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Earthworms in *Chromolaena odorata* (L.) King and Robinson (Asteraceae) fallows along a chronosequence: Changes in community structure and identification of persistent and indicator species

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ABSTRACT

The species *Chromolaena odorata* (Asteraceae) is a notorious invasive shrub spreading throughout West and Central Africa and as such, there is a need to determine its environmental impact, particularly on soil biodiversity and functioning. Indeed, soil organisms such as earthworms are known to strongly influence soil properties and biogeochemical cycles. This study, conducted in Central Côte d'Ivoire, aims to investigate the temporal dynamics of earthworm communities in *C. odorata* fallows of different ages and to identify associated indicators and persistent species. Three distinct classes of fallows identified by local farmers, were considered: young (1–3 years, C1), medium-aged (4–8 years, C2) and old (>9 years, C3). Each of the classes included four plot replicates where earthworms were sampled using the Tropical Soil Biology and Fertility (TSBF) 25 cm × 25 cm × 30 cm soil monolith method. The study of earthworm communities was focused on density, biomass, diversity and complementarity. Indicator values (IndVals) were used to identify indicator species of the classes of fallows. The shrub exerted a mixed influence on earthworms depending on the functional group, with litter feeders and polyhumics declining over time as a result of a reduction of the litter availability on the soil surface. The species richness was significantly greater in C1 than in the other classes although the Shannon–Weaver's index did not vary significantly. However, a cluster analysis performed on densities highlighted marked differences between C2 and the two other classes in terms of community composition. Indicator species were found for C1 and C2. The geophagous *Millsonia omodeoi* has emerged as a persistent species as its density and biomass steadily increased so that it became the dominant species in old fallows. The roles of litters and soil parameters in influencing earthworm communities are discussed.

Introduction

Native to Central America, the species *Chromolaena odorata* (L.) King and Robinson (Asteraceae) was introduced to Africa – in Nigeria in 1937 and thereafter the species spread throughout West and Central Africa (Obatolu and Agboola 1993) taking advantage of vegetation disturbance caused by agricultural activities or other activities (logging, roads,. . .). The weed spread rapidly due to its high production of wind-dispersed seeds (Gautier 1992) and has shifted into fallow systems, which are now well integrated into perennial systems in forest and forest-savanna transition zones (Slaats 1995; Koutika et al. 2004; Koné et al. 2012a). In Côte d'Ivoire, *C. odorata* bushes are encountered on most agricultural lands and used by the majority (*ca.* 80%) of farmers (Bouadi 2009). It is an aggressive invasive species, which colonizes fields even during the cropping period. Immediately after land conversion to fallow, it rapidly establishes and prevails over the other species covering up to 95% of the land surface within one year. However, there have been very few investigations that have looked at the long term influence of the weed on earthworm communities despite the latter's recognized impacts on soil properties and biogeochemical cycles. An understanding of any influence will be useful in evaluating the consequences of land invasion by *C. odorata* in terms of biodiversity and ultimately ecosystem functioning (Hooper et al. 2000; Ehrenfeld 2003; Milcu et al. 2006).

A body of research works dealing with ecosystem functioning has focused on linkages between aboveground and belowground diversity, and the general conclusion is that the evidence for correlation between the two domains is mixed (Hooper et al. 2000). Nonetheless, high diversity in plant species or specific functional groups may result in high diversity of belowground organisms (Yeates 1999; Hooper et al. 2000). Because plant species differ in

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both the quantity and quality of resources (litters, root exudates) supply to soil, individual plant species may have idiosyncratic effects on components of the soil biota and the processes they regulate (Gastine et al. 2003; Wardle et al. 2004). Thus, a diversity of carbon source entering the belowground subsystem will lead to greater diversity of soil organisms through greater niche differentiation (Sulkava and Huhta 1998; Wardle et al. 1999; Yeates 1999). Although soil organisms are responsive to the nature of organic inputs from aboveground (Swift et al. 1979), the effects of plant composition on soil biota may be restricted to some species (Wardle et al. 2004; Eisenhauer et al. 2009). On the other hand, the absence of correlation (Wardle et al. 1999; Laossi et al. 2008) or no clear trend (Eisenhauer et al. 2009) between aboveground vegetation and soil organisms can occur.

The inconsistencies observed in the "aboveground–belowground" interactions hold even when more restricted groups of soil organisms such as earthworms are concerned. Some studies showed evidence of correlation between belowground and aboveground systems (Spehn et al. 2000; Milcu et al. 2008) while others did not (Wardle et al. 1999; Milcu et al. 2006). However, the existence of correlation between aboveground and belowground diversity does not necessarily imply mechanistic linkages (Hooper et al. 2000). Overall, the influence of a plant species on soil organisms is strongly dependent on its relative abundance in the community (dominant *versus* rare or subordinate species) and types of soil organisms considered (Wardle et al. 2004). That is because aboveground vegetation might influence the attributes of belowground organisms (abundance and diversity) through the litter quality and biomass or modifying microhabitats (temperature, humidity) (Anderson 1994). These litter attributes were sometimes found to be more influential than diversity alone (Hooper et al. 2000). In this regard, Barros (1999) reported a positive correlation between soil macrofauna diversity and aboveground plant biomass but not with plant diversity across secondary succession plots in the Amazon basin.

The invasion of an area by a plant species may greatly affect aboveground–belowground interactions and in the long term, these interactions may be influenced by the traits of the dominant plant species as well as by the quantity and quality of resource inputs to soil and their effect on soil organisms (Wardle et al. 1999; Ehrenfeld 2003). According to Slaats (1995), great changes occur in the invasive weed *C. odorata* bushes over time, particularly regarding biomass. The author reported values of 8, 14 and 18 Mg ha^{-1} dry biomass for 1-year, 2-year and 3-year old fallows, respectively. He also reported increasing litter and nutrient quantities provided to the soil as the fallow aged. All these changes may impact earthworms either at the species or the community level as evidenced by previous studies (Mboukou-Kimbasta et al. 2007; Milcu et al. 2006, 2008; Belote and Jones 2009; Eisenhauer et al. 2009; Koné et al. 2012b). Also, *C. odorata* was found to reduce plant diversity (Goodall and Erasmus 1996) as observed for many others invasive species.

