

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

Marie Sauvadet, Stéphane Saj, Grégoire T. Freschet, Jean-Daniel Essobo, Seguy Enock, Thierry Becquer, Philippe Tixier, Jean-Michel Harmand

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25 **Abstract**

- 26 1. Manipulating plant functional diversity to improve agroecosystem multifunctionality is a central
27 challenge of agricultural systems worldwide. In cocoa agroforestry systems (cAFS), shade trees
28 are used to supply many services to farmers, yet their impact on soil functioning and cocoa
29 yields is likely to vary substantially among tree species.
- 30 2. Here, we compared the impact of five shade tree species (*Canarium schweinfurthii* (Canarium),
31 *Dacryoides edulis* (Safou), *Milicia excelsa* (Iroko), *Ceiba pentandra* (Kapok tree), *Albizia*
32 *adanthifolia* (Albizia)) and unshaded conditions on the functioning of poor sandy savannah soils
33 within eight cocoa farms in Central Cameroon. We assessed the effects of plant functional traits,
34 leaf litterfall and fine root biomass on a range of soil functions and on cocoa yield.
- 35 3. Shade trees generally improved soil pH, NH_4^+ , NO_3^- and Olsen P content, biomass production
36 of bioassays, and soil total C and N content, while leaving cocoa yields unchanged. However,
37 these effects varied largely among species. Improvements of soil functions were low under the
38 two fruit trees (*Canarium* and *Dacryodes*), medium under the legume tree *Albizia*, and high
39 under the two timber trees (*Milicia* and *Ceiba*). Low litter recalcitrance was most strongly
40 associated with increases in soil fertility indicators such as N and P availability, whereas soil C
41 and N content increased with litter Ca restitution.
- 42 4. *Synthesis and applications.* We demonstrate that cocoa agroforest multifunctionality is
43 substantially influenced by the functional traits of shade tree species. Shade tree species with
44 the most dissimilar traits to cocoa (cocoa showing the lowest leaf litter quality) showed the
45 largest improvement of soil functions. Therefore, selection of shade trees based on their
46 functional traits appears as a promising practice to adequately manage soil functioning. In order
47 to fully assess the beneficial role of shade trees in these agroecosystems, future research will
48 need to extend this approach to other belowground traits and other aspects of multifunctionality
49 such as long-term cocoa health and yield.

50
51 **Keywords:** agroecosystem multifunctionality, agroforestry, litter recalcitrance, cacao tree, fertility, plant
52 functional traits, shade type, soil functions

53 **French abstract**

- 54 1. Manipuler la diversité fonctionnelle végétale pour améliorer la multifonctionnalité des
55 agroécosystèmes est un défi majeur à l'échelle mondiale. Dans les systèmes agroforestiers à
56 base de cacaoyers, les arbres d'ombrage sont utilisés pour fournir de nombreux services aux
57 agriculteurs. Cependant, leur impact sur le fonctionnement du sol et le rendement des
58 cacaoyers est susceptible de varier considérablement d'une espèce à l'autre.
- 59 2. Nous avons comparé les effets de cinq espèces d'arbres d'ombrage (*Canarium schweinfurthii*
60 (*Canarium*), *Dacryoides edulis* (Safoutier), *Milicia excelsa* (Iroko), *Ceiba pentandra* (Fromager
61 ou Kapokier), *Albizia adianthifolia* (*Albizia* d'Afrique de l'Ouest) et d'un témoin sans arbres sur
62 le fonctionnement du sol dans huit exploitations cacaoyères sur sol pauvre au Centre du
63 Cameroun. Nous avons ensuite relié les traits fonctionnels des arbres et des litières aériennes
64 ainsi que la biomasse de racines fines à plusieurs fonctions du sol et au rendement des
65 cacaoyers.
- 66 3. Les arbres d'ombrage ont globalement amélioré le pH, les teneurs en NH_4^+ , NO_3^- , P Olsen,
67 Carbone et Azote totaux du sol, et les biomasses produites en bioessais, tout en maintenant
68 les rendements de cacao. Toutefois, ces effets ont considérablement varié d'une espèce à
69 l'autre. Ces améliorations étaient de faible amplitude sous les deux arbres fruitiers (*Canarium*
70 et *Dacryodes*), moyennes sous la légumineuse *Albizia* et élevées sous les deux arbres de bois
71 d'œuvre (*Milicia* et *Ceiba*). La faible récalcitrance des litières aériennes a été associée à
72 l'amélioration de la biodisponibilité en N et P du sol, tandis que les teneurs en C et N totaux du
73 sol ont augmenté avec la quantité de Ca restituée par les litières aériennes.
- 74 4. *Synthèse et applications*. Nous démontrons que la multifonctionnalité des systèmes
75 agroforestiers à base de cacaoyers est fortement liée aux traits fonctionnels des espèces
76 d'arbres d'ombrage qui les composent. Les espèces d'ombrage présentant les traits les plus
77 dissemblables des cacaoyers (les cacaoyers présentant la qualité de litière aérienne la plus
78 faible) améliorent davantage la multifonctionnalité du sol que les autres espèces. La sélection
79 des arbres d'ombrage basé sur leurs traits fonctionnels apparaît donc comme une pratique
80 prometteuse pour améliorer le fonctionnement du sol. Afin d'évaluer pleinement le rôle
81 bénéfique des arbres d'ombrage sur ces agroécosystèmes, les futures recherches devront

82 élargir cette approche à d'autres traits souterrains et à d'autres composantes de la
83 multifonctionnalité, telles que la santé et le rendement à long terme des cacaoyers.

84 **1. Introduction**

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

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

104 Improving agroecosystem multifunctionality by managing plant community composition represents an
105 opportunity to increase the yield in cocoa agroforests (cAFS) from West Africa, where 70% of world
106 cocoa is produced. Farmers introduce shade trees in cAFS to provide an understory shade that reduces
107 cocoa physiological stress, pest and diseases outbreaks (Andres et al., 2016). The shade tree species
108 used in cAFS are very diverse and are selected both for their shade cover and for the provision of
109 additional goods to local populations (firewood, fruit, timber, medicine), which may reach up to 60% of
110 total cAFS plot revenue when adequately managed (Juhrbandt, 2010). Nonetheless, shade trees can
111 decrease cocoa growth and yield because of light interception (Sanchez 1995). Yet, this potential
112 disservice is not always observed (Wartenberg et al., 2019), and may be reduced in low fertility systems
113 (Isaac et al., 2007a). These studies suggest that (i) in poor soils, soil fertility increase with shade tree

114 introduction may compensate for their light interception effects on cocoa yield (Isaac et al., 2007a), and
115 that (ii) these effects are expected to vary strongly with shade tree species (Wartenberg et al., 2019). In
116 this context, testing whether differences among shade trees functional traits can affect cocoa yield and
117 soil fertility while providing goods for farmers is of high interest.

