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Patch area and current coffee management determine woody plant diversity in patches of semi-forest coffee embedded in an agricultural matrix

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ABSTRACT

Effective conservation of biodiversity in patches of (semi-) natural vegetation is dependent on an understanding of the influence of management as well as spatial and temporal factors. In southwestern Ethiopia coffee generally grown under a rather dense layer of indigenous trees (so called semi-forest coffee - SFC) often in patches embedded in an open agricultural landscape. The aim of the study was to disentangle what governs the variation in species richness of woody species among such patches. We collected data on species and possible explanatory factors in 40 × 40 m plots centered in 40 SFC patches, measured the patch area for 1987 and 2013, and the amount of surrounding SFC-area for each patch. We recorded the number of coffee stems and the level of disturbance caused by slashing of the understory vegetation. Species richness of large coffee shade trees (>20 cm in diameter) was higher in larger patches with even slightly better fit of the statistical models when the historical area was taken into account. However, most species of large trees also occurred as seedlings showing that there is still a potential to conserve these species in the patches. Coffee management negatively affected the richness and density of woody species, especially in the intermediate size class (1.6–20 cm diameter). Disturbances accompanying coffee management such as slashing of the ground vegetation also negatively affected tree seedling density as well as species richness. There was no effect of connectivity on species richness. Based on the combination of these results we conclude that small patches of semi-forest coffee had fewer species of large trees, not because of a lack of tree seedlings, but probably because of differentiated local extinctions, perhaps during the time when the species were intermediate sized. To maintain the species richness of large trees in semi-forest coffee patches, the sites need to be actively managed.

1. Introduction

Habitat loss is considered the major cause of declining biodiversity, especially in tropical forest ecosystems (Mortelliti et al., 2010; Botello et al., 2015). Since agricultural mosaic landscapes have become common on previously forested areas we

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need a better understanding of the drivers of species richness and composition associated with trees and embedded forest fragments in such landscapes (Chazdon et al., 2009; Gardner et al., 2009; Häger et al., 2015).

The number of species in a forest patch is affected by many different factors. A larger patch generally has higher species richness due to higher habitat heterogeneity or simply because more individuals are present (Rosenzweig, 1995). If the number of species increases with patch area also when comparing same-size plots (for example one plot in the center of each of the patches), it might be an indication that the pattern is instead related to colonization–extinction dynamics following predictions of island-biogeography and metapopulation models (MacArthur and Wilson, 1967; Munguía-Rosas and Montiel, 2014). Here, not only area through its effect on both extinction and colonization rates, but also isolation, by decreasing the colonization rate are regarded as an important predictors of patch species richness. The degree of the impact of isolation is also dependent on the matrix between the patches (Laurance, 1997; Bender and Fahrig, 2005). However, many other variables than area and isolation could affect the number of species in a patch and even change the predicted species–area relationship (Ewers and Didham, 2006). In human dominated landscapes where generalist species from the matrix can penetrate the patches, pronounced edge related effects and various effects of management will influence species richness (Hundera et al., 2013).

History of the past land use can also affect the biodiversity of the patches. This can arise due to time lagged responses of species to landscape change both regarding extinctions and colonizations (Jackson and Sax, 2009). Extinction debts could be caused by delays due to both changes in habitat quality, quantity and connectivity (Hylander and Ehrlén, 2013), changes which often goes hand in hand when forests are becoming fragmented (Hanski and Ovaskainen, 2002; Franken and Hik, 2004). For example, bigger trees in Amazonian forest fragments did go extinct only after two decades after fragmentation (Laurance et al., 2000). The length of the delay period can vary among species due to differences in life history traits. For example, short-lived plants might go extinct quickly after a landscape change compared to long-lived species which may persist (Morris et al., 2008). Therefore, recognition of the legacy of the historical land use plays an indispensable role in explaining the present-day vegetation patterns in fragmented landscapes (Lindborg and Eriksson, 2004; Ewers et al., 2013).

