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Soil macrofauna abundance under dominant tree species increases along a soil degradation gradient

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ABSTRACT

Soil macrofauna contribute to key soil functions underpinning soil-mediated ecosystem services. There is limited understanding about the role of trees as 'resource islands' for soil macrofauna in agricultural landscapes and how this interaction is affected by soil degradation status. The study assessed the spatial influence of three dominant trees namely, *Croton megalocarpus*, *Eucalyptus grandis* and *Zanthoxylum gilletii*, on soil macrofauna abundance, along a soil degradation gradient resulting from continuous cultivation for 10, 16 and 62 years. It was hypothesised that spatial variation in soil macrofauna abundance is affected by duration of cultivation, tree species and distance from the tree trunk. Soils cultivated for 10 years showed highest soil nutrient levels. Notably, soil C and N were higher below the canopy of *C. megalocarpus* (64.6 g kg^{-1} C; 6.7 g kg^{-1} N), than *E. grandis* (58.7 g kg^{-1} C; 5.9 g kg^{-1} N) and *Z. gilletii* (54.5 g kg^{-1} C; 5.6 g kg^{-1} N) after 10 years of cultivation. Similar trends were also found after 16 and 62 years of cultivation, although the mean values for the two elements were below 40.0 g kg^{-1} and 4.0 g kg^{-1}, respectively. Higher soil macrofauna abundance was found after 16 and 62 years of cultivation, though this was dependent on tree species and soil macrofauna group. Earthworm abundance was highest below the canopy of *Z. gilletii* averaging 389 individuals and 160 individuals m^{-2}, respectively, compared to 14 individuals m^{-2} after 10 years of cultivation. Conversely, beetles showed higher numbers under *E. grandis* and *C. megalocarpus* than under *Z. gilletii*. Highest numbers of termites and centipedes were found under *E. grandis* after 16 years of cultivation. These findings support the importance of a diverse tree cover in agricultural landscapes to conserve soil macrofauna communities and the contribution of their activity to soil ecological functions.

1. Introduction

Soil biota is a central constituent of any ecosystem, whether natural or managed, due to their role in regulating key soil functions such as organic matter decomposition, nutrient cycling and soil structure maintenance (Brussaard et al., 1997; Barrios, 2007). Soil macrofauna constitute an important component of soil biota given the significant impact of their activities on soil properties (Lavelle, 1997; Ayuke et al., 2009). Earthworms and termites, for example, have earned recognition as 'ecosystem engineers' due to their significant effects on soil structure and functions through their soil-feeding, nesting and burrowing habits (Jones et al., 1994). However, their activities could be affected by management practices largely through changes in organic inputs to soil which affect food availability, and through soil disturbance (e.g. tillage) which often kill the larger species (e.g. earthworms) or the structures they inhabit and interfere with their activities (Lavelle et al., 2003; Ayuke et al., 2011; Mbau et al., 2015). Furthermore, these management practices can also contribute to the spatial heterogeneity in soil properties which underlies the distribution of soil macrofauna. Consequently, soil macrofauna are usually not uniformly

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distributed within the soil in any given space and time, but rather, aggregated in 'hotspots' of carbon-rich areas such as the rhizosphere, soil aggregates and organic detritus (Beare et al., 1995; Lavelle, 1997; Barrios et al., 2012a; Kuzyakov and Blagodatskaya, 2015). Therefore, farmer practices involving tillage, application of agricultural inputs and/or the types of plants grown on their farms may have significant positive or negative effects on soil macrofauna abundance and distribution in any given location.

Smallholder farmers often intercrop trees with annual crops for various reasons such as provision of food, forage, wood and/or charcoal, among other products (Akinnifesi et al., 2010; Nyaga et al., 2015). In some occasions, farmers deliberately retain indigenous trees during conversion of forest to cultivated lands for similar reasons (Fonte et al., 2010; Pauli et al., 2012). Trees are known to modify conditions beneath the canopy through shading, root turnover and litter inputs which significantly influence soil moisture, temperature, carbon substrate availability and nutrient regimes (Lavelle et al., 2003; Lin, 2010; Barrios et al., 2012a). Earlier research has shown predictable patterns in the variation of soil properties resulting from individual trees where litter deposition around the trees produces characteristic concentric rings of influence that are proportional to the size of the crown (Rhoades, 1997). Other studies have shown gradual decline in the content of organic carbon, nitrogen, phosphorus and exchangeable bases with increasing distance from the tree stem due to differences in litter deposition (Kater et al., 1992; Tomlinson et al., 1998; Jonsson et al., 1999). Root turnover is also a critical component of soil carbon and nutrients and therefore an important driver of belowground processes and ecological functions (Gill and Jackson, 2000; Iversen and O'Brien, 2010). Due to the feeding preference of some soil macrofauna groups for specific organic substrate types, the quality of litter and its deposition patterns as well as root turnover may therefore affect their distribution (Lavelle et al., 2003; Pauli et al., 2010). For instance, Warren and Zou (2002), Caner et al. (2004) and Frouz et al. (2013) have reported differential effects of litter quality on soil macrofauna in different systems. Further, in their recent review, Korboulewsky et al. (2016) highlighted that the litter quality from a given tree species can significantly contribute to the changes observed in soil fauna communities. Besides tree leaf litter and root turnover, stemflow could also contribute nutrients to the soil at the base of trees through the washing of dust, insect remains or bird droppings from the leaves and bark (Rhoades, 1997). Changes in soil chemistry beneath the tree could potentially affect the occurrence of soil macrofauna since soil chemical properties have been used to partially explain the variations in distribution of soil macrofauna (Ayuke et al., 2009; Pauli et al., 2011; Mbau et al., 2015). The spatial patterns of soil macrofauna abundance are thus expected to be structured in a manner that corresponds to the heterogeneity of soil resources around the tree (Korboulewsky et al., 2016). The soil beneath tree canopy can therefore be hypothesised as a distinct area of favourable or unfavourable conditions to the abundance of some soil macrofauna group(s), thus becoming an important determinant of their spatial distribution patterns. As such, in-depth research that addresses spatial-temporal patterns of soil macrofauna abundance as affected by tree attributes under contrasting soil degradation levels could significantly contribute towards the design of sustainable farming systems (Barrios et al., 2012a). Though the spatial arrangement of single trees has been shown to affect soil properties (Belsky et al., 1989; Kater et al., 1992; Rhoades, 1997; Tomlinson et al., 1998; Jonsson et al., 1999; Amiotti et al., 2000), little is known about the magnitude and pattern of their influence on soil macrofauna abundance in agricultural landscapes particularly in tropical Africa.

In this study, we assessed effects of three dominant tree species; *Croton megalocarpus* Hutch., *Eucalyptus grandis* W.Hill and *Zanthoxylum gilletii* (De Wild.) P.G.Waterman, on soil macrofauna abundance and biomass across three catchments that represent a soil degradation gradient resulting from different times since conversion from primary forest to agriculture (Kimetu et al., 2008). This provided a chronosequence experimental set-up where short/medium term effects of tree species and long-term effects of land-use change could be systematically studied. It was hypothesised that i) soil nutrient stocks and availability would decrease with increasing duration of cultivation and distance from the tree trunk, and ii) soil macrofauna abundance and biomass would decrease with increasing distance from the tree trunk and duration of cultivation but the magnitude of these effects would be modulated by tree identity.

2. Materials and methods

2.1. The study sites

The study site is located in Kapchorwa, Nandi County in several farms along the Kakamega-Nandi forest complex which lies at Latitude 0° 10′ 00″ N and Longitude: 35° 0′ 00″ E. Altitude ranges between 1600 and 1900 m above sea level. The area receives an annual precipitation of approximately 2000 mm; the rainfall is bimodal, with 'long rains' occurring between April and June (approximately 1200 mm), and 'short rains' between August and October (approximately 800 mm) (Güereña et al., 2015). Being near the equator, temperatures are relatively constant throughout the year with an average maximum daily temperature of 26 °C, an average minimum of 11 °C and a mean annual temperature of 19 °C. Soils are classified as kaolinitic Acrisols (FAO/UNESCO classification) or Ultisols (USDA classification) showing deep reddish-brown coloration and thick humic topsoil with 45–49% clay, 15–25% silt and 26–40% sand on predominantly heavier-textured Ultisols and 11–14% clay, 21–27% silt and 59–68% sand, on lighter-textured Ultisols (Kimetu et al., 2008). The indigenous vegetation is primarily highland rainforest, an extension of Guinean-Congolian belt, and dominated by *Funtumia africana* (Benth.) Stapf, *Prunus africana* (Hook.f.) Kalkman, *Ficus* spp., *Croton* spp. and *Celtis* spp. (Glenday, 2006). The farms are dominated by cereal cultivation and rarely use any form of inorganic inputs. If applied, the amounts used are barely enough to meet crop needs. Farmlands are therefore characterised by low soil fertility and crop productivity. Study farms were selected from three catchments which were under continuous cultivation for 10 years, 16 years and 62 years, since conversion from primary forest to agricultural lands. The three catchments are located within an area of 6 km^2, with their sizes ranging from 9 to 14 ha. Detailed description of these catchments can be found in Recha et al. (2013) and Güereña et al. (2015).

