprophagous invertebrate communities under sugarcane cultivation and (2) to investigate the effects of organic conversion on these communities under real sugarcane cultivation conditions.

2. Materials and methods

2.1. Study site

The study was conducted in a sugarcane plantation (Distillerie Neisson) on the Caribbean coast of Martinique. The landscape is made up of a mosaic of sugarcane fields, dry forest, pasture and urban areas (Fig. 1). Martinique is a volcanic island located in the middle of the Lesser Antilles archipelago. The climate is tropical with a dry season from February to May. Mean annual temperature at the closest meteorological station (Saint Pierre, 6 km away) is 26.6 °C and mean annual precipitation is 2000 mm (average 1981–2010). The year before this study (2014) had been particularly dry; the precipitation deficit was 716 mm, i.e. 36% less than an average year (Fig. 1). The soils are shallow with a sandy texture (74% sand and 10% clay). They have developed from recent volcanic material (pyroclastic flow made of ash and pumice) and could be classified as young Andosols. The sugarcane fields investigated were mostly mechanically harvested and sugarcane dry leaves (straw) were left behind, forming a thick litter layer (approximately 30 cm). On average, fields were ploughed and manually replanted every seven years.

For the past two years, the farm has been taking steps to convert to organic farming. This study focuses on five sugarcane fields all located within 1 km of the distillery and having the same soil properties and cropping history (sugarcane for more than 20 years).

The conversion to organic farming concerns three fields covering 2.6 ha. Two fields have been undergoing conversion for two years and one field is one year into the conversion process. The conversion to organic farming has involved halting the use of herbicides and mineral fertilizers. Weeding is conducted by a combination of one to two passes with a spading machine per year (depending on weed growth) and manual weeding. Fertilization is based on three commercially available AB'FLOR© brand organic fertilizers, with the following formulations: 2N-10P-10K, 8N-4P-12K and 14N. The N from these fertilizers comes from organic substrates such as composted oil cakes and sterilized pig bristles and feathers, P and K come mostly from mineral powder approved for organic farming. These fertilizers are spread at a rate calculated to reach the same nitrogen input as in conventional farming (i.e. approximately 150 kg.ha^{-1}).

Simultaneously, two other sugarcane fields covering 2.5 ha were managed using conventional practices. In these fields, sugarcane is fertilized with mineral fertilizers (16N-7P-2K) and herbicides are used for weed control inside fields and for edge cleaning. Six commercially available herbicides are used for this purpose. As some commercial products are made of mixtures, the conventional fields received a total of eight active ingredients (S-metolachlor, mesotrione, benoxacor, pendimethalin, 2,4-D sodium salt, glyphosate, 2,4-D-ethyl ester and triclopyr) during the two years preceding the sampling. Such practices are representative of sugarcane cultivation in Martinique and in other countries in the region where high crop yields are achieved.