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

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

138 **2. Materials and methods**

139

140 *2.1. Site description and experimental design*

141 The study was conducted in cocoa farms previously studied by Nijmeijer et al. (2019), in the villages of
142 Bakoa and Guéfigué, in the Bokito district (4°30 N, 11°10 E) of Cameroon. This site is located in a forest-
143 savannah transition zone, in a hilly area with gentle slopes at an altitude between 400 and 550 m a.s.l.
144 Yearly average temperature is of 25°C, with annual rainfall between 1300 and 1400 mm and a main dry

145 season between November and March (Jagoret et al., 2012). Eight farms growing *Theobroma cacao*
146 were selected, all established between 1950 and 2000 on savannah and located downhill. The eight
147 farms selected were on Orthic Ferrasol, with similar soil texture (approx. 12% clay, 17% silt and 71%
148 sand).

149 We chose five associated shade tree species, with contrasting characteristics and uses, regularly
150 occurring in these agroecosystems: *Canarium schweinfurthii* and *Dacryodes edulis* (fruit trees,
151 evergreen), *Milicia excelsa* and *Ceiba pentandra* (timber trees, deciduous), and *Albizia adianthifolia* (N₂-
152 fixing tree, deciduous). Individuals of each shade tree species were selected within the eight farms in
153 order to assess (i) their individual attributes and (ii) cocoa yield and soil functions under their canopy.
154 Since the farms presented different tree species diversities, not all five species could be studied in each
155 farm, resulting in a slightly unbalanced replication scheme. One individual tree by farm could be sampled
156 for *Dacryodes* and *Ceiba*, whereas only seven, five and three individuals could be sampled across all
157 eight farms for *Milicia*, *Canarium* and *Albizia*, respectively (see Table S1 for more details). For each
158 shade tree individual, a subplot of 10 m x 10 m was defined beneath the canopy in order to estimate
159 maximum cocoa yield and to sample soil. In each of the eight cocoa farms, we also selected one subplot
160 of cocoa trees (10 m x 10 m) away from the canopy of any shade tree (at least at a distance
161 corresponding to the height of the nearest shade tree, *i.e.* between 17 m and 45 m), as the reference
162 treatment (called “unshaded”). Cocoa density was on average 14±3 cocoa 100 m² across all the
163 sampled subplots and did not differ between treatments (Table 2).

164

165

2.2. Soil sampling and analyses

166 One composite sample of the 0-10 cm soil layer (2 kg dry soil) was prepared in May 2017 in each
167 10 x 10 m subplot, at intermediate distance between the shade tree trunk and its canopy edge, and from
168 10 locations always situated 1 m away from the base of cocoa trunks. Because only three *Albizia* trees
169 were found across the eight farms, two composite samples were taken beneath each tree of this species
170 (for a total of six sub-samples).

171 Fresh, coarsely crumbled soil was used for a greenhouse plant bioassay in order to provide a general
172 index of “soil biochemical fertility” of the ecosystem. According to Dybziński et al. (2008), the greenhouse
173 plant bioassay is an off-site assessment of soil fertility, relying on a short-term growth of seedlings of a
174 model plant in soils collected beneath plant communities. Biomass production of the model plant in this
175 controlled environment is considered as a direct response to soil fertility. Plant bioassay is thus only

176 influenced by soil properties, while cocoa yield (also measured in this study) results from specific
177 interactions between climate, soil, pest and disease pressure, shade trees, and the structure of the
178 cocoa stand. In our study, maize was chosen as the bioassay model plant for its short-term sensitivity
179 to soil nutrient limitations, as shown by Sauvadet et al. (2019). Briefly, 2-L pots were filled with 1.4 kg of
180 soil at water holding capacity from each composite soil sample. Each pot was then sown with four seeds
181 of maize (*Zea mays* L.) cv. CIRAD 412; only two plants were left in each pot after sprouting of the seeds.
182 Maize seedlings were grown in a greenhouse (25°C average temperature, 81% average humidity) with
183 manual watering to maintain soil at its water holding capacity. After 45 days of vegetative growth, shoots
184 and roots of the plants were harvested, washed, dried at 65°C, and weighed to obtain the above- and
185 below-ground dry biomasses. Fresh, coarsely crumbled soil was also used for the measurement of soil
186 inorganic N content. After extraction from 5 g (dry weight) of fresh soil, with 20 mL of a 1 M KCl solution,
187 NO_3^- and NH_4^+ were determined by continuous flow colorimetry (TRAACS 2000, Bran and Luebbe,
188 Norderstedt, Germany).

189 After thorough mixing of the remaining soil, an aliquot of about 260 g (dry weight) of soil was sieved at
190 2 mm and air-dried before analysis of total C, total N, Olsen P, pH (H_2O) and basal C and N
191 mineralization. Total soil organic C and N were determined by dry combustion of dry soil subsamples
192 ground to 0.2 mm, using a CHN microanalyzer (Carlo Erba NA 2000). Soil pH (H_2O) was determined by
193 mixing 2 g of dry soil with 10 mL of deionized water for 30 min. Olsen P content was measured after
194 Olsen et al. (1954). Briefly, 250 mg of dry soil were extracted with 5 mL of 0.5 M NaHCO_3 at pH 8.5 by
195 30 min shaking. The P within the extract was then measured according to the malachite green method
196 (Rao et al., 1997). To measure soil C basal mineralization and nitrification, two aliquots of respectively
197 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
198 $193 \text{ g H}_2\text{O kg}^{-1}$ soil, then pre-incubated for one week at 20°C. At the end of the pre-incubation, NO_3^- was
199 extracted from the 10 g dry soil aliquot with 40 mL 1 M KCl, as the initial NO_3^- content. Jars containing
200 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
201 NaOH). The traps were changed at 7, 14 and 28 days and analyzed for carbonates within the day. The
202 remaining NaOH was titrated with 1 M HCl. The final soil NO_3^- was assessed after 28 days of incubation
203 at 28°C of the 25 g jars in the same way.

204

205 2.3. *Trees and cocoa characteristics*

206 Main attributes of individual shade trees and cocoa trees were characterized between August 2017 and
207 March 2018. Succession guild, leaf habit and legume vs non-legume were documented after Saj et al.
208 (2017a). Tree height was estimated using a rangefinder (TRUPULSE 360, Laser Technology Inc) for
209 shade trees and a graduated stick for cocoa trees. Average crown diameter of each shade tree was
210 estimated from four measurements of crown diameter done in cardinal and intercardinal directions (N-
211 S, E-O, NO-SE, NE-SO) using a compass and a tape decameter, and canopy area was calculated
212 accordingly. Diameter at breast height (DBH) of cocoa and shade trees was measured using a diameter
213 tape. As differences in cocoa attributes (cocoa height, leaf nutrient content) between unshaded and
214 shaded cocoa were not significant (data not shown), only unshaded cocoa attributes were considered.