2.2. Identification and selection of tree species

Selection of tree species of interest was conducted using participatory action research tools in the context of focus group discussions involving randomly-selected farmers from all the three catchments (Barrios et al., 2012b). A ranked list of the most common trees within the area of study was identified and the top three most abundant trees were selected, namely, *Croton megalocarpus, Eucalyptus grandis* and *Zanthoxylum gilletii*. Selection of trees to be sampled within the three catchments was based on the following criteria: (i) dominance: for each species selected, at least three single trees could be located within each catchment. Each tree species represented a treatment; (ii) distribution: the selected trees occurred singly within the farms and were located at least 4 times their crown diameter from other trees, thus free from tree interferences; (iii) attributes: the height, shape and age of the single

trees were comparable; (iv) farm management practices: study trees were all found under the same small-holder maize-based cropping system, involving minimal superficial disturbance at planting (e.g. hand hoe) and manual weeding, across all sampling distances.

2.3. Soil macrofauna sampling protocol

In order to study the effects of tree species and canopy on soil macrofauna, soil monoliths (0.25 by 0.25 by 0.30 m) were excavated following the standard Tropical Soil Biology and Fertility Programme (TSBF) sampling protocol (Anderson and Ingram, 1993) at predetermined points around the tree (Fig. 1). The area around the selected trees was subdivided into four concentric zones, A, B, C and D based on modifications to the method used by Bayala et al. (2004). Modifications included: i) Zone A was located 0.25 m from the tree stem on all the occasions, whereas in the former it could vary between 0 and 2 m and ii) Zone D was located away from edge of the tree crown at an equivalent distance to that between A and C, whereas in the former it was located 2 m from the edge of the crown. Zone B and C were not modified and remained at the middle of the tree crown and at the tree crown edge respectively. Soil monoliths were excavated from each concentric zone following four transects at right angles from each other, for a total of 16 monoliths per tree. Sampling was conducted towards the end of the short rain season in the month of November 2014. The excavated soil was placed in plastic trays and large clods gently broken to enable hand picking of soil macrofauna. All soil macrofauna were first placed in 75% ethanol. At the end of the sampling exercise, the macrofauna (except earthworms) were transferred into fresh 75% ethanol and sealed in vials. Earthworms were transferred into 4% formaldehyde for preservation. The preservative solution was replaced when coloration change was observed. Soil macrofauna were separated into seven broad taxonomic units (orders or families), i.e. earthworms (Oligochaeta), ants (Hymenoptera), termites (Isoptera), centipedes (Chilopoda), millipedes (Diplopoda), beetles (Coleoptera) and spiders (Araneae). Other observed soil invertebrates included crickets (Orthoptera), cockroaches (Blattodea) and earwigs (Dermaptera); due to their low numbers, they were pooled together as 'other soil macrofauna'. The soil macrofauna abundance was calculated as number of individuals per square meter (individuals m^{-2}) and their biomass in grams per square meter (g m^{-2}).

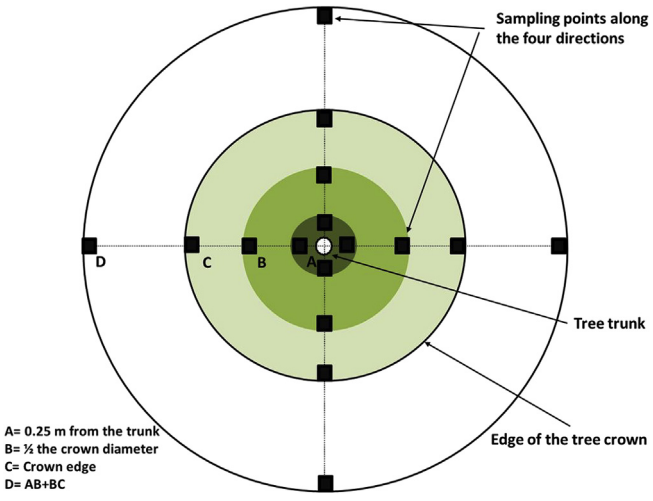

Fig. 1. Schematic representation of the sampling protocol from beneath the trees.

2.4. Collection and chemical characterisation of tree litter and roots

Leaf litter was collected in January 2015, at the beginning of the dry season when leaf fall takes place, using litter traps placed below the selected trees for a period of two weeks. Fine roots (<5 mm diameter) were dug out from several locations below the canopy concurrent with soil macrofauna sampling. After collection, the materials were air dried in the field, bulked and taken to the laboratory, where they were further dried in the oven at 60 °C to a constant weight. The dried samples were then ground and passed through a 2 mm sieve. Total macro-elements (total nitrogen (N), phosphorous (P), potassium (K), calcium (Ca) and magnesium (Mg)), total carbon (C), lignin and polyphenols were analysed from the samples. Total C and N were determined using CN-analyser while P, K, Ca and Mg were extracted through closed-vessel microwave-assisted digestion system (Miller, 1998) and determined using inductively coupled plasma atomic emission spectroscopy (Isaac and Johnson, 1998). Lignin were analysed using the acid detergent fibre method, while polyphenols were analysed using the Folin-Denis method (Anderson and Ingram, 1993).

2.5. Soil sampling and nutrient analysis

Immediately after handpicking the soil macrofauna, soil from each tree zone for the four directions (Fig. 1), was mixed thoroughly to make a composite sample of about 500 g for analysis. All soil samples were initially scanned using near-infrared (NIR) spectroscopy for the selection of 10% of total samples as reference samples to undergo conventional soil chemical analysis (Shepherd and Walsh, 2007). Soil parameters measured included: total N and C, available P, soil pH and exchangeable bases (Ca, Mg and K). Total C and N were determined using a CN-analyser, while P and the bases were extracted by the Mehlich-3 procedure (Mehlich, 1984) and measured through inductively coupled plasma atomic emission spectroscopy (Isaac and Johnson, 1998). Soil pH was determined using a pH meter with soil-water ratio of 1:2.5 (Anderson and Ingram, 1993). Soil chemical data from these reference soil samples was used to generate a calibration curve using partial least-squares regression analysis through mid-infrared spectroscopy (MIR) which was then used to determine soil parameters of the remaining 90% of the samples.

2.6. Statistical analysis

Given that the soil macrofauna data showed deviation from normality, based on Shapiro-Wilk test, and lack of homogeneity of variance (Levene's test), coupled with the complex sampling design, generalised linear mixed models (GLMM) were used to test the effects of duration of cultivation (i.e. catchment conversion age), tree species and zone of sampling using the package lme4 (Bates et al., 2015) in R (R Core Team, 2015). Further, given that the data had a considerable proportion of zero values, negative binomial regression was chosen as an extension of the Poisson distribution, using (1|Tree replicates: Tree species: Duration of cultivation) as a random term. However, it should be noted that 'duration of cultivation' is not a randomly allocated treatment and the differences between catchments could be due to other factors in addition to the duration of cultivation. The best fitting models were chosen based on the lowest Akaike Information Criterion (AIC). The high frequency of zeros values in the biomass data, however, meant that the usual statistical models were not appropriate since the models available either describe discrete distributions in which the variable can take only a few specific values or continuous distributions in which the variable can take any value in a range. In our case, we had a mixture of a continuous distribution

of non-zero values and a clump of zero values. Hence we did the analysis in two stages. First, we performed a logistic regression analysis to determine whether the response outcome was positive (e.g. presence/absence). Conditional on the outcome being positive, the second stage was to determine how these positive outcomes depended on the explanatory variables using the log-normal distribution. Multivariate principal component analysis (PCA) and Monte Carlo test were performed to assess the influence of tree species and duration of cultivation. We also conducted a redundancy analysis (RDA) to determine factors explaining soil macrofauna abundance. Soil macrofauna were entered as dependent variables whereas soil chemical properties as explanatory variables. The analysis was conducted using the Vegan package of R (Oksanen et al., 2015).

3. Results

3.1. Quality parameters of litter derived from tree species

Tree species had a considerably greater influence on litter quality parameters than the duration of cultivation (Table 1). All the chemical elements were significantly different between the different tree species. Duration of cultivation only influenced the lignin content and the L/N ratio of leaf litter, decreasing in *Z. gilletii* with time. Total C was higher in *E. grandis* (514.0 g kg^{-1}) and low in *C. megalocarpus* tree litter (472.7 g kg^{-1}), whereas total N content was low in *E. grandis* (9.1 g kg^{-1}) compared to *Z. gilletii* (13.5 g kg^{-1}) and *C. megalocarpus* (18.1 g kg^{-1}). Thus C/N values were low in the litter of native trees, *C. megalocarpus* and *Z. gilletii*, with values of 27:1 and 36:1, respectively, compared to 57:1 in litter derived from the exotic tree *E. grandis*. Phosphorous was more than 3 times higher in *C. megalocarpus* and *Z. gilletii* litter than that of *E. grandis*. Like the C/N, the C/P ratios were higher in *E. grandis* than the native trees. Therefore, the quality of *E. grandis* litter was very low as measured by C/N and C/P ratios, compared to that of the two indigenous trees, *C. megalocarpus* and *Z. gilletii*. Exchangeable bases (K, Ca and Mg) were remarkably higher in *C. megalocarpus* litter than that of the other two trees species. *C. megalocarpus* contained the lowest concentration of polyphenols (6.5%) whereas *E. grandis* had the highest (13.5%). Due to the low concentration of N in *E. grandis*, the ratios L/N, PP/N and (L + PP)/N, were also higher in *E. grandis* litter.