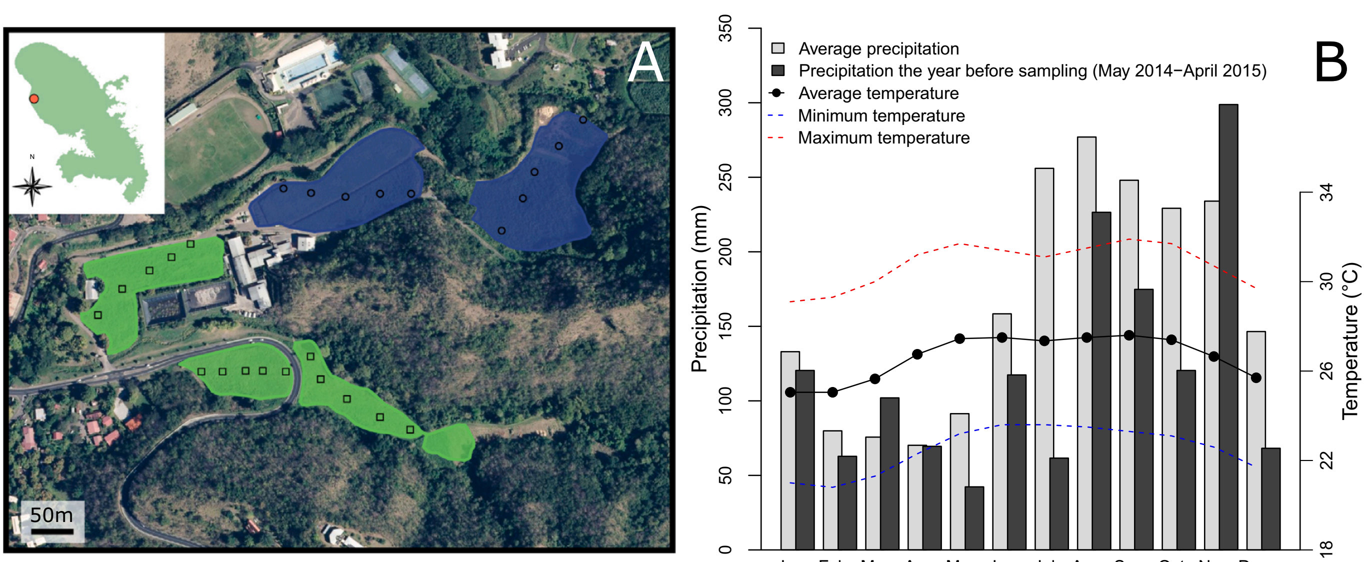

Fig. 1. Geographical localization and climate chart of the study site. (A) Sampling sites in organic and conventional fields are marked on the aerial view with green squares and blue dots respectively (image source: © IGN, 2019). (B) Monthly precipitation during the year before sampling (complete seasonal cycle from May 2014 to April 2015) plotted with the long-term means of monthly precipitation and air temperature (average 1981–2010). All data are from the St Pierre meteorological station (14°45′N, 61°10′W, 40 m a.s.l.), located 6 km from the study site (source: Météo France).

2.2. Macrofauna sampling and identification

Macrofauna sampling was carried out in the five sugarcane fields between March 20 and April 21, 2015. In each field, five sites were established along a transect, making a total of 25 independent sampling sites (Fig. 1). In each site, two complementary methods were used to sample macrofauna: a Barber pitfall trap for five days and the sampling of a 25 × 25 × 12 cm soil monolith in the vicinity. The monolith was delimited using a quadrat made of a metal frame, and the litter layer and topsoil were collected and placed in a Tullgren extractor for seven days to extract soil macrofauna. The volume of soil below was manually sorted using a 2 mm mesh sieve until a depth of approximately 12 cm. This depth corresponds to the limit of Ap horizon; deeper than this the soil has many pumice stones and macrofauna have never been found in this material. Fauna extracted with Tullgren and sorted from the soil below were brought gather together in a single tube for each monolith and preserved in 70° ethanol until identification.

More than 500 specimens of soil saprophagous macrofauna (size > 2 mm) were collected. In the first step, all specimens were sorted according to morphospecies. Then, depending on the availability of documentation and the availability of specialists for each group, specimens were identified to the species level.

2.3. Micro-habitat characterization

In order to characterize the micro-habitat of soil invertebrate, five variables concerning weeds and soil characteristics were measured on each sampling site ($n = 25$). All weeds were collected on 2 m^2 around the monolith sample, plant species were then identified and dried at 60 °C over 48 h. These data made it possible to measure weed richness (number of weed species per site) and weed biomass ($g.m^{-2}$). Then, samples of litter and surface soil (depth of 0 to 10 cm) were collected and dried at 65 °C and 105 °C respectively in order to measure their gravimetric water content (% of dry mass). After Tullgren extraction, the litter collected in the quadrat was dried at 60 °C in order to estimate the standing litter mass ($g.m^{-2}$).

2.4. Community indices

Abundance and biomass were estimated using data from only the soil monolith. Abundance is given in number of individuals per square meter ($ind.m^{-2}$). In order to accurately estimate the biomass, all the specimens collected by hand sorting were kept alive and brought to the lab for individual weighing and photographing. These data were used to develop allometric equations for estimating the fresh biomass of earthworms and diplopods from body size measurements (for more details see Coulis and Joly, 2017). For other invertebrate taxa (Gastropoda, Isopoda and Insecta), the fresh body mass was measured on a subset of specimens for each species, then an averaged biomass value was attributed to each individual of the same species. Though this method is less accurate, it concerned less than 10% of the biomass data. The combination of direct measurements and indirect biomass calculations made it possible to accurately estimate the biomass of all specimens sampled through the quadrat method, which is expressed in fresh mass per square meter ($mg.m^{-2}$). Biodiversity metrics were calculated using data from both soil monoliths and Barber pitfall traps. The species richness, the Shannon diversity index (using a natural logarithm base) and the Shannon evenness index were calculated for each site independently.

2.5. Statistical analyses

The micro-habitat variables (weed biomass, mean weed richness, litter mass, litter and soil gravimetric water content) were analyzed for differences between conventional and organic practices using a Generalized Linear Mixed-Effects Model procedure (using the glmer function of the lme4 package). A model for each variable was built including the farming practices (organic versus conventional) as a fixed effect and position of the sample along the gradient (on the edge or in the center of the field) as a random factor, to take into account intra-field variability. As visual diagnostics revealed a skewed distribution for all variables, Poisson distribution was considered to be the best descriptor for data. Residuals of each model were checked for normality.

Data for abundance, biomass and mean diversity were analyzed for differences between conventional and organic conversion fields using Generalized Linear Models (using the glm function of the lme4 package). The distribution of all variables was considered to be Poisson (link function = Quasipoisson) and co-variable accounting for different micro-habitat conditions in every site were included as fixed factors in the model. After testing for several micro-habitat factors, the gravimetric soil water content was shown to have the most important effect on soil macrofauna and was retained as a co-variable for all models.

In order to test which micro-habitat variables best explain invertebrate diversity, paired correlation tests were conducted between biodiversity and micro-habitat variables. The correlations between variables were explored with the SMA regression method (using the smartr package).