215 For all subplots, fine roots (diameter < 1 cm) were sampled in March 2018 in the 0-10 cm layer near
216 each soil sampling location, using an 8 cm diameter root auger. Roots from each sampling point were
217 washed, sorted out manually by species (cocoa vs. shade tree), dried for one week at 37°C, and weighed
218 separately. Leaf litterfall was measured during 8 months (including the dry season) when most of the
219 annual litterfall occurs (Nijmeier et al., 2019). Briefly, one 0.45 m² collector was placed above each soil
220 and fine roots sampling location of each subplot. Leaf litter was collected every 15 days between
221 September 2017 and March 2018 and dried at 37°C for one week. For each collector and sampling date,
222 dry weight of the collected litter was measured by species, then summed through all the sampling period.

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

226 *2.4. Leaf litter traits*

227 Leaf litter collected from each litterfall collector was then used to measure C, N, P, Ca, Mg, K and tannin
228 content, Van Soest fractions and pH (H₂O). In order to have enough material to retain three replicates
229 by species, 1.5 g composite samples were made by pooling the litter across the farms with the closest
230 proximity (see Table S1 for further details).

231 Total C and N contents were determined by dry combustion using a CHN micro-analyzer (Carlo Erba
232 NA 2000). After acid extraction, Ca, Mg, and K contents were determined by atomic absorption
233 spectroscopy. Litter P content was analyzed using Murphy and Riley reagent, and readings were done
234 by colorimetry. Water-soluble compounds, hemicellulose, cellulose and lignin contents were obtained

235 by the van Soest method (Van Soest, 1963) with a Fibersac 24 fiber analyser (Ankom, Macedon, NJ,
236 USA). Condensed tannins were measured according to the acid butanol method (Coq et al. 2010). For
237 pH, 0.15 mL of each ground sample was shaken with 1.2 mL demineralized water in an Eppendorf tube
238 for 1 h at 250 rpm. After centrifugation at 9000 g for 5 min, pH of the supernatant solution was measured
239 (Cornelissen et al., 2006). Lignocellulose Index (van Soest lignin / [van Soest hemicellulose + cellulose
240 + lignin]) and Lignin: N ratio (van Soest lignin / leaf litter N content) were calculated.

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

246 2.5. Data analyses

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

$$251 \text{CWM}_x = p_{\text{cocoa}} \times t_{\text{cocoa}} + p_{\text{shade}} \times t_{\text{shade}} \quad (1)$$

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

262 We considered the following agroecosystem functions: total soil organic C, total N, NO_3^- , NH_4^+ , Olsen P
263 content, soil pH, C mineralization, nitrification, bioassay, cocoa yield, as well as the type of production

264 by shade trees: fruit or timber. An agroecosystem multifunctionality index was calculated under each
265 treatment. Briefly, values of each function were standardized by its maximum across all treatments, and
266 thus ranged between 0 and 100%. Multifunctionality was then defined as the number of standardized
267 functions under each cocoa – shade tree association that had a value above a threshold T (30, 50, 70
268 and 90%). C mineralization, which is considered as a negative process relative to cAFS functioning,
269 was inverted before being standardized. Fruit and timber production were either attributed a value of 0
270 (non-producing) or 100% (producing) under a given shade tree species (Figure S1).

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

286 3. Results

287

288

3.1. Cocoa and shade tree characteristics

289 Shade tree species characteristics differed significantly between each other and from *Theobroma cacao*.
290 Among shade trees, *Dacryodes* was the smallest and the thinnest species, while *Ceiba* was the tallest
291 and widest species (Table 1). Litter N and P contents were higher for the deciduous (*Milicia*, *Ceiba* and
292 *Albizia*) than for the evergreen species (*Canarium* and *Dacryodes*), the latter being at the same level as
293 cocoa. Cocoa had higher leaf N and P resorption efficiencies than shade trees (except for *Dacryodes* N
294 resorption), and higher or similar litter Mg content and pH. Litter from the evergreen trees had lower pH

295 (< 6), higher tannin content and Lignin:N ratio than litter from the deciduous shade tree species (Table
296 1). Among the deciduous species, litter from N₂-fixing *Albizia* had the highest N content, and the lowest
297 lignin:N ratio, Mg and tannin contents.

298 Association with shade trees affected strongly leaf litterfall but did not modify patterns of fine roots
299 biomass significantly (Table 2). Cocoa litterfall was decreased by half under shade trees, regardless of
300 the shade species considered. Shade tree litterfall varied between species and ranged from 2.6 to 4.7 t
301 DM ha⁻¹ (Table 2). The total amount of litterfall was lower for unshaded cocoa and cocoa shaded with
302 *Canarium* than for the other associations. Cocoa leaf litterfall amounted for only 21 to 36% of total leaf
303 litterfall under shade trees (Table 2). As a result, community weighted mean litter traits in association
304 were thus mostly driven by the characteristics of the shade tree species (Table S2).

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

310 3.2. *cAFS multifunctionality*

311 Shade trees greatly altered the agroecosystem functions linked to soil fertility. Soil NO₃⁻ and Olsen P
312 content, and the biomass produced by the maize bioassay were significantly improved under the
313 influence of deciduous trees (Table 3). Soil pH was only improved under *Milicia* and *Ceiba*, while soil
314 under *Albizia* was acidified compared to the other associations (Table 3). Only association with *Ceiba*
315 led to a significant increase in soil C and N contents. Overall, shade trees had relatively little impact on
316 soil C mineralization, nitrification and cocoa yield.

317 Agroecosystem multifunctionality was higher under cocoa – shade tree associations than under
318 unshaded cocoa, yet depended on the shade tree species and the threshold considered (Figure 2).
319 These improvements were more obvious at the threshold value of 50%, where multifunctionality index
320 increased from 2 for unshaded cocoa, to 4 for associations with *Dacryodes*, 6 with *Canarium* and *Albizia*,
321 and 8 for associations with the two timber trees. Higher multifunctionality under the deciduous trees as
322 compared to unshaded cocoa corresponded to higher NO₃⁻, Olsen P content and bioassay production,
323 as well as the additional fruit or timber production of all shade trees except *Albizia* (Figure S1). Impacts

324 of shade trees on multifunctionality decreased for higher threshold values (70 and 90%) and became
325 null for *Albizia* relatively to unshaded cocoa. Multifunctionality improvement under the other shade trees
326 at the 90% threshold corresponded respectively to edible fruit production under *Canarium* and
327 *Dacryodes*, and to timber production and soil pH increase under *Milicia* and *Ceiba* (Figure 2 and S1).

328 3.3. Relationships between cocoa - shade tree association characteristics and soil 329 functions

330 The model averaging and redundancy analyses both suggested that litter N, Ca, soluble and tannin
331 content were among the most important contributors to the changes in soil functions (Figure 3a; Table
332 4). Cocoa association with the two timber species, *Ceiba* and *Milicia*, increased total litterfall, CWM litter
333 P and Ca content, and were linked with higher soil NO_3^- , Olsen P content, bioassay production and soil
334 C and N content (Figure 3). Cocoa association with *Albizia* led to litter N enrichment, linked to increased
335 soil NH_4^+ and NO_3^- content but also to a decrease of soil pH. Association with evergreen *Canarium* and
336 *Dacryodes* had limited effects both on CWM litter traits and agroecosystems functions changes from
337 unshaded cocoa (Figure 3b). The model averaging approach highlighted most particularly the role of
338 litter Ca content, which contributed to most of the soil functions considered (RI > 0.64 for soil C, N, NO_3^-
339 content, soil pH and bioassay production). Further, litter tannin content was negatively associated with
340 soil NH_4^+ and Olsen P content (RI of 0.96 and 0.76, respectively), while litter soluble content was
341 negatively associated with NH_4^+ and litter N, P, K and Ca were associated with soil pH.

