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A B S T R A C T

The inclusion of shade trees into cocoa (*Theobroma cacao* L.) systems can generate livelihood opportunities for smallholder farmers. Yet, there is the need to examine the ecological context within which shade trees, and their functional traits, have a positive impact on ecosystem services in cocoa systems. Here, we used a network of farms of similar aged hybrid cocoa, in a nested design consisting of agroforestry or monoculture management, on three initial soil quality levels (poor, moderate or good) in two agroecological zones (humid or sub-humid) to investigate whether shade tree functional traits are linked with soil-based and cocoa-based ecosystem services. Initial soil quality level was the main driver of differences in soil organic matter, soil N, soil C:N, soil total C, soil permanganate-oxidizable C, while agroecological zone largely explained differences in cocoa yield and aboveground C. The inclusion of shade trees increased soil macrofauna abundance and mass but decreased cocoa aboveground C compared to cocoa monoculture plots. Importantly, within agroforestry systems, shade tree leaf traits expressed as community weighted means of SLA, leaf N, and leaf dry matter content explained differences in soil-based and cocoa-based ecosystem services. These results show that agroforestry systems have the potential to enhance soil-based ecosystem services without notably decreasing cocoa yield. And a trait-based approach to describe shade tree diversity can advance our understanding and management of shade tree-ecosystem service relationships in cocoa agroforestry systems.

1. Introduction

Ghana is the second largest producer of cocoa (*Theobroma cacao*, L.) beans in the world, with a market share of 20% of the total global cocoa production, which represents over US$ 2 billion annually in foreign exchange (GCB, 2022) and supports the livelihood of more than 600,000 households across Ghana (Ghana Statistical Service, 2020). However, decreases in productivity and income earning by smallholder farmers, have emerged during the last decade (Kroeger et al., 2017; GCFRP, 2021; Bermudez et al., 2022), currently affecting ~ 40% of cocoa farms, with relatively low yields (Aneani and Ofori-Frimpong, 2013; Kalischek et al., 2023). Several factors have been attributed to these decreases, such as high pest incidence, the use of low-yielding varieties, over-aged cocoa stands and, importantly, soil fertility loss (Baah et al., 2011; Akrofi et al., 2015; Doe et al., 2022). Soil fertility maintenance in cocoa systems is an on-going research priority to sustain yield (Ahenkora et al., 1987; Appiah et al., 1997; Isaac et al., 2007; Konger et al., 2019; Asante et al., 2021; Doe et al., 2023). Indeed, many years of harvesting cocoa without replenishing the lost nutrients may contribute to soil fertility loss, which eventually affects yield (Appiah et al., 1997; Hartemink, 2005). While this loss may be compensated in some systems with high fertilizer inputs, these additions may acidify the soil and interfere with the availability of critical soil nutrients, such as phosphorus (Koko, 2013).

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There have been concerted efforts to promote the inclusion of shade trees into cocoa agroforestry systems to improve both the environment and livelihood opportunities for smallholder farmers (Asare et al., 2014; Nyantakyi-Frimpong et al., 2019; Isaac et al., 2021; Sanial et al., 2020; UNEP, 2022). Indeed, the shade trees in cocoa agroforestry systems can alter light, water and nutrient supply into cocoa systems through its direct influence on the canopy structure (Asare and Ræbild, 2016), soil structure (Saputra et al., 2020), rooting systems (Isaac et al., 2014) and soil fertility (Sauvadet et al., 2020; Asigbaase et al., 2021), and thus provide various supporting ecosystem services such as enhanced nutrient cycles, and regulating ecosystem services such as biomass and soil carbon (C) storage (Ofori-Frimpong et al., 2007; Tscharntke et al., 2011; Mortimer et al., 2018). Nonetheless, to our knowledge, most studies on the role of shade trees in cocoa agroforests have focused on broad assessments of shade tree characteristics, such as shade taxa and related shade tree height or canopy measures, as well as the impacts of shade trees on soil fertility indicators and cocoa yield (Isaac et al., 2007; Blaser et al., 2017, 2018; Asare et al., 2017, 2019; Asitoakor et al., 2022; but see Blaser-Hart et al., 2021), which have produced mixed results. For example, studies in Ghana and elsewhere that have compared soil fertility in cocoa monoculture and cocoa agroforests have reported similar fertility levels in the two systems (reviewed in Niether et al., 2020; Asitoakor et al., 2022), with some instances of shade trees reducing cocoa yield through various direct—pests— and indirect –light, water and soil nutrient competition— mechanisms (e.g., Ofori-Frimpong et al., 2007; Wade et al., 2010; Wartenberg et al., 2017). However, other studies have found that shade trees can improve soil fertility in cocoa agroforests, especially in farms with poor soils such as Ferralsols or Acrisols, but that these benefits depended on shade tree species (Isaac et al., 2007; Sauvadet et al., 2020; Wartenberg et al., 2020).

The impact of tree diversity benefits have been linked to their functional traits, defined as any morphological, chemical, physiological or phenological characteristics that reflect the life history of individuals (Violle et al., 2007). Specifically for cocoa agroforestry systems, Sauvadet et al. (2020) show that higher soil fertility was observed under shade tree species with the highest leaf chemical trait dissimilarity with cocoa leaves in a Cameroonian cocoa agroforest, while Moço et al. (2010) observed higher soil biodiversity under the shade trees producing litter of the highest quality (i.e. low lignin and polyphenols contents, high nutrient contents). These examples point to the fact that trait-based approaches offer one of the best options to disentangle the effects of shade trees on ecosystem services provided by cocoa agroforestry systems (Martin and Isaac, 2015, 2018; Wood et al., 2015; Sauvadet et al., 2020), including soil-based ecosystem services and cocoa-based ecosystem services (Isaac et al., 2024). Such an approach provides the opportunity to optimize the selection of the most suitable tree species to be incorporated into cocoa farms to achieve key trait-environment relationships. However, there are still knowledge gaps that need to be addressed. First, most of the shade tree benefits on soil-based ecosystem services are localized under their canopies, and not detectable away from these zones (Blaser et al., 2017; Wartenberg et al., 2020), in line with the current knowledge of tree spatialized influence in other agroforestry systems (Cardinael et al., 2017). Nonetheless, while the observations of shade tree influence on soil properties at the farm scale are more seldom, they may still occur (e.g., Abou Rajab et al., 2016) but are harder to link to shade tree community traits due to the coarseness of their characterization in these studies. Second, the influence of shade trees – and on a larger scale agroecosystems diversification – is also dependent on soil inherent properties (e.g., Waithaisong et al., 2020; Sauvadet et al., 2021), yet soil type sensitivity to shade tree species introduction have been seldom studied.