Coffee (*Coffea arabica* L.) is a major crop in SW Ethiopia. It is a native species in the understory of forests (Teketay, 1999), but is also actively managed in many different parts of the landscapes (Hundera et al., 2013). The most common traditional coffee cultivation system in Ethiopia is semi-forest coffee (SFC) characterized by an active management of coffee, but still under a more or less natural canopy of original forest trees (Senbeta and Denich, 2006; Aerts et al., 2011). It is not only the naturally occurring plants that are nurtured, but often farmers also practice enrichment planting with wild coffee seedlings or cultivars. SFC system is similar to the rustic coffee system in Latin America, where however the coffee shrubs grown under the original forest trees is not a native species (Hernandez-Martinez et al., 2009). SFC cultivation is affecting the biodiversity in Ethiopia in different ways. It hosts native woody plant biodiversity (Tadesse et al., 2014) and has contributed to an overall reduction of tree cover but also deforestation rates at coffee growing altitudes by buffering the conversion of larger forest remnants (Hylander et al., 2013). In addition, SFC patches have been found to support high bird species diversity (Buechley et al., 2015). On the other hand, SFC management includes the slashing of the undergrowth herbs and the removal of shrubs and emergent trees with the aim to increase coffee productivity (Senbeta and Denich, 2006; Schmitt et al., 2009). Coffee management often also includes the thinning of the upper canopies to allow more light to penetrate down to the coffee (Gole, 2003; Labouisse et al., 2008) and certain shade trees are favored over others (Hundera et al., 2013). In some landscapes with SFC management one can find numerous small SFC patches embedded in a matrix of agricultural fields. Such patches might have a legacy as forest fragments after agricultural expansion, but over the last 40 years some of the patches have actually increased in area as coffee has been planted at the edges of the patches (Hylander et al., 2013; Ango et al., 2014).

The study aims at understanding the variation in species richness of woody plants in SFC patches in a mosaic landscape in SW Ethiopia. For this purpose we investigated 40 SFC patches surrounded by an open agricultural landscape, of which half of them have increased and the rest have decreased in area over the last 25 years. We studied small patches that in general have a rather homogenous management (pers. observation) due to only one or in a few cases a few owners. We explored how historical, spatial and management factors influenced species richness and density. Specifically we hypothesized that: 1. seedling densities would decrease with increasing levels of disturbance due to slashing; 2. coffee cover would negatively influence density and species richness of similar sized plants due to the management for avoiding competition; 3. Focal sites surrounded by high cover of SFC-areas would be more easily colonized than more isolated areas; and 4. the historical patch area would better explain the present species richness than current patch area for trees with large diameter, due to the inherent time lag between a tree seedling and a big tree. An improved understanding of the processes generating the species richness patterns of SFC patches would not only increase our general understanding on how species richness is governed in fragmented human dominated landscapes, but also guide conservationists since SFC patches probably house the last forest associated biodiversity in some regions (Tadesse et al., 2014).

2. Methods

2.1. Study area

The study was carried out around the town of Agaro in southwest Ethiopia, Oromia National Regional State, Gomma district located at 7°48′-7°53′N and 36°33′-36°36′E (Fig. 1). The area is characterized by a rolling topography and is dissected by many streams. The district is a variegated landscape of annual crop fields and semi-forest coffee patches. The closest

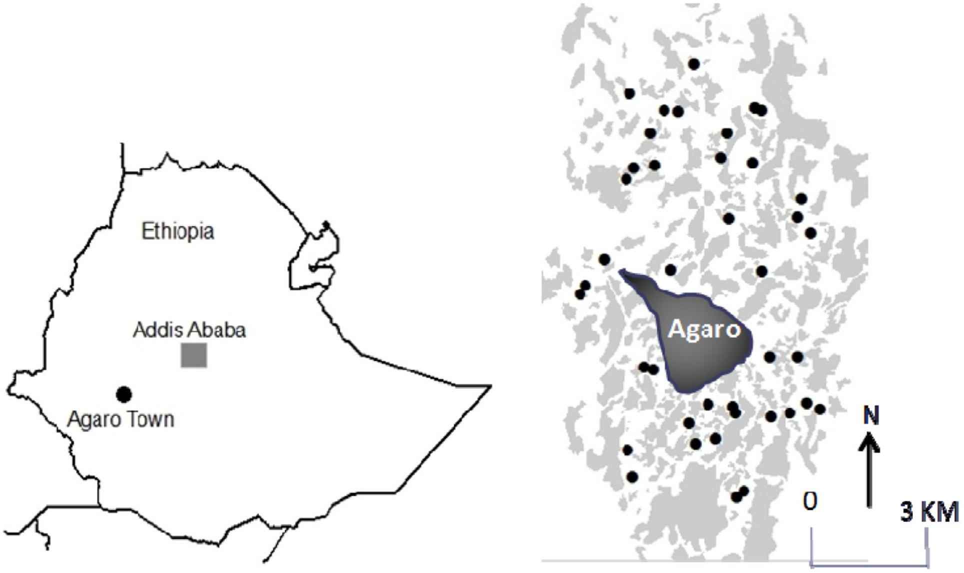

Fig. 1. Study area in South-westen Ethiopia in the Gomma district surrounding the town of Agaro. Semi-forest coffee patches are denoted with light gray color embedded in the open agricultural landscape (white on the map). Black points denote the 40 semi-forest coffee patches used for this study.

more natural forests are found 15 kms to the west in the Gera district. The annual average rainfall of the area is about 2000 mm. The climax vegetation in the study region is moist afro-montane forests with characteristic tree species such as *Pouteria adolfi-friederici, Croton macrostachyus, Ficus sur, Apodytes dimidiata, Cordia africana, Syzygium guineense, Allophyllus abyssinicus, Millettia ferruginea, Sapium ellipticum, Albizia spp., Acacia abyssinica* and *Olea welwitschii* (Friis et al., 2010).

