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RESEARCH ARTICLE

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Cocoa agroforest multifunctionality and soil fertility explained by shade tree litter traits

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Abstract

1. Manipulating plant functional diversity to improve agroecosystem multifunctionality is a central challenge of agricultural systems world-wide. In cocoa agroforestry systems (cAFS), shade trees are used to supply many services to farmers, yet their impact on soil functioning and cocoa yields is likely to vary substantially among tree species.
2. Here we compared the impact of five shade tree species (*Canarium schweinfurthii* (Canarium), *Dacryodes edulis* (Safou), *Milicia excelsa* (Iroko), *Ceiba pentandra* (Kapok tree), *Albizia adianthifolia* (Albizia)) and unshaded conditions on the functioning of poor sandy savanna soils within eight cocoa farms in Central Cameroon. We assessed the effects of plant functional traits, leaf litterfall and fine root biomass on a range of soil functions and on cocoa yield.
3. Shade trees generally improved soil pH, NH_4^+, NO_3^- and Olsen P content, biomass production of bioassays and soil total C and N content, while leaving cocoa yields unchanged. However, these effects varied largely among species. Improvements of soil functions were low under the two fruit trees (*Canarium* and *Dacryodes*), medium under the legume tree *Albizia* and high under the two timber trees (*Milicia* and *Ceiba*). Low litter recalcitrance was most strongly associated with increases in soil fertility indicators such as N and P availability, whereas soil C and N content increased with litter Ca restitution.
4. *Synthesis and applications*. We demonstrate that cocoa agroforest multifunctionality is substantially influenced by the functional traits of shade tree species. Shade tree species with the most dissimilar traits to cocoa (cocoa showing the lowest leaf litter quality) showed the largest improvement of soil functions. Therefore, selection of shade trees based on their functional traits appears as a promising practice to adequately manage soil functioning. In order to fully assess the beneficial

role of shade trees in these agroecosystems. Future research will need to extend this approach to other below-ground traits and other aspects of multifunctionality such as long-term cocoa health and yield.

KEYWORDS

agroecosystem multifunctionality, agroforestry, cacao tree, fertility, litter recalcitrance, plant functional traits, shade type, soil functions

1 | INTRODUCTION

Ecosystems are expected to provide multiple functions and services for human society. Hence, ecosystems' health is now mainly assessed through their multifunctionality (Maestre, Castillo-Monroy, Bowker, & Ochoa-Hueso, 2012; Wagg, Bender, Widmer, & Heijden, 2014). Ecosystem multifunctionality is assumed to be maintained with high levels of above-ground and below-ground biodiversity (Delgado-Baquerizo et al., 2016). However, the identity of species that live in the ecosystem, as well as their functional traits (defined as any morphological, physiological or phenological feature measurable at the individual level; Violle et al., 2007), are at least as important as biodiversity per se in explaining the effects of species richness on ecosystem multifunctionality (Maire et al., 2018; Peltzer et al., 2009). In the agricultural sector, stakeholders and managers are increasingly considering the identity of species that are associated with the crop, and their functional traits, in order to improve agroecosystem multifunctionality (Martin & Isaac, 2015, 2018). For instance, Blesh (2018) recently found that cover crop mixtures with complementary functional traits increased multifunctionality. Likewise, Damour, Navas, and Garnier (2018) proposed a trait-based approach framework which uses traits to select optimal plant community compositions and design agroecological cropping systems.

While the use of plant functional traits to improve agroecosystems multifunctionality has been conceptualized in several recent works, it has yet scarcely been put into practice in the field. Improving agroecosystems functioning through plant diversification mainly relies on gross functional classification as N-fixing ability or rooting type (Martin & Isaac, 2015 and citations therein). Finer characterization of plants introduced within agroecosystems and their impact on services and disservices provision would bestow more mechanistic keys to improve plant community composition management.

Improving agroecosystem multifunctionality by managing plant community composition represents an opportunity to increase the yield in cocoa agroforests (cAFS) from West Africa, where 70% of world cocoa is produced. Farmers introduce shade trees in cAFS to provide an understorey shade that reduces cocoa physiological stress, pest and diseases outbreaks (Andres et al., 2016). The shade tree species used in cAFS are very diverse and are selected both for their shade cover and for the provision of additional goods to local populations (firewood, fruit, timber, medicine), which may reach up to 60% of total cAFS plot revenue when adequately managed (Juhrbandt, Duwe, Barkmann, Gerold, & Marggraf, 2010). Nonetheless, shade trees can decrease cocoa growth and yield because of light interception (Sanchez, 1995). Yet, this potential disservice is not always observed (Wartenberg, Blaser, Roshetko, Noordwijk, & Six, 2019), and may be reduced in low fertility systems (Isaac, Ulzen-Appiah, Timmer, & Quashie-Sam, 2007). These studies suggest that (a) in poor soils, soil fertility increase with shade tree introduction may compensate for their light interception effects on cocoa yield (Isaac, Ulzen-Appiah, et al., 2007), and that (b) these effects are expected to vary strongly with shade tree species (Wartenberg et al., 2019). In this context, testing whether differences among shade trees' functional traits can affect cocoa yield and soil fertility while providing goods for farmers is of high interest.

Shade tree effects on cocoa yield, nutritional status and soil fertility has been studied both at the community (Blaser, Oppong, Yeboah, & Six, 2017; Niether, Schneidewind, Fuchs, Schneider, & Armengot, 2019) and at the species level (Isaac, Timmer, & Quashie-Sam, 2007; Wartenberg et al., 2019). Depending on the study, observed effects are explained by a variety of individual or community properties such as above-ground biomass (Isaac, Timmer, et al., 2007; Niether et al., 2019; Wartenberg et al., 2019), leaf biomass nutrient concentration (Isaac, Timmer, et al., 2007; Wartenberg et al., 2019) or canopy architecture and/or cover (Blaser et al., 2017; Isaac, Timmer, et al., 2007; Wartenberg et al., 2019). Nonetheless, to our knowledge, there is no study considering the specific relationships between shade tree functional traits and agroecosystem functioning in cAFS. Studies on natural ecosystems underline positive relationships between leaf litter N, P and Ca concentrations and soil nutrient availability (Hobbie, 2015), whereas soil C storage may mostly depend on plant below-ground traits such as root biomass, length, or mycorrhizal associations (Clemmensen et al., 2013; DuPont et al., 2014). However, whether the theoretical expectations that the traits of shade trees could be directly used to select for trees promoting greater cAFS multifunctionality remain to be tested.