3.2. Quality parameters of fine roots derived from tree species

Similar to the litter, duration of cultivation had little influence on root quality parameters (Table 2). Only root C content was significantly affected by duration of cultivation, particularly in *Z. gilletii*. All the chemical elements (except K and Mg) differed significantly among the tree species. Total N was very low in *E. grandis* (5.5 g kg^{-1}) compared *C. megalocarpus* (14.0 g kg^{-1}) and *Z. gilletii* (17.1 g kg^{-1}). Phosphorous was at least 60% higher in *C. megalocarpus* and *Z. gilletii* roots than those of *E. grandis*. Due to the low N and P content, C/N and C/P ratios were large in *E. grandis* with values exceeding 75:1 and 700:1, respectively compared to lowest values < 40:1 and < 400:1, respectively recorded in *C. megalocarpus* fine roots. Contrary to the other elements, Ca was significantly higher (16.9 g kg^{-1}) in *E. grandis* roots, while averages of 13.3 g kg^{-1} and 10.9 g kg^{-1} were found in *C. megalocarpus* and *Z. gilletii* roots, respectively. Lignin was about 25% and polyphenols about 8% in *E. grandis* roots compared to *C. megalocarpus* (14.1%; 0.9%) and *Z. gilletii* (13.3%; 2.6%).

3.3. Effects of duration of cultivation and tree species on soil chemical properties

Duration of cultivation and tree species had significant effects on soil chemical properties (Table 3). Soil below *E. grandis* was slightly lower in pH with values of 5.9 compared to the other two tree species *C. megalocarpus* and *Z. gilletii*, both with values of 6.2. There was significantly higher C and N in soil after 10 years of cultivation compared 16 and 62 years (Table 4). Notably, these elements were higher below the canopy of *C. megalocarpus*, (64.5 g kg^{-1} C; 6.7 g kg^{-1} N), compared to *E. grandis* (58.7 g kg^{-1} C; 5.9 g kg^{-1} N) and *Z. gilletii* (54.5 g kg^{-1} C; 5.6 g kg^{-1} N). The C and N content under the trees in soil after 16 and 62 years of cultivation was generally below 40.0 g kg^{-1} and 4.0 g kg^{-1}, respectively, except under the canopy of *C. megalocarpus* in soil after 16 years of cultivation. Thus due to the lower N content, the soil C/N ratios were relatively higher in the farms with longer duration of cultivation compared to farms with shorter conversion age. Exchangeable Ca and Mg showed a similar trend with the highest values recorded below the canopy of *C. megalocarpus* (4.8 g Ca; 376.9 mg Mg kg^{-1}) and lowest on *Z. gilletii* (3.9 g Ca; 352.3 mg Mg kg^{-1}) in soil after 10 years of cultivation. Available P was significantly different as a function of duration of cultivation but not between tree species. In particular, P was higher in soil after 16 and 62 years (15.8 mg and

Table 1
Tree litter quality parameters (mean ± SE) as influenced by duration of cultivation and tree species.

Parameter	Tree species									*p*-value	
	Croton megalocarpus			*Eucalyptus grandis*			*Zanthoxylum gilletii*				
	10 years	16 years	62 years	10 years	16 years	62 years	10 years	16 years	62 years	Duration of cultivation	Species
C (g kg^{-1})	466.3 (3.0)	473.7 (3.0)	478.0 (5.0)	511.0 (3.0)	514.7 (1.0)	516.3 (1.0)	492.7 (1.0)	492.3 (4.0)	477.0 (5.0)	0.255	**<0.001*****
N (g kg^{-1})	16.2 (0.8)	21.2 (0.3)	17.0 (0.3)	9.1 (1.4)	8.4 (0.3)	9.7 (1.0)	14.7 (1.7)	13.1 (1.0)	12.8 (0.4)	0.545	**<0.001*****
P (g kg^{-1})	0.8 (0.1)	1.2 (0.1)	1.2 (0.1)	0.2 (0.1)	0.2 (0.0)	0.4 (0.1)	0.8 (0.1)	0.6 (0.0)	0.6 (0.1)	0.115	**<0.001*****
K (g kg^{-1})	17.2 (2.0)	16.2 (2.0)	15.8 (0.2)	6.5 (1.0)	4.1 (1.0)	5.9 (0.2)	5.8 (2.0)	6.9 (1.0)	8.4 (4.0)	0.756	**<0.001*****
Ca (g kg^{-1})	33.8 (2.0)	23.7 (3.0)	28.8 (2.0)	15.7 (2.0)	13.1 (0.2)	10.5 (0.3)	18.4 (5.0)	16.9 (1.0)	22.3 (6.0)	0.239	**<0.001*****
Mg (g kg^{-1})	4.9 (0.1)	5.5 (1.0)	4.3 (1.0)	1.4 (0.2)	1.3 (0.1)	1.4 (0.2)	2.8 (0.3)	2.8 (1.0)	3.0 (1.0)	0.859	**<0.001*****
C/N	28.9 (1.5)	22.6 (0.6)	27.9 (0.7)	59.6 (11.1)	61.4 (2.0)	54.1 (4.3)	34.2 (3.1)	37.7 (2.0)	37.4 (0.9)	0.975	**<0.001*****
C/P	606.7 (56.7)	418.4 (43.5)	406.4 (48.1)	2320.1 (192.7)	2209.5 (65.8)	1595.6 (379.6)	673.5 (70.7)	804.4 (50.8)	782.2 (53.6)	0.075	**<0.001*****
L (%)	33.5 (0.6)	35.5 (0.9)	36.1 (0.4)	30.9 (0.5)	30.7 (0.8)	31.1 (0.9)	37.2 (2.8)	23.4 (1.4)	18.6 (0.5)	**<0.001*****	**<0.001*****
PP (%)	6.0 (0.7)	6.6 (0.9)	6.8 (0.5)	12.8 (0.6)	13.9 (0.2)	13.9 (0.1)	9.7 (0.8)	8.9 (0.5)	8.3 (0.6)	0.843	**<0.001*****
L/N	20.8 (1.2)	16.8 (0.4)	21.3 (0.3)	35.7 (5.9)	36.6 (1.0)	32.5 (1.9)	25.5 (0.9)	17.8 (0.7)	14.6 (0.6)	**0.014***	**<0.001*****
PP/N	3.7 (0.5)	3.1 (0.4)	4.0 (0.3)	15.0 (3.1)	16.5 (0.4)	14.5 (1.1)	6.7 (0.4)	6.9 (0.5)	6.5 (0.6)	0.958	**<0.001*****
(L + PP)/N	24.5 (1.4)	19.9 (0.8)	25.3 (0.5)	50.7 (9.1)	53.2 (1.3)	47.0 (3.1)	32.2 (1.3)	24.7 (1.1)	21.1 (1.2)	0.118	**<0.001*****

Abbreviations: C = carbon, N = nitrogen, P = phosphorous, K = potassium, Ca = calcium, Mg = magnesium, L = lignin, PP = polyphenols. *p*-values marked in bold are significant:$^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Table 2
Tree root quality parameters (mean ± SE) as influenced by the duration of cultivation and tree species.

Parameter	Tree species									*p*-value	
	Croton megalocarpus			*Eucalyptus grandis*			*Zanthoxylum gilletii*				
	10 years	16 years	62 years	10 years	16 years	62 years	10 years	16 years	62 years	Duration of cultivation	Species
C (g kg^{-1})	437.5 (2.8)	433.1 (6.8)	431.5 (1.5)	434.3 (1.1)	432.4 (0.9)	430.8 (1.7)	442.1 (12.1)	465.7 (8.4)	415.7 (17.7)	**0.047***	0.448
N (g kg^{-1})	15.3 (1.3)	13.5 (1.8)	13.1 (2.6)	5.7 (0.6)	5.5 (0.9)	5.2 (0.2)	15.6 (2.0)	23.1 (3.4)	12.6 (2.6)	0.119	**<0.001*****
P (g kg^{-1})	1.6 (0.04)	1.3 (0.3)	1.3 (0.4)	0.6 (0.03)	0.5 (0.1)	0.6 (0.03)	0.7 (0.02)	1.5 (0.5)	0.7 (0.1)	0.420	**<0.001*****
K (g kg^{-1})	7.5 (0.8)	6.9 (0.6)	7.6 (1.4)	8.3 (0.7)	8.7 (0.6)	8.2 (0.3)	5.5 (0.3)	13.0 (4.2)	6.7 (1.2)	0.232	0.657
Ca (g kg^{-1})	13.1 (0.7)	13.3 (0.1)	13.4 (0.4)	16.3 (1.0)	16.7 (1.1)	17.6 (1.0)	9.9 (1.4)	10.5 (0.7)	12.3 (1.2)	0.221	**<0.001*****
Mg (g kg^{-1})	2.2 (0.3)	1.9 (0.3)	2.1 (0.4)	1.7 (0.3)	1.7 (0.2)	1.8 (0.1)	1.7 (0.2)	2.0 (0.2)	1.8 (0.2)	1.000	0.276
C/N	29.0 (2.6)	33.1 (4.0)	36.0 (8.0)	77.2 (6.8)	82.6 (11.2)	83.5 (3.1)	29.3 (3.5)	21.2 (3.2)	35.2 (5.5)	0.272	**<0.001*****
C/P	267.3 (6.4)	398.2 (12.8)	400.6 (13.8)	755.5 (40.6)	830.1 (82.3)	703.1 (35.2)	614.2 (7.1)	391.0 (15.3)	654.1 (60.5)	0.705	**<0.001*****
L (%)	12.1 (3.0)	13.5 (2.3)	16.8 (3.4)	28.2 (2.1)	22.0 (0.3)	25.1 (0.8)	18.4 (6.2)	9.5 (0.7)	11.9 (1.9)	0.233	**<0.001*****
PP (%)	1.0 (0.2)	1.1 (0.2)	0.8 (0.1)	7.9 (0.9)	8.1 (0.2)	8.6 (0.6)	2.4 (0.8)	3.3 (0.4)	2.0 (0.9)	0.381	**<0.001*****
L/N	8.0 (1.8)	10.8 (3.1)	13.8 (3.7)	49.6 (1.8)	41.8 (5.3)	48.6 (2.0)	11.9 (3.4)	4.5 (1.1)	9.9 (1.9)	0.102	**<0.001*****
PP/N	0.7 (0.1)	0.9 (0.1)	0.7 (0.1)	14.1 (2.1)	15.6 (2.3)	16.5 (1.0)	1.4 (0.4)	1.5 (0.3)	1.8 (1.0)	0.686	**<0.001*****
(L + PP)/N	8.7 (1.7)	11.7 (3.1)	14.4 (3.7)	63.7 (2.6)	57.4 (7.6)	65.1 (2.7)	13.4 (3.3)	5.9 (1.3)	11.7 (1.8)	0.136	**<0.001*****

Abbreviations: C = carbon, N = nitrogen, P = phosphorous, K = potassium, Ca = calcium, Mg = magnesium, L = lignin, PP = polyphenols. *p*-values marked in bold are significant: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Table 3
p-values associated with the soil chemical properties as influenced by duration of cultivation, tree species and tree zone.

