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Agroecosystem diversification with legumes or non-legumes improves differently soil fertility according to soil type

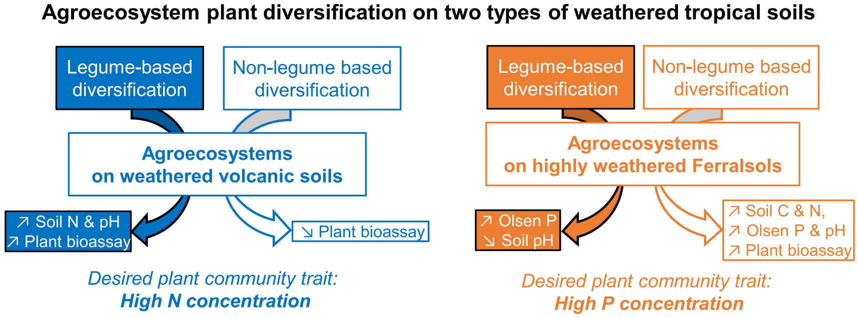
Marie Sauvadet [a,b,c,*], Jean Trap [a], Gaëlle Damour [b,c], Claude Plassard [a], Karel Van den Meersche [b,d,e], Raphaël Achard [b,c,f], Clémentine Allinne [b,e,g], Patrice Autfray [b,h,i], Isabelle Bertrand [a], Eric Blanchart [a], Péninna Deberdt [b,j], Séguy Enock [k], Jean-Daniel Essobo [k], Grégoire T. Freschet [l,m], Mickaël Hedde [a], Elias de Melo Virginio Filho [e], Bodovololona Rabary [i], Miora Rakotoarivelo [n], Richard Randriamanantsoa [i], Béatrice Rhino [b,j], Aude Ripoche [b,h,i], Elisabeth Rosalie [b,c,f], Stéphane Saj [b,g,k], Thierry Becquer [a], Philippe Tixier [b,c], Jean-Michel Harmand [b,d,k]

[a] Eco&Sols, Institut Agro, Univ Montpellier, CIRAD, INRAE, IRD, F-34060 Montpellier, France
[b] Univ Montpellier, F-34398 Montpellier, France
[c] CIRAD, UPR GECO, F-34398 Montpellier, France
[d] CIRAD, UMR Eco&Sols, F-34398 Montpellier, France
[e] CATIE (Tropical Agricultural Research and Higher Education Center), Turrialba 7170, Costa Rica
[f] CIRAD, UPR GECO, F-97285 Le Lamentin, Martinique, France
[g] SYSTEM, Univ Montpellier, CIHEAM-IAMM, CIRAD, INRAE, Institut Agro, F-34060 Montpellier, France
[h] CIRAD, UPR AIDA, BP 110 Antsirabe, Madagascar
[i] FOFIFA SRR, BP 230 Antsirabe, Madagascar
[j] CIRAD, UPR HORTSYS, F-97285 Le Lamentin, France
[k] ICRAF (World Agroforestry), West and Central Africa Regional Program, Yaounde, Cameroon
[l] CNRS, Station d'Ecologie Théorique et Expérimentale, F-09200 Moulis, France
[m] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Univ Paul Valéry Montpellier 3, Institut Agro, INRAE, F-34293 Montpellier, France
[n] Université d'Antananarivo, Ecole Supérieure des Sciences Agronomiques, BP 175 Antananarivo, Madagascar

HIGHLIGHTS

- We compared plant diversification impacts on soil fertility across 6 agroecosystems.
- Benefits of plant diversification depended on both legume presence and soil type.
- Legume-based diversification was mostly beneficial on the younger soils.
- Ferralsols' fertility was improved with plant communities' litter P content.
- Plant communities' traits were linked with diversification impacts on contrasting soils.

GRAPHICAL ABSTRACT



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ABSTRACT

Plant diversification through crop rotation or agroforestry is a promising way to improve sustainability of agroecosystems. Nonetheless, criteria to select the most suitable plant communities for agroecosystems diversification facing contrasting environmental constraints need to be refined. Here, we compared the impacts of 24

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[*] Corresponding author at: CIRAD, UPR GECO, F-97285 Le Lamentin, Martinique, France.
E-mail address: marie.sauvadet@cirad.fr (M. Sauvadet).

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different plant communities on soil fertility across six tropical agroecosystems: either on highly weathered Ferralsols, with strong P limitation, or on partially weathered soils derived from volcanic material, with major N limitation. In each agroecosystem, we tested several plant communities for diversification, as compared to a matching low diversity management for their cropping system. Plant residue restitution, N, P and lignin contents were measured for each plant community. In parallel, the soil under each community was analyzed for organic C and N, inorganic N, Olsen P, soil pH and nematode community composition. Soil potential fertility was assessed with plant bioassays under greenhouse controlled climatic conditions.

Overall, plant diversification had a positive effect on soil fertility across all sites, with contrasting effects depending on soil type and legumes presence in the community. Communities with legumes improved soil fertility indicators of volcanic soils, which was demonstrated through significantly higher plant biomass production in the bioassays (+18%) and soil inorganic N (+26%) compared to the low diversity management. Contrastingly, communities without legumes were the most beneficial in Ferralsols, with increases in plant biomass production in the bioassays (+39%), soil Olsen P (+46%), soil C (+26%), and pH (+5%). Piecewise structural equation models with Shipley's test revealed that plant diversification impacts on volcanic soil fertility were related to soil N availability, driven by litter N. Meanwhile, Ferralsols fertility was related to soil P availability, driven by litter P. These findings underline the importance of multifactorial and multi-sites experiments to inform trait-based frameworks used in designing optimal plant diversification in agroecological systems.

1. Introduction

Plant diversification is an important lever to ensure environmentally and nutritionally sustainable food supply in agroecosystems (Dawson et al., 2019). Agroecosystem diversification can either be achieved by increasing sequential crop diversity (Tiemann et al., 2015) and/or by simultaneously cultivating several species within the field, such as cereal – cover crop intercropping or cocoa – shade trees intercropping (Tscharntke et al., 2011). Both forms of plant diversification are known to provide a wide range of services such as pest regulation (Ratnadass et al., 2012), the diversification of farm income sources, and a higher food production stability at national levels (Renard and Tilman, 2019; Díaz et al., 2020). Plant diversification can also improve soil carbon (C) storage and soil fertility, by promoting soil biological activity and facilitating access to nutrients otherwise inaccessible to the main crop (Latati et al., 2016; Duchene et al., 2017). Legume species are especially favored for plant diversification for their ability to fix atmospheric nitrogen (N_2), hence reducing the need of synthetic N fertilizers of the agroecosystems (Jensen et al., 2012). However, the services and disservices provided by legume and non-legume plants vary with both the species used and the agroecosystems' environmental constraints (Fujii et al., 2018; Waithaisong et al., 2020). A better mechanistic understanding of how plant diversity and its management alter agroecosystem functions will help design efficient cropping systems under a range of environmental conditions.

Greater plant species diversity is assumed to lead to higher ecosystem functionality (Martin and Isaac, 2015; Isbell et al., 2017), since increasing the number of species within an ecosystem increases the probability for plants to display complementary resource requirements and use within the community (Barry et al., 2019). The understanding of plant community relationships with their environment and the effects of plant diversity has benefited from trait-based approaches in ecology rather than relying solely taxonomic diversity. Plant functional traits are defined as any morphological, anatomical, physiological, or phenological features measurable at the individual level (Violle et al., 2007). They are tightly linked with plant resource acquisition strategies and plant effects on resource cycling in ecosystems (Freschet and Roumet, 2017). A trait-based framework using plant traits to design optimal plant community compositions for agroecosystems sustainability has been proposed on this principle by Damour et al. (2018). This approach has been promoted by several reviews and conceptual papers (Garnier and Navas, 2012; Wood et al., 2015). However, it lacks both (i) plant trait data in agroecosystems (Martin and Isaac, 2015) and (ii) multi-sites studies to consider the influence of contrasting environmental constraints on plant traits – ecosystem functions relationships.

While soil fertility has been linked to plant traits in many studies, how these relationships may be influenced by local ecosystem environmental constraints are less well known (Freschet et al., 2021). For instance, plant P acquisition can be achieved through the development of its root network and/or through root association with mycorrhizas (Sawers et al., 2017). However, the efficiency of either plant roots network or mycorrhizal symbioses for P acquisition highly depends on overall soil P level, which decreases with soil age (Lambers et al., 2008). Differences in soil P level also impacts the fixation of atmospheric N by legume species (Augusto et al., 2013; Batterman et al., 2013); however, while legume species are known to differ in their efficiency to provide N (e.g. Blesh, 2018), how P limitation can affect these differences remains less well known. This question is especially important for tropical agroecosystems, displaying strong contrasts of N and P limitations because of the wide range of soil alteration found in these latitudes (Lambers et al., 2008; Hou et al., 2020). Aged, weathered soils such as Ferralsols, which are widely spread in tropical countries, are typically more P-limited than younger soils, which are more N-limited.

Global-scale studies across soil fertility gradients have evidenced the importance of litter N and P restitution for soil N and P availability in natural ecosystems, both for aboveground (Hobbie, 2015; Maire et al., 2015) and belowground litter (Bardgett et al., 2014) – although the latter is less studied due to the difficulty of their measurements. Nutrient release from litter decomposition is driven by the soil food web, yet both its composition and functioning are heavily altered by anthropic management in agroecosystems (de Vries et al., 2013). Nonetheless, several key food web components such as bacterial-feeding nematodes have been observed to promote litter and soil organic N and P mineralization in agroecosystems (Trap et al., 2016; Ranoarisoa et al., 2018, 2020). While these food web components can be favored by specific plant communities in natural ecosystems (Wardle et al., 2003; De Deyn et al., 2004), the relationships between plant traits, soil food web and soil fertility have seldom been studied as a whole in agroecosystems. We clearly need to improve our understanding on how plant community traits relate to soil fertility both directly through litter-mediated nutrient cycling feedbacks, and indirectly through food web activity promotion. This could provide new leads to set up a trait-based approach framework for agroecosystem plant diversification (Bender et al., 2016).