2.2. Data collection

2.2.1. Selection of semi-forest coffee patches

To our knowledge everything that looks like forest in a satellite image covering our study area is under SFC management and has been so for long time. The district is known for its long history of coffee production and still traditional management with old coffee shrubs dominates the area (Birhan et al., 2014). In this area there are no signs of certain remnant forests trees (e.g. *Pouteria adolfi-friederici* and *Syzygium guineense*) that are common both in forests and in shade coffee areas recently converted from forests in the neighborhood Gera district (pers. obs.). We selected an area of 144 km^2 surrounding the town of Agaro (12 km in N–S direction and 6 km in E–W direction; Fig. 1), which had many SFC patches. Using Landsat imagery data obtained from USGS GLOVIS, we delineated semi-forest coffee patches in one Landsat ETM image (spatial resolution 30 m) from 1987 and identified the same patches in another Landsat ETM+ image from 2013. We used image enhancement techniques for increasing the visual distinctions between features in a scene. The minimum mapping unit was 0.36 ha, which correspond to four pixels. The preprocessing operations and area calculations were done using the software ERDAS IMAGINE 9.1 (ESRI, 2010). We selected 44 SFC patches (22 patches which had increased in area and 22 which had decreased between the years 1987 and 2013). After visiting the sites in the field we omitted four patches because two patches were burial areas and two others were found to have houses built inside; otherwise all patches had SFC management of varying intensity. In addition, we avoided patches near streams (less than 300 m from the streams) and patches outside the altitudinal band of 1500–1900 m asl to reduce environmental gradients among the patches and since coffee is most abundant at these altitudes. We only selected rather small patches ranging from 0.8 to 4.9 ha as measured in the 2013 satellite image. The included patches had varied in area from a decrease of a maximum of 1.2 ha to an increase with up to 1.7 ha between the two measurements in 1987 and 2013 (Table 1). The minimum distance between two patches was 34 m (as measured in Google Earth imagery from 2013 and the maximum distance between two closest patches was 1744 m. However, in our selected landscape there is seldom more than 300 m distance between a focal patch and another SFC patch in the landscape (see Fig. 1 for an overview of the spatial arrangement of SFC areas).

2.2.2. Vegetation sampling

The fieldwork for the major data collection was conducted from March to April 2014. In the center of each of the 40 selected semi-forest coffee patches we established a plot of 40 × 40 m. In the plots, we identified all individuals and species of woody plants and designated as tree (a woody plant with a single main stem and a distinct upper crown); shrub (a woody plant with 2 or more stems arising from the base) and climber (woody plant that uses other plants as a means of support but has its roots in the ground) based on the description given in the Flora of Ethiopia and Eritrea (Hedberg and Edwards,

Table 1
Range and average of management, spatial and environmental variables in 40 semi-forest coffee patches, Gomma, Southwest Ethiopia. Disturbance and coffee cover was measured in a 40 × 40 m plot.

Variables	Range	Average	Standard deviation
Area 1987 (ha)	0.36–4.9	2.4	1.2
Area 2013 (ha)	0.80–4.9	2.3	1.1
Aerial change (ha)	−1.2–(+1.7)	0.01	0.59
Disturbance (%)	25–62	44	11
Coffee cover (coffee density/ha)	125-550	458	88
SFC cover within 500 m (%)	5.7–60.4	26.2	12.0
SFC cover within 1000 m (%)	3.7–46.5	18.9	11.4
Altitude (m asl)	1501–1889	1661	91

1989) and own observations in the field. For species which were not identified in the field we collected plant samples, which were enumerated and identified to species level later on by using the Flora of Ethiopia and Eritrea. The voucher specimens are stored in the National Herbarium of Ethiopia, Addis Ababa University. We measured the DBH of all individuals of woody species. To assess vegetation structure, we categorized the individuals as seedlings (DBH $<$ 1.6 cm), middle size trees (DBH 1.6–20 cm) and large trees (DBH $>$ 20 cm).

2.2.3. *Management and spatial variables*

In the plots of all SFC patches, we estimated the percent of disturbance (slashing of the under-growth that could heavily influence regeneration of trees) by measuring the area of the slashed parts of the plot and dividing it with the total area. We assumed that areas that were slashed this year also were slashed other years and vice versa. We also counted the number of coffee plants, which could be assumed to affect the number of similar sized shrubs and trees of other species. In a Google Earth image from 2013, we delineated all patches manually by creating polygons in the study area and then created a raster layer of SFC area in ArcGIS (ESRI, 2010). Based on that layer we calculated the amount of SFC cover in buffers of 500 m and 1000 m radii around each focal plot using proximity toolset in ArcToolbox of ArcGIS (ESRI, 2010). We chose the 500 m and 1000 m buffer radii to cover typical variation in the landscape. Since, many tropical trees are dispersed by birds (Datta and Rawatt, 2008; Corlett, 2009), even longer distances might have been valuable to evaluate. However, our setting did not allow for that since larger buffers would have overlapped too much. In all the SFC patches the altitude and geographic coordinates at the center of each plot were recorded using a handheld global positioning device (eTrex Vista HCx; Garmin, Kansas City).