For describing changes in community composition between conventional and organic conversion fields, the community matrix was analyzed using Non-metric Multidimensional Scaling (NMDS) and Analysis of similarities (ANOSIM) procedures (using the functions MetaMDS and anosim of the vegan package). All statistical analyses were conducted with R version 3.3.2 (R Core Team, 2016) and with an alpha level of 0.05.

3. Results

3.1. Effect of conversion to organic farming on micro-habitat variables

Conversion to organic farming significantly affected the micro-habitat variables measured at the scale of the sampling site. Weed biomass was more than 2.5 times higher in sugarcane fields under conversion, however the mean weed richness was not significantly affected by conversion (Table 1). The standing litter mass was more than 1.5 times higher and relative humidity nearly doubled in sugarcane fields under conversion (Table 1). In contrast, soils were slightly wetter in conventionally farmed fields (Table 1).

3.2. Effect of conversion to organic farming on soil saprophagous macrofauna abundance and biomass

Conversion to organic farming had a profound effect on the community of soil saprophagous macrofauna. The abundance of the community was 342 ± 78 $ind.m^{-2}$ in fields under conversion, compared to 146 ± 34 $ind.m^{-2}$ in fields under conventional practices (mean ± SE). However, conversion had different effects according to the taxonomic

Table 1
Micro-habitat variables according to farming practice. Measurements concerning weed and soil characteristics were made on each sampling site (n = 15 for organic farming and n = 10 for conventional farming). For each variable, a glm model was used to test for the significance of the farming practice.

Micro-habitat variables	Organic farming (mean ± SE)	Conventional farming (mean ± SE)	*p*-Value
Weed biomass ($g.m^{-2}$)	41.7 ± 9.5	16.3 ± 9.4	<0.0001***
Mean weed richness (per sample)	2.5 ± 0.4	1.9 ± 0.3	0.299
Litter mass ($g.m^{-2}$)	22.8 ± 2.8	14.9 ± 3.2	<0.0001***
Litter gravimetric water content (%)	20.5 ± 2.6	11.2 ± 1.9	<0.0001***
Soil gravimetric water content (%)	8.3 ± 0.5	9.9 ± 0.7	<0.0001***

group (Fig. 2, Table S1). Conversion had a marked effect on isopod and gastropod abundance. In contrast, no significant difference between conventional and organic farming was observed for diplopod abundance. Between these contrasting responses, earthworms were shown to have an intermediate response to conversion: earthworm abundance was not significantly different but its biomass increased significantly from 3.2 g.m^{-2} in conventional fields to 11 g.m^{-2} in organic ones (Figs. 2–3). The biomass of the whole community followed the same trend as abundance, with an increase from 11.6 g.m^{-2} in conventional fields to 35 g.m^{-2} in organic ones (Table S2). Each taxonomic group also revealed a trend for a higher biomass (Fig. 3, Table S2). It is worth noting that gastropod biomass drastically increased due to the sampling of an individual *Achatina fulica*, the African giant snail, which created heterogeneity in the data.

3.3. Effect of conversion to organic farming on soil saprophagous macrofauna diversity

Across all the samples, 25 (morpho)species were identified (see Table S3). The earthworm community had two exotic introduced species: *Pontoscolex corethrurus* (endogeic) and *Amynthas rodericensis* (epigeic). The diplopod community had seven species and was dominated by two iuliform species: *Anadenobolus monilicornis* and *Trigoniulus corallinus* (Table S3). The isopoda community had five morphospecies and was dominated by *Pseudotyphloscia alba*, *Philosciidae* sp. and *Trichorhina* sp. The snail community had four species and was clearly dominated by *Subulina octona*. Finally, few saprophagous insects were collected; they were mostly coleoptera among which a small scarab (*Ataenius* sp.) is the most abundant.

Unlike abundance, the diversity of soil saprophagous macrofauna was similar between conventional and organic fields (Fig. 4). The mean specific richness per sampling unit, the Shannon index and the evenness were all non-significantly different between sugarcane fields under each farming system. The NMDS analysis showed a strong overlap of the space representing communities occurring in each farming system (Fig. S1). This was confirmed by ANOSIM, indicating non-significant differences between organic conversion and conventional fields ($P = 0.059$). All the micro-habitat variables were investigated but the only factor affecting significantly the diversity of soil saprophagous invertebrate was the amount of litter on the soil. The litter mass at each sampling site was positively related to the mean specific richness per site (Fig. 5).

4. Discussion

This study makes a significant contribution to increasing our knowledge on the soil saprophagous macroinvertebrates of tropical agroecosystems in Martinique. Despite being part of a Caribbean biodiversity hotspot, soil biodiversity in Martinique has received little attention apart from two studies on collembolans and nematodes (Loranger et al., 1998a; Queneherve and Van den Berg, 2005). The macrofauna of Martinique was still largely unknown (see Blanchart (2002) and Loranger et al. (1998b)). Diplopod and earthworm species found in the present study were already known to be present in Guadeloupe (Csuzdi and Pavliček, 2009; James and Gamiette, 2016; Loranger-Merciris et al., 2007) where they occur in the same habitats as in Martinique. Such homogeneity in community composition (low beta diversity) at the Lesser Antilles scale can be explained by the fact that a large proportion of communities in cultivated areas comprises exotic introduced species which have been homogenized by past intense exchanges between the islands of the Lesser Antilles archipelago.