In this context, we studied six tropical agroecosystems – either on highly weathered Ferralsols or on more recent, partially weathered soils derived from volcanic parent material – to compare the influence of plant diversification on soil fertility and soil micro-food web composition. We tested whether (i) plant diversification with legume or non-legume species could improve soil fertility in these contrasting tropical agroecosystems and soil types, (ii) diversification impacts on soil fertility could be linked to plant communities' traits, and (iii) soil fertility – plant communities relationships understanding could be improved with the characterization of changes in soil micro-food web composition.

2. Materials and methods

2.1. Sites and sampling strategy

Six experimental sites, within the CIRAD – IRD network and collaborating institutions in tropical countries (Cameroon, Costa Rica, Madagascar and Martinique, West Indies) (Table 1) were selected. Two main types of plant diversification were considered: rotational diversification (at 3 sites; tomato, rice and banana based-cropping systems) and agroforestry (at 3 sites; shade trees intercropping in cocoa, organic coffee and conventional coffee based-cropping systems). For each focal crop (tomato, rice, banana, cocoa, organic coffee and conventional coffee), three to five combinations of crop / additional species (hereafter called "plant communities") were replicated in three to eight blocks, accounting for a total of $n = 142$ observations (Table 1).

The trials were carried out on soils with two contrasting levels of soil mineral fertility: highly weathered Ferralsols with high P-limitation for Rice and Cocoa agroecosystems, and partially weathered soils derived from volcanic parent material for Tomato, Banana, Organic and Conventional Coffee sites (Nitisols, Cambisols and Acrisols), with expected major limitation in N (Lambers et al., 2008). Crop rotational diversification (i.e. diversification over time) corresponded to a plant community growing in rotation with the focal crop. At the end of the first growing season, the plant communities were cut and left in the field as a mulch on soil surface until crop sowing. One notable exception was the residues of *Allium fistulosum* from the Tomato site, whose integral aboveground biomass was harvested and hence exported from the field in both *A. fistulosum* / Tomato and *A. fistulosum* + *Crotalaria spectabilis* / Tomato rotations (Table 1). Although banana is a multiannual crop, only the sowing and cutting of different plant communities and the subsequent first year of banana cropping was considered, to be comparable with the other sites testing rotational diversification (i.e. Tomato and Rice). On the other hand, the agroforestry trials (i.e. simultaneous association in the same area) compared coffee or cocoa intercropped with different shade tree species with unshaded coffee or cocoa systems, respectively (Table 1).

Each of the six sites was hence designed to assess the impact of plant diversification compared to a reference treatment. The reference treatment in each site was the treatment that represented the lowest diversity management: crop without shade tree in agroforestry sites, rice / rice two-stages rotation in Rice site, and 170-days spontaneous grassing (i.e. no active sowing) / tomato and 245-days spontaneous grassing / banana in Tomato and Banana sites (Table 1).

2.2. Plant sampling and community traits measurements

Assessment of annual aboveground biomass restitution depended on diversification type. In rotational systems, plant communities' aboveground biomass was cut, and restituted as a mulch on soil surface during the first growing season. Residue restitution was assessed by harvesting and weighing one subplot of 1 m^2 in each block. Plant communities consisted of one to several species per treatment (Table 1) that were studied jointly (i.e. not separated by species during the sampling and analysis processes). In coffee and cocoa agroforestry systems, aboveground biomass restitution was assessed with litter collectors placed under the canopies of shade trees and crop; leaf litterfall from both the focal crop (cocoa or coffee) and the intercropped shade trees was collected and weighed at several times throughout the main litterfall season (see Sauvadet et al. (2020) for further details).

A composite sample of the litter collected from each community was then used to analyze plant community litter traits (Table S1). Total C and N contents were determined by dry combustion using a CHN micro-analyzer (Carlo Erba NA 2000, Milan, Italy). For total P content, 50 mg of ground litter were mixed with 65% HNO_3, then mineralized at 200 °C during 15 min in a Milestones ETHOS ESAY microwave, together with standard and blank. Phosphorus content was quantified colorimetrically using the yellow vanadomolybdate reagent (Neves et al., 2008) with modification. Briefly, ammonium heptamolybdate tetrahydrate (20 g L^{-1}) was first dissolved in 200 mL of deionized water with ammonia (2 mL L^{-1}). Ammonium vanadate (0.47 g L^{-1})

Table 1
Sites presentation. Legume species are in bold. Coffee site tested plant diversification impacts for organic and conventional systems.

	Experimental sites				
	Tomato	Banana	Rice	Coffee (organic & conventional)	Cocoa
Country	Martinique (West Indies)	Martinique (West Indies)	Madagascar	Costa Rica	Cameroon
Position	14°66 N, 61°00 W	14°66 N, 61°00 W	19°33 S, 46°25 E	9°53 N, 83°40 W	4°30 N, 11°10 E
Altitude	54 m a.s.l	54 m a.s.l	930 m a.s.l	600 m a.s.l	400–550 m a.s.l
Annual Precipitation	2000 mm y^{-1}	2000 mm y^{-1}	1330 mm y^{-1}	2915 mm y^{-1}	1300–1400 mm y^{-1}
Average temperature	25 °C	25 °C	24 °C	22 °C	25 °C
Soil information	Nitisol Clay	Nitisol Clay	Ferralsol Sandy clay - Loam	Acrisol – Cambisol Loam – Clay loam	Ferralsol Sandy loam
Soil type	Volcanic soil	Volcanic soil	Ferralsol	Volcanic soil	Ferralsol
Main crop	Tomato	Banana	Rice	Coffee	Cocoa
Fertilization	None to 138 kg N ha^{-1}, 138 kg P ha^{-1}, 276 kg K ha^{-1}	205 kg N ha^{-1}	5 t ha^{-1} manure	Organic: 5 t ha^{-1} coffee pulp Conventional: 150 kg N ha^{-1}, 10 kg P ha^{-1}, 75 kg K ha^{-1}	None
Diversification mode	Rotation	Rotation	Rotation	Agroforestry	Agroforestry
Reference treatment	1. 170-days grass*	1. 245-days grass*	1. Rice	1. Unshaded coffee	1. Unshaded cocoa
Plant communities tested for diversification	2. *Allium fistolusum* 3. ***Crotalaria spectabilis*** 4. ***C. spectabilis*** + *Allium fistolusum*	2. *Brachiaria decumbens* 3. ***Stylosanthes guianensis***	2. ***Arachis hypogaea*** 3. ***Mucuna cochinchinensis + C. spectabilis*** 4. *Sorghum bicolor* + ***Vigna unguiculata***	2. ***Chloroleucon eurycyclum***** 3. ***Erythrina poepiggiana*** 4. *Terminalia amazonia*	2. ***Albizia adianthifolia*** 3. *Canarium schweinfurthii* 4. *Ceiba pentandra* 5. *Dacryodes edulis* 6. *Milicia excelsa*
Year of sampling	2017	2018	2018	2017	2017
Site age at sampling	1 year	1 year	3 years	>17 years	>17 years
Numb. observations	20	18	16	49 (28 + 21)	39
Reference publication	Deberdt and Fernandes (2017)	Tixier et al. (2011)	Ripoche et al. (2019)	Sauvadet et al. (2019)	Sauvadet et al. (2020)

* Grass correspond to spontaneous grassing (dominated by gramineous species) in Tomato and Banana sites.
** Chloroleucon eurycyclum was only studied in the organic coffee system.

was added into 100 mL of hot deionized water and slowly acidified with 1 mL of 65% HNO_3. After addition of 100 mL of water and cooling, both solutions were mixed together with 90 mL of 65% HNO_3 and completed to 1 L with deionized water. The colored reaction was carried out by mixing the extract with deionized water and vanadomolybdate reagent. Overall, the sensitivity of the assay was 0.36 mg P g^{-1} DM. Lignin content was obtained by the van Soest method (Van Soest, 1963) with a Fibersac 24 fiber analyzer (Ankom, Macedon, NJ, USA). Litter quality of *C. arabica* in both Costa Rican sites (Organic Coffee and Conventional Coffee) and of *E. poepiggiana* and *T. amazonia* in the Conventional Coffee site could not be analyzed. We therefore estimated them from the review of Petit-Aldana et al. (2019) and from results in the Organic Coffee site, respectively.

2.3. Soil sampling, nematodes and soil fertility indices measurements

All soil analyses were performed on one composite soil sample per block of about 2 kg fresh soil from the 0–10 cm soil layer, corresponding to the zone of influence of aboveground litter deposition, at the key stage of crop development (i.e. flowering for rice and tomato and fruiting for banana, coffee and cocoa). The composite soil sample was obtained from 7 to 10 random locations within the main crop interrows in rotational systems, and around coffee and cocoa plants; in the case of agroforestry systems, the sampling was performed around coffee and cocoa plants that were under the canopy of the associated shade trees. Composite soils were carefully homogenized before being subsampled for nematode extraction and identification (used as a proxy of soil food web), and soil fertility components: plant bioassay production and soil chemical fertility (Table S1).

Nematode communities were characterized both to assess the impacts of agricultural practices on soil health (Ritz and Trudgill, 1999) and for their key roles in C, N and P cycling through the microbial loop theory (Bonkowski, 2004). Nematodes were extracted from 250 g fresh soil samples by elutriation (Seinhorst, 1950) and were counted with a stereomicroscope (×40). Nematodes were fixed in a 4% formaldehyde solution. Then, 200 specimens per sample were randomly selected on glass slides and identified to the genus level with a compound microscope (×400) (Nematrops Laboratory, Dakar, Senegal). Nematode community composition was used to calculate genera richness and Shannon diversity index at the level of the genus. Each nematode genus was then assigned to a trophic group (Yeates et al., 1993), which allowed us to calculate the Enrichment Index (EI), Basal Index (BI), Structure Index (SI) and the Nematode Channel Ratio (NCR). EI, BI and SI indicate the proportion of opportunistic, basal and specialists' taxa within the micro-food web, respectively (Ferris et al., 2001; Berkelmans et al., 2003). NCR indicates the proportion of bacterial-feeding nematodes – considered important for nutrient cycling promotion – within microbial-feeder nematodes (Yeates, 2003).

