



Long-term dynamics of cocoa agroforestry systems established on lands previously occupied by savannah or forests



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ABSTRACT

Cocoa agroforestry systems (cAFS) in Central Cameroon are established on lands which were either forest or savannah. The functioning and ecosystem services (ES) delivery of an agroecosystem can be influenced by past land-use. We hypothesised that savannah-derived cocoa agroforestry systems (S-cAFS) and forest-derived cocoa agroforestry systems (F-cAFS) would (i) progressively drift away from past land-use, and (ii) eventually converge and support comparable levels of ecosystem services. We selected 25 ecosystem attributes directly related to at least one of the following six ecosystem (dis)services (ES): species conservation, carbon storage, crop production, nutrient cycling, soil quality and soil pollution. We followed their temporal evolution in S- and F-cAFS along > 70-year chronosequences. Our results showed that the attributes and services studied followed typical temporal trajectories in S- and F-cAFS while generally tending to reach comparable levels on the long run. However, the time needed to do so varied strongly and ranged from 20 to 30 years for perennial species diversity to more than 70 years for C storage or some components of soil quality. The results also demonstrated that S-cAFS could sustainably improve many of the studied attributes and ES. Regarding the attributes related to the cocoa stand, both S- and F-cAFS seemed influenced by their previous land-use up until 15 and 30 years, respectively, after their establishment. With respect to soil quality, nutrient cycling and carbon storage, only S-cAFS could be significantly distinguished from their past land-use, after 15 to 30 years.

1. Introduction

Ecosystem services and underlying functions depend on both current ecosystem ecological attributes and historical legacies. Disturbances, natural or anthropogenic, can lead to long-term fluctuations in ecosystem structure and functioning. The frequency, type, size, timing and intensity of a disturbance determines its impact which could eventually lead to land-use change (Chapin et al., 2011). In general, the impact of human interference, for example in the form of agricultural activities, is larger than that of natural events (Foster et al., 2003). All organic components, above- and below- ground, seem to be highly influenced by past land-use (Bellemare et al., 2002; Jangid et al., 2011; Perring et al., 2016). Such legacies are demonstrated for an array of ecosystem attributes such as nutrient cycling (Dupouey et al., 2002),

carbon storage (Freschet et al., 2014), soil microbial community and heterotrophic respiration (Kallenbach and Stuart Grandy, 2015). Yet, land-use legacies might be overruled if current disturbances are strong and long enough, ultimately leading to novel ecosystems (Hobbs et al., 2006).

Agricultural systems can be established from contrasting ecosystems. The conversion of a tropical forest into an agricultural suitable environment is mainly achieved by slash-and-burn technics, which are very similar all over the world (Nepstad et al., 1999; Achard et al., 2002; Palm et al., 2005). Tropical grasslands are also used for agricultural purposes after vegetation burning (Kugbe et al., 2012). Over the last century, half of the tropical grasslands and savannahs had been converted to agricultural land (UNDP, 2005). Often, the same crops are grown on differing past land-uses. This is the case of cocoa agroforestry

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systems (cAFS) from the forest–savannah transition zone of Central Cameroon which are either created on forest or on savannah land (Jagoret et al., 2012). In the forest-derived cAFS (F-cAFS), farmers operate a selective clearing of forest trees for the provision of shade along with food and/or additional income (Jagoret et al., 2014; Saj et al., 2017a). In the savannah-derived cAFS (S-cAFS), farmers use specific techniques to build up a tree canopy (Jagoret et al., 2012). Central Cameroon farmers' practices are known to drive cAFS' structure, tree species composition and biomass on the long run (Jagoret et al., 2012; Saj et al., 2017a; Jagoret et al., 2018a). Interestingly, full-grown S-cAFS and F-cAFS seem to exhibit comparable multi-strata structure, cocoa yields and C storage abilities despite differing previous land-use and *a fortiori* differing legacies (Jagoret et al., 2012; Saj et al., 2013; Nijmeijer et al., 2018).

Land-use change from savannah or forest into cAFS probably affects both above- and below- ground ecosystem functioning and related services. For instance, conversion of forest into cAFS was shown to alter litter inputs and soil properties, putatively altering nutrient cycling (Beer et al., 1998; Schroth et al., 2001; Hartemink, 2005; Adeniyi et al., 2017). Similarly, transitioning from savannah to another (agro or eco) system or vice-versa was shown to alter both litter inputs and soil properties (Don et al., 2011; Nouvellon et al., 2012; Sugihara et al., 2014). In this paper we explored the long-term legacies of past land-use in F- and S-cAFS from Central Cameroon.

First, we hypothesised that S- and F- cAFS ecosystem attributes were likely to progressively drift away from those of their initial ecosystem. We expected that the timespan needed to observe significant changes would depend both on the previous land-use (PLU) and the considered ecosystem attribute. Secondly, we hypothesised that the magnitude and the direction of the temporal evolution, hereafter called trajectories, of some ecosystem attributes were to differ between S- and F-cAFS. We expected these differential trajectories to attain comparable levels for some of the studied attributes. We tested both hypotheses using a selected number of attributes in cAFS, whose levels were studied through decade-long chronosequences. On the one hand, we focused on S-cAFS trajectories and their PLU, savannah, and on the other hand, we studied F-cAFS trajectories and their PLU, forest. Each of the 25 ecosystem attributes studied (plant biomass, production, litter production and storage, soil organic matter and nutrient contents and associated perennials diversity...) relates directly to at least one of the following six (dis)services: species conservation, carbon storage, crop production, nutrient cycling, soil quality and soil pollution.

2. Material and methods

2.1. Site characteristics and sampled plots

The study was carried out in the district of Bokito, in the villages Bakoa and Guéfigué (4°30 latitude N and 11°10 longitude E), located in a forest–savannah transition zone in Central Cameroon. The landscape consists of hills with gentle slopes at an altitude between 400 and 550 m a.s.l. and is characterised by a patchwork of forests, agroforests and herbaceous savannahs (Jagoret et al., 2012). Annual rainfall ranges from 1300 to 1400 mm with a main dry season lasting from mid-November to the beginning of March (Jagoret et al., 2012). The region is dominated by desaturated ferrallitic soils (Elangwe, 1979). Here the cocoa plantations consist mainly of decade-old diversified agroforestry systems (cAFS) containing many associated trees (Sonwa et al., 2007; Jagoret et al., 2011; Saj et al., 2013). We selected 16 plots of cAFS created on savannah (S-cAFS) and 16 plots created on secondary forest (F-cAFS) whose age was distributed along a gradient from 1 (farmers just started the planting process of cocoa) to over 70 years old. Besides, five control plots of each past land-use (savannah and forest) were selected for comparison with the S- and F-cAFS. Savannahs in the area are annually burned and periodically cultivated, therefore we chose plots where no agricultural activity could be noticed for the last seven years,

as savannah controls. The forest patches are degraded compared to other secondary forests that can be found in the region (Saj et al., 2017a). Plot size was of 40 m x 60 m (2400 m²), each containing a subplot of 20 m x 40 m (800 m²; see below and Nijmeijer et al., 2018).

2.2. Ecosystem attributes

2.2.1. Conservation

A floristic survey enabled us to compute two attributes which relate to species conservation, *i.e.* perennial species richness and diversity. We also computed species rarefaction curves. We surveyed all the perennial plants found in the studied systems including both typical trees and “tree-like” perennials, *i.e.*: cocoa, associated trees, palms and bananas. All the perennials with a diameter at breast height (DBH) over 30 cm were surveyed in 2400 m² plots. Those with a DBH between 5 and 30 cm were surveyed in 800 m² subplots within the 2400 m² area already selected. Height, DBH and species were recorded as described in Nijmeijer et al. (2018). When the DBH couldn't be measured, we followed the recommendations from Weyerhaeuser and Tennigkeit (2000) to indirectly estimate it. In total, we counted 3036 cocoa trees and 670 associated perennials in the cAFS studied. In the forest and savannah control plots, we identified 304 and 92 perennials, respectively. Associated perennials were classified according to their species: (i) native species from the African continent and (ii) exotic species introduced from other continents. Among all the individuals counted in cAFS, forest and savannah plots, 88.4% could be identified at the species level. The number of individuals per species in the plots were extrapolated to number of individuals per species per hectare. Abundance and diversity data of associated perennials were used to calculate species richness using Shannon-Wiener and Sørensen indices (Peet, 1974; Magurran, 2004).

2.2.2. Carbon storage

Using the above-cited survey we calculated the total biomass of large associated trees (DBH > 30 cm) and the biomass of cocoa trees, two attributes directly relating to carbon storage (Saj et al., 2013). Aboveground biomass (AGB) of associated trees was estimated after Chave et al. (2014). Their belowground biomass (BGB) was estimated after (Cairns et al., 1997). The biomass of each tree was then calculated as the sum of AGB and BGB.

