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The effect of land use on aboveground biomass and soil quality indicators in spontaneous forests and agroforests of eastern Amazonia

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Abstract This study unites physicochemical indicators of aboveground vegetation, litter layer and topsoil (0–20 cm) in contrasting vegetation types commonly found in the eastern Amazonia. We compare three agroforestry systems (enriched fallows, homegardens and commercial plantations) with three spontaneous forest types (young and old secondary forests and mature rainforests) via one-way ANOVA, linear and non-linear regressions and multivariate analyses. Agroforests had significantly lower understory biomass when compared with young secondary forest. Commercial plantation agroforests had higher topsoil pH and Ca-contents and homegardens had higher K-contents and P-availability hotspots, as revealed by their higher variance and single very high values. Agroforests and spontaneous forests were similar in their litter biomass (both leaves and twigs) and C:N ratio, and in soil organic matter and P contents. The overstory negatively impacted the understory ($r^2 = 0.20, p < 0.05$) and the understory correlated significantly with the litter layer ($r^2 = 0.11, p < 0.07$). By contrast, there were no direct relationships between overstory and the litter layer, pointing to a major discontinuity between vegetation and topsoil. Principal component analysis depicted a successional sequence of systems, with homegardens closest to mature rainforests. According to co-inertia analysis, plant biomass was more strongly related to topsoil in spontaneous forests than in agroforests. Altogether, agroforests were similar to mature rainforests in a wide range of variables of the vegetation, litter and topsoil, and co-inertia analysis indicated that agroforestry management can alter this continuum. Our results point to an outstanding position of homegardens in the study region, with higher aboveground biomass and elevated nutrient availability which may have been caused by the traditional sweep-and-burn low-intensity fire regime prevalent throughout Amazonia and beyond.

Keywords Homegardens · Enriched fallows · Commercial plantation agroforestry · Secondary forest · Shifting cultivation · Sweep-and-burn

Introduction

Anthropogenic pressure on agricultural lands continues to be high throughout the tropics and notably in eastern and southern Amazonia, an area also known as

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the ‘arc of deforestation’. After the first deforestation cycle of pristine rainforests (de las Heras et al. 2011), spontaneous regrowth of secondary forest develops on abandoned pastures and shifting cultivation fields. Shifting cultivation is the predominant land-use system adopted by the majority of low-income rural populations in the region.

However, this land-use system contributes to environmental degradation, slower secondary forest regeneration, lower biodiversity, increased dominance of aggressive ruderal species, and impoverished soil fertility, altogether leading to rural poverty (Satyam Verma 2012). The soils of the humid tropics are particularly vulnerable to degradation because of fast organic matter decomposition and mineralization as well as nutrient losses caused by leaching (Markewitz et al. 2004). Degradation caused by repeated slash-and-burn practice and reduced fallow periods lowers agricultural productivity and ultimately leads to rural poverty (Varma 2003). Maintenance or restoration of the soil ‘productive potential’ is a central pillar of sustainable land use (Boddey et al. 2003). Agroforestry has been proposed as a viable alternative for shifting cultivation in the tropics, as it can improve soil quality (Pinho et al. 2012), increase system stability (Mohri et al. 2013) and reduce economic risks because of better market flexibility via multiple products (Souza et al. 2012). Trees are a key factor for maintaining soil fertility in agroforestry due to nutrient pumping and safety-net mechanisms (Seneviratne et al. 2006).

Depletion of soil nutrients as the outcome of non-sustainable land-use intensification can cause reductions in above- and belowground biodiversity, ecosystem functioning and stability (Thiele-Bruhn et al. 2012). The diversity of agroforestry systems is very large (Atangana et al. 2014); therefore, the ecological and social sustainability of these systems is likewise expected to vary widely. Here, we assess the impact of different land-use forms, which are three agroforestry systems: enriched fallows, homegardens and commercial plantations; and three types of spontaneous vegetation: young and old secondary regrowth and mature rainforests on aboveground vegetation, litter layer and topsoil physical and chemical characteristics in eastern Amazonia (north-central Maranhão and eastern Pará states), and we explore system-related differences along the vegetation–litter-topsoil continuum.

Materials and methods

Study region and site clusters

Research was conducted on 32 study sites in the eastern periphery of Amazonia across five counties aggregated into two regional clusters (Table 1). Pastures and secondary forests have almost entirely replaced the original rainforests in central Maranhão and eastern Pará states. Maximum distance between sites within each county was less than 30 km while the maximum distance between counties in each regional cluster was less than 150 km. Seventeen of the 32 sites were located in central-northern Maranhão state and the others were located approximately 400 km further west in Tomé-açu county in eastern Pará state. Climate is classified according to Köppen as *Aw* and *Ami* and varies slightly between the two regional clusters, with 2100 and 2300 mm annual rainfall, and with 6 and 5 months hydric deficit in central Maranhão and eastern Pará states, respectively. Soils are nutrient-poor acid Oxisols and Ultisols (USDA 2010). The topsoil texture was classified as ‘loamy/fine-sand’ and varied little between sites and clusters (sand average = 72.88 ± 17.11 %, silt average = 12.97 ± 18.63 % and clay average = 14.15 ± 7.21 %). There were no differences in soil texture between systems, counties and regional clusters.

Spontaneous forest and agroforest system classification

We compared three types of spontaneous forest with three types of agroforest, which were distributed into two regional clusters and five counties (Table 1). Site classification was based on previous work by Cardozo et al. (2015) as follows.

Spontaneous forest types

Secondary forests Spontaneous secondary forest regrowth following slash-and-burn shifting cultivation or on abandoned pastures. We divided these into ‘young’ (≤12 years old; SFY) and ‘old’ (20–26 years old; SFO). The most common species were the babassu palm (*Attalea speciosa* Mart.), together as *Cecropia* sp., *Inga* sp., *Astrocaryum vulgare* Mart., *Lecythis* sp., and *Carica microcarpa* Jacq.