Soil chemical parameter	*p*-value					
	Duration of cultivation	Tree species	Tree zone	Duration × Species	Species × Zone	Duration × Species × Zone
pH (water)	**<0.001*****	**0.050***	0.091	**0.033***	0.091	0.315
Total C	**<0.001*****	0.263	**0.009****	0.292	**<0.001*****	0.136
Total N	**<0.001*****	0.184	**0.009****	0.213	**0.001****	0. 061
C/N ratio	**<0.001*****	**0.027***	0.6107	**<0.001*****	0.8130	0.7854
Available P	**0.011***	0.220	0.452	0.122	0.833	0.404
Exchangeable K	**<0.001*****	**0.042***	0.740	**0.050***	0.910	0.394
Exchangeable Ca	**<0.001*****	**0.033***	0.063	0.102	0.060	0.508
Exchangeable Mg	**<0.001*****	0.374	**0.030***	**0.042***	0.395	0.556

Abbreviations: C = Carbon, N = Nitrogen, P = Phosphorous, K = Potassium, Ca = Calcium, Mg = Magnesium. Values marked in bold are significant: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

15.5 mg kg^{-1} respectively), than 10 years (11.3 mg kg^{-1}) of cultivation. This was contrary to all the other nutrient elements which, on average, were higher shortly after forest conversion and decreased with duration of cultivation. Generally, soil under *E. grandis* canopy had a lower concentration of chemical elements compared to the two indigenous tree species. Projection of the differences based on PCA showed significant ($p < 0.01$) separation of *E. grandis* from *C. megalocarpus* and *Z. gilletii* along the second axis of Fig. 2a. Separation between soils after 10 years of cultivation, which had considerably higher stocks of soil nutrients than after 16 and 62 years of cultivation, was also evident. The first principal component axis thus expressed a significant ($p < 0.001$) gradient in soil degradation (Fig. 2b).

3.4. Effects of duration of cultivation and tree species on soil macrofauna abundance

Ten soil macrofauna groups were identified across the study area, but four of these; earthworms, beetles, ants and termites, were the dominant groups. Generally, the abundance of soil macrofauna was influenced differently by tree species (Table 5). Though there was evidence of tree species effects on earthworms abundance, this was dependent on duration of cultivation as shown by the interactions of the two factors. For instance, a significantly high number of earthworms was found below the canopy of *Z. gilletii* in the farms after 16 and 62 years of cultivation with an average of 389 individuals m^{-2} and 160 individuals m^{-2} respectively, compared to only 14 individuals m^{-2} in the farms after 10 years of cultivation under the same tree species (Table 6). These values represented 40%, 16% and 1% of the total earthworm counts beneath tree canopies, respectively. The number of earthworms associated with *E. grandis* and *C. megalocarpus* followed a similar trend to that of *Z. gilletii*, but with lower abundances. Beetles showed a contrasting trend to that of earthworms with higher numbers associated with *E. grandis* and *C. megalocarpus* and lower below the canopy of *Z. gilletii*. However, unlike earthworms, duration of cultivation had no significant influence on beetles. An exceptionally high number of termites was found to be associated with *E. grandis* after 16 years of cultivation with an average of 82 individuals m^{-2}, representing about 38% of the total termite counts. Centipedes were significantly higher below the canopy of *E. grandis* with an average of 11 individuals m^{-2} constituting 56% of total centipede counts, compared to an average of 4 individuals m^{-2} recorded below the canopy of the other two tree species, *C. megalocarpus* and *Z. gilletii*. Based on the duration of cultivation, the abundance of centipedes was higher in soils after 16 years of cultivation than after 10 or 62 years of cultivation. Ants showed a similar trend to that of termites and centipedes, except that soils after 10 years of cultivation also showed relatively high number associated with *E. grandis*. Higher spider numbers were found to be associated with *C. megalocarpus* in soils after 16 years of cultivation with an average of 8 individuals m^{-2}, constituting 28% of the total spider counts beneath the canopy of trees. Generally, soil macrofauna beneath *Z. gilletii* showed significant separation ($p < 0.01$) from that of *E. grandis* and *C. megalocarpus* as shown by the PCA along the first axis (Fig. 3a). A clear separation was also observed along the first principal component axis ($p < 0.001$) between soils after 10 years of cultivation and those with greater duration of cultivation (Fig. 3b).

Table 4
Soil chemical properties (mean and *SE*) as influenced by the duration of cultivation, tree species and tree zone.