342 4. Discussion

343

344 Shade trees management in cocoa plantation has been discussed for decades regarding their benefits
345 and disadvantages for cAFS (Sanchez, 1995; Andres et al., 2016; Blaser et al., 2017; Niether et al.,
346 2019). The microclimatic regulation introduced by shading decreases diseases' outbreaks, which are
347 known to hamper both cocoa yield and sustainability (Andres et al., 2016). However, light interception
348 by shade trees decreases cocoa photosynthesis activity and may lead to yield decrease, as reviewed
349 by Sanchez (1995). However, this decrease may not occur in systems with poor soils, where nutrient
350 availability may be more limiting to cocoa production than light (Isaac et al., 2007a). Here, we
351 demonstrated that several species of shade trees were able to improve contrasting aspects of soil
352 fertility, without affecting cocoa yield. This result is in line with recent findings from Wartenberg et al.
353 (2019). The five shade tree species studied generally improved nutrient restitution from litter, through
354 increased litterfall and litter quality over the year, as compared with cocoa alone, and had positive effects

355 on a range of soil functions linked to soil fertility. Together, these results suggest that the putative
356 negative impact of shading has been compensated here by the relief of soil nutrient limitation for cocoa
357 production and/or improved cocoa nutrient use efficiency under their canopy (Niether et al., 2019). The
358 lack of increase in cocoa production under shade trees suggests nonetheless that light would have
359 become a limiting resource, setting an upper threshold to the benefits of such improved soil nutrient
360 conditions. Finally, our results suggest that, in places where soils are naturally poor or impoverished by
361 decades of cocoa monocultures with low input levels, such as in Côte d'Ivoire or Ghana, the plantation
362 of shade trees is likely to allow a gain in sustainability since positive effects on soil nutritional status
363 would counterbalance the effects of competition for light.

364 The number of soil functions improved under cocoa - shade tree associations varied greatly between
365 shade tree species, as driven by differences in litter quality. Shade tree litter constitutes indeed a
366 significant source of organic matter inputs in most cAFS, with important effects on carbon and nutrient
367 cycling (Nesper et al., 2019). This was particularly true in conditions of poor sandy soil. Out of all the
368 parameters tested, CWM litter Ca and, to a lesser extent, tannin content had the highest explanatory
369 weights for many soil functions. In our systems, these two litter traits, which typically drive litter
370 decomposability and turnover rate in soils (Kraus, Dahlgren, & Zasoski, 2003; Hobbie, 2015), proved to
371 be of higher significance for soil fertility and C sequestration than classical indices of litter N and P
372 content, amount of aboveground litterfall and belowground fine root biomass.

373 Associations with the evergreen fruit trees *Canarium* and *Dacryodes* led to the lowest improvement of
374 soil functions compared to the unshaded reference. These were the species with the closest
375 characteristics to cocoa (leaf life span strategy, litter nutrient content) and the lowest nutrient restitution
376 levels by litterfall. Further, the high recalcitrance of *Canarium* and *Dacryodes* litters (high tannins
377 content, low pH) may also have limited litter nutrient release and availability to plants due to their low
378 turnover rate (Hättenschwiler et al., 2011; Hobbie, 2015). In contrast, the three deciduous tree species
379 exhibited more contrasting properties compared to cocoa, and generally led to a more substantial
380 improvement of soil fertility. More specifically, the increased soil pH induced by the associations with
381 the deciduous timber tree species (*Milicia* and most particularly *Ceiba*), could be at least partly attributed
382 to the higher amount of Ca and Mg restituted by their litter (Reich et al., 2005). In addition, *Milicia* is an
383 oxalic species known to accumulate calcium carbonate in soil (Cailleau et al., 2005). In contrast,
384 association with *Albizia* decreased soil pH to lower levels than cocoa alone. Soil acidification are often

385 observed in legume plantations and could be caused by their N₂-fixing activity (Jensen & Hauggaard-
386 Nielsen, 2003). Soil pH decrease under legume can also result in soil P release (Hinsinger et al, 2003)
387 and could be responsible to the high Olsen P content under *Albizia* associations. Finally, the positive
388 impact of associations with deciduous species on soil N and P availability may be linked to the high
389 quality of the deciduous species litters (low lignin:N ratio and tannin content) as much as to its high N
390 and P content. Indeed, despite similar N and P content, litter from the evergreen tree *Dacryodes*, with
391 lower overall quality, improved less soil N and P availability than the deciduous tree species.

392 Our finding that litter low recalcitrance is associated with higher soil C sequestration is in line with the
393 recent paradigm that plant species with rapid litter decomposition may be associated with relatively
394 greater accumulation of soil C (Hobbie, 2015). However, this process may be hampered by soil
395 acidification by legume N₂-fixing activity in the case of *Albizia* association. Indeed, high litter Ca content
396 generally favors litter consumption by soil fauna (Holdsworth, Frelich, & Reich, 2008) which is
397 increasingly considered as favoring soil C storage (Berg, 2000; 2014). Secondary transformations during
398 the production of decomposer necromass and faeces favor organic matter mixing and binding with soil
399 mineral matrix and hence its stabilization (Lehman and Rillig, 2015). Despite increasing recognition of
400 the important role of fine root biomass and turnover in soil C storage (Clemmensen et al., 2013; DuPont
401 et al., 2014), the similar fine-root biomass observed here could not explain the differences in soil C
402 content. In order to adequately capture root carbon and nutrient inputs to the soil (Matamala et al. 2003),
403 further studies will need to go beyond classical measurements of standing biomass and to focus more
404 specifically on root turnover, exudation rates and mycorrhizal associations.