Table 1 Numbers (in parentheses) and distribution of the 32 study sites within the two regional clusters and five counties, showing wegetation characteristics and site use histories of the study sites in Eastern Amazonia

Forest system	System type	Region	County	Location[a]
Spontaneous forest (9)	Young secondary forest (4)	Maranhão	São Luís (2)	2°59′12.0″S–44°20′52.2″W
				2°59′11.2″S–44°20′52.6″W
		Pará	Tomé-açu (2)	2°24′06.6″S–48°11′48.4″W
				2°24′29.0″S–48°11′52.3″W
	Old secondary forest (3)	Maranhão	São Luís (2)	2°58′44.5″S–44°21′14.5″W
				2°58′44.2″S–44°20′52.6″W
		Pará	Tomé-açu (1)	2°24′45.7″S–48°11′51.2″W
	Mature forest (2)	Pará	Tomé-açu (2)	2°23′39.1″S–48°09′51.6″W
				2°30′05.6″S–48°17′26.2″W
Agroforest (23)	Enriched fallow (6)	Maranhão	Anajatuba (2)	3°26′58.2″S–44°23′13.3″W
				3°11′31.3″S–44°35′29.3″W
			Morros (3)	2°53′10.0″S–44°09′23.5″W
				2°59′48.9″S–43°55′05.0″W
		Pará	Tomé-açu (1)	2°32′38.4″S–48°16′26.7″W
	Homegarden (11)	Maranhão	Anajatuba (3)	3°14′59.0″S–44°36′46.8″W
				3°15′00.6″S–44°36′43.5″W
			Arari (5)	3°33′40.8″S–44°49′57.3″W
				3°33′08.6″S–44°49′10.5″W
		Pará	Tomé-açu (3)	2°11′31.9″S–48°08′41.9″W
				2°11′55.9″S–48°09′17.2″W
	Commercial plantation (6)	Pará	Tomé-açu (6)	2°12′32.2″S–48°17′44.2″W
				2°33′11.0″S–48°07′39.2″W

[a] For counties with more than two sampling sites per system, we give regional coordinates

Mature rainforest (MF) Original mature forest without visible human perturbation (one site) or with low-intensity selective logging >60 years ago (one site). The most common species were *Holopyxidium latifolium* (Ducke) R. Knuth, *Manilkara* sp., *Copaifera langsdorffii* Desf., *Carapa guianensis* Aubl., and *Protium* sp.

Agroforest types

Enriched fallow agroforest (EFA) Established by enrichment planting of fruit and timber species in the understory of 15- to 25-year-old secondary forest. The most common crops were cupuassu (*T. grandiflorum* K. Schum), açaí (*Euterpe oleracea* Mart.), and cacao (*Theobroma cacao* L.), spaced at distances of 3–4 m.

Homegarden agroforest (HA) Tall multistrata agroforests surrounding houses, virtually omnipresent in our study region and elsewhere. This system has a particular fire regime called 'sweep-and-burn' (Winklerprins 2009), the regular sweeping and subsequent burning of litter piles in order to keep the surroundings of the houses 'clean' and to avoid mosquitoes, spiders, snakes, etc. Dominant overstory plants are mango (*Mangifera indica* L.), jackfruit (*Artocarpus integrifolia* L.) and açaí, with banana (*Musa* spp.), cupuassu and cacao in the understory,

Commercial plantation agroforest (CPA) Regularly-spaced plantations with inorganic fertilization and liming. This system was inspired and developed by Japanese immigrants. Main products are fruits of cacao, cupuassu, açaí and black pepper (*Piper nigrum* L.).

Not all systems occurred in both regional clusters. Implications of the resulting unbalanced scheme are further discussed in "Variables under investigation" and "Vegetation, litter and topsoil variables across land-use systems and between regions" sections.

Within-site sampling scheme

We adopted a joint sampling scheme to guarantee compatibility between all of our datasets. Vegetation and litter sampling methods strive to capture 'plant influence zones'; sensu Rhoades (1996). We estimated large tree aboveground biomass in a main circular plot and minor vegetation and litter in five subplots (Coomes et al. 2002) (see Fig. 1a). Topsoil (0–20 cm) was collected as composite samples from the centers of the five subplots.

In the CPA sites, we adapted our sampling-scheme to the predominating regular spacing. Instead of a circle, we used six sub-plots (3 × 5 m) in three quadrangular main plots of 25 × 25 m (Fig. 1b). This sampling scheme has been shown to generate reliable estimates of system totals and to be superior to circular sampling geometry in regularly spaced plantations (Kato et al. 2009). We subsequently corrected for the 4.5 % smaller total sampling area in this alternate scheme. During site selection, we discarded large border zones to neighboring vegetation.

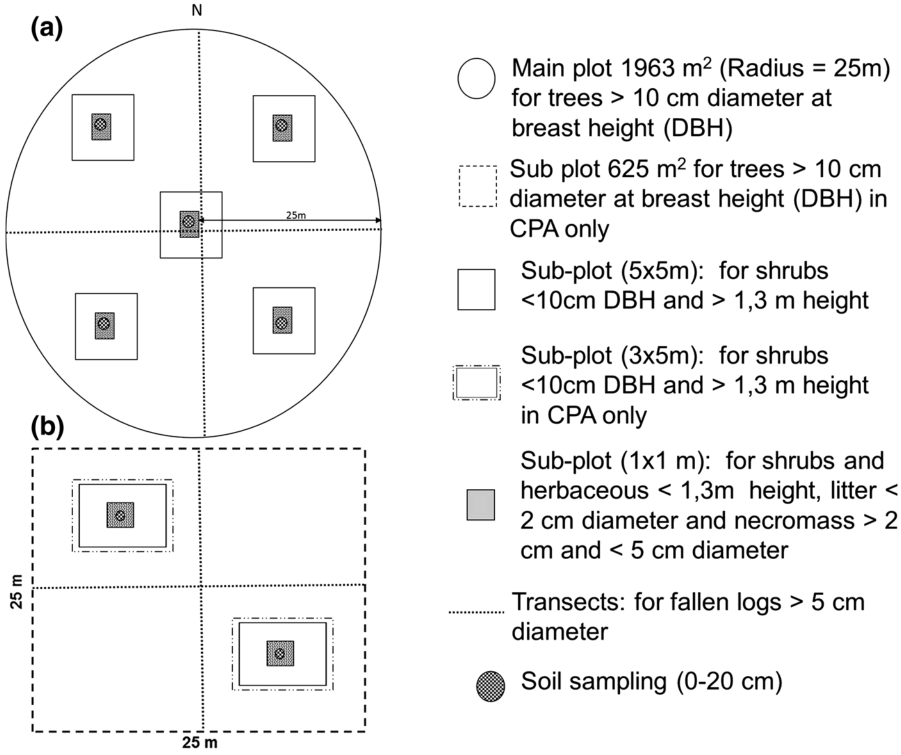
Variables under investigation

Large biomass components were estimated allometrically by Muchavisoy (2013) by utilizing diameter-based equations as well as conversions between diameter at breast height (dbh) and diameter measured at 30 cm height for smaller vegetation components (Gehring et al. 2008). These and further species-specific equations utilized in this study are detailed in Annex 1.