2.2.3. Crop production

Five attributes related to crop production were computed using the above-cited floristic survey and cocoa pod production counts, namely: cocoa tree stand density and basal area, cocoa tree basal area share (CTBAS), accessible cocoa yield and banana stem density. CTBAS was calculated as: [basal area of cocoa trees (at 1.30 m height): basal area of whole stand] (Saj et al. (2017b)). Cocoa pod production and subsequent yield in cocoa beans were estimated for three consecutive production cycles in 2014, 2015 and 2016. Pods with a length > 10 cm were counted four to five times during the year (April, June, August, October and December) to get most of the annual production cycle. Such a count indicates the maximum number of pods per plot that can be produced and physiologically reach maturity within a production cycle. This has been defined as the “accessible” production of pods from which we can then derive the “accessible” yield in cocoa beans used in this study with calculations described in Saj et al. (2017b).

2.2.4. Nutrient cycling

Six attributes related to nutrient cycling were computed, namely: annual leaf and total litterfalls, leaf and total standing litters, leaf litter and total litter cycling indicators. Litterfall was monitored from November 2015 to October 2016. Three 0.5 m² collectors were randomly placed within the 2400 m² area of each plot, and once a month their positions were changed to account for spatial variability (12 different positions for each collector during the study; Schroth, 2003).

They were emptied every two weeks (111 collections in total). Once collected, the litter was air-dried and sorted to distinguish leaf litter from total (ie. leaf + branches + reproductive organs) litter. Sub-samples were then dried at 60 °C for 72 h and weighed for dry matter content calculation. Standing litter was measured at the end of the rainy season (October 2016), when decomposition started to slow down due to seasonal climate transition. In each plot, litter was collected in four randomly distributed 1 m² quadrants for fresh weight measurement. Litters from a 0.0625 m² (25 x 25 cm) sub-quadrant were then dried at 60 °C for 72 h and weighed for dry matter content calculation. These subsamples were also sorted to distinguish leaf litterfall from total (ie. leaf + branches + reproductive organs) litterfall. Standing litter and litterfall were not measured in the savannah control plots due to the very low density of perennials in these plots. Two indicators of litter decomposition were calculated after [Tripathi and Singh \(1994\)](#): (i) one including all the organs constituting the litter (leaves, branches and reproductive organs), which we called “total litter cycling”: [total litterfall : (total litterfall + total standing litter)]; (ii) one including only leaves, hereafter called “leaf litter cycling”: [leaf litterfall : (leaf litterfall + leaf standing litter)].

2.2.5. Soil quality and contamination

Ten attributes related to soil quality and possible contamination by pesticide-driven Cu were computed, namely: pH, organic carbon (C), total N, C:N, Inorganic P, exchangeable K, cation exchange capacity, as well as exchangeable Ca, Mg and Cu. A composite soil sample of 0–15 cm depth was built from eight subsamples (each of 135 cm³) systematically distributed in each 800 m² subplot after brushing off the litter layer. Particle size distribution and soil chemical composition and particle size distribution were determined by the IITA soil laboratory in Yaoundé (November 2016; www.iita.org). Soils were air-dried and sieved at 2 mm. Particle size distribution (three fractions) of sieved soil samples (0–2 mm) was estimated after [Bouyoucos \(1951\)](#); pH in water was determined in a 1:2.5 (10w:v) soil:water suspension. To determine soil organic C (SOC), soils were further ground to reach a particle size ≤ 0.5 mm before proceeding to chromic acid digestion and spectrophotometric analysis ([Heanes, 1984](#)). Total nitrogen (N) was determined from a wet acid digest ([Buondonno et al., 1995](#)) and analyzed by colorimetry ([Anderson and Ingram, 1993](#)). Inorganic phosphorus (P) was extracted using Bray 1 extractant and analyzed using the molybdate blue procedure ([Murphy and Riley, 1962](#)). Exchangeable cations (calcium (Ca), magnesium (Mg), potassium (K)) were extracted by ammonium acetate at pH 7 and analyzed by flame atomic absorption spectrophotometry ([David, 1960](#)). Exchangeable copper (Cu) was extracted using the Mehlich-3 procedure and determined by atomic absorption spectrophotometry ([Mehlich, 1984](#)).

2.3. Chronosequence validation

We defined four cAFS age categories [0–14], [15–30], [31–50] and [> 50] years to represent the different temporal stages of cAFS while trying to balance the number of plots per category. Yet we noticed a significant soil clay content heterogeneity among the plots sampled ([Nijmeijer et al., 2018](#)) which challenged the validity of the chronosequence ([Pickett, 1989](#)). To take into account a putative soil texture effect, a preliminary ANCOVA, including age categories, past land-use and soil clay content as a covariate, was run on the whole set of cAFS. It showed that the soil clay content still significantly impacted - and interacted with - cAFS age and/or previous land-use on numerous ecosystem attributes (data not shown). This was probably due to the fact that most of the S-cAFS in the sampled region were located at the foot of gentle slopes while F-cAFS were located slightly higher ([Nijmeijer, 2017](#)). Consequently, we split the studied plots into two according to their clay content: a group with low clay content soils (LCCS; containing between 9.8 to 16.2% of clay), a group with high clay content soils (HCCS; containing more than 19.6% of clay). The number of F-cAFS

plots in the LCCS group and the number of S-cAFS plots in the HCCS group were too low to establish chronosequences. Hence, we ended up studying a S-cAFS chronosequence on LCCS, and a F-cAFS chronosequence on HCCS. The LCCS group was comprised of 20 plots (n S-AFS = 11, n savannah controls = 3, n F-cAFS = 3, n forest controls = 3). The HCCS group contained 18 plots (n S-AFS = 4, n savannah controls = 2, n F-cAFS = 10, n forest controls = 2). We further used ANOVAs to check, separately for each soil clay content group, that cAFS age categories did not differ in soil clay content. Appendix A shows the mean values resulting from ANOVA and post-hoc (SNK) of the 25 studied attributes for the 4 land-use types regardless of plot age and soil texture (42 plots in total).

2.4. Data analyses

We performed all statistical analyses for the LCCS and HCCS groups separately. Two principal component analyses (PCA) followed by a Varimax rotation were performed on the whole set of ecosystem attributes studied to estimate cAFS plot positions in multivariate space of ecosystem attributes and identify major axes of variations. The scores of each S- or F-cAFS plot on the two axes of the PCA were then extracted and, for each axis, one-way ANOVAs with post-hoc SNK tests were run to determine which age categories significantly differed from their respective control (ie. past land-use). Each of the 25 ecosystem attributes ([Table 1](#)) studied were then tested separately to check for differences between age categories and control plots with one-way ANOVAs followed by SNK as post-hoc (or with non-parametric Kruskal–Wallis tests followed by the Steel–Dwass–Critchlow–Fligner test when variables did not exhibit homogeneity of variance). These analyses were followed by the study of the temporal evolution of each attribute using linear, polynomial or logarithmic regressions – choosing for each the best fitted model (RMSE). The significance of each regression was then tested comparing the model’s residuals against their predicted values (F-test). All statistical analyses were performed using XLStat ([Addinsoft, 2015](#)) and statistical significance was set at $P < 0.05$. Finally, (associated) perennial species rarefaction curves were computed to check for differences between the four land-use types. These curves were computed using EstimateS (version 9.1.0) from [Colwell \(2013\)](#) and their visual comparison was used to evaluate the differences between land-uses ([Barlow et al., 2007](#)).

3. Results

3.1. Principal component analyses

The first two axes of the PCA explained 63% and 54.7% of the total variance of the two systems studied i.e. S-cAFS in the low clay content soil group (LCCS) and F-cAFS in the high clay content soil group (HCCS), respectively ([Fig. 1a,b](#)). For both groups, the attributes related to soil quality, nutrient cycling and carbon storage were the main contributors to the first axis (D1), accounting respectively for 40.27% of the total variance in LCCS group and 36.58% in HCCS group. For both groups, the attributes related to cocoa stands were the main contributors to the second axis (D2), accounting respectively for 22.73% of the total variance in the LCCS group and 18.12% in the HCCS group ([Fig. 1a,b; Table 1](#)). Standing leaf litter significantly participated to the D2 of the LCCS group ([Fig. 1a,b; Table 1](#)). The projection of the plots from both groups clearly discriminated between forest and savannah control plots while showing significant evolutions of the agroforestry systems created on savannah ([Fig. 2a,b](#)). Agroforestry systems established on savannah (S-cAFS), could be distinguished from savannah on D1 and D2 as soon as their age reached 15–30 years ($p = 0.002$ and $p = 0.01$, respectively; [Fig. 2a](#)). Agroforestry systems established on forest lands (F-cAFS) could not be distinguished from forest lands on D1 ($p = 0.103$) but could be distinguished on D2 as soon as their age was over 30–50 years ($p = 0.016$; [Fig. 2b](#)).

Table 1

Regressions coefficients (R^2) of the principal component analyses (PCA) of the studied attributes after Varimax rotation for the first two dimensions, D1 and D2, run for S-cAFS in low clay content soils and for F-cAFS for high clay content soils (in bold: $R^2 > 0.5$).