Earthworms are major ecosystem engineers and the most important macro-decomposer group (Scheu 2003; Lavelle et al. 2006) whose impact on soil varies with feeding behavior. Thus, linkages between *C. odorata* and these organisms may be important at the ecosystem scale in terms of soil functioning or ecosystem services (nutrient cycling, carbon sequestration, water infiltration, soil structuring, microbial activity, *etc.*) and the promotion of keystone species or a combination of species with significant effect on soil fertility (Wall and Moore 1999; Lavelle et al. 2006). Therefore, studying the effect of *C. odorata*, which is still invading new areas, on earthworm community dynamics, appears to be a research priority.

The influence of aboveground vegetation on soil organisms may occur at different levels of the faunal community (Wolters et al. 2000). The research reported here aimed to investigate (i) changes in earthworm community structure (density, biomass and diversity) in *C. odorata* fallows along a chronosequence, and (ii) to identify both persistent species and indicator species of fallow age. The following hypotheses were tested: (1) changes in earthworm community structure occur under *C. odorata* fallow over time, (2) these changes are linked to changes in litter quality and quantity; and (3) some earthworm species are specific to fallow stages while others proliferate or decline irrespective of fallow age.

Material and methods

Study site

The study was conducted in a humid savanna zone in Central Côte d'Ivoire, around the village of Ahérémou-2 (6′10–6′15N; 4′55–5′00W). The vegetation structure was a mosaic of secondary forests, savannas, *C. odorata* fallows and various agroecosystems. The climate is subequatorial with four seasons, namely: a long dry season from December to February, a long wet season from March to July, a short dry season in August, and a short wet season from September to November. The temperature is nearly constant throughout the year, averaging 27 °C and the annual rainfall is around 1200 mm. Soils are moderately leached Ferralsols (Delmas 1967), with granite as the underlying bedrock. Upper soil layers generally have a sandy texture. Clays consist of illites and slightly crystallized kaolinites, with a low adsorption capacity.

Experimental design and plot description

The study consisted of a set of 12 plots under *C. odorata* fallows, which are dense tangled bushes 1.5–2.0 m in height. These fallows were categorized into three classes according to age, by local farmers (Bouadi 2009): class 1 (C1) consisted of young (1–3 years) fallows; class 2 (C2) was composed of medium (4–8 years) fallows, cultivated by most farmers and producing satisfactory yields; and class 3 (C3) consisted of older fallows (>9 years) and only observed among landowners. Each class consisted of four plots of 1302 m^2 (42 m × 31 m) size, distant from each other (as depicted by the GPS) and located either at the top of slope or mid-slope in the landscape (Appendix 1). All the plots were located on a sandy clay soil surface. Except for the plot C1-1, these fallows were preceded by a maximum cropping period of three years with most following the traditional cultural succession (Appendix 2) of a main yam (*Dioscorea* spp.) crop mixed with plantain (*Musa* spp.) and vegetables in the first year; a main crop of plantain, mixed with vegetables and sometimes cassava (*Manihot esculenta*) in the second year, and plantain cropped either alone or with cassava in the final year. Before being cropped, plots were either secondary forest or *C. odorata* fallows. Land preparation was similar in all plots, consisting of slash and burn.

Leaf litter sampling and chemical analyses

Leaf-litter was characterized quantitatively and qualitatively. Leaf-litter sampling was carried out within a 1 m × 1 m quadrant, at three points distributed randomly over each plot and then, the mean biomass was obtained using the three quadrants.

The chemical composition of leaf litter from each plot was determined on composite samples obtained by mixing litter materials from the three quadrants. Total carbon (C) and total nitrogen (N) were determined by dry combustion using a CHN autoanalyzer (EA1112 Thermo Finnigan Series, France) for 4 mg samples that had been dried and ground to less than 0.1 mm. Total phosphorus was determined after hydrochloric digestion and extracts were analyzed for orthophosphate using the molybdenum blue colorimetric method (Murphy and Riley 1962). Major cations were extracted in an ammonium acetate buffer (1 N; pH 7; litter:extractant ratio of

1:20, g:ml), and determined by atomic absorption spectrophotometry techniques (Varian SpectrAA 220 SF model).

Soil sampling and analyses

Soil sampling was conducted concurrently to earthworm sampling. On each of the plots, samples were collected with a soil auger from 0 to 10 cm layer at five points in the plots: one in the center and one in each corner of the plot. These samples were pooled and thoroughly mixed to give a single composite sample, which was air-dried for one week, sieved through a 2 mm sieve and kept in plastic bags for chemical analyses. Therefore, for each of the fallow classes, there were four composite samples.

Total carbon was determined using a modified Anne method (Nelson and Sommers 1982). Total N was extracted according to Nelson and Sommers (1980) and determined using Technicon autoanalyzer (Technicon Industrial Systems 1977). Plant available P was extracted according to the Bray-1 procedure (Olsen and Sommers 1982) and determined using a Technicon AutoAnalyzer (Technicon Industrial Systems 1977). Soil acidity (pH) was ascertained with a glass electrode in 1:2.5, soil:water, g:ml ratio. Cation exchange capacity (CEC) was obtained using standard methods (Anderson and Ingram 1993). Soil texture was determined using the standard Na-hexametaphosphate suspension method: organic matter was destroyed using hydrogen peroxide, the coarse soil fraction was then obtained by sieving, and clay and silt were separated using the Robinson pipette method (Anderson and Ingram 1993). Soil bulk density was determined on core samples obtained by the cylinder (diameter: 5 cm, height: 10 cm). Samples were collected in the first 10-cm soil layer, oven-dried at 105 °C for 48 h and then weighed.

Earthworm sampling and identification

In general, earthworms are sampled using ethological (chemicals, electricity, heat) or physical (hand sorting from soil monoliths) methods. The hand sorting method was shown to be efficient in tropical soils and has been widely used by other authors (Lavelle 1978; Tondoh and Lavelle 2005; Blanchart et al. 2006; Mboukou-Kimbasta et al. 2007; Laossi et al. 2008) as well as in the present study. Earthworms were sampled in early July 2009, at the end of the long rainy season, following a modified tropical soil biology and fertility (TSBF) method (Anderson and Ingram 1993). Soil monoliths of 25 cm × 25 cm × 30 cm size were excavated at five distinct points as was described for soil sampling. Before excavating a soil monolith, a trench was dug out around it to prevent earthworm from escaping. In the rainy season, most earthworms prefer living in the top 0–30 cm soil layer thus facilitating capture with the TSBF monoliths. Collected earthworm specimens were then stored in a 4% formaldehyde solution until identification. They were identified to species level using reference specimens confirmed by the Natural History Museum of Budapest (Hungary) or, when this proved difficult, to numbered morpho-species. Individuals were grouped according to species, counted and weighed (dry biomass) at the soil monolith level. The same measurements were done regarding the feeding behavior. We found mainly litter feeders, which feed at or near the soil surface on plant litter and geophagous earthworms, which feed deeper in the soil and derive their nutrition from soil organic matter and dead roots ingested with mineral soil (Lee 1985). The geophagous species were divided into three groups, on the basis of their dependence upon soil organic matter (Lavelle 1981): the polyhumics, which feed on decaying residues mixed with little mineral soil, the mesohumics, which feed on soil fairly rich in organic matter and the oligohumics, which feed on organic matter–poor soil.

