

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: semiplantation coffee, semiforest coffee, and forest coffee. 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 analysis of variance. The study showed 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 semiforest

coffee, which has significant negative effects on tree seedling abundance. Further intensification leads to the conversion of semiforest to semiplantation coffee, causing significant diversity losses and the collapse of forest structure (decrease 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 the decrease of ecosystem resilience and disruption of ecosystem services related to coffee yield, such as pollination and pest control.

Keywords Afromontane forest · *Coffea arabica* · Coffee certification · Ecosystem services · Extinction debt · Traditional coffee management · Wild coffee

Kitessa Hundera and Raf Aerts contributed equally in this work.

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Introduction

Global forest habitat in the tropics has decreased much during 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 (Ahr-ends and others 2010; DeFries and others 2010). Next to decreasing forest cover and associated forest fragmentation, forest structure is also being affected by logging and forest management, creating forests that strongly differ from the predisturbance conditions (Hobbs and others 2006; Gardner and others 2009). These ongoing deforestation and forest degradation processes put forest-dependent biodiversity, as well as the ecosystem functions and services of forests and their biota, at risk (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 m 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 because 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 understorey 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) because this yield is directly proportional to the 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 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 subcanopy 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): (1) the forest coffee (FC) system, in which farmers harvest coffee from essentially wild coffee shrubs with little or no intervention in the canopy and subcanopy layers; (2) the semiforest 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 (3) the semiplantation coffee (SPC) system, which involves modification of the forest similar to the SFC system, 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 shown that decreasing shade to increase coffee production causes

losses of species diversity in Latin American (Perfecto and others 2005) and Ethiopian coffee agroecosystems (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 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 an FC system over to an SFC system to an SPC system—on forest diversity, structure, and regeneration potential. The specific aims were to quantify the impact of coffee management intensity on (1) woody species diversity; (2) tree seedling and sapling abundance; and (3) 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 the SPC and SFC 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, and 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 (*e.g.*, *Prunus africana* (Hook. f.) Kalkman) in the farmlands and coffee fragments as well as information gathered from elderly inhabitants 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 (United States Department of Agriculture [USDA]: ultisol). The mean annual rainfall of the area varies between 1,800 and 2,300 mm with maximum rainfall between the months of