Small vegetation (<1.30 m height) was estimated destructively jointly with the litter layer in the 1 × 1 m subplots, by complete harvesting and subsequent in situ separation into biomass fractions wood and leaf of trees, lianas and palms, herbaceous, gramineous, as well as leaf and twig litter. We estimated dry-matter content in representative subsamples of each of these fractions by comparing the fresh weights (in situ) and the dry weights, which were taken after 2 weeks at 65 °C.

We distinguish biomass of the following components: large vegetation (trees with dbh ≥ 10 cm and palms >2 m height) were grouped as aboveground biomass (AGB) of plants larger than 10 cm dbh (AGB ≥ 10 cm dbh), mid-sized vegetation (trees, shrubs and lianas with dbh < 10 cm and palms <2 m height), and small vegetation (destructively sampled herbaceous and shrubs smaller than 1.30 m height). For statistical analyses, we combined mid-sized and small vegetation as the above ground

Fig. 1 Sampling units with differently-sized and replicated sampling areas for vegetation, litter and topsoil for **a** the spontaneous forests, enriched fallow and homegardens and for **b** CPA only



biomass smaller than 10 cm dbh (AGB $<$ 10 cm dbh). We estimated the necromass of fallen logs in four transects (Van Wagner 1968) and standing dead logs in the circular main plots, following the methods of Arevalo et al. (2002). We destructively quantified and sampled the litter layer during the rainy season, in five 1 × 1 m sub-quadrants within each sampling unit, distinguishing between leaf and twig litter biomass. Total aboveground biomass (TAGB) was considered as the sum of all above-mentioned components.

To characterize topsoil physical quality, we measured (1) soil bulk density (volumetric rings), and (2) soil texture (pipette method), utilizing procedures described in Klute et al. (1986). To characterize topsoil chemistry, we measured the pH (0.01 M $CaCl_2$ suspension), soil organic matter content (Walkley–Black method; Walkley and Black 1934), available P (extraction with synthetic anion exchange resin Amberlite IRA-400) and exchangeable K (Mehlich I), Ca, Mg (KCl extraction) and H + Al (SMP method), following IAC (2001) routines. C- and N-concentrations in leaf-litter samples were determined with Walkley–Black and Kjeldåhl digestion (Tedesco et al. 1995), respectively.

Statistical analyses

Basic and univariate statistics

Kolmogorov–Smirnov and Lilliefor's tests were used for checking the normality of the data. Most variables followed a normal distribution or could be normalized via $\log_{10}$ or $\log_{10}(x + 1)$ transformation, with the exception of the leaf litter C:N-ratio, for which we utilized non-parametric procedures (Spearman correlations, Kruskal–Wallis ANOVA with rank-based Dunn's test). Homogeneity of variance was checked by using Brown–Forsythe test for unequal replication numbers. Outliers and extremes ($>$1.5 × SE) were excluded: one value for organic matter, two for twig biomass and one for total aboveground biomass (in a CPA with Brazil-nut trees). For between-group comparisons and regressions, significance-level as 5 % default and tendencies with $<$10 % significance-level were established.

Two single systems or groups of vegetation-types were investigated via *t* tests, and multiple systems jointly via one-way ANOVAs and subsequent post hoc Spjøtfoll–Stoline tests (HSD Tukey for unequal replication numbers). Relationships between pairs of variables via linear and non-linear regressions were investigated. These analyses were conducted with Statistica 8.0 (StatSoft, 2007), graphs were generated with SigmaPlot 11.0 (Systat, 2008) and in R.

Multivariate statistics

Principal component analysis (PCA), between-class analysis (BCA) (Chessel et al. 2004), co-inertia analysis (CIA) (Dray et al. 2003) and permutation Monte Carlo significance tests were used for data synthesis. PCA was adopted to investigate variation of the entire dataset and BCA to isolate the system grouping contributions to data variability.

CIA investigates relationships between two or more datasets (Dray et al. 2003), which in our case were the biomass and soil datasets. We utilized a between-class CIA, which is a procedure that maximizes the covariance between groups, rather than between individual cases. We measured overall similarities using a multivariate extension of the Pearson correlation, the Rv coefficient.

R environment (R Development Core Team 2007) and "ade4" library were used for the multivariate analyses (Chessel et al. 2004).

Analysis of regional variance

Our experimental design was unbalanced, due to the non-occurrence of some systems in some clusters (see "Spontaneous forest and agroforest system classification"). We addressed the unbalanced design by searching for between-region (states) differences for the two systems which occurred in sufficient replications in both regions, via *t* tests between the regions central Maranhão and western Pará (Tomé-açu approximately 400 km west) via BCA.

A multivariate BCA was used to investigate the potential effect of regional differences on secondary forests and on homegarden agroforests (which occurred in both regions; see Table 1). Furthermore, the regional effect on the sum of variation of the entire dataset was quantified by suing Monte Carlo randomization procedure with 9999 permutations for significance testing.

Results

Vegetation, litter and topsoil variables across land-use systems and between regions

Total aboveground biomass (TAGB) differed significantly between systems (Fig. 2a, left scale). Within the spontaneous forests, TAGB increased from 68.08 Mg ha^{-1} in SFY to 92.98 Mg ha^{-1} in SFO, and it was 2.73-fold higher in MF (253.55 Mg ha^{-1}). TAGB likewise differed strongly among agroforests. TAGB of HA (178.52 Mg ha^{-1}) was 3.5-fold higher than in CPA (50.95 Mg ha^{-1}).