We aim to determine whether shade tree functional traits in a range of environmental conditions predict key soil-based ecosystem services related to soil fertility and C storage, including soil C (total and active), soil N, macrofauna communities, and cocoa-based ecosystem services including yield and aboveground C storage. To do this, we used a network of farms along a gradient of agroecological zones and soil quality in Ghana, with the same cocoa hybrid of similar age, in a nested design of: farm management (cocoa in monoculture or in agroforestry), initial soil quality level (poor, moderate and good quality) and climate (humid and sub-humid agroecological zone). Our objectives were to 1) describe leaf functional trait variability among shade trees in agroforestry systems, 2) determine the soil properties related to soil-based ecosystem services and cocoa-based ecosystem services in cocoa monocultures and agroforestry systems, and 3) link shade tree functional traits and ecosystem services in cocoa agroforestry systems.

2. Materials and methods

2.1. Study sites

Eighteen smallholder cocoa farms were purposely selected from the 130 experimental trials of the CocoaSoils program (Asante et al., 2021). The CocoaSoils program is being implemented in Ghana and other West African countries to promote integrated soil fertility management practices to achieve sustainable cocoa production and improvement in the livelihoods of smallholder famers, and to reduce deforestation (Rusinamhodzi et al., 2020). The CocoaSoils experimental trials were established in 2020 on already existing smallholder cocoa farms distributed across six Global Agro-ecological Zones (CocoaSoils Annual Report, 2019, Table 1) adapted from the zonation framework of IIASA/FAO (2012). The Global Agroecological zones framework provides a classification of biophysical factors that are relevant for agricultural production systems, by grouping areas with similar climatic and edaphic conditions (IIASA/FAO, 2012). This zonation classification is a coarse-scale measure, but it provides a standardized framework for characterizing climate, soil and field conditions relevant for agricultural production (Bunn et al., 2019).

In this study, the cocoa farms were selected in areas representing gradients of moisture regime and initial soil quality (see details in Table 1) through 10 cocoa districts spread across seven cocoa-growing regions of Ghana, including Ahafo, Ashanti, Bono, Central, Eastern, Western and Western North regions (Table S1). These regions fall within three agro-ecological zones ranging from semi deciduous through moist evergreen to wet evergreen forests zones – and communities are located between latitudes 5.3° N and 7.2° N and longitudes 0.5° W and 3.0° E, within the six Climate-smart Hotspot Intervention Areas identified in the Ghana Cocoa Forest REDD+ programme (Forestry Commission, 2021).

Table 1
Description of Global Agroecological Zones and Soil Quality types of the Food and Agriculture Organization (FAO) and International Institute for Applied Systems Analysis (IIASA).

Agro-ecological Zone	Description
Humid	Moisture regime of 0.65
Sub-humid	Moisture regime of > 1.15
Poor soil	Soil Quality Index ≤ 0–0.333
Moderate soil	Soil Quality Index of 0.333–0.666
Good soil	Soil Quality Index > 0.666

The Agro-ecological zonation is adopted from the Global Agro-ecological Zones for farming systems (IIASA/FAO, 2012). The cocoa areas were classified into agro-ecological zones according to two moisture regimes (humid and sub-humid) and three soil quality indices (poor, moderate and good soils). The moisture regime was calculated as Precipitation/Potential Evapotranspiration, and it is an indication of the length of the growing period (that is the number of days in the year when both water availability and temperature permit crop growth). Subhumid conditions have a moisture regime of > 1.15 for a growing period of 180–269 days, and humid conditions have a moisture regime between 0.65 and 1.15 for 270–364 days of growing period (FAO and IIASA, 2012; Bunn et al., 2019). Soil Quality Index ranges between value of 1 for the high quality soil and 0 for poor quality soil.

Mean annual rainfall in the last 30 years ranged from 1300 mm to 2300 mm (Baidu et al., 2017). Mean annual temperature ranged between 26.5 °C and 26.8 °C, and elevation of 66–361 m above sea level. The communities experience bimodal rainfall pattern; the major rainfall season occurs from April to July, and the minor rainfall season starts from September and ends in November (Asante et al., 2021). The areas have deeply weathered and well-drained soils, and the dominant soil types include Acrisols, Nitisols, Ferralsols, Leptosols and Lixisols according to the FAO soil classification system (Adei-Gyapong and Asiamah, 2000).

Cocoa farms that serve as controls (no fertilizer application) for the CocoaSoils trials were used. The selected cocoa farms met the following criteria: (i) cocoa farms were grown from the same hybrids, (ii) covered an area of > 1 ha, (iii) a section of the farm in agroforestry and in monoculture, and (iv) cocoa farms were between the ages of 5–15 years – the age range considered as the active productive stage of the developmental cycle of the cocoa plant (Dawoe et al., 2010). We employed a nested design that included three cocoa farms (n = 3) with two farm-level management practices (monoculture and agroforestry; n = 2) nested in the three soil quality classes (poor, moderate and good soils; n = 3), and nested in two agro-ecological zones reflecting moisture regimes (humid and sub-humid; n = 2), for a total of 36 individual research sites among 18 farms. Within each cocoa farm, three 10 m x 10 m plots (100 m^2) were established in an area dominated by shade trees for the agroforestry plots and three 10 m x 10 m plots containing only cocoa trees were established away from the canopy of any shade tree at a distance of at least 45 m away from the nearest shade tree, and used as cocoa monoculture plots.