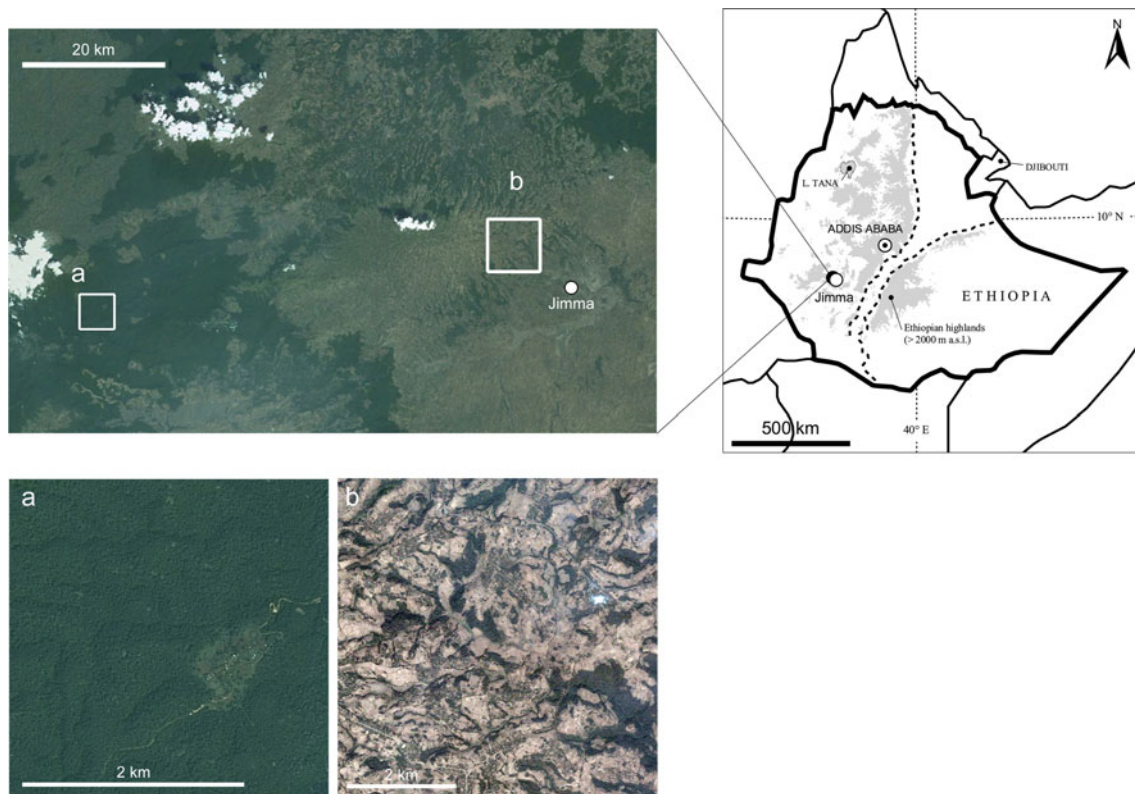


Fig. 1 Afromontane moist forests in southwest Ethiopia. *Insets* show detail of **a** the FC and **b** the SFC/SPC landscape. Satellite imagery © 2012 DigitalGlobe, GeoEye, and Cnes/Spot Image by way of Google Earth

June and September. The mean annual temperature is between 15 and 22 °C (Ethiopian Mapping Authority 1988).

Vegetation Data

Vegetation was sampled in 84,400 m² plots (20 × 20 m) established in the three localities. To avoid edge effects related to the high degree of forest fragmentation, which covaries with the differences in forest-management intensity in the 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 m² (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 3.0 (Stand Visualization System, USDA Forest Service, Portland, OR). 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 global positioning device (eTrex Vista

HCx; Garmin, Kansas City). 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 (4 subsamples/plot) at a depth of 0–20 cm. Subsamples from each plot were merged, and the composite samples were air-dried, sieved (<2 mm), and then oven-dried (24 h at 80 °C). According to standard soil analysis methods (Van Reeuwijk 2002), each sample was analyzed for potential soil acidity pH(KCl), available phosphorus, cation exchange capacity, soil nutrients (calcium, manganese, potassium and nitrogen), 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: (1) slashing of undergrowth; (2) cutting of large trees; and (3) practice of

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

systematic planting of coffee seedlings (Table 1). The different practices were assessed as “intensive” when systematically visible over the entire 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 (H') and Simpson’s (D) diversity 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 multiresponse permutation procedure test (MRPP). Indicator species analysis (ISA) and Monte Carlo permutations (5,000 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 analysis of variance (ANOVA). In 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, Gleneden Beach, OR). All other statistical procedures were conducted in IBM SPSS Statistics 20 (IBM, New York).

Results

Species Richness and Diversity Among Coffee-Production Systems

A total of 69 woody species with DBH \geq 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 SPC systems, the FC system harbored a greater total species richness (γ). Total species richness in the FC system was 44 species compared with 38 in the SFC system and 26 in the SPC system. The average species richness α (and SE) per plot showed a similar decrease over the FC-SFC-SPC system gradient: 11.2 (1.2), 8.2 (0.8), and 4.4 (0.4) species in the FC, SFC, and SPC systems, 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 system were the early successional species *Albizia gummifera* C.A.Sm. and *A. schimperiana* Oliv., whereas in the SFC and FC systems, the indicator species were late-successional species of the moist evergreen Afromontane forest, such as *Olea welwitschii* Gilg and G. Schellenb and *Schefflera abyssinica* Harms for the SFC system and *P. africana*, *Teclea nobilis* Delile, and *Syzygium guineense* DC for the FC system (Table 2).