Service	Attribute	Abbreviation	S-cAFS		F-cAFS	
			low clay content soils (65%)		high clay content soils	
			D1	D2	D1	D2
Conservation	Perennials shannon index	Shannon	0.36	0.03	0.36	0.19
	Perennials species richness (nb ha ⁻¹)	Species R	0.28	0.13	0.31	0.05
C Storage	Large associated trees biomass (t ha ⁻¹)	LT biomass	0.53	0.03	0.53	0.00
	Cocoa trees biomass (t ha ⁻¹)	Cac biomass	0.05	0.87	0.00	0.16
Crop production	Density of cocoa trees (nb ha ⁻¹)	Cac dens	0.00	0.70	0.02	0.72
	Basal area of cocoa trees (m ² ha ⁻¹)	BA Cac	0.06	0.89	0.01	0.75
	Cocoa trees basal area share (%)	CTBAS	0.01	0.76	0.01	0.25
	Mean accessible yield (kg ha ⁻¹)	Cac yield	0.06	0.88	0.00	0.00
Nutrient cycling	Density of banana stems (nb ha ⁻¹)	Ban dens	0.02	0.08	0.07	0.12
	Leaf litterfall (t ha ⁻¹)	LLF	0.56	0.11	0.04	0.08
	Total litterfall (t ha ⁻¹)	TLF	0.59	0.15	0.23	0.09
	Leaf standing litter (t ha ⁻¹)	LSL	0.05	0.28	0.00	0.11
	Total standing litter (t ha ⁻¹)	TSL	0.08	0.31	0.19	0.23
	Leaf litter cycling	L cycle	0.52	0.02	0.39	0.36
	Total litter cycling	T cycle	0.70	0.05	0.56	0.46
Soil quality	pH	pH	0.72	0.02	0.81	0.76
	Organic C (%)	Org C	0.86	0.03	0.79	0.00
	Total N (%)	N	0.80	0.01	0.92	0.02
	C:N	C/N	0.60	0.00	0.54	0.07
	Inorganic P (ppm)	P	0.64	0.00	0.63	0.01
	CEC (cmol kg ⁻¹)	CEC	0.83	0.03	0.62	0.00
	Exchangeable K (cmol kg ⁻¹)	K	0.34	0.14	0.45	0.00
	Exchangeable Ca (cmol kg ⁻¹)	Ca	0.76	0.06	0.80	0.05
	Exchangeable Mg (cmol kg ⁻¹)	Mg	0.54	0.02	0.62	0.00
	Soil contamination	Exchangeable Cu (ppm)	Cu	0.10	0.07	0.24

3.2. Ecosystem services levels and trajectories

3.2.1. Conservation

S-cAFS exhibited equivalent associated perennials diversity and species richness to F-cAFS and savannah but lower than those of forest (Table 2a). While no significant differences in Shannon index and species richness were observed between local forest and young F-cAFS (< 30 years), mature and old F-cAFS (more than 30 years old) exhibited lower associated perennials diversity values (Table 2b). Regressions showed that, around 30 years old, S-cAFS and F-cAFS reached

comparable diversity levels (Fig. 3a). S-cAFS associated perennial species richness appeared constant (ca. 7.8 sp ha⁻¹) while it decreased with time in F-cAFS reaching that of S-cAFS ca. 90–100 years after establishment (Fig. 3b). Rarefaction curves were computed for African and total (associated) perennial species identified in each system type (Fig. 4a,b). Forested systems (forest control, F- and S-cAFS) revealed comparable curve shapes while their levels underlined clear differences. These systems were found to exhibit very different species accumulation abilities than those exhibited by savannah (Fig. 4 a,b). Furthermore, the sampling effort needed in cAFS to reach forest control

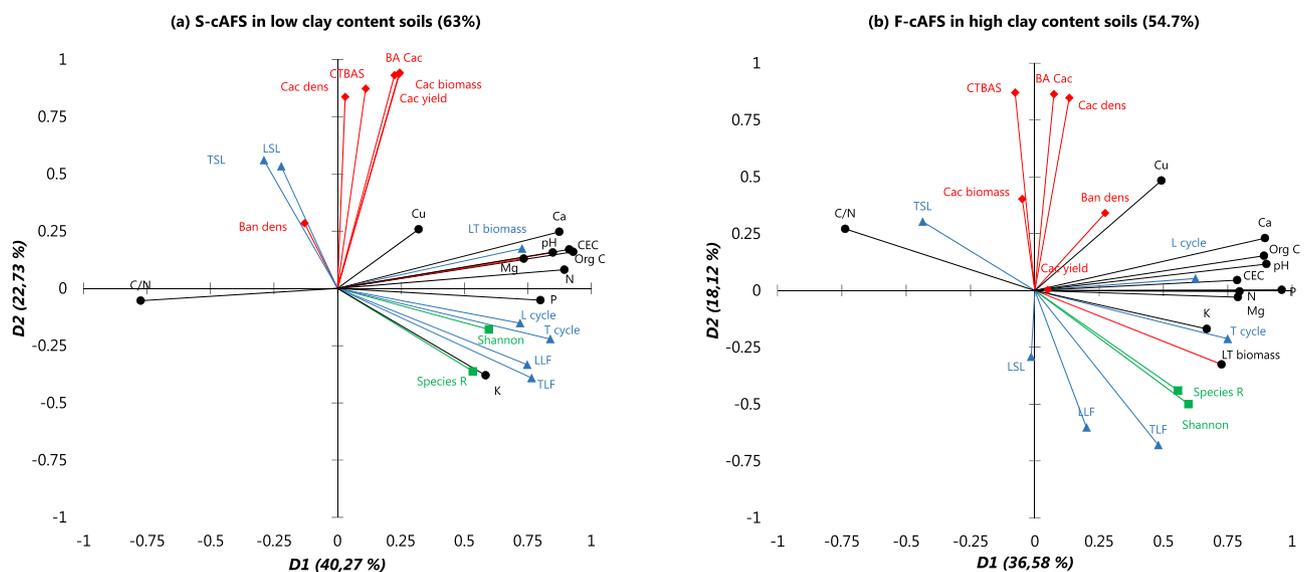


Fig. 1. Vectors of the principal component analysis (PCA) after Varimax rotation for the low clay content soils group (a) and the high clay content soils group (b). Abbreviations are explained in Table 1. The colour and the shape of the ending point of each vector display the ecosystem service to which each attribute has been related to: big violet dot = carbon storage; red diamond = crop production; green square = species conservation; blue triangle = nutrient cycling; small black dot = soil quality and contamination.

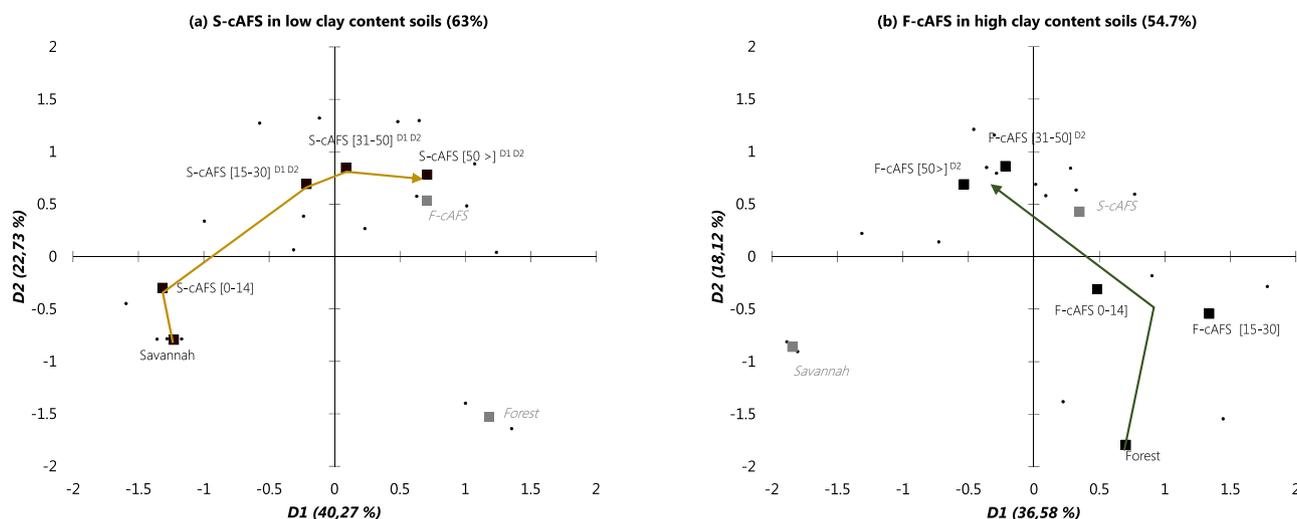


Fig. 2. Biplot of the PCA for the forest, savannah and cAFS plots on (a) low clay content soils or (b) high clay content soils. Dots represent individual plots, squares represent systems' means. The name of each agroforestry system age category, noted in (a) S-cAFS [age 1 – age2] and in (b) F-cAFS [age 1 – age2], is followed by an exponent stating for which dimension (D1 and/or D2) its mean was found significantly different from past land-use mean. In (a), forests and F-cAFS plots and means appear in grey. These plots contributed to the PCA but were not included in the ANOVA made on plot scores to distinguish between S-cAFS age categories and savannah. In (b), savannah and S-cAFS plots and means appear in grey. These plots contributed to the PCA but were not included in the ANOVA made on plot scores to distinguish between F-cAFS age categories and local forest. Arrows between savannah and S-cAFS (a, orange) and between forest and F-cAFS (b, green) were added manually on the biplot to highlight the “virtual” path followed by the agroforestry systems according to their past land-use.

species richness levels appeared at least three times higher. S-cAFS exhibited slightly lower abilities to accumulate species than F-cAFS – notably due to their lower associated tree abundance (Nijmeijer et al., 2018). The share of African individuals in S-cAFS and F-cAFS appeared close, being respectively of 44.1 and 47.6% (Fig. 3a,b). Forest control plots exhibited a fair number of exotic individuals (> 10%, Fig. 4a,b). Finally, F- and S-cAFS shared 29 and 19 African species with forest plots, respectively (Sørensen index: 0.68 and 0.48). S and F-cAFS shared 22 African species (Sørensen index = 0.61).