2.3. *Data analysis*

The difference in richness and density among the four different size classes: trees seedlings, shrub and climber seedlings, middle size trees (diameter at breast height or DBH 1.6–20 cm) and large trees (DBH $>$ 20 cm) were tested using ANOVA. We assessed the impact of spatial, management and environmental variables on species richness and density of individuals using general linear modeling (GLM). We modeled total species richness as well as species richness and density separately for the four size classes. We used the following explanatory variables: patch area, level of ground disturbance, coffee cover (number of coffee stems), and percentage of forest cover in 500 m and 1000 m buffers surrounding the focal plot. For each response variable we run two models with the same explanatory variables, but with historical patch area (1987) and present (2013) patch area in two different models, respectively. This was because these two variables were correlated (see Appendix B for a correlation matrix among the explanatory variables). We also calculated the range and average of the aerial changes of the SFC patches between the two measurement years.

In the modeling procedure a stepwise backward selection was employed where spatial and environmental variables were dropped based on their contribution to the Akaike Information Criterion (AIC); within the MASS package in the R program (Venables and Ripley, 2002). The final reported model was the one with the smallest AIC value. We found GLM with Poisson error to fit best the data for the species richness and for the density of the largest sizes of woody species (DBH $>$ 20 cm). Linear models (with the logarithm of the response variable to meet assumptions of normality of the residuals) were fitted for the rest of the density classes. We inspected the performance of the models in relation to model assumptions (i.e. normality of the residuals) using a panel of four diagnostic plots in R (Venables and Ripley, 2002). In addition, we assessed possible over-dispersion of the GLM models. Since four SFC patches has lower coffee cover than the rest we also re-run the models without them to cross-check the robustness of the results (Results only shown in those cases when it had a profound effect).

Using the presence–absence data of species in the different patches, we conducted ordination analyses (Non-metric multidimensional scaling, NMDS with Bray-Curtis distance measure) to explore the general patterns of species composition in the separate size class groups. We then tested if management, spatial and environmental variables correlated to the sites scores in the separate ordinations employing the *envfit* command in the package in R (Oksanen, 2013). The statistical significance was calculated by Montecarlo permutations. We also conducted an NMDS ordination for a pooled matrix of both the largest DBH class and their seedlings (using presence–absence data) to examine if the species compositions of the two groups overlapped or not, by visually examining the distribution of site scores. We tested if there was a significant shift or not in species composition between the larger trees and their seedlings by employing an *adonis* analysis in *vegan*

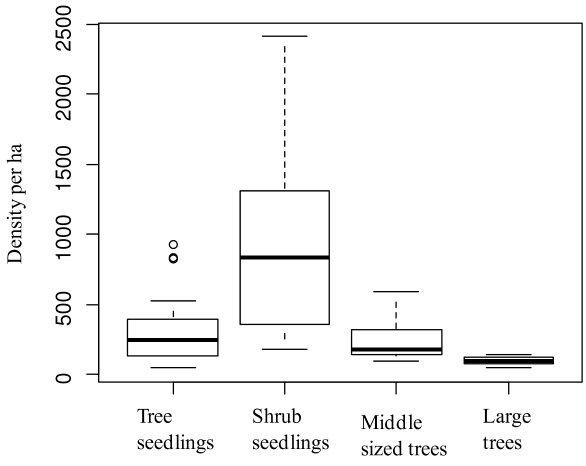

Fig. 2. Densities of woody species in 40 semi-forest coffee patches divided by diameter class and for the smallest class between shrubs and trees. Data collected in 40 × 40 m plots and calculated to density per ha (DBH = diameter at breast height).

Table 2
Final models for densities of individuals of the different DBH classes in relation to management and spatial variables in 40 Semi-forest coffee patches. Linear model for tree seedlings (DBH < 1.6 cm), shrub seedlings (DBH < 1.6 cm) and Middle size class (DBH 1.6–20 cm) and GLM with Poisson error structure for the Higher DBH size class (DBH > 20 cm). Model A uses patch area in 1987 and model B patch area in 2013. Area change is a categorical variable (increase or decrease between 1987 and 2013). coef = coefficient.