Soil parameter	Tree species											
	Croton megalocarpus				*Eucalyptus grandis*				*Zanthoxylum gilletii*			
	Tree zone											
	A	B	C	D	A	B	C	D	A	B	C	D
10 years of cultivation												
pH (water)	6.6 (0.1)	6.6 (0.0)	6.6 (0.0)	6.1 (0.0)	6.6 (0.1)	6.6 (0.1)	6.4 (0.1)	6.5 (0.0)	6.3 (0.1)	6.3 (0.1)	6.5 (0.1)	5.9 (0.0)
Total C (g kg^{-1})	66.1 (3.1)	65.6 (3.0)	62.2 (4.8)	47.0 (3.7)	55.1 (3.1)	60.6 (5.3)	60.5 (4.4)	61.1 (4.5)	54.5 (2.9)	54.5 (2.5)	54.6 (2.7)	45.4 (3.0)
Total N (g kg^{-1})	7.0 (0.5)	6.8 (0.5)	6.4 (0.5)	5.8 (0.3)	5.5 (0.4)	6.0 (0.5)	6.2 (0.5)	6.3 (0.5)	5.5 (0.3)	5.7 (0.3)	5.6 (0.3)	5.1 (0.3)
C/N ratio	9.5 (0.4)	9.7 (0.4)	9.7 (0.2)	8.1 (0.3)	10.2 (0.4)	10.2 (0.3)	9.8 (0.2)	9.7 (0.2)	9.8 (0.2)	9.6 (0.2)	9.8 (0.1)	8.9 (0.2)
Av. P (mg kg^{-1})	11.9 (1.4)	10.9 (0.4)	10.8 (0.5)	11.0 (0.7)	13.9 (2.1)	13.2 (2.6)	12.4 (0.8)	10.7 (0.9)	10.5 (0.5)	10.2 (0.2)	10.8 (0.3)	9.2 (0.9)
Exc. K (mg kg^{-1})	455.4 (9.1)	446.4 (9.8)	437.8 (8.0)	455.7 (14.9)	472.1 (23.4)	446.8 (55.9)	455.9 (11.5)	451.4 (15.8)	433.4 (51.2)	438.6 (39.8)	443.0 (41.5)	417.9 (26.0)
Exc. Ca (g kg^{-1})	4.9 (0.2)	4.9 (0.2)	4.6 (0.3)	4.3 (0.3)	4.0 (0.3)	4.4 (0.4)	4.4 (0.3)	4.4 (0.2)	3.8 (0.4)	3.9 (0.3)	3.9 (0.3)	3.2 (0.2)
Exc. Mg (mg kg^{-1})	387.2 (0.0)	371.0 (7.2)	372.4 (7.2)	356.7 (5.6)	351.0 (7.2)	346.1 (2.8)	367.0 (9.6)	359.8 (7.4)	356.4 (6.8)	353.3 (8.3)	347.3 (2.4)	345.8 (5.4)
16 years of cultivation												
pH (water)	6.2 (0.3)	6.1 (0.2)	6.1 (0.1)	5.2 (0.0)	5.4 (0.0)	5.4 (0.0)	5.4 (0.0)	5.5 (0.1)	6.0 (0.4)	6.0 (0.4)	5.8 (0.3)	5.8 (0.3)
Total C (g kg^{-1})	48.9 (5.7)	48.4 (0.9)	39.9 (2.2)	36.1 (4.2)	38.8 (2.5)	38.3 (2.8)	39.6 (3.5)	38.1 (2.9)	33.0 (3.9)	32.0 (4.5)	32.2 (4.9)	30.7 (2.5)
Total N (g kg^{-1})	5.0 (0.6)	4.9 (0.2)	3.9 (0.3)	3.6 (0.4)	3.5 (0.1)	3.5 (0.2)	3.7 (0.4)	3.5 (0.3)	2.9 (0.4)	2.7 (0.5)	2.9 (0.5)	2.1 (0.2)
C/N ratio	9.8 (0.5)	9.8 (0.5)	10.2 (0.9)	10.0 (0.3)	11.0 (0.7)	10.9 (0.5)	10.8 (0.3)	11.0 (0.2)	11.3 (0.3)	11.9 (1.0)	11.3 (1.0)	14.6 (0.7)
Av. P (mg kg^{-1})	20.8 (1.4)	18.3 (1.2)	16.7 (1.3)	14.8 (0.9)	15.3 (4.0)	16.0 (3.7)	15.6 (4.1)	17.2 (3.3)	14.5 (2.5)	15.4 (3.8)	11.4 (1.9)	13.3 (1.1)
Exc. K (mg kg^{-1})	385.6 (9.4)	331.4 (30.7)	265.4 (60.4)	305.1 (41.4)	198.7 (41.7)	214.9 (35.9)	205.7 (20.6)	240.9 (28.4)	386.1 (39.3)	391.2 (82.1)	337.9 (20.9)	338.5 (26.9)
Exc. Ca (g kg^{-1})	3.5 (0.4)	3.4 (0.2)	2.5 (0.4)	2.7 (0.2)	1.6 (0.1)	1.6 (0.0)	1.8 (0.1)	1.8 (0.1)	1.9 (0.4)	1.8 (0.5)	1.8 (0.5)	1.7 (0.1)
Exc. Mg (mg kg^{-1})	325.7 (6.5)	327.5 (5.4)	289.1 (8.0)	297.2 (24.7)	203.8 (23.3)	213.2 (15.8)	212.3 (19.1)	222.7 (31.5)	276.5 (39.3)	285.5 (59.2)	246.0 (24.1)	225.4 (22.0)
62 years of cultivation												
pH (water)	5.9 (0.2)	5.9 (0.2)	5.8 (0.2)	5.8 (0.2)	5.8 (0.2)	5.9 (0.1)	5.8 (0.2)	5.8 (0.2)	6.3 (0.1)	6.3 (0.0)	6.3 (0.1)	5.6 (0.1)
Total C (g kg^{-1})	31.4 (7.0)	31.6 (6.8)	31.9 (6.7)	26.3 (5.4)	40.1 (1.7)	37.2 (0.1)	38.6 (1.2)	36.4 (1.0)	36.1 (5.4)	35.8 (4.7)	36.7 (5.0)	35.2 (3.3)
Total N (g kg^{-1})	2.8 (0.8)	2.8 (0.7)	2.8 (0.7)	2.7 (0.6)	3.6 (0.2)	3.2 (0.2)	3.3 (0.2)	3.1 (0.1)	3.3 (0.6)	3.2 (0.6)	3.4 (0.7)	2.1 (0.4)
C/N ratio	11.5 (0.9)	11.5 (0.8)	11.5 (0.9)	9.7 (0.9)	11.1 (0.6)	11.7 (0.5)	11.6 (0.4)	11.6 (0.2)	11.0 (0.6)	11.3 (1.3)	11.2 (1.3)	16.8 (0.4)
Avail. P (mg kg^{-1})	18.1 (3.8)	19.9 (2.3)	19.7 (2.2)	13.2 (2.6)	12.7 (0.7)	10.7 (1.2)	12.3 (1.2)	12.3 (1.2)	16.7 (2.6)	18.5 (1.0)	19.2 (3.8)	12.4 (2.2)
Exc. K (mg kg^{-1})	317.9 (9.3)	305.7 (8.1)	306.5 (6.4)	318.5 (74.4)	361.9 (33.0)	376.8 (5.0)	348.1 (21.2)	348.1 (21.2)	455.6 (4.3)	443.5 (4.7)	435.5 (37.2)	423.8 (18.5)
Exc. Ca (g kg^{-1})	2.1 (0.6)	2.1 (0.7)	2.0 (0.6)	1.7 (0.4)	1.9 (0.1)	1.8 (0.1)	1.6 (0.7)	1.6 (0.7)	2.2 (0.3)	2.4 (0.2)	2.5 (0.5)	2.1 (0.2)
Exc. Mg (mg kg^{-1})	255.1 (6.7)	238.1 (9.2)	236.8 (9.7)	235.2 (36.6)	299.5 (17.6)	287.0 (20.7)	267.9 (15.3)	267.9 (15.3)	297.4 (27.6)	300.3 (24.9)	308.4 (21.4)	247.0 (24.5)

Abbreviations: C = Carbon, N = Nitrogen, P = Phosphorous, K = Potassium, Ca = Calcium, Mg = Magnesium. Avail. = available; Exc. = exchangeable.

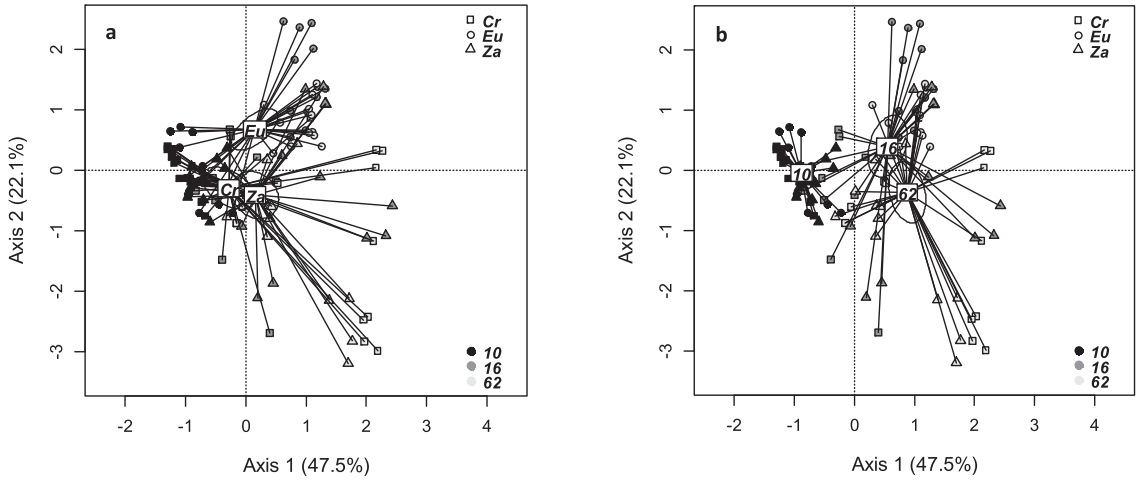

Fig. 2. Projection of soil chemical parameters sampling points along the two principal component (PC) axes using the *ordiellipse* and *ordispider* functions in package Vegan. The ellipses are standard errors, while the letters indicate the location of centroids for each **(a)** tree species and **(b)** duration of cultivation. Abbreviations; Cr = *Croton megalocarpus*, Eu = *Eucalyptus grandis*, Za = *Zanthoxylum gilletii*. The numbers 10, 16 and 62 represent the years of cultivation. $p < 0.001$ for both tree species and duration of cultivation; Monte Carlo permutation test is based on 999 random permutations.

Table 5
p-values associated with the soil macrofauna abundance as influenced by the duration of cultivation, tree species and tree zone.

Soil macrofauna group	*p*-value					
	Duration of cultivation	Tree species	Tree zone	Duration × Species	Species × Zone	Duration × Species × Zone
Ants	0.122	**0.008****	0.555	0.474	0.088	1.000
Beetles	0.176	**0.017***	**0.031***	0.779	0.298	0.307
Centipedes	**0.013***	**0.006****	0.062	0.078	0.965	0.365
Earthworms	<**0.001*****	0.149	0.083	<**0.001*****	0.299	0.130
Millipedes	0.072	0.110	0.805	0.226	0.482	1.000
Spiders	0.792	0.309	0.911	**0.019***	<**0.001*****	1.000
Termites	0.836	0.804	0.196	**0.003****	0.859	0.339
Other soil macrofauna	0.564	0.805	0.469	0.931	0.205	0.319

Values marked in bold are significant: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Table 6
Soil macrofauna abundance (mean individuals m^{-2} ± SE) as influenced by the duration of cultivation, tree species and tree zone.