Fresh, coarsely homogenized soil was used for the measurement of soil inorganic N content with a 1:4 soil 1 M KCl solution mixture. NO_3^- and NH_4^+ were determined by continuous flow colorimetry (TRAACS 2000, Bran and Luebbe, Norderstedt, Germany). Another aliquot of fresh, coarsely homogenized soil was used for a greenhouse plant bioassay, an off-site assessment of "soil biochemical fertility" of the ecosystem, which relies on the short-term growth of seedlings of a model plant in soils collected beneath plant communities (Dybzinski et al., 2008). Briefly, 2-L pots were filled with 1.40 ± 0.01 kg of fresh soil from composite soil samples per block. Four seeds of maize (*Zea mays* L.) cv. CIRAD 412 were then sown into each pot; only two seedlings were left in each pot after sprouting of the seeds. The maize seedlings were grown in a greenhouse with manual watering to maintain soil at its optimal water holding capacity. After 45 days of vegetative growth, shoots and roots of the plants were harvested, washed, dried at 65 °C for 2 days, and weighed to obtain the above- and belowground dry biomasses. We refer to the biomass obtained by this method as "plant bioassay" in the rest of the article and in the illustrations.

A final soil subsample of 260 g was thoroughly mixed, then sieved at 2 mm and air-dried before analysis of total C, total N, Olsen P and pH (H_2O). Total soil organic C and N were determined by dry combustion of dry soil subsamples ground to 0.2 mm, using a CHN microanalyzer (Carlo Erba NA 2000, Milan, Italy). Soil pH (H_2O) was determined by mixing 2 g of dry soil with 10 mL of deionized water for 30 min. Olsen P content was measured from Olsen (1954). Briefly, 250 mg of dry soil were extracted with 5 mL of 0.5 M $NaHCO_3$ at pH 8.5 by 30 min shaking. P in the extract was then measured according to the malachite green method (Rao et al., 1997).

2.4. Statistical analyses

Inherent site differences in soil fertility and nematode community composition were first assessed through a comparison between each site reference treatment (Table 1) with generalized linear models coupled with post hoc HSD Tukey tests (Table 2).

In a second step, site reference treatments were used to assess the impact of plant diversification on soil fertility according to Hedges et al. (1999). First, log response ratio (LRR_i) was calculated for each site and soil variable:

$$LRRi = \ln\left(\frac{\text{Treatment i}}{\text{Reference Treatment}}\right) \tag{1}$$

where *"Treatment i"* is the treatment value at the plot i, and *"Reference Treatment"* the reference treatment mean value for the corresponding site. The log response ratio of nematode indices was calculated similarly after the addition of the value 1 to both the numerator and denominator to avoid errors caused by null values. This metric reflects a change of the variable relative to the site reference treatment; positive and negative values of LRR_i represent respectively a positive and negative effect of plant diversification relatively to its reference treatment. For each variable, we then assessed the mean log response ratio LRR_m according to two crossed factors: presence of legume in the community (with legume – without legume), and soil type (volcanic soils – Ferralsols), resulting in four different categories. LRR_m was calculated according to eq. 2 and estimated the 95% confidence interval around LRR_m using bootstrapping (1000 iterations) for each category with the {boot} R package.

$$LRRm = \frac{\sum \text{LRRi}}{n} \tag{2}$$

where n corresponds to the total number of observations of each category. LRR_m was calculated for all soil fertility and nematodes indices and was considered significant if its 95% confidence interval did not overlap with zero.

The plant community traits were first used in a principal component analysis (PCA) to identify trait covariation patterns and the main differences between plant communities across all sites. We then used generalized linear models coupled with the post hoc HSD Tukey test to assess the significance of legume presence and soil type on plant community traits. A first global analysis of relationships between plant community traits, soil fertility and nematode indices was performed with a Pearson correlation coefficient matrix, corrected for multiple comparison with the Benjamini-Hochberg method. This analysis allowed selecting the most pertinent variables to include in a following analysis of piecewise Structural Equation Models (pSEMs). The *psem* function of the {piecewiseSEM} R package (Lefcheck et al., 2015) was used in order to include the site identity as a random effect for each linear mixed-effects equation. Linear mixed effects equations were built as a first step according to the observed bivariate and multivariate relationships. Shipley's test of d-separation (Shipley, 2009) was then used to assess the overall fit of the pSEMs and whether paths were missing from the model. All statistical analyses were performed using R software (R-3.6.2) and the following packages: ade4, boot, emmeans, factoextra,

Table 2
Soil fertility and nematode indices of the reference site treatments.

	Experimental sites					
	Tomato	Banana	Rice	Conv. coffee	Org. coffee	Cocoa
Soil type	Volcanic soil	Volcanic soil	Ferralsol	Volcanic soil	Volcanic soil	Ferralsol
Reference treatment	170-days grass	245-days grass	Rice	Conv. Unshaded coffee	Org. Unshaded coffee	Unshaded cocoa
Soil biochemistry						
Soil C *(g C kg^{-1} soil)*	20.1 ± 1.1 bc	21.6 ± 1.4 b	18.0 ± 0.9 c	36.9 ± 4.9 a	39.3 ± 5.0 a	15.4 ± 5.3 c
Soil N *(g N kg^{-1} soil)*	1.9 ± 0.1 b	2.0 ± 0.1 b	1.3 ± 0.0 c	3.5 ± 0.4 a	3.6 ± 0.5 a	1.2 ± 0.4 c
Soil C:N ratio	10.9 ± 0.3 b	11.0 ± 0.2 b	13.6 ± 0.5 a	10.6 ± 0.3 b	10.8 ± 0.3 b	12.5 ± 1.1 a
Inorganic N *(mg N kg^{-1} soil)*	7.1 ± 0.9 c	16.1 ± 3.3 a	3.5 ± 1.6 d	11.1 ± 1.3 b	20.8 ± 3.6 a	10.7 ± 3.7 bc
Olsen P *(mg P kg^{-1} soil)*	12.3 ± 2.8 c	34.6 ± 2.6 a	4.4 ± 0.1 d	26.7 ± 5.0 b	39.0 ± 10.2 ab	8.0 ± 4.8 cd
pH H_2O	5.5 ± 0.1 c	6.1 ± 0.0 b	5.5 ± 0.0 c	5.0 ± 0.1 d	6.2 ± 0.1 b	6.6 ± 0.1 a
Plant bioassay *(g DM produced per plant)*	0.9 ± 0.2 c	1.6 ± 1.0 b	1.3 ± 1.3 bc	3.4 ± 1.3 a	4.2 ± 1.0 a	1.5 ± 0.5 b
Soil nematode community						
Bacterial-feeders *(ind kg^{-1} soil)*	1696 ± 900 a	219 ± 241 b	1260 ± 346 a	267 ± 185 b	2652 ± 1776 a	2088 ± 943 a
Fungal-feeders *(ind kg^{-1} soil)*	775 ± 298 a	106 ± 83 b	1069 ± 759 a	56 ± 83 b	705 ± 638 a	353 ± 177 a
Omn + Carn *(ind kg^{-1} soil)*	484 ± 257 b	661 ± 881 ab	1068 ± 329 a	9 ± 16 c	465 ± 291 b	885 ± 326 ab
Total free-living *(ind kg^{-1} soil)*	2955 ± 1290 a	986 ± 1163 b	3398 ± 770 a	332 ± 22 b	3822 ± 1680 a	3326 ± 1245 a
Plant-feeders *(ind kg^{-1} soil)*	2519 ± 1343 bc	6978 ± 3679 a	3112 ± 987 b	95 ± 70 d	1150 ± 857 c	4201 ± 1960 ab
Enrichment Index (EI)	72 ± 9 a	71 ± 24 a	36 ± 14 b	24 ± 25 b	31 ± 14 b	52 ± 18 ab
Basal Index (BI)	16 ± 3 b	6 ± 4 c	18 ± 9 b	70 ± 29 a	43 ± 29 ab	15 ± 4 b
Structure Index (SI)	69 ± 5 c	93 ± 5 a	78 ± 12 abc	13 ± 21 d	48 ± 33 bcd	81 ± 5 b
Nematodes Channel Ratio (NCR)	67 ± 9 c	68 ± 19 abc	58 ± 18 bc	87 ± 15 ab	74 ± 24 abc	85 ± 7 a
Genera richness	12 ± 1 b	8 ± 4 bc	9 ± 1 c	3 ± 2 d	12 ± 4 abc	16 ± 2 a
Shannon Index	2.02 ± 0.13 b	1.69 ± 0.51 b	1.88 ± 0.09 b	0.68 ± 0.47 c	1.55 ± 0.73 abc	2.31 ± 0.11 a

Significant differences were tested by GLS followed by Tukey HSD post hoc tests and bear different letters for P-values <0.05.

FactoMineR, ggplot2, lme4, multcomp, nlme, piecewiseSEM, psych, readxls, reshape2 and stats.

3. Results

3.1. Plant community traits

Plant community traits greatly differed between the communities according to (i) the presence of legumes in the community and (ii) the type of soil where the community was grown (Fig. 1). Legume presence in plant communities significantly increased litter N content (2.3 ± 1.2 against 1.3 ± 0.4%DM without legumes, P-value <0.01) across all sites, but did not impact significantly litter P content or the amount of aboveground biomass returned to the soil (Fig. S1). On the other hand, plant communities from Ferralsols (i.e. Rice and Cocoa sites) had lower litter P contents than sites on volcanic soils (0.08 ± 0.03 against 0.21 ± 0.07% DM, respectively, P-value <0.001), and higher lignin content (39.2 ± 7.9 against 26.6 ± 8.4% DM, respectively, P-value <0.001, Fig. S1). The amount of biomass restitution did not differ between volcanic soils and Ferralsols and was higher in Banana and Tomato sites than in the other sites (Fig. 1).

3.2. Differences in soil fertility and nematode indices across sites references

Soil pH was acid to slightly acid across all sites and ranged between 5.0 ± 0.1 for the Conventional Coffee site to 6.6 ± 0.1 for the Cocoa site (Table 2). Sites on Ferralsols (Rice and Cocoa) had the lowest total C (18.0 ± 0.9 and 15.4 ± 5.3 g C kg^{-1} soil, respectively) and N contents, the highest soil C to N ratio, and the lowest Olsen P content (inferior to 8.0 mg P kg^{-1} soil). On the other hand, Conventional and Organic Coffee sites presented the highest soil C, N and Olsen P contents, and produced 2.1 to 4.7 times more biomass in the plant bioassay than the other sites (Table 2). Tomato and Banana sites presented intermediate values for most soil fertility indices, except for inorganic N content and plant bioassay, which were one of the lowest for Tomato site.

