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Agroforestry improves soil fauna abundance and composition in the Atlantic Forest of Paraguay

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Abstract Edaphic fauna is a major determinant of agricultural soil quality, but few studies have investigated soil fauna in different agroforestry systems. The objective of this study was to evaluate the effect of agroforestry plantations of *Ilex paraguariensis* on the abundance and composition of ants, earthworms, and nematodes in two agronomic systems, conventional and agroecological, and three plantation types (pathsides, agricultural field edges, and islets) in the Atlantic Forest in Paraguay. The study was conducted on 26 plots distributed in the different agronomic systems and plantation types (three plots per combination of agronomic system and plantation type, with a total of 18 plots, plus eight control plots). We compared agroforestry plots with non-agroforestry plots and with natural forests. Eighteen individuals of different native species (*Cordia americana*, *Cedrela fissilis*, *Handroanthus impetiginosus, Handroanthus albus*, *Peltophorum dubium*, and *Cordia trichotoma*) were planted in each plot, together with five individuals of *I. paraguariensis* (total of 2300 individuals ha^{-1}). The agroforestry scheme increased the abundance and improved the composition of beneficial soil fauna in the two agricultural systems. The agroecological system showed 238% higher abundance of ants and 90% higher abundance of earthworms than the conventional one. In both systems, the agroforestry scheme led to lower abundance of deleterious *Atta sexden* and *Acromyrmex spp*. leafcutter ants and higher abundance of beneficial species. The three plantation types increased the abundance of beneficial species. Agroforestry plots, particularly those in an agroecological system, were more similar to reference forest than to non-agroforestry plots. Our results suggest that the composition of soil fauna at the study site was significantly affected by the agroforestry scheme and, agronomic system, but not by plantation type. These results support the advantages of agroforestry and agroecological systems for favoring the diversity of soil fauna and related ecosystem services, which may help guide the design of successful agroforestry interventions.

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Introduction

In a world increasingly exploited by humans, who in turn need the services provided by ecosystems (Alcamo et al. 2005; Rey-Benayas et al. 2020), ecological restoration is of great importance for biodiversity conservation (Strassburg et al. 2020; Garibaldi et al. 2020). Agriculture and farming have caused 80% of historical global deforestation (FAO 2019) and have intensified in recent years. As a result, more than a third of agricultural land is moderately or severely degraded (CEPAL/FAO/IICA 2019). In tropical ecosystems, modern intensive agriculture is the main factor contributing to degradation of cultivated land (Bedano and Domínguez 2016, Le et al. 2020) and biodiversity reduction (Phalan et al 2013; Tsiafouli et al 2015; FAO 2019). In these areas, agricultural expansion and intensification are predicted to lead to the loss of 30% of vertebrate species abundance (Kehoe et al. 2017) and an increase in greenhouse gas emissions, highlighting the need for urgent improvements in agronomic practices (Clark et al. 2020).

Reversing soil degradation and recovering edaphic (soil) fauna, which is at the core of this study, require biodiversity-friendly agricultural practices, including the maintenance or ecological restoration of spaces with natural and semi-natural vegetation and the prioritization of native species when restoring degraded forest habitats (Dainese et al. 2015; Matos et al. 2020). An effective approach is agroforestry, which integrates trees and shrubs into farming systems (Torralba et al. 2016) and can provide the proper habitat for a large number of species characteristic of tropical forests (Haggar et al. 2019), particularly soil organisms (Socarrás and Izquierdo 2014, Harrison and Gassner 2020). Spaces with minimally disturbed vegetation are sources of biodiversity (Muluneh et al. 2021) and favor soil ecosystem function (Chen et al. 2020).

In agricultural systems, soil biodiversity is important for supporting terrestrial ecosystem services (Wagg et al. 2014; Tsiafouli et al. 2015), such as productivity (Crowther et al. 2019), mineralization of organic matter (Frouz 2018), nutrient recycling and availability (Chen et al. 2020), formation of macropores and water infiltration (Arnol and Williams 2016), degradation of pollutants, and soil structure formation (Botinelli et al. 2015, Arnol and Williams 2016, Yang et al. 2018). Soil biodiversity depends on macrofauna and microfauna. Macrofauna includes invertebrates with a body size greater than 2 mm, such as earthworms and ants, among other taxonomic groups (Bedano and Domínguez 2016). Microfauna consists of organisms with a body diameter of 1–100 µm (Neher 1999) and includes bacteria, fungi, and nematodes, among other taxonomic groups.

Soil species can be detrimental or beneficial to crops. Some ant species are considered harmful to crops (Amarilla and Arias 2011), while others are beneficial due to their functions in natural and cultivated systems (Escobar et al. 2010). Cutter ants of the *Atta* and *Acromyrmex* genera, which are native to the Neotropics (Brandão et al. 2011, Della et al. 2013, Castaño-Quintana 2019) and difficult to control (Lajarthe 2000), can severely damage agricultural and forest plantations (Lopes Vinha et al. 2020; Pimentel et al. 2022). In contrast, many ant species provide valuable services: they regulate agricultural pests, aerate the soil, increase drainage and penetration by plant roots (Sousa-Souto et al. 2008, Della et al. 2013), favor water infiltration (Gilibert et al. 2022) and cation exchange, and increase the mineralization and availability of organic matter and nutrients (Della et al. 2013; Offenberg 2015), which can improve crop yields. On the other hand, earthworms benefit agricultural soils (Valdez-Ibañez et al. 2019). They promote the rapid decomposition of organic matter, particularly leaf litter (Frouz 2018), as well as soil formation and nutrient cycling (Bertrand et al. 2015; Cardinael et al. 2019). Finally, soil nematodes, together with springtails, protozoa, and mites, constitute a critical link between macrofauna and primary decomposers due to their effect on the release of immobilized nutrients (George 2006). Several nematode species are beneficial (Yeates 1987), playing fundamental roles in carbon fluxes (Jiang et al. 2018) and biogeochemical cycles (Trap et al 2016), and they are bioindicators of soil health (Gao et al. 2020; Schlüter et al. 2022). There are saprophagous or bacteriophagous nematode species that feed on bacteria associated with soil organic matter, predator species that feed on other nematodes and soil organisms, and phytophagous species that attack plants (Valiente 2010; Gitanjali & Jisna 2018).