We aim to determine whether shade tree traits could be used to identify the shade tree species with the highest improvement of cAFS multifunctionality components compared with unshaded cocoa. We first hypothesize that shade trees promote cAFS multifunctionality through increase of soil nutrient availability, C storage and goods production. We then hypothesize that soil nutrient availability and C content are positively influenced by shade trees' leaf litter nutrient concentration and root biomass respectively.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

The study was conducted in cocoa farms previously studied by Nijmeijer et al. (2019), in the villages of Bakoa and Guéfigué, in the Bokito district (4°30 N, 11°10 E) of Cameroon. This site is located in a forest–savanna transition zone, in a hilly area with gentle slopes at an altitude between 400 and 550 m a.s.l. Yearly average temperature is of 25°C, with annual rainfall between 1,300 and 1,400 mm and a main dry season between November and March (Jagoret, Michel-Dounias, Snoeck, Ngnogué, & Malézieux, 2012). Eight farms growing *Theobroma cacao* were selected, all established between 1950 and 2000 on savanna and located downhill. The eight farms selected were on Orthic Ferrasol, with similar soil texture (*c*. 12% clay, 17% silt and 71% sand).

We chose five associated shade tree species, with contrasting characteristics and uses, regularly occurring in these agroecosystems: *Canarium schweinfurthii* and *Dacryodes edulis* (fruit trees, evergreen), *Milicia excelsa* and *Ceiba pentandra* (timber trees, deciduous) and *Albizia adianthifolia* (N_2-fixing tree, deciduous). Individuals of each shade tree species were selected within the eight farms in order to assess (a) their individual attributes and (b) cocoa yield and soil functions under their canopy. Since the farms presented different tree species diversities, not all five species could be studied in each farm, resulting in a slightly unbalanced replication scheme. One individual tree by farm could be sampled for *Dacryodes* and *Ceiba*, whereas only seven, five and three individuals could be sampled across all eight farms for *Milicia*, *Canarium* and *Albizia* respectively (see Table S1 for more details). For each shade tree individual, a subplot of 10 m × 10 m was defined beneath the canopy in order to estimate maximum cocoa yield and to sample soil. In each of the eight cocoa farms, we also selected one subplot of cocoa trees (10 m × 10 m) away from the canopy of any shade tree (at least at a distance corresponding to the height of the nearest shade tree, i.e. between 17 m and 45 m), as the reference treatment (called 'unshaded'). Cocoa density was on average 14 ± 3 cocoa 100 m^{-2} across all the sampled subplots and did not differ between treatments (Table 2).

2.2 | Soil sampling and analyses

One composite sample of the 0–10 cm soil layer (2 kg dry soil) was prepared in May 2017 in each 10 × 10 m subplot, at intermediate distance between the shade tree trunk and its canopy edge, and from 10 locations always situated 1 m away from the base of cocoa trunks. Because only three *Albizia* trees were found across the eight farms, two composite samples were taken beneath each tree of this species (for a total of six subsamples).

Fresh, coarsely crumbled soil was used for a greenhouse plant bioassay in order to provide a general index of 'soil biochemical fertility' of the ecosystem. According to Dybzinski, Fargione, Zak, Fornara, and Tilman (2008), the greenhouse plant bioassay is an off-site assessment of soil fertility, relying on a short-term growth of seedlings of a model plant in soils collected beneath plant communities. Biomass production of the model plant in this controlled environment is considered as a direct response to soil fertility. Plant bioassay is thus only influenced by soil properties, while cocoa yield (also measured in this study) results from specific interactions between climate, soil, pest and disease pressure, shade trees and the structure of the cocoa stand. In our study, maize was chosen as the bioassay model plant for its short-term sensitivity to soil nutrient limitations, as shown by Sauvadet, Van den Meersche, et al. (2019). Briefly, 2-L pots were filled with 1.4 kg of soil at water holding capacity from each composite soil sample. Each pot was then sown with four seeds of maize (*Zea mays* L.) cv. CIRAD 412; only two plants were left in each pot after sprouting of the seeds. Maize seedlings were grown in a greenhouse (25°C average temperature, 81% average humidity) with manual watering to maintain soil at its water holding capacity. After 45 days of vegetative growth, shoots and roots of the plants were harvested, washed, dried at 65°C and weighed to obtain the above- and below-ground dry biomasses. Fresh, coarsely crumbled soil was also used for the measurement of soil inorganic N content. After extraction from 5 g (dry weight) of fresh soil, with 20 ml of a 1 M KCl solution, NO_3^- and NH_4^+ were determined by continuous flow colorimetry (TRAACS 2000; Bran and Luebbe).

After thorough mixing of the remaining soil, an aliquot of about 260 g (dry weight) of soil was sieved at 2 mm and air-dried before analysis of total C, total N, Olsen P, pH (H_2O) and basal C and N mineralization. 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). 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 after Olsen (1954). Briefly, 250 mg of dry soil was extracted with 5 ml of 0.5 M $NaHCO_3$ at pH 8.5 by 30 min shaking. The P within the extract was then measured according to the malachite green method (Rao et al., 2008). To measure soil C basal mineralization and nitrification, two aliquots of respectively 10 g and 25 g of dry soil were put in sealed jars after fixing their water content at a potential of pF 2.5 at 193 g H_2O/kg soil, then pre-incubated for 1 week at 20°C. At the end of the pre-incubation, NO_3^- was extracted from the 10 g dry soil aliquot with 40 ml of 1 M KCl, as the initial NO_3^- content. Jars containing the 25 g dry soil aliquot were then incubated at 28°C for 28 days with an alkali trap (15 ml of 0.5 M NaOH). The traps were changed at 7, 14 and 28 days and analysed for carbonates within the day. The remaining NaOH was titrated with 1 M HCl. The final soil NO_3^- was assessed after 28 days of incubation at 28°C of the 25 g jars in the same way.