2.2. Whole plant and leaf sampling and trait determination

All shade trees in the agroforestry subplots were identified by vernacular names; for trees that could not be identified *in situ*, leaf specimens were pressed and sent to the herbarium of CSIR-FORIG for identification. Species identification and nomenclature followed Hawthorne and Gyakari (2006). Whole plant traits were then determined on the shade trees species in the agroforestry plots. Maximum heights were measured using LaserAce hysometer, while the diameter was measured as diameter at breast height (DBH) at 1.3 m from the ground using a diameter tape. For the few shade trees with irregular bole or buttress, diameter was measured *ca.* 50 cm above the buttress or estimated using ocular approach.

Leaf morphological (specific leaf area, SLA and leaf dry matter content, LDMC) traits were determined following standardized protocol (Pérez-Harguindeguy et al., 2013). These traits were selected because they comprised the widely used traits from the '*leaf economic spectrum*' (Reich, 2014), and they have been reported to relate to soil fertility and biomass production in agroecosystems (Wood et al., 2015; Wendling et al., 2016). On each tree, six mature fully expanded leaves without obvious herbivore damage were collected from two branches detached from the shaded lower portion and outer canopy, which receives full sunlight. The leaves were stored in tightly sealed plastic bags, and immediately sent them to the laboratory for further analysis. At the laboratory, the leaf samples were scanned using a flatbed scanner (CanoScan LiDE 110) attached to a laptop after rehydration. We scanned only complete leaves with rachis and the petiole attached. We later analyzed the digital images using IMAGEJ to estimate leaf area. After scanning, the leaf fresh mass was determined and then the leaves were oven-dried at 60° C to determine their dry mass. Specific leaf area (SLA) and LDMC were calculated using the leaf area, fresh and dry mass values following standardized protocol (Pérez-Harguindeguy et al., 2013). Specific leaf area ($cm^2\ g^{-1}$) was calculated as one-sided leaf area divided by leaf dry mass and LDMC ($mg\ g^{-1}$) was calculated as leaf dry mass divided by leaf fresh mass. Leaf C, N and C:N were determined on oven-dried and ground leaf samples with elemental analysis on a LECO CN628 Elemental Analyzer (LECO Corporation).

2.3. Cocoa-based ecosystem services

Approaches such as farmer yield reports, counting of the total number of cherelles and matured pods, harvested pods, and then weighing the dried beans from pods after fermentation and obtaining yield records from farmers 'Cocoa Passbooks' have been used to quantify on-farm cocoa yield (e.g., Asare et al., 2019). We estimated cocoa yield using only the total number of cherelles and matured pods on productive cocoa trees, then the density of cocoa trees per unit area according to a formula proposed by UTZ-Rainforest Alliance (2018).

To do so, all productive cocoa trees (trees that had cherelles and matured cocoa pods on them) were counted in each subplot to determine the density of cocoa trees per 100 m^2. We subsequently counted all the pods on the trunk and branches of each cocoa tree, to calculate cocoa yield per hectare as follows:

$$Apt = \frac{\Sigma P}{\Sigma T} \tag{1}$$

$$A_{cp}\ (\text{kg tree}^{-1}) = A_{pt}\ x\ A_{cpi} \tag{2}$$

$$Y(\text{kg ha}^{-1}) = A_{cp}\ x\ A_t \tag{3}$$

Where A_{pt} is the average number of cocoa pods per productive tree, ΣP is the total number of pods sampled on productive trees, ΣT is the density of productive trees per 100 m^2, A_{cp} *(kg tree*$^{-1}$*)* is average cocoa production per tree, A_{cpi} is the average weight of one cocoa pod, which was taken as equivalent to 0.04 kg of cocoa beans (UTZ-Rainforest Alliance, 2018); A_t, average number of productive trees per hectare; and *Y (kg ha*$^{-1}$*)*, estimated cocoa yield per hectare.

To estimate the aboveground biomass of cocoa trees, the total height and DBH of each cocoa tree in agroforestry and monoculture systems were measured using a graduated stick and a diameter tape at 1.3 m from the ground, respectively. The aboveground biomass (AGB) was then deduced from the allometric equation of Andrade et al. (2008):

$$AGB = 10^{\,(-1.625\ +\ 2.63\ x\ \log\ (\text{DBH}))} \tag{4}$$

Where *AGB* is aboveground tree biomass in kg and DBH is the diameter at breast height in cm. We then calculated plot-level AGB ($Mg\ ha^{-1}$) by summing the biomass values of all trees in each plot, and then converted the values into $Mg\ C\ ha^{-1}$ using a carbon content of 0.5 of dry mass (IPCC, 2003).

2.4. Soil macrofauna

Soil macrofauna were sampled using a soil monolith sampling procedure adapted from Rousseau et al. (2012). Within each subplot in the agroforestry and monoculture plots, soil monoliths of 20 cm×20 cm x 10 cm depth were excavated at two random locations. In the agroforestry plots, the two soil monoliths were sampled semi-randomly in areas where the canopies of shade trees and cocoa trees were in contact under the shade tree canopy. The soil and surface litter were taken and placed on a black plastic sheet, and soil animals were manually sorted immediately. Earthworms were preserved in 4% formalin, whilst other invertebrates were preserved in 70% ethanol (Rousseau et al., 2012). Sample specimens were then transported to the laboratory for further analyses. In the laboratory, soil fauna individuals were counted and identified at the order level following standard procedure (Gibb and Oseto, 2006). After the identification, all individuals were scanned using a flatbed scanner (CanoScan LiDE 110). Fauna fresh mass was calculated from body size measurements using allometric equations (Coulis and Joly, 2017). These measurement allowed to assess both soil fauna abundance (individuals per m^2) and biomass (kg per m^2) at the plot scale, by dividing either the number of individuals collected or their estimated biomass by the area sampled in each plot (two monoliths of 20 cm×20 cm, corresponding in total to 0.08 m^2).