After removing the effect of environmental variation by way of 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 system 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 system (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 ($F_{2,81} = 12.73$,

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

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

The indicator value IV ranges from 0 (no indication) to 100 (perfect indication), and significance *P* is the proportion of 1,000 randomized trials with IV equal to or exceeding the observed IV. All species with significance *P* < 0.10 are listed

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). Pairwise comparisons between the three coffee-management systems showed that tree density, basal area, and crown closure (Fig. 3a through 3c) were significantly greater in the FC and SFC systems compared with the SPC system. Crown cover and dominant tree height were lower in the SPC system than in the SFC system (Fig. 3d, e), and the number of seedlings significantly decreased over the FC-SFC-SPC system gradient (Fig. 3f). Mean tree height did not vary significantly between management systems.

The regeneration of six late-successional tree species (*S. guineense*, *Afrocarpus falcatus* (Thunb.) C.N. Page, *O. welwitschii*, *P. africana*, *Ilex mitis* Radlk., and *Pouteria adolfi-friederici* (Engl.) Baehni) was consistently greater in the FC than in the SFC and SPC systems ($19.20 \leq F_{2,81} \leq 57.43$, all *P* < 0.001) (SupplementalFig. S1). The

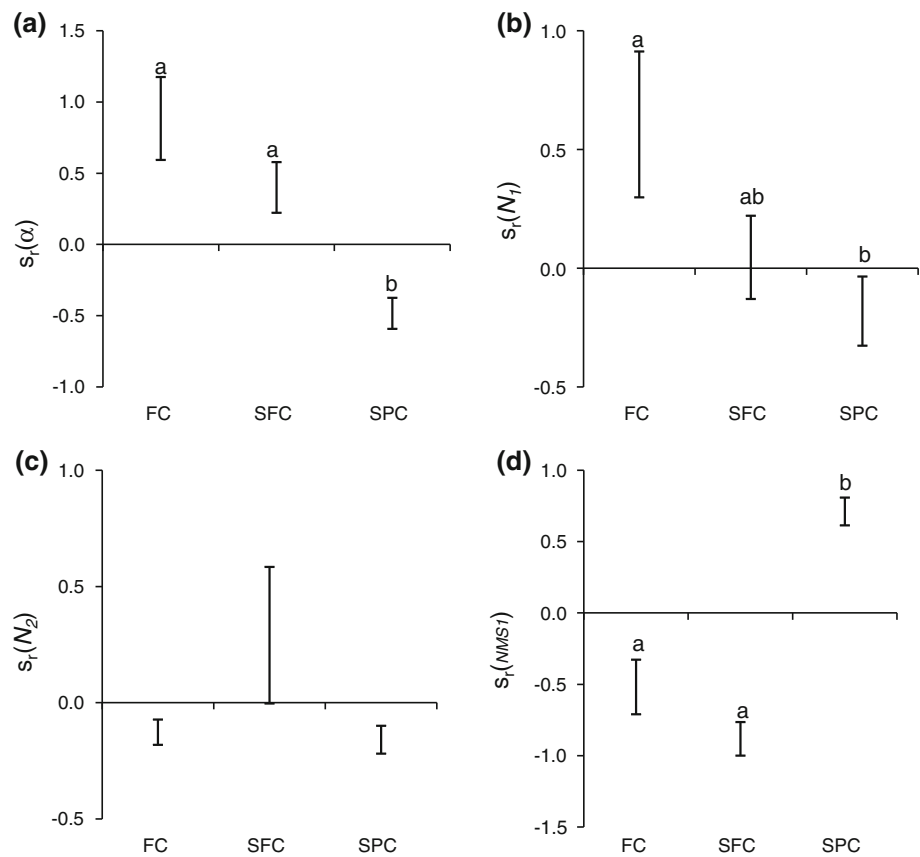
stand profile diagrams of the different coffee-production systems show that the SPC system is the most degraded and impoverished system, with only few selected coffee shade trees, such as *A. schimperiana*, *A. gummifera*, and gap colonizers, such as *Croton macrostachys*, and the absence of small trees and shrubs in the understorey. The stand profiles also clearly illustrate the decrease of the maximum and dominant tree heights, the notable decrease in stem number, and the decrease of canopy closure from an FC system over an SFC system to an SPC system (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 toward 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 undergrowth. Clearly, repeated cutting of emerging saplings in the understorey in the SFC and SPC systems limits the potential for recruitment of late-successional and secondary tree species or even pioneer tree species.