2.3 | Trees and cocoa characteristics

Main attributes of individual shade trees and cocoa trees were characterized between August 2017 and March 2018. Succession guild, leaf habit and legume versus non-legume were documented after Saj, Durot, Mvondo Sakouma, Tayo Gamo, and Avana-Tientcheu (2017). Tree height was estimated using a rangefinder (TRUPULSE 360; Laser Technology Inc) for shade trees and a graduated stick for cocoa trees. Average crown diameter of each shade tree was estimated from four measurements of crown diameter done in cardinal and intercardinal directions (N–S, E–O, NO–SE, NE–SO) using a compass and a tape decameter, and canopy area was calculated accordingly. Diameter at breast height (DBH) of cocoa and shade trees was measured using a diameter tape. As differences in cocoa attributes (cocoa height, leaf nutrient content) between unshaded and shaded cocoa were not significant (data not shown), only unshaded cocoa attributes were considered.

For all subplots, fine roots (diameter <1 cm) were sampled in March 2018 in the 0–10 cm layer near each soil sampling location, using an 8-cm diameter root auger. Roots from each sampling point were washed, sorted out manually by species (cocoa vs. shade tree), dried for 1 week at 37°C, and weighed separately. Leaf litterfall was measured during 8 months (including the dry season) when most of the annual litterfall occurs (Nijmeijer et al., 2019). Briefly, one 0.45 m^2 collector was placed above each soil and fine root sampling location of each subplot. Leaf litter was collected every 15 days between September 2017 and March 2018 and dried at 37°C for 1 week. For each collector and sampling date, dry weight of the collected litter was measured by species, then summed through all the sampling period.

Cocoa estimated maximum yield was assessed according to Saj, Jagoret, et al. (2017), by counting every 7 weeks the number of pods on all the cocoa plants of every 10 × 10 m subplots, between June and December 2017 (four campaigns).

2.4 | Leaf litter traits

Leaf litter collected from each litterfall collector was then used to measure C, N, P, Ca, Mg, K and tannin content, Van Soest fractions and pH (H_2O). In order to have enough material to retain three replicates by species, 1.5 g composite samples were made by pooling the litter across the farms with the closest proximity (see Table S1 for further details).

Total C and N contents were determined by dry combustion using a CHN micro-analyzer (Carlo Erba NA 2000). After acid extraction, Ca, Mg, and K contents were determined by atomic absorption spectroscopy. Litter P content was analysed using Murphy and Riley reagent, and readings were done by colorimetry. Water-soluble compounds, hemicellulose, cellulose and lignin contents were obtained by the Van Soest method (Van Soest, 1963) with a Fibersac 24 fibre analyser (Ankom). Condensed tannins were measured according to the acid butanol method (Coq, Souquet, Meudec, Cheynier, & Hättenschwiler, 2010). For pH, 0.15 ml of each ground sample was shaken with 1.2 ml of demineralized water in an Eppendorf tube for 1 hr at 250 rpm. After centrifugation at 9,000 *g* for 5 min, pH of the supernatant solution was measured (Cornelissen et al., 2006). Lignocellulose Index (van Soest lignin/[van Soest hemicellulose + cellulose + lignin]) and Lignin:N ratio (van Soest lignin/leaf litter N content) were calculated.

Leaf N and P resorption efficiencies were estimated as described by Freschet, Cornelissen, Logtestijn, and Aerts (2010), by measuring the proportional difference between green leaves (collected from the crown of each shade tree and from cocoa plants in each unshaded area in October 2017) and leaf litter nutrient content. This ratio was corrected for fractional change in the measurement basis using lignin content as a reference value (Freschet et al., 2010).

2.5 | Data analyses

Litterfall and soil properties data from *Albizia* pseudo-replicates were averaged under each *Albizia* tree (i.e. one value by tree) for all the subsequent statistical analyses. In order to understand the impacts of cocoa–shade tree associations on cAFS functions, we first calculated the community weighted mean (CWM) leaf litter trait values above each soil sampling location, according to the formula (1):

$$\mathrm{CWM}_x = p_{\mathrm{cocoa}} \times t_{\mathrm{cocoa}} + p_{\mathrm{shade}} \times t_{\mathrm{shade}} \qquad (1)$$

where CWM_x is the CWM for trait *x*, *p* is the relative proportion of either cocoa or shade tree to the total leaf litterfall collected above each soil sampling location, and *t* is the leaf litter trait value for cocoa or shade tree for the corresponding location (Table S1). We first confirmed with linear mixed-effects models that there were no farm (replicate) effects on CWM traits and soil functions (Tables S3 and S4). CWM traits and soil functions differences between cocoa–shade tree associations were then assessed with generalized linear models coupled with the post hoc HSD Tukey tests. Finally, CWM traits were drawn in principal component analyses (PCAs) in order to differentiate the main characteristics of cocoa–shade tree associations between the studied species. These analyses, coupled with Pearson correlation matrix (Figure S2), allowed us to select the most pertinent CWM traits to explain soil functions in the subsequent analyses.

We considered the following agroecosystem functions: total soil organic C, total N, NO_3^-, NH_4^+, Olsen P content, soil pH, C mineralization, nitrification, bioassay, cocoa yield, as well as the type of production by shade trees: fruit or timber. An agroecosystem multifunctionality index was calculated under each treatment. Briefly, values of each function were standardized by its maximum across all treatments, and thus ranged between 0% and 100%. Multifunctionality was then defined as the number of standardized functions under each cocoa–shade tree association that had a value above a threshold T (30%, 50%, 70% and 90%). C mineralization, which is considered as a negative process relative to cAFS functioning, was inverted before being standardized. Fruit and timber production were either attributed a value of 0 (non-producing) or 100% (producing) under a given shade tree species (Figure S1).