The agroforest and spontaneous forest systems differed significantly in their shrubs and herbaceous biomass (AGB < 10 cm dbh; Fig. 2a, right scale). SFY had an approximately 100-fold higher shrub biomass than HA (64.97 and 0.42 Mg ha^{-1}, respectively), and MF a nearly five-fold higher shrub biomass than CPA. There was no significant difference in necromass of standing and fallen logs greater than 5 cm, nor in litter mass (twigs or leaf litter, data not shown). Within the spontaneous forests (i.e., excluding all agroforests from statistical analysis), there were tendencies ($p < 0.10$) of decreasing leaf litter and increasing twig litter along succession ($p < 0.10$) (Fig. 2b). A t test comparison between mature forest and homegardens revealed a significant ($p < 0.03$) difference in total litter biomass (Table 2, as indicated by the capital letters).

No significant differences in any variable were detected by t tests between the two regional clusters (central Maranhão state and Tomé-açu in eastern Pará state). Furthermore, the BCA of clusters on the land-use systems partitioned by region indicated that the difference between regions explains only 7.72 % of the total variance for the dataset of secondary forests fallow (SFY and SFO) and homegardens agroforests (HA), because both occurred in sufficient replications in both regions. According to the Monte Carlo test of 9999 random simulations, between-region variation was neither relevant nor significant ($p = 0.114$).

We found no overall between-system differences in topsoil organic matter (OM) concentration. Excluding agroforests, i.e., concentrating on spontaneous succession, there was a significant ($p < 0.05$) increase of OM concentration from young to old secondary forests and the highest values in MF (Table 2, letters in parentheses). Bulk soil density was significantly higher in SFY than in SFO, MF and HA ($p < 0.05$). Topsoil pH was highest in CPA and lowest in MF and HA ($p < 0.05$) (Table 2). Available P concentration was non-normally distributed and, due to high data variability, did not differ between systems, according to Dunńs non-parametric test (Fig. 3a).

Topsoil K concentration was three times higher in HA than in the spontaneous forests (SFY, SFO and MF) ($p < 0.05$), and topsoil Ca concentration was higher in CPA and SFO than in HA and MF

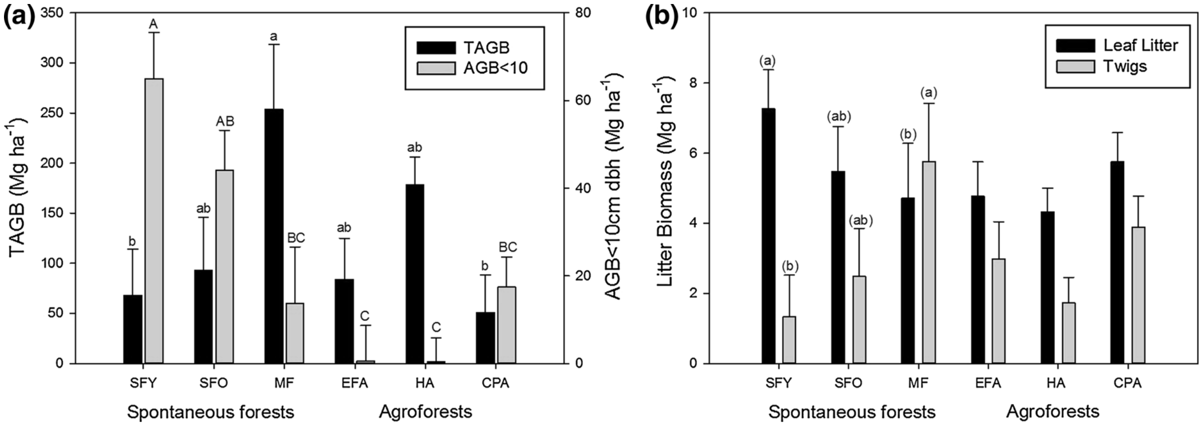


Fig. 2 **a** Total aboveground biomass (*TAGB*) and biomass of small (<10 cm dbh) trees, lianas, shrubs and herbaceous plants and **b** twigs and leaf litter in the understory of spontaneous forests and agroforests. Note differences for the *black* (*left scale*) and *gray* (*right scale*) columns. *SFY* young secondary forest; *SFO* old secondary forest; *MF* mature forest; *EFA* enriched fallow agroforest; *HA* homegarden agroforest; *CPA* commercial plantation agroforest. In (**a**) means + SE followed by the *same letter* do not differ between another, as indicated by Spjøtfoll–Stoline tests at the 5 % probability-level. In (**b**) *letters in parentheses* correspond to Spjøtfoll–Stoline tests for spontaneous forests only (analysis excluding agroforests), at a 10 % probability level

Table 2 Topsoil (0–20 cm) organic matter concentration, bulk soil density, pH value, concentrations of K and Ca, and of littermass and leaf litter N concentration in spontaneous forests and in agroforests

	Spontaneous forests			Agroforestry systems		
	SFY	SFO	MF	EFA	HA	CPA
Organic matter (OM) ($g\ dm^{-3}$)	22.63 ± 2.95(b)	31.03 ± 3.41(ab)	32.30 ± 4.17 (a)	30.64 ± 2.64	28.53 ± 1.78	26.00 ± 2.23
Bulk density (BD) ($g\ cm^{-3}$)	1.37 ± 0.03 a	1.21 ± 0.04 b	1.17 ± 0.05 b	1.27 ± 0.03 ab	1.22 ± 0.02 b	1.32 ± 0.03 ab
pH	4.28 ± 0.14 ab	4.34 ± 0.17 ab	3.77 ± 0.20 b	4.19 ± 0.13 ab	4.03 ± 0.09 b	4.68 ± 0.11 a
K ($mg\ dm^{-3}$)	9.75 ± 5.4 9b	14.02 ± 6.34 b	12.82 ± 7.76 b	26.05 ± 4.91 ab	37.95 ± 3.31 a	25.64 ± 4.15 ab
Ca ($mg\ dm^{-3}$)	115.00 ± 43.47 ab	246.67 ± 50.20 a	10.00 ± 61.48 b	212.00 ± 38.88 ab	112.73 ± 26.22 b	251.43 ± 32.86 a
H + Al ($mmol_c\ dm^{-3}$)	40.25 ± 8.82 ab	50.33 ± 10.19 ab	85.00 ± 12.48 a	41.80 ± 7.89 ab	63.09 ± 5.32 a	34.86 ± 6.67 b
Total litter ($Mg\ ha^{-1}$)	8.61 ± 1.54	7.97 ± 1.78	10.47 ± 2.18 (A)	7.76 ± 1.38	6.07 ± 0.93 (B)	9.63 ± 1.17
Leaf litter N ($g\ kg^{-1}$)	9.75 ± 1.04 c	12.53 ± 1.48 ab	13.32 ± 1.48 a	9.58 ± 1.04 c	10.64 ± 0.64 bc	10.74 ± 0.85 bc