Model	R^2	AIC	Area		Area change		Coffee cover		Disturbance		% of SFC in 500 m buffer		% of SFC in 1000 m buffer	
			coef	*p*	coef	*p*	coef	*p*	coef	*p*	coef	*p*	coef	*p*
Tree seedlings	0.23	95.7	–	–	−0.21	0.030	0.01	0.024	−0.01	0.008	–	–	–	–
Shrub seedlings A	0.25	−95.6	0.06	0.165	0.13	0.17	–	–	−0.01	0.010	0.01	0.055	−0.01	0.023
Shrub seedling B	0.23	96.2	–	–	–	–	–	–	−0.01	0.011	0.01	0.082	−0.01	0.037
Middle DBH class	0.37	−133.1	–	–	–	–	−0.01	<0.001	–	–	0.004	0.13	–	–
Higher DBH class	–	204.2	–	–	–	–	0.02	<0.001	–	–	–	–	–	–

package in R (Oksanen, 2013). An *adonis*-analysis is analogous to a multivariate analysis of variance using dissimilarity distance matrices. To characterize which species that contributed most, and in which direction, to the difference in species composition between the higher DBH trees and the seedlings, we conducted an indicator species analysis using *indval* in the *labdsv* package in R (Dufrêne and Legendre, 1997). The method builds on calculating relative frequencies among sites. The indicator values were calculated from species-site matrix of the presence/absence data and the statistical significances were tested using permutation.

3. Results

3.1. Variation in management and spatial variables

The plots displayed a large variation in ground disturbance (25%–63% of the inventoried plot) and coffee cover (20–88 shrubs per plot corresponding to 125–550 shrubs per hectare; Table 1). The amount of SFC-cover in buffers of 500 m and 1000 m, varied from a few percentages to 60% and 47%, respectively (Table 1).

3.2. Density of individuals

The average densities of woody plant individuals varied among the different size classes ($F = 46.36$, $p < 0.001$) and were more than 10 times higher for seedlings (DBH < 1.6 cm) than of trees with a diameter >20 cm (Fig. 2). In the smallest diameter class (<1.6 cm) the shrub seedlings had higher average density (906 individuals per ha) compared to tree seedlings (291 individuals per ha) (Fig. 2).

The number of seedlings in a plot was negatively affected by the level of disturbance ($p = 0.008$, Table 2). Tree seedlings, for example, decreased from around 60 per plot when the disturbance was negligible to 20 when ∼60% of the plot was

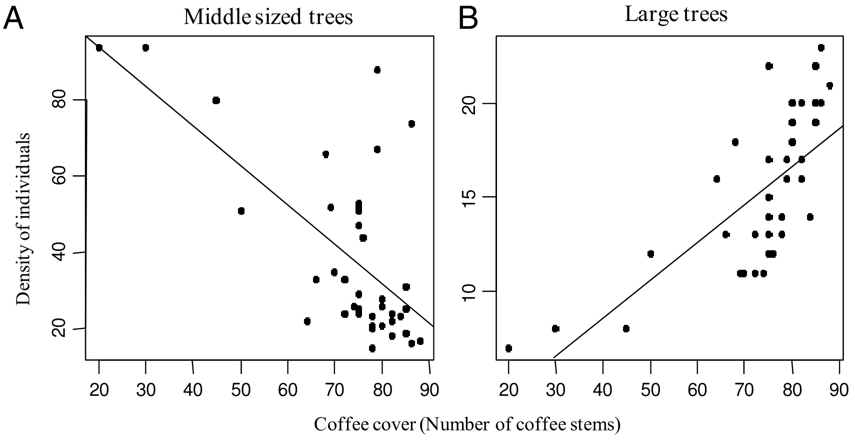

Fig. 3. Density of individuals of woody species in different diameter classes within 40 ×40 m plots versus coffee cover i.e., (A) middle sized trees and shrubs (1.6–20 cm) and (B) large tree (DBH >20 cm). Linear trend lines are imposed on the data for better interpretability. For statistical details see Table 2.

Table 3
Species richness of the different size classes of woody species within 40 semi-forest coffee plots of 40 × 40 m (DBH = diameter at breast height).

Variables	Range	Average
Tree seedling richness, DBH < 1.6 cm	2–8	4
Shrub seedling richness, DBH < 1.6 cm	3–18	9
All woody species richness, DBH 1.6–20 cm	1–18	8
All woody species richness, DBH > 20 cm	1–8	4
Total woody species richness	7–26	17

disturbed due to slashing of the understory vegetation. Coffee cover was found to be one of the most important predictors of density. However, its effect varied among the different size classes being positive for tree seedlings and trees >20 cm DBH and negative for the intermediate size class (Table 2, Fig. 3(A) and (B)). However, numbers of tree seedlings were mostly affected by the level of disturbance (Table 2). If the four sites with lowest coffee cover were removed the relationship with that variable was not longer significant.