Beforehand analyses showed that soil functions under cocoa–shade tree associations were better explained with CWM litter traits than tree height and DBH. Only CWM litter traits were hence used to assess the associations' impact on soil functions, with two complementary analyses. First, a redundancy analysis (RDA) was performed in order to visualize the global trends between the two sets of variables (the observed relationships between soil parameters and litter CWM were mostly linear, supporting the use of RDA). In a second time, each soil function responding significantly to shading was then regressed with all CWM traits. For each function, regression models were calculated with the *dredge* function from {MuMIn} r package. The parameters of the most parsimonious models (with lowest Akaike's information criterion; delta <2) were then used to calculate the relative importance (RI) of each trait using the *model.averaging* function {MuMIn} r package (Giam & Olden, 2016). The model averaging approach provides synthetic information on which functional traits contribute most consistently to the models with lowest AICs, making them the most likely contributors to the ecosystem function of interest. All statistical analyses were performed using R software (R-3.3.1) and the following packages: ggtern (Hamilton & Ferry, 2018), lme4 (Bates, Mächler, Bolker, & Walker, 2015), multcomp (Hothorn, Bretz, & Westfall, 2008), MuMIn (Barton & Barton, 2018), psych (Revelle, 2017), stats (R Core Team, 2018) and vegan (Oksanen et al., 2018).

3 | RESULTS

3.1 | Cocoa and shade tree characteristics

Shade tree species characteristics differed significantly between each other and from *Theobroma cacao*. Among shade trees, *Dacryodes* was the smallest and the thinnest species, while *Ceiba* was the tallest and widest species (Table 1). Litter N and P contents

TABLE 1 Shade tree and cocoa characteristics

	Reference	**Shade tree species**				
	Cocoa	***Canarium***	***Dacryodes***	***Milicia***	***Ceiba***	***Albizia***
Tree characteristics						
Succession guild	Shade tolerant	Pioneer	Pioneer	Pioneer	Pioneer	Non-pioneer light demander
Leaf habit	Semi-deciduous	Evergreen	Evergreen	Deciduous	Deciduous	Deciduous
Legume versus non-legume	Non-legume	Non-legume	Non-legume	Non-legume	Non-legume	Legume
Height (m)	6 ± 0 c	**29 ± 2 a**	**12 ± 3 b**	**31 ± 4 a**	**31 ± 4 a**	**17 ± 9 b**
DBH (cm)	13 ± 4 d	**119 ± 27 b**	**36 ± 14 c**	**129 ± 61 b**	**321 ± 83 a**	**86 ± 24 b**
Canopy area (m^2)	Na	446 ± 211 a	102 ± 65 b	252 ± 260 ab	513 ± 314 a	411 ± 238 a
Leaf N resorption efficiency (%)	51 ± 3 ab	**41 ± 5 cd**	53 ± 1 a	**34 ± 5 d**	44 ± 4 bc	**21 ± 1 e**
Leaf P resorption efficiency (%)	73 ± 2 a	**31 ± 17 b**	44 ± 6 ab	52 ± 10 ab	**38 ± 10 b**	**36 ± 19 b**
Leaf litter traits						
N (mg/g DM)	10.5 ± 0.5 cd	9.6 ± 0.8 d	12.2 ± 1.2 bcd	15.1 ± 4.6 bc	**16.1 ± 0.7 b**	**30.2 ± 6.8 a**
P (mg/g DM)	0.6 ± 0.1 c	0.8 ± 0.2 bc	1.0 ± 0.2 abc	1.0 ± 0.1 abc	**1.3 ± 0.2 a**	**1.2 ± 0.5 ab**
K (mg/g DM)	5.8 ± 1.2 b	5.2 ± 0.5 b	7.4 ± 0.3 b	**14.2 ± 5.9 a**	5.9 ± 0.9 b	6.9 ± 2.1 b
Ca (mg/g DM)	17.7 ± 1.7 b	19.9 ± 3.1 b	14.6 ± 1.9 b	18.2 ± 4.4 b	**32.7 ± 5.0 a**	15.4 ± 1.7 b
Mg (mg/g DM)	7.0 ± 1.8 a	**3.2 ± 0.8 cd**	**2.7 ± 0.5 cd**	**4.7 ± 0.6 bc**	5.1 ± 0.4 ab	**2.2 ± 0.3 d**
pH (H_2O)	7.0 ± 0.0 a	**5.9 ± 0.3 b**	**4.8 ± 0.3 c**	7.1 ± 0.2 a	7.0 ± 0.2 a	6.7 ± 0.2 a
Soluble VS (mg/g DM)	209 ± 10 bc	162 ± 18 c	**280 ± 27 a**	224 ± 34 ab	157 ± 12 c	**77 ± 33 d**
Cellulose VS (mg/g DM)	149 ± 56 ab	127 ± 8 b	130 ± 34 ab	112 ± 5 b	116 ± 11 b	195 ± 23 a
Hemicellulose VS (mg/g DM)	214 ± 23 a	220 ± 48 a	178 ± 20 a	236 ± 53 a	272 ± 35 a	260 ± 48 a
Lignin VS (mg/g DM)	428 ± 46 a	491 ± 43 a	412 ± 42 a	428 ± 92 a	455 ± 48 a	468 ± 63 a
Tannin (mg/g DM)	25 ± 7 b	**127 ± 17 a**	47 ± 13 b	**7 ± 2 c**	39 ± 14 b	**6 ± 4 c**
Lignocellulose Index (LCI)	54 ± 6 a	59 ± 5 a	57 ± 6 a	55 ± 10 a	54 ± 5 a	51 ± 5 a
Lignin:N ratio	41 ± 6 a	51 ± 8 a	34 ± 5 a	32 ± 18 ab	28 ± 2 ab	**16 ± 5 b**

Note: Significant differences were tested by GLM followed by Tukey HSD post hoc tests and bear different letters for $p < .05$. LCI represent the proportion of lignin within the cell wall. Shade tree species characteristics are emphasized in bold when different from the reference cocoa. Abbreviation: VS, van Soest.