Total free-living and bacterial-feeding nematodes densities were the highest (more than 2900 and 1600 in. kg^{-1} soil, respectively) in Organic Coffee, Cocoa, Rice and Tomato sites, and the lowest in Conventional Coffee and Banana sites (less than 1000 and 300 in. kg^{-1} soil, respectively) (Table 2). Densities of fungal-feeders were the greatest in Rice, Tomato and Organic Coffee sites, while Omnivores, Carnivores and Plant-feeding nematodes were more abundant in Banana, Cocoa and Rice sites (Table 2). Nematode genera richness and Shannon Index were the highest in Organic Coffee, Cocoa and Tomato sites, and the lowest in Conventional Coffee site. Nematode communities under the agroforestry systems (Cocoa, Organic and Conventional Coffee) presented higher Nematode Channel Ratio (NCR), while communities under Tomato and Banana sites presented higher Enrichment Index (EI). Nematode communities in Organic and Conventional Coffee sites presented higher Basal Index (BI), but lower Structure Index (SI).

3.3. Effects of plant diversification on soil fertility and nematodes indices

Plant diversification impacts on soil fertility and nematode communities depended on both plant communities and soil type (Fig. 2). First, legume inclusion in the system globally increased soil inorganic N content in both volcanic soils and Ferralsols, albeit only significantly for the former (Fig. 2a). However, the other fertility indices responded differently depending on both legume presence in plant communities and soil type. Indeed, on volcanic soils, diversification with legumes significantly increased plant bioassay, soil N content, soil pH, decreased soil C:N ratio and showed no impact on soil Olsen P, while the non-legume communities had no or negative impacts on volcanic soil fertility (e.g. significant decrease of plant bioassay).

Contrastingly, plant diversification on Ferralsols significantly increased soil Olsen P content, regardless of the presence of legumes within the communities. Non-legume communities were the most beneficial to Ferralsols, with a significant increase of plant bioassay, soil total C and N contents, and soil pH. In contrast, diversification with legumes in Ferralsols decreased soil pH, increased soil C:N ratio and had no significant impacts on plant bioassay and soil C and N contents (Fig. 2a).

The introduction of legumes decreased the total abundance of omnivorous and plant-feeding nematode populations in both soil types, albeit only significantly in Ferralsols (Fig. 2b). The introduction of legumes also increased the nematodes Basal Index in Ferralsols and decreased the total free-living nematode taxonomic richness in volcanic

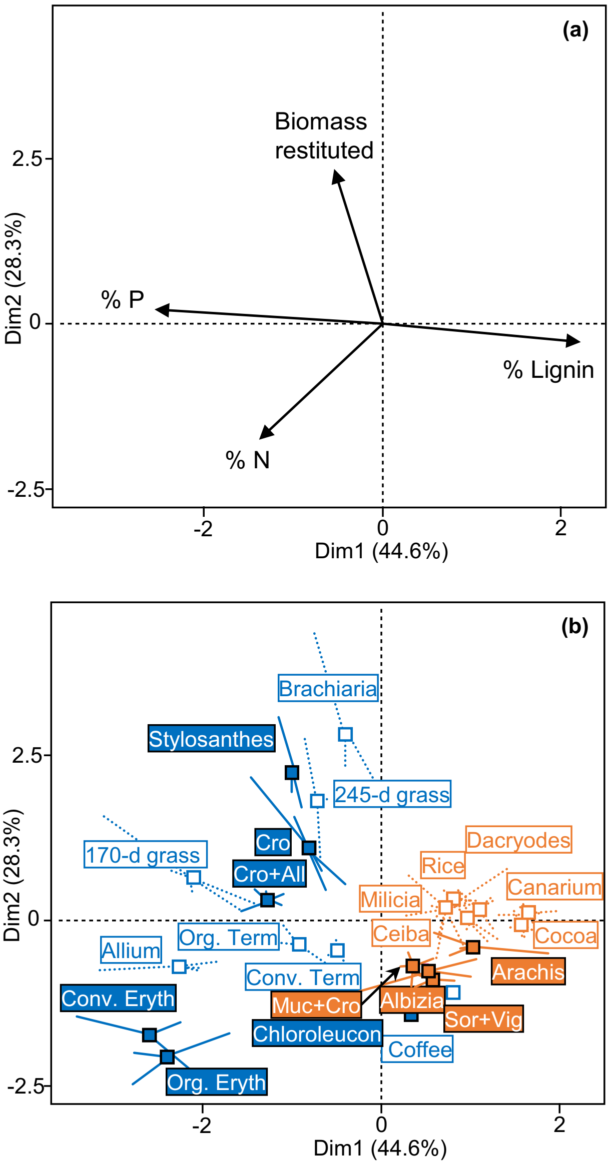


Fig. 1. Principal component analysis of plant community traits (a) variables and (b) individual factor map in the six experimental sites. Plant communities studied on Ferralsols and on volcanic soils are represented in orange and blue, respectively. Full and empty symbols indicate plant communities with and without legumes, respectively. Ferralsols: Rice and Cocoa sites; Volcanic soils: Tomato, Banana, Organic and Conventional Coffee sites. For a full description of the plant communities, see Table 1. Cro: *Crotalaria spectabilis*; Cro + All: *C. spectabilis* + *Allium fistulosum*; Muc + Cro: *Mucuna cochinchinensis* + *C. spectabilis*; Sor + Vig: *Sorghum bicolor* + *Vigna unguiculate*; Conv. Eryth: *Erythrina poepiggiana* + *Coffea arabica* in conventional system; Org. Eryth*:* *E. poepiggiana* + *C. arabica* in organic system; Conv. Term: *Terminalia amazonia* + *C. arabica* in conventional system; *Org. Term: T. amazonia* + *C. arabica* in organic system. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

soils. Finally, plant diversification decreased the nematodes Basal Index in volcanic soils, regardless of legume presence in the community.

3.4. Relationships between plant community traits, soil fertility, and nematode indices

Litter N and P contents were positively correlated to soil inorganic N and Olsen P contents, respectively (r of 0.55 and 0.29, respectively, Fig. 3). Litter N and P contents were also positively correlated with soil C and N contents (*p*-value <0.05 in all cases). However, soil C content presented better correlations with soil inorganic N and Olsen P (r of 0.68 and 0.68, respectively, *p*-values <0.001) than with any plant community traits (Fig. 3). Similarly, plant bioassay was better correlated with soil variables than with plant community traits, especially with soil C ($r = 0.81$, p-value <0.001), soil inorganic N ($r = 0.77$, p-value <0.001) and soil Olsen P ($r = 0.65$, p-value <0.001) contents (Fig. 3 and S2). Nematode indices presented only weak correlations with plant community traits; nematode bacterial-feeders abundance and Basal Index showed significant yet weak correlations with soil inorganic N and soil C content, respectively ($r = 0.26$ and 0.30, respectively, p-values <0.05) (Fig. 3). However, soil pH was the best variable correlated to several nematode indices, such main trophic groups abundance, diversity and food web indexes (Fig. 3 and S3).

Based on these observations, piecewise structural equation models were built and included a random site effect for each equation (Fig. 4). Application of the model to the whole dataset showed that plant bioassay increased significantly with both soil N and P availability (*P*-values <0.001) (Fig. 4a). Soil N availability increased with plant community litter N and soil C content, while soil P availability increased with soil C content and to a lesser extent with nematodes Basal Index. Separate analyses per soil type showed contrasting relationships between plant community traits, soil fertility and nematode indices (Fig. 4b and c). In Ferralsols (Rice and Cocoa sites), soil P availability increased with both plant community litter P and soil C content (Fig. 4b), and was significantly correlated with plant bioassay. In these sites, soil N availability increased significantly with litter N content but had no significant relationship with plant bioassay. In volcanic soils (Tomato, Banana and Coffee sites), both plant community litter N and soil C contents explained soil N availability, while nematode Basal Index increased significantly with soil P availability. In these soils, the soil N availability – plant bioassay correlation was four times stronger than the soil P availability – plant bioassay correlation (r of 0.52 and 0.13, respectively), despite being both significant (*P*-values inferior to 0.001 and 0.05, respectively).

4. Discussion

4.1. Plant community traits – soil fertility – micro-food web relationships vary with soil type

In line with our expectations, plant diversification had overall positive effects on soil fertility across all sites, yet these effects varied greatly with the pedological conditions. First, each site tested a set of plant communities susceptible to improve agroecosystem services in its local context. Therefore, not only soil fertility, but also plant community traits varied greatly among the six sites. This was especially apparent for sites on Ferralsols (Rice and Cocoa sites) which presented lower soil P availability (Walker and Syers, 1976), but also plant communities with lower litter P content, as a consequence of P limitation for growth (Han et al., 2011; Raminoarison et al., 2020). Differences in nutrient limitations for plant growth between Ferralsols and volcanic soils were also evidenced by the greenhouse plant bioassay, an off-site assessment of soil potential fertility (Dybzinski et al., 2008, Sauvadet et al., 2019, 2020). Plant bioassay presented strong correlations with the most limiting element for its growth (Fig. S2) – i.e., P in Ferralsols, and N more than P in volcanic soils. These results are in line with the common findings in literature, describing a shift between N and P limitation with soil weathering stage (Lambers et al., 2008; Hou et al., 2020), and were consistent between the sites despite their differences in management and fertilization.