Means + SE followed by the same letter do not differ between another, as indicated by Spjøtfoll–Stoline tests at the 5 % probability-level. Letters in parentheses correspond to Spjøtfoll-Stoline tests for spontaneous forests only (analysis excluding agroforests), at a 10 % probability-level. Capital letters in parentheses correspond to the *t* test applied for mature forest and homegardens only at a 3 % level of probability

SFY young secondary forest, *SFO* old secondary forest, *MF* mature forest, *EFA* enriched fallow agroforest, *HA* homegarden agroforest, *CPA* commercial plantation agroforest

($p < 0.05$). Soil potential acidity (H + Al) was higher in MF and HA than in CPA ($p < 0.05$) (Table 2).

Neither leaf nor twig litter layer C content differed significantly between systems (data not shown). By contrast, leaf-litter N content was highest in MF (average 20 % above CPA and HA, and 30 % above SFY and EFA) (Table 2). Leaf-litter C:N was significantly higher in both SFY and CPA compared to EFA (Fig. 3b).

Relationships between variables

Here, we explore the bivariate relationships between aboveground vegetation–litter–topsoil over the 32 study sites.

Within-vegetation and vegetation litter relationships

We found a negative logarithmic relationship in spontaneous forests between AGB ≥ 10 cm dbh and AGB < 10 cm dbh over the 32 study sites ($r^2 = 0.19$, $p < 0.04$). Our results also established a positive logarithmic relationship between AGB < 10 cm dbh and total litter biomass ($r^2 = 0.11$, $p < 0.07$). However, when treated separately for leaves and twigs, this relationship was significant only for leaf litter ($r^2 = 0.14$, $p < 0.05$). There was no apparent relationship between AGB ≥ 10 cm dbh and leaf, twig or total litter mass, though there was a positive relationship (Spearman rank $R = +0.61$, $p < 0.05$) between total litter mass and its C:N ratio.

Litter–topsoil relationships

Neither total nor leaf-litter biomass were significantly related with topsoil organic matter (all $p > 0.57$). In contrast, there was a significant positive relationship between twig biomass and topsoil organic matter content ($r^2 = 0.13, p < 0.05$). Plant-available P and K concentrations were negatively related to total litter biomass ($r^2 = 0.22$, $p < 0.01$ and $r^2 = 0.20$, $p < 0.02$).

Within-topsoil relationships

Soil organic matter (OM) content was positively related to clay content ($r^2 = 0.20$, $p < 0.01$) and negatively related to soil bulk density ($r^2 = 0.20$, $p < 0.01$). Clay content correlated negatively with soil

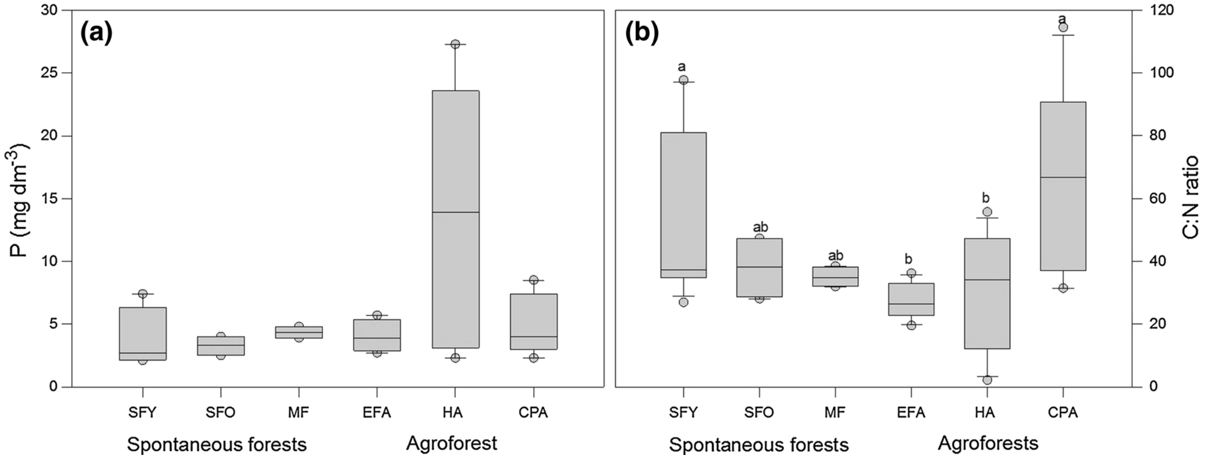


Fig. 3 **a** Topsoil (0–20 cm) resin-extractable P concentrations and **b** carbon:nitrogen ratios in leaf litter in spontaneous forests and agroforests. *SFY* young secondary forest; *SFO* old secondary forest; *MF* mature forest; *EFA* enriched fallow agroforest; *HA* homegarden agroforest; *CPA* commercial plantation agroforest. *Lines* and *boxes* represent medians and 25–75 percentiles of P concentrations, *whiskers* are the 90 and 10 percentiles. Systems with the *same letter* do not differ between another, as indicated by Dunn's nonparametric test at the 5 % probability-level

bulk density ($r^2 = 0.18, p < 0.03$), whereas the other granulometric fractions did not significantly affect soil density.

We detected no significant relationships between OM and pH or nutrients (data not shown). Within the soil chemical indicators, we found a positive relationship between P and K ($r^2 = 0.32, p < 0.01$), as well as between pH and Ca ($r^2 = 0.67, p < 0.01$).

