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Effects of coffee management intensity on composition, structure and regeneration status of Ethiopian moist evergreen Afromontane forests

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Abstract: The effect of arabica coffee management intensity on composition, structure and regeneration of moist evergreen Afromontane forests was studied in three traditional coffee management systems of Southwest Ethiopia: semi-plantation coffee (SPC), semi-forest coffee (SFC) and forest coffee (FC). Vegetation and environmental data were collected in 84 plots from forests varying in intensity of coffee management. After controlling for environmental variation (altitude, aspect, slope, soil nutrient availability and soil depth), differences in woody species composition, forest structure and regeneration potential among management systems were compared using one way ANOVA. The study revealed that intensification of forest coffee cultivation to maximize coffee production negatively affects diversity and structure of Ethiopian moist evergreen Afromontane forests. Intensification of coffee productivity starts with the conversion of forest coffee to semi-forest coffee, with significant negative effects on tree seedling abundance. Further intensification leads to the conversion of semi-forest to semi-plantation coffee, causing significant diversity losses and the collapse of forest structure (decline of stem density, basal area, crown closure, crown cover and dominant tree height). Our study underlines the need for shade certification schemes to include variables other than canopy cover, and that the loss of species diversity in intensively managed coffee systems may jeopardize the sustainability of coffee production itself through reduction of ecosystem resilience and disruption of ecosystem services related to coffee yield, such as pollination and pest control.

Key words: Afromontane forest; *Coffea arabica;* coffee certification; ecosystem services; extinction debt; traditional coffee management; wild coffee

Introduction

Global forest habitat in the tropics has decreased much over the last century (Priess and others 2007; Hansen and others 2010). Forest cover in the tropics continues to decrease, mainly by forest conversion to agriculture (Ahrends and others 2010; DeFries and others 2010). Next to decreasing forest cover and associated forest fragmentation, also forest structure is being affected by logging and forest management, creating forests that strongly differ from the pre-disturbance conditions (Hobbs and others 2006; Gardner and others 2009). These ongoing deforestation and forest degradation processes put forest-dependent biodiversity at risk, as well as the ecosystem functions and services of forests and their biota (Trauernicht and Ticktin 2005; Priess and others 2007; Aerts and Honnay 2011).

The moist evergreen Afromontane forests of Southwest Ethiopia (Friis 1992) are the center of origin and diversity of *Coffea arabica* L. and hold the wild gene pool of all cultivated arabica coffee (Anthony and others 2002). Wild coffee occurs as an understorey shrub in these forests at an altitude between 1,500 and 1,900 meters above sea level, but cultivated plants are found over a wider range, between 1,000 and 2,800 m (Hedberg and others 2003; Gole and others 2008). These Afromontane moist forests are traditionally managed by local people for coffee production, as coffee forms the livelihood basis for many rural communities (Gole 2003; Senbeta and Denich 2006; Schmitt and others 2009). The traditional coffee production and management systems in Southwest Ethiopia are similar to the rustic coffee production system in Latin America where coffee is grown under a canopy cover of indigenous trees (Hernández-Martínez and others 2009), but with the difference that arabica coffee shrubs are indigenous understory plants in Ethiopia and thus a functional component of the autochthonous plant community and food web (Aerts and others, 2011). The forest management typically removes canopy trees to increase coffee yield (Senbeta and Denich 2006; Schmitt and others 2009; Aerts and others 2011), as this yield is directly proportional to growth of primary (orthotropic) and secondary (plagiotropic) branches (Gebre-Egziabher 1978; Aerts and others 2011). Opening up the canopy and clearing of competing lower vegetation enhance the vegetative growth through side branching, and hence increase coffee yield (Aerts and others 2011). Depending on the intensity of the forest management, the population structure of the coffee shrubs and the diversity of canopy and sub-canopy tree species, three major traditional coffee production systems can be recognized within the forest environment in Ethiopia (Senbeta and Denich 2006; Labouisse and others 2008; Schmitt and others 2009; Aerts and others 2012): a) the forest coffee (FC) system, where farmers harvest coffee from essentially wild coffee shrubs with little or no intervention in the canopy and sub-canopy layers; b) the semi-forest coffee (SFC) system, in which herbs, shrubs other than coffee and emerging tree seedlings in the understorey are removed annually, the upper canopy is selectively thinned and coffee saplings are locally planted; and c) the semi-plantation coffee (SPC) system, which involves modification of the forest similar to the SFC, but more intensively, and including the systematic planting of coffee seedlings, often locally improved coffee berry disease resistant varieties.

The conservation and sustainable management of moist evergreen Afromontane forests in Southwest Ethiopia requires a thorough understanding of the effects of coffee management intensity on the forest. It has been demonstrated that reducing shade to increase coffee production causes losses of species diversity in Latin American (Perfecto and others 2005) and Ethiopian coffee agro-ecosystems (Senbeta and Denich 2006; Schmitt and others 2009). Because of the dramatic species losses known from intensively managed forests, negative effects on structural diversity and the regeneration potential can also be expected, but very little information on the effects of increasing coffee management intensity on forest structure and regeneration capacity is currently available. The general aim of the current study was therefore to document the impact of coffee management intensity – increasing from FC over SFC to SPC – on forest diversity, structure and regeneration potential. The specific aims were to quantify the impact of coffee management intensity on (i) woody species diversity; (ii) tree seedling and sapling abundance; and (iii) forest structural variables such as canopy cover, canopy closure and basal area. The results will assist the conservation and sustainable management of coffee forests and their associated forest dependent biodiversity and ecosystem services.