3.2.2. Carbon storage

In S-cAFS, large (DBH > 30 cm) associated tree and cocoa tree biomass increased with age, especially between [15–30] and [31–50] years old categories (Table 2a). Large associated tree biomass did not differ significantly between F-cAFS age categories, S-cAFS and forest plots (Table 2b). Regressions showed that large associated tree biomass in S-cAFS reached about the same values (140 t ha⁻¹) as F-cAFS ca. 70 years after establishment (Fig. 3c). Regressions showed that cocoa tree biomass followed similar trends and reached ca. 20–25 t ha⁻¹ 50 years after establishment (Fig. 3d).

3.2.3. Crop production

For the attributes related to cocoa production, no significant differences were found between F-cAFS age categories and S-cAFS (Table 2b). For S-cAFS, basal area of cocoa trees, cocoa tree basal area share (CTBAS) and accessible yield were found to increase with time, especially between [0–14] and [15–30] years old categories (Table 2a). Regressions underlined that S-cAFS exhibited more cocoa trees during the first 20 years (> 1500 ha⁻¹) (Fig. 5a). Cocoa tree density reached a maximum when S-cAFS were around 20 years old and when F-cAFS were approx. 40–50 years old. They then slowly decreased and stabilised around 1000 trees ha⁻¹ for both systems (Fig. 5a). Cocoa tree basal area regressions followed the same trend for S-cAFS and F-cAFS up until 60–70 years of age. Afterwards, basal areas decreased in F-cAFS (Fig. 5b). Cocoa tree basal area share (CTBAS) followed the same trend in S- and F-cAFS while it appeared consistently higher in S-cAFS. After 60 years, regressions showed that CTBAS reached a value of ca. 40% in S-cAFS versus ca. 30–32% in F-cAFS (Fig. 5c). F-cAFS accessible yields did not evolve significantly with time and showed a mean of 693 kg

ha⁻¹. S-cAFS accessible yield increased with time and tended to reach values of 800 kg ha⁻¹ or higher 40 years after establishment (Fig. 5d). Banana stems appeared more numerous in F-cAFS that were [15–30] years of age (Table 2b). Banana density did not however show any significant trend on the long-term (mean of 97.5 in. ha⁻¹) in F-cAFS. Contrastingly, it quickly decreased after S-cAFS establishment as banana stems were then barely found in plots older than 5 years of age (Fig. 5e).

3.2.4. Nutrient cycling

In S-cAFS, leaf litterfall increased the first 20 years after establishment and could not be distinguished from F-cAFS and forest levels from 20 to 30 years onwards (Table 2a; Fig. 6a). S-cAFS total litterfall increased with time but remained lower than that of local forest (Table 2a, Fig. 6d). In F-cAFS, leaf litterfall did not significantly evolve with time and showed a mean of 4.88 t year⁻¹ ha⁻¹. Total litterfall was found lower than that of forest in old F-cAFS (> 50 years) (Table 2b). Total litterfall increased significantly until ca. 40 years in S-cAFS, time at which it reached the F-cAFS total litterfall mean (7.93 t year⁻¹ ha⁻¹; Fig. 6d). No significant differences could be detected for standing litters for both S and F-cAFS (Table 2a, b). Yet, in F-cAFS, regressions showed that leaf standing litter increased with time and could reach values close to 2 t ha⁻¹ for plots older than 80 years – a value corresponding to the mean obtained in S-cAFS at the same age (Fig. 6b). In S-cAFS, total standing litter increased marginally with time (p < 0.1) to reach equivalent amounts to those in F-cAFS already 15–20 years after establishment (mean F-cAFS = 4.19 t ha⁻¹; Fig. 6e). In S-cAFS, total litter cycling significantly increased and could not be distinguished from F-cAFS or forest total litter cycling when over 30 years of age (Table 2a). For F-cAFS, both litter cycling indicators decreased with time and ended up lower than forest indicators, after 30 years for leaf cycling and 50 years for total cycling (Table 2b). Regressions showed that both leaf litter and total litter cycling indicators displayed significant opposite trends between S-cAFS (increasing) and F-cAFS (decreasing) to eventually reach comparable values at ca. 60 years of age (Fig. 6c,e).

3.2.5. Soil quality and contamination

In S-cAFS, soil pH, cation exchange capacity (CEC) as well as soil organic C, total N, exchangeable Ca and Cu concentrations increased

Table 2

Results from ANOVA (F) or Kruskal-Wallis (H) and mean values for the 25 attributes in S- and F-cAFS, savannah and forest controls, from plots with low clay content soils (LCCS, 2a) and plots with high clay content soils (HCCS, 2b). In the case of LCCS plots, age categories were applied only on S-cAFS (2a). In the case of HCCS plots, age categories were applied only on F-cAFS (2b) (see text). °: $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. Differences at $P < 0.05$ between the different age categories and land-uses are indicated by different letters after the mean.

(2a)			Low clay content soils						
Service	Attribute	F or H	savannah	S-cAFS [0-14] years	S-cAFS [15-30] years	S-cAFS [31-50] years	S-cAFS [50 >] years	F-cAFS	forest
Conservation	Perennials shannon index	8.134 ***	1.094 b	1.423 b	1.820 b	1.700 b	1.731 b	1.958 b	2.832 a
	Perennials species richness (nb ha ⁻¹)	25.644 ***	5.0 b	8.0 b	8.0 b	7.3 b	8.0 b	10.7 b	26.0 a
Carbon storage	Large associated trees biomass (t ha ⁻¹)	4.330 *	0.8 b	31.0 b	22.5 b	134.1 ab	103.7 ab	220.0 a	177.2 ab
	Cocoa trees biomass (t ha ⁻¹)	6.531 **	–	2.0 b	11.9 ab	20.7 a	20.1 a	17.5 a	–
Crop production	Density of cocoa trees (nb ha ⁻¹)	0.456	–	1170.8	1593.8	1316.7	1087.5	1320.8	–
	Basal area of cocoa trees (m ² ha ⁻¹)	6.154 *	–	1.272 b	5.906 a	8.504 a	9.081 a	7.442 a	–
	Cocoa trees basal area share (%)	16.448 ***	–	8.4 c	49.0 a	33.6 ab	41.9 a	21.2 bc	–
	Mean accessible yield (kg ha ⁻¹)	4.422 *	–	129.4 b	699.0 ab	919.7 a	1000.8 a	947.6 a	–
Nutrient cycling	Density of banana stems (nb ha ⁻¹)	2.304 °	–	116.7	6.3	4.2	12.5	37.5	–
	Leaf litterfall (t ha ⁻¹)	4.448 *	–	2.3 b	5.4 a	6.1 a	6.2 a	6.3 a	7.4 a
	Total litterfall (t ha ⁻¹)	8.745 **	–	3.4 c	6.4 bc	8.6 bc	7.6 bc	9.0 b	14.7 a
	Leaf standing litter (t ha ⁻¹)	1.313	–	2.1	2.7	2.4	1.1	1.2	0.5
	Total standing litter (t ha ⁻¹)	1.063	–	4.1	5.9	6.4	3.0	5.4	3.2
Soil quality	Leaf litter cycling	2.669	–	0.448	0.517	0.530	0.712	0.591	0.854
	Total litter cycling	3.934 *	–	0.666 b	0.681 b	0.752 ab	0.862 ab	0.869 ab	0.963 a
	pH	4.460 *	5.8 ab	5.5 b	5.8 ab	5.9 ab	6.4 a	6.5 a	6.3 ab
	Organic C (%)	9.132 ***	1.10 bc	0.99 c	1.34 ab	1.52 a	1.54 a	1.58 a	1.61 a
	Total N (%)	6.298 **	0.05 bc	0.04 c	0.10 abc	0.10 ab	0.12 a	0.11 ab	0.14 a
	C:N	5.675 **	20.5 ab	22.3 a	16.1 abc	14.8 bc	13.5 bc	14.6 bc	11.6 c
	Inorganic P (ppm)	2.456 °	1.80	2.83	1.90	6.48	5.22	6.53	7.98
	CEC (cmol kg ⁻¹)	4.733 **	3.0 bc	2.6 c	4.2 abc	4.4 abc	5.6 a	5.0 abc	5.3 ab
	Exchangeable K (cmol kg ⁻¹)	1.902	0.16	0.17	0.17	0.13	0.17	0.20	0.31
	Exchangeable Ca (cmol kg ⁻¹)	5.092 **	1.59 b	1.72 b	3.39 ab	3.32 ab	5.82 a	4.58 ab	4.33 ab
Soil contamination	Exchangeable Mg (cmol kg ⁻¹)	1.712	0.87	0.74	1.34	0.82	1.17	1.27	1.18
	Exchangeable Cu (ppm)	5.165 **	6.20 ab	0.79 b	1.47 b	3.42 ab	8.54 a	3.51 ab	1.57 b