How agroforestry systems influence the characteristics of soil fauna on yerba mate plantations has not been studied in Paraguay. Therefore, the objective of this study was to evaluate the effects of an agroforestry scheme on soil fauna (ants, earthworms, and nematodes) in the Atlantic Forest in Paraguay. We examined these effects under two agricultural systems, conventional and agroecological, and three plantation types (pathsides, agricultural field edges, and islets). We investigated how the agroforestry scheme affected soil fauna, particularly ants, worms and nematodes, within a six-year period. Our hypotheses were that (1) an agroforestry scheme would increase the abundance of soil fauna in both agricultural systems, particularly of fauna beneficial to crops; (2) the agroecological system would lead to greater abundance of soil fauna than the conventional system because of higher soil quality; and (3) soil fauna would be more abundant in forest islets and pathsides than in agricultural field edges due to lower interior area in the field edges. As controls, we included non-agroforestry plots and reference forests. This study expands knowledge about the soil fauna in agroecosystems in the region, which may help guide efforts to improve agricultural practices and ensure the sustainability of food production.

Material and methods

Study area and study groups

The study was conducted between 2010 and 2016 on two farms in the Repatriation District in the Department of Caaguazú in eastern Paraguay (Fig. 1). The farms were located at coordinates 25°33′11.25'', S 55°55′38.02'' W and 25°34′37.30'' S, 55°45′01.53'' W, within the Atlantic Forest (World Wildlife Fund 2019). Of the original 47,120,400 ha of the Atlantic Forest (Di Bitetti et al. 2003) only approximately 9% remain as scattered fragments in Paraguay (Da Ponte 2017, Kubota et al. 2021). The study area has a subtropical climate. During the seven years of field work, annual temperature averaged 23.5 °C; annual precipitation, 1642 mm (Grassi 2020); maximum insolation, 9.0 h day^{-1}; and minimum insolation, 7.5 h day^{-1} (DINAC 2021).

Our study focused on three groups of invertebrates important for soil functioning: ants, worms and nematodes. In Paraguay, around 541 species of ants typical of the Neotropical region have been reported (Fernandez and Sendoya 2004, Wild 2002, 2005). Earthworm species, on the contrary, have not been studied, but at least 18 species of the families *Acanthodrilidae*, *Glossoscolecidae*, *Megascolecidae*, *Rhinodrilidae*, and *Ocnerodrilidae* have been identified in the Atlantic Forest ecoregion in Brazil (Santos et al. 2018). Some species exist only in soils of good quality (Shipitalo and Gibbs 2000), and are therefore sensitive to disturbance (Bedano 2011). Land use and management practices have been reported to affect earthworm abundance and diversity (Cluzeau et al. 2012; Frazão et al. 2017). Finally, eight genera of nematodes have been linked to cultivation of yerba mate (*Ilex paraguariensis)* in Paraguay: *Criconemella, Helicotylenchus, Meloidogyne, Pratylenchus, Scutellonema, Tylenchorhynchus, Trichodorus,* and *Xiphidorus* (Caballero-Mairesse et al. 2021). Many more nematode species likely exist in the Atlantic Forest ecoregion but have not yet been characterized (Müller et al. 2019).

Experimental design

Two agricultural farms with different agronomic systems were selected (Table S1). One farm was under a conventional management system and the other farm was under an agroecological management system.

The agroforestry scheme implemented at both farms included six native tree species and the perennial crop *I. paraguariensis,* which was selected because of its economic importance for farmers in the study area. These species were planted at three plots in different plantation types: pathsides, agricultural field edge, and forest islets (Figure S1). Control plots (one for each system and plantation type) were included, leading to a total of 12 plots in each agronomic system. As another control, a plot of remnant forest close to each agronomic system was studied. All plots measured 100 m^2 overall; islets and pathsides had dimensions of 10 m × 10 m, while agricultural field edge had dimensions of 2.5 m × 40 m (Figure S2). The six native tree species planted were *Handroanthus albus*, *Handroanthus impetiginosus*, *Peltophorum dubium*, *Cedrela fissilis*, *Cordia americana*, and *Cordia trichotoma*. These species are