Multivariate synthesis of variables and systems

We explored the degree of covariation via PCA (Fig. 4). The two main factors (axes 1 and 2) together explained 44.14 % of total variability of the combined vegetation, litter and topsoil physicochemical data. Figure 4a shows a successional trajectory of spontaneous forests from SFY via SFO and EFA to MF, aligned along axis 1 as a result of the influence of the aboveground biomass (i.e. TAGB and AGB < 10 cm dbh) and of soil physicochemical properties (bulk soil density, pH, K and Ca content). Remarkably, HA were closest to MF. CPA formed a distinct group clearly separated from the other systems, with one extreme value presumably caused by the high biomass of Brazil-nut trees (*Bertholia excelsa* Humb. & Bonpl.) on this site only. Figure 4b delimits the PCA correlation circle over all variables of this study. Axis 1 captured most of the variability related to the soil physicochemistry (base saturation, soil potential acidity, pH, K concentration, clay, bulk soil density) and the litter layer and small vegetation components, whereas axis 2 represented the variability driven by OM, litter layer N content and total and large vegetation biomass (these latter two also contribute strongly to axis 1). In summary, our results of PCA (1) partitioned two main axes (soil physicochemistry vs. large vegetation), (2) indicated successional pathways, and (3) positioned HA close to MF and CPA as a distinct group distant from all others.

We investigated differences between land-use systems using BCA (Fig. 5). The between-group inertia corresponded to 30.3 % of the total PCA variation ($p = 0.0001$). The first and second axes together represented 75.5 % of the total data variation. The successional trajectory from SFY to MF was less apparent than in the PCA, which may be expected since the BCA method maximizes the inertia between-groups rather than between-sites. Further similarities were found with the PCA result: HA systems were most similar to MF, CPA again formed a distinct group. EFA were similar to SFO, HA and CPA, while SFY formed a separate group. Homegardens had the most widespread spread of points in the two axes, reflecting a high variability, whereas the market-oriented CPA exhibited the lowest data-spread.

Between-class CIA measured the overall similarity between aboveground biomass and litter biomass with soil physicochemistry datasets. Over all systems, the

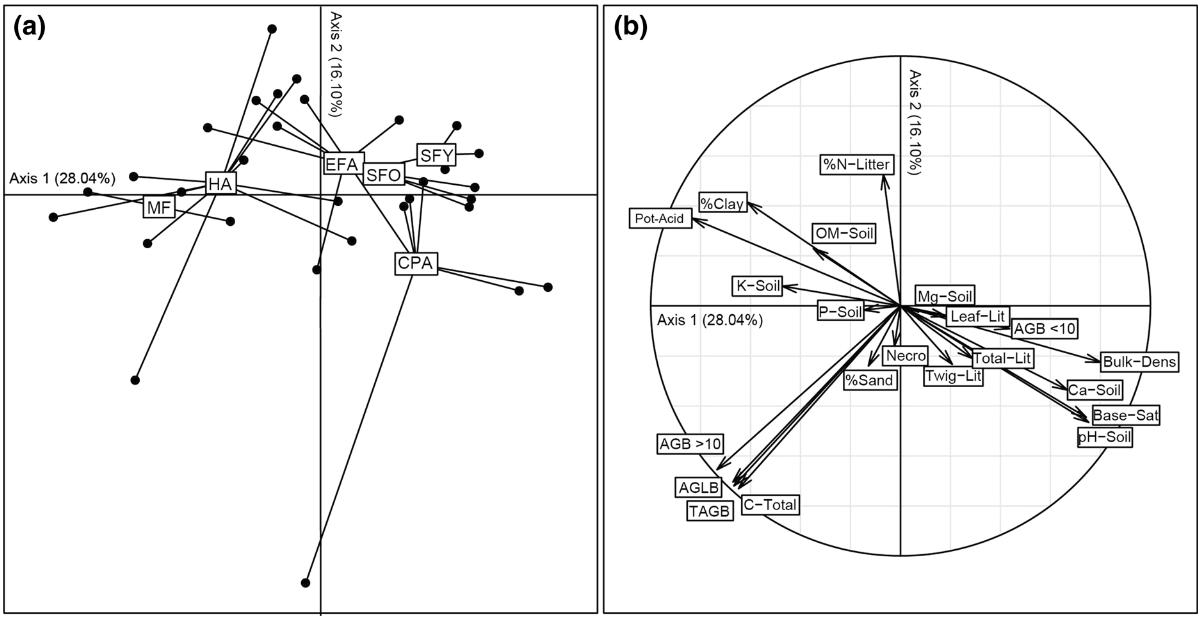


Fig. 4 **a** Principal component analysis (PCA) over the 32 sites of spontaneous forests and agroforests in eastern Amazonia, and **b** PCA correlation circle of soil physical and chemical indicators and vegetation components. *SFY* young secondary forest; *SFO* old secondary forest; *MF* mature forest; *EFA* enriched fallow agroforest; *HA* homegarden agroforest; *CPA* commercial plantation agroforest

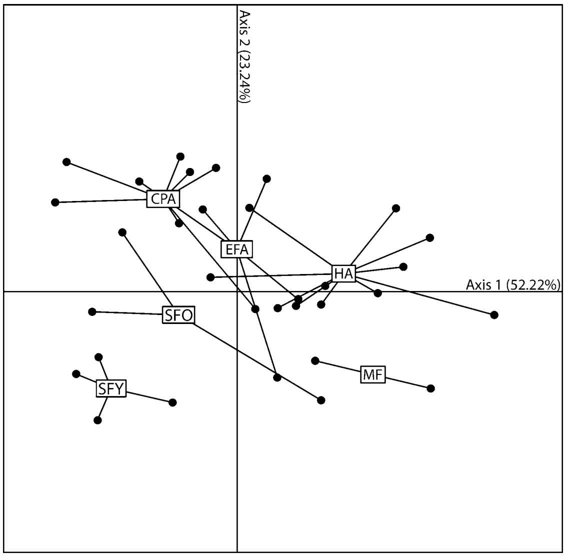


Fig. 5 Between-class analysis (BCA) of the 32 sites of spontaneous forests and agroforestry systems in eastern Amazonia. *SFY* young secondary forest; *SFO* old secondary forest; *MF* mature forest; *EFA* enriched fallow agroforest; *HA* homegarden agroforest; *CPA* commercial plantation agroforest. The inertia between classes was of 30.29 %, and the Monte Carlo permutation level of significance was $p = 0.001$

similarity between aboveground and litter biomass with soil physicochemistry was significant but weak (Rv = 21.76 %, $p < 0.05$). When considering only spontaneous forests (SFY, SFO and MF), the multiple correlation coefficient was three times higher (Rv = 75.50 %, $p < 0.01$), whereas the same correlation coefficient in agroforest systems (EFA, HA and CPA) was only 25.73 % and also less significant ($p < 0.09$) (Table 3). The spontaneous forests retained more information of variability in the first two axes (95.14 %) than the agroforests.