Data analysis

Earthworm sampling completeness was tested by calculating the abundance-based coverage estimator (ACE) of species richness using Estimates 7.5 (Colwell 2004) to determine whether the samples were close to species saturation, and by recording the auto-similarity to determine whether there was any difference in species assemblage between plots from the same fallow class (Colwell 2004). The diversity of earthworms in each class of fallow was evaluated through the average number of species, the cumulative number of species, and the Shannon–Weaver's diversity index (H') as well as its evenness (Pielou 1966). The calculations were made as follows: first, the parameters were determined at the plot level providing an average of the values obtained in the five soil monoliths, and second, they were determined at the fallow class level, giving an average value for the four replicates (plots). Variations in earthworm species composition with fallow age were examined using the complementarity index (C) of Colwell and Coddington (1994) ($C = 1 -$ Jaccard similarity index). Values of complementarity vary from zero (identical species lists) to unity (completely distinct species lists). To better visualize the similarity of fallow plots, a dendogram of plots was produced using the unweighted pair-group clustering method, which is based on distances between two plots; this dendogram was done using Statistica 6.0 Software program (Statistica, Tulsa, OK).

The indicator value (IndVal) method (Dufrêne and Legendre 1997) was used to identify characteristic (or indicator) earthworm species for each *C. odorata* fallow class or group of plots yielded by the cluster analysis. High IndVals indicate that the associated earthworm species make reliable indicator species because they are specific to a fallow class and they have a high probability of being sampled at that fallow stage. This index is calculated based on the density of the earthworm species sampled in each plots and species with significant IndVals were then considered as indicator species.

Mean comparisons (litter parameters, earthworms density and biomass, and diversity parameters) were carried out using a one-way ANOVA following verification of the homogeneity of variances with the Levene's test. The least significant difference (LSD) test was used to determine significant differences between fallow classes. Significant temporal changes in earthworm abundance were tested using Pearson's correlation test. Multiple regressions using GLM (general linear model) procedures were performed on the data for analyzing relationships between earthworms and both soil and litter parameters. These statistical analyses were processed using the R ver. 2.13.1 software (http://www.r-project.org/).

Results

Soil attributes

The soil pH was nearly neutral and did not vary significantly among fallow classes (Table 1). Surface soil fine fraction was low (*ca.* 16%) and did not show any significant variation between fallow classes. However, total C ($F_{2,9} = 4.4$, $P = 0.04$, $n = 4$) and the C:N ratio ($F_{2,9} = 4.2$, $P = 0.04$, $n = 4$) varied significantly, with inverse trends. The former increased while the latter decreased from C1 to C3. Significant differences were also observed in soil bulk density ($F_{2,9} = 3.8$, $P = 0.04$, $n = 4$) with an increasing trend from C1 to C3. No significant difference among classes was observed in total N, soluble P and soil moisture.

Biomass and quality of leaf litters

The litter biomass measured in C2 was significantly higher ($F_{2,9} = 12.6$, $P = 0.04$, $n = 4$) than in the other classes of fallow

Table 1
Main soil attributes (mean ± SE) in the different classes of fallows.

	Fallow classes		
	C1	C2	C3
pH water	6.8 ± 0.1^{a}	7.2 ± 0.1^{a}	6.9 ± 0.2^{a}
Clay+silt (%)	15.7 ± 0.7^{a}	16.4 ± 0.9^{a}	16.8 ± 1.2^{a}
Total C (g kg^{-1})	11.0 ± 0.8^{a}	12.2 ± 1.0^{ab}	15.1 ± 1.2^{b}
Total N (g kg^{-1})	1.0 ± 0.2^{a}	1.2 ± 0.2^{a}	1.3 ± 0.1^{a}
C/N ratio	18.0 ± 3.6^{a}	10.9 ± 0.6^{b}	12.0 ± 1.0^{b}
Soluble P (mg kg^{-1})	13.7 ± 5.5^{a}	8.2 ± 2.5^{a}	11.2 ± 4.2^{a}
Bulk density (g cm^{-3})	1.0 ± 0.0^{a}	1.1 ± 0.0^{ab}	1.2 ± 0.1^{b}
Moisture (%)	12.1 ± 2.0^{a}	11.1 ± 2.7^{a}	13.0 ± 2.4^{a}

For the same parameter, means with the same letter are not significantly different at the 5% level.

(Table 2) which showed similar values. Overall, the chemical properties across the different classes were similar; except for nitrogen which showed significantly increasing values from C1 to C3 ($F_{2,9} = 6.3$, $P = 0.04$, $n = 4$).

Earthworm sampling efficiency

The species detected in this study belonged to the Acanthodrilidae and the Eudrilidea families. In total, 19 species were detected, of which two could not be identified to species level (Table 3).

The total number of species detected in C1 (16), C2 (11) and C3 (12) were 97.7%, 86.6% and 86.3%, respectively, of those predicted by the ACE estimator. The value of auto-similarity in C1 (0.45) was slightly lower than 50%; suggesting some differences between plots from C1 in terms of taxonomic composition. However, C2 and C3 were higher than 50% (0.57 and 0.53, respectively) suggesting that plots from each of these classes did not highly differ in their taxonomic composition.

Earthworm abundance

At the community level

The density of earthworms significantly varied between fallow classes ($F_{2,9} = 4.2$, $P = 0.03$, $n = 4$), although C1 and C2 showed similar values (Fig. 1a). In C3, total density declined by almost 50%. Overall, total density was significantly and negatively correlated to fallow age ($r = -0.58$, $P = 0.04$, $n = 12$).

Earthworm density within trophic groups also varied across the fallow classes except for the oligohumics (Fig. 1b). Litter feeders ($F_{2,9} = 4.0$, $P = 0.04$, $n = 4$) and the polyhumics ($F_{2,9} = 6.0$, $P = 0.02$, $n = 4$) had the highest density in C1 and the lowest in C3. A significant negative correlation ($r = -0.6$, $P = 0.04$, $n = 12$) was observed with fallow age for polyhumics. Mesohumic density was significantly higher in C2 ($F_{2,9} = 3.9$, $P = 0.05$, $n = 4$) than in C1 and C3 which were similar. No significant correlation with fallow age was found.