Soil C content also presented strong positive correlation with plant bioassay, supporting the concept of soil fertility promotion by soil organic matter (Manlay et al., 2007), which was further supported by the positive correlations found with soil N and P availability. Indeed, due to constrained stoichiometric ratios of soil organic matter, soil C enrichment implies soil total N and P increase (e.g. Kirkby et al., 2011), along with improved biological activity, leading to faster N and P turnover (Craswell and Lefroy, 2001). Interestingly, correlations strength

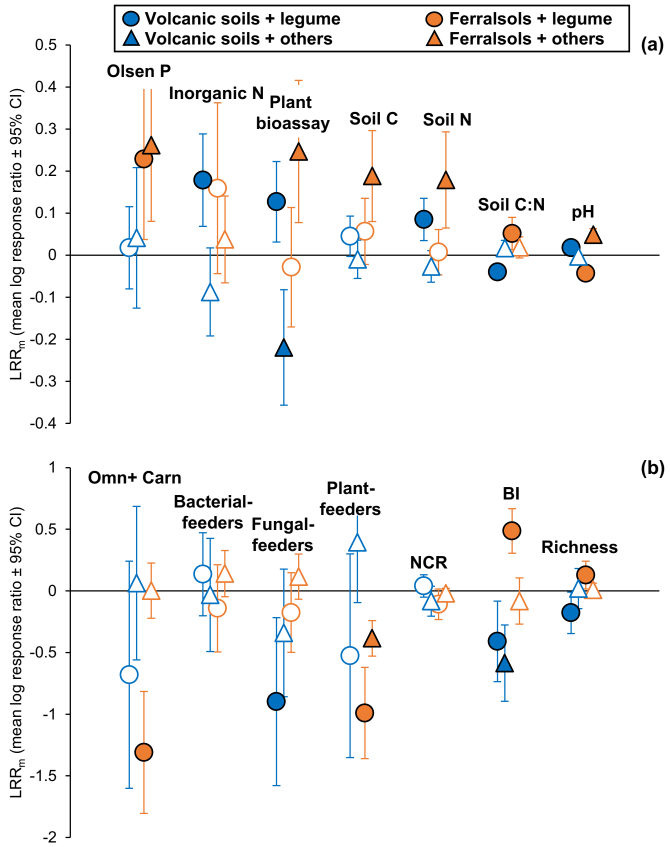
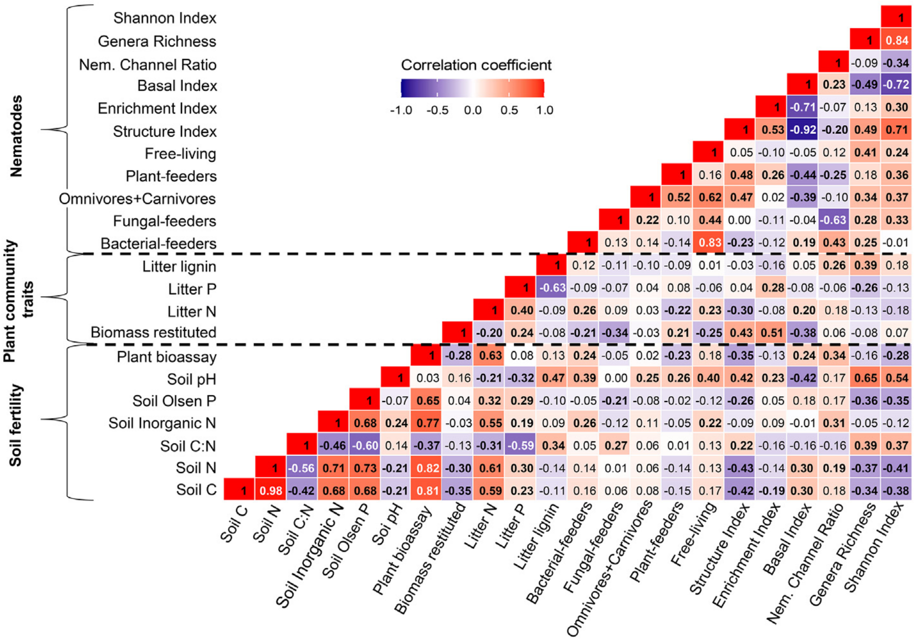


Fig. 2. Plant diversification impacts on soil fertility (a) and nematode indices (b). Data were calculated as mean log response ratio (LRR_m) of diversification as compared to the reference treatment of each site. Full and empty symbols indicate significant and non-significant effects, respectively. Vertical bars correspond to 95% confidence intervals. Ferralsols: Rice and Cocoa sites; Volcanic soils: Tomato, Banana, Organic and Conventional Coffee sites. For a full description of reference treatments, see Table 2.

between soil C and nutrient availability depended on the most limiting nutrient for plant growth; soil C – P availability link was significant only in Ferralsols, while soil C – N availability relationship was significant only in volcanic soils (P-values <0.01 and 0.001, respectively, Fig. 4). While soil C relationships with N and P availability are not so easily found because of differences in turnover time or P sorption mechanisms on soil constituents (Kruse et al., 2015; Plassard et al., 2015), our experimental design allowed to focus on plant communities – based relationships for both soil types. Consequently, relationships between soil C and soil N and P availability mirrored these between soil C and plant community litter N and P content in this study, suggesting that the plant communities producing litter of high nutrient contents could have provided the additional N and P required to store more C in soil superficial layer, while keeping soil organic matter stoichiometric ratio (Bertrand et al., 2019). These relationships are likely to occur due to cumulative effect over several years. In support for our second objective we demonstrate here that key plant community traits can be linked with soil fertility increase across contrasting agroecosystems.

Soil N availability was indeed linked with litter N content, and to a lesser extent to bacterial-feeder nematode abundance. While the impacts of plant litter N on soil N dynamics has long been acknowledged (Manzoni et al., 2008; Hobbie, 2015), the promoting effects of bacterial-feeder nematodes on soil N availability through bacterial grazing (Bonkowski, 2004) has more recently been considered at different scales (de Vries et al., 2013; Trap et al., 2016). Given the sensitivity of this trophic group to soil pH (van den Hoogen et al., 2019), avoiding practices with strong soil acidification impacts such as massive ammonium-based fertilization is of upmost importance (Stumpe and Vlek, 1991; Goulding, 2016). Similarly, soil P availability was both correlated with litter P and nematode community structure, albeit with a lesser strength than for N availability. Indeed, while the role of litter P content (Damon et al., 2014; Maire et al., 2015) and nematode top-down regulation (Ranoarisoa et al., 2018, 2020) has been recognized to improve soil P availability, the diversity of P forms and their complex interactions with soil matrix hampers the generalization of these relationships across agroecosystems (Kruse et al., 2015; Plassard et al., 2015). Plant diversification has hence been shown to impact contrastingly P cycling through the promotion of different P forms and P



	Soil C	Soil N	Soil C:N	Soil Inorganic N	Soil Olsen P	Soi pH	Plant bioassay	Biomass restituted	Litter N	Litter P	Litter lignin	Bacterial-feeders	Fungal-feeders	Omnivores+Carnivores	Plant-feeders	Free-living	Structure Index	Enrichment Index	Basal Index	Nem. Channel Ratio	Genera Richness	Shannon Index
Shannon Index																						**1**
Genera Richness																					**1**	**0.84**
Nem. Channel Ratio																				**1**	-0.09	**-0.34**
Basal Index																			**1**	**0.23**	**-0.49**	**-0.72**
Enrichment Index																		**1**	**-0.71**	-0.07	0.13	**0.30**
Structure Index																	**1**	**0.53**	**-0.92**	**-0.20**	**0.49**	**0.71**
Free-living																**1**	0.05	-0.10	-0.05	0.12	**0.41**	**0.24**
Plant-feeders															**1**	0.16	**0.48**	**0.26**	**-0.44**	**-0.25**	0.18	**0.36**
Omnivores+Carnivores														**1**	**0.52**	**0.62**	**0.47**	0.02	**-0.39**	-0.10	**0.34**	**0.37**
Fungal-feeders													**1**	**0.22**	0.10	**0.44**	0.00	-0.11	-0.04	**-0.63**	**0.28**	**0.33**
Bacterial-feeders												**1**	0.13	0.14	-0.14	**0.83**	**-0.23**	-0.12	**0.19**	**0.43**	**0.25**	-0.01
Litter lignin											**1**	0.12	-0.11	-0.10	-0.09	0.01	-0.03	-0.16	0.05	**0.26**	**0.39**	0.18
Litter P										**1**	**-0.63**	-0.09	-0.07	0.04	0.08	-0.06	0.04	**0.28**	-0.08	-0.06	**-0.26**	-0.13
Litter N									**1**	**0.40**	-0.09	**0.26**	0.09	0.03	**-0.22**	**0.23**	**-0.30**	-0.08	**0.20**	0.18	-0.13	-0.18
Biomass restituted								**1**	**-0.20**	**0.24**	-0.08	**-0.21**	**-0.34**	-0.03	**0.21**	**-0.25**	**0.43**	**0.51**	**-0.38**	0.06	-0.08	0.07
Plant bioassay							**1**	**-0.28**	**0.63**	0.08	0.13	**0.24**	-0.05	0.02	**-0.23**	0.18	**-0.35**	-0.13	**0.24**	**0.34**	-0.16	**-0.28**
Soil pH						**1**	0.03	0.16	**-0.21**	**-0.32**	**0.47**	**0.39**	0.00	**0.25**	**0.26**	**0.40**	**0.42**	**0.23**	**-0.42**	0.17	**0.65**	**0.54**
Soil Olsen P					**1**	-0.07	**0.65**	0.04	**0.32**	**0.29**	-0.10	-0.05	**-0.21**	-0.08	-0.02	-0.12	**-0.26**	0.05	0.18	0.17	**-0.36**	**-0.35**
Soil Inorganic N				**1**	**0.68**	**0.24**	**0.77**	-0.03	**0.55**	**0.19**	0.09	**0.26**	-0.12	0.11	-0.05	**0.22**	-0.09	0.09	-0.01	**0.31**	-0.05	-0.12
Soil C:N			**1**	**-0.46**	**-0.60**	0.14	**-0.37**	-0.13	**-0.31**	**-0.59**	**0.34**	0.05	**0.27**	0.06	0.01	0.13	**0.22**	-0.16	-0.16	-0.16	**0.39**	**0.37**
Soil N		**1**	**-0.56**	**0.71**	**0.73**	**-0.21**	**0.82**	**-0.30**	**0.61**	**0.30**	-0.14	0.14	0.01	0.06	-0.14	0.13	**-0.43**	-0.14	**0.30**	**0.19**	**-0.37**	**-0.41**
Soil C	**1**	**0.98**	**-0.42**	**0.68**	**0.68**	**-0.21**	**0.81**	**-0.35**	**0.59**	**0.23**	-0.11	0.16	0.06	0.08	-0.15	0.17	**-0.42**	**-0.19**	**0.30**	0.18	**-0.34**	**-0.38**

Fig. 3. Pearson correlation coefficient matrices of soil fertility, plant community traits and nematode indices on the whole dataset ($n = 142$). Correlations were corrected for multiple comparisons with the Benjamini-Hochberg method. Significant correlations (p-value <0.05) are written in boldface.