TABLE 2 Leaf litterfall and fine root (diameter < 1 cm) biomass under the different associations

		Under shade trees				
	Unshaded	***Canarium***	***Dacryodes***	***Milicia***	***Ceiba***	***Albizia***
Cocoa density (plant 100/m^2)	14 ± 3 ab	14 ± 3 ab	14 ± 2 ab	13 ± 2 ab	17 ± 3 a	11 ± 5 b
Fine root biomass (kg DM/m^2)						
From cocoa	0.16 ± 0.06 a	0.15 ± 0.08 a	0.12 ± 0.08 a	0.18 ± 0.06 a	0.15 ± 0.11 a	0.08 ± 0.02 a
From shade tree	0.03 ± 0.04 a	0.02 ± 0.02 a	0.05 ± 0.04 a	0.06 ± 0.05 a	0.02 ± 0.03 a	0.03 ± 0.01 a
Total	0.19 ± 0.08 a	0.18 ± 0.07 a	0.17 ± 0.11 a	0.24 ± 0.05 a	0.17 ± 0.10 a	0.10 ± 0.02 a
Leaf litterfall (kg DM/m^2)						
From cocoa	0.28 ± 0.09 a	**0.15 ± 0.07 b**	**0.13 ± 0.04 b**	**0.13 ± 0.08 b**	**0.15 ± 0.07 b**	**0.11 ± 0.03 b**
From shade tree	0.02 ± 0.04 c	**0.26 ± 0.06 b**	**0.34 ± 0.14 ab**	**0.47 ± 0.17 a**	**0.36 ± 0.14 ab**	**0.36 ± 0.04 ab**
Total	0.31 ± 0.08 b	0.41 ± 0.07 ab	**0.47 ± 0.13 a**	**0.60 ± 0.21 a**	**0.51 ± 0.14 a**	0.46 ± 0.03 ab

Note: Significant differences were tested by GLM followed by Tukey HSD post hoc tests and bear different letters for $p < .05$. Values under shade tree species are emphasized in bold when different from the unshaded treatment.

were higher for the deciduous (*Milicia*, *Ceiba* and *Albizia*) than for the evergreen species (*Canarium* and *Dacryodes*), the latter being at the same levels as cocoa. Cocoa had higher leaf N and P resorption efficiencies than shade trees (except for *Dacryodes* N resorption), and higher or similar litter Mg content and pH. Litter from the evergreen trees had lower pH (<6), higher tannin content and Lignin:N ratio than litter from the deciduous shade tree species (Table 1). Among the deciduous species, litter from N_2-fixing *Albizia* had the highest N content, and the lowest lignin:N ratio, Mg and tannin contents.

Association with shade trees affected strongly leaf litterfall but did not modify patterns of fine root biomass significantly (Table 2). Cocoa litterfall was decreased by half under shade trees, regardless of the shade species considered. Shade tree litterfall varied between species and ranged from 2.6 to 4.7 t DM/ha (Table 2). The total amount of litterfall was lower for unshaded cocoa and cocoa shaded with *Canarium* than for the other associations. Cocoa leaf litterfall amounted for only 21%–36% of total leaf litterfall under shade trees (Table 2). As a result, community weighted mean litter traits in association were thus mostly driven by the characteristics of the shade tree species (Table S2).

Community weighted mean litter quality was improved in cocoa–deciduous species associations with increased litter pH and decreased lignin:N ratio (Figure 1a; Table S2), as well as increased litter N, P, K, and Ca contents (with the steepest increase of Ca content with *Ceiba* and N content *with Albizia*; Figure 1b; Table S2). Association with evergreen species decreased the averaged litter quality through an increase of tannin content and a decrease in litter pH and Mg content (Figure 1; Table S2).

3.2 | cAFS multifunctionality

Shade trees greatly altered the agroecosystem functions linked to soil fertility. Soil NO_3^- and Olsen P content, and the biomass produced by the maize bioassay were significantly improved under the influence of deciduous trees (Table 3). Soil pH was only improved under *Milicia* and *Ceiba*, while soil under *Albizia* was acidified compared to the other associations (Table 3). Only association with *Ceiba* led to a significant increase in soil C and N contents. Overall, shade trees had relatively little impact on soil C mineralization, nitrification and cocoa yield.

Agroecosystem multifunctionality was higher under cocoa–shade tree associations than under unshaded cocoa, yet depended on the shade tree species and the threshold considered (Figure 2). These improvements were more obvious at the threshold value of 50%, where multifunctionality index increased from 2 for unshaded cocoa, to 4 for associations with *Dacryodes*, 6 with *Canarium* and *Albizia* and 8 for associations with the two timber trees. Higher multifunctionality under the deciduous trees as compared to unshaded cocoa corresponded to higher NO_3^-, Olsen P content and bioassay production, as well as the additional fruit or timber production of all shade trees except *Albizia* (Figure S1). Impacts of shade trees on multifunctionality decreased for higher threshold values (70% and 90%) and became null for *Albizia* relatively to unshaded cocoa. Multifunctionality improvement under the other shade trees at the 90% threshold corresponded respectively to edible fruit production under *Canarium* and *Dacryodes*, and to timber production and soil pH increase under *Milicia* and *Ceiba* (Figure 2; Figure S1).

3.3 | Relationships between cocoa–shade tree association characteristics and soil functions

The model averaging and redundancy analyses both suggested that litter N, Ca, soluble and tannin content were among the most important contributors to the changes in soil functions (Figure 3a; Table 4). Cocoa association with the two timber species, *Ceiba* and *Milicia*, increased total litterfall, CWM litter P and Ca content, and were linked