3.3. Species richness

In total we found 88 species of woody plants from the 40 plots of which 39 were classified as shrubs, 10 woody climbers and 39 as trees (Appendix A). The average number of species per plot was 17, but the species were distributed differently among the different growth forms and size classes (Table 3). The average species richness was similar for tree seedlings (4 species) and the largest trees (>20 cm) (4 species), but higher in the shrub seedlings and intermediate size classes (DBH 1.6–20 cm) (Table 3). The lowest minimum richness in a single plot was only one species in one plot for DBH 1.6–20 cm and one species of DBH greater than 20 cm in another plot (Table 3).

The total species richness of woody plants in a plot varied from 7 to 26 species (Table 3). Different spatial, temporal and management factors were related to the variation in the different size classes (Table 4). Disturbance was the major predictor of both tree and shrub seedling richness. The number of tree species seeedlings dropped from around 6 to 3 along the disturbance gradient ($p = 0.015$, Table 4, Fig. 4(A)). For the intermediate sized class (DBH 1.6–20 cm), coffee cover was instead the most important predictor with a strong negative effect on number of species ($p < 0.001$, Table 4, Fig. 4(B)). Number of species of trees with DBH >20 cm in a plot varied from 1 to 8 and was best explained by the area 25 years prior to the inventory ($p = 0.001$, Table 4, Fig. 4(C)). Richness of large trees was also higher in sites that had large area in 2013, since there was a correlation between area in 1987 and 2013. However, that model of the richness of the larger trees had somewhat a better fit when including historical patch area compared to using only current patch area. This is also shown by the inclusion of the variable "increased or decreased area" in the final model using area from 2013 instead of 1987 as the predictor (Table 2). Here a recent increase in area did not positively affect the number of species (as it did for shrub seedlings and smaller trees, Table 2), but instead showed a negative trend, indicating that the historical area is an important predictor. The cover of SFC areas surrounding the focal sites did not significantly contribute to explain richness in any of the models.

3.4. Species composition

Shrub seedlings species composition significantly correlated with coffee cover in the NMDS analysis ($p = 0.024$, stress $= 0.20$). For the other strata there were no significant correlations between the species composition and the measured

Table 4
Final models for species richness of the different size classes in 40 semi-forest coffee plots of 40 × 40 m. Model A uses patch area in 1987 and model B patch area in 2013. Area change is a categorical variable (increase or decrease between 1987 and 2013). coef = coefficient, Middle DBH class has DBH 1.6–20 cm and Higher DBH class has DBH > 20 cm. Data from final models based on their AIC-value.

Model	AIC	Area		Area change		Coffee cover		Disturbance	
		coef	*p*	coef	*p*	coef	*p*	coef	*p*
Tree seedlings	154. 8	–	–	–	–	–	–	−0.02	0.015
Shrub seedlings	201.7	–	–	0.23	0.038	–	–	−0.02	<0.001
Middle DBH class A	217.3	–	–	0.20	0.092	−0.01	<0.001	−0.01	0.089
Higher DBH class A	147.9	0.21	0.001	–	–	–	–	–	–
Higher DBH class B	149.1	0.21	0.003	−0.31	0.055	–	–	–	–
Total species A	230.1	–	–	0.17	0.025	–	–	−0.01	<0.001

Table 5
Indicator values of large trees (higher DBH class i.e. DBH > 20 cm) and their seedlings, respectively, and *p*-values from Montecarlo permutation test. A presence/absence matrix was used for the calculations.

Tree species	Indicator value for higher DBH size class	Indicator value of seedlings	*P* value
A. abyssinica	0.28	0.08	0.095
Albizia grandibracteata	0.03	0.03	1
Albizia gummifera	0.34	0.19	0.27
Albizia schimperiana	0.26	0.17	0.52
Bersama abyssinica	0.002	0.20	0.01
Cassipourea malosana	0.012	0.012	1
C. africana	0.41	0.03	0.002
C. macrostachyus	0.4	0.24	0.23
Dracaena steudneri	0.03	0.03	1
Ehretia cymosa	0.10	0.03	0.48
Ekebergia capensis	0.012	0.012	1
Entada abyssinica	0.03	0.01	1
Euphorbia ampliphylla	0.03	0	1
Ficus thonningii	0.03	0	1
Ficus vasta	0.05	0	0.49
Flacourtia indica	0.02	0.07	0.70
Ilex mitis	0.05	0	0.51
Macaranga capensis	0	0.03	1
M. ferruginea	0.07	0.17	0.39
Mimusops kummel	0.03	0	1
Prunus africana	0.01	0.06	0.63
Psidium guajava	0.01	0.21	0.02
Sapium ellipticum	0.12	0.22	0.46
Spathodea campanulata	0.03	0	1
Strychnos mitis	0.21	0	1