405 Overall, cocoa - *Ceiba* was the association that increased most cAFS multifunctionality, along with cocoa
406 – *Milicia* associations. Litter from these shade tree species were both characterized by high Ca
407 restitution levels in litterfall and low litter recalcitrance, and presented overall the highest level of
408 dissimilarity with cocoa litter. This trend may suggest that shade trees that differ most from cocoa may
409 provide stronger benefits in cAFS. In a context where tree species should be selected for (i) the desired
410 shade cover and production of goods for local population, with (ii) traits favoring soil multifunctionality
411 (i.e. low litter recalcitrance and high nutrient content), our results suggest that the selection of a small
412 number of tree species may provide better results than including a large range of species. Nonetheless,
413 multifunctionality in our study was mainly centered on soil functions. The relative importance of other
414 goods provision for local population, including timber and fruit, should not be overlooked as they are

415 valued by farmers (Jagoret et al., 2014) and may constitute a fair share of total cAFS plot revenue when
416 adequately managed (Juhrbandt, 2010). Furthermore, our results once again underline the empirical
417 knowledge of farmers on the impact of their associations and the trade-offs they sometimes imply (Saj
418 et al., 2017 a,b). In this respect, long-term studies integrating socio-economical aspects of cocoa and
419 goods' production, together with soil fertility indicators are further needed to meaningfully attribute a
420 weighting to each components of the agroecosystem functioning for profitable and sustainable
421 management. Considering other benefits potentially associated with maintaining high tree diversity at
422 the field scale, such as complementarity in resource use (Gross et al., 2017), stability of ecosystem
423 functioning in conditions of climate change (Eisenhauer et al., 2018) and their resistance to perturbations
424 (Loreau & de Mazancourt, 2013) would also be useful.

425 **Conclusions**

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

437

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448 **Authors' contributions**

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

452 **Data availability statement**

453 Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.dz08kp6> (Sauvadet et al.,
454 2019).

455 **ORCID**

456 *Marie Sauvadet* <https://orcid.org/0000-0002-7520-8565>

457 *Stéphane Saj* <https://orcid.org/0000-0001-5856-5459>

458 *Grégoire T. Freschet* <https://orcid.org/0000-0002-8830-3860>

459 *Thierry Becquer* <https://orcid.org/0000-0001-5846-5810>

460 *Philippe Tixier* <https://orcid.org/0000-0001-5147-9777>

461 *Jean-Michel Harmand* <https://orcid.org/0000-0002-8065-106X>

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595 **Figure captions**

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

600

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

603

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

Tables

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 vs 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 ⁻¹ 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 ⁻¹ 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 ⁻¹ 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 ⁻¹ 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 ⁻¹ 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 ₂ O)	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 ⁻¹ DM)	209±10 bc	162±18 c	280±27 a	224±34 ab	157±12 c	77±33 d
Cellulose VS (mg.g ⁻¹ DM)	149±56 ab	127±8 b	130±34 ab	112±5 b	116±11 b	195±23 a
Hemicellulose VS (mg.g ⁻¹ DM)	214±23 a	220±48 a	178±20 a	236±53 a	272±35 a	260±48 a
Lignin VS (mg.g ⁻¹ DM)	428±46 a	491±43 a	412±42 a	428±92 a	455±48 a	468±63 a
Tannin (mg.g ⁻¹ 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

Significant differences were tested by GLM followed by Tukey HSD post hoc tests and bear different letters for *P*-values < 0.05. VS: van Soest. LCI represent the proportion of lignin within the cell wall. Shade tree species characteristics are emphasized in bold when different from the reference cocoa.

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

	Unshaded	Under shade trees				
		<i>Canarium</i>	<i>Dacryodes</i>	<i>Milicia</i>	<i>Ceiba</i>	<i>Albizia</i>
Cocoa density (<i>plant 100 m⁻²</i>)	14±3 ab	14±3 ab	14±2 ab	13±2 ab	17±3 a	11±5 b
Fine root biomass (<i>kg DM m⁻²</i>)						
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 (<i>kg DM m⁻²</i>)						
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

Significant differences were tested by GLM followed by Tukey HSD post hoc tests and bear different letters for *P*-values < 0.05. Values under shade tree species are emphasized in bold when different from the unshaded treatment.

TABLE 3 Soil functions under the different associations.

	Unshaded	Under shade trees				
		<i>Canarium</i>	<i>Dacryodes</i>	<i>Milicia</i>	<i>Ceiba</i>	<i>Albizia</i>
Soil C (<i>g C kg⁻¹ soil</i>)	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 (<i>g N kg⁻¹ soil</i>)	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
NH₄⁺ (<i>mg N kg⁻¹ soil</i>)	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
NO₃⁻ (<i>mg N kg⁻¹ soil</i>)	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 (<i>mg P kg⁻¹ soil</i>)	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 H₂O	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 (<i>g DM produced per plant</i>)	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 (<i>nb pods per tree</i>)	22±7 a	26±9 a	21±5 a	24±11 a	22±6 a	25±16 a
C mineralization (<i>mg C kg⁻¹ soil d⁻¹</i>)	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 (<i>mg N kg⁻¹ soil d⁻¹</i>)	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

Significant differences were tested by GLM followed by Tukey HSD post hoc tests and bear different letters for *P*-values < 0.05. Values under shading are emphasized in bold when different from unshaded treatment.

TABLE 4 Model averaging of soil functions by cocoa – shade tree association litterfall and community weighted mean litter traits, performed on centered-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

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 correspond to significant variables ([†] $P < 0.10$; *; $P < 0.05$; **; $P < 0.01$; ***; $P < 0.001$) with positive and negative coefficient, respectively (see Table S6 for further details).

- Unshaded
- Albizia
- Canarium
- Millicia
- Dacryodes
- Ceiba

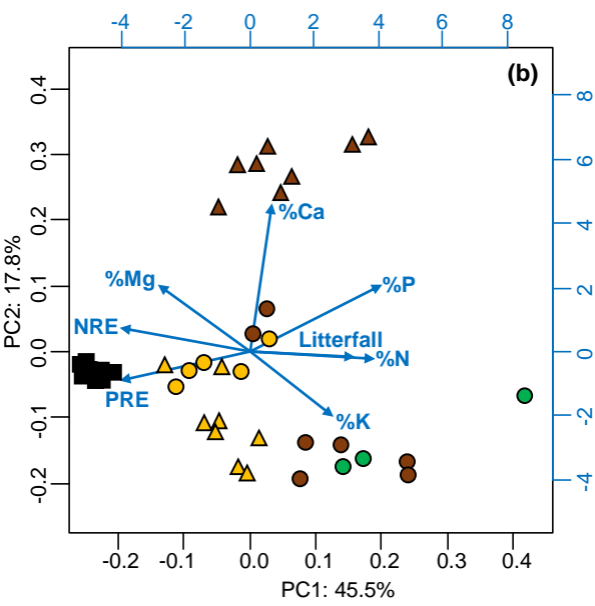
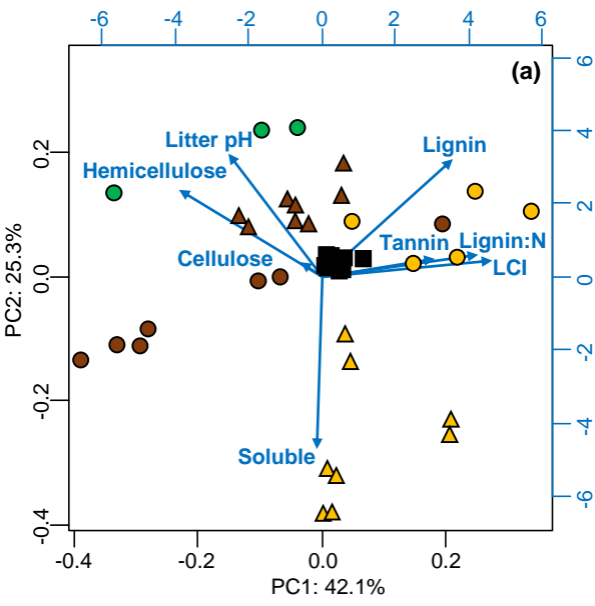