(2b)			High clay content soils						
Service	Attribute	F or H	forest	F-cAFS [0-14] years	F-cAFS [15-30] years	F-cAFS [31-50] years	F-cAFS [50 >] years	S-cAFS	savannah
Conservation	Perennials shannon index	4.237 *	2.571 a	2.276 ab	1.681 ab	1.500 b	1.583 b	1.775 ab	1.452 b
	Perennials species richness (nb ha ⁻¹)	6.492 **	20.5 a	14.0 ab	13.0 ab	9.7 bc	8.3 bc	8.0 bc	2.500 c
Carbon storage	Large associated trees biomass (t ha ⁻¹)	2.113	284.4	248.6	267.5	182.2	124.9	191.2	14.3
	Cocoa trees biomass (t ha ⁻¹)	4.463 *	–	5.3 b	5.1 b	25.9 a	18.2 a	19.2 a	–
Crop production	Density of cocoa trees (nb ha ⁻¹)	3.693 *	–	870.8	937.5	1633.3	895.8	1040.6	–
	Basal area of cocoa trees (m ² ha ⁻¹)	3.795 *	–	2.545	2.548	10.515	8.154	8.369	–
	Cocoa trees basal area share (%)	1.140	–	18.5	6.6	36.5	30.5	30.2	–
	Mean accessible yield (kg ha ⁻¹)	0.080	–	630.9	669.6	723.5	732.6	801.2	–
Nutrient cycling	Density of banana stems (nb ha ⁻¹)	4.842 *	–	62.5 b	175.0 a	112.5 ab	58.3 b	18.8 b	–
	Leaf litterfall (t ha ⁻¹)	3.094 °	7.7 a	5.4 a	7.6 a	5.5 a	5.0 a	5.4 a	–
	Total litterfall (t ha ⁻¹)	4.220 *	15.1 a	8.9 ab	15.4 a	9.1 ab	6.8 b	10.3 ab	–
	Leaf standing litter (t ha ⁻¹)	3.121 °	0.7 a	0.9 a	1.0 a	0.9 a	2.2 a	1.0 a	–
	Total standing litter (t ha ⁻¹)	0.370	4.5	3.5	4.6	4.1	4.8	4.8	–
Soil quality	Leaf litter cycling	10.405 **	0.836 a	0.674 b	0.812 a	0.622 b	0.573 b	0.638 b	–
	Total litter cycling	6.176 **	0.947 a	0.890 a	0.928 a	0.905 a	0.732 b	0.892 a	–
	pH	4.872 *	6.5 a	7.1 a	7.0 a	6.3 a	5.7 ab	6.6 a	4.9 b
	Organic C (%)	1.598	2.18	2.10	2.96	1.76	1.78	2.49	1.43
	Total N (%)	2.233	0.20	0.17	0.24	0.13	0.12	0.19	0.08
	C:N	3.832 *	11.2 b	12.1 b	12.4 b	13.8 ab	15.1 ab	13.4 ab	18.8 a
	Inorganic P (ppm)	4.800 *	7.215 ab	5.716 ab	–	3.977 ab	3.332 b	9.110 a	2.270 b
	CEC (cmol kg ⁻¹)	1.500	8.0	7.3	11.3	5.5	6.9	9.5	5.5
	Exchangeable K (cmol kg ⁻¹)	2.246	0.29	0.33	0.50	0.19	0.19	0.34	0.18
	Exchangeable Ca (cmol kg ⁻¹)	2.356	8.56	10.23	15.86	5.09	4.69	10.16	1.61
Soil contamination	Exchangeable Mg (cmol kg ⁻¹)	1.076	2.14	2.15	2.86	1.38	1.92	2.17	1.11
	Exchangeable Cu (ppm)	0.928	3.44	2.78	4.39	3.48	15.79	14.83	1.93

significantly with time - reaching levels comparable to F-cAFS and/or local forest after 30 or 50 years. Oppositely, the C:N ratio significantly decreased with time (Table 2a). In F-cAFS, soil attributes didn't reveal much significant differences with time, inorganic P was found lower after 50 years old, C:N ratio tended to increase with time while pH

exhibited an opposite trend (Table 2b). Regressions showed that S-cAFS soil pH increased over time to reach that of F-cAFS (ca. 6.1–6.2) 50 years after establishment (Fig. 7a). No significant evolution was found for soil organic C in F-cAFS, these values had large variability (mean = 2%). Soil organic C increased significantly in S-cAFS where

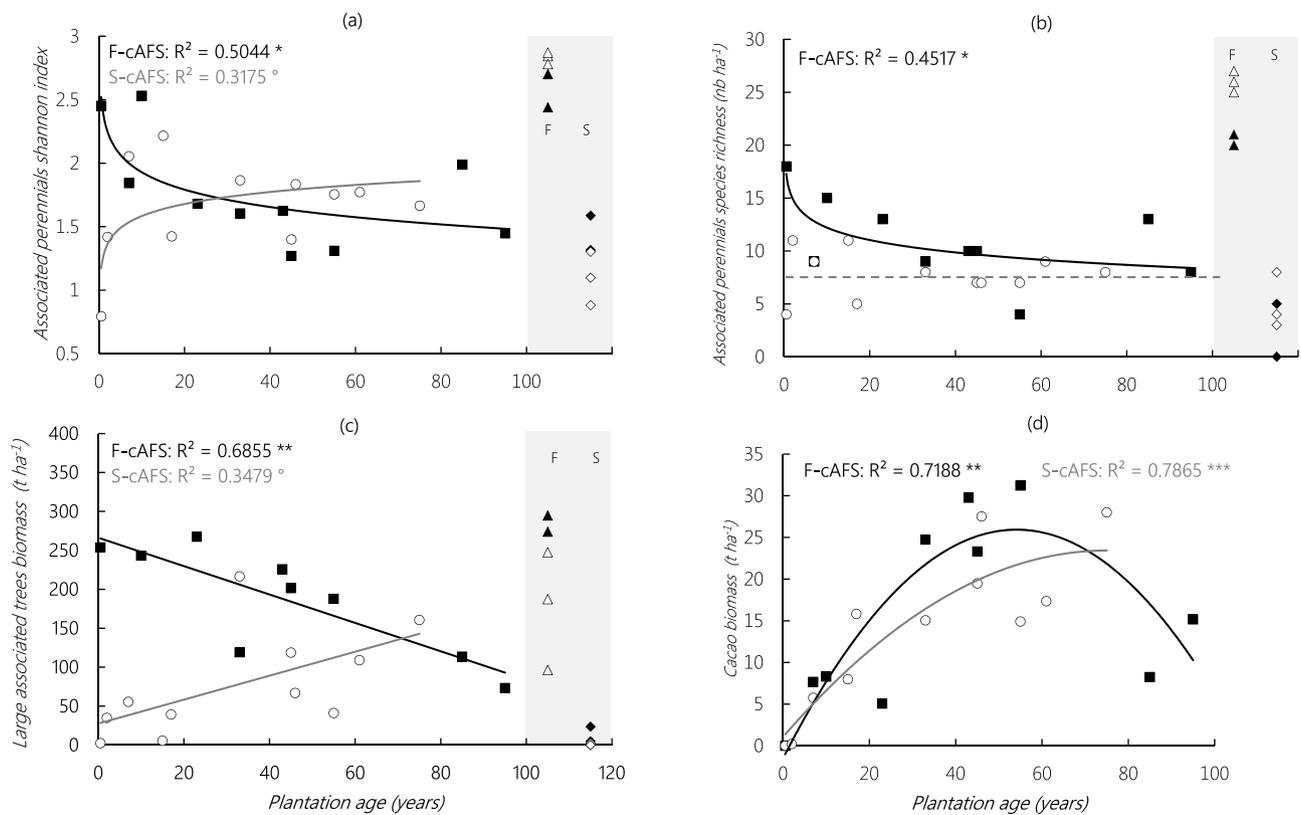


Fig. 3. Temporal evolution of perennial plant Shannon index (a) and species richness (b), large associated trees biomass (c) and cocoa trees biomass (d), in S- and F-cAFS. Plots from the LCCS group (low-clay content soils) are represented with white symbols. Plots from the HCCS (high-clay content soils) are represented with black symbols. Squares: F-cAFS; circles: S-cAFS; triangles: forest (F); diamonds: savannah (S). Control plots (F and S) are shown on the right side of each sub-figure which background appears in light grey. For each indicator, significant temporal evolution is represented by a solid regression line or curve which is black for F-cAFS and grey for S-cAFS. Dashed lines (black for F-cAFS and grey for S-cAFS) correspond to the variables' means when no significant temporal evolution could be found. °: $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$.

the regression showed a ca. 50% increase 70–80 years after plot establishment (Fig. 7b). Regressions showed that 65–70 years after establishment, S-cAFS and F-cAFS exhibited similar levels of soil total N i.e. approx. 0.13% (Fig. 7c). Regressions for soil C:N ratio showed an increase for F-cAFS and a steady decrease for S-cAFS - similar levels (ca. 14) being reached around 50–55 years after plot establishment (Fig. 7d). No significant regression was found for soil exchangeable P in S-cAFS, however a marginal decrease was detected in F-cAFS (mean P

in S-cAFS = 4.8 ppm; Fig. 7e). Regressions made on CEC were not significant in F-cAFS (mean = 7 cmol kg^{-1}) whilst a significant increase was found in S-cAFS (Fig. 7f). No significant regression was found for soil exchangeable K content in S-cAFS (mean = 0.16 cmol kg^{-1}) while the decrease was significant in F-cAFS (Fig. 7g). Regressions made on exchangeable Ca showed a marginal decrease in F-cAFS and a significant increase in S-cAFS - similar levels (ca. 5–5.5 cmol kg^{-1}) being met around 65 years after plot establishment (Fig. 7h).