2.5. Soil-based ecosystem services

Soil was sampled with a hand-driven soil auger (diameter 5.5 cm) at five locations to 20-cm depth along an X-shape in each 10 m x 10 m subplot. The collected samples were composited into one sample per plot, and transferred into labelled plastic bags for laboratory processing at the CSIR-Forestry Research Institute of Ghana (CSIR-FORIG). At the laboratory, the soil samples were air-dried, crushed and sieved at 2-mm after removing gravels, roots, and other debris. The samples were then transferred to the University of Toronto Scarborough, Canada to determine Soil Organic Matter (SOM), soil C pools (total C and Soil Permanganate Oxidizable – C (POXC)) and total soil N. Soil organic matter was determined with loss on ignition methods (Schulte and Hopkins, 1996). Soil Permanganate Oxidizable – C (POXC) often considered as active soil C (Culman et al., 2012) was determined following the method of Weil et al. (2003). Briefly, a diluted, 0.2 *M* alkaline potassium permanganate ($KMnO_4$) solution was added to 2.5 g of soil, shaken, centrifuged and measured on a spectrophotometer at 550 nm (Thermo Scientific GENESYS UV-Vis Spectrophotometer, Thermo Fisher Scientific Inc., USA). Total C and N were determined on a sample subaliquot that was crushed beforehand at 200 μm, before being analyzed by combustion on a LECO CN628 Elemental Analyzer (LECO Corporation, Minnesota, USA).

2.6. Data analyses

First, functional traits of shade tree species were aggregated at the community level for each subplot via Community Weighted Mean (CWM), according to Lavorel et al. (2008):

$$CWM = \sum_{i=1}^{N} bixi \quad (5)$$

Where *bi* is the relative biomass of *i*th species, *xi* is the trait value of *i*th species, and *N* is the total number of species observed in a given subplot.

Variables were first checked for normality using Shapiro-Wilk test and for homoscedasticity with Levene's test, and log transformed when necessary. In addition, the data were checked for extreme outliers using the box plot method in R and the ROUT method of the GraphPad Prism 10 software. A three-factor Analysis of Variance (ANOVA) with agroecological zone (humid and sub-humid), initial soil quality level (poor, moderate and good soil) and management type (agroforestry and monoculture) as fixed factors and farm as a random factor were first performed on all soil and cocoa parameters. CWM traits were analyzed on the same logic with two-factors ANOVA of agroecological zone and soil quality type. Multiple comparisons among paired means were then tested using Tukey's Honest Significant Difference (HSD) post-hoc test to adjust for paired comparisons.

Shade tree functional traits and ecosystem services were then assessed with a Principal Component Analysis (PCA). We also applied redundancy analyses (RDA) to determine if differences in soil properties and cocoa yield and carbon storage relate to shade tree CWM functional traits and macrofauna indicators in either agroecological zones. Significance of each variable was assessed using a PERMANOVA implemted using the 'vegan' R package (with 9999 permutations used). All data analyses were performed using R Programming (R Core Development Team 2018) and GraphPad Prism 10 (GraphPad Software, Inc., California, USA).

3. Results

3.1. Shade tree traits

Shade tree composition consisted of 23 different tree species (Table S2). The most abundant tree species were *Morinda lucida* (18.8%), *Milicia excelsa* (11.8%), *Terminalia ivorensis* (10.6%), *Terminalia superba* (9.4%) and *Newbouldia laevis* (8.2%). Moderately represented species, all around 5% of the species composition, were *Amphimas pterocarpoides*, *Entandrophragma angolense*, *Holarrhena floridunda*, *Ficus sur* and *Spathodia campanulata*. And a suite of 13 other tree species with <2% representation on cocoa farms.

Traits of shade trees are reported as Community Weighted Means (CWM). CWM_Leaf N had a narrow range among all agroforestry plots (Table 2) whereas CWM_SLA had a much larger range of 4.52–138.40 cm^2 g^{-1}. The agroecological zone ($p = 0.015$) and interaction between agroecological zone and soil quality ($p = 0.015$) explained differences in shade tree CWM_SLA (Table 3); SLA was higher in the sub-humid zone (Fig. S1). CWM_Leaf N though not significant, showed slightly higher values in sub-humid zone as well (Fig. S1). CWM_Leaf C:N also had a large range (7.88–70.70). Soil type explained the differences between CWM_Leaf C:N ($p = 0.036$) as well as DBH ($p = 0.051$; Table 3) with no clear trends in the direction of the other traits (Fig. S1).

3.2. Soil and cocoa properties

Soil-based ecosystem services varied among factors within the nested level, with the initial soil quality level (poor, moderate, good) explaining the largest amount of variance (Table 4). Soil quality level was a significant factor explaining differences in SOM ($p < 0.002$), soil total N ($p = 0.002$), soil C:N ratio ($p < 0.001$), macrofauna abundance ($p = 0.009$),

Table 2
Community weighted mean (CWM), standard error (S.E.), minimum and maximum values, and lower and upper 95% of Confidence Interval of mean of shade trees leaf and plant functional traits in cocoa agroforestry plots on three soil quality levels representing soil quality indices in humid and sub-humid agroecological zones in Ghana.

CWM of variable	Mean ± S.E.	Minimum-Maximum	CI of mean
CWM_Leaf N (%)	0.80 ± 0.05	0.11 – 1.86	0.69 – 0.92
CWM_Leaf C:N	28.55 ± 1.88	7.88 – 70.70	24.78 – 32.31
CWM_SLA (cm^2 g^{-1})	45.62 ± 3.56	4.52 – 138.40	38.48 – 52.76
CWM_LDMC (mg g^{-1})	37.31 ± 2.56	5.80 – 83.76	32.17 – 42.45
CWM_DBH (cm)	14.45 ± 1.86	0.98 – 70.03	10.71 – 18.19
CWM_Maximum H (m)	5.84 ± 0.50	0.73 – 18.16	4.85 – 6.84

Leaf N, leaf nitrogen concentration; Leaf C:N: leaf carbon-to-nitrogen ratio; SLA, specific leaf area; LDMC, leaf dry matter content; DBH, diameter at breast height; H, maximum tree height.

Table 3
ANOVA results of six community weighted mean (CWM) shade tree traits (specific leaf area (SLA), leaf nitrogen (Leaf N), leaf carbon (C) to N (Leaf C:N), leaf dry matter content (LDMC), tree diameter at breast height (DBH) and maximum tree height (H)) explained by three factors and their interactions: agroecological zone (A), initial soil quality level (S), agroecological zone-by-soil quality type interaction (A x S). Factors with significant effects on variables are presented in bold.