In the study area, intensification of coffee cultivation from an FC to an SPC system entailed a γ diversity loss of approximately 41 % (from 44 species in the SFC system to 26 species in the SPC system). Similar effects have already been reported in coffee agroecosystems in Latin America and Ethiopia (Senbeta and Denich 2006; Philpott and others 2008; Schmitt and others 2009) as well as other systems, such as cocoa agroecosystems in Cameroon (Bisseleua and others 2008). The decrease of α diversity in SPC compared with other systems, in particular the FC system (Fig. 2a), reflects the selective removal of certain tree species in the process of decreasing shade for coffee production. Emergent tree species, such as *P. adolfi-friederici*, *O. welwitschii*, and *A. 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, 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).

Fig. 2 Effects of forest management in FC, SFC, and 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 . **d** community composition $NMS1$. Values are standardized residuals of the regression analysis. Error bars denote SE. Letters show significant differences between groups (ANOVA LSD test, $\alpha = 0.05$)



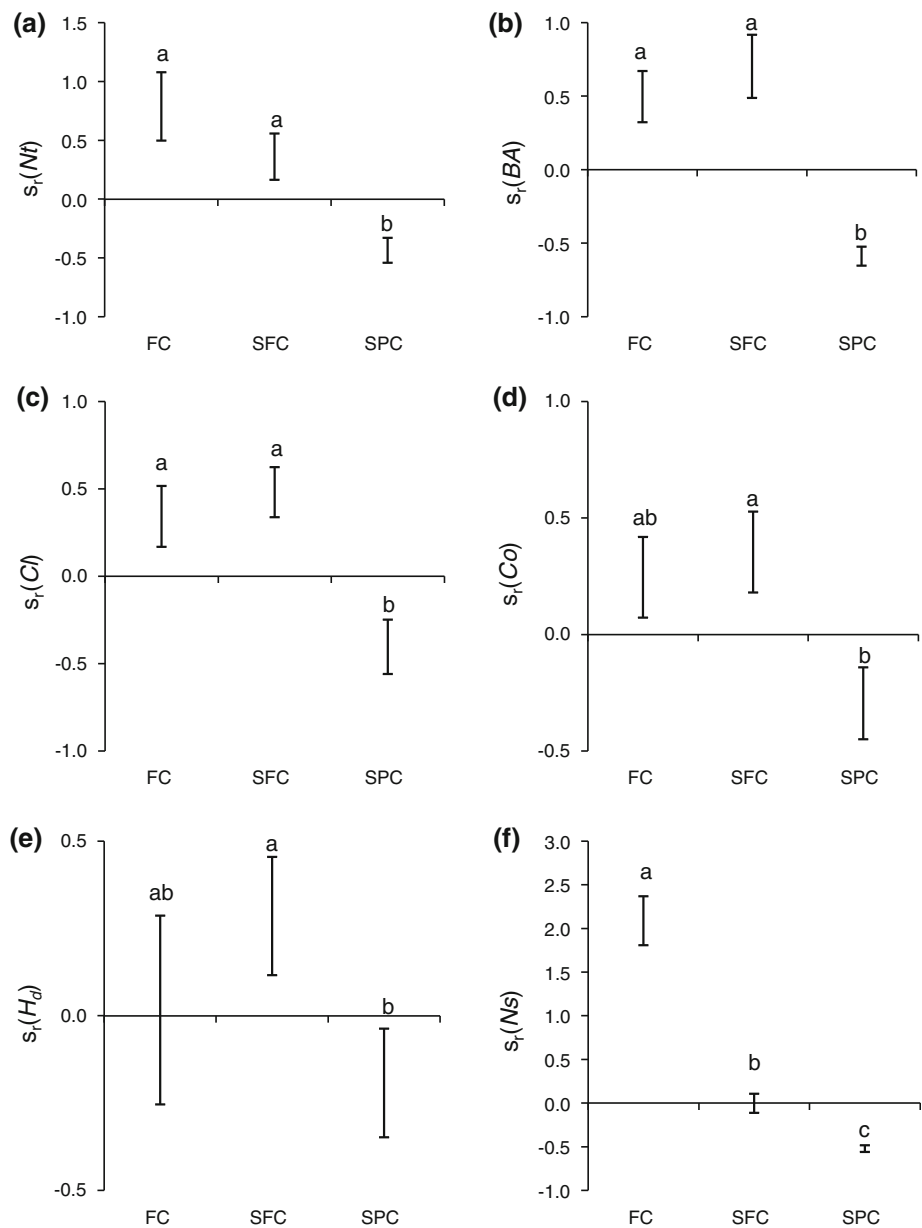
Tree seedling density in the SPC system is decreased by >95 % compared with the FC system (approximately 10,000/ha in the FC system vs. approximately 400/ha in the SPC system) due to slashing of the undergrowth. Conversion of an FC to an SFC system also decreased seedling density, in this case by >70 % (approximately 10,000/ha in the FC system vs. approximately 3,000/ha in the SFC system). Greater tree diversity in the SFC system compared with the SPC system (Fig. 2a) may therefore represent an extinction debt (see, e.g., Tilman and others 1994; Vellend and others 2006) because in both systems understorey clearing is systematically eliminating all regenerating trees. In addition, thinning of the canopy exposes seedlings and juvenile trees 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 decreased by 75 and 68 %, respectively, when comparing FC with the SPC system, whereas tree abundance in the SFC system was only approximately 30 % lower (952/ha in the FC system vs. 655/ha in the SFC system) (Figs. 3a, b). The SPC system 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 system has resulted in two-way biotic homogenization, i.e., taxonomic homogenization (few tree species; Figs. 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 *C. arabica* itself, it has recently been shown that intensive management drives cryptic genetic erosion (Aerts and others 2012).