Discussion

Regional variance and plot-size effects

We investigated the possible problem of regional variability unduly affecting our results in secondary forests and in homegardens, both of which were present in sufficient replications in central Maranhão and in Pará states. According to between-region BCA, the regional effects on data variability were small (only 7.7 % of total variance), and *t* tests between

Table 3 Coefficient of matrix correlation (Rv) between data-sets of soil and biomass for spontaneous forests and agroforests

Systems	Co-inertia ratio (Rv)	Cumulative project inertia (%)[a]	p^b
All systems	0.2176*	81.96	0.0429
Spontaneous forests	0.7550**	95.14	0.0026
Agroforests	0.2573	87.72	0.0817

* Co-inertia ratio was significant at $p < 0.05$

** Co-inertia was significant at the level of $p < 0.01$

[a] Total inertia percentage of the two principal axis of CIA

[b] Significance-level based on 9999 Monte Carlo permutations

regions did not detect any significant differences. Thus, regional variability did not bring a relevant bias to our key findings.

We estimated AGB $\geq$ 10 cm dbh in a 0.20-ha sampling unit per site, similar in size to sampling units successfully employed in studies of tall spontaneous forests (Keller et al. 2001). However, we recorded two very high (>80 Mg ha^{-1}) estimates of shrubs, treelets and lianas (AGB 1–10 cm dbh), one for SFY and another for CPA. A possible explanation for these outliers may be insufficient subplot-size for reliable estimation of mid-sized vegetation. TAGB was overall strongly dominated by the large vegetation components.

Vegetation and land-use-related differences

Aboveground biomass of large ($\geq$10 cm dbh) trees and palms and of understory (<10 cm dbh) plants both varied widely between systems, though frequently in opposite directions in consequence of the negative logarithmic relationship between large and small plants, presumably the outcome of light and nutrient competition (Schwinning and Weiner 1998). Within the spontaneous forests, we observed successional trajectories of increasing overstory biomass and of decreasing understory biomass (Fig. 2a). Within agroforests, we observed direct management effects, such as differing regimes of understory clearing, and of sweep-and-burn in the homegardens (Fig. 2a). Overall, understory biomass was much lower in agroforests than in spontaneous forests, reflecting the management objective of reducing competition and maximizing crop resource use. Neither topsoil OM nor bulk density differed significantly between spontaneous forests and agroforests (Table 2). Soil organic matter content was the lowest in SFY, intermediate in SFO and the highest in MF (Table 2), pointing to organic matter restoration along succession (Silver et al. 2000). Management also influenced topsoil chemistry, with higher pH and Ca-concentrations in CPA (Table 2), presumably caused by liming and significant chemical fertilizer input.

The increase of leaf litter N content from young secondary forests to mature forests (Table 2) would be in accordance with a decreasing N limitation and also a decreasing relevance of biological N_2 fixation along secondary forest succession (Davidson et al. 2007). N concentrations in the litter layer of agroforests (Table 2) were lower than reported elsewhere (Moço et al. 2010), probably due to the low quantity of N_2-fixing legumes in our agroforests.

Next to N, litter layer C:N ratios are key for litter–topsoil N dynamics (Constantinides and Fownes 1994). Plant tissues tend to mineralize with C:N ratios of less than 25 while those greater than 25 tend to immobilize mineral N (Hobbie et al. 2006). Thus, N immobilization predominated in litter layers (Fig. 3b), with the exception of one HA and two EFA sites. We observed a significant positive relationship between twig littermass (but not leaf littermass) and topsoil OM contents (see "Litter–topsoil relationships"), which may be due to the elevated lignin/polyphenol contents typical for twigs (Tu et al. 2011). Twigs decompose slower than leaves within the litter layer, due to the higher concentrations of less degradable components, especially lignins and other polyphenols, which form precursors for the build-up of soil organic matter (Rahman et al. 2013). Thus, a higher portion of twigs in litter mass can be more important for organic matter buildup than the leaf litter layer. Agroforestry species with larger twig input could therefore improve soil carbon sequestration.

Multivariate analysis permitted deeper insights into the interrelationships between variables, and the appreciation of land use and management effects on such relationships. Here, our results of PCA (1) partitioned two main axes (soil physicochemistry vs. large vegetation) (Fig. 4b), (2) indicated successional pathways, and (3) positioned HA close to MF, whereas CPA formed a distinct proper group (Fig. 4a).

According to BCA analysis (Fig. 5), the homegardens had the most widespread point projection in both axes, pointing to high management variability. By contrast, the market-oriented commercial plantation agroforests exhibited the lowest within-system variability. This high variability within homegardens suggests a large potential of management improvement, by selecting sites with low indicator values and implementing agricultural practices to increase agronomic efficiency of this traditional system. Such beneficial effects could be maximized by combining plots with contrasting functions in a strategically designed landscape mosaic (Lovell and Johnston 2009).

Plant litter–topsoil interactions

Plants and soils interact via a complex network of relationships between the vegetation components, the litter layer and the topsoil (van der Putten et al. 2013). We observed, first, a negative relationship between aboveground biomass of large and small plants, presumably the outcome of competition for light and soil resources (Schwinning and Weiner 1998). However, this direct effect of canopy tree on understory is likely more complex since the spatial patterns of the light environment are not entirely dependent on stem height and the diameter at breast height (Montgomery and Chazdon 2001), the input variables measured to estimate aboveground plant biomass in this study. Second, litter-layer biomass was affected by small vegetation but not by large trees, and was influenced mainly by the portion of leaves in the litter. This could be a consequence of the tradeoffs between light use efficiency and light interception efficiency (Onoda et al. 2014) which results in fast changes of leaves in the understory rather than in the overstory. Third, litter-layer twigs but not leaves contributed to soil organic matter build-up, probably due to their contrasting decomposition dynamics, with fast leaf litter decomposition contributing little to soil organic matter build-up, as opposed to the more recalcitrant twigs which are less easily degraded and form precursors of soil organic matter (Wang et al. 2010). A further explanation for the weak relationships between the litter layer and topsoil organic matter is in the decisive role of (mainly fine) root biomass to soil organic matter formation (Zhang et al. 2013), not covered in our study. Fourth, leaf litter mass increased with a widening of its C:N ratio and related negatively with ‘plant available’ topsoil P and K concentrations; similar results have been found in other studies throughout Amazonia (review by McGrath et al. (2001). And, fifth, we found the expected relationships within topsoil, such as the positive relationship between clay content and soil organic matter (Desjardins et al. 2004) and the negative relationship between OM and bulk density (Feller and Beare 1997).