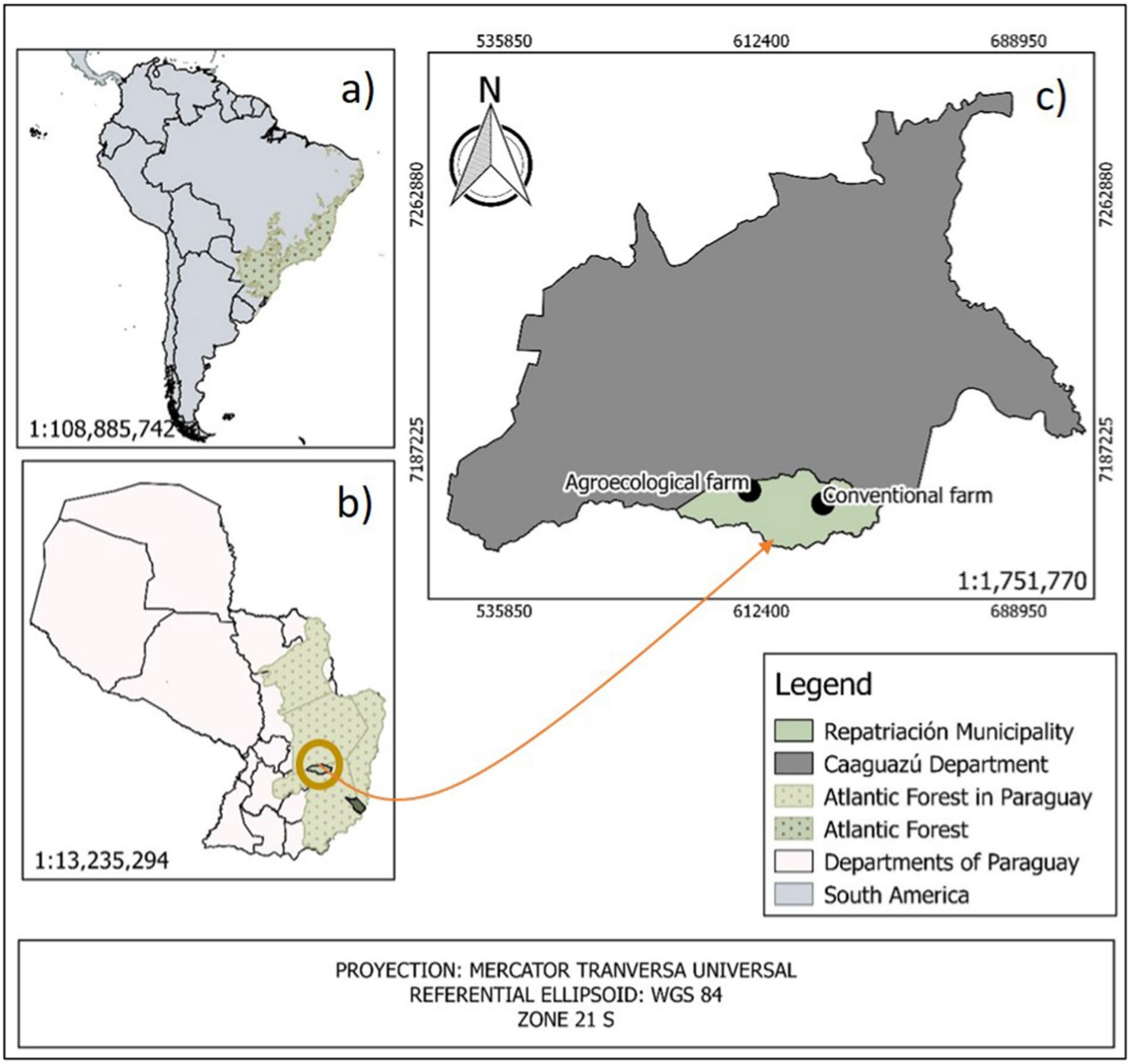

Fig. 1 Location of the study area (**a**) within the Neotropics and (**b**) in the eastern region of Paraguay and (**c**) of the experimental plantations in Caaguazú. Panels **a** and **b** show the distribution area of the Atlantic Forest according to the World Wildlife Fund (2019)

considered trees of the first stratum, achieving heights of 20–30 m (Degen et al. 2017); the species are also valuable for the ecosystem services they provide in the Atlantic Forest (Insfrán et al. 2022). Plantation density was 1,800 individuals ha^{-1} of native forest species (18 individuals/plot) and 500 individuals ha^{-1} of *I. paraguariensis* (5 individuals/plot; Table 1). The mean planting distance between individuals was 2.5 m (Figure S2). The plantations were established on 20–21 October 2010 in both agronomic systems.

Sampling of soil characteristics

The soils of the study area were of sandstone taxonomic origin, of the ultisol order, arenic rhodic paleudult subgroup, and sandy-clay textural subdivision. The soils contained 20–30% clay, showed strong water erosion and severe degradation (MAG 1995). The predominant land use was class III, with moderate limitations for agricultural use, implying conservation actions (López Gorostiaga 1995).

Table 1 Experimental design used to investigate the effects of different agronomic systems (conventional and agroecological) and plantation types (pathside, field edge, and forest islet) on the soil fauna abundance and composition. Control plots were included for all combinations of agronomic system and plantation type

Agronomic system	Plantation type	No. plots	Plot size (m^2)	Monitoring period*	Control plots	
					Non-agroforestry	Reference forest
Conventional	Pathside	3	100	2010–2016	1	1
	Field edge	3	100	2010–2016	1	
	Islet	3	100	2010–2016	1	
Agroecological	Pathside	3	100	2010–2016	1	1
	Field edge	3	100	2010–2016	1	
	Islet	3	100	2010–2016	1	
Total		18	–	–	6	2

*Monitoring years: 2010, 2012, 2014, and 2016

Soil parameters were measured in 2010 to obtain a baseline of the soil quality (Table 2). Soil compaction was measured using a 30° cone penetrometer (ASAE-R313-NN1981) at five points in each plot. Compaction was assessed according to US Department of Agriculture guidelines (Fitzpatrick et al. 2001). Samples from each plot were analyzed for pH, organic matter, and exchangeable aluminum ($Al^{+3}H^{+}$) at the Soil Laboratory of the National University of Asunción. Soils in the conventional system were quite compact, contained a medium level of organic matter, and had acidic pH and high content of $Al^{+3}H^{+}$. Soils in the agroecological system showed medium compaction, low to medium content of organic matter, acid to slightly acid pH, and low to medium content of $Al^{+3}H^{+}$ (Table 2). The higher organic matter content in the conventional system than in the agroecological system is attributed to (1) surface erosion towards the conventional system plots and organic matter loss in the agroecological system plots due to their lower and upper topographic positions, respectively; and (2) texture (sandy clay loam with 55% sand, 35% clay and 10% silt in the conventional system plots and sandy loam with 82% sand, 10% clay and 8% silt in the agroecological system plots; Soil Survey Staff 2022).