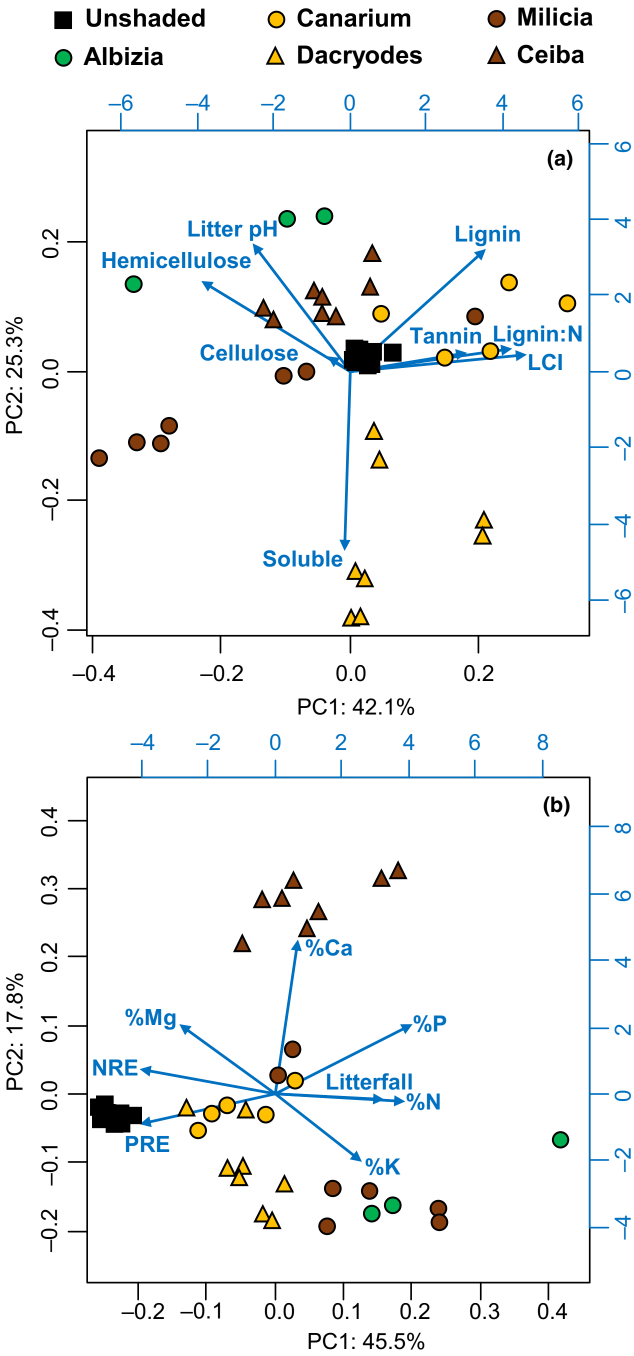

FIGURE 1 Principal component analyses of (a) averaged leaf litter C quality and (b) leaf nutrient contents and litterfall. Only variables significantly impacted by shade tree species are represented. %N, P, K, Ca, Mg: leaf litter N, P, K, Ca, Mg content; LCI: Litter lignocellulose Index; NRE: leaf N resorption efficiency; PRE: leaf P resorption efficiency

with higher soil NO_3^-, Olsen P content, bioassay production and soil C and N content (Figure 3). Cocoa association with *Albizia* led to litter N enrichment, linked to increased soil NH_4^+ and NO_3^- content but also to a decrease of soil pH. Association with evergreen *Canarium* and *Dacryodes* had limited effects both on CWM litter traits and agroecosystem functions changes from unshaded cocoa (Figure 3b). The model averaging approach highlighted most particularly the role of litter Ca content, which contributed to most of the soil functions considered (RI > 0.64 for soil C, N, NO_3^- content, soil pH and bioassay production). Furthermore, litter tannin content was negatively associated with soil NH_4^+ and Olsen P content (RI of 0.96 and 0.76, respectively), while litter soluble content was negatively associated with NH_4^+ and litter N, P, K and Ca were associated with soil pH.

4 | DISCUSSION

Shade tree management in cocoa plantation has been discussed for decades regarding their benefits and disadvantages for cAFS (Andres et al., 2016; Blaser et al., 2017; Niether et al., 2019; Sanchez, 1995). The microclimatic regulation introduced by shading decreases diseases' outbreaks, which are known to hamper both cocoa yield and sustainability (Andres et al., 2016). However, light interception by shade trees decreases cocoa photosynthesis activity and may lead to yield decrease, as reviewed by Sanchez (1995). However, this decrease may not occur in systems with poor soils, where nutrient availability may be more limiting to cocoa production than light (Isaac, Ulzen-Appiah, et al., 2007). Here we demonstrated that several species of shade trees were able to improve contrasting aspects of soil fertility, without affecting cocoa yield. This result is in line with recent findings from Wartenberg et al. (2019). The five shade tree species studied generally improved nutrient restitution from litter, through increased litterfall and litter quality over the year, as compared with cocoa alone, and had positive effects on a range of soil functions linked to soil fertility. Together, these results suggest that the putative negative impact of shading has been compensated here by the relief of soil nutrient limitation for cocoa production and/or improved cocoa nutrient use efficiency under their canopy (Niether et al., 2019). The lack of increase in cocoa production under shade trees suggests nonetheless that light would have become a limiting resource, setting an upper threshold to the benefits of such improved soil nutrient conditions. Finally, our results suggest that, in places where soils are naturally poor or impoverished by decades of cocoa monocultures with low input levels, such as in Côte d'Ivoire or Ghana, the plantation of shade trees is likely to allow a gain in sustainability since positive effects on soil nutritional status would counterbalance the effects of competition for light.

The number of soil functions improved under cocoa–shade tree associations varied greatly between shade tree species, as driven by differences in litter quality. Shade tree litter constitutes indeed a significant source of organic matter inputs in most cAFS, with important effects on carbon and nutrient cycling (Nesper, Kueffer, Krishnan, Kushalappa, & Ghazoul, 2019). This was particularly true in conditions of poor sandy soil. Out of all the parameters tested, CWM litter Ca and, to a lesser extent, tannin content had the highest explanatory weights for many soil functions. In our systems, these two litter traits, which typically drive litter decomposability and turnover rate in soils (Hobbie, 2015; Kraus, Dahlgren, & Zasoski, 2003), proved to be of higher significance for soil fertility and C sequestration than