Table 2
Leaf litter biomass and quality parameters (mean ± SE, $n = 4$).

Liter parameters	Fallow classes		
	C1	C2	C3
Biomass (Mg ha^{-1})	207.8 ± 58.4^{a}	555.1 ± 123.7^{b}	356.5 ± 85.8^{ab}
C (g kg^{-1})	427.3 ± 3.7^{a}	436.6 ± 8.5^{a}	434.4 ± 4.9^{a}
N (g kg^{-1})	17.9 ± 1.0^{a}	22.0 ± 3.9^{ab}	25.3 ± 2.4^{b}
P (g kg^{-1})	1.6 ± 0.3^{a}	1.5 ± 0.2^{a}	1.8 ± 0.2^{a}
Ca (g kg^{-1})	22.3 ± 0.9^{a}	22.4 ± 1.5^{a}	22.5 ± 2.1^{a}
Mg (g kg^{-1})	8.3 ± 0.8^{a}	7.1 ± 0.6^{a}	6.9 ± 0.7^{a}
K (g kg^{-1})	4.4 ± 0.7^{a}	3.7 ± 0.8^{a}	3.5 ± 0.4^{a}
C/N	24.0 ± 1.4^{a}	21.0 ± 3.4^{a}	17.5 ± 1.7^{a}

For a specific litter parameter, means with the same letter are not significantly different at the 5% level.

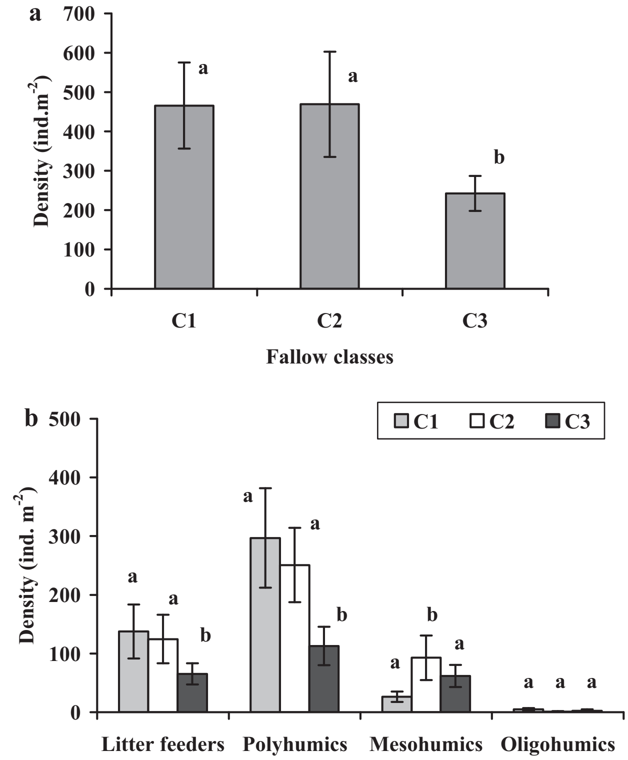

Fig. 1. Total earthworm density (a) and earthworm density within feeding groups (b). Means with the same letter within the same feeding group are not significantly different at the 5% level. Vertical bars represent standard errors.

Total earthworm biomass ranged between $29.8 \pm 6.0\,\mathrm{g\,m^{-2}}$ (in C1) and $55.0 \pm 12.4\,\mathrm{g\,m^{-2}}$ (in C2). Unlike density, biomass did not show any significant variation between fallow classes although value in C2 was nearly twice that in C1 and C3 (Fig. 2a). Also, no significant correlation was found with fallow age.

With regard to the feeding groups, significant variation was observed for polyhumics ($F_{2,9} = 4.7$, $P = 0.03$, $n = 4$) and mesohumics ($F_{2,9} = 4.2$, $P = 0.04$, $n = 4$). In the former group, biomass was the highest in C2, intermediate in C1 and the lowest in C3 while in the latter one, it was the highest in C2, intermediate in C3 and the lowest in C1 (Fig. 2b). None of the feeding groups significantly correlated with fallow age.

At species level

Among litter feeders, the species *Dichogaster mamillata* and *Dichogaster ehrhardti* were only observed in C2, with densities of 47.0 ± 18.6 individuals m^{-2} (ind m^{-2}) and 41.0 ± 27.1 ind m^{-2}, and biomass of $0.5 \pm 0.2\,\mathrm{g\,m^{-2}}$ and $2.5 \pm 2.2\,\mathrm{g\,m^{-2}}$, respectively. Both *Dichogaster saliens* (64.8 ± 16.9 ind m^{-2}; $2.4 \pm 1.6\,\mathrm{g\,m^{-2}}$) and *Dichogaster* sp. (32.1 ± 24.0 ind m^{-2}; $0.3 \pm 0.3\,\mathrm{g\,m^{-2}}$) were primarily present in C1. The two species significantly decreased with time in terms of density (*D. saliens*: $r = -0.55$, $P = 0.04$, $n = 12$; *Dichogaster* sp.: $r = -0.63$, $P = 0.04$, $n = 12$) while only *D. saliens* showed the same trend with respect to biomass.

Among polyhumics, the density of *Stuhlmannia zielae* varied significantly with fallow classes ($F_{2,9} = 4.8$, $P = 0.04$, $n = 4$), similarly to *Stuhlmannia palustris* ($F_{2,9} = 3.6$, $P = 0.05$, $n = 4$). The highest density was recorded in C1 (232.8 ± 82.2 ind m^{-2}) for the former and in C2 (177.8 ± 71.8 ind m^{-2}) for the latter. Significant correlation with fallow age was observed only for *S. zielae* ($r = -0.6$; $P = 0.04$, $n = 12$), showing a sharply decreasing trend with age. As a result, the density of *S. zielae* decreased by 75% in oldest fallows. In terms of biomass, only *S. zielae* ($F_{2,9} = 4.2$, $P = 0.04$, $n = 4$) and *S. palustris* ($F_{2,9} = 3.8$, $P = 0.04$, $n = 4$) significantly varied among fallow classes,

Table 3
List of species and morpho-species of earthworms and their abundance in the different fallow classes.