As shown in Andean ecosystems, farmers can benefit from the conservation of natural, diverse habitat through ecosystem services, such as decreased pest damage and increased yields (Poveda and others 2012). In addition, coffee benefits from ecosystem services of the forest (Millard 2011), and therefore the loss of species diversity in the 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).

Fig. 3 Effects of forest management in FC, SFC, and 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 . **f** Number of seedlings Ns . Error bars denote SE. Letters show significant differences between groups (ANOVA LSD test, $\alpha = 0.05$)



Management Implications

Intensification of coffee productivity starts with the conversion of an FC to SFC system 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 semiforest to the SPC system and disintegration of the entire forest structure: stem density, basal area, crown closure, crown cover, and dominant tree height all decrease 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 semiforest and semiplantation 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 SFC system has the potential to improve economic performance and biodiversity conservation. In the SFC system, coffee productivity is greater 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 the SPC and SFC systems. These temporarily

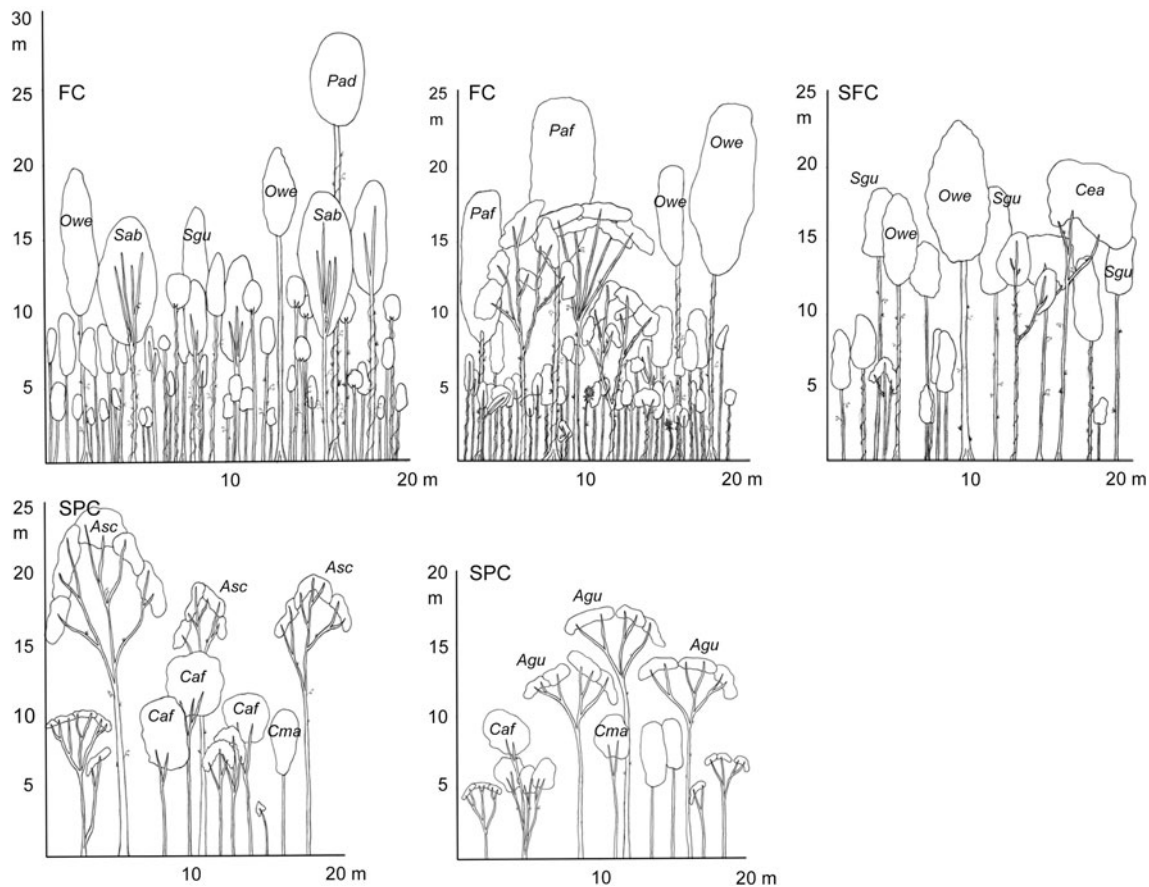


Fig. 4 Representative stand profiles from five 20 × 20 m plots in FC, SFC, and SPC systems in moist evergreen Afromontane forests in southwest Ethiopia. Upper canopy tree species are labeled as follows: Ag = *A. gummifera*; Asc = *A. schimperiana*; Caf = *Cordia africana*;

Cea = *Celtis africana*; *Cma* = *C. macrostachys*; *Owe* = *O. welwitschii*; *Pad* = *P. adolfi-friederici*; *Paf* = *P. africana*; *Sab* = *S. abyssinica*; and *Sgu* = *S. guineense*. The uniform understorey of *C. arabica* in the SFC and SPC systems is not shown