The saprophagous invertebrate abundance measured in this study falls within the range measured by Loranger-Merciris et al. (2007) in the secondary forests of Guadeloupe (i.e. between 75 and 250 ind.m^{-2}). Even if the species pool was different, the specific richness of diplopods was similar (seven species in both studies).This result emphasized that current sugarcane cultivation practices allow for the development of an important community of soil saprophagous invertebrates. Large amounts of organic matter are left in the fields after the cane harvest, creating a thick mulch that is both a habitat and a resource for such organisms. Previous sugarcane production practices involved preharvest burning that might be a very strong perturbation to populations by directly killing and removing potential resources for saprophagous invertebrates. This hypothesis is supported by previous data from Martinique (Blanchart and Bernoux, 2005) indicating a lower abundance of saprophagous macrofauna in sugarcane fields using preharvest burning (110 ind.m^{-2}) compared to green cane harvesting (220 ind.m^{-2}). Similar effects of burning on earthworm populations are reported by Dlamini and Haynes (2004) in South Africa and Spain et al. (1990) in Australia. These examples clearly illustrate how agricultural practices shape soil invertebrate communities. Even though herbicides contain active substances that do not especially target soil invertebrates, their intensive use in sugarcane cultivation (Ibrahim, 1984; Nachimuthu et al., 2016) is a practice that could strongly influence the soil invertebrate community. Correia and Moreira (2010) have proved the toxicity of two herbicides (2,4 D and glyphosate) for earthworms in laboratory experiments. These herbicides are used worldwide in sugarcane cultivation as well as in the conventional fields of this study. However, barely

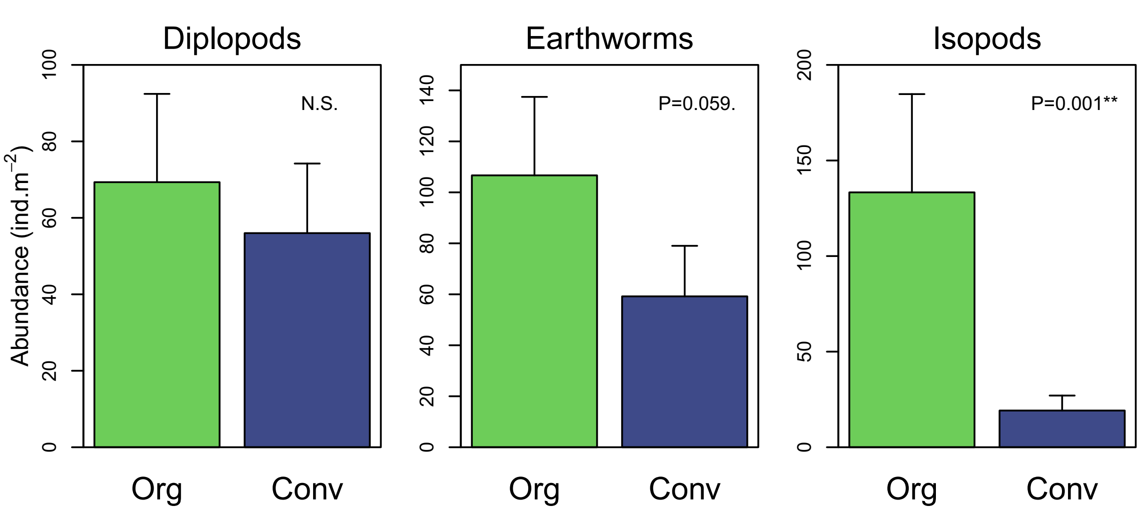

Fig. 2. Abundance of the three main invertebrate groups according to farming practice (mean ± SE, $n = 15$ for organic farming and $n = 10$ for conventional farming).