MATERIALS AND METHODS

Description of the study area

The study was conducted in semi-plantation and semi-forest coffee systems at Garuke and Fetche (see also Aerts and others 2011), and in a forest coffee system in the Gera sector of the Belete-Gera National Forest Priority Area (see also Aerts and others 2012; Takahashi and Todo 2012). The three study areas are located in the Jimma zone, Oromia region, Southwest Ethiopia (Fig 1). The Garuke study locality comprises different isolated forest fragments, managed for coffee production in an undulating landscape consisting of a mosaic of crop land, pasture, riverine wetland, small human settlements and isolated farmsteads (Aerts and others 2011). The presence of scattered mature canopy trees characteristic of the moist evergreen Afromontane forest (for example *Prunus africana* (Hook. f.) Kalkman) in the farmlands and coffee fragments, and information gathered from elderly people indicates that these fragments were once part of a larger Afromontane forest block. The Fetche locality consists of a more continuous (> 100 ha) forest fragment in the same landscape as Garuke. The Gera forest, finally, is a large continuous forest with a size of > 100,000 ha. Despite the currently ongoing processes of internal degradation and fragmentation, Gera forest is one of the last remaining, least disturbed moist evergreen Afromontane forests in the area.

Soils of the study area are largely volcanic in origin and relatively fertile. The dominant soil type is nitosol (USDA: ultisol). The mean annual rainfall of the area varies between 1800 mm and 2300 mm with maximum rainfall between the months of June and September. The mean annual temperature is between 15°C and 22°C (EMA 1988).

Vegetation data

Vegetation was sampled in eighty-four 400 m^2 plots (20 × 20 m) established in the three localities. To avoid edge effects related to the high degree of forest fragmentation, which co-varies with the differences in forest management intensity in our study area, the plots were laid out at a sufficient distance (>50 m) from the forest edge. The abundance of all tree and shrub species with diameter at breast height ≥ 5 cm was recorded in each plot and their circumference at breast height and height were measured with tape meter and clinometer, respectively. In each plot, one subplot of 25 m^2 (5 × 5 m) was established for recording the abundance of tree seedlings and saplings. Percent crown cover was calculated from vertical crown projections using SVS (Stand Visualization System, USDA Forest Service). Crown closure (%) was calculated from four readings in the cardinal directions with a spherical densiometer.

Environmental data

Altitude of the plots was recorded in the centre of the plot using a handheld GPS device (eTrex Vista HCx, Garmin). Aspect was recorded as the azimuth (θ) measured in degrees from true north and was transformed to a relative measure for heat load (*HL*) using the equation $HL = 0.5[1-\cos(\theta)]$ (McCune and Keon 2002). Slope was measured using a clinometer. Soil nutrient availability was quantified using soil samples randomly collected inside each plot (four sub-samples per plot) at a depth of 0–20 cm. Sub-samples from each plot were merged and the composite samples were air-dried, sieved (< 2 mm) and oven-dried (24h at 80°C). Following standard soil analysis methods (Van Reeuwijk 2002), each sample was analyzed for potential soil acidity pH(KCl), available phosphorus P, CEC, soil nutrients (Ca, Mg, K, N), soil carbon and organic matter. Soil penetration resistance was measured as a proxy for soil depth and soil compaction. We used the rod penetration method (Eriksson and Holmgren 1996) based on 10 systematic steel bar depth measurements per plot.

Data analysis

The plots were assigned to the three traditional coffee management systems based on three criteria that were easily distinguishable in the field: (i) slashing of the undergrowth; (ii) cutting of large trees; and (iii) practice of systematic planting of coffee seedlings (Table 1). The different practices were assessed as 'intensive' when systematically visible over the whole of the established plot. They were assessed as 'present' when apparent but in a non systematical way. Tree and seedling count data and basal area were converted to values per hectare. From tree height data, we calculated mean tree height and dominant tree height (defined as the average height of the five tallest trees in the plot). Alpha diversity was calculated as mean number of tree species observed per plot. We calculated Hill's numbers N_1 and N_2 (Hill 1973) as measures of species diversity because they are relatively unaffected by species richness and tend to be independent of sample size. N_1 (= $e^{H'}$) and N_2 (= D^{-1}) were calculated from Shannon's diversity

(*H'*) and Simpson's diversity (*D*) indices. We used non-metrical multidimensional scaling (NMS) to determine community composition using tree abundance data, the Sørensen distance measure, 250 iterations and an instability criterion of 10^{-5}. Multivariate differences in species composition between coffee management systems were tested with a multi-response permutation procedure test (MRPP). Indicator Species Analysis (ISA) and Monte Carlo permutations (5000 runs) were used to calculate indicator values for all species and their significances within the three coffee management systems.