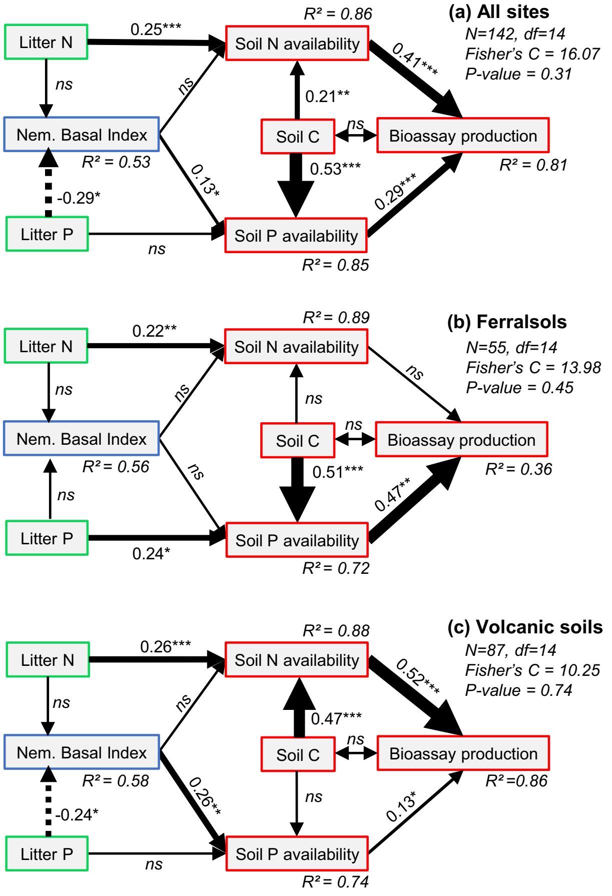


Fig. 4. Piecewise structural equation models on plant community traits impacts on soil fertility for all sites (a), sites on Ferralsols (b), and sites on volcanic soils (c). Variables of plant community traits, nematodes, and soil fertility are represented in green, blue and red, respectively. The numbers on the arrows are path coefficients; dashed line arrows indicate negative effects, and double arrows covariation relationships. The R^2 value represents the proportion of total variance explained by the model. Asterisks represent the level of significance of the paths; * stands for P-values <0.05; ** for P-values <0.01; *** for P-values <0.001 Ferralsols: Rice and Cocoa sites; Volcanic soils: Tomato, Banana, Organic and Conventional Coffee sites. The analyses were performed on standardized normally distributed data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

solubilization processes, depending on both plant communities and soil type (Waithaisong et al., 2020). Differences in P cycling processes between soil types could explain the absence of nematode community – Olsen P correlations in Ferralsols (Fig. 4), however this assumption would have needed the characterization of more P forms to be fully answered. These differences of P assimilation strategy could also have been further comforted with the characterization of root traits and mycorrhizal symbioses indicative of plant P uptake capacity, as well as the activity of P-mineralizing and -solubilizing microorganisms in addition to their nematodes grazers (indicating soil P potential availability) (e.g. Becquer et al., 2014).

4.2. Implications for plant community selection for agroecosystems diversification

Plant community traits – soil fertility – micro-food web composition relationships give useful insights to understand the impacts of managed plant community composition on agroecosystems functioning. On the one hand, volcanic soils, presenting higher limitation for N, benefitted more from plant communities including legumes, which produced N-enriched litter due to their N_2-fixing ability and improved soil total N and inorganic N contents along with plant bioassay (see Sauvadet et al., 2019, for more details). These results are in line with global findings in temperate, N-limited agroecosystems (Drinkwater et al., 1998). Further, the introduction of legume species led to similar increase of plant community litter-N and soil N availability in both Ferralsols and volcanic soils, suggesting that the legume species grown on the Ferralsols sites may be well adapted to fix atmospheric N_2 in limited P-availability conditions (Augusto et al., 2013), likely thanks to their high capacity to mobilize soil P (Hinsinger et al., 2003). However, increases in N availability under legume communities did not improve plant bioassay in Ferralsols as they did in volcanic soils. This lack of effects may be caused by Ferralsols P- rather than N-limitation for plant growth, which was not improved by the presence of legume (Fig. 2). Even more, the increased N provision by legumes in Ferralsols, combined with low N uptake, may have led to nitrification and subsequent nitrate leaching, leading to proton production (van Breemen et al., 1983; de Vries and Breeuwsma, 1987), and causing the observed Ferralsols acidification under legume communities (Fujii et al., 2018).

Ferralsols acidification by legumes may have hampered biological activity, which could explain the absence of other benefits of plant community diversity on soil fertility as observed with non-legume communities, despite similar levels of nutrient availability. First, soil acidification by legumes may have decreased in part P availability (Plassard et al., 2015), in particular in the Rice site which had a low initial pH. This process may not have been detected in this study because of the use of the Olsen P protocol (pH 8.5 extractant) to assess P availability (Kruse et al., 2015), as the absence of significant soil pH – Olsen P relationships in Fig. 3 may suggest. Second, soil acidification under legumes likely disturbed soil biological activity and led in some cases to soil C loss despite good nutrient availability (see Sauvadet et al. (2020) for more details). Overall, these results question the use of legumes for agroecosystem diversification when soil P availability is too low, and highlight the strong dependency of plant community traits – soil fertility relationships with the local pedoclimatic context. This dependency underlines the importance of assessing the limiting factors of agroecosystems' soil fertility, and their interactions with other soil properties, in order to determine which plant community traits to favor when diversifying agroecosystems.

5. Conclusion

Our study highlighted the importance to consider both pedoclimatic constraints and plant community traits to build diversified agroecological cropping systems. The presence of legumes – widely favored for their well-known benefits in N-limited agroecosystems – does not appear determinant for soil fertility in more weathered soils presenting strong P limitation such as Ferralsols. Soil fertility in such soils was driven by plant community traits directly linked with P cycling. This was evidenced by a shift of the key traits promoting soil fertility between volcanic soils and Ferralsols in pSEMs analysis. While the traits used in this work were generic because of the heterogeneity of the agroecosystems studied (annual and agroforestry systems), these first results highlight the need to further test a range of more specific traits linked to N and P acquisition and build-up in soil, such as root traits and more specifically mycorrhizal symbiosis, (Freschet et al., 2021). Furthermore, practices improving both soil pH and soil C should be promoted for their strong links with nematode indices (and likely microbial community structure), and N and P availability for plants, respectively. Overall, our findings evidenced important challenges that will have to be solved before a framework can be laid out for designing trait-based plant communities suited for tropical agroecosystems for a wide range of pedoclimates.

CRediT authorship contribution statement

Marie Sauvadet: Investigation, Formal analysis, Software, Writing – original draft, Writing – review & editing. **Jean Trap:** Methodology, Investigation, Formal analysis, Software, Writing – review & editing. **Gaëlle Damour:** Formal analysis, Writing – review & editing. **Claude**

Plassard: Methodology, Formal analysis, Writing – review & editing. **Karel Van den Meersche:** Resources, Methodology, Formal analysis, Investigation, Writing – review & editing. **Raphaël Achard:** Resources, Methodology, Investigation, Writing – review & editing. **Clémentine Allinne:** Resources, Methodology, Writing – review & editing. **Patrice Autfray:** Methodology, Investigation, Writing – review & editing. **Isabelle Bertrand:** Writing – review & editing. **Eric Blanchart:** Methodology, Investigation, Writing – review & editing. **Péninna Deberdt:** Resources, Methodology, Writing – review & editing. **Séguy Enock:** Investigation, Writing – review & editing. **Jean-Daniel Essobo:** Investigation, Writing – review & editing. **Grégoire T. Freschet:** Writing – review & editing. **Mickaël Hedde:** Software, Formal analysis, Writing – review & editing. **Elias de Melo Virginio Filho:** Methodology, Investigation, Writing – review & editing. **Bodovololona Rabary:** Methodology, Investigation, Writing – review & editing. **Miora Rakotoarivelo:** Investigation, Writing – review & editing. **Richard Randriamanantsoa:** Methodology, Investigation, Writing – review & editing. **Béatrice Rhino:** Resources, Methodology, Writing – review & editing. **Aude Ripoche:** Resources, Methodology, Investigation, Formal analysis, Writing – review & editing. **Elisabeth Rosalie:** Investigation, Writing – review & editing. **Stéphane Saj:** Methodology, Formal analysis, Writing – review & editing. **Thierry Becquer:** Resources, Supervision, Project administration, Funding acquisition, Methodology, Formal analysis, Writing – review & editing. **Philippe Tixier:** Resources, Supervision, Project administration, Funding acquisition, Methodology, Software, Formal analysis, Writing – review & editing. **Jean-Michel Harmand:** Resources, Supervision, Project administration, Funding acquisition, Methodology, Investigation, Formal analysis, Writing – review & editing.

Declaration of competing interest

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Data availability

Data associated with this article can be found online in the Dryad repository, at https://doi.org/10.5061/dryad.2fqz612ph.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.148934.

References

Augusto, L., Delerue, F., Gallet-Budynek, A., Achat, D.L., 2013. Global assessment of limitation to symbiotic nitrogen fixation by phosphorus availability in terrestrial ecosystems using a meta-analysis approach. Glob. Biogeochem. Cycles 27, 804–815. https://doi.org/10.1002/gbc.20069.

Bardgett, R.D., Mommer, L., De Vries, F.T., 2014. Going underground: root traits as drivers of ecosystem processes. Trends Ecol. Evol. 29, 692–699. https://doi.org/10.1016/j.tree.2014.10.006.

Barry, K.E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A.J., Bai, Y., Connolly, J., Deyn, G.B.D., Kroon, H. de, Isbell, F., Milcu, A., Roscher, C., Scherer-Lorenzen, M., Schmid, B., Weigelt, A., 2019. The future of complementarity: disentangling causes from consequences. Trends Ecol. Evol. 34, 167–180. https://doi.org/10.1016/j.tree.2018.10.013.