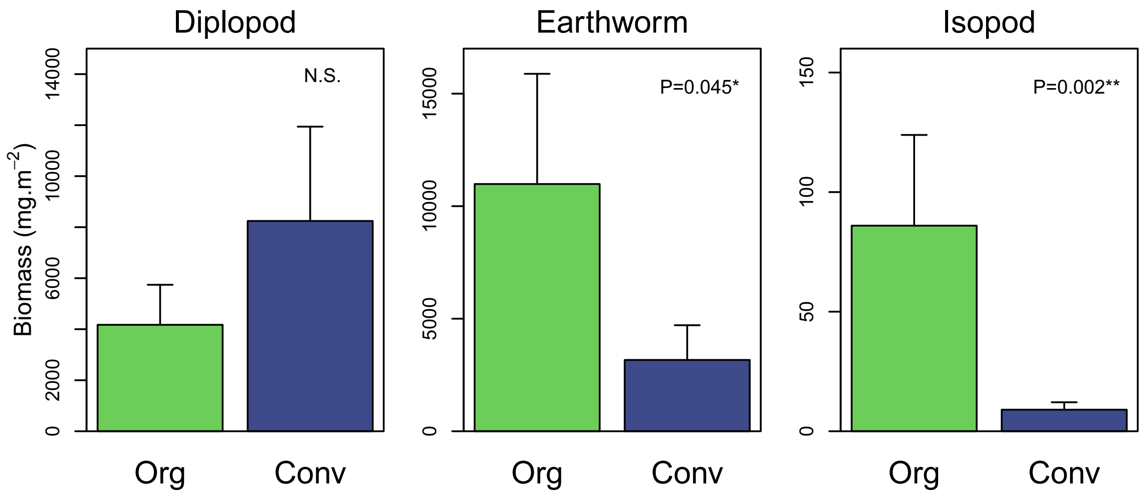

Fig. 3. Biomass of the three main invertebrate groups according to farming practice (mean ± SE, n = 15 for organic farming and n = 10 for conventional farming).

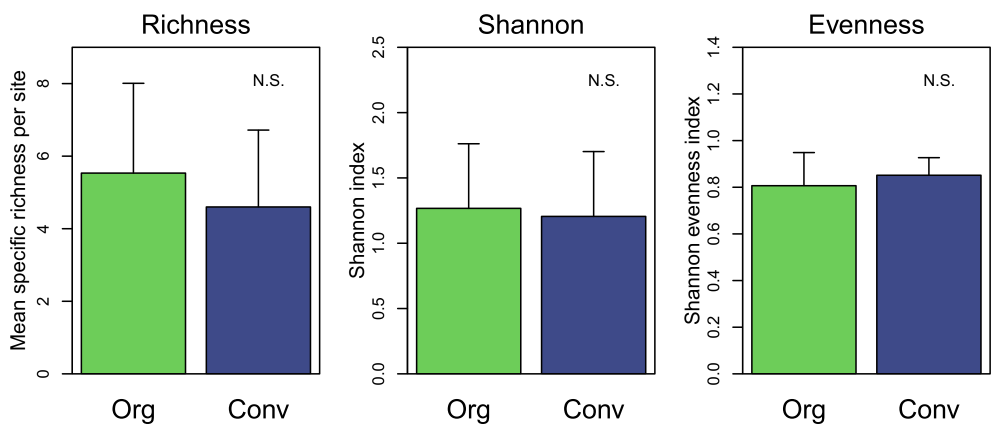

Fig. 4. Diversity of the saprophagous invertebrate community according to farming practice. Each index was calculated at the site scale (mean ± SE, n = 15 for organic farming and n = 10 for conventional farming).

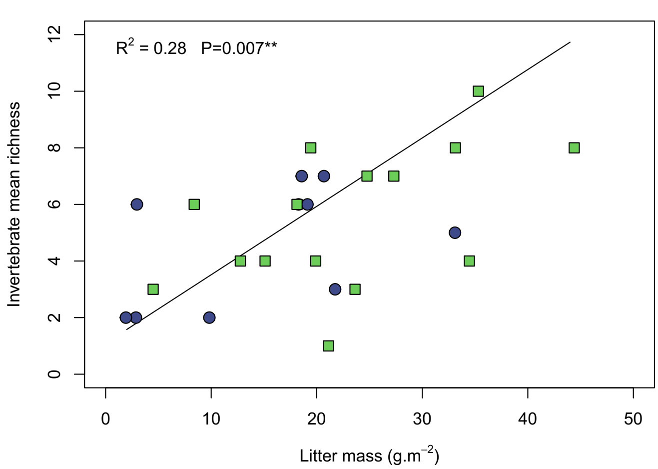

Fig. 5. Relationship between litter standing mass and invertebrate mean richness per site. The line plotted was estimated using the SMA regression method. Green squares and blue circles indicate data from organic and conventional farming respectively.

nothing is known about how a mixture of herbicides (cocktail effect) can affect populations of soil organisms in the field (Kortenkamp et al., 2009; Relyea, 2009).

The results of this study show that the conversion to organic farming had a positive effect on the abundance of saprophagous macrofauna. No chemical fertilizers nor herbicides were used in fields under organic conversion, consequently the differences with conventional fields could be explained by a diminution of the toxic effect of herbicides, which are the main pesticide used in sugarcane cultivation.