We used a principal component analysis (PCA) with varimax rotation to summarize the environmental variables (altitude, aspect, slope, soil nutrient composition, and soil depth) at the plot level. To control for environmental variation between plots, and to separate the effects of environmental variation from the effect of management intensity, we first performed linear regressions between the two derived PCA axes (cumulative variance explained by PCA1 and PCA2: 53.7%) and the different vegetation variables and diversity indices. Then, we related the standardized residuals (r_s) of these linear regressions to the three management intensity types, using ANOVA. This way we tried to explain the residual variation between plots after accounting for the environmental variables. Post-hoc multiple comparisons between the three management intensity types were conducted using the Least Significant Difference (LSD) test. To visualize changes in forest structure, stand profiles representing the three traditional coffee production systems were drawn. The profile diagrams were created from data from five plots. NMS, MRPP and ISA were performed in PC-ORD 5.31 (MjM Software, Oregon, U.S.A.). All other statistical procedures were conducted in IBM SPSS Statistics 20 (IBM Corp., New York, U.S.A.).

RESULTS

Species Richness and Diversity among Coffee Production Systems

A total of 69 woody species with DBH ≥ 5 cm were recorded. The vegetation characteristics and forest structure of each coffee production system reflected a clear gradient in management intensity. Although the number of plots sampled in the FC system was lower than in the SFC and FC systems, FC harbored a higher total species richness (γ). Total species richness in FC was 44 species, compared to 38 in SFC, and 26 in SPC. The average species richness α (and SE) per plot showed a similar decline over the FC-SFC-SPC gradient: 11.2 (1.2), 8.2 (0.8) and 4.4 (0.4) species in FC, SFC and SPC, respectively. Tree species composition varied significantly between forest management systems (MRPP T = -18.97; A = 0.079; $p < 0.001$). The indicator species for the SPC were the early-successional species *Albizia gummifera* C.A.Sm. and *A. schimperiana* Oliv., while in the SFC and FC systems, the indicator species were late-successional species of the moist evergreen Afromontane forest such as *Olea welwitschii* Gilg & G.Schellenb and *Schefflera abyssinica* Harms for the SFC and *Prunus africana*, *Teclea nobilis* Delile and *Syzygium guineense* DC for the FC (Table 2).

After removing the effect of environmental variation via linear regression with the PCA axes, the three traditional coffee production systems varied significantly in alpha diversity ($F_{2.81}$=16.59, $p < 0.001$) and community composition ($F_{2.81}$=16.59, $p < 0.001$). Post-hoc multiple comparisons between the three management systems showed that the SPC had significantly lower alpha diversity (Fig. 2a) and different community composition (Fig. 2d) than the SFC and FC systems and a lower N_1 than the FC (Fig. 2b). N_2 did not vary significantly between management systems.

Structure and Regeneration among Coffee Production Systems

After analogous removal of the effect of environmental variation, the three traditional coffee management systems varied significantly in tree abundance ($F_{2.81}$=12.73, $p < 0.001$), basal area ($F_{2.81}$=26.85, $p < 0.001$), crown closure ($F_{2.81}$=9.35, $p < 0.001$), crown cover ($F_{2.81}$=4.52, p = 0.014) and seedling density ($F_{2.81}$=29.95, $p < 0.001$). Pair-wise comparisons between the three coffee management systems showed that tree density, basal area and crown closure (Fig. 3a-c) were significantly higher in the FC and SFC systems compared to the SPC. Crown cover and dominant tree height were lower in the SPC than in the SFC (Fig. 3d-e), and the number of seedlings significantly declined over the FC-SFC-SPC gradient (Fig. 3f). Mean tree height did not vary significantly between management systems.

The regeneration of six late-successional tree species (*Syzygium guineense*, *Afrocarpus falcatus* (Thunb.) C.N. Page, *Olea welwitschii*, *Prunus africana*, *Ilex mitis* Radlk., and *Pouteria adolfi-friederici* (Engl.) Baehni) was consistently higher in the FC than in the SFC and SPC ($19.20 \leq F_{2,81} \leq 57.43$, all $p < 0.001$) (Fig. S1). The stand profile diagrams of the different coffee production systems show that the SPC system is the most degraded and impoverished system, with only few selected coffee shade trees such as *Albizia schimperiana, A. gummifera* and gap colonizers such as *Croton macrostachys,* and the absence of small trees and shrubs in the understorey. The stand profiles also clearly illustrate the decline of the maximum and dominant tree heights, the notable decrease in stem number and the reduction of canopy closure from FC over SFC to SPC (Fig. 4).

DISCUSSION

Intensification of forest coffee cultivation to maximize coffee production in Ethiopian moist evergreen Afromontane forests results in structural degradation and causes a shift in tree species composition towards an early-successional community (Table 2, Fig. 4). Our study confirms that intensive coffee cultivation has a negative impact on species diversity (Senbeta and Denich 2006; Schmitt and others 2009), leads to impoverished tree communities (Aerts and others 2011), and affects structure and regeneration potential. This variation was strongly related to differences in tree thinning and slashing of the undergrowth. Clearly, repeated cutting of emerging saplings in the understorey in the SFC and SPC limits the potential for recruitment of late-successional and secondary tree species, or even pioneer tree species.