Fig. 1

12 functions tested:
 - Soil C, N, NH_4 , NO_3 and Olsen P contents and pH
 - Soil nitrification and [1 / C mineralization]
 - Bioassay, Cocoa yield, Fruits and Timber productions

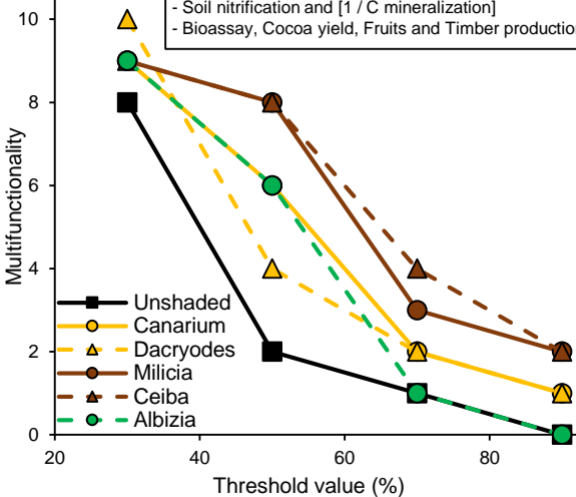


Fig. 2

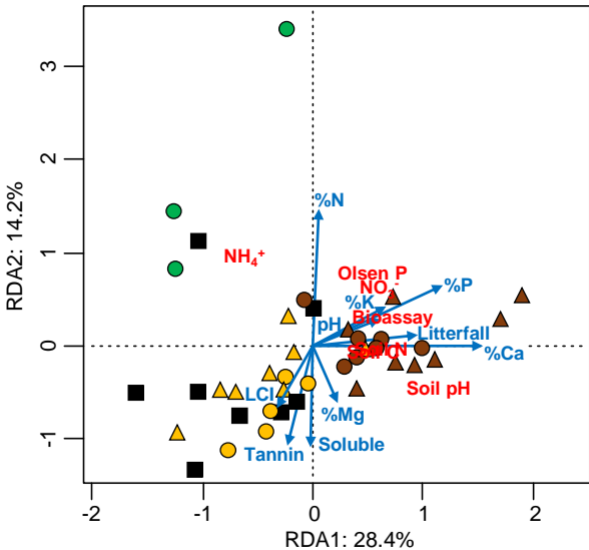


Fig. 3

Supporting Information from Sauvadet et al. (2019)

TABLE S1 Summary of the experimental design strategy. One soil sampling and litter collectors were set up in 10 m x 10 m subplot under the canopy of each studied shade trees, excepted under *Albizia adianthifolia* where two sampling subplots per tree were performed because of the few tree number of this species. The Unshaded treatment refers to sampling subplots under cocoa outside any shade tree canopies.

	Unshaded cocoa	Canarium	Dacryodes	Milicia	Ceiba	Albizia
Number of studied trees / unshaded plots						
Farm #1	1	2	1	1	1	1
Farm #2	1	1	1		1	
Farm #3	1		1		1	1
Farm #4	1		1		1	1
Farm #5	1	1	1	2	1	
Farm #6	1		1	1	1	
Farm #7	1		1	2	1	
Farm #8	1	1	1	1	1	
Studied trees	na	5	8	7	8	3
Sampling subplots	8	5	8	7	8	6
Litter sample pools for traits analysis	[Farms # 1+2]; [Farms # 3+4]; [Farms # 5+6+7+8]	[Farm #1]^a ; [Farm #2]; [Farm #5]; [Farm #8]	[Farms # 1+2]; [Farms # 3+4]; [Farms # 5+6+7+8]	[Farm #1+ Tree#1 of Farm#5] ^b ; [Tree#2 of Farm#5]*; [Farms # 6+7+8]	[Farms # 1+2]; [Farms # 3+4]; [Farms # 5+6+7+8]	[Farm #1]; [Farm #3]; [Farm #4]

a : Canarium litter was not pooled between Farm #1 and #2 for traits analysis, because of a pods disposal close to the Farm #2 Canarium, which may have artificially enriched Canarium leaf P content; b: Farm #1 Milicia tree did not provide enough litter to perform all the analyses, and was thus pooled with Farm #5 Milicia tree #1

TABLE S2 Cocoa – shade tree associations community weighted mean attribute and elemental restitution by litterfall. Under shade tree, each community attribute was averaged between cocoa and shade tree litter traits, relatively to its contribution to litterfall (presented in Table 2). C and nutrient restitution correspond to the sum of nutrient restituted (litterfall x litter nutrient content) by shade tree and cocoa litterfall.

	Unshaded	Under shade trees				
		<i>Canarium</i>	<i>Dacryodes</i>	<i>Milicia</i>	<i>Ceiba</i>	<i>Albizia</i>
Physiological traits						
N resorption efficiency (%)	51±0 a	45±3 b	52±0 a	37±4 c	45±3 b	28±1 d
P resorption efficiency (%)	73±0 a	45±10 b	53±4 b	53±7 b	47±8 b	44±15 b
Litter traits						
N (mg.g ⁻¹ DM)	10.5±0.0 d	9.9±0.5 d	12.0±0.8 cd	15.4±2.6 b	14.3±1.0 bc	25.8±5.7 a
P (mg.g ⁻¹ DM)	0.6±0.0 c	0.7±0.1 bc	0.8±0.1 ab	0.9±0.1 a	1.1±0.1 a	1.0±0.4 a
K (mg.g ⁻¹ DM)	5.4±0.1 b	5.3±0.3 b	6.7±0.2 b	13.8±4.6 a	5.8±0.4 b	6.5±1.7 b
Ca (mg.g ⁻¹ DM)	17.3±0.1 bc	18.7±2.1 b	15.3±1.2 c	18.5±2.5 b	26.8±1.7 a	15.8±1.3 bc
Mg (mg.g ⁻¹ DM)	7.2±0.1 a	4.7±0.8 c	4.0±0.8 cd	5.3±0.4 bc	5.9±0.3 b	3.3±0.3 d
pH (H ₂ O)	7.0±0.0 a	6.3±0.2 b	5.4±0.4 c	7.2±0.2 a	7.0±0.1 a	6.7±0.2 a
Soluble VS (mg.g ⁻¹ DM)	209±0 b	181±16 c	265±23 a	233±23 b	176±10 c	108±22 d
Cellulose VS (mg.g ⁻¹ DM)	140±3 b	133±5 bc	137±23 bc	120±5 c	121±9 c	182±15 a
Hemicellulose VS (mg.g ⁻¹ DM)	209±2 b	214±28 b	184±14 c	248±33 a	251±14 a	249±38 ab
Lignin VS (mg.g ⁻¹ DM)	442±5 ab	473±28 a	413±29 b	399±59b	452±25 a	461±50 ab
Tannin (mg.g ⁻¹ DM)	26±0 c	90±16 a	38±5 b	12±3 d	38±10 b	11±2 d
Lignocellulose Index (LCI)	56±1 a	58±3 a	56±4 a	52±6 a	55±2 a	52±4 a
Lignin : N ratio	42±1 ab	48±5 a	35±4 bc	29±10 cd	33±1 c	22±5 d
Elemental restitution by litterfall						
C (kg m ⁻²)	0.13±0.00 e	0.19±0.00 d	0.22±0.00 c	0.26±0.01 a	0.24±0.00 b	0.23±0.00 bc
N (g m ⁻²)	3.3±0.1 f	4.1±0.2 e	5.6±0.3 d	9.2±1.4 b	7.4±0.2 c	11.9±2.5 a
P (g m ⁻²)	0.18±0.03 d	0.28±0.04 c	0.40±0.06 b	0.54±0.02 a	0.56±0.03 a	0.47±0.16 ab
K (g m ⁻²)	1.7±0.3 c	2.2±0.2 c	3.2±0.2 b	8.2±2.6 a	3.0±0.3 bc	3.1±0.9 b
Ca (g m ⁻²)	5.5±0.2 d	7.6±0.9 c	7.3±0.4 c	11.0±1.4 b	14.0±1.7 a	7.4±0.4 c
Mg (g m ⁻²)	2.1±0.4 b	2.0±0.4 b	1.9±0.3 b	3.2±0.3 a	3.0±0.3 a	1.5±0.1 c