Earthworm species	Feeding groups	Density-based presence			Biomass-based presence		
		C1	C2	C3	C1	C2	C3
Dichogaster leroyi Omodeo, 1958	Litter feeder	**	**	**	*	*	*
Dichogaster Baeri Sciacchitano, 1952	Litter feeder	*	*		*		*
Dichogaster saliens Beddard, 1893	Litter feeder	****		*	*		*
Dichogaster papillosa Omodeo, 1958	Litter feeder	**	*	**	*	*	*
Dichogaster mamillata Omodeo, 1963	Litter feeder		**			*	
Dichogaster notabilis Omodeo, 1958	Litter feeder	*		**	**		**
Dichogaster ehrhardti Michaelsen, 1898	Litter feeder	***	*	*			
Dichogaster sp.	Litter feeder	***			*		
Millsonia lamtoiana Omodeo and Vaillaud, 1967	Litter feeder	*		*			***
Millsonia omodeoi Sims, 1986	Mesohumic	**	***	****	***	*****	*****
Millsonia sp.	Mesohumic	*		*		****	*
Millsonia schlegeli Horst, 1884	Mesohumic		*		*		
Dichogaster terrae-nigrae Omodeo and Vaillaud, 1967	Oligohumic	*			**		*
Agastrodrilus multivesiculatus Omodeo and Vaillaud, 1967	Oligohumic	*	*	*	*		*
Hyperiodrilus africanus Beddard, 1891	Polyhumic	*	**		*	***	
Eudrilus eugeniae Kinberg, 1867	Polyhumic	*		*	*		
Stuhlmannia zielae Omodeo, 1963	Polyhumic	*****	****	****	**	*	*
Stuhlmannia sp	Polyhumic	*		*		*	
Stuhlmannia palustris Omodeo and Vaillaud, 1967	Polyhumic	***	*****	***	*	***	*

Asterisk (*) indicates presence.

[*] <10, for density; 0–2.5, for biomass.

[**] 11–30, for density; 2.5–5, for biomass.

[***] 1–50, for density; 5–10, for biomass.

[****] 51–100, for density; 10–15, for biomass.

[*****] 100–200, for density; 15–20 g m^{-2}, for biomass.

[******] >200 individuals m^{-2}, for density.

with the highest value in C1 (4.5 ± 1.2 g m^{-2}) for the former and in C2 (7.3 ± 3.0) for the latter. Significant decrease in biomass with fallow age was observed with *S. zielae* ($r = -0.55$, $P = 0.04$, $n = 12$).

Among the three mesohumics identified, only *Millsonia omodeoi* showed significant variation ($F_{2,9} = 6.4$, $P = 0.03$, $n = 4$) in density between fallow classes, increasing from 23.2 ± 8.1 ind m^{-2} in C1 to 57.3 ± 15.3 ind m^{-2} in C3 – a 2.5-fold increase. As a result, this species showed a positive correlation ($r = 0.7$, $P = 0.03$, $n = 12$) with fallow age. On the other hand, its biomass significantly varied between fallow classes ($F_{2,9} = 4.8$, $P = 0.04$, $n = 4$), from 6.8 ± 2.3 g m^{-2} in C1 to 19.8 ± 6.1 g m^{-2} in C2 and 19.2 ± 5.2 g m^{-2} in C3 but no significant correlation was found over time. *Millsonia schlegeli* was observed only in C2 with a density of 47.0 ± 23.2 ind m^{-2}. Oligohumics were present at low density with no significant variation in the community.

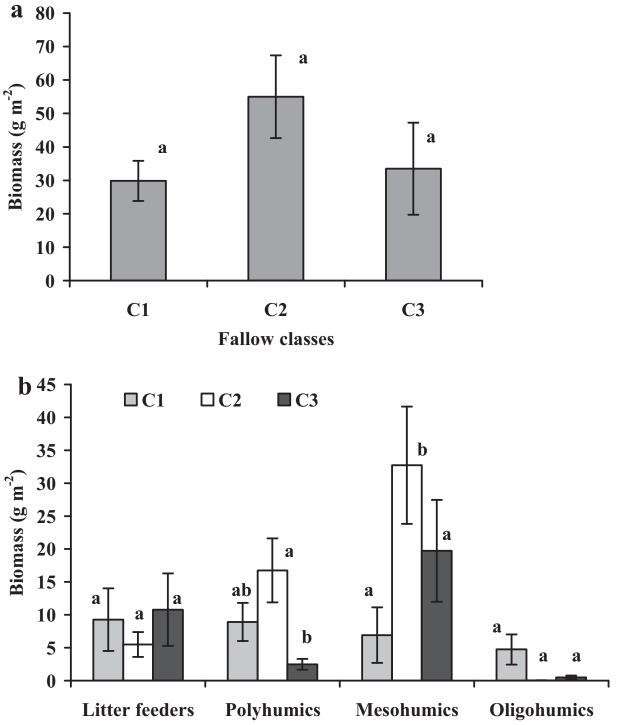

Fig. 2. Total earthworm biomass (a) and earthworm biomass within feeding groups (b). Means with the same letter within the same feeding group are not significantly different at the 5% level. Vertical bars represent standard errors.

Overall, the most common worm species in the youngest fallows were *S. zielae* representing 50% of the total earthworm density, followed by *D. saliens* (13.9%) and *S. palustris* (9.6%). In C2, *S. palustris* (38% of the total earthworm density) was dominant, followed by *M. schlegeli* (10%), *M. omodeoi* (10%) and *D. mamillata* (10%). In the oldest fallows (C3), *M. omodeoi* (24%), *S. zielae* (23.2%) and *S. palustris* (21%) were found to be the most common species.

When considering biomass, the dominant species in C1 were *M. omodeoi* (22.7%), *Dichogaster notabilis* (16%), *S. zielae* (15%), *Dichogaster terrae-nigrae* (11%), *Eudrilus eugeniae* (8.3%) and *D. saliens* (8%); in C2, *M. omodeoi* (36%), *M. schlegeli* (23.5%), *Hyperiodrilus africanus* (16%) and *S. palustris* (13.3%). In the oldest fallows, the dominant species was *M. omodeoi*, with more than half of the total biomass (57.2%), followed by *D. notabilis* (9%).