Macrofauna group	Tree species											
	Croton megalocarpus				*Eucalyptus grandis*				*Zanthoxylum gilletii*			
	Tree zone											
	A	B	C	D	A	B	C	D	A	B	C	D
10 years of cultivation												
Ants	8.0 (4.6)	33.3 (21.8)	13.3 (6.2)	17.3 (14.5)	16.0 (7.9)	9.3 (3.1)	94.7 (73.5)	33.3 (17.1)	10.7 (5.3)	10.7 (10.7)	9.3 (8.0)	4.0 (2.1)
Beetles	26.7 (5.7)	34.7 (9.6)	34.7 (11.8)	22.7 (5.7)	33.3 (13.4)	28.0 (6.6)	41.3 (10.1)	38.7 (17.2)	20.0 (4.9)	20.0 (5.6)	26.7 (7.7)	12.0 (5.3)
Centipedes	0.0	1.3 (1.3)	5.3 (2.3)	2.7 (1.8)	4.0 (2.1)	10.7 (6.9)	6.7 (2.4)	4.0 (2.9)	1.0 (1.0)	1.3 (1.3)	0.0	0.1 (0.1)
Earthworms	8.0 (4.2)	30.7 (10.9)	29.3 (14.5)	10.7 (4.1)	26.7 (8.7)	36.0 (18.6)	26.7 (8.2)	24.0 (6.4)	8.0 (3.7)	20.0 (7.1)	13.3 (4.8)	4.0 (2.9)
Millipedes	0.0	0.0	14.7(13.3)	0.0	2.7 (2.7)	1.3 (1.3)	0.0	2.7 (2.7)	0.0	1.3(1.3)	0.0	0.0
Spiders	0.0	0.0	5.3(2.3)	0.0	1.3 (1.3)	1.3 (1.3)	2.7 (2.7)	1.3 (1.0)	0.0	4.0 (2.9)	4.0 (2.9)	1.3 (1.0)
Termites	58.7 (54.4)	26.7 (26.7)	2.7 (1.8)	24.0 (13.1)	22.7 (19.8)	8.0 (5.4)	1.3 (1.3)	2.7 (1.8)	6.7 (6.7)	44.0 (37.1)	0.0	12.0 (8.2)
Other soil macrofauna	4.0 (3.1)	0.1 (0.1)	6.7 (3.1)	2.7 (1.8)	0.0	4.0 (2.1)	5.3 (4.1)	1.3 (0.5)	4.0 (2.9)	8.0 (4.2)	9.3 (4.2)	4.7 (2.0)
16 years of cultivation												
Ants	4.0 (2.9)	46.7 (30.1)	36.0 (11.3)	36.0 (21.9)	96.0 (49.6)	2.7 (2.7)	32.0 (22.1)	48.0 (35.2)	10.7 (6.6)	13.3 (8.1)	17.3 (7.7)	6.7 (5.4)
Beetles	42.7 (7.2)	48.0 (11.3)	72.0 (18.9)	26.7 (6.0)	73.3 (14.0)	45.3 (10.6)	49.3 (16.5)	37.3 (8.4)	20.0 (5.3)	52.0 (20.5)	24.0 (7.0)	20.0 (4.0)
Centipedes	4.0 (4.0)	9.3 (4.6)	4.0 (2.9)	2.7 (1.8)	24.0 (9.3)	10.7 (3.6)	22.7 (9.5)	14.7 (4.6)	10.7 (3.6)	10.7 (6.9)	8.0 (3.1)	6.7 (3.1)
Earthworms	62.7 (26.1)	42.7 (12.0)	26.7 (7.5)	42.7 (12.0)	85.3 (29.0)	92.0 (20.4)	89.3 (15.3)	68.0 (20.9)	381.3 (59.6)	370.7 (91.8)	414.7 (72.8)	186.7 (41.5)
Millipedes	2.7 (1.8)	0.0	4.0 (2.1)	4.0 (2.9)	1.3 (1.3)	0.0	1.3 (1.3)	5.3 (4.1)	5.3 (3.0)	4.0 (2.9)	2.7 (2.7)	1.3 (1.3)
Spiders	2.7 (1.8)	9.3 (5.4)	12.0 (5.3)	1.3 (1.3)	0.0	0.0	4.0 (2.3)	2.7 (1.8)	1.3 (1.3)	0.0	2.7 (1.8)	0.0
Termites	0.0	2.7 (1.8)	2.7 (2.7)	0.0	197.3 (117.2)	20.0 (11.2)	29.3 (20.7)	65.3 (32.1)	18.7 (6.8)	58.9 (24.8)	34.7 (24.8)	0.1 (0.1)
Other soil macrofauna	5.3 (3.0)	13.3 (5.9)	16.0 (7.1)	2.7 (1.8)	5.3 (2.3)	1.3 (1.3)	5.3 (2.3)	1.3 (1.0)	6.7 (2.4)	5.3 (2.3)	2.0 (1.0)	1.3 (1.0)
62 years of cultivation												
Ants	2.7 (1.8)	2.7 (1.8)	33.3 (20.5)	21.3 (9.3)	8.0 (4.6)	0.0	30.7 (17.4)	6.7 (5.4)	25.3 (21.3)	0.0	6.7 (6.7)	6.7 (3.1)
Beetles	57.3 (17.1)	34.7 (6.5)	49.3 (10.9)	32.0 (8.4)	41.3 (13.7)	24.0 (4.6)	33.3 (13.7)	38.7 (10.9)	24.0 (5.4)	20.0 (5.9)	36.0 (9.5)	33.3 (7.2)
Centipedes	2.7 (2.7)	4.0 (2.1)	5.3 (2.3)	4.0 (3.7)	5.3 (3.0)	6.7 (3.1)	4.0 (2.1)	2.7 (2.7)	5.3 (2.3)	1.3 (1.3)	1.3 (1.3)	0.0
Earthworms	222.7 (99.0)	93.3 (24.7)	98.7 (32.7)	161.3 (32.9)	66.7 (18.4)	92.0 (25.2)	122.7 (19.4)	94.7 (32.4)	150.7 (57.5)	161.3 (24.0)	166.7 (43.2)	164.0 (46.2)
Millipedes	6.7 (3.1)	5.3 (3.6)	9.3 (4.6)	9.3 (3.7)	4.0 (2.9)	4.0 (2.9)	4.0 (2.1)	1.3 (1.3)	2.7 (1.8)	4.0 (2.9)	2.7 (2.7)	1.3 (1.3)
Spiders	2.7 (1.8)	1.3 (1.3)	6.7 (3.1)	1.3 (1.3)	1.3 (1.3)	0.0	2.7 (1.8)	0.0	1.3 (1.3)	2.7 (1.8)	0.0	4.0 (2.1)
Termites	8.0 (4.6)	10.7 (10.7)	68.0 (36.0)	25.3 (17.3)	20.0 (20.0)	1.3 (1.3)	12.0 (5.6)	12.0 (10.6)	1.3 (1.3)	0.0	9.3 (9.3)	5.3 (4.1)
Other soil macrofauna	4.0 (2.1)	5.3 (2.3)	13.3 (5.5)	2.0 (0.1)	1.3 (1.3)	5.3 (3.0)	5.3 (3.0)	1.3 (1.3)	2.7 (1.8)	10.7 (4.1)	2.7 (1.8)	2.3 (1.3)

3.5. Effects of duration of cultivation and tree species on soil macrofauna biomass

Except for a few soil macrofauna groups, the biomass was not significantly affected by tree species, duration of cultivation or the zone of sampling (Tables S1 and S2). Earthworm biomass was greatest in soils after 16 years of cultivation (20.4 g m^{-2}), compared to 10 years (17.1 g m^{-2}) and 16 years (16.4 g m^{-2}). Tree species

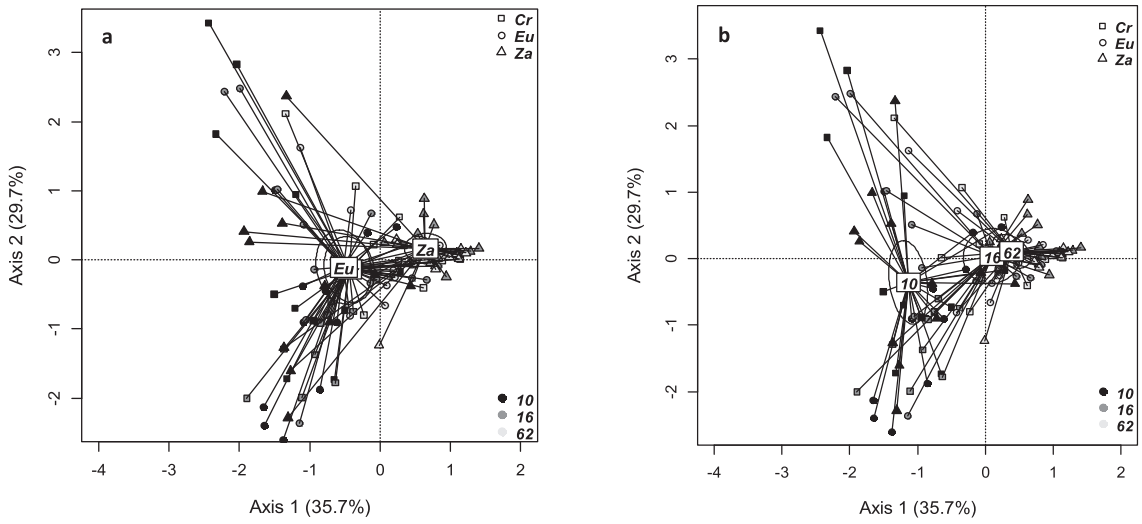

Fig. 3. Projection of soil macrofauna sampling points along the two principal component (PC) axes using the *ordiellipse* and *ordispider* functions in package Vegan. The ellipses are standard errors, while the letters indicate the location of centroids for each **(a)** tree species and **(b)** duration of cultivation. Abbreviations; Cr = *Croton megalocarpus*, Eu = *Eucalyptus grandis*, Za = *Zanthoxylum gilletii*. The numbers 10, 16 and 62 represent the years of cultivation. $p < 0.01$ (tree species) and $p < 0.001$ (duration of cultivation); Monte Carlo permutation test is based on 999 random permutations).

played a significant role in determining the biomass of termites only, but this occurred at specific time under cultivation. For instance, an average of 4.1 g m^{-2} or 36% of the total termite biomass, was associated with *E. grandis* in soils after 16 years of cultivation. Of all the soil macrofauna groups, only biomass of spiders showed significant differences between tree zones. Higher biomass values were found below the canopy of *E. grandis* and *C. megalocarpus* in soils after 62 years of cultivation, while *E. grandis* and *Z. gilletii* in soils after 10 years of cultivation showed greater biomass away from the trees.