Table 2 Baseline physical and chemical properties of the soil in experimental plots

Agronomic system	Plantation type	pH	Organic matter (%)	$Al^{+3+}H^{+}$ ($Cmol.kg^{-1}$)	Compaction (kpa^{-1})	Depth (cm)
Conventional	Pathside	4.53 ± 0.07	1.65 ± 0.20	2.19 ± 0.25	0.97 ± 0.06	10.35 ± 0.86
	Islet	4.80 ± 0.21	2.27 ± 0.11	1.33 ± 0.39	0.89 ± 0.04	11.18 ± 1.24
	Field border	4.83 ± 0.30	2.36 ± 0.29	1.33 ± 0.53	0.47 ± 0.04	12.57 ± 0.78
	Reference forest	6.50	2.91	1.25	0.18	22.34
Agroecological	Pathside	5.27 ± 0.37	0.81 ± 0.05	0.47 ± 0.54	0.31 ± 0.04	16.58 ± 1.22
	Islet	5.43 ± 0.14	0.81 ± 0.07	0.24 ± 0.30	0.29 ± 0.04	17.33 ± 1.08
	Field border	6.32 ± 0.72	1.29 ± 0.78	0	0.26 ± 0.02	19.12 ± 1.23
	Reference forest	6.52	2.88	0	0.16	24.20

pH values: acidic, < 5.59; slightly acidic, 5.60–6.49; neutral, 6.50–7.49

Organic matter content: low, < 1.29; medium, 1.30–2.79; high, > 2.8

Exchangeable aluminum ($Al^{+3+}H^{+}$) content: low, < 0.39; medium, 0.40–0.89; high, > 0.90

Compaction: very compact, > 0.50; firm, 0.20–0.49; soft, < 0.19

Soil fauna sampling

Sampling of ants and earthworms was performed using soil monoliths (Figure S3) extracted according to the methodology of the Tropical Soil Biology and Fertility Program (Römbke 2007, Kist et al. 2013). The ants sampled were diurnal feeding species that are active during the sampling period (09:00 to 12:00 h); therefore, it is likely that due to their social habit they represent a subset of the total diversity of ants at the sampled site. Monoliths were distributed in an inverted "M" in islets, pathsides, and control forests, but in "zig-zags" in agricultural field edges (López-Nicora et al. 2021). Each monolith had the dimensions 25 cm × 25 cm × 30 cm (0.0188 m^3). Every two years sampling was performed in spring (October), starting in 2010 and ending in 2016. Sampling was always conducted from 9:00 a.m. to 12:00 p.m. at a temperature of 25–32 °C and relative humidity of 60–80%. Individuals of each species were counted in a pool of five samples extracted from soil monoliths from each plot (Figure S3). The collected individuals were placed in glass containers containing 70% alcohol for transfer to the Entomology Laboratory of the Faculty of Agrarian Sciences of the National University of Asunción for identification at family, genus, and species level whenever possible. Nematode sampling was based on a 20-cm deep soil layer extracted with a 10-cm diameter half-round probe. The distribution was the same for soil samples analyzed for nematodes, ants or earthworms (Figure S3). The sampling was performed once at the establishment of the agroforestry plantations (October 2010) and again at the end of the study (December 2016), from 9:00 a.m. to 12:00 p.m. on the same day for all plots at temperatures of 27–34 °C and relative humidity of 50–70%. Five samples from each plot were pooled for analysis in the Phytopathology Laboratory of the Faculty of Agrarian Sciences of the National University of Asunción in order to identify individuals at the genus level. Nematodes were extracted from 100 cm^3 of soil per plot using the Cobb method of centrifugal flotation in a 45% sucrose solution (Jenkins 1964).

Data analysis

The abundance of macrofauna and microfauna was analyzed at the genus level, which is often appropriated for soil studies (Gupta and Yeates 1997). The effects of agroforestry plantations as a restoration scheme, the agronomic system and the plantation type on the abundance of ants, earthworms, and nematodes over time were analyzed using generalized linear mixed models (GLMM). Possible effects of over-dispersion were accounted for using a negative binomial distribution error. The most complete model featured the following fixed effects: restoration scheme (restored using agroforestry *or* not restored), agronomic system (conventional *or* agroecological), plantation type (pathside, agricultural field edge, *or* islet), and all their interactions (including triple ones), as well as time since restoration, which was included as a covariate. Plot (sampled over time) was considered as a random factor. Models were compared using the Akaike Information Criterion corrected for small samples (AICc). The models that had a $\Delta AICc \leq 2$ with respect to the best model were selected (Burnham and Anderson 2002). Random effects were first evaluated, then fixed effects. Since models without random effects proved more parsimonious (lower AICc) than models with plot as a random effect, we proceeded testing fixed effects with generalized linear models (GLM). In cases with more than one best model, the most complete one served as a benchmark to evaluate predictions. The residuals of the best model(s) were explored using simulations (Dunn and Smyth 1996). These analyses were performed in R (R Development Core Team 2019) using the R packages 'lme4' (Bates et al. 2015), 'MuMIn' (Bartón 2019), and 'DHARMA' (Hartig 2019).

The effects of agroforestry restoration scheme, agronomic system, and plantation type on composition of soil fauna was investigated using a permutational multivariate analysis of variance (PERMANOVA) based on distance matrices (Anderson 2001) and non-metric multidimensional scaling (NMDS) analysis. PERMANOVA tested the response of the three fauna groups to each predictor, as well as possible interactions among these variables. Since no data were available for nematodes in 2012 or 2014, all the analyses were performed separately at the start (2010) and end (2016) of the study period. The NMDS is an indirect ordination that allows the similarity of the plots to be visualized on a two-dimensional space using distance matrices based on species composition and abundance. The distance matrices between plots for the NMDS were calculated with the

Bray–Curtis index and 999 permutations. The first two axes of the NMDS were correlated with species abundance, and the squared correlation coefficient (r^2) and corresponding p-value were calculated. The species that correlated significantly with the ordination axes were plotted in the NMDS ordination diagram. PERMANOVA and NMDS were performed using the 'vegan' package in R (Oksanen et al. 2019).