Influence of environmental factors on earthworm abundance

Multiple regression analyses showed that the total density of earthworm ($R^2 = 0.9$, $P = 0.01$, $F = 7.1$) and polyhumics ($R^2 = 0.9$, $P = 0.02$, $F = 6.3$) was significantly influenced by soil parameters, although no significant partial coefficient was found. Densities of *M. omodeoi* ($R^2 = 0.9$, $P = 0.04$, $F = 4.8$), *S. zielae* ($R^2 = 0.9$, $P = 0.04$, $F = 5.3$) and *S. palustris* ($R^2 = 0.8$, $P = 0.04$, $F = 4.3$) were also significantly influenced by soil parameters. Particularly, *D. notabilis* was linked to the soil pH ($\beta = -0.9$, $P = 0.03$), *M. omodeoi* to total soil C ($\beta = 1.3$, $P = 0.05$), *S. zielae* to the C:N ratio ($\beta = 0.7$, $P = 0.02$) and *S. palustris* to both C:N ratio ($\beta = -0.7$, $P = 0.02$) and soluble P ($\beta = -0.8$, $P = 0.01$). Earthworm biomass was also significantly influenced by soil parameters. The polyhumic group ($R^2 = 0.9$, $P = 0.04$, $F = 4.8$) was positively correlated with soil pH ($\beta = 0.8$, $P = 0.01$) and moisture

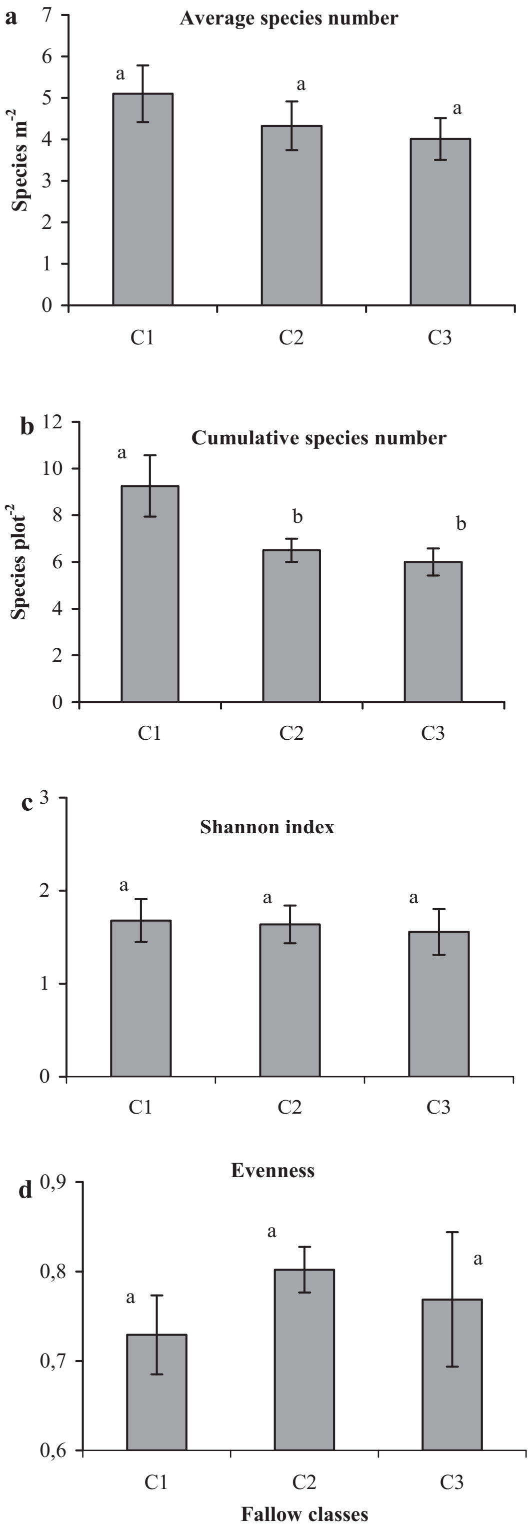

Fig. 3. Diversity parameters of earthworm's communities in the different fallow classes. Means with the same letter are not significantly different at the 5% level. Vertical bars represent standard errors.

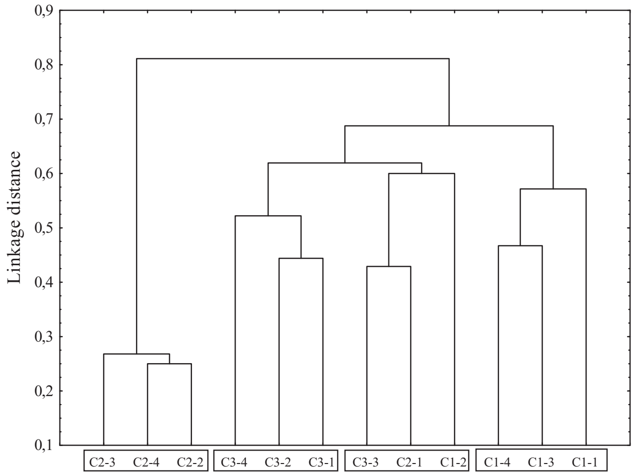

Fig. 4. Cluster analysis. Dendrogram of *Chromolaena odorata* plots based on the complementarity index (1 – Jaccard similarity index) of Colwell and Coddington (1994).

($\beta = 0.8$, $P = 0.03$); *S. zielae* ($R^2 = 0.9$, $P = 0.02$, $F = 7.7$) was significantly and positively correlated with the C:N ratio ($\beta = 0.9$, $P = 0.003$).

Earthworm abundance was also significantly influenced by leaf litters. In terms of density, leaf litter primarily influenced polyhumic species such as *S. zielae* ($R^2 = 0.9$, $P = 0.04$, $F = 5.2$) and *E. eugeniae* ($R^2 = 0.98$, $P = 0.02$, $F = 21.2$), the two species being negatively linked to litter C content ($\beta = -28.3$, $P = 0.04$ for the former, and $\beta = -0.9$, $P = 0.04$ for the latter). Leaf litter also significantly influenced the biomass of the polyhumic group ($R^2 = 0.91$, $P = 0.03$, $F = 5.6$) primarily through leaf litter quantity ($\beta = -1.3$, $P = 0.04$) and C ($\beta = -44$, $P = 0.03$). At the species level, leaf litter influenced *S. zielae* biomass ($R^2 = 0.95$, $P = 0.04$, $F = 6.2$) through C ($\beta = -45.3$, $P = 0.01$) and Mg ($\beta = 16.5$, $P = 0.01$) contents.