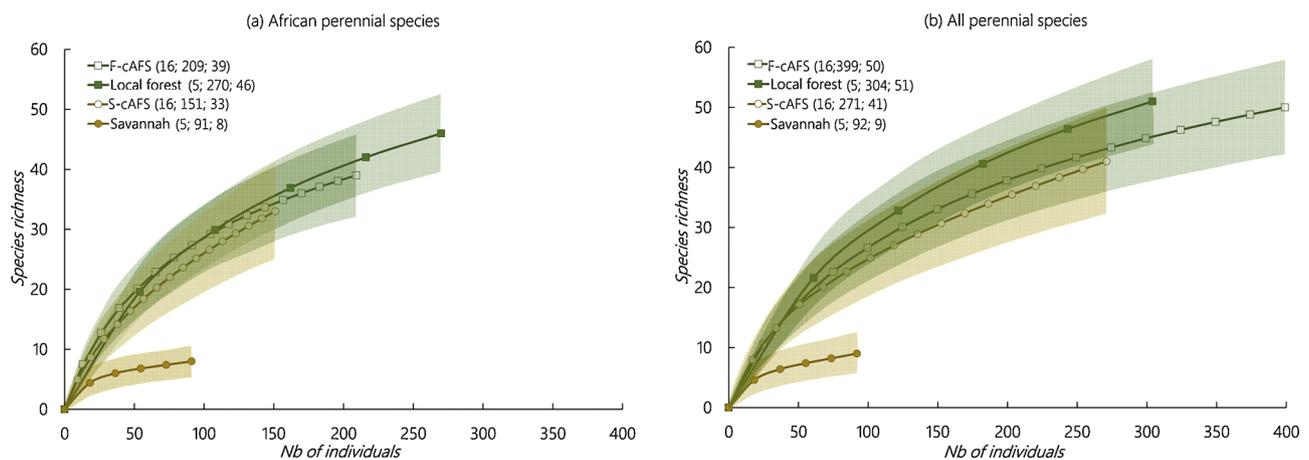


Fig. 4. African (a) and total (b) perennial plant species rarefaction curves for forest (green line with green squares), F-cAFS (green line with white squares), S-cAFS (orange line with white circles) and savannah (orange line with orange circles) plots. The 95% intervals (shaded regions) were obtained by a bootstrap method based on 100 replications. The numbers within the brackets next to the system type correspond to: the number of plots needed (first number) to reach the sample size, the number of individuals counted (second number) and the number of species (third number) obtained for the studied sample size.

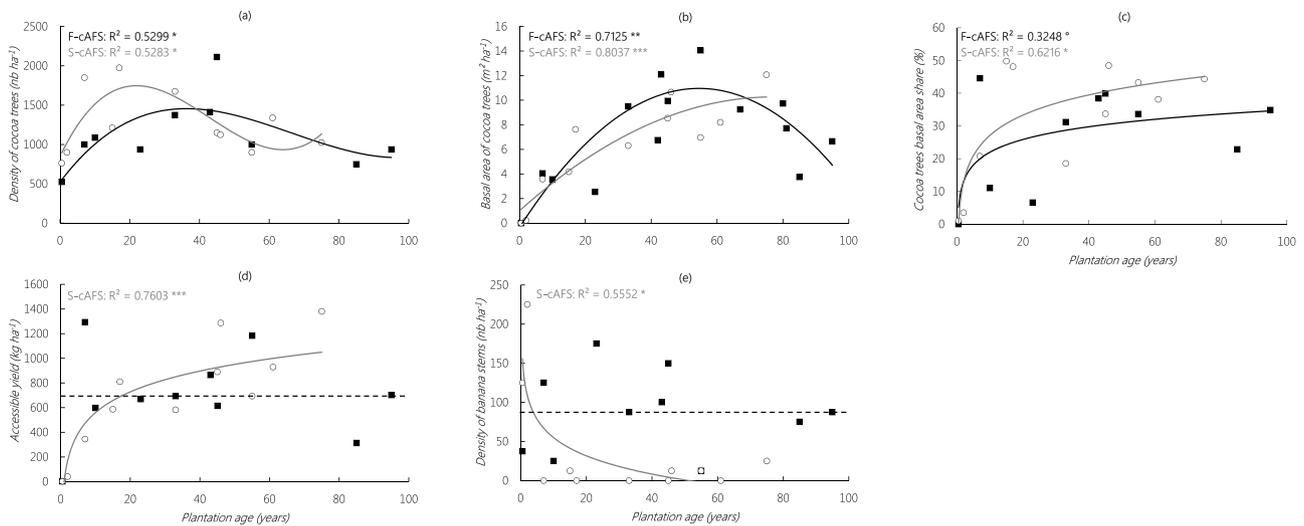


Fig. 5. Temporal evolution of crop production indicators (a to e) in S- and F-cAFS. Plots from the LCCS group (low-clay content soils) are represented with white symbols. Plots from the HCCS (high-clay content soils) are represented with black symbols. Squares: F-cAFS; circles: S-cAFS; triangles: forest (F); diamonds: savannah (S). Control plots (F and S) are shown on the right side of each sub-figure which background appears in light grey. For each indicator, significant temporal evolution is represented by a solid regression line or curve which is black for F-cAFS and grey for S-cAFS. Dashed lines (black for F-cAFS and grey for S-cAFS) correspond to the variables' means when no significant temporal evolution could be found. °: $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

Regressions showed no significant evolution for exchangeable Mg, neither in S-cAFS nor in F-cAFS (mean: S-cAFS = 1 cmol kg⁻¹; F-cAFS = 1.9 cmol kg⁻¹; Fig. 7i). Finally, regressions made on soil exchangeable Cu content showed a significant increase in S-cAFS while no trend could be established for F-cAFS (mean = 7 ppm, Fig. 7j).

4. Discussion

4.1. S-cAFS and F-cAFS general trajectories

Our results demonstrated that F- and S-cAFS underwent highly contrasting trajectories after their establishment. Ecosystem attributes related to soil quality, plant diversity and nutrient cycling appeared to generally converge among S-cAFS and F-cAFS along the chronosequences studied, whereas attributes related to crop production varied in a more similar way. Overall our results revealed that, for the pool of attributes and services studied, agroforestry systems always

evolved away from their past land-use state. Such differences became statistically apparent after 15 to 30 years for S-cAFS and after 30 to 50 years for F-cAFS. Hence, depending on attributes, past land-use legacies differed in magnitude and lasted from a few years to several decades. S- and F-cAFS displayed comparable levels of most attributes after a certain timespan, as previously suggested by other studies in the same region (Jagoret et al., 2012; Saj et al., 2017a; Nijmeijer et al., 2018). However, for other attributes the temporal projections did not seem to display a stabilization phase at later stages. It suggests that these attributes, after converging at intermediate time scales, may keep evolving in contrasting directions for S- and F-cAFS. This could be related to the different types of soils studied (Adeniyi et al., 2017) as well as farmers' differential management within a generation and between generations (Jagoret et al., 2018a) - both putatively altering ecosystem's functioning. Answering this question would need further investigations on a broader array of soil types and longer timespans.