Significant differences were tested by GLM followed by Tukey HSD post hoc tests and bear different letters for P-values < 0.05. Values under shading are emphasized in bold when different from unshaded treatment.

TABLE S3 Linear mixed-effects models of farms identity impacts on cocoa – shade tree associations community weighted mean attributes, with associations identity set as random effects. The analyses were performed on the treatments represented by one modality per farm (i.e. unshaded cocoa, cocoa - *Dacryodes edulis* and cocoa - *Ceiba pentandra* associations).

	Degree of freedom	F-value	P-value
Physiological traits			
N resorption efficiency (%)	7	0.76	0.63
P resorption efficiency (%)	7	2.30	0.09
Litter traits			
N (mg.g ⁻¹ DM)	7	0.46	0.85
P (mg.g ⁻¹ DM)	7	0.57	0.77
K (mg.g ⁻¹ DM)	7	1.49	0.25
Ca (mg.g ⁻¹ DM)	7	0.87	0.55
Mg (mg.g ⁻¹ DM)	7	0.49	0.83
pH (H ₂ O)	7	1.04	0.45
Soluble VS (mg.g ⁻¹ DM)	7	2.20	0.10
Cellulose VS (mg.g ⁻¹ DM)	7	0.20	0.98
Hemicellulose VS (mg.g ⁻¹ DM)	7	0.08	0.99
Lignin VS (mg.g ⁻¹ DM)	7	0.51	0.81
Tannin (mg.g ⁻¹ DM)	7	0.19	0.98
Lignocellulose Index (LCI)	7	0.19	0.98
Lignin : N ratio	7	1.23	0.35
Elemental restitution by litterfall			
C (kg m ⁻²)	7	3.82	0.02
N (g m ⁻²)	7	0.20	0.98
P (g m ⁻²)	7	0.63	0.73
K (g m ⁻²)	7	6.83	0.001
Ca (g m ⁻²)	7	1.45	0.26
Mg (g m ⁻²)	7	17.02	<0.001

TABLE S4 Linear mixed-effects models of farms identity impacts on soil functions, with cocoa – shade tree associations identity set as random effects. The analyses were performed on the treatments represented by one modality per farm (i.e. unshaded cocoa, cocoa - *Dacryodes edulis* and cocoa - *Ceiba pentandra* associations).

	Degree of freedom	F-value	P-value
Soil C (<i>g C kg⁻¹ soil</i>)	7	0.57	0.77
Soil N (<i>g N kg⁻¹ soil</i>)	7	0.57	0.77
NH₄⁺ (<i>mg N kg⁻¹ soil</i>)	7	1.27	0.33
NO₃⁻ (<i>mg N kg⁻¹ soil</i>)	7	0.59	0.75
Olsen P (<i>mg P kg⁻¹ soil</i>)	7	1.17	0.38
pH H₂O	7	1.77	0.17
Bioassay (<i>g DM produced per plant</i>)	7	2.51	0.07
Cocoa yield (<i>nb pods per tree</i>)	7	2.92	0.04
C mineralization (<i>mg C kg⁻¹ soil d⁻¹</i>)	7	0.92	0.52
Nitrification (<i>mg N kg⁻¹ soil d⁻¹</i>)	7	0.55	0.78

FIGURE S1 Values of the standardized soil functions under each cocoa – shade tree associations. Each function was standardized by expressing them as a percentage of the maximum values observed across all plots. As such, 100% correspond to one single plot and treatments do not necessarily show value up to 100%.

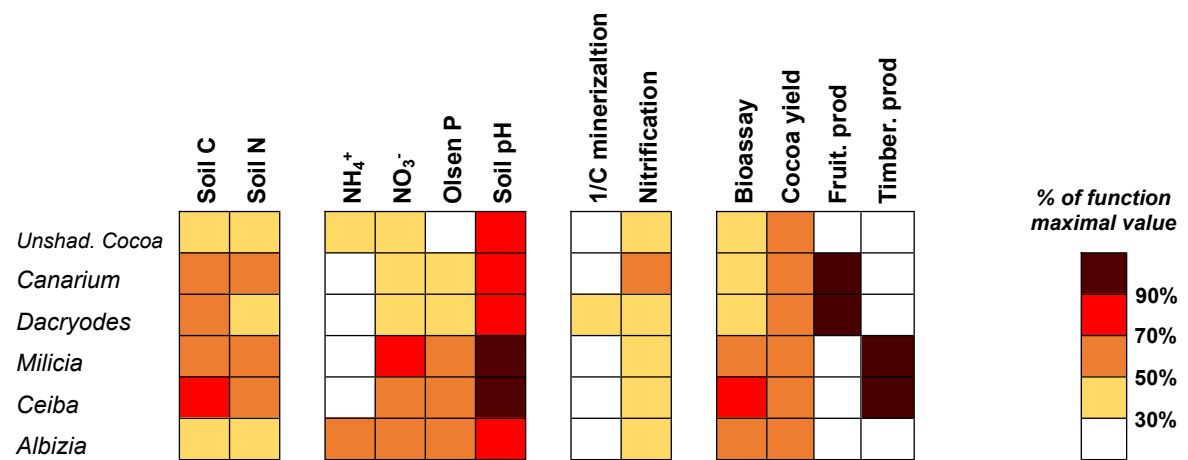


FIGURE S2 Cocoa - Shade tree associations characteristics (on the left) and soil functions (on the right) Pearson correlation coefficient matrices (n=42). Correlations were corrected for multiple comparisons with the Benjamini-Hochberg method. Significance correlations: * P-values < 0.05; ** P-values < 0.01; *** P-values < 0.001. NRE: N nutrient resorption Efficiency; PRE: P nutrient resorption Efficiency; LCI: proportion of lignin in litter cell wall (lignin / [lignin+ cellulose+hemicellulose]).