Source of variance	CWM_Leaf N (%)	CWM_Leaf C:N	CWM_SLA (cm g^{-1})	CWM_LDMC (mg g^{-1})	CWM_DBH (cm)	CWM_H (m)
	F (P)	*F(P)*	*F (P)*	*F (P)*	*F (P)*	*F (P)*
A	0.310 (0.607)	1.048 (0.364)	**8.230 (0.015)**	2.604 (0.182)	0.092 (0.909)	0.223 (0.707)
S	0.112 (0.879)	**5.988 (0.036)**	0.115 (0.879)	1.447 (0.304)	4.820 (0.051)	2.590 (0.136)
A x S	1.349 (0.320)	**6.056 (0.030)**	**6.296 (0.015)**	3.227 (0.102)	0.482 (0.630)	0.370 (0.699)

Table 4
ANOVA results of SOM, soil total N, soil C:N, macrofauna abundance and mass, soil total C, POXC and aboveground C (AGC), and yield variable explained by three factors and their interactions: agroecological zone (A), initial soil quality level (S), agroforestry or monoculture management (M), agroecological zone-by-soil quality type interaction (A x S), agroecological zone-by-management interaction (A x M), Soil quality type-by-management interaction (S x M) and agroecological zone-by-soil quality type-by-management (A x S x M) interaction. Factors with significant effects on variables are presented in bold.

Source of variance	SOM	Soil Total N	Soil C:N ratio	Macrofauna abundance	Log-macrofauna mass	Soil Total C	POXC	AGC	Log-Cocoa Yield
	F (P)	*F (P)*	*F (P)*	*F (P)*	*F (P)*	*F (P)*	*F (P)*	*F (P)*	*F (P)*
A	0.009 (0.925)	0.009 (0.925)	0.031 (0.860)	2.747 (0.101)	1.880 (0.174)	0.326 (0.569)	**4.460 (0.038)**	**18.820 (<0.000)**	**9.939 (0.002)**
S	**6.615 (0.002)**	**6.615 (0.002)**	**7.848 (<0.000)**	**4.888 (0.009)**	0.015 (0.985)	**7.877 (<0.000)**	**2.262 (0.001)**	**6.222 (0.003)**	1.797 (0.172)
M	1.953 (0.166)	1.953 (0.166)	0.027 (0.869)	**22.878 (<0.000)**	**5.362 (0.023)**	1.816 (0.181)	0.281 (0.598)	**17.744 (<0.000)**	0.367 (0.546)
A x S	1.997 (0.142)	1.997 (0.142)	**3.185 (0.040)**	1.340 (0.267)	2.070 (0.132)	**3.548 (0.033)**	**3.325 (0.040)**	2.296 (0.106)	2.328 (0.104)
A x M	0.185 (0.669)	0.185 (0.669)	0.852 (0.358)	0.635 (0.428)	0.049 (0.825)	0.000 (0.999)	0.094 (0.760)	3.599 (0.061)	0.623 (0.432)
S x M	0.522 (0.595)	0.522 (0.595)	0.011 (0.989)	0.769 (0.467)	2.234 (0.113)	0.513 (0.600)	0.868 (0.423)	2.541 (0.084)	0.524 (0.594)
A x S x M	0.335 (0.716)	0.335 (0.716)	0.522 (0.595)	1.090 (0.341)	1.620 (0.204)	0.231 (0.794)	0.357 (0.701)	0.149 (0.862)	0.691 (0.504)

as well as all C based services: soil total C ($p < 0.001$), POXC ($p < 0.001$) and AGC ($p = 0.003$). In some cases, mean values tended to increase from poor to moderate to good initial soil quality levels (Fig. 1B-F). Initial soil quality level had the largest impact on SOM values, moderating any effects from agroecological zone or management. Management (agroforestry or monoculture) was only significant in explaining differences in macrofauna mass ($p = 0.023$) and abundance ($p < 0.001$; Table 4), with higher macrofauna mass and abundance in agroforestry plots in all scenarios except sub-humid poor soils, where monoculture plots had higher macrofauna mass (Figs. 1H and 1I). In fact, overall, the number of individuals and mass of soil macrofauna taxa were significantly higher in the agroforestry plots than the cocoa monoculture plots. Fauna abundance was significantly higher in cocoa agroforestry plots (155.00 ± 18.26 ind.m^{-2}) compared to the cocoa monoculture plots (82.29 ± 8.85 ind.m^{-2}) ($p < 0.001$). Mean fauna mass also differed significantly between the two management types ($p = 0.023$), with the agroforestry plots recording higher fauna mass (70.65 ± 11.27 gm^{-2}) than the monoculture plots (46.04 ± 9.22 gm^{-2}). In addition, more macrofauna taxonomic groups (Blattaria, Gastropods and Isopoda) that are classified as litter transformers were distributed in only the agroforestry plots, while Isoptera were only found in cocoa monocultures (Table S3). Agroecological zone explained differences in cocoa-based services: AGC ($p < 0.001$) and yield ($p = 0.002$; Table 4), with yield being marginally higher in the humid zone (Fig. 1G).

3.3. *Shade tree trait relationships with soil and cocoa properties*

Under agroforestry management, variations in all soil-based ecosystem services (SOM, soil total N, soil C:N, soil total C, POXC) and soil fauna were greatly associated with PCA axis 1, and negatively covaried with cocoa yield, CWM_H and CWM_DBH (Table 5 and Fig S2). On the other hand, CWM_Leaf N and CWM_SLA were associated with PCA axis 2, and covaried negatively with CWM_LDMC (Table 5).

These relationships between shade tree traits and soil-based and cocoa-based ecosystem services also varied with the agroecological zone; indeed, redundancy analysis (RDA) in the sub-humid zone showed soil-based ecosystem services were positively associated with soil fauna indicators but negatively covaried with shade tree CWM_DBH, CWM_LDMC and CWM_H, along with cocoa yield (Fig. 2A). Cocoa AGC on the other hand was mostly negatively associated with CWM_Leaf N ratio on the RDA2 axis (Fig. 2A). While the positive relationships between soil fauna mass and soil-based ecosystem services remained in the humid climate (Fig. 2B), cocoa-based ecosystem services both negatively covaried with CWM_Leaf C:N and CWM_SLA (Fig. 2B).