Batterman, S.A., Wurzburger, N., Hedin, L.O., 2013. Nitrogen and phosphorus interact to control tropical symbiotic N2 fixation: a test in Inga punctata. J. Ecol. 101, 1400–1408. https://doi.org/10.1111/1365-2745.12138.

Becquer, A., Trap, J., Irshad, U., Ali, M.A., Claude, P., 2014. From soil to plant, the journey of P through trophic relationships and ectomycorrhizal association. Front. Plant Sci. 5. https://doi.org/10.3389/fpls.2014.00548.

Bender, S.F., Wagg, C., van der Heijden, M.G.A., 2016. An underground revolution: biodiversity and soil ecological engineering for agricultural sustainability. Trends Ecol. Evol. (Amst.) 31, 440–452. https://doi.org/10.1016/j.tree.2016.02.016.

Berkelmans, R., Ferris, H., Tenuta, M., van Bruggen, A.H.C., 2003. Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil management. Appl. Soil Ecol. 23, 223–235. https://doi.org/10.1016/S0929-1393(03)00047-7.

Bertrand, I., Viaud, V., Daufresne, T., Pellerin, S., Recous, S., 2019. Stoichiometry constraints challenge the potential of agroecological practices for the soil C storage. A review. Agron. Sustain. Dev. 39, 54. https://doi.org/10.1007/s13593-019-0599-6.

Blesh, J., 2018. Functional traits in cover crop mixtures: biological nitrogen fixation and multifunctionality. J. Appl. Ecol. 55, 38–48. https://doi.org/10.1111/1365-2664.13011.

Bonkowski, M., 2004. Protozoa and plant growth: the microbial loop in soil revisited. New Phytol. 162, 617–631. https://doi.org/10.1111/j.1469-8137.2004.01066.x.

van Breemen, N., Mulder, J., Driscoll, C.T., 1983. Acidification and alkalinization of soils. Plant Soil 75, 283–308. https://doi.org/10.1007/BF02369968.

Craswell, E.T., Lefroy, R.D.B., 2001. The role and function of organic matter in tropical soils. In: Martius, C., Tiessen, H., Vlek, P.L.G. (Eds.), Managing Organic Matter in Tropical Soils: Scope and Limitations: Proceedings of a Workshop Organized by the Center for Development Research at the University of Bonn (ZEF Bonn) — Germany, 7–10 June, 1999, Developments in Plant and Soil Sciences. Springer Netherlands, Dordrecht, pp. 7–18 https://doi.org/10.1007/978-94-017-2172-1_2.

Damon, P.M., Bowden, B., Rose, T., Rengel, Z., 2014. Crop residue contributions to phosphorus pools in agricultural soils: a review. Soil Biol. Biochem. 74, 127–137. https://doi.org/10.1016/j.soilbio.2014.03.003.

Damour, G., Navas, M.L., Garnier, E., 2018. A revised trait-based framework for agroecosystems including decision rules. J. Appl. Ecol. 55, 12–24. https://doi.org/10.1111/1365-2664.12986.

Dawson, I.K., Park, S.E., Attwood, S.J., Jamnadass, R., Powell, W., Sunderland, T., Carsan, S., 2019. Contributions of biodiversity to the sustainable intensification of food production. Global Food Security 21, 23–37. https://doi.org/10.1016/j.gfs.2019.07.002.

De Deyn, G.B., Raaijmakers, C.E., Van Ruijven, J., Berendse, F., Van Der Putten, W.H., 2004. Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. Oikos 106, 576–586. https://doi.org/10.1111/j.0030-1299.2004.13265.x.

Deberdt, P., Fernandes, P., 2017. Agroecological management of bacterial wilt of tomato in Martinique, in: Agroecological Crop Protection / Deguine Jean-Philippe (Ed.), Gloanec Caroline (Ed.), Laurent Philippe (Ed.), Ratnadass Alain (Ed.), Aubertot Jean-Noel (Ed.). Springer; Ed. Quae, Dordrecht, pp. 120–124.

Díaz, S., Settele, J., Brondízio, E., Ngo, H., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K., Butchart, S., Chan, K., Garibaldi, L., Ichii, K., Liu, J., Subrmanian, S., Midgley, G., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R., Shin, Y., Visseren-Hamakers, I., Wilis, K., Zayas, C., 2020. Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Drinkwater, L.E., Wagoner, P., Sarrantonio, M., 1998. Legume-based cropping systems have reduced carbon and nitrogen losses. Nature 396, 262–265. https://doi.org/10.1038/24376.

Duchene, O., Vian, J.-F., Celette, F., 2017. Intercropping with legume for agroecological cropping systems: complementarity and facilitation processes and the importance of soil microorganisms. A review. Agric. Ecosyst. Environ. 240, 148–161. https://doi.org/10.1016/j.agee.2017.02.019.

Dybzinski, R., Fargione, J.E., Zak, D.R., Fornara, D., Tilman, D., 2008. Soil fertility increases with plant species diversity in a long-term biodiversity experiment. Oecologia 158, 85–93. https://doi.org/10.1007/s00442-008-1123-x.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29. https://doi.org/10.1016/S0929-1393(01)00152-4.

Freschet, G., Roumet, C., Comas, L., Weemstra, M., Bengough, A., Rewald, B., Bardgett, R., Deyn, G.B., Johnson, D., Klimešová, J., Lukac, M., Mccormack, M., Meier, I., Pagès, L., Poorter, H., Prieto, I., Wurzburger, N., Zadworny, M., Bagniewska-Zadworna, A., Stokes, A., 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. New Phytol. https://doi.org/10.1111/nph.17072 (press).

Freschet, G.T., Roumet, C., 2017. Sampling roots to capture plant and soil functions. Funct. Ecol. 31, 1506–1518. https://doi.org/10.1111/1365-2435.12883.

Fujii, K., Shibata, M., Kitajima, K., Ichie, T., Kitayama, K., Turner, B.L., 2018. Plant–soil interactions maintain biodiversity and functions of tropical forest ecosystems. Ecol. Res. 33, 149–160. https://doi.org/10.1007/s11284-017-1511-y.

Garnier, E., Navas, M.-L., 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. Agron. Sustain. Dev. 32, 365–399. https://doi.org/10.1007/s13593-011-0036-y.

Goulding, K.W.T., 2016. Soil acidification and the importance of liming agricultural soils with particular reference to the United Kingdom. Soil Use Manag. 32, 390–399. https://doi.org/10.1111/sum.12270.

Han, W.X., Fang, J.Y., Reich, P.B., Woodward, F.I., Wang, Z.H., 2011. Biogeography and variability of eleven mineral elements in plant leaves across gradients of climate, soil and plant functional type in China. Ecol. Lett. 14, 788–796. https://doi.org/10.1111/j.1461-0248.2011.01641.x.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156. https://doi.org/10.2307/177062.

Hinsinger, P., Plassard, C., Tang, C., Jaillard, B., 2003. Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: a review. Plant Soil 248, 43–59. https://doi.org/10.1023/A:1022371130939.

Hobbie, S.E., 2015. Plant species effects on nutrient cycling: revisiting litter feedbacks. Trends Ecol. Evol. 30, 357–363. https://doi.org/10.1016/j.tree.2015.03.015.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., Mauro da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutiérrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Martín, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., Carlos Pereira da Silva, J., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergård, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194–198. https://doi.org/10.1038/s41586-019-1418-6.

Hou, E., Luo, Y., Kuang, Y., Chen, C., Lu, X., Jiang, L., Luo, X., Wen, D., 2020. Global meta-analysis shows pervasive phosphorus limitation of aboveground plant production in natural terrestrial ecosystems. Nat. Commun. 11, 637. https://doi.org/10.1038/s41467-020-14492-w.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G.M., Wardle, D.A., O'Connor, M.I., Duffy, J.E., Turnbull, L.A., Thompson, P.L., Larigauderie, A., 2017. Linking the influence and dependence of people on biodiversity across scales. Nature 546, 65–72. https://doi.org/10.1038/nature22899.

Jensen, Erik Steen, Peoples, Mark B., Boddey, Robert M., Gresshoff, Peter M., Hauggaard-Nielsen, Henrik, Alves, Bruno J.R., Morrison, Malcolm J., 2012. Legumes for mitigation of climate change and the provision of feedstock for biofuels and biorefineries. A review. Agronomy for Sustainable Development 32 (2), 329–364. https://doi.org/10.1007/s13593-011-0056-7.

Kirkby, C.A., Kirkegaard, J.A., Richardson, A.E., Wade, L.J., Blanchard, C., Batten, G., 2011. Stable soil organic matter: a comparison of C:N:P:S ratios in Australian and other world soils. Geoderma 163, 197–208. https://doi.org/10.1016/j.geoderma.2011.04.010.

Kruse, J., Abraham, M., Amelung, W., Baum, C., Bol, R., Kühn, O., Lewandowski, H., Niederberger, J., Oelmann, Y., Rüger, C., Santner, J., Siebers, M., Siebers, N., Spohn, M., Vestergren, J., Vogts, A., Leinweber, P., 2015. Innovative methods in soil phosphorus research: a review. J. Plant Nutr. Soil Sci. 178, 43–88. https://doi.org/10.1002/jpln.201400327.

Lambers, H., Raven, J.A., Shaver, G.R., Smith, S.E., 2008. Plant nutrient-acquisition strategies change with soil age. Trends Ecol. Evol. 23, 95–103. https://doi.org/10.1016/j.tree.2007.10.008.

Latati, M., Bargaz, A., Belarbi, B., Lazali, M., Benlahrech, S., Tellah, S., Kaci, G., Drevon, J.J., Ounane, S.M., 2016. The intercropping common bean with maize improves the rhizobial efficiency, resource use and grain yield under low phosphorus availability. Eur. J. Agron. 72, 80–90. https://doi.org/10.1016/j.eja.2015.09.015.

Lefcheck, J.S., Byrnes, J.E.K., Isbell, F., Gamfeldt, L., Griffin, J.N., Eisenhauer, N., Hensel, M.J.S., Hector, A., Cardinale, B.J., Duffy, J.E., 2015. Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat. Commun. 6, 6936. https://doi.org/10.1038/ncomms7936.