3.6. Correlation of tree litter/root quality parameters and soil macrofauna abundance

Earthworms, centipedes and termites showed significant correlation with litter quality parameters (Table 7). Earthworm abundance correlated negatively with litter K, lignin and C/P, while correlation with P was significantly positive. Centipedes on the other hand were significantly correlated with all the chemical parameters measured (except K and lignin). They were positively correlated with C and plant tissue quality indicators (e.g. C/N, C/P, L/N, PP/N, L + PP/N), but negatively correlated with N, P, Ca and Mg of litter. Like centipedes, termites were also positively and significantly correlated with Mg and all the ratios, but negatively and significantly correlated with N and P. Beetles, millipedes, ants and spiders showed no significant correlation with any of the tree litter quality parameters. Only earthworms and centipedes showed significant response towards root quality parameters (Table 7). Earthworm abundance was positively correlated with root C, N, P and K but negatively correlated with lignin. Centipede abundance was positively correlated with K, Ca, polyphenols and PP/N ratio of roots.

Table 7
Pearson correlation matrix between soil macrofauna and selected tree litter and root quality parameters.

Soil macrofauna group	Tree litter quality parameters												
	C	N	P	K	Ca	Mg	C/N	C/P	L	PP	L/N	PP/N	(L + PP)/N
Ants	0.22	0.07	0.15	0.23	0.06	0.13	0.04	0.10	−0.10	−0.10	−0.07	−0.10	−0.10
Beetles	−0.06	−0.02	0.14	0.16	−0.1	−0.15	0.11	0.17	−0.03	−0.10	0.01	−0.04	−0.01
Centipedes	**0.53****	**−0.42***	**−0.43***	−0.32	**−0.48***	**−0.44***	**0.48***	**0.55****	−0.12	**0.48***	**0.42***	**0.51****	**0.46***
Earthworms	−0.26	−0.33	**0.49***	**−0.65****	−0.15	−0.05	−0.07	**−0.48****	**−0.60****	0.03	−0.20	−0.10	0.03
Millipedes	−0.32	0.10	0.17	−0.04	−0.31	0.02	−0.18	−0.24	0.02	−0.13	−0.08	−0.13	−0.13
Spiders	−0.09	0.32	0.28	0.23	−0.29	−0.07	−0.21	−0.05	−0.03	−0.09	−0.09	−0.14	−0.14
Termites	0.01	**−0.68****	**−0.53****	−0.29	0.01	**0.43***	**0.74****	**0.50****	**0.54****	0.18	**0.77****	**0.44***	**0.85****
	Tree roots quality parameters												
Ants	−0.01	−0.29	−0.19	−0.06	0.18	−0.16	0.38	0.27	0.27	0.33	0.36	0.32	0.38
Beetles	0.09	−0.08	0.14	−0.03	0.20	0.14	0.02	−0.17	−0.04	−0.03	−0.01	−0.04	−0.02
Centipedes	0.16	−0.07	−0.01	**0.43***	**0.44***	0.03	0.32	0.17	0.08	**0.42***	0.28	**0.40***	0.32
Earthworms	**0.38***	**0.54****	**0.40***	**0.66****	−0.23	0.15	−0.29	−0.26	**−0.44***	−0.09	−0.32	−0.19	−0.29
Millipedes	0.01	0.19	0.35	0.21	0.11	0.04	−0.13	−0.33	−0.32	−0.23	−0.19	−0.18	−0.19
Spiders	−0.17	0.04	−0.05	−0.26	−0.15	−0.12	−0.20	−0.03	−0.14	−0.34	−0.20	−0.30	−0.23
Termites	0.10	−0.04	0.02	0.22	0.03	0.06	0.19	0.10	−0.04	0.16	0.11	0.22	0.14

Abbreviations: C = carbon, N = nitrogen, P = phosphorous, K = potassium, Ca = calcium, Mg = magnesium, L = lignin, PP = polyphenols. Correlation between variables with values marked in bold are significant. $^{*}p < 0.05$; $^{**}p < 0.01$.

3.7. Correlation between soil macrofauna and selected soil chemical properties

Soil degradation status varied considerably as shown by the redundancy analysis (RDA). The sampling points were aligned along axis 1 which corresponded to the different duration of cultivation, and the separation was significant ($p < 0.001$; Fig. 4). The axis (45.9% of explained variance) clearly revealed that there was a difference in soil chemical properties amongst soils with different time under cultivation. All the elements entered into the RDA (except available P), were projected on one side along the first axis, therefore revealing a degradation gradient between soils after relatively short-term cultivation and long-term cultivation. Soil macrofauna abundance tended to increase with duration of cultivation and therefore negatively correlated with most soil chemical properties along the first axis. Notably, however, earthworms and millipedes were strongly correlated with available P. On the other hand, correlations between either centipedes or termites with available P were generally weak. The second axis (9.3%) reflected the variability within catchments and/or tree species.

4. Discussion

4.1. Effects of duration of cultivation and tree species on soil chemical properties

There are at least two major mechanisms which could explain the observed higher soil nutrients under the canopy of the trees: i) trees often exploit nutrients from deep layers in the soil profile, or laterally, and redistribute them under the canopy in the form of organic inputs aboveground (litter) and belowground (root turnover) or ii) leguminous trees fix N which goes back to the soil through the first mechanism (Rhoades, 1997; Schroth et al., 2003). In this study, only the first mechanism can explain the nutrient increases below the tree canopy since none of the three species are N-fixing trees. Therefore, the differences in nutrient elements below the canopy of the three tree species could be a reflection of their organic input quality and/or deposition patterns. The higher nutrient contents below the canopy of *C. megalocarpus* and *Z. gilletii* could therefore be attributed to either a higher nutrient content in their litter (as observed in Table 1), and/or a higher rate of litter deposition (which was not measured in this study). On the other hand, trees with higher nutrient use efficiency have been reported to produce litter with lower nutrient contents (Aerts and Chapin, 1999). In an early study done by Poggiani (1985), it was reported that *Eucalyptus saligna* Sm. produced litter with lower N and K concentration compared to that of *Pinus caribaea var. hondurensis* (Sénécl) Barr. et Golf. In addition, the author reported that the amount of litter deposited by *E. saligna* was nearly half of that deposited by *P. caribaea*. In this case, the tree had the capacity to reduce nutrient loss through two ways; reabsorption of the nutrients before leaf senescence and reduced shedding of leaves. In another study, Kater et al. (1992) noted that the lower available Ca and K in the upper soil layers under the canopy of *Parkia biglobosa* G.Don compared to *Vitellaria paradoxa* C.F.Gaertn. may be an indication of the high capacity of *P. biglobosa* to absorb and retain scarce soil nutrients. This could suggest that the exotic *E. grandis* has greater capacity to hold nutrients in its biomass than *C. megalocarpus* and *Z. gilletii*. Such outcome emphasises the importance of native trees as 'resource islands' supporting nutrient cycling in farms where no inputs or only minimal external nutrients are available to farmers. On the other hand, intensive cultivation with minimal or no external inputs leads to degradation of soil, manifested in form of nutrient depletion, poor soil structure, and low soil biodiversity (Lal, 2009). In this study, soils from farms with greater duration of cultivation were particularly lower in soil nutrients compared to the younger farms. This trend is expected since some of the farms had been cultivated with low, if any nutrient inputs, for over 60 years since conversion from the native forest compared to the younger farms which were barely 10 years under cultivation. These trends are in agreement with those reported by Recha et al. (2013) who had previously worked in the same area. The authors attributed the lower nutrient contents in the older farms to losses through crop off-take, as well as microbial mineralisation and leaching losses. It should be noted, however, that since duration of cultivation was not randomly allocated to catchments and there was only one replicate of each, other differences between the catchments instead of, or in addition to, time of cultivation will be implicated in observed differences in soils. Nevertheless, the mechanism described above along with the fact that there are no other striking differences in soils or topography of the catchments provide good evidence that duration of cultivation has a dominant effect. Contrary to other nutrients, available P was higher in the farms with longer duration of cultivation. In their study, Recha et al. (2013) reported that farmers did not apply organic or inorganic fertilisers in the young farms while estimated applications of P fertiliser in soils after 16 and 62 years of cultivation was 2.8 and 4.1 kg ha^{-1} respectively. Despite the small amounts of fertiliser-P applied, the low mobility of P in the soil matrix could have resulted in the accumulation with increasing duration of cultivation. Therefore, in addition to the contribution of trees to the redistribution of soil P, the observed higher soil available P in the older farms could have been influenced by the small, but repeated external P inputs.

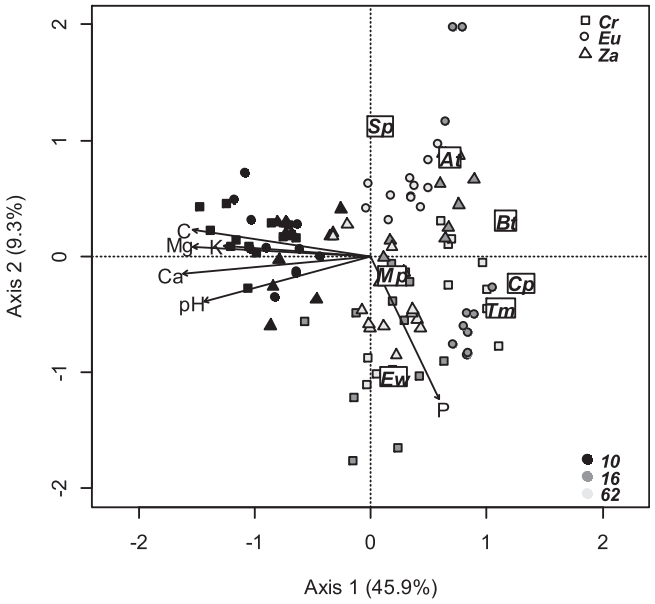

Fig. 4. A Redundancy Analysis (RDA) biplot showing correlation between soil macrofauna groups and soil chemical properties. Abbreviations; At = Ants, Bt = Beetles, Cp = Centipedes, Ew = Earthworms, Mp = millipedes, Sp = Spiders and Tm = Termites. The numbers 10, 16 and 62 represent the years of cultivation.