In our study area, intensification of coffee cultivation from FC to SPC entailed a γ diversity loss of ca. 41 % (from 44 species in the SFC to 26 species in the SPC). Similar effects have already been reported in coffee agro-ecosystems in Latin America and Ethiopia (Senbeta and Denich 2006; Philpott and others 2008; Schmitt and others 2009) but also in other systems, such as cocoa agro-ecosystems in Cameroon (Bisseleua and Vidal 2008). The reduction of α diversity in SPC compared to the other systems, in particular FC (Fig. 2a), reflects the selective removal of certain tree species in the process of reducing shade for coffee production. Emergent tree species such as *Pouteria adolfi-friederici, Olea welwitschii* and *Afrocarpus falcatus* are generally considered to cast too much shade or to produce unsuitable litter (see also Soto-Pinto and others 2007). It is not surprising that these species are the first to experience local extinction through selective cutting and recruitment failure when also considering their valuable and sought-after timber (see e.g. Lemmens 2007; Aerts 2008; Aerts 2011), and the fact that in fragmented forests late-successional, shade-tolerant tree species have limited regeneration potential because of fragmentation effects *per se* (Puetz and others 2011).

Tree seedling density in SPC is reduced by more than 95 percent as compared to the FC (~10,000/ha in FC vs. ~400/ha in SPC), due to slashing of the undergrowth. The conversion of the FC to the SFC system also reduced seedling density, in this case by more than 70 percent (~10,000/ha in FC vs. ~3000/ha in SFC). A higher tree diversity in the SFC compared to the SPC (Fig. 2a) may therefore represent an extinction debt (see e.g. Tilman and others 1994; Vellend and others 2006), as in both systems understorey clearing is systematically eliminating all regenerating trees. Additionally, the thinning of the canopy exposes seedlings and juveniles to more extreme temperatures and drought (Ramírez-Marcial and others 2001), which would cause undoubtedly increased mortality in the seedling bank if it would not be systematically cut (Allen and others 2010).

Basal area and tree abundance was also reduced by 75 percent and 68 percent, respectively, when comparing FC to SPC, while the tree abundance in SFC was only about 30 percent lower (952/ha in FC vs. 655/ha in SFC) (Fig 3a-b). The SPC was characterized by a rather low tree canopy without intermediate layers, and a uniform understorey of *C. arabica*. In other words, intensive coffee management in the SPC has resulted in two-way biotic homogenization, i.e. taxonomic homogenization (few tree species; Fig. 2a-b) and structural homogenization (low tree abundance, basal area, canopy closure, cover and dominant height; Fig 3) (see also Aerts and others 2011). Because of the various, complex interactions between species in tropical forests (see e.g. Zytynska and others 2011), it is expected that this homogenization in intensively managed coffee forests is also occurring in other taxa, such as birds or epiphytic orchids (Hundera and others, 2012), and at other levels, such as functional and genetic diversity. At least for the *Coffea arabica* itself, it has recently been shown that intensive management drives cryptic genetic erosion (Aerts and others 2012).

As demonstrated in Andean ecosystems, farmers can benefit from the conservation of natural, diverse habitat through ecosystem services such as reduced pest damage and increased yields (Poveda and others 2012). Also coffee benefits from the ecosystem services of the forest (Millard 2011), and therefore the loss of species diversity in SPC system may jeopardize the sustainability of coffee production itself. Diversity losses are very likely to lower ecosystem resilience and disrupt ecosystem services related to coffee yield, such as pollination (e.g. Priess and others 2007; Vergara and Badano 2009), and pest control (e.g. Soto-Pinto and others 2002).

Management implications

Intensification of coffee productivity starts with the conversion of forest coffee to semi-forest coffee, with significant negative effects on seedling abundance and noticeable impacts on stem densities and diversity. Basal area and crown closure are not extensively affected at this stage and are therefore less sensitive indicators for intensification in the forest coffee system. Further intensification, however, leads to the conversion of semi-forest to semi-plantation coffee, and the disintegration of the entire forest structure: stem density, basal area, crown closure, crown cover and dominant tree height all decline significantly.

Our results imply that indicator species (late-successional tree species) and seedling numbers are guiding variables to follow-up the conservation status of forest coffee systems and that forest stand variables such as crown closure and basal area can be used to discriminate semi-forest and semi-plantation systems. This underlines the need for shade certification schemes to include variables other than canopy cover (see also Perfecto and others 2005; Philpott and others

2007). Second, our results show that the semi-forest coffee system has the potential to improve economic performance and biodiversity conservation. In the SFC, coffee productivity is higher because of the intensive canopy management, yet effects on structure and diversity are (statistically) limited. Third, the repeated removal of the seedlings and saplings of shade trees seems to call for the establishment of small exclosures (Aerts and others 2009) in both SPC and SFC systems. These temporarily fenced areas where slashing is suspended, may facilitate tree recruitment or could be used for seedling planting to maintain healthy populations of preferred shade trees for coffee production and late-successional tree species for biodiversity conservation.