Maire, V., Wright, I.J., Prentice, I.C., Batjes, N.H., Bhaskar, R., van Bodegom, P.M., Cornwell, W.K., Ellsworth, D., Niinemets, Ü., Ordonez, A., Reich, P.B., Santiago, L.S., 2015. Global effects of soil and climate on leaf photosynthetic traits and rates. Glob. Ecol. Biogeogr. 24, 706–717. https://doi.org/10.1111/geb.12296.

Manlay, R.J., Feller, C., Swift, M.J., 2007. Historical evolution of soil organic matter concepts and their relationships with the fertility and sustainability of cropping systems. Agric. Ecosyst. Environ. 119, 217–233. https://doi.org/10.1016/j.agee.2006.07.011.

Manzoni, S., Jackson, R.B., Trofymow, J.A., Porporato, A., 2008. The global stoichiometry of litter nitrogen mineralization. Science 321, 684–686. https://doi.org/10.1126/science.1159792.

Martin, A.R., Isaac, M.E., 2015. REVIEW: plant functional traits in agroecosystems: a blueprint for research. J. Appl. Ecol. 52, 1425–1435. https://doi.org/10.1111/1365-2664.12526.

Neves, M.S.A.C., Souto, M.R.S., Tóth, I.V., Victal, S.M.A., Drumond, M.C., Rangel, A.O.S.S., 2008. Spectrophotometric flow system using vanadomolybdophosphate detection chemistry and a liquid waveguide capillary cell for the determination of phosphate with improved sensitivity in surface and ground water samples. Talanta, 14th International Conference on Flow Injection Analysis and Related Techniques 77, 527–532. https://doi.org/10.1016/j.talanta.2008.03.014.

Olsen, S.R., Sterling, R., 1954. Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate. U.S. Dept. of Agriculture, Washington, D.C.

Petit-Aldana, J., Rahman, M.M., Parraguirre-Lezama, C., Infante-Cruz, A., Romero-Arenas, O., 2019. Litter decomposition process in coffee agroforestry systems. Journal of Forest and Environmental Science 35, 121–139. https://doi.org/10.7747/JFES.2019.35.2.121.

Plassard, C., Robin, A., Cadre, E.L., Marsden, C., Trap, J., Herrmann, L., Waithaisong, K., Lesueur, D., Blanchard, E., Chapuis-Lardy, L., Hinsinger, P., 2015. Ameliorer la biodisponibilite du phosphore : comment valoriser les competences des plantes et les mecanismes biologiques du sol ? Innovations Agronomiques 43, 115–138.

Raminoarison, M., Razafimbelo, T., Rakotoson, T., Becquer, T., Blanchart, E., Trap, J., 2020. Multiple-nutrient limitation of upland rainfed rice in ferralsols: a greenhouse nutrient-omission trial. J. Plant Nutr. 43, 270–284. https://doi.org/10.1080/01904167.2019.1676906.

Ranoarisoa, M.P., Morel, C., Andriamananjara, A., Jourdan, C., Bernard, L., Becquer, T., Rabeharisoa, L., Rahajaharilaza, K., Plassard, C., Blanchart, E., Trap, J., 2018. Effects of a bacterivorous nematode on rice 32P uptake and root architecture in a high P-sorbing ferrallitic soil. Soil Biol. Biochem. 122, 39–49. https://doi.org/10.1016/j.soilbio.2018.04.002.

Ranoarisoa, M.P., Trap, J., Pablo, A.-L., Dezette, D., Plassard, C., 2020. Micro-food web interactions involving bacteria, nematodes, and mycorrhiza enhance tree P nutrition in a high P-sorbing soil amended with phytate. Soil Biol. Biochem. 143, 107728. https://doi.org/10.1016/j.soilbio.2020.107728.

Rao, A.S., Reddy, K.S., Takkar, P.N., 1997. Malachite green method compared to ascorbic acid for estimating small amounts of phosphorus in water, 0.01 M calcium chloride, and olsen soil extracts. Commun. Soil Sci. Plant Anal. 28, 589–601. https://doi.org/10.1080/00103629709369813.

Ratnadass, A., Fernandes, P., Avelino, J., Habib, R., 2012. Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: a review. Agron. Sustain. Dev. 32, 273–303. https://doi.org/10.1007/s13593-011-0022-4.

Renard, D., Tilman, D., 2019. National food production stabilized by crop diversity. Nature 571, 257–260. https://doi.org/10.1038/s41586-019-1316-y.

Ripoche, A., Blanchard, E., Trap, J., Sauvadet, M., Autfray, P., Randriamanantsoa, R., Rabary, B., 2019. Does an increase in plant diversity enhance agroecosystem services? Case study in rainfed rice based cropping systems in Madagascar. Presented at the 6th International SYmposium for Farming Systems Design. Universidad de la República Uruguay, Montevideo, Uruguay.

Ritz, K., Trudgill, D.L., 1999. Utility of nematode community analysis as an integrated measure of the functional state of soils: perspectives and challenges. Plant Soil 212, 1–11. https://doi.org/10.1023/A:1004673027625.

Sauvadet, M., den Meersche, K.V., Allinne, C., Gay, F., de Melo Virginio Filho, E., Chauvat, M., Becquer, T., Tixier, P., Harmand, J.-M., 2019. Shade trees have higher impact on soil nutrient availability and food web in organic than conventional coffee agroforestry. Sci. Total Environ. 649, 1065–1074. https://doi.org/10.1016/j.scitotenv.2018.08.291.

Sauvadet, M., Saj, S., Freschet, G.T., Essobo, J.-D., Enock, S., Becquer, T., Tixier, Harmand, J.-M., 2020. Cocoa agroforest multifunctionality and soil fertility explained by shade tree litter traits. J. Appl. Ecol. 57, 476–487. https://doi.org/10.1111/1365-2664.13560.

Sawers, R.J.H., Svane, S.F., Quan, C., Grønlund, M., Wozniak, B., Gebreselassie, M.-N., González-Muñoz, E., Chávez Montes, R.A., Baxter, I., Goudet, J., Jakobsen, I., Paszkowski, U., 2017. Phosphorus acquisition efficiency in arbuscular mycorrhizal maize is correlated with the abundance of root-external hyphae and the accumulation of transcripts encoding PHT1 phosphate transporters. New Phytol. 214, 632–643. https://doi.org/10.1111/nph.14403.

Seinhorst, J.W., 1950. De betekenis van de toestand van de grond voor het optreden van aantasting door het stengelaaltje (*Ditylenchus dipsac*i (KÜHN) Filipjev). Tijdschrift Over Plantenziekten 56, 289–348. https://doi.org/10.1007/BF01989990.

Shipley, B., 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90, 363–368. https://doi.org/10.1890/08-1034.1.

Stumpe, J.M., Vlek, P.L.G., 1991. Acidification induced by different nitrogen sources in columns of selected tropical soils. Soil Sci. Soc. Am. J. 55, 145–151. https://doi.org/10.2136/sssaj1991.03615995005500010026x.

Tiemann, L.K., Grandy, A.S., Atkinson, E.E., Marin-Spiotta, E., McDaniel, M.D., 2015. Crop rotational diversity enhances belowground communities and functions in an agroecosystem. Ecol. Lett. 18, 761–771. https://doi.org/10.1111/ele.12453.

Tixier, P., Lavigne, C., Alvarez, S., Gauquier, A., Blanchard, M., Ripoche, A., Achard, R., 2011. Model evaluation of cover crops, application to eleven species for banana cropping systems. Eur. J. Agron. 34, 53–61. https://doi.org/10.1016/j.eja.2010.10.004.

Trap, J., Bonkowski, M., Plassard, C., Villenave, C., Blanchart, E., 2016. Ecological importance of soil bacterivores for ecosystem functions. Plant Soil, 1–24 https://doi.org/10.1007/s11104-015-2671-6.

Tscharntke, T., Clough, Y., Bhagwat, S.A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., Wanger, T.C., 2011. Multifunctional shade-tree management in tropical agroforestry landscapes – a review. J. Appl. Ecol. 48, 619–629. https://doi.org/10.1111/j.1365-2664.2010.01939.x.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x.

Vries, de, de, F.T., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Jørgensen, H.B., Brady, M.V., Christensen, S., Ruiter, P.C. de, d'Hertefeldt, T., Frouz, J., Hedlund, K., Hemerik, L., Hol, W.H.G., Hotes, S., Mortimer, S.R., Setälä, H., Sgardelis, S.P., Uteseny, K., Putten, W.H. van der, Wolters, V., Bardgett, R.D., 2013. Soil food web properties explain ecosystem services across European land use systems. PNAS 110, 14296–14301. https://doi.org/10.1073/pnas.1305198110.

de Vries, W., Breeuwsma, A., 1987. The relation between soil acidification and element cycling. Water Air Soil Pollut. 35, 293–310. https://doi.org/10.1007/BF00290937.

Waithaisong, K., Robin, A., Mareschal, L., Bouillet, J.-P., Laclau, J.-P., Deleporte, P., Gonçalves, J.L. de M., Harmand, J.-M., Plassard, C., 2020. Introducing N2-fixing trees (Acacia mangium) in eucalypt plantations rapidly modifies the pools of organic P and low molecular weight organic acids in tropical soils. Sci. Total Environ. 742, 140535. https://doi.org/10.1016/j.scitotenv.2020.140535.

Walker, T.W., Syers, J.K., 1976. The fate of phosphorus during pedogenesis. Geoderma 15, 1–19. https://doi.org/10.1016/0016-7061(76)90066-5.

Wardle, D.A., Yeates, G.W., Williamson, W., Bonner, K.I., 2003. The response of a three trophic level soil food web to the identity and diversity of plant species and functional groups. Oikos 102, 45–56. https://doi.org/10.1034/j.1600-0706.2003.12481.x.

Wood, S.A., Karp, D.S., DeClerck, F., Kremen, C., Naeem, S., Palm, C.A., 2015. Functional traits in agriculture: agrobiodiversity and ecosystem services. Trends Ecol. Evol. (Amst.) 30, 531–539. https://doi.org/10.1016/j.tree.2015.06.013.

Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils 37, 199–210. https://doi.org/10.1007/s00374-003-0586-5.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. J. Nematol. 25, 315–331.