4. Discussion

Using a trait-based approach to disentangle the effects of shade tree functional traits on soil-based ecosystem services in smallholder cocoa farms, we demonstrate that shade trees have a beneficial impact on key soil properties, including macrofauna mass and macrofauna abundance. We show that these positive effects are predicted by community-weighted shade tree traits. We also found initial soil quality level (poor, moderate or good soil) was the most significant nested factor that explained differences in SOM, soil total N, soil C:N ratio, macrofauna abundance, soil total C, POXC and AGC.

4.1. *Contrasting shade tree CWM traits between agroecological zones and soil quality levels*

Agroecological zone, initial soil quality level, and their interactions accounted for differences in shade tree SLA and leaf C:N at the community level. Notably, SLA at the community scale was higher in the sub-humid agroecological zone, suggesting that the quality of shade trees in sub-humid zones are higher, given that SLA correlates well with rates of resource acquisition (Reich, 2014) and biomass production (Liu

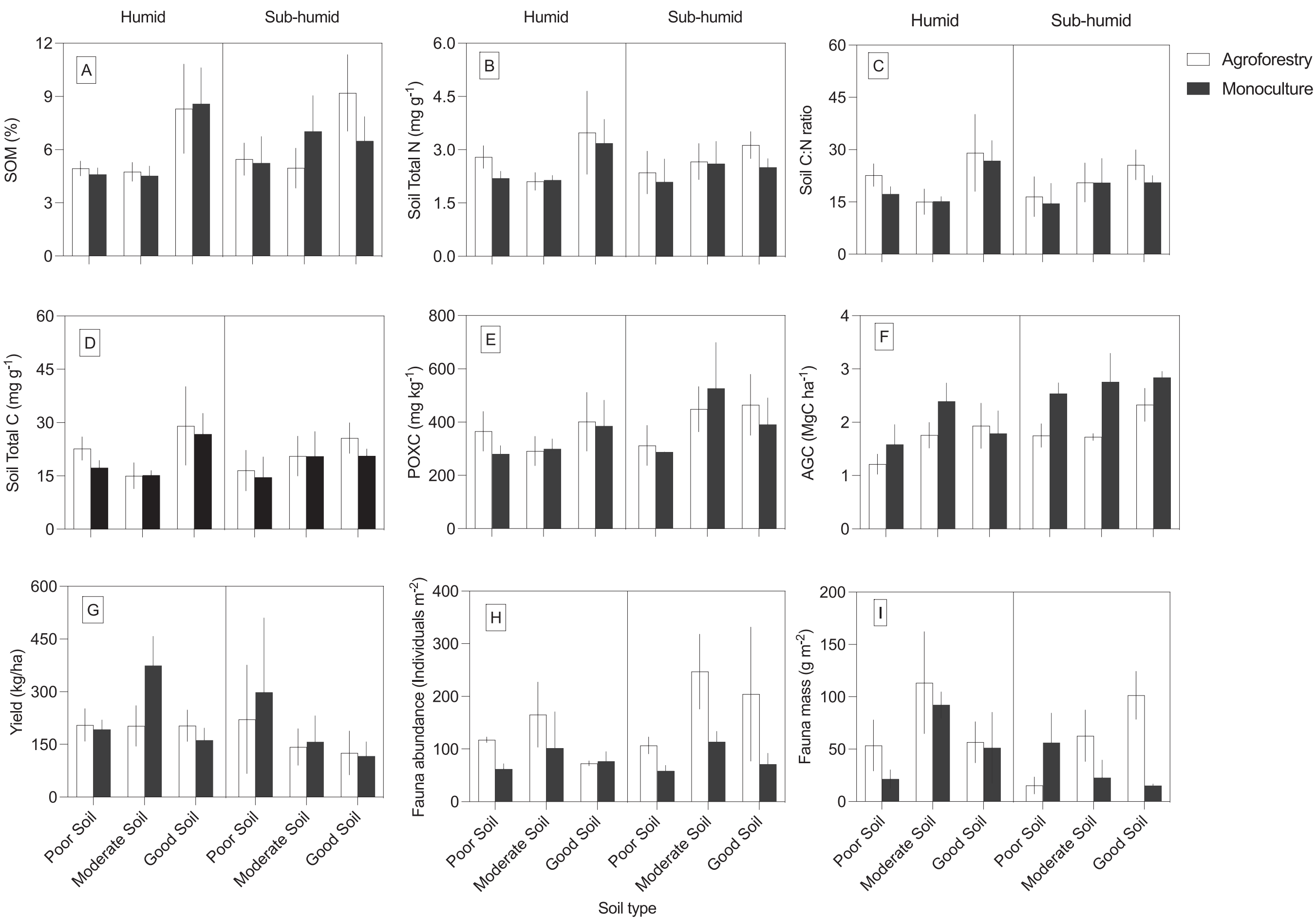

Fig. 1. Soil-based and cocoa-based ecosystem services in cocoa agroforestry (open bars) and cocoa monoculture (black bars) plots in farms distributed across three initial soil quality levels (poor, moderate and good soils) in humid and subhumid agroecological zones in Ghana. Also included in aboveground carbon and cocoa yield.

Table 5
Soil-based and cocoa-based ecosystem services and biomass-weighted community means (CWM) of shade tree functional trait correlations to PCA's eigenvectors (Figure S2). Correlations above 0.5 are deemed relevant (in bold). Leaf N, leaf nitrogen concentration; Leaf C:N, leaf carbon-to-nitrogen ratio; SLA, specific leaf area; LDMC, leaf dry matter content; DBH, diameter at breast height; H, maximum tree height.