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Tables

Table 1 Management practices in three traditional coffee production systems and number of plots sampled in each system in SW Ethiopia

Coffee management practice	SPC	SFC	FC
Slashing of undergrowth	++	+	-
Planting of coffee seedlings	++	+	-
Tree cutting	++	+	-/+
Number of plots sampled	44	29	11

++ very intensive; + present; - absent

Table 2 Indicator tree species, indicator values and significance for three traditional coffee production systems in SW Ethiopia

Management system	Species	IV	*p*
FC	*Prunus africana* (Hook. f.) Kalkman	61.4	<0.001
	Teclea nobilis Delile	48.9	<0.001
	Syzygium guineense DC.	44.4	0.005
	Polyscias fulva (Hiern) Harms	41.0	0.001
	Millettia ferruginea Hochst	38.6	0.015
	Coffea arabica L. (tree layer)	32.8	0.010
	Ilex mitis Radlk.	32.8	0.008
	Oxyacantha Medic *sp.*	24.5	0.050
	Premna schimperi Engl.	22.5	0.014
	Maytenus gracilis Loes.	21.4	0.030
	Sapium ellipticum Pax	20.5	0.046
	Rytigynia neglecta Robyns	18.5	0.080
SFC	*Olea welwitschii* Gilg & G.Schellenb.	28.3	0.047
	Schefflera abyssinica Harms	26.9	0.010
	Rhus glutinosa Hochst. ex A.Rich.	20.2	0.042
	Mimusops kummel Bruce ex A.DC.	18.8	0.055
	Vepris dainellii (Pic.Serm.) Kokwaro	10.3	0.074
SPC	*Albizia gummifera* C.A.Sm.	38.2	0.014
	Albizia schimperiana Oliv.	35.4	0.017
	Croton macrostachys Hochst. ex A.Rich.	31.5	0.094

The indicator value IV ranges from 0 (no indication) to 100 (perfect indication) and the significance *p* is the proportion of 1000 randomized trials with IV equal to or exceeding the observed IV. All species with significance $p < 0.10$ are listed.

Fig. 1 Afromontane moist forests in Southwest Ethiopia. Insets show detail of (a) the forest coffee and (b) the semi-forest coffee/semi-plantation landscape. Satellite imagery © 2012 DigitalGlobe, GeoEye and Cnes/Spot Image, via Google Earth.

Fig. 2 Effects of forest management in forest coffee (FC), semi-forest coffee (SFC) and semi-plantation coffee (SPC) systems in Southwest Ethiopia on tree diversity after accounting for environmental variability: (a) alpha diversity α, (b) Hill's N_1, (c) Hill's N_2, and (d) community composition *NMS1*. Values are standardized residuals of the regression analysis. Error bars denote SE. Letters show significant differences between groups (ANOVA LSD, $\alpha = 0.05$).

Fig. 3 Effects of forest management in forest coffee (FC), semi-forest coffee (SFC) and semi-plantation coffee (SPC) systems in Southwest Ethiopia on forest structure after accounting for environmental variability: (a) stem density *Nt*, (b) basal area *BA*, (c) crown closure *Cl*, (d) crown cover *Co*, (e) dominant tree height *Hd*, and (f) number of seedlings *Ns*. Error bars denote SE. Letters show significant differences between groups (ANOVA LSD, $\alpha = 0.05$).

Fig. 4 Representative stand profiles from five 20 × 20 m plots in forest coffee (FC), semi-forest coffee (SFC) and semi-plantation coffee (SPC) systems in moist evergreen Afromontane forests in Southwest Ethiopia. Upper canopy tree species are labeled: *Agu, Albizia gummifera*; *Asc, Albizia schimperiana*; *Caf, Cordia africana*; *Cea, Celtis africana*; *Cma, Croton macrostachys*; *Owe, Olea welwitschii*; *Pad, Pouteria adolfi-friederici*; *Paf, Prunus africana; Sab, Schefflera abyssinica;* and *Sgu, Syzygium guineense*. The uniform understorey of *Coffea arabica* in the SFC and SPC is not shown.

Fig. S1 Effects of forest management in forest coffee (FC), semi-forest coffee (SFC) and semi-plantation coffee (SPC) systems in Southwest Ethiopia on regeneration of late-successional tree species after accounting for environmental variability: (a) *Syzygium guineense*, (b) *Afrocarpus falcatus*, (c) *Olea welwitschii*, (d) *Prunus africana*, (e) *Ilex mitis*, and (f) *Pouteria adolfi-friederici*. Error bars denote SE. Letters show significant differences between groups (ANOVA LSD, $\alpha = 0.05$).