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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References

- Aerts R (2008) *Afrocarpus falcatus* (Thunb.) C.N.Page. In: Louppe D, Oteng-Amoako AA, Brink M (eds) Record from Protabase. PROTA (Plant Resources of Tropical Africa/Ressources Végétales de l’Afrique tropicale), Wageningen, Netherlands. Available at: <http://database.prota.org/search.htm>. Accessed: July 23, 2012
- Aerts R (2011) *Olea capensis* L. In: Lemmens RHMJ, Louppe, D, Oteng-Amoako AA (eds) Record from Protabase. PROTA (Plant Resources of Tropical Africa/Ressources Végétales de l’Afrique tropicale), Wageningen, Netherlands. Available at: <http://database.prota.org/search.htm>. Accessed: July 23, 2012
- Aerts R, Honnay O (2011) Forest restoration, biodiversity and ecosystem functioning. *BMC Ecol*. doi:10.1186/1472-6785-11-29
- Aerts R, Nyssen J, Haile M (2009) On the difference between “exclosures” and “enclosures” in ecology and the environment. *J Arid Environ* 73:762–763
- Aerts R, Hundera K, Berecha G, Gijbels P, Baeten M, Van Mechelen M et al (2011) Semi-forest coffee cultivation and the conservation of Ethiopian Afromontane rainforest fragments. *Forest Ecol Manage* 261:1034–1041
- Aerts R, Berecha G, Gijbels P, Hundera K, Van Glabeke S, Vandepitte K, et al. (2012) Genetic variation and risks of introgression in the wild *Coffea arabica* gene pool in southwestern Ethiopian Montane rainforests. *Evol Appl*. doi:10.1111/j.1752-4571.2012.00285.x
- Ahrends A, Burgess ND, Milledge SAH, Bulling MT, Fisher B, Smart JCR et al (2010) Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city. *Proc Natl Acad Sci U S A* 107:14556–14561
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol Manage* 259:660–684
- Anthony F, Combes MC, Astorga C, Bertrand B, Graziosi G, Lashermes P (2002) The origin of cultivated *Coffea arabica* L.