In a temperate climate, Henneron et al. (2015) have shown that conversion to organic farming had a beneficial effect on most soil invertebrates. Pelosi et al. (2014) have reviewed the effects of pesticides on earthworms at the individual level as well as at the community scale. At the individual scale, the effects mostly concerned a reduction of fertility rather than direct toxicity increasing mortality. At the community scale, a summary of six studies comparing organic and conventional farming shows that conversion to organic farming causes an increase in the abundance and biomass of earthworms. Our study confirms this general trend and shows that conversion to organic farming had a positive effect on earthworms and, more generally, on the community of saprophagous macrofauna in a tropical context. However, the response to farming practices was dependent on soil invertebrate taxa. Isopods and gastropods were strongly affected, reinforcing the knowledge we have on these organisms (not very mobile, with a high assimilation rate and bio-accumulation of pollutants) which are often used as bio-indicators (Oehlmann and Schulte-Oehlmann, 2003; Paoletti, 2012). Although earthworms were affected by farming practices, they responded in a less pronounced manner (only biomass but not abundance was significantly affected). This more pronounced effect on biomass was probably the combination of a slightly smaller abundance and a slightly smaller mean individual weight in conventional farming. Despite earthworms responding in a less pronounced manner than other invertebrate groups, this result still confirms the trend towards increased earthworm biomass in organic farming, as was previously observed in temperate regions (Pelosi et al., 2014). In contrast, diplopods were not significantly affected by a change in farming practices. Ecotoxicological studies suggest a weak toxicity of herbicides in diplopods (Da Silva Souza et al., 2014). Several field studies have also shown that diplopods are less affected (Paoletti et al., 1995) or do not even respond to a conversion to organic farming (Henneron et al., 2015). This seems to confirm that diplopods are less sensitive to pesticides than other soil invertebrates.

The results of this study show no change in any diversity metric in fields under conversion to organic farming compared to fields conventionally farmed. Even if biodiversity can change according to farming practices (Hole et al., 2005), it is also strongly constrained by other factors affecting the local species pool and acting at the landscape level, such as the diversity of habitats surrounding the field, proportion of non-cultivated area, hedges or other ecological corridors (Bengtsson et al., 2005; Tscharntke et al., 2002). As suggested by Bengtsson et al. (2005), it is likely that the effect of organic farming on biodiversity depends on the landscape structure, with a more pronounced effect in uniform landscapes dominated by intensive agriculture and less pronounced effects in heterogeneous landscapes providing a mosaic of habitats. The varied landscape in this study could explain why fields under conventional farming have quite good diversity and why the conversion to organic farming did not significantly impact biodiversity. It is also possible that the short period since conversion had not yet allowed new species to colonize the fields, especially because of the poor dispersal abilities (no wings) of most saprophagous invertebrates.

Even if numerous potentially toxic active substances draw attention at first sight, the observed effect of organic conversion cannot be attributed to only the detrimental effect of herbicides but also the potential beneficial effects of organic fertilizer. Indeed, the beneficial effects of organic fertilizers on soil fauna have been demonstrated many times (D'Hose et al., 2018; Edwards, 1983; Whalen et al., 1998) and could explain the results of our field study. However, there is no reason that organic fertilizers strongly stimulated earthworms and isopods but not diplopods, which are recognized as important litter consumers. Therefore, this result indicates that the effect of organic conversion is more likely assignable to a halt in herbicide use. Nevertheless, the way herbicides affect soil fauna remains a complex topic. Herbicides not only affect soil organisms through direct toxicity, but they also eliminate plant cover and consequently strongly modify the micro-habitat of soil fauna (Brust, 1990). In our study, we clearly observed different micro-habitat conditions in organic fields compared to conventional ones (Table 1). Both weed biomass and litter mass were significantly higher in organic fields and litter also had a higher water content. Previous works have shown that herbicides change habitat structure (plant height) and could alter soil temperature and humidity, leading to a decrease in the abundance of various predators (Hawes et al., 2003) such as web-spinning spiders (Haughton et al., 2001) and large carabid beetles (Brust, 1990). Hawes et al. (2003) have shown a negative impact of herbicides on the green food web (herbivores and pollinators) but found mitigated results for the brown food web (detritivores), suggesting an herbicide effect mediated by the suppression of trophic resource. Although the link between herbicide habitat modification and macrofauna of the brown food web has been poorly investigated, House et al. (1987) suggest that herbicide effects could be mediated by such habitat modification. In our work, it is likely that micro-habitat destruction or alteration (see Table 1) has been an important pathway by which herbicides have affected soil saprophagous invertebrates. It is striking to note the importance of mulch since it provides "bed and board" for saprophagous invertebrates. Independently of herbicide use, the biodiversity of invertebrates was correlated to litter mass (Fig. 5), indicating that keeping the soil covered with a mulch is an agricultural practice which must be promoted in order to achieve the restoration of soil biological processes and sustained soil biodiversity.

5. Conclusion

In summary, communities of saprophagous macrofauna in sugarcane cultivation have shown a marked response to the conversion to organic farming, even after a short period of conversion. However, the response was taxa-specific, isopods and gastropods exhibiting marked responses both in terms of abundance and biomass. Earthworm biomass increased but not earthworm abundance, and diplopods were not affected by the conversion to organic farming. This pattern probably reflects the contrasted functional traits of invertebrates (Hedde et al., 2012). Future work should search for functional traits related to invertebrate response to herbicide disturbance in order to advance our understanding of the mechanisms responsible for herbicide effects. In the present work it is hypothesized that herbicides had an indirect effect via the modification of the micro-habitat of macrofauna (change in standing litter mass and litter humidity) caused by a drastic reduction in plant biomass in conventional fields.

Declaration of competing interest

The author declares that he have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

I would like to thank the following specialists: Francis Deknuydt (Coleoptera), Regis Delannoye (Gastropda), Jean-Jacque Geoffroy and Jean-Paul Mauriès (Diplopoda), Frank Noël (Isopoda) and Malalatiana Razafindrakoto (Oligochaeta) for their help in soil invertebrate identification.