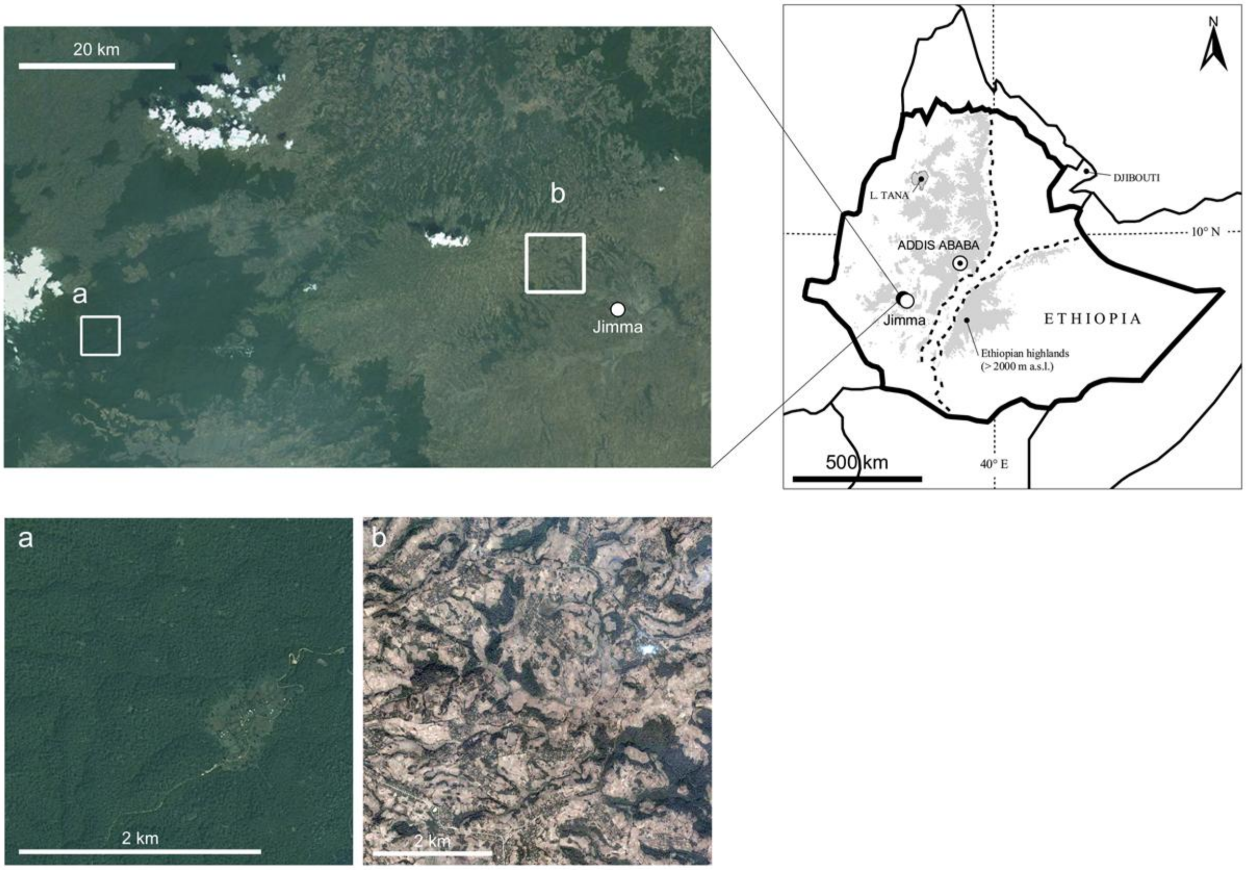


Figure 1 (preview version-high resolution TIFF provided)