4.2. Tree effects on soil macrofauna abundance

Trees differ in the quantity and quality of their aboveground and belowground organic inputs, which potentially determines the patterns of influence on soil macrofauna (Korboulewsky et al., 2016). Vohland and Schroth (1999), for instance, reported that the overall faunal abundance were significantly higher under *Bactris*

gasipaes Kunth and *Bixa orellana* L. compared to that obtained under *Bertholletia excelsa* Bonpl. and *Theobroma grandiflorum* (Willd. ex Spreng.) K.Schum as a result of differences in plant tissue quality. In our study, it was noted that there was a significant difference between the litter and root tissue quality of native trees *C. megalocarpus* and *Z. gilletii*, and exotic tree *E. grandis*. These organic inputs, through litter decomposition and root turnover, could have played a key role in shaping the observed differences in the soil macrofauna population abundance below the trees. For instance, it was observed that earthworms were strongly and positively correlated with P of the litter, and N and P of the roots, which were both higher in *C. megalocarpus* and *Z. gilletii* roots compared to that of *E. grandis*. Further, *Z. gilletii* particularly recorded exceptionally higher number of earthworms in soils after 16 years of cultivation which corresponded to the higher N and P content observed in the roots of this tree in that specific catchment. In agreement with these findings, Barrios et al. (2005) reported highest earthworm counts under slash and mulch of *Tithonia diversifolia* (Hemsl.) Gray known to accumulate soil P in plant tissues given its profuse root development and association with native arbuscular mycorrhizal fungi (Sharrock et al., 2004). Furthermore, Mbau et al. (2015) reported that P could have been the main driver of the high number of earthworms recorded in plots treated with filtermud compost. The higher soil macrofauna generally recorded below the canopies of *C. megalocarpus* and *Z. gilletii* could therefore, be associated with the higher quality of litter and root turnover than that of *E. grandis*. Differences found in C/N and (L + PP)/N ratios, frequently used as measures of organic resource quality (Tian et al., 1997; Vanlauwe et al., 2005; Cobo et al., 2002), support the argument that plant tissue quality can significantly contribute to differences in abundance of soil macrofauna. In this study, the C/N ratio of the litter and fine roots was relatively lower in the litter and roots derived from the two native trees, *C. megalocarpus* and *Z. gilletii,* than that from *E. grandis*. In addition, lignin and polyphenols contents were also lower in the litter and fine roots of the native trees. This suggests that organic inputs derived from native trees would likely be more palatable to some soil macrofauna than those from *E. grandis*. In contrast to other soil macrofauna, termites showed higher abundance under the canopy of *E. grandis*. Termites are known to produce a large variety of enzymes from the associated gut microflora which enables them to digest low quality organic matter (Lavelle, 1997). Due to this diverse preference in food substrates, the quality of organic inputs below tree canopies could therefore be an important determinant of soil macrofauna abundance. Like termites, centipedes were also higher under the canopy of *E. grandis*. Since centipedes are known to be predators, the high numbers under this tree may not be linked directly to the litter or root biomass as substrates, but rather to the presence of prey.

Apart from soil organic matter influence, the differences observed in soil macrofauna in the current study may partly be attributed to tree influence on microclimatic conditions of the soil under its canopy. It has been documented in several studies that trees intercept significant amount of incident solar radiation depending on the size and species (Belsky et al., 1989; Lott et al., 2009). In an early study in Tsavo, Kenya, Belsky et al. (1989) reported a reduction in solar irradiance of between 45 and 65% under *Adansonia digitata* L. and *Acacia tortilis* (Forssk.) Hayne, which led to a 5–12 °C lower temperature below the two trees than in the open grassland. Vandenbeldt and Williams (1992) reported that a nearly leafless *Faidherbia albida* (Delile) A.Chev. intercepted almost half of the incoming radiation resulting in a soil temperature decrease of up to 10 °C at 0.02 m depth. More recently, Ong et al. (2000) and Lott et al. (2009) reported amelioration of soil temperature as a result of shading from *Grevillea robusta* A.Cunn. while Lin (2010) and De Souza et al. (2012) observed that incorporating trees in coffee farms helped in protecting extreme fluctuations in soil temperature. Such moderation in temperature also reduces the rate of evapotranspiration hence soil moisture content is likely to be higher than in the adjacent open sites. Apart from shading, some trees/shrubs such as *Piliostigma reticulatum* (DC.) Hochst. and *Guiera senegalensis* J. F. Gmel. have also been shown to directly increase moisture of the surface soil by drawing out water from the subsoil through hydraulic redistribution processes (Diedhiou-Sall et al., 2013; Kizito et al., 2012). Though we did not measure soil moisture and temperature below the tree canopies, we believe that differences in these two parameters may have also contributed to the observed patterns in soil macrofauna, given the sensitivity of numerous soil organisms to soil moisture and temperature regimes (Pflug and Wolters, 2001; Lindberg et al., 2002; Tsiafouli et al., 2005).

4.3. Effects of duration of cultivation on soil macrofauna abundance

Land-use change from natural forest to plantations, pasture or cultivated lands often results in intense and rapid changes in soil that are likely to affect soil macrofauna abundance and distribution patterns (Beare et al., 1997; Giller et al., 1997; Decaëns et al., 2004). The effects are linked to direct induced mortality through physical destruction or loss of food resources (Fragoso et al., 1993; Palm et al., 1996; Blanchart and Julka, 1997) or indirectly through changes in microhabitats resulting from damage of nests and burrows (Ayuke et al., 2011; Orgiazzi et al., 2016). This is especially notable in cropped lands, perhaps due to the higher levels of intensification and disturbance (Decaëns et al., 2004; Eggleton et al., 2005; Rossi and Blanchart, 2005). Nonetheless, even in intensively cultivated lands, there is usually a re-establishment of soil macrofauna after such disturbances. The re-establishment is, however, largely dependent on the soil macrofauna group in consideration and the soil management practices applied. Agricultural practices which increase soil organic matter inputs therefore, may be vital in accelerating the rate of soil macrofauna survival and re-establishment. The observed greater soil macrofauna abundance with increasing time under cultivation supports the increasing importance of trees as 'resource islands' (Liu et al., 2011; Dossa et al., 2013). Furthermore, Pauli et al. (2010) and Diedhiou-Sall et al. (2013) also found greater soil biological activity beneath trees with increasing soil resource and environmental limitations in Central America and the Sahel respectively, thus supporting the role of trees in contributing to greater functional resilience in agro-ecosystems (Barrios et al., 2015). In the study area, it was evident that farms on soils after 62 years of cultivation had more trees incorporated as live fences or hedgerows to delineate farm boundaries, intercropped with annual crops or as small pockets of woodlots. This is a common practice in smallholder farms in Kenya as the farm fragmentation increases as highlighted by Nyaga et al. (2015). On the farms after 10 years of cultivation, however, the plant cover was predominantly annual crops (maize and beans) including only a few sparse trees within the farms. The increased importance of trees could therefore be one of the contributors to the observed impacts of duration of cultivation on soil macrofauna abundance. Numerous studies have also reported similar outcomes. For instance, Mathieu et al. (2005) reported that the species richness of soil macrofauna fell from an initial 76 species in the primary forest to 30 in deforested plots under rice crop. However, the authors noted that soil macrofauna re-established based on the land-use type, with the higher recovery being observed in old fallow plots. The higher population in the fallow plots, they noted, could have been as a result of the higher litter retention and creation of microclimatic conditions that resemble

more closely those in the forests. This shows that following soil disturbance in the form of cultivation, soil macrofauna may generally re-establish where the management options provide them with better living conditions. Furthermore, agroforestry practices used to restore degraded and eroded soils safeguard the already accumulated soil organic matter, and enhance the availability of vital food resource to a large number of soil-dwelling organisms (Barrios et al., 2005). This could therefore have indirectly favoured soil macrofauna proliferation on the older farms compared to the younger ones. However, some soil macrofauna may be more sensitive to disturbance and changes in soil, and still are negatively affected by agriculture. This could partly explain why, in this study, some soil macrofauna such as millipedes, spiders, crickets, cockroaches and earwigs occurred in low numbers. Most of these occurred either below the tree canopy or in the farms with greater duration of cultivation, perhaps attracted by better microclimatic conditions under the trees or improved soil conditions, respectively. Therefore, introduction of trees is likely to play a major role in shaping spatial patterns of soil macrofauna distribution and abundance.

5. Conclusions

Land-use conversions from natural forest to cultivated lands often results in soil nutrient losses that are likely to negatively affect soil macrofauna. However, our study shows that soil macrofauna studied responded differently to soil degradation and tree identity highlighting the complexity of the soil ecosystem. The quality of tree organic inputs showed an important effect on soil macrofauna abundance and spatial distribution. Promoting diversity of land-use at the landscape and farm scale has been identified as central to maintaining biodiversity and ecosystem services. Our results indicate that increasing diversity of tree species in agroecosystems can play a major role in such a strategy.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2017.04.016.

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