Results

Identified genera and species

We identified an ant species (*Atta sexden*) and seven genera (*Atta*, *Acromyrmex*, *Crematogaster*, *Solenopsis*, *Pheinole*, *Camponotus*, and *Pachycondyla*), corresponding to three subfamilies (Myrmicinae, Formicinae, and Ponerinae) and one family (Formicidae), one earthworm species (*Lombricus terrestrial*, Lumbricidae) and 13 genera of nematodes (*Acrobele*, *Aphelenchoides*, *Criconemoides*, *Diplogaster*, *Dorylaimus*, *Helicotylenchus*, *Hoplolaimus*, *Mononchus*, *Paratrichodorus*, *Pratylenchus*, *Rhabditis*, *Trichordorus*, and *Tylenchus*) corresponding to 10 families (Tables S2 and S3).

Abundance of edaphic fauna

At six years after the establishment of the agroforestry scheme, the agroforestry scheme increased the abundance of ants and earthworms over time (Table 3). In general, the abundance of ants and earthworms differed between the agronomic systems, but not among plantation types (Fig. 2a, b; Tables 3, S2 and S3). Ant abundance also differed substantially among reference forests, control plots, and agroforestry plots. The increase in ant and earthworm abundance was greater in the agroecological than in the conventional system (Fig. 2a, b; Tables 3, S2 and S3). The abundance of beneficial species *Crematogaster* spp., *Solenopsis* spp. and *L. terrestris* increased more in agroecological plots than in conventional ones, and some, such as the genera *Pheidole* and *Camponotus,* appeared over time in the agroecological system but not in the conventional one (Tables S2, S3 and S4). The abundance of beneficial ant species was greatest in the

Table 3 Abundance of soil fauna (individuals per 0.0188 m^3 soil) by agronomic system, plantation type, and year

Plantation type	Agronomic system			
	Conventional		Agroecological	
	2010	2016	2010	2016
Ants				
Pathside	188.00 ± 32.78	258.00 ± 36.95	312.33 ± 41.79	676.33 ± 116.80
Field edge	102.33 ± 13.29	198.33 ± 28.18	591.67 ± 59.68	943.00 ± 106.45
Islet	256.33 ± 43.04	248.00 ± 34.75	443.67 ± 45.62	766.33 ± 94.82
Control[a]	128.33 ± 30.38	114.33 ± 25.24	387.67 ± 45.91	346.67 ± 42.46
Forest[b]	560 ± 77.76	496 ± 67.35	560 ± 77.76	496 ± 67.460
Earthworms				
Pathside	0	46.96 ± 4.00	32.33 ± 6.81	52.67 ± 9.45
Field edge	16.00 ± 3.00	42.38 ± 5.04	48.33 ± 3.51	101.33 ± 9.45
Islet	16.00 ± 2.00	59.00 ± 6.56	81.00 ± 6.93	127.78 ± 8.78
Control[a]	10.67 ± 9.24	10.67 ± 9.24	43.91 ± 17.50	35.73 ± 10.89
Forest[b]	96.00 ± 16.00	80.00 ± 9.238	80 ± 18.48	80.00 ± 9.238
Nematodes				
Pathside	62.62 ± 110.50	103.15 ± 286.22	22.19 ± 38.15	26.69 ± 40.76
Field edge	56.77 ± 97.66	92.92 ± 192.25	33.57 ± 59.13	45.69 ± 78.07
Islet	76.00 ± 256.86	114.92 ± 252.33	47.98 ± 92.44	81.69 ± 137.84
Control[a]	87.85 ± 279.04	188.31 ± 578.05	34.33 ± 63.06	37.38 ± 76.79
Forest[b]	15.50 ± 37.06	12.75 ± 21.86	32.60 ± 55.30	31.50 ± 60.98