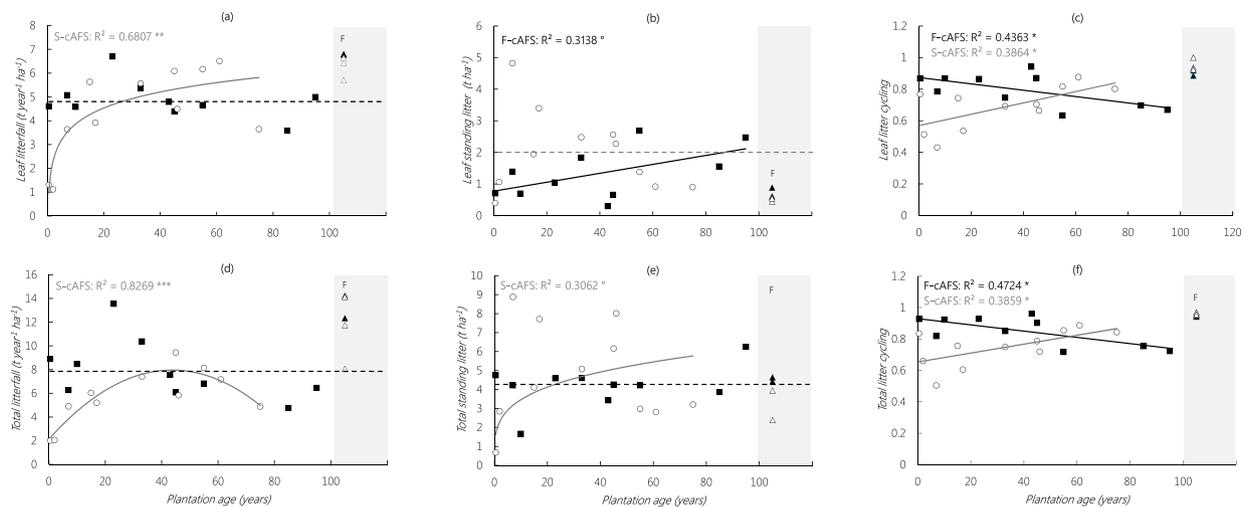


Fig. 6. Temporal evolution of litter dynamic indicators (a to f) in S- and F-cAFS. Plots from the LCCS group (low-clay content soils) are represented with white symbols. Plots from the HCCS (high-clay content soils) are represented with black symbols. Squares: F-cAFS; circles: S-cAFS; triangles: forest (F); diamonds: savannah (S). Control plots (F and S) are shown on the right side of each sub-figure which background appears in light grey. For each indicator, significant temporal evolution is represented by a solid regression line or curve which is black for F-cAFS and grey for S-cAFS. Dashed lines (black for F-cAFS and grey for S-cAFS) correspond to the variables' means when no significant temporal evolution could be found. °: $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

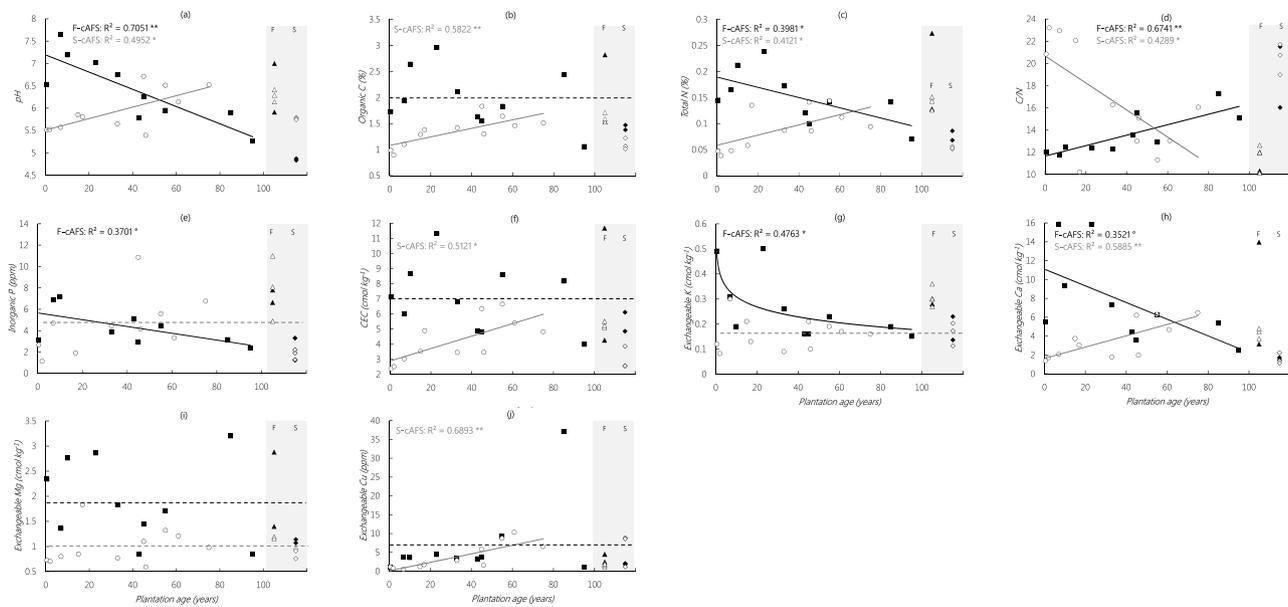


Fig. 7. Temporal evolution of soil quality (a to i) and pollution (j) indicators in S- and F-cAFS. Plots from the LCCS group (low-clay content soils) are represented with white symbols. Plots from the HCGS (high-clay content soils) are represented with black symbols. Squares: F-cAFS; circles: S-cAFS; triangles: forest (F); diamonds: savannah (S). Control plots (F and S) are shown at the right side of each sub-figure which background appears in light grey. For each indicator, significant temporal evolution is represented by a solid regression line or curve which is black for F-cAFS and grey for S-cAFS. Dashed lines (black for F-cAFS and grey for S-cAFS) correspond to the variables' means when no significant temporal evolution could be found. *: $P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

4.2. Ecosystem services temporal trajectories

4.2.1. Species conservation

Our results underlined the relatively fast (ca. 20 years) convergence in terms of perennial species diversity between S- and F-cAFS. Interestingly, S-cAFS exhibited a large number of African species. This high number of native species in S-cAFS could be explained by the important gene bank (native trees, seeds and seedlings) present in their soils or in that of nearby forests or agroforests. Such a result also points at the active introduction, preservation or transfer of these species into S-cAFS (Jagoret et al., 2018b). Interestingly, rarefaction curves highlighted the similarity of species accumulation between S- and F-cAFS. Yet, despite a fair proportion of African species (over 50% of associated individuals), S-cAFS demonstrated an overall lower potential of conservation since the abundance of associated perennials was found lower than in F-cAFS (Nijmeijer et al., 2018). Besides, some species occurred in S- or F-cAFS even they were not present in forest controls. This was the case of locally consumed *Cola* species but also of *Entandrophragma cylindricum*, a commercial timber species, which is currently classified 'vulnerable' in the IUCN red list (IUCN, 2018). All in all, F-cAFS still exhibited a forest legacy a century after establishment whilst both S- and F-cAFS showed an ability to enrich the local pool of species. Our study emphasised the important role that both agroforestry systems may currently play in the region in perennial species conservation, even though they do not preserve as many species as forests (De Beenhouwer et al., 2013; Mortimer et al., 2017). Furthermore, since associated diversity and abundance are largely driven by the practices and uses of associated flora (Jagoret et al., 2014; Saj et al., 2017a), a particular attention shall be given to old systems which rejuvenation depends on farmer strategies and may eventually lead to less multifunctional and simplified systems (Saj and Jagoret, 2017; Jagoret et al., 2018b).

4.2.2. Carbon storage

In terms of C storage, the land-use legacy appeared very significant in young systems and tended to disappear on the long term. While the biomass of large associated trees of S-cAFS increased steadily over decades, it decreased in F-cAFS. These results underline the ability of S-cAFS to gain in C storage with ageing, at least up to a certain point (Saj

et al., 2013). The results further emphasised the slow, but steady, decrease in C storage abilities in F-cAFS. In a region where old cAFS are numerous (Jagoret et al., 2011), such results point to the need to include selection/management (at the species and individual level) of potentially large trees in the renewal process of these systems (Jagoret et al., 2018b). Such management schemes would lead to the renewal of mature and old systems whilst keeping good C storage abilities. However, the timespans - and levels - of C storage of Cameroonian cAFS remain highly significant in comparison to other agricultural systems or cocoa monocultures (Schroth et al., 2015; Schneidewind et al., 2018).

4.2.3. Crop production

The attributes chosen to indicate cocoa production abilities correspond to cocoa stands' or system attributes known for their contribution to yield in the studied systems (Saj et al., 2017b). The higher density of cocoa trees in S-cAFS compared to F-cAFS up to 20–30 years after establishment may reflect the insurance practices of local farmers which often "overseed" their S-cAFS to control grasses such as *Imperata cylindrica* (Jagoret et al., 2012). These practices probably support successful establishments since accessible yields in S-cAFS appeared overall similar or slightly higher than that of F-cAFS plots. Except for very young S-cAFS, where banana stems provide beneficial shade to young cocoa seedlings and temporary income/food/feed (Jagoret et al., 2012), banana stems appeared more numerous in F-cAFS than in older S-cAFS. This discrepancy could underline farmer practices favouring cocoa in soils where competition for water can be harsh as the S-cAFS studied were established on relatively sandy soils (van Vliet and Giller, 2017). It could also underline the differential role S- and F-cAFS may have in the provision of co-products (Jagoret et al., 2012; Saj et al., 2013). Such differentiations may be interpreted as management legacies inherited from past land-use or adaptation to soil type. Furthermore, cocoa yields reached comparable levels at the latest 15 years after cAFS establishment. This confirms that, despite unfavourable conditions in savannah (such as low soil fertility, weed competition and almost no shade trees), afforestation is clearly achievable using shaded cocoa (Jagoret et al., 2012). Finally, the constantly lower basal area share of cocoa trees in F-cAFS compared to S-cAFS may be considered as a legacy from previous land use (forest) as mature trees are already

present at establishment. It can be hypothesised that the maintenance of these trees with an already developed canopy may alter light capture on the long term (Blaser et al., 2017).