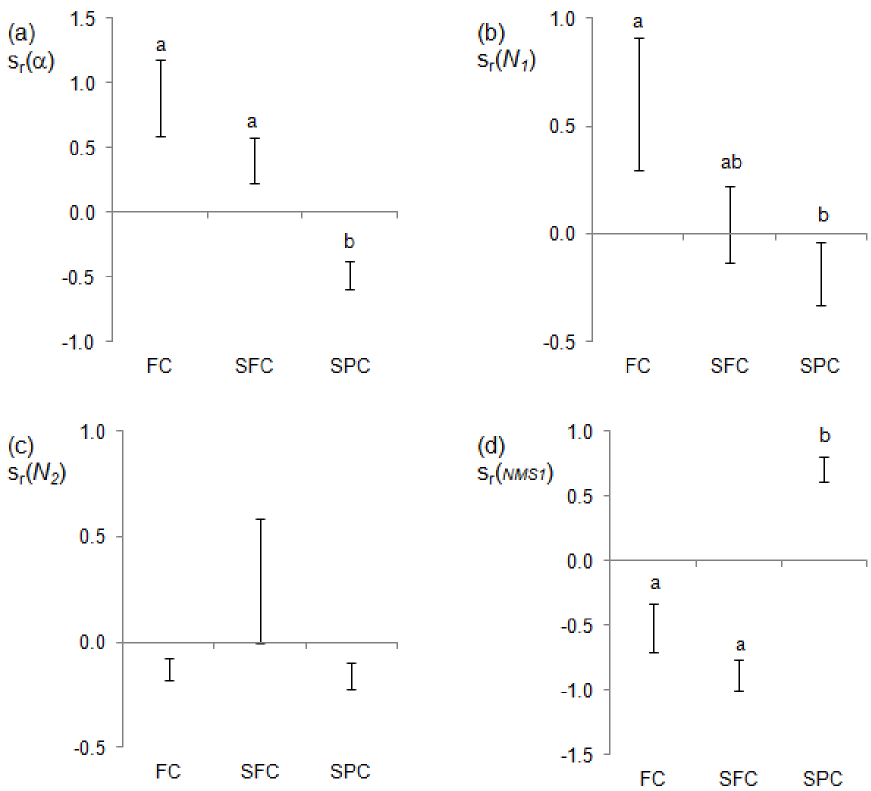
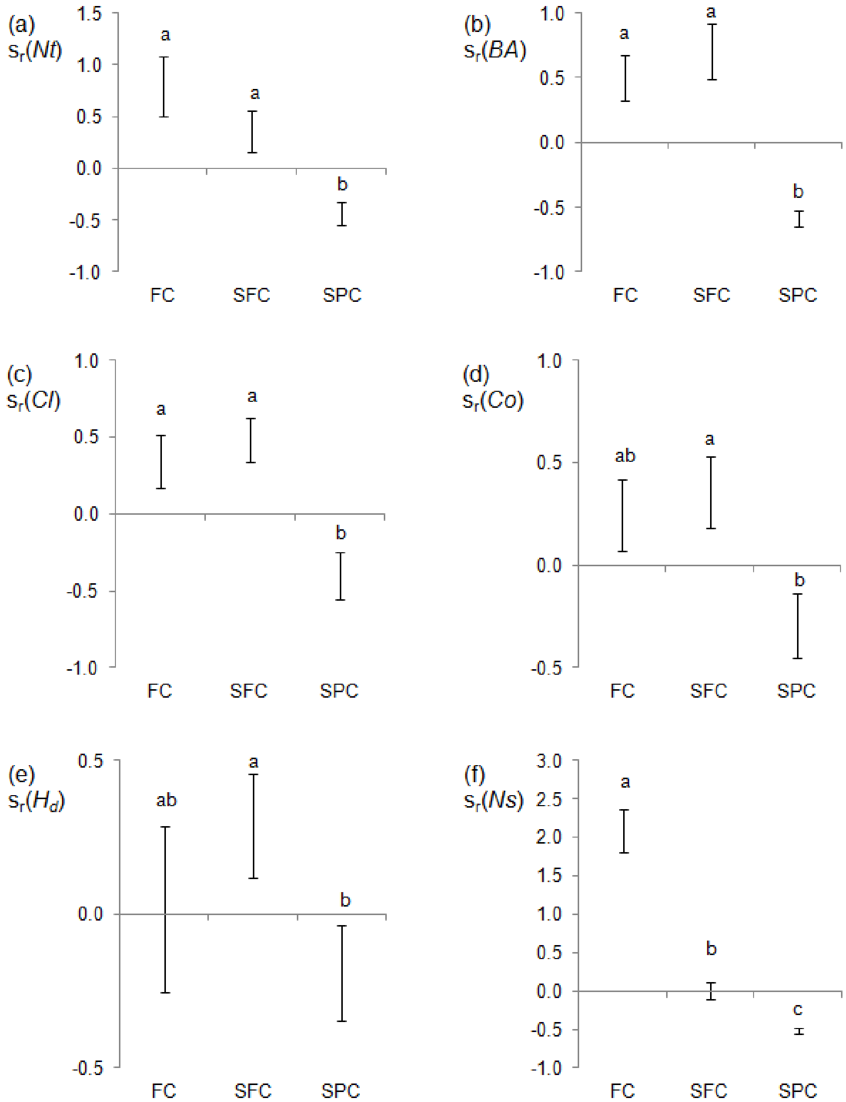


Figure 2 (preview version-vector XLS file provided)



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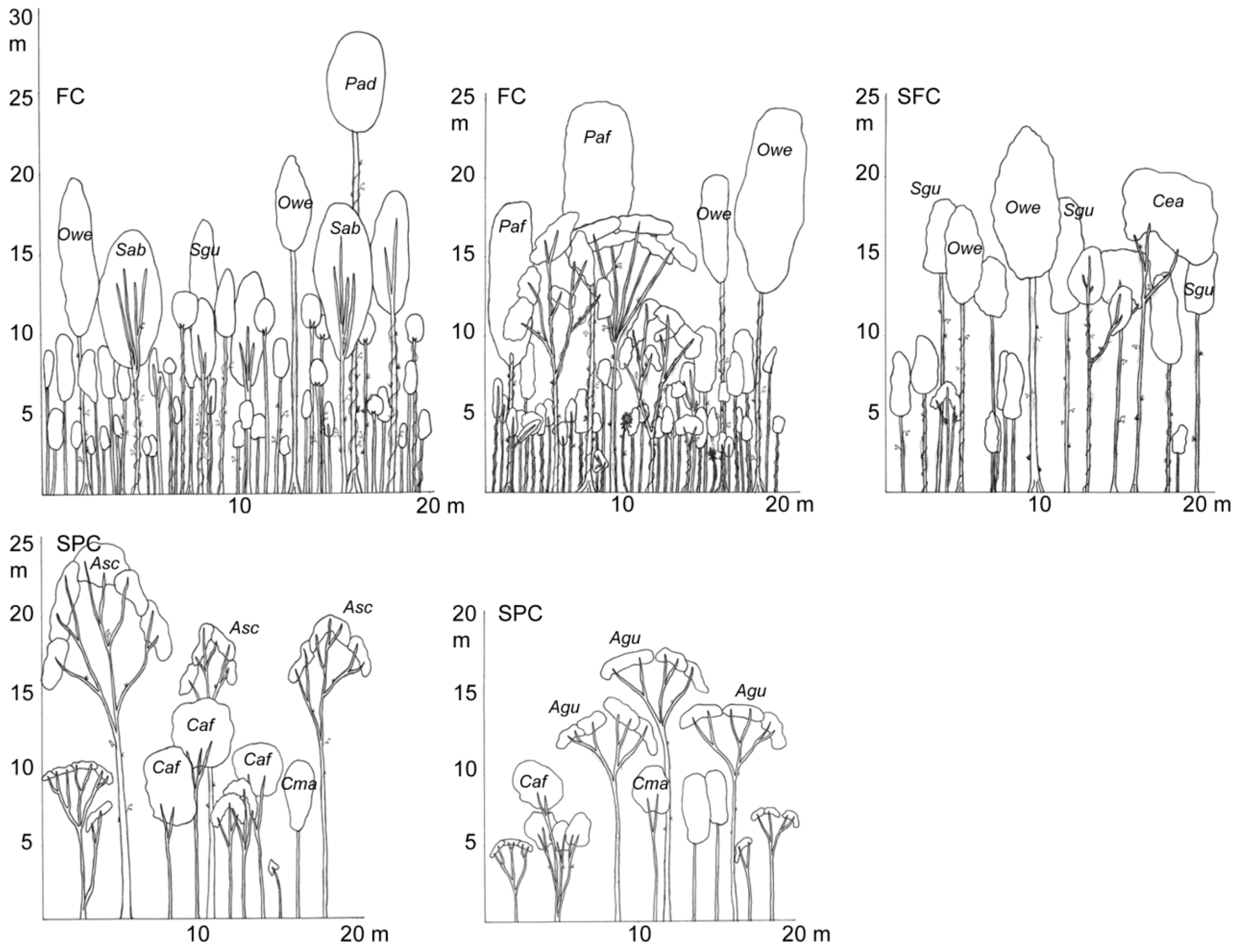