TABLE 3 Soil functions under the different associations

		Under shade trees				
	Unshaded	*Canarium*	*Dacryodes*	*Milicia*	*Ceiba*	*Albizia*
Soil C (g C/kg soil)	15.4 ± 5.3 b	17.8 ± 5.0 ab	16.8 ± 6.5 ab	18.9 ± 3.9 ab	**23.5 ± 5.5 a**	13.9 ± 2.8 ab
Soil N (g N/kg soil)	1.2 ± 0.4 b	1.4 ± 0.4 ab	1.2 ± 0.4 b	1.5 ± 0.3 ab	**1.9 ± 0.5 a**	1.1 ± 0.2 b
NH_4^+ (mg N/kg soil)	4.6 ± 3.0 b	2.2 ± 0.8 b	2.6 ± 0.9 b	2.7 ± 1.0 b	2.6 ± 0.9 b	**9.6 ± 4.0 a**
NO_3^- (mg N/kg soil)	6.1 ± 1.6 c	7.0 ± 1.2 abc	7.1 ± 2.3 bc	**10.9 ± 1.9 a**	**10.5 ± 3.1 a**	**10.5 ± 3.6 ab**
Olsen P (mg P/kg soil)	9.3 ± 5.3 b	10.9 ± 2.1 ab	14.4 ± 5.7 ab	**17.2 ± 5.7 a**	**18.7 ± 7.2 a**	**21.0 ± 10.6 a**
pH H_2O	6.6 ± 0.1 b	6.7 ± 0.1 b	6.6 ± 0.1 b	**7.1 ± 0.2 a**	**7.2 ± 0.1 a**	**6.0 ± 0.3 c**
Bioassay (g DM produced per plant)	1.5 ± 0.6 b	1.3 ± 0.5 b	1.8 ± 0.6 b	2.1 ± 0.5 ab	**2.7 ± 0.8 a**	2.1 ± 0.4 ab
Cocoa yield (pods per tree)	22 ± 7 a	26 ± 9 a	21 ± 5 a	24 ± 11 a	22 ± 6 a	25 ± 16 a
C mineralization (mg C kg^{-1} soil day^{-1})	17.7 ± 7.8 a	22.2 ± 15.1 a	8.2 ± 5.5 a	11.8 ± 5.8 ab	16.5 ± 7.7 a	13.7 ± 5.4 a
Nitrification (mg N kg^{-1} soil day^{-1})	1.7 ± 0.7 a	2.4 ± 1.4 a	1.3 ± 0.6 a	1.3 ± 0.6 a	2.0 ± 0.5 a	1.4 ± 0.1 a

Note: Significant differences were tested by GLM followed by Tukey HSD post hoc tests and bear different letters for $p < .05$. Values under shading are emphasized in bold when different from unshaded treatment.

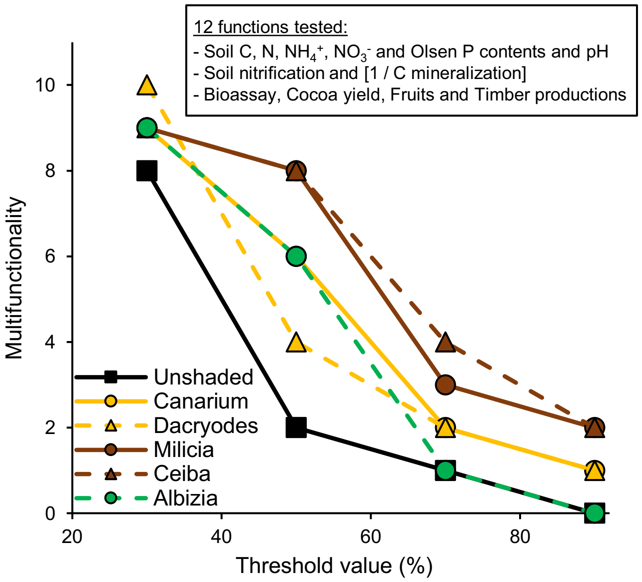

FIGURE 2 Shade tree association effects on soil multifunctionality. Each of the 12 functions tested was standardized by its maximal value, then compared to the threshold values of 0%, 30%, 50%, 70% and 90%

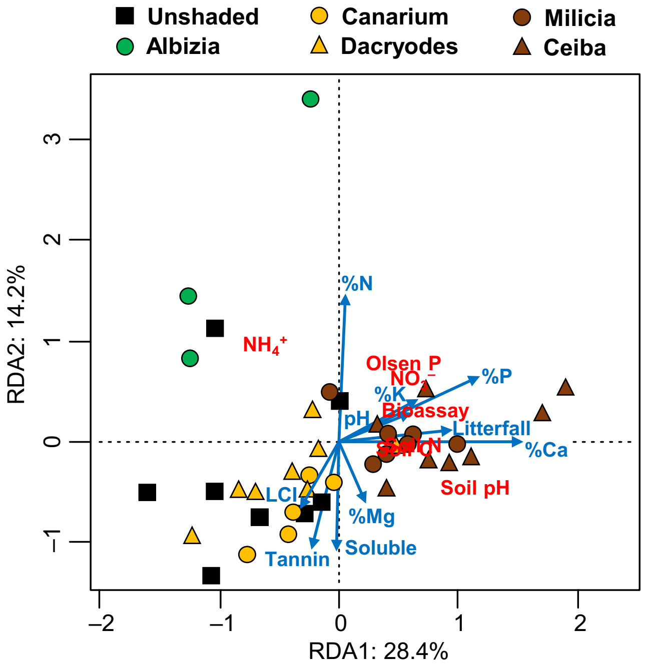

FIGURE 3 Redundancy analysis of soil functions (in red) constrained by cocoa–shade tree association characteristics (in blue). Only the tree characteristics and soil functions selected in the models from Table 4 were used to build the RDA. %N, P, K, Ca, Mg: leaf litter N, P, K, Ca, Mg content

classical indices of litter N and P content, amount of above-ground litterfall and below-ground fine root biomass.

Associations with the evergreen fruit trees *Canarium* and *Dacryodes* led to the lowest improvement of soil functions compared to the unshaded reference. These were the species with the closest characteristics to cocoa (leaf life span strategy, litter nutrient content) and the lowest nutrient restitution levels by litterfall. Furthermore, the high recalcitrance of *Canarium* and *Dacryodes* litters (high tannins content, low pH) may also have limited litter nutrient release and availability to plants due to their low turnover rate (Hättenschwiler, Coq, Barantal, & Handa, 2011; Hobbie, 2015). In contrast, the three deciduous tree species exhibited more contrasting properties compared to cocoa, and generally led to a more substantial improvement of soil fertility. More specifically, the increased soil pH induced by the associations with the deciduous

TABLE 4 Model averaging of soil functions by cocoa–shade tree association litterfall and community weighted mean litter traits, performed on centred-reduced data. For each function, the relative importance (RI) was estimated for all variables