This work was supported by the European Regional Development Fund (ERDF) and the Martinique Regional Authority (CTM) [grant number 33115]. The field research was conducted at EARL Domaines Thieubert (Distillerie Neisson) thanks to the involvement of C. Neisson-Vernant, G. Vernant and J. Mocquot. I thank A. Bobi and all the workers from the factory for their technical help.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.103923.

References

Bengtsson, J., Ahnström, J., Weibull, A.-C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. J. Appl. Ecol. 42, 261–269.
Blanchart, E., 2002. Diversité de la faune du sol dans les systèmes cultivés en Martinique. Cah. PRAM 2, 15–17.
Blanchart, E., Bernoux, M., 2005. Déterminants des stocks de carbone des sols des Petites Antilles (Martinique, Guadeloupe). Alternatives de séquestration du carbone et spatialisation des stocks actuels et simulés (c. r. du programme GESSOL). IRD, Montpellier, France.
Brust, G.E., 1990. Direct and indirect effects of four herbicides on the activity of carabid beetles (Coleoptera: Carabidae). Pestic. Sci. 30, 309–320.
Correia, F.V., Moreira, J.C., 2010. Effects of glyphosate and 2, 4-D on earthworms (*Eisenia foetida*) in laboratory tests. Bull. Environ. Contam. Toxicol. 85, 264–268.
Coulis, M., Joly, F.-X., 2017. Allometric equations for estimating fresh biomass of five soil macroinvertebrate species from neotropical agroecosystems. Eur. J. Soil Biol. 83, 18–26.
Csuzdi, C., Pavlíček, T., 2009. New records of earthworms from Guadeloupe with description of a new species (Oligochaeta: Glossoscolecidae, Acanthodrilidae, Megascolecidae and Eudrilidae). Opusc. Zool. Bp. 40, 9–15.
Da Silva Souza, T., Christofoletti, C.A., Bozzatto, V., Fontanetti, C.S., 2014. The use of diplopods in soil ecotoxicology–a review. Ecotoxicol. Environ. Saf. 103, 68–73.

De Silva, P.M.C.S., Pathiratne, A., van Gestel, C.A., 2010. Toxicity of chlorpyrifos, carbofuran, mancozeb and their formulations to the tropical earthworm *Perionyx excavatus*. Appl. Soil Ecol. 44, 56–60.

D'Hose, T., Molendijk, L., Vooren, L.V., van den Berg, W., Hoek, H., Runia, W., van Evert, F., ten Berge, H., Spiegel, H., Sandèn, T., Grignani, C., Ruysschaert, G., 2018. Responses of soil biota to non-inversion tillage and organic amendments: an analysis on European multiyear field experiments. Pedobiologia 66, 18–28.

Dlamini, T.C., Haynes, R.J., 2004. Influence of agricultural land use on the size and composition of earthworm communities in northern KwaZulu-Natal, South Africa. Appl. Soil Ecol. 27, 77–88.

Edwards, C.A., 1983. Earthworm ecology in cultivated soils. In: Satchell, J.E. (Ed.), Earthworm Ecology: From Darwin to Vermiculture. Springer Netherlands, Dordrecht, pp. 123–137.

FAO, 2017. FAO Global Statistical Yearbook [WWW Document]. URL. http://www.fao.org/faostat/en/#data/QC (accessed 1.21.20).

Fox, C.J.S., 1964. The effects of five herbicides on the numbers of certain invertebrate animals in grassland soil. Can. J. Plant Sci. 44, 405–409.

Hassan, S.A., Bigler, F., Bogenschütz, H., Boller, E., Brun, J., Calis, J.N.M., Coremans-Pelseneer, J., Duso, C., Grove, A., Heimbach, U., others, 1994. Results of the sixth joint pesticide testing programme of the IOBC/WPRS-Working Group «Pesticides and Beneficial Organisms». Entomophaga 39, 107–119.

Haughton, A.J., Bell, J.R., Boatman, N.D., Wilcox, A., 2001. The effect of the herbicide glyphosate on non-target spiders: part II. Indirect effects on *Lepthyphantes tenuis* in field margins. Pest Manag. Sci. 57, 1037–1042.

Hawes, C., Haughton, A.J., Osborne, J.L., Roy, D.B., Clark, S.J., Perry, J.N., Rothery, P., Bohan, D.A., Brooks, D.R., Champion, G.T., 2003. Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the farm scale evaluations of genetically modified herbicide-tolerant crops. Philos. Trans. R. Soc. B Biol. Sci. 358, 1899.

Hedde, M., Van Oort, F., Lamy, I., 2012. Functional traits of soil invertebrates as indicators for exposure to soil disturbance. Environ. Pollut. 164, 59–65.

Henneron, L., Bernard, L., Hedde, M., Pelosi, C., Villenave, C., Chenu, C., Bertrand, M., Girardin, C., Blanchart, E., 2015. Fourteen years of evidence for positive effects of conservation agriculture and organic farming on soil life. Agron. Sustain. Dev. 35, 169–181.