[a]Plots not restored with agroforestry

[b]Reference forest

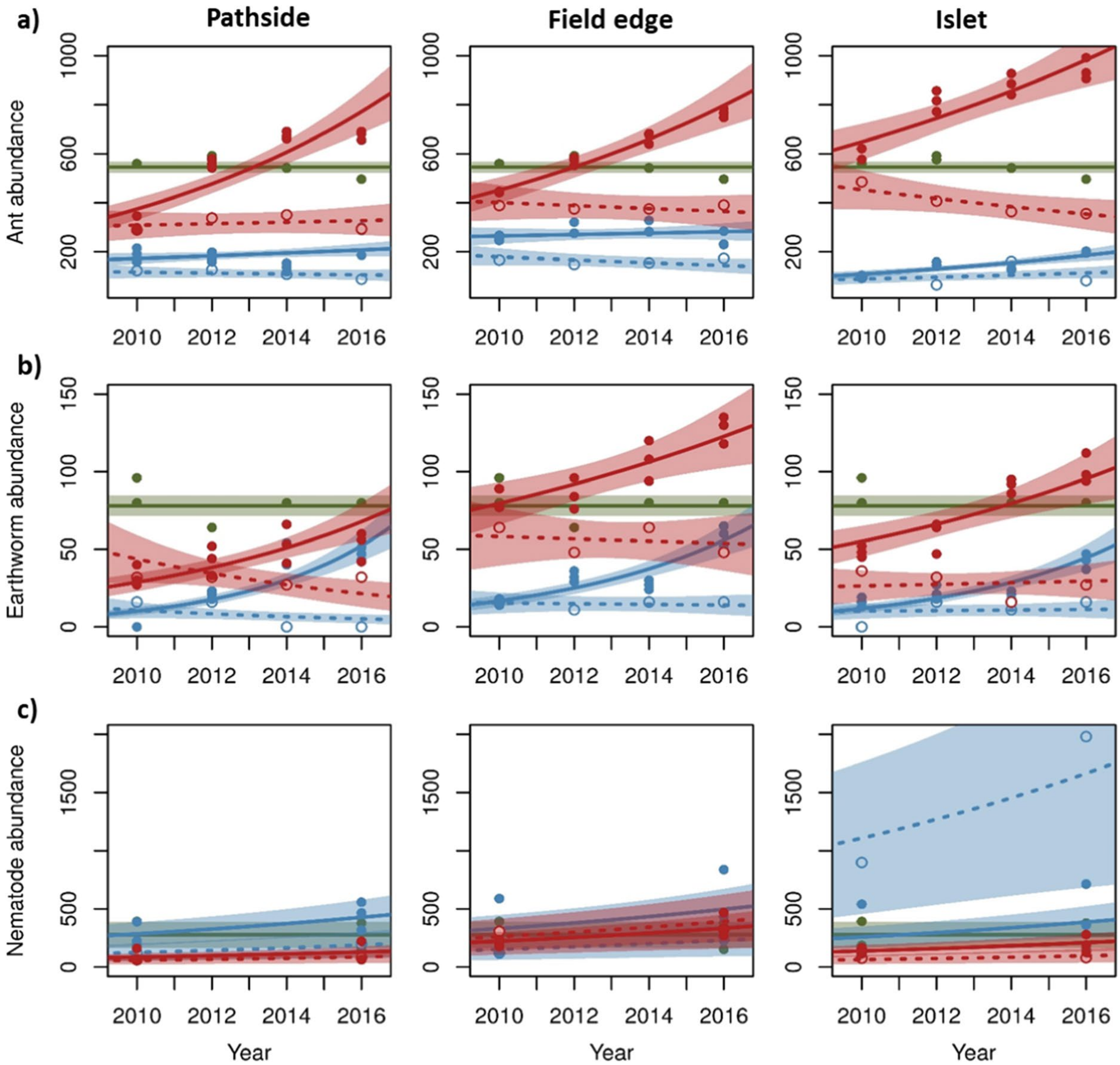

Fig. 2 Predictions of the abundance (individuals per 0.0188 m^3 soil) of soil fauna over time for (**a**) ants, (**b**) earthworms, and (**c**) nematodes in pathsides (*left* panels), field edge (*center*), and forest islets (*right*). Blue lines and dots represent the conventional agronomic system; red lines and dots, the agroecological agronomic system; and green lines and dots, the reference forest (not included in the statistical models). Dashed lines and open dots represent, in each agronomic system, the non-restored system, while the solid lines and filled dots represent the systems restored by agroforestry. Colored bands indicate the 95% confidence intervals, and overlap of bands indicates no statistically significant difference

islets of agroecological plots and in the agricultural field edges of conventional plots (Tables S5 and S7). Conversely, restoration with agroforestry reduced the abundance of leafcutter ants *A. sexden* and *Acromyrmex spp.* in both agroecological and conventional plots (Tables S2, S3). The abundance of *L. terrestris* was higher in all plantation types in the agroecological system compared to the conventional one (Tables S5 and S7).

In contrast to the results for ants and earthworms, the agroforestry scheme increased the abundance of nematodes in the conventional system, without affecting their abundance in the agroecological system (Fig. 2c; Tables 3, S2, S3 and S4). Both at the beginning of the study and after six years, conventional plots showed greater abundance of nematodes than agroecological ones for all plantation types, even higher than the abundance in the reference forest (Fig. 2c, Table 3). Abundance of beneficial nematode species was higher in the agroecological system than in the conventional one. In the agroecological system, abundance of the phytoparasite *Helicotylenchus* decreased due to the effect of the agroforestry system (Table 3). The highest abundance of this nematode genus was found in non-agroforestry plots (Table S6).

Species composition

PERMANOVA indicated that soil species composition was significantly affected by all the predictors and their interactions, both at the beginning and end of the study (Table 4). After six years, the factors that most determined the species composition were the agroforestry scheme and the type of agronomic system. NMDS ordination showed segregation of the plots depending on whether they were restored through agroforestry, on the agronomic system, and on whether they were control plots or reference forests. Agroforestry restoration, particularly under the agroecological system, led to plots more similar to natural forests (Fig. 3). In fact, only agricultural field edge showed some similarity in species composition with the agroecological system and reference forest.

The correlations between individual taxa and the first two axes of the NMDS indicated positive associations of the agroforestry scheme and the agroecological system with beneficial species, as well as the positive associations of lack of agroforestry and the conventional system with harmful species. Thus, the presence of several beneficial species (*Camponotus* spp., *Crematogaster* spp., *L. terrestris*, *Pheidole* spp., and *Solenopsis* spp.) positively correlated with each other both at the beginning and end of the study. There were five positive correlations between *Camponotus spp*., *Crematogaster spp*., *L. terrestris, Pheidole spp.* and *Solenopsis spp*.; likewise, *Helicotylenchus spp*., *Atta sexden* and *Pachycondyla spp*. showed negative correlations (Fig. 3 and Table S8).