- varieties revealed by AFLP and SSR markers. *Theor Appl Genet* 104:894–900
- Bisseleua D, Hervé B, Stefan V (2008) Plant biodiversity and vegetation structure in traditional cocoa forest gardens in southern Cameroon under different management. *Biodivers Conserv* 17:1821–1835
- DeFries RS, Rudel T, Uriarte M, Hansen M (2010) Deforestation driven by urban population growth and agricultural trade in the twenty-first century. *Nat Geosci* 3:178–181
- Eriksson CP, Holmgren P (1996) Estimating stone and boulder content in forest soils—evaluating the potential of surface penetration methods. *Catena* 28:121–134
- Ethiopian Mapping Authority (1988) National atlas of Ethiopia. EMA, Addis Ababa
- Friis I (1992) Forests and forest trees of Northeast tropical Africa. Kew Bulletin Additional Series No 15. Her Majesty's Stationery Office, London, UK
- Gardner TA, Barlow J, Chazdon RL, Ewers R, Harvey CA, Peres CA et al (2009) Prospects for tropical forest biodiversity in a human-modified world. *Ecol Lett* 12:61–582
- Gebre-Egziabher T (1978) Some vegetative parameters of coffee, *Coffea arabica* L., proportional to yield. *Ethiopian J Sci* 1:51–57
- Gole TW (2003) Vegetation of the Yayu Forest in SW Ethiopia: Impacts of human use and implications for in situ conservation of wild *Coffea arabica* L. populations. Ecology and Development Series No. 10. Centre for Development Research, University of Bonn, Bonn, Germany
- Gole TW, Borsch T, Denich M, Teketay D (2008) Floristic composition and environmental factors characterizing coffee forests in southwest Ethiopia. *Forest Ecol Manage* 255:2138–2150
- Hansen MC, Stehman SV, Potapov PV (2010) Quantification of global gross forest cover loss. *Proc Natl Acad Sci U S A* 107:8650–8655
- Hedberg I, Edwards S, Nemomissa S (eds) (2003) Flora of Ethiopia and Eritrea. Volume 4, part 1. *Apiaceae* to *Dipsacaceae*. The National Herbarium, Addis Ababa University, Addis Ababa, Ethiopia, and The Department of Systematic Botany, Uppsala University, Uppsala, Sweden
- Hernández-Martínez G, Manson RH, Contreras Hernández A (2009) Quantitative classification of coffee agroecosystems spanning a range of production intensities in central Veracruz, Mexico. *Agric Ecosyst Environ* 134:89–98
- Hill MO (1973) Diversity and evenness. *Ecology* 54:427–432
- Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA et al (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecol Biogeogr* 15:1–7
- Hundera K, Aerts R, De Beenhouwer M, Van Overtveld K, Helsen K, Muys B, and others. (2012, in press) Both forest fragmentation and coffee cultivation negatively affect epiphytic orchid diversity in Ethiopian moist evergreen Afromontane forests. *Biol Conserv*. doi:10.1016/j.biocon.2012.10.029
- Labouisse JP, Bellachew B, Kotecha S, Bertrand B (2008) Current status of coffee (*Coffea arabica* L.) genetic resources in Ethiopia: implications for conservation. *Gen Resour Crop Evol* 55:1079–1093
- Lemmens RHMJ (2007) *Pouteria adolfi-friederici* (Engl.) A.Meeuse. In: Louppe D, Oteng-Amoako AA, Brink M (eds) Record from Protabase. PROTA (Plant Resources of Tropical Africa/Ressources Végétales de l'Afrique tropicale), Wageningen, Netherlands. Available at: <http://database.prota.org/search.htm>. Accessed: July 23, 2012
- McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. *J Veg Sci* 13:603–606
- Millard E (2011) Incorporating agroforestry approaches into commodity value chains. *Environ Manage* 48:365–377
- Perfecto I, Vandermeer J, Mas A, Soto-Pinto L (2005) Biodiversity, yield, and shade coffee certification. *Ecol Econ* 54:435–446
- Philpott SM, Bichier P, Rice R, Greenberg R (2007) Field-testing ecological and economic benefits of coffee certification programs. *Conserv Biol* 21:975–985
- Philpott SM, Arendt WJ, Armbrrecht I, Bichier P, Diestch TV, Gordon C et al (2008) Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conserv Biol* 22:1093–1105
- Poveda K, Martínez E, Kersch-Becker MF, Bonilla MA, Tschamtké T (2012) Landscape simplification and altitude affect biodiversity, herbivory and Andean potato yield. *J Appl Ecol* 49:513–522
- Priess JA, Mimler M, Klein AM, Schwarze S, Tschamtké T, Steffan-Dewenter I (2007) Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems. *Ecol Appl* 17:407–417
- Puetz S, Groeneveld J, Alves LF, Metzger JP, Huth A (2011) Fragmentation drives tropical forest fragments to early successional states: a modelling study for Brazilian Atlantic forests. *Ecol Model* 222:1986–1997
- Ramírez-Marcial N, González-Espinosa M, Williams-Linera G (2001) Anthropogenic disturbance and tree diversity in montane rain forests in Chiapas, Mexico. *Forest Ecol Manage* 154:311–326
- Schmitt CB, Senbeta F, Denich M, Preisinger H, Boehmer HJ (2009) Wild coffee management and plant diversity in the montane rainforest of southwestern Ethiopia. *Afr J Ecol* 48:78–86
- Senbeta F, Denich M (2006) Effects of wild coffee management on species diversity in the Afromontane rainforests of Ethiopia. *Forest Ecol Manage* 232:68–74
- Soto-Pinto L, Perfecto I, Caballero-Nieto J (2002) Shade over coffee: its effects on berry borer, leaf rust and spontaneous herbs in Chiapas, Mexico. *Agroforest Syst* 55:37–45
- Soto-Pinto L, Villalvazo-López V, Jiménez-Ferrer G, Ramírez-Marcial N, Montoya G, Sinclair F (2007) The role of local knowledge in determining shade composition of multistrata coffee systems in Chiapas, Mexico. *Biodivers Conserv* 16:419–436
- Takahashi R, Todo Y (2012) Impact of community-based forest management on forest protection: evidence from an aid-funded project in Ethiopia. *Environ Manage* 50:396–404
- Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371:65–66
- Trauernicht C, Ticktin T (2005) The effects of non-timber forest product cultivation on the plant community structure and composition of a humid tropical forest in southern Mexico. *Forest Ecol Manage* 219:269–278
- Van Reeuwijk LP (2002) Procedures for soil analysis. International Soil Reference and Information Centre, Wageningen
- Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, Peterken G et al (2006) Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87:542–548
- Vergara CH, Badano EI (2009) Pollinator diversity increases fruit production in Mexican coffee plantations: the importance of rustic management systems. *Agric Ecosyst Environ* 129:117–123
- Zytynska SE, Fay MF, Penney D, Preziosi RF (2011) Genetic variation in a tropical tree species influences the associated epiphytic plant and invertebrate communities in a complex forest ecosystem. *Philos Trans R Soc Lond B Biol Sci* 366:1329–1336