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A.D., 2005. Does organic farming benefit biodiversity? Biol. Conserv. 122, 113–130.

House, G.J., Worsham, A.D., Sheets, T.J., Stinner, R.E., 1987. Herbicide effects on soil arthropod dynamics and wheat straw decomposition in a North Carolina no-tillage agroecosystem. Biol. Fertil. Soils 4, 109–114.

Ibrahim, A.a.S., 1984. Weed competition and control in sugarcane. Weed Res. 24, 227–231.

James, S.W., Gamiette, F., 2016. New species of *Dichogaster* Beddard, 1888 (Clitellata: Benhamiidae) with additional records of earthworms from Guadeloupe (French West Indies). Zootaxa 4178, 391–408.

Kortenkamp, A., Backhaus, T., Faust, M., 2009. State of the art report on mixture toxicology. Rep. Comm. Eur. Comm. DG Environ. 22–25.

Lavelle, P., 1996. Diversity of soil fauna and ecosystem function. Biol. Int. 33, 3–16.

Lavelle, P., Spain, A.V., Blanchart, E., Martin, A., Martin, S., 1992. Impact of soil fauna on the properties of soils in the humid tropics. In: Myths and Science of Soils of the Tropics. Soi Science Society of America Special Publication, pp. 157–185.

Lavelle, P., Barros, E., Blanchart, E., Brown, G., Desjardins, T., Mariani, L., Rossi, J.-P., 2001. SOM management in the tropics: why feeding the soil macrofauna? Nutr. Cycl. Agroecosystems 61, 53–61.

Loranger, G., Ponge, J.-F., Blanchart, E., Lavelle, P., 1998a. Impact of earthworms on the diversity of microarthropods in a vertisol (Martinique). Biol. Fertil. Soils 27, 21–26.

Loranger, G., Ponge, J.-F., Blanchart, É., Lavelle, P., 1998b. Influence of agricultural practices on arthropod communities in a vertisol (Martinique). Eur. J. Soil Biol. 34, 157–165.

Loranger-Merciris, G., Imbert, D., Bernhard-Reversat, F., Ponge, J.-F., Lavelle, P., 2007. Soil fauna abundance and diversity in a secondary semi-evergreen forest in Guadeloupe (Lesser Antilles): influence of soil type and dominant tree species. Biol. Fertil. Soils 44, 269–276.

Merlini, V.V., Nogarol, L.R., Marin-Morales, M.A., Fontanetti, C.S., 2012. Toxicity of trifluralin herbicide in a representative of the edaphic fauna: histopathology of the midgut of *Rhinocricus padbergi* (Diplopoda). Microsc. Res. Tech. 75, 1361–1369.

Nachimuthu, G., Halpin, N.V., Bell, M.J., 2016. Effect of sugarcane cropping systems on herbicide losses in surface runoff. Sci. Total Environ. 557–558, 773–784.

Oehlmann, J., Schulte-Oehlmann, U., 2003. Molluscs as bioindicators. Trace Met. Contam. Environ. 6, 577–635.

Paoletti, M.G., 2012. Invertebrate Biodiversity as Bioindicators of Sustainable Landscapes: Practical Use of Invertebrates to Assess Sustainable Land Use. Elsevier.

Paoletti, M.G., Schweigl, U., Favretto, M.R., 1995. Soil macroinvertebrates, heavy metals and organochlorines in low and high input apple orchards and a coppiced woodland. Pedobiologia 39, 20–33.

Pelosi, C., Barot, S., Capowiez, Y., Hedde, M., Vandenbulcke, F., 2014. Pesticides and earthworms. A review. Agron. Sustain. Dev. 34, 199–228.

Queneherve, P., Van den Berg, E., 2005. Liste des nématodes phytoparasites (Tylenchida et Dorylaimida) des départements français d'Amérique (Guadeloupe, Martinique et Guyane) et dispositions réglementaires. EPPO Bull. 35, 519–530.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Relyea, R.A., 2009. A cocktail of contaminants: how mixtures of pesticides at low concentrations affect aquatic communities. Oecologia 159, 363–376.

Spain, A.V., Saffigna, P.G., Wood, A.W., 1990. Tissue carbon sources for *Pontoscolex corethrurus* (Oligochaeta: Glossoscolecidae) in a sugarcane ecosystem. Soil Biol. Biochem. 22, 703–706.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A., Thies, C., 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecol. Appl. 12, 354–363.

Whalen, J.K., Parmelee, R.W., Edwards, C.A., 1998. Population dynamics of earthworm communities in corn agroecosystems receiving organic or inorganic fertilizer amendments. Biol. Fertil. Soils 27, 400–407.

Wolters, V., Ekschmitt, K., 1997. Gastropods, isopods, diplopods, and chilopods: neglected groups of the decomposer food web. In: Fauna in Soil Ecosystems: Recycling Processes, Nutrient Fluxes, and Agricultural Production. Marcel Dekker, inc., New York, pp. 265–306.