Discussion

How agroforestry systems involving yerba mate cultivation influence the characteristics of soil fauna has

Table 4 Permutational multivariate analysis of variance to identify predictors of species composition at the beginning and end of the study

Factor	Df	Sums of sqs	Mean sqs	F model	r^2	Pr (> F)
2010						
System	1	0.805	0.805	20.891	0.262	0.001 ***
Type	2	0.539	0.269	6.991	0.176	0.001 ***
Agrof	1	0.109	0.109	2.841	0.036	0.020 *
System:Type	2	0.499	0.250	6.488	0.163	0.001 ***
System:Agrof	1	0.095	0.095	2.469	0.031	0.025 *
Type:Agrof	2	0.266	0.133	3.456	0.087	0.001 ***
System:Type:Agrof	2	0.290	0.145	3.766	0.095	0.002 **
Residuals	12	0.462	0.039	0.151		
Total	23	3.066		1.000	0.850	
2016						
System	1	1.037	1.037	37.504	0.286	0.001 ***
Type	2	0.366	0.183	6.620	0.101	0.001 ***
Agrof	1	0.682	0.682	24.677	0.188	0.001 ***
System:Type	2	0.249	0.124	4.493	0.069	0.001 ***
System:Agrof	1	0.298	0.298	10.771	0.082	0.001 ***
Type:Agrof	2	0.338	0.169	6.115	0.093	0.001 ***
System:Type:Agrof	2	0.326	0.163	5.887	0.090	0.001 ***
Residuals	12	0.332	0.028	0.091		
Total	23	3.332		1.000	0.909	

System = agronomic system, Type = type of plantation, Agrof = agroforestry

P-values: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

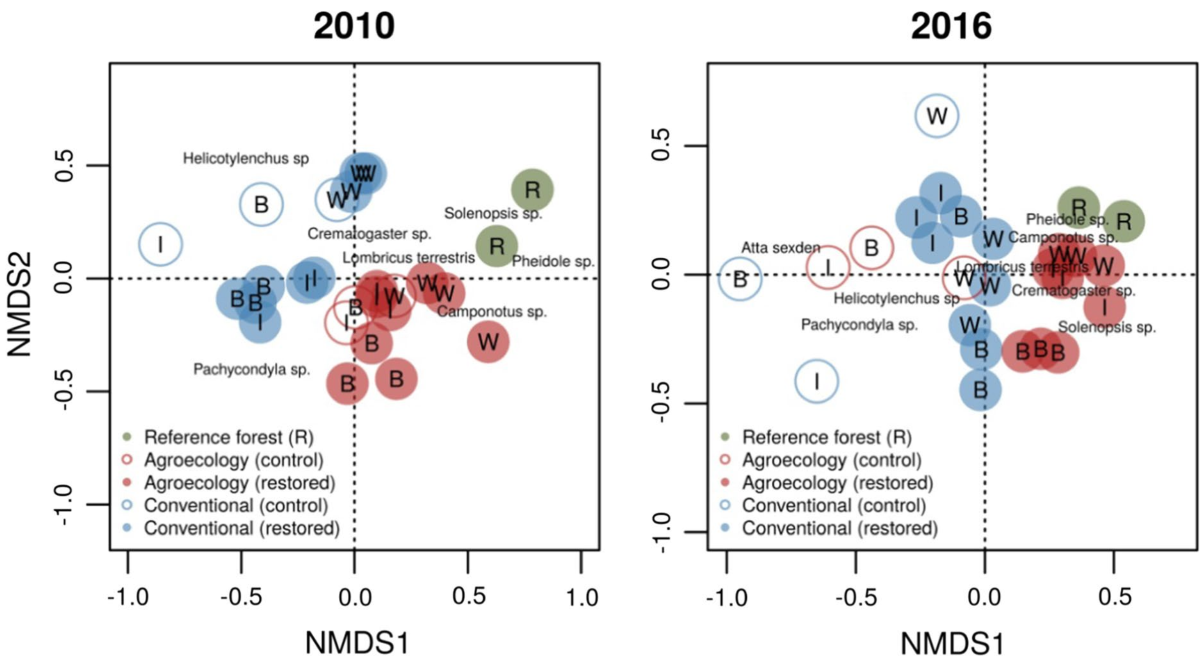

Fig. 3 Graphic representations of non-metric multidimensional scaling (NMDS) analysis of soil fauna species, including ants, earthworms, and nematodes, at the beginning of the study (2010) and at the end (2016). Blue circles represent the conventional agronomic system; red, agroecological agronomic system; green, natural forest; transparent, plots not restored through agroforestry. Letters identify the types of plantations along pathsides (B), field edges (W), and islets (I), as well as reference forest (F). Species that significantly correlated with the ordination axes are also represented, illustrating their (indirect) relationship with agroforestry restoration, agronomic system, and plantation type in the study

not been studied in Paraguay. Here, we analyzed how the establishment of different agroforestry schemes affected the abundance and composition of soil fauna six years after plantation took place. We compared the effects between two agronomic systems (conventional or agroecological) and different plantation types (pathsides, agricultural field edges, or forest islets). In general, the agroforestry scheme increased the abundance and improved the composition of beneficial soil fauna in both agricultural systems, in support of our first hypothesis. Consistent with our second hypothesis, soil fauna abundance, particularly for beneficial species, increased in the agroecological system compared to the conventional one. However, contrary to our third hypothesis, we did not find any significant effect of plantation type.

Agroforestry effects

Agroforestry restoration increased the abundance of ants and earthworms over time. These results are consistent with other studies in similar ecosystems (Meli et al. 2017; Tsufac et al. 2021). However, the abundance of macrofauna was similar to that of a degraded primary forest in the Brazilian Amazon (Barros et al. 2002). Restoration brought the species composition of plots, particularly those in the agroecological system, closer to the species composition in reference forest. This can be explained by the beneficial effect of agroforestry schemes in alleviating soil acidity and associated toxicity, restoring nutrient concentration, and reducing surface soil erosion (Tscharntke et al. 2011; Jose 2012, Marsden 2020).

The present study also demonstrates that agroforestry schemes can reduce the abundance of deleterious leafcutter species of the *Atta* and *Acromyrmex* genera, consistent with other studies in the Atlantic Forest (Pimentel et al. 2022). At the same time, the agroforestry scheme in our study increased the abundance of five beneficial species. For example, the cosmopolitan genus *Solenopsis* (Karaman 2010) controls up to 80% of green stink bug eggs (*Nezara viridula*) in crops in India (Olson and Ruberson 2012), and it regulates the abundance of mites (Offenberg 2015).