Earthworm diversity and indicator species

The average number of species (measured at the soil monolith level) remained almost constant among fallow classes (Fig. 3a). As for the cumulative number of species (measured at the plot level), it decreased significantly ($F_{2,9} = 4.2$, $P = 0.05$, $n = 4$) from 9.3 ± 1.3 species plot^{-1} in C1 to 6.5 ± 0.5 species plot^{-1} in C2 and 6.0 ± 0.6 species plot^{-1} in C3 (Fig. 3b). The Shannon–Weaver did not show any significant change with fallow age (Fig. 3c). In general, the evenness of earthworm community was similarly high (>0.7) for all of the fallow classes (Fig. 3d).

The multiple regression test revealed that the cumulative number of species was influenced by soil parameters ($R^2 = 0.9$, $P = 0.01$, $F = 14.1$), it was particularly negatively impacted by the bulk density ($\beta = -1.4$, $P = 0.02$). Leaf litter significantly influenced the average number of species ($R^2 = 0.95$, $P = 0.003$, $F = 30.5$) and the Shannon index ($R^2 = 0.92$, $P = 0.02$, $F = 8.9$). The first was linked to litter C ($\beta = -2.3$, $P = 0.03$) and K ($\beta = 2.2$, $P = 0.01$) contents while the second was only linked to litter C ($\beta = -2.5$, $P = 0.004$).

The cluster analysis of plot data revealed a clear pattern (Fig. 4). At the first subdivision level, two major groups emerged, one consisting of three plots from the medium-aged fallows (C2) (major group 1) and the other including all the remaining plots (major group 2). At the second subdivision level, the major group 2 was subdivided into two further groups, one consisting of three plots from the youngest fallows (C1) (sub-group 1) and the other containing the rest (sub-group 2). At the third partitioning level, the sub-group 2 was subdivided in a group containing three plots from the oldest fallows (C3) and another consisting of plots belonging to each of the three fallow classes. Accordingly, the complementarity index showed that the earthworm community composition from C2 was dissimilar to those from C1 (57.9%) and C3 (64.7%), these two being closer to each other (25%).

Seven out of the 19 earthworm species were found to be characteristic (or indicators) of a fallow class or a group of plots yielded by the cluster analysis. The indicator values (IndVals) are presented in

Table 4
Indicator values (%) for the groups produced by cluster analysis. Only characteristic species are reported.

Species	Subdivision 1		Subdivision 2			Subdivision 3			
	C2	Rest	C1	C2	Rest	C1	C2	C3	Rest
M. schlegeli	90.64	–[a]	–	85.32	–	–	–	–	
D. terrae-nigrae	–	–	–	–	–	–	–	–	47.71
D. saliens	–	–	93.53	–	–	89.97	–	–	–
D. mamillata	95.48	–	–	92.68	–	–	92.68	–	–
D. ehrhardti	100	–		100	–	–	–	–	–
H. africanus	82.7	–	–	–	–	–	–	–	–
S. zielae	–	–	70.7	–	–	67.28	–	–	–

[a] The species was not characteristic of the correspondent group.

Table 4 for each of the clustering steps. In the two first subdivisions, C2 had a greater number of characteristic species compared to the other clusters. In the third subdivision, however, the C1 had the greatest number. The species *M. schlegeli*, *D. mamillata*, *D. ehrhardti* and *H. africanus* which were indicators in C2 had their maximum IndVals at the first subdivision of the plots while those of *D. saliens* and *S. zielae*, indicators in C1, were observed in the second subdivision. No earthworm species was found to be characteristic of C3. Also, no species was found to be an indicator in more than one group of plots, suggesting that the indicator species is fallow class-specific.

Discussion

Earthworm abundance

Compared to older fallows, C1 displayed a higher abundance of earthworms with the community being dominated by litter feeders and polyhumics. This observation is in line with what has been reported in other studies conducted in tropical regions (Lavelle et al. 2000; Thomas et al. 2004). In this study, the total density of earthworms recorded in the classes C1 and C2 fall within the range of 300–500 ind m^{-2} given for tropical areas (Lavelle and Spain 2001).

Previous studies evidenced the prevalence of litter quality and quantity over litter diversity in influencing soil fauna where aboveground vegetation was dominated by one species (Barros 1999; Wardle et al. 1999; Ehrenfeld 2003). Therefore, in this study, we used litter characteristics to account for the influence of *C. odorata* on earthworms. The importance of litter quantity and quality supplied by plants in influencing earthworms was widely shown in earlier studies (Briones et al. 2001; Curry et al. 2008; Belote and Jones 2009; Koné et al. 2012b). Although there were significant changes in the aboveground vegetation attributes (biomass and quality) in our study, a significant correlation was only found with some of the earthworm species. Probably other factors were determinant for the remaining species as suggested by Hooper et al. (2000) and Wardle et al. (2004). The impact of *C. odorata* over time depended on the functional group of earthworms with the largest effects on litter feeders and polyhumics. This result is in accordance with those of Eisenhauer et al. (2009) and Koné et al. (2012b). Equally, Spehn et al. (2000) found that anecic earthworms more strongly suffer from a decrease in plant residues than endogeic earthworms, which feed on soil with intermediate content in organic matter. In old fallows where preceding crop-derived residues presumably have almost completely disappeared, the decline in litter biomass resulted in a decline in litter feeder and more particularly, polyhumics, as shown by multiple regressions. As a consequence, the gap between densities of earthworm species has narrowed, resulting in a slight increase in the evenness. Although the quantity of preceding crop residues in C2 presumably declined relative to C1, total earthworm density remained constant. This could have been due to compensation through increased litter fall in C2. The decline in the polyhumic density and biomass could also be linked to an increase in litter content in C as revealed by the multiple regression tests. In older fallows (C3), stems of *C. odorata* become climbers, making them easy to tangle and form a barrier that retains some of the dead leaves. This may partly explain the decline of litter biomass on the soil surface. However, these conditions were less restricting for mesohumics and oligohumics, which both feed on soil.

Litters with high N content were reported to be of good quality and beneficial to earthworms (Curry 2004; Mboukou-Kimbasta et al. 2007; Laossi et al. 2008; Koné et al. 2012b). In this study, although litter N increased and the C:N ratio decreased as the fallow aged, no positive impact was recorded on earthworms, particularly litter feeders and polyhumics. This is most likely due to (i) the fact that a significant part of the litter was not in contact with soil and (ii) the probable increased lignin content as a consequence of the increased C. Indeed, lignin-to-N ratio was reported to reduce litter palatability to earthworms (Mboukou-Kimbasta et al. 2007). Inconsistencies in the food preference of earthworms have been widely reported in the literature. Some authors found litter N to be determinant (Martin and Lavelle 1992; Koné et al. 2012b) while others suggest that litter C is determinant (Tiunov and Scheu 2004). Nonetheless, it is probable that plant diversity in C1 was higher than in the other classes, and that it might account for the higher density of earthworms, as suggested by Mboukou-Kimbasta et al. (2007). Indeed, before the fallow land was completely covered by *C. odorata*, several other plant species were growing and providing residues probably a food source for earthworms, given that *C. odorata* hardly produces litter in its younger stage.