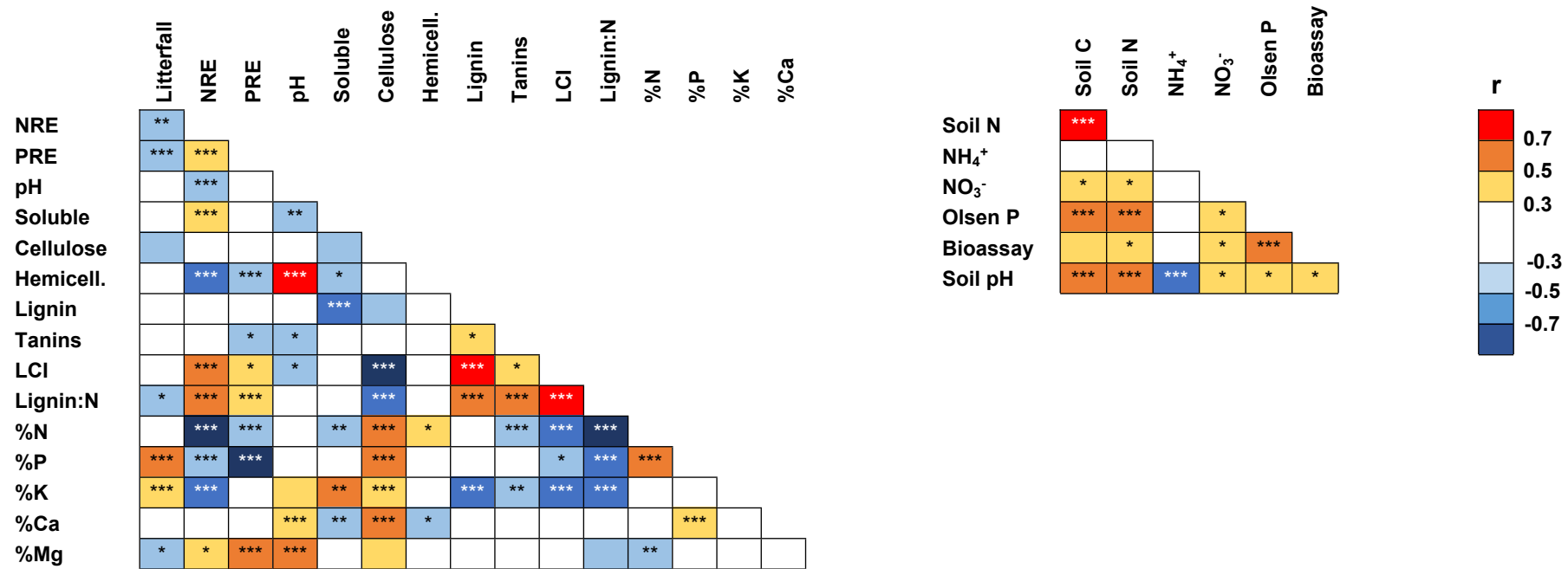
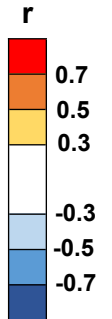


TABLE S5 Pearson correlation coefficient matrix between cocoa - Shade tree associations characteristics and soil functions (n=42).

	Soil C	Soil N	NH ₄ ⁺	NO ₃ ⁻	Olsen P	Soil pH	Bioassay
Litterfall	0.12	0.14	-0.26	0.26	0.28	0.35	0.38
Soluble	-0.04	-0.14	-0.46*	-0.24	-0.17	0.15	-0.08
Tannins	-0.02	-0.04	-0.33	-0.26	-0.30	0.03	-0.22
LCI	0.06	0.04	-0.11	-0.35	-0.16	-0.08	-0.23
Litter pH	0.10	0.23	0.14	0.33	0.06	0.33	0.17
%N	-0.05	-0.01	0.40*	0.42*	0.32	-0.26	0.27
%P	0.26	0.28	-0.11	0.48**	0.38	0.32	0.46*
%K	-0.03	-0.03	-0.11	0.36	0.20	0.30	0.21
%Ca	0.42*	0.51**	-0.21	0.35	0.18	0.66***	0.45*
%Mg	0.10	0.17	-0.07	-0.06	-0.27	0.30	-0.09



Correlations were corrected for multiple comparison with the Benjamini-Hochberg method. Significance correlations:
 * P-values < 0.05; ** P-values < 0.01; *** P-values < 0.001. LCI: proportion of lignin in litter cell wall (lignin / [lignin + cellulose + hemicellulose]).

TABLE S6 Variables coefficients from model averaging of soil functions by cocoa – shade tree association litterfall and community weighted mean litter traits. For each function, the parameter estimates of each variable have been averaged on the models selected on Akaike information criterion (for $\Delta < 2$). Models were performed on centered-reduced data.

	Soil C	Soil N	NH ₄ ⁺	NO ₃ ⁻	Olsen P	Bioassay	Soil pH
Litterfall	0.06	0.10	-0.19	0.00	0.14	0.28[†]	0.10
Soluble	0.12	0.07	-0.81*	-0.44	-0.36	0.10	0.10
Tannins	-0.11	-0.12	-0.46**	-0.14	-0.45[†]	-0.27	-0.13
LCI	0.14	0.14	-0.23	-0.06	-0.14	-0.09	0.13
Litter pH	-0.08	0.01	-0.62	-0.26	0.01	-0.11	-0.03
%N	-0.19	-0.08	0.06	0.27	-0.38	0.12	-0.60***
%P	0.25	0.14	-0.30	0.32	0.30	0.20	0.31**
%K	0.04	0.07	0.33	0.50	0.16	0.19	0.49***
%Ca	0.43*	0.51***	-0.35*	0.35[†]	0.30	0.49**	0.66***
%Mg	0.02	0.04	0.30	0.23	-0.48	-0.24	0.03

[†], *, ** and *** stands for traits whose P-value < 0.10, 0.05, 0.01 and 0.001, respectively

Linking cocoa – shade tree associations litter traits to soil functions in a cocoa agroforest

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Cocoa agroforest
in Central Cameroon



8 farms on sandy soils

Journal of Applied Ecology

Cocoa – shade tree
associations

■ *Unshaded cocoa*

Cocoa shaded with:

● *Canarium schweinfurthii*

▲ *Dacryodes edulis*

● *Milicia excelsa*

▲ *Ceiba pentandra*

● *Albizia adianthifolia*