Management impacted strongly on plant–soil interactions and may have influenced the strength of the plant litter–topsoil relationships. One conspicuous result of our study was the absence of significant relationships between topsoil OM content and nutrient concentrations or pH. In CPA (and partially in EFA), which can be attributed to liming (CPA only) and localized synthetic fertilizer inputs. Low biomass estimates of small plants and litter in the agroforest systems likely reflect the management practice of regular weeding (for the CPA and the EFA systems) and in the homegardens of ‘sweep-and-burn’ in the house surroundings (Benjamin et al. 2001). On the other hand, the lower values found in the mature forests are probably a result of the influence of the overstory (Schwinning and Weiner 1998).

Relationships between components of plant biomass within vegetation, vegetation litter and litter–topsoil physicochemistry were altogether weak. Several explanations are likely responsible for this. First, compared to regularly ploughed fields or species-poor grasslands, spatial variability in spontaneous forests is high both in vegetation (Punchi-Manage et al. 2014) and soil (Fromin et al. 2013). Second, we are confident that our sampling scheme well reflects the ‘grain’ of spatial variability of the different components covered, and a previous study (Somarriba et al. 2013) has shown similar sampling schemes to successfully represent the different vegetation, litter and soil components under investigation. However, an unavoidable problem of any sampling scheme is the assumption of ‘homogenous’ characteristics throughout the sampling units, whereas both above- and belowground plant–soil interactions vary in strength and expression from the plant center (stem position used for biomass estimation) towards the crown rim and neighboring vegetation (Rhoades 1996). And, third, our study showed how management can affect soil nutrient availability via inputs such as liming, fertilization, and, in homegardens, the addition of crop residues from the outside (Rugalema et al. 1994), and how it can affect its spatial variability via pruning, weeding, and sweeping and burning of litter piles. Thus, systems-specific management will alter plant–soil interactions and—over all systems—reduce the strength of these relationships.

CIA (Table 3) helped us to synthesize the multivariate relationships between vegetation–litter–soil. Overall vegetation impacts on topsoil were stronger in spontaneous forests than in agroforests and did not occur (i.e. discontinuity) in two agroforestry-systems (CPA and HA). Our results indicate that even agroforestry systems, commonly accepted as a low impact land use, may face sustainability challenges (Nair 2014), as specific management practices can affect the relationships within the plant–litter–soil interface.

The special case of homegardens

Omnipresent homegardens are complex multistrata systems, typically with high plant diversity and are subsistence- rather than market-oriented (Mohri et al. 2013).

Homegardens are also special in their specific 'sweep-and-burn' fire regime of the litter layer (Benjamin et al. 2001; Winklerprins 2009) practised by the house residents in order to reduce the occurrence of insects and snakes, and to keep the homegarden 'clean' around the farmers' houses. Benjamin et al. (2001) suggested that this practice could offset carbon liberation and negatively affect nutrient cycling. We found elevated K concentrations (Table 2) and widespread P concentrations or P hotspots (Fig. 3a) in the topsoil of homegardens, similar to results reported by Pinho et al. (2011) in homegardens of Roraima, Brazil. Potassium in the soil is easily lost via leaching (He and Chen 2013), whereas P is immobile but subject to P fixation especially in highly weathered tropical soils (Gama-Rodrigues et al. 2014; Melo et al. 2015). Protection against leaching by the large trees could explain the higher topsoil K content in homegardens, whereas the widespread values of topsoil P availability point to high soil heterogeneity in homegardens. Both findings could be the outcome of spatially irregular burning of litter piles (the burning of which releases K and P into the soil in the locations of the burns). Thus, sweep-and-burn may be a fire regime capable of creating a mosaic of edaphic conditions, and such heterogeneity could benefit ecosystem stability (Tittonell et al. 2013). By contrast, pH values were low in homegardens, similar with mature rainforest and significantly lower than in CPA (Table 2), possibly the result of the low burning temperatures in the litter piles being insufficient to increase pH (Certini 2005). Sweep-and-burn combines quick nutrient mineralization and the creation of spatial heterogeneity with protection against leaching by the large trees with their dense canopies and root systems. Further nutrient-relevant mechanisms in homegardens include the influence of nutrient pumping by larger plants, and nutrient inputs by the addition of crop and food residues from outside plantations and the house (crop residues, household refuse, animal manure) (Rugalema et al. 1994; Seneviratne et al. 2006).

In spite of their omnipresence (Mohri et al. 2013) and socioeconomic success (Cardozo et al. 2015), homegarden agroforests remain under-researched (Nair 2014). Complex geometries and interactions have so far largely evaded science (Seneviratne et al. 2006), and homegardens have never been part of systematic agronomic improvement efforts. The high between-site data variability found here (Figs. 4, 5) points to a substantial potential for management improvements (optimized composition, spacing, pruning, etc.).

Conclusions

We found strong impacts of land use on soil quality indicators and aboveground biomass within agroforests partly related to contrasting effects of understory and soil management, whereas changes in spontaneous forests are related to successional trajectories. We also detected a disruption in the plant–litter–soil continuum for the agroforests, presumably the result of management. Altogether, biomass in agroforests was statistically similar with mature rainforests and litter and topsoil nutrients were higher than in young secondary forests, confirming their ecological sustainability and potential as alternative to slash-and-burn in eastern Amazonia.

Our study highlights the outstanding characteristics of traditional homegarden agroforestry in terms of biomass, with homegardens ranked next to mature rainforests. The traditional 'sweep-and-burn' practice combines rapid nutrient mineralization with protection against leaching by large trees and a closed canopy. The large between-site variability pointed to a significant potential of improved management, and homegardens need to be a part of strategies for sustainable rural development.

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