On the other hand, the increase in soil organic matter beneficially impacted the mesohumic worm *M. omodeoi.* The species consistently increased both in terms of density and biomass to ultimately account for a quarter of the total earthworm density and more than half of the total earthworm biomass in old fallows. Such a positive influence of soil organic matter on *M. omodeoi* was also reported by Gilot-Villenave (1994). Although the abundance (density and biomass) of mesohumic such as *M. omodeoi* increased as *C. odorata* fallow aged whereas that of litter feeders (*D. saliens*) and polyhumics (*Dichogaster zielae*) decreased, this antithetic pattern was likely not due to competitive interaction, as individuals of these groups have distinct niches dictated by their feeding behavior. Moreover, root biomass would have provided a partial explanation to the trend observed for *M. omodeoi* or other earthworm species, had we investigated this parameter (Eisenhauer et al. 2009). Nevertheless, further field experiments are needed to explain the declining trend in litter feeders and polyhumics; but also the increasing trend observed for the mesohumic *M. omodeoi.*

Species composition and characteristic species of fallows

The sampling method of earthworm used in this study allowed for the detection of at least 86% of the expected number of earthworm species in all fallow classes. In addition, auto-similarity values recorded within fallow classes were relatively high. Overall, this method can be considered efficient.

It is important to mention that information about the earthworm species composition in the agricultural fields before fallowing could have been useful for a better explanation of variability within fallow classes, particularly in young fallows (C1), which were directly derived from agricultural fields. Indeed, earthworm species composition in fallows could, to some extent, reflect diversity in crops in agricultural fields. For instance, the value of auto-similarity in C1 was lower than 50%, and this may be an indication that earthworms were subtly influenced by the history of plots, particularly the latest food crops, which were different from one plot to the other. Tondoh et al. (2007) also argued that the variety of residues accounted for the increased diversity of earthworms in croplands, compared to other types of land-use in Center-West Côte d'Ivoire. However, this was not the case in C2 and C3 (higher auto-similarity), which consisted of older fallows with more homogenous environmental conditions and which came from fields with more homogeneity in the latest food crops. Earthworm diversity was also found to be influenced by *C. odorata* litter biomass; these findings are consistent with that of Laossi et al. (2008).

As shown by the cluster analysis, great changes occurred in the earthworm community composition, especially in the medium-aged fallows (C2). The phenomenon of community succession that occurs in ecosystems such as fallows is well-known (Stamou et al., 2011). The distinctive demarcation of plots of C2 from the others in the first subdivision of the dendogram is indicative of a marked change in species composition. However, in older fallows, the species composition was similar to what was observed in the younger ones. This is probably a consequence of close overlapping compositions from the two classes.

Of the seven indicator species identified, five were either litter feeders or polyhumics. Thus, one can state that the presence of organic residues at the soil surface account for a great part in the distribution of earthworm species compared to others parameters such as soil organic matter. Although *M. omodeoi* was the most represented in the oldest fallows, it was not an indicator for any class of fallows. The persistence of this species along the chronosequence at a relatively high density is likely the reason for this pattern.

Implications of the persistence of M. omodeoi for soil bio-functioning

The species *M. omodeoi* is generally large (adult: 15–25 cm) and is predominantly found in the humus soil layer (0–20 cm). It is known for the large amounts of soil it processes, which range from 450 to 800 t ha^{-1} year^{-1} (Lavelle 1978). Based on its activity in soils, its relatively high density, the numerous burrows the species creates in the soil profile leading to better aeration and effective water infiltration (Blanchart et al. 1997; Lavelle et al. 2006), this species is likely to be of great significance in continually affecting the soil fertility parameters under *C. odorata* fallows. However, the increase observed in *M. omodeoi* density might be detrimental, at a certain level, to its own survival and to soil fertility as well. Because this species is not able to reingest the large casts it egested, it may starve and die after having ingested large quantities of soil (Gilot-Villenave 1994; Blanchart et al. 1997). In field experiments in which soil was inoculated with *M. omodeoi*, a significant reduction in the species biomass (from 25 g m^{-2} to 3 g m^{-2} within three years) was observed, as a result of the concentration of large aggregates all consisting of egested casts (Gilot-Villenave 1994). Other consequences could be soil compaction and a reduction in water infiltration into soil (Guéi et al. 2012). Fortunately, in natural ecosystems, this effect was likely balanced by the presence of small filiform earthworms of the family Eudrilidae, namely *S. zielae* and *S. palustris* and other larger species such as *E. eugeniae* which have the ability to break down casts of larger worms into smaller aggregates (Blanchart et al. 1997; Guéi et al. 2012). On the other hand, the decline in these polyhumic earthworms, as well as in litter feeders would lower litter turnover.

Conclusion

The weed *C. odorata* significantly impacted earthworm community structure over time. This impact depended on the functional group of earthworms with the strongest effects found for litter feeders and polyhumics. Indeed, their density and biomass was adversely affected by the reduced availability of litter material on the soil surface, and its quality as well; thus validating our first hypothesis. Hypothesis 2 was partially confirmed given that litter attributes only influenced some of the earthworm species. However, the observed changes may have consequences either on soil physical parameters or nutrient cycling in this fallow system.

Some species were found to be indicators of fallow age; while others, persisted across *C. odorata* fallows. Among them, *M. omodeoi* was the only species whose density increased steadily as the fallow aged. Although this species was among those with the lowest densities in younger fallows (C1), it was one of the dominant ones in older ones, followed by *S. zielae* and *S. palustris* providing evidence to support hypothesis 3. Therefore, *M. omodeoi* may be considered a relevant candidate for studies dealing with long term interactions between earthworms and soil fertility parameters under *C. odorata* fallows.

We primarily based the mechanistic understanding of the influence of *C. odorata* on earthworm communities on the quality and quantity of resources that the weed produced. However unknown factors such as allelopathy may have played a significant role that needed to be explored. Also, further studies are needed, taking into consideration fine root biomass as a determinant factor.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pedobi.2012.02.001.

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