Solenopsis and *Pheidole* ants, dominant soil omnivores, tolerate degraded environments (Sandoval-Gómez et al. 2012) and prey on fly larvae (Carrero et al. 2013).

Solenopsis as well as *Camponotus* species are detritivorous and can remove the same amount of soil as earthworms (Noguera-Talavera et al. 2017). In fact, they are common in cultivation of *I. paraguariensis* (Junqueira et al. 2001). We also identified ants of the genus *Pachycondyla*, which defend their nests aggressively. This genus was less abundant, even in the agroforestry scheme, reflecting the situation in Atlantic Forest (Wild 2002). Most species of this genus are generalist predators of arthropods (Orivel and Dejean 2001), while some others are specialized predators of termites. In Paraguay, two species of this genus have been recorded, *Pachycondyla obscuricornis* and *Pachycondyla verenae*; the latter has been described in Caaguazú Department (Wild 2005).

The only earthworm species identified in this study, *L. terrestris*, is considered beneficial because it decomposes organic matter, recycles nutrients, and forms biopores in the soil (Valdez-Ibañez et al. 2019). Agroforestry restoration increased its abundance in our study, in line with previous research in France (Cardinael et al. 2019). This effect may reflect higher soil fertility (Barros et al. 2002; Cardinael et al 2020; Tsufac et al. 2021) and more favorable soil temperature and humidity due to tree shade (Santos et al. 2018).

The agroforestry scheme incremented nematode abundance in conventional plots, but not in agroecological plots. However, agroforestry schemes increase the abundance of beneficial free-living nematodes, similar to the results of Puissant et al. (2021). Among the 13 genera of nematodes identified in the present study, *Acrobeles* and *Rhabdistis* (bacterivores), *Aphelenchoides* (fungivores), and *Mononchus* (predators of other nematodes) are considered beneficial for the agroecosystem (Maina et al. 2021), while all others are considered plant parasites (Valiente 2010; Schlüter et al. 2022).

Agronomic system effects

The agroforestry scheme promoted beneficial soil macrofauna to a greater extent in the agroecological system than in the conventional one, consistent with the diversified agroecosystem prediction (Rodríguez & Salazar 2021). One explanation is that the use of agrochemicals in conventional systems disturbs the biotic community, especially earthworms (Murchie et al. 2015). Agroforestry restoration increases soil cover by dry branches and leaf litter, which favors nest building by *Pheidole* ants (Camargo-Vanegas and Guerrero 2020), which would explain the results found in our study.

The abundance of the different genera of nematodes varied between conventional and agroecological plots. This was the case for *Paratrichodorus* and *Trichodorus*, transmitters of viral diseases; *Pratylenchus*, a polyphagous phytonematode (Goulart 2008; López-Nicora et al. 2021) and migratory endoparasite that, in tropical areas, promotes root rotting of certain crops associated with fungi; and *Tylenchus*, present in crop roots, with a deleterious effect on yield (Valiente 2010). Phytoparasites of the *Helicotylenchus* genus, which inhabit the soil-root interface (Jones et al. 2016), were more abundant in conventional plots and the agroecological system; they presented the highest value of the predatory and omnivorous trophic groups, coinciding with the study by Salas (2019). The abundance of the genus *Hoplolaimus*, an ectoparasite linked to various crops (Ma et al. 2022), increased in both agronomic systems during the six years of monitoring.

Plantation type effects

Agroforestry schemes implemented in either form of linear elements (pathsides and agricultural field edge) or islets increased the abundance and improved the composition of beneficial species, particularly an ant and the earthworm, similar to a study in an agricultural landscape in Northwest Germany (Schirmel et al. 2016). Beneficial ants provide ecosystem services in agrosystems such as plant pollination, soil bioturbation and regulation of harmful insects to crops (Diamé et al. 2017). However, most of the nematode genera in crops are harmful, in particular the *Helycotilenchus* genus. These nematodes are ectoparasites and semi-endoparasites of roots (Quénéhervé et al. 1995) and generally reduce crop yields (Guzmán-Piedravita 2011).

Our research reports that six years after planting, the abundance of macrofauna increased on the pathsides and fields edges. However, previous work in Mediterranean ecosystem cropping plot showed that the abundance of soil macrofauna strongly depends on season (D´Hervilly et al. 2022) and ecological interactions (Marsden et al. 2020).

The increase in the abundance of ants and earthworms as a result of the agroforestry system was greater on pathsides and field edges with no-tilled soils. Earthworms are highly sensitive to conventional tillage (Briones and Schmidt 2017) and semi-natural areas favor their presence and abundance. There is a need of further investigation on the interactions of earthworms with soil elements and other fauna groups given their importance for the functioning of tropical agroecosystems.

Applications and conclusions

In general, our results show that agroforestry restoration with native tree species combined with *I. paraguariensis* influences the abundance of taxonomic groups of soil macrofauna and microfauna within a timespan as short as six years. According to the NMDS and the PERMANOVA, these effects were observed since the first year of our experiment. Our agroforestry scheme increased the abundance of beneficial species, reduced deleterious species, and improved the composition of ants, earthworms, and nematodes, especially in agroecological systems. In particular, our agroforestry scheme reduced the abundance of the leaf-cutter ant species *A. sexden* and *Acromyrmex* spp., which can promote tree establishment, especially of the sensitive tree species. Our scheme also increased the abundance of ants, earthworms and, potentially, beneficial nematodes in all three plantation types. These results may encourage farmers to implement successful agroforestry systems.

Future studies should continue to deepen our understanding of the abundance and composition of soil fauna in tropical agroforestry systems, as well as clarify soil-vegetation-water interactions. As another step to ensure successful restoration of agricultural land, agroforestry models should consider key interspecific interactions. In these ways, restoration efforts on agricultural land can maintain or increase biodiversity and associated ecosystem services.

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Declarations

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Informed consent Not applicable.

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