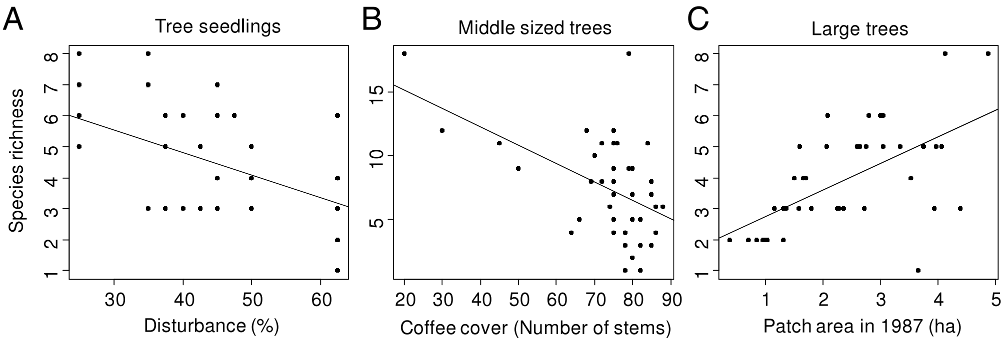

Fig. 4. Species richness of (A) tree seedlings versus disturbance, (B) middle sized trees and shrubs (DBH 1.6–20 cm) versus coffee cover, and (C) large trees (DBH > 20 cm) patch area in 1987 within 40 × 40 m plots. Linear trend lines are imposed on the data for better interpretability. For statistical details see Table 4.

management and spatial variables. The species composition of tree-seedlings differed from the composition of the large trees ($F = 4.26$, $p = 0.004$). However, the difference seems small with much overlap as seen in the NMDS graph (Fig. 5). Moreover, the indicator species analysis revealed only few differences between the seedling and adult composition (Table 5). The only species that was overrepresented as adult was *Cordia africana* ($p = 0.002$, Table 5).

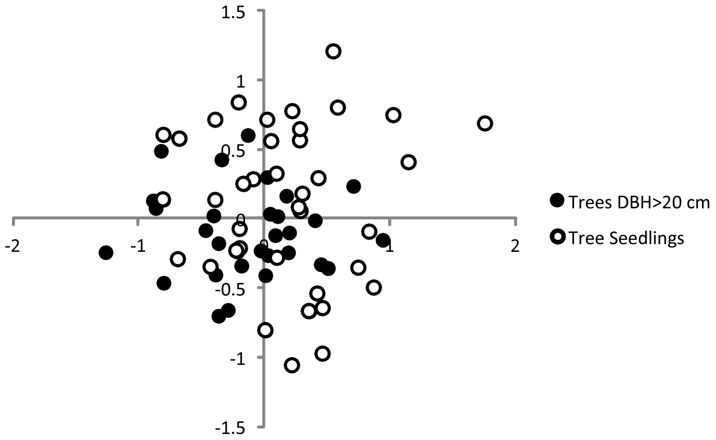

Fig. 5. NMDS of higher DBH trees and their seedling species compositions of pooled data (based on presence/absence) from 40 SFC patches of 40 × 40 m plots.

4. Discussion

In this study we show that patches of so called semi-forest coffee embedded in an open agricultural landscape vary much in how many species of woody plants they contain. We show that the species richness of larger trees is higher in plots located in patches of larger area. Moreover we show that coffee cover may have either a positive or a negative association to local species richness, depending on if we analyzed the richness of large or middle size trees. These are important information to incorporate in management plans, given that for long term conservation of the earth's biodiversity we need not only knowledge of pattern and processes in areas with little influence of human management, but also to what extent human dominated landscape, not least in a tropical context, can harbor species (Tscharntke et al., 2005; Vandermeer and Perfecto, 2006; Hylander and Nemomissa, 2008).

4.1. Time lags

The effect of history on species richness of larger trees is likely due to the longevity of the trees, as they germinate some times before and respond slowly to landscape changes as opposed to short lived plants (cf. Metzger et al., 2009). If historical variables affect current patterns of species richness there is a possibility that there could be an extinction debt (Kuussaari et al., 2009). For example long lived plants could be present even if they do not reproduce (Eriksson, 1996). However, it is not necessary that the correlation to historical variables imply an extinction debt and in our case we found seedlings of most of the canopy trees indicating that this was not the case in our system, except perhaps for *C. africana* (see Table 5). This species is popular for its valuable timber by the local communities and is listed as a threatened species (IBC, 2012).