	PC1	PC2
SOM	**-0.841**	0.056
Soil Total N	**-0.905**	0.164
Soil C:N	**-0.887**	0.142
Soil Total C	**-0.941**	0.162
POXC	**-0.803**	0.248
AGC	0.141	-0.265
Yield	**0.740**	0.374
Fauna abundance	-0.246	-0.361
Fauna mass	**-0.760**	-0.057
CWM_Leaf N	-0.287	**-0.654**
CWM_Leaf C:N	0.058	0.171
CWM_SLA	**-0.530**	**-0.706**
CWM_LDMC	0.260	**0.858**
CWM_DBH	**0.488**	-0.430
CWM_Maximum H	**0.615**	-0.462

et al., 2016). This finding is in line with the common assumption that climatic factors, especially precipitation, drives SLA in woody plants (Gong and Gao, 2019). On the other hand, initial soil quality levels drove the differences in CWM leaf N and C:N ratios in the sub-humid but not the humid zone; while information on the relationship between shade tree leaf stoichiometry and soil properties in cocoa systems is scarce, previous studies in forest ecosystems supports our findings (e.g., Liu and Wang, 2021). Indeed, leaf C:N ratios usually decreases with soil quality and/or fertility levels (e.g. Zhang et al., 2020). Interestingly, while not significant, we note trends in higher shade tree DBH and height in sub-humid agroecological zones, indicating that shade trees are selected for larger size, and possibly higher growth rate, in these resource limited sites. What these shade tree functional trait trends also reveal is that some traits, such as leaf N and LDMC, are conserved across climatic and soil gradients, suggesting that prescriptions for shade trees may be applicable across conditions.

4.2. *Variation in key soil-based and cocoa-based ecosystem services*

Our results show that the management practice of shade trees in cocoa agroforestry systems did not necessarily lead to categorical improvement in soil-based ecosystem services at the plot scale (Blaser et al., 2017; Wartenberg et al., 2020), but did enhance the abundance and mass of soil macrofauna. Indeed, retaining or integrating shade trees in cocoa agroforests is crucial for promoting the abundance and diversity of soil macrofauna and other important ecosystem services such as aboveground C. The higher abundance and mass of soil macrofauna in the cocoa agroforestry plots compared to the monoculture plots is in agreement with other studies that reported of higher number of soil animals in cocoa agroforestry systems in Ghana and elsewhere (Bigger, 1981; Bisseleua et al., 2009; Felicitas et al., 2018; Niether et al., 2020, but see Rizali et al., 2013). Often, non-cocoa trees and their associated

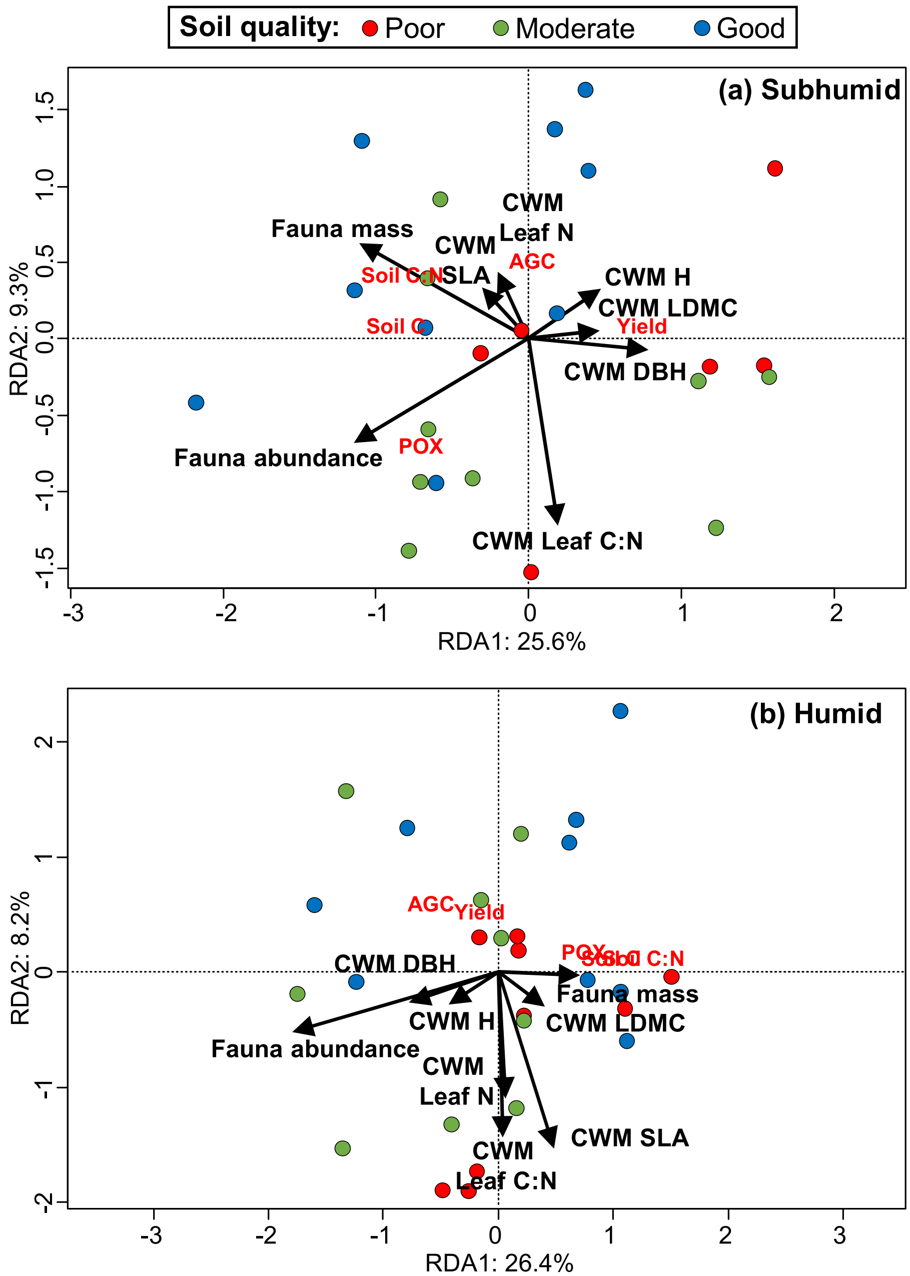

Fig. 2. Redundancy analyses (RDA) performed on soil properties in a) subhumid and b) humid agroecological zones. Colors represent three initial soil quality levels (poor, moderate, good). Arrows correspond to vectors representing shade tree functional traits (CWM_leaf N, CWM_leaf C:N, CWM_SLA, CWM_LDMC, CWM_DBH and CWM_H) and macrofauna measures (mass and abundance).

litter layer provide sustained habitat, which supports high taxonomic groups of soil fauna (Rousseau et al., 2013). In addition, the presence of shade trees can induce a denser rhizosphere, producing more food for the detritivore soil macrofauna organisms (Brussaard, 1998). Soil fauna communities such as the litter transformers that were recorded in this study (e.g., Blattaria, Isopoda, Diplopoda and Gastropoda) are recognized as an important indicator of soil biodiversity (Rousseau et al., 2013), and are critical for the general health of cocoa farms (Tsufac et al., 2021). Clearly, regardless of agroecological zones or initial soil quality level, agroforestry systems stimulate the amount and diversity of macrofauna, providing the drivers of key soil fertility processes not found in monocultures.