	Soil C	Soil N	NH_4^+	NO_3^-	Olsen P	Bioassay	Soil pH
Litterfall	0.20	0.23	0.35	0.19	0.24	*0.54*†	0.26
Soluble	0.24	0.21	**1.00***	0.47	0.39	0.22	0.21
Tannins	0.23	0.24	**0.96****	0.24	*0.76*†	0.51	0.38
LCI	0.24	0.26	0.37	0.22	0.22	0.21	0.27
Litter pH	0.22	0.20	0.56	0.36	0.29	0.24	0.19
%N	0.27	0.22	0.26	0.39	0.37	0.26	**0.99*****
%P	0.33	0.24	0.49	0.50	0.42	0.28	**0.88****
%K	0.20	0.21	0.29	0.72	0.25	0.29	**0.99*****
%Ca	**0.85***	**0.98*****	**0.68***	*0.64*†	0.48	**0.96****	**1.00*****
%Mg	0.20	0.20	0.30	0.28	0.68	0.36	0.19

Note: RI varies from 0 to 1 and represents the sum of the Akaike weights of the models in which each variable is used. RI represented in red and blue corresponds to significant variables ($^{\dagger}p < .10$; $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$) with positive and negative coefficient respectively (see Table S6 for further details).

timber tree species (*Milicia* and most particularly *Ceiba*), could be at least partly attributed to the higher amount of Ca and Mg restituted by their litter (Reich et al., 2005). In addition, *Milicia* is an oxalic species known to accumulate calcium carbonate in soil (Cailleau, Braissant, Dupraz, Aragno, & Verrecchia, 2005). In contrast, association with *Albizia* decreased soil pH to lower levels than cocoa alone. Soil acidification is often observed in legume plantations and could be caused by their N_2-fixing activity (Jensen & Hauggaard-Nielsen, 2003). Soil pH decrease under legume can also result in soil P release (Hinsinger, Plassard, Tang, & Jaillard, 2003) and could be responsible to the high Olsen P content under *Albizia* associations. Finally, the positive impact of associations with deciduous species on soil N and P availability may be linked to the high quality of the deciduous species litters (low lignin:N ratio and tannin content) as much as to its high N and P content. Indeed, despite similar N and P content, litter from the evergreen tree *Dacryodes*, with lower overall quality, improved less soil N and P availability than the deciduous tree species.

Our finding that litter low recalcitrance is associated with higher soil C sequestration is in line with the recent paradigm that plant species with rapid litter decomposition may be associated with relatively greater accumulation of soil C (Hobbie, 2015). However, this process may be hampered by soil acidification by legume N_2-fixing activity in the case of *Albizia* association. Indeed, high litter Ca content generally favours litter consumption by soil fauna (Holdsworth, Frelich, & Reich, 2008) which is increasingly considered as favouring soil C storage (Berg, 2000, 2014). Secondary transformations during the production of decomposer necromass and faeces favour organic matter mixing and binding with soil mineral matrix and hence its stabilization (Lehmann & Rillig, 2015). Despite increasing recognition of the important role of fine root biomass and turnover in soil C storage (Clemmensen et al., 2013; DuPont et al., 2014), the similar fine-root biomass observed here could not explain the differences in soil C content. In order to adequately capture root carbon and nutrient inputs to the soil (Matamala, Gonzàlez-Meler, Jastrow, Norby, & Schlesinger, 2003), further studies will need to go beyond classical measurements of standing biomass and to focus more specifically on root turnover, exudation rates and mycorrhizal associations.

Overall, cocoa–*Ceiba* was the association that increased most cAFS multifunctionality, along with cocoa–*Milicia* associations. Litter from these shade tree species were both characterized by high Ca restitution levels in litterfall and low litter recalcitrance, and presented overall the highest level of dissimilarity with cocoa litter. This trend may suggest that shade trees that differ most from cocoa may provide stronger benefits in cAFS. In a context where tree species should be selected for (a) the desired shade cover and production of goods for local population, with (b) traits favouring soil multifunctionality (i.e. low litter recalcitrance and high nutrient content), our results suggest that the selection of a small number of tree species may provide better results than including a large range of species. Nonetheless, multifunctionality in our study was mainly centered on soil functions. The relative importance of other goods provision for local population, including timber and fruit, should not be overlooked as they are valued by farmers (Jagoret, Kwesseu, Messie, Michel-Dounias, & Malézieux, 2014) and may constitute a fair share of total cAFS plot revenue when adequately managed (Juhrbandt et al., 2010). Furthermore, our results once again underline the empirical knowledge of farmers on the impact of their associations and the trade-offs they sometimes imply (Saj, Durot, et al., 2017; Saj, Jagoret, et al., 2017). In this respect, long-term studies integrating socio-economical aspects of cocoa and goods' production, together with soil fertility indicators are further needed to meaningfully attribute a weighting to each component of the agroecosystem functioning for profitable and sustainable management. Considering other benefits potentially associated with maintaining high tree diversity at the field scale, such as complementarity in resource use (Gross et al., 2017), stability of ecosystem functioning in conditions of climate change (Eisenhauer et al., 2018) and their resistance to perturbations (Loreau & de Mazancourt, 2013) would also be useful.

5 | CONCLUSIONS

Our study highlighted the benefits of introducing shade trees on agroecosystem multifunctionality on poor sandy soils, where the balance between lower light availability and higher soil nutrient availability maintain similar cocoa yield. Such benefits ranged from improved soil fertility to higher soil C sequestration. Nonetheless, multifunctionality improvement from unshaded cocoa strongly depended on the tree species, with lower effects of the evergreen fruit trees *Canarium* and *Dacryodes*, intermediate improvements by the legume tree *Albizia* and strong improvement by the two timber trees *Milicia* and *Ceiba*. Our results suggest that the traits of some shade trees were too similar to those of cocoa to induce consistent change in soil functioning. High leaf litter Ca and low tannin contents of shade trees appeared particularly important to improve the local poor sandy soil conditions. These results underline the need to go beyond classical indicators of litter quality and soil functioning and the importance to consider aspects of long-term litter cycling in assessments of agroecosystem multifunctionality.

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AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology; M.S., G.T.F., J.-D.E., S.E. and J.-M.H. collected the data; M.S. analysed the data; M.S., S.S., G.T.F., T.B., P.T. and J.-M.H. led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.dz08kprt6 (Sauvadet, Saj, et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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