4.2.4. Nutrient cycling

Litterfall and its subsequent decomposition are considered to be effective in the improvement and conservation of soil quality and, as such, play an important role in the regulation of nutrient cycling (Vitousek and Sanford, 1986; de Carvalho et al., 2014). Litterfall in S-cAFS increased steadily up to 40–50 years after establishment, reaching the levels of F-cAFS litterfall. In F-cAFS the forest legacy maintained a leaf litterfall amount close to that of the initial forest. The litter cycling indicators clearly showed an increase in S-cAFS contrasting with a decrease in F-cAFS. These indicators show comparable levels around 50 years, suggesting a convergence for both S- and F-cAFS. The temperature and moisture levels in forests with a closed canopy generally favour decomposition of litter and could explain the lower standing litter of the forest control plots compared to the more open canopy of cAFS (Prescott, 2002; Steffan-Dewenter et al., 2007). The probably drier and warmer conditions in young S-cAFS, which are still lacking a closed canopy and producing mainly low quality cocoa litter (Dawoe et al., 2010), could also explain the higher litter stock in young S-cAFS, despite their lower litter production. Overall, the similar cocoa productivity after savannah and forest conversions may suggest that, while young cocoa plantations established after savannah benefited less from the nutrients released by litter decomposition than those established on forest, the lower competition for light they encountered offset the low soil fertility and actually authorised an equivalent productivity level compared to young F-cAFS (Blaser et al., 2017). Besides, as cAFS mature and the cocoa stands develop, the poor quality of cocoa leaf litter and its subsequent lower decomposition rate (Dawoe et al., 2010) may account for the slight increasing leaf standing litter noticed in F-cAFS chronosequence.

4.2.5. Soil quality and contamination

In S-cAFS established on low clay content soils many of the studied attributes exhibited a steady evolution with time underlining an overall improvement of soil quality and nutrient availability. This improvement can be explained by the increase of litter - and linked litter cycling - in S-cAFS over time when compared to the very low soil organic content (SOC) content and litter cycling of the initial savannahs. This was not the case in F-cAFS established in high clay content soils where a decrease in pH, K and Ca and an increase of the C:N ratio may point to a low but steady decline of soil quality and nutrient availability – results in line with the recent study of Adeniyi et al. (2017). Noticeably, soil Cu concentrations seemed to increase with time at least in S-cAFS and could point to a putative soil contamination by pesticides, as farmers use copper oxide or hydroxide to treat against black pod disease (Sonwa et al., 2008; Jagoret et al., 2011). As a result of the differences in previous land-uses (savannah vs. forest) - emphasised by the differences in soil texture (LCCS vs HCCS) – the convergence of soil attributes between S- and F-cAFS took a long the timespan: 40–60 years after plot establishment. This timespan may have been increased by the lower soil clay content of the initial savannah. Indeed, Nijmeijer et al. (2018) found that the annual increase in SOC concentration of S-cAFS was lower in soils with low clay content (10–15%) than in soils with higher clay content (20–25%). In the same way, Feller et al. (2001) reported that the annual rate of soil carbon increase was lower in a degraded than in a non-degraded soils. Soil organic C concentration is generally positively related to fine silt and clay content (Plante et al., 2006). As CEC is a positive function of soil clay and organic carbon concentrations, forest soils also may have had intrinsically larger nutrient contents than savannah soils.

The values found for macronutrients fell within the range already

noticed in Cameroonian cAFS (Duguma et al., 2001). Yet, soil organic matter (represented here by the SOC) did not decrease in F-cAFS after conversion contrasting with other studies (Yang et al., 2004; Snoeck et al., 2010). The forest control plots in our study region were highly disturbed with low and rather similar litter production as in F-cAFS, which may explain the rather similar SOC contents of both systems. Furthermore, the production of cocoa was reported to be linked to the acidification of the soil (Hartemink, 2005; Snoeck et al., 2010; Adeniyi et al., 2018). However, despite a clear decrease over the long term, pH in F-cAFS did not show significant differences with the forest control. Other studies revealed idiosyncratic results (Dawoe et al., 2010; Isaac and Kimaro, 2011) and it may be hypothesised that the composition and abundance of associated trees and their diverse litter restitution to the soil could account for such results (Finzi et al., 1998). This could also partly explain the pH increase with time in S-cAFS. The overall lower pH and nutrient contents in savannah plots might be explained by annual burning and periodical cultivation of savannah with staple crops, practices which are known to lead to extensive carbon and nutrient losses resulting in soil desaturation (Kugbe et al., 2012; Dubiez et al., 2018). The low levels of soil C and N in savannah plots are in accordance with previous studies (Lal and Bruce, 1999; Jagoret et al., 2012). However, the increase of organic C in older S-cAFS showed that the systems were able to build-up SOC over time and increase their soil fertility which may support cocoa yield (Adeniyi et al., 2018). The decreasing trajectory exhibited by K in the soils of F-cAFS after conversion may be linked to lower recycling of K in cAFS than in forest and high absorption of K by cocoa trees and its exportation with cocoa-beans harvest (van Vliet and Giller, 2017). Yet, in S-cAFS, the relative stability of K at a minimum level over time and the trend towards these K levels in F-cAFS after around 80 years suggests that K input to the top soil through recycling (litter and throughfall) (Hartemink, 2005) could, at least partly, compensate K loss through cocoa bean exports.

5. Conclusion

As a whole, the 25 attributes related to the six ecosystem (dis)services (ES) studied underwent distinct temporal trajectories and showed that S- and F-cAFS could be significantly distinguished from their past land-use, savannah and forest, after 30 and 50 years, respectively. Past land-use legacies were strong enough to last decades but, in the end, S- and F-cAFS agroforests revealed typical and largely convergent profiles despite different initial systems and soil types. Such results indirectly point to the role of farmers in the establishment and maintenance of decade-old agroforestry systems as well as the significant contribution of associated plant diversity to ES provision in these systems. The levels and timespans at which the studied complex cAFS provide multiple ES are worth comparing with simpler (or full sun) systems. In the current context of climate change, where the choice of species and densities of associated perennials in cocoa plantations are debated, such multifunctionality comparisons could help determine long-term strategies which would use plant biodiversity as an actionable lever to adapt and mitigate climate change.

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Appendix A. Results from ANOVA (F) and mean values of the 25 studied ecosystem attributes in S- and F-cAFS, savannah and local forest controls, irrespective to their soil clay content and age. °: P < 0.1; *: P < 0.05; **: P < 0.01; *: P < 0.001. Differences at P < 0.05, after SNK test, between land-uses are indicated by different letters after the mean**

Service	Attribute	F	savannah	S-cAFS	F-cAFS	forest
Conservation	Perennials shannon index	15.141 ***	1.238 c	1.707 b	1.749 b	2.727 a
	Perennials species richness (nb ha ⁻¹)	48.072 ***	4.0 c	8.1 b	10.6 b	23.8 a
Carbon storage	Large associated trees biomass (t ha ⁻¹)	5.629 **	6.2 b	107.1 a	161.9 a	220.1 a
	Cocoa trees biomass (t ha ⁻¹)	0.13	–	15.4	14.19	–
Crop production	Density of cocoa trees (nb ha ⁻¹)	0.027	–	1174.2	1197.7	–
	Basal area of cocoa trees (m ² ha ⁻¹)	0.049	–	6.812	6.509	–
	Cocoa trees basal area share (%)	0.779	–	31.5	26.3	–
	Mean accessible yield (kg ha ⁻¹)	0.011	–	716.7	701.9	–
	Density of banana stems (nb ha ⁻¹)	4.225 *	–	33.6 b	97.7 a	–
Nutrient cycling	Leaf litterfall (t ha ⁻¹)	4.451 *	–	4.5 b	5.2 b	6.5 a
	Total litterfall (t ha ⁻¹)	8.951 **	–	6.7 b	8.0 b	12.1 a
	Leaf standing litter (t ha ⁻¹)	0.705	–	4.8	4.7	3.7
	Total standing litter (t ha ⁻¹)	3.031 °	–	1.8 a	1.4 ab	0.6 b
	Leaf litter cycling	3.522 *	–	0.497 b	0.533 b	0.640 a
	Total litter cycling	5.964 *	–	0.785 b	0.844 b	0.952 a
Soil quality	pH	4.249 *	5.4 b	6.1 a	6.4 a	6.4 a
	Organic C (%)	1.958	1.23	1.660	1.85	1.84
	Total N (%)	3.687 *	0.06 b	0.116 ab	0.14 a	0.16 a
	C:N	4.625 **	19.8 a	15.9 b	14.4 b	11.4 b
	Inorganic P (ppm)	4.379 *	1.99 b	5.44 a	4.74 a	7.67 a
	CEC (cmol kg ⁻¹)	1.189	4.0	5.6	6.2	6.4
	Exchangeable K (cmol kg ⁻¹)	1.680	0.17	0.21	0.24	0.30
	Exchangeable Ca (cmol kg ⁻¹)	2.016	1.60	5.20	6.34	6.02
Soil contamination	Exchangeable Mg (cmol kg ⁻¹)	1.921	0.97	1.30	1.70	1.56
	Exchangeable Cu (ppm)	0.469	4.49	6.79	5.44	2.32

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