4.2. Area and isolation effects

The positive area effect on species richness of larger trees, which even a somewhat better model fit for the area 25 years ago, need to be scrutinized, since there could be many processes creating a positive species–area relationship (Turner and Tjørve, 2005). Among the many explanations for high species diversity in larger patches is that they are more heterogeneous and that more heterogeneous habitats provide more niche space (Rosenzweig, 1995; Honnay et al., 1999). However, since we used same-sized sample plots for all different sized patches, it is unlikely that habitat heterogeneity contributed to the observed richness–area relation for large trees. Both the island biogeography and metapopulation theories, predict higher colonization in larger patches contributing to high species richness as compared to small patches (MacArthur and Wilson, 1967; Hanski and Gilpin, 1991). However, since we did not find any effect of our connectivity measure (amount of SFC in the surrounding area) on the number of tree seedlings or their species richness, there is little evidence that our current or historical area effect is due to higher colonization in the larger patches. Instead, a possible explanation for the exhibited species–area relations could be lower extinction in larger patches than in smaller patches, which is the second major prediction from island biogeography and metapopulation biology. We believe that beside stochastic effects related to mortality of certain species in the smaller patches, perhaps also deterministic extinctions of certain species due to edge effects could be involved. For instance, sharply elevated tree mortality is encountered near forest edges due to wind effects in the Amazon (Laurance et al., 2000; D'Ângelo et al., 2004). Note, however, that the densities of large trees were the same in small and large patches in our case. Perhaps the process of converting the shade tree composition to a more homogenous and favorable one (Hundera et al., 2013) is easier in smaller than larger patches, both from a microclimatic and a labor point of view (e.g. closer to take timber to the edges). If we had known the longer history of the patches we would have known whether there is a legacy of the patches as old forest fragments from a continuous afromontane forest, which could have guided our interpretations.

The lack of any effect of connectivity (amount of forest in a 500 or 1000 m buffer) on the species richness and species composition in any of the strata may suggest that most forest species in this region can easily disperse across this landscape. However, more likely it has to do with the limited area we have studied. In fact several dominant climax species of the moist afromontane forest type (Friis et al., 2010) are missing in our entire data set and might be limited by dispersal to this area. For example, neither any adults nor seedlings were found of the three characteristic species *P. adolfi-friederici*, *O. welwitschii* and *S. guineense*, which are frequent in the larger continuous Gera forest some 15 km to the west of our area (Gebrehiwot and Hundera, 2014).

4.3. Coffee management

As hypothesized, coffee management was an important driver of woody species density and diversity. As also suggested by several other studies, one of the largest effects of coffee management in Ethiopian forests is the decline of similar sized trees and shrubs (Senbeta and Denich, 2006; Hundera et al., 2013; Tadesse et al., 2014), which also was the most clear effect in our data both for density and species richness (Fig. 3(A)–(B) and Fig. 4(B)). However, more surprisingly were the findings of positive relationships between coffee cover and density of large canopy shade trees (Fig. 3(B)). Perhaps it is the lower density of larger trees in sites with less coffee that needs an explanation, rather than the many trees apparently retained in dense coffee sites. If so, one could hypothesize that selective logging was more common in sites with less coffee. An alternative hypothesis is that large trees do not attain the same density in sites with a larger variation in tree sizes (i.e. including middle sized trees). From our results it is also clear that the disturbance due to annual slashing accompanying coffee cultivation is a strong negative force on both density and richness of seedlings. Even if we found most canopy trees regenerating in the semi-forest coffee patches, the densities may still be reduced compared to in undisturbed forests (cf. Hundera et al., 2013). Not only coffee forests but also many other disturbed forests have poor regeneration of trees, for example due to grazing (Telila et al., 2015). Some of the unexplained variation in our data could be attributed to unmeasured variation in environmental variables among the patches and plots. For example aspect and slope may be important drivers of vegetation.

5. Conclusions

Total species richness was mainly driven by the seedlings due to the higher richness in their size classes compared to the larger trees. This highlights the importance of understanding the processes affecting richness and density of the different size classes in order to be able to evaluate which actions might be needed for conservation. From this study it is clear that there is a risk that the traditional coffee management in semi-forest coffee patches not only will negatively affect species richness of the intermediate DBH woody species, but also in the long term the richness of the larger shade trees. Although there was now a positive effect of coffee cover on richness of large trees, it is likely that the richness in this layer also eventually will decrease, since there were few intermediate sized individuals that could grow into large trees. However, on the positive side was that there were many tree seedlings of different species that, if allowed, could possibly regenerate into larger trees. Thus, it would be possible to maintain or even increase the diversity of semi-forest coffee patches if the management would focus not only on coffee production, but also on biodiversity conservation. In addition, for biodiversity conservation purposes there need also to be certain areas with less coffee cover that can accommodate intermediate sized species that never grow high, since they always will be competing with coffee for light and space. However, even with such measures semi-forest coffee sites will never be able to replace undisturbed natural forests in terms of conservation values (e.g. Senbeta and Denich, 2006; Hundera et al., 2013; Buechley et al., 2015). However, it is also worth repeating that besides its negative influence on plant species diversity, semi-forest coffee management overall also plays an important role in buffering against deforestation (Hylander et al., 2013). Thus, the future challenge is to maintain the positive role of coffee cultivation for biodiversity conservation, while mitigating the negative effects.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2016.09.012.

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