Figure 4 (high resolution TIFF)

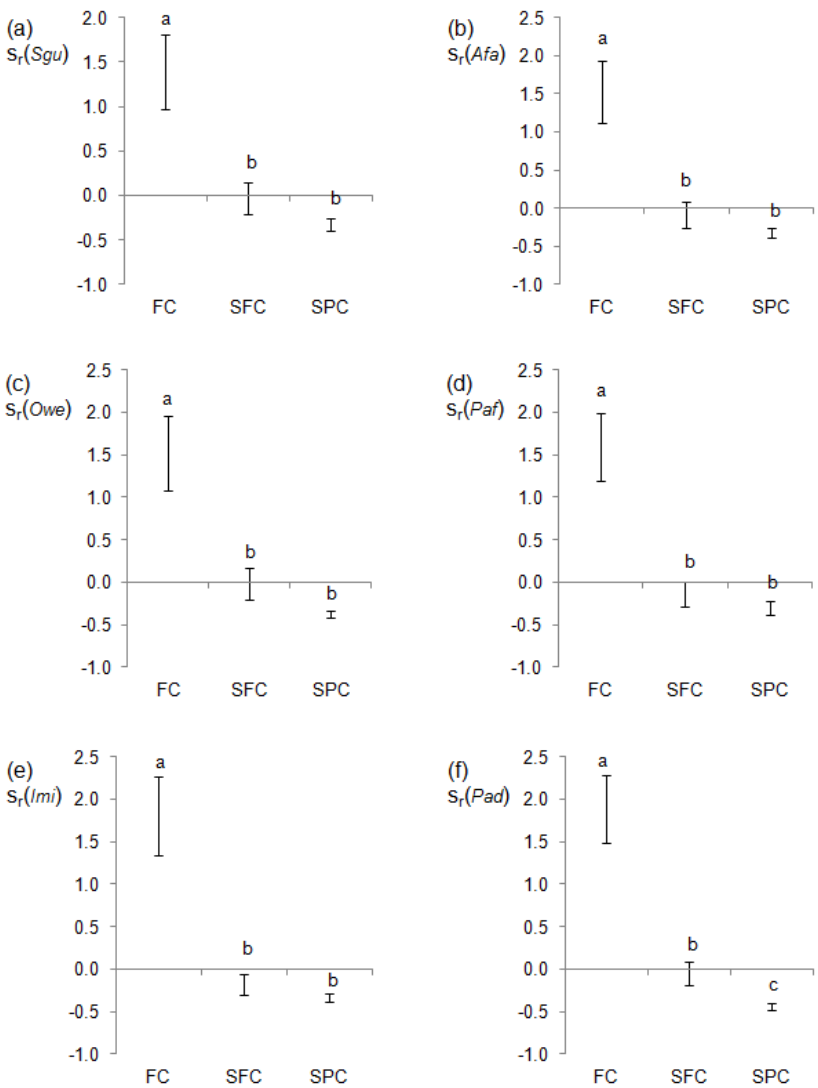
(a)
$s_r(Sgu)$
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
a
b
b
FC
SFC
SPC
(b)
$s_r(Afa)$
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
a
b
b
FC
SFC
SPC
(c)
$s_r(Owe)$
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
a
b
b
FC
SFC
SPC
(d)
$s_r(Paf)$
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
a
b
b
FC
SFC
SPC
(e)
$s_r(Imi)$
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
a
b
b
FC
SFC
SPC
(f)
$s_r(Pad)$
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
a
b
c
FC
SFC
SPC

Figure S1