Agroecological zone largely explained differences in cocoa-based services; aboveground cocoa carbon pools tended to be higher in subhumid zone, while cocoa yield was marginally higher in the humid zone. These trends are not unexpected as cocoa may allocate higher biomass to aboveground components in more limited conditions (Borden et al., 2019), while yield is slightly limited when climatic conditions are marginal (Abdulai et al., 2018).

4.3. Community-level shade tree traits predict soil-based and cocoa-based ecosystem services

Efforts to establish linkages between shade tree functional traits and the maintenance and supply of ecosystem services in cocoa agroforestry systems, although in the nascent stage, is gaining attention for theoretical and practical implications on shade management to derive multiple benefits within cocoa agroforest systems (Martin and Isaac, 2015). Yet, most of these studies focuses on multiple individual shade trees rather than global shade tree community composition (e.g Blaser-Hart et al., 2021; Sauvadet et al., 2020). Our results provide empirical evidence on shade tree functional traits at the community level to predict variables representing important soil-based ecosystem services. The association of CWM shade tree traits, such as CWM of SLA, LDMC, leaf N, leaf C:N and DBH, with soil-based services at the farm scale supports the theories that emphasize traits as direct drivers of ecosystem processes and responses (Lavorel and Garnier, 2002; Martin and Isaac, 2018; Meidema Brown and Anand, 2022).

It is established that traits including leaf N, leaf C:N, SLA and LDMC affect soil fertility through their influence on decomposition, mineralization and nutrient conservation (Lavorel and Garnier, 2002; Ordoñez et al., 2009). In particular in cocoa agroforestry systems, the mixing of low-quality and high-quality litter can modify decomposition rates and thus soil fertility (Sari et al., 2022; Bai et al., 2022). In addition, conservative traits such as leaf C:N and LDMC, which partly determine leaf quality, relate to macrofauna abundance and macrofauna mass (Giweta, 2020), through an effect on leaf litter palatability and thus affect the abundance, composition and diversity of soil macrofauna (Moço et al., 2010; Rousseau et al., 2021). This is in line with the positive covariation of acquisitive trait CWM SLA with soil fauna mass found in our study. On the other hand, soil fauna mass was negatively associated with CWM of maximum height and DBH, in line with recent studies in experimental grasslands, which showed that these CWM traits explained soil fauna variability due to their overall influence of plant litter inputs (Beugnon et al., 2019). These impacts on soil fauna, and to a broader extent soil biological activity, likely benefitted to soil C content and quality, hence explaining the relationships found between these indicators in our study. These pathways provide the often missing leaf level traits linking trees to soil dynamics and outcomes, critical to optimizing shade tree management for key soil-based ecosystem services.

Cocoa-based ecosystem services presented contrasting sensitivity to farms environmental and management constrains. Indeed, cocoa AGC, in spite of being higher under the sub-humid climate, responded positively to the soil quality gradient, but also to the shade tree CWM traits associated with increased fertility and soil biological activity (i.e. acquisitive shade tree leaf traits, leaf N and SLA), suggesting a strong dependency of cocoa AGC on soil quality in these systems. Nonetheless, and in spite of these effects on cocoa AGC, cocoa yield was not significantly decreased under shade trees, and presented contrasted sensitivity to soil quality and shade tree traits depending on the agroecological zone. Cocoa yield was lower in the sub-humid zone, with no clear relationships with soil quality, but rather with CWM maximum height and DBH, suggesting a more important limitation of the microclimate rather than soil quality for cocoa production in this zone.

5. Conclusions

Cocoa is often cultivated in full-sun monocultures in order to maximize short-term productivity and profitability because of the uncertainty about the functional relevance of shade trees in cocoa agroforestry systems. Our results show that shade tree functional traits at the community level can predict multiple ecosystem services within cocoa agroforests. Specifically, integrating shade trees, with the expression of certain functional trait strategies, is key to promoting the activity of soil macrofauna, which has a coupling effect on soil biodiversity and related ecological functions. This has implications for our understanding and management of the context within which the positive influence of shade trees can be optimized. We also show that while some shade tree functional traits are more variable, other shade tree functional traits at the community scale are similar across agroecological zones, suggesting certain traits are conserved over climatic regions. This allows for the use of traits over taxa among agroecological zones when selecting for appropriate shade trees. Finally, soil quality plays a mediating role in the ability of cocoa systems to provide and maintain critical ecosystem services. Thus, shade tree management prescriptions should consider these local environmental constraints. This ecological approach to understanding shade tree diversity will achieve important ecosystem services for enhanced environmental benefits and farmer livelihoods.

CRediT authorship contribution statement

Shalom D. Addo-Danso: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Richard Asare:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Conceptualization. **Abigail Tettey:** Writing – review & editing, Resources, Methodology, Investigation. **Jennifer E. Schmidt:** Writing – review & editing, Methodology, Conceptualization. **Marie Sauvadet:** Writing – review & editing, Methodology, Conceptualization. **Mathieu Coulis:** Writing – review & editing, Methodology, Formal analysis. **Nelly Belliard:** Methodology, Formal analysis. **Marney E. Isaac:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Marney E Isaac reports financial support was provided by Canada Research Chairs Program. One co-author is employed by Mars Wrigley in the Cocoa Plant Science division. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109090.

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