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Species composition and diversity of small Afromontane forest fragments in northern Ethiopia

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Abstract

In the highlands of northern Ethiopia, remnants of the original Afromontane forest vegetation are largely restricted to church yards and other sacred groves in a matrix of cropland and semiarid degraded savanna. To assess the potential for natural forest regeneration, species composition and diversity of all forest fragments (10) in a study area of 13,000 ha were analyzed in relation to environmental and soil variables. Using a random design and a density of approximately one plot per two ha in all fragments, thirty-one 20 m × 20 m plots were sampled. Indicator species analysis and MRPP tests yielded five communities representing two forest types and one degraded savanna habitat.

The forest fragments had a species-poor tree and shrub community in which plots were rather homogeneous and most species abundant. NMDS and analysis of variance indicated that a topographical gradient correlated to soil phosphorus, soil depth, stoniness and the proximity to the river system explained the major differences in species composition and separated moist and dry Afromontane forest communities. The grazing intensity further partitioned the habitats. Present communities and their environmental correlates indicate that the secondary climax forest in the area probably consisted of dry Afromontane forest interlaced by broad strips of moist Afromontane forest along rivers and streams and not a continuous, mono-dominant *Juniperus* forest as is often presumed.

Negative effects of the degraded matrix on forest fragments increased with decreasing patch area and increasing shape irregularity. Nevertheless, all remaining fragments are important for their role in the landscape ecology of the region as refuges and species pools and should be protected and managed accordingly.

If seed dispersal from forest fragments into exclosures and subsequent tree recruitment are both successful, the vegetation type most likely to establish is Afromontane savanna woodland, and if managed properly, eventually dry Afromontane forest may arise. Increasing the size of small patches and placing forest plantations and exclosures in the vicinity of small forest fragments is expected to yield the most immediate results. This approach may increase the likelihood of patch colonisation by frugivorous forest birds and thus foster the regeneration of native woody species.

Introduction

Changes in land cover triggered by cultivation and heavy livestock grazing pressure are proximate causes for severe dryland degradation and desertification in many parts of Sub-Saharan Africa (Zeleke & Hurni 2001; Geist & Lambin 2004; Lemenih et al. 2005). In northern Ethiopia, and in particular in the northernmost regional state of Tigray, where almost all available land is under cultivation or used as grazing land, a network of exclosures has been established to control further degradation of natural ecotopes (Aerts et al. 2004; Nyssen et al. 2004; Mengistu et al. 2005). Land rehabilitation efforts in these exclosures, which are protected areas several hectares in size where removal of remnant vegetation and free grazing is no longer permitted or strictly controlled, aim to restore the natural forest vegetation.

To facilitate natural forest regeneration in these exclosures, an understanding of the ecology of indigenous forest communities and tree species is required. Trees perform a range of ecological functions with respect to disturbance regimes and they may regenerate from various sources, including dormant seeds in the seed bank, seed rain, advanced regeneration, and resprouts from damaged adults (Horvitz et al. 1998). Characteristic species of Afromontane forest such as *Juniperus procera* Hochst. ex Endl., *Olea europaea* ssp. *cuspidata* (Wall. ex G. Don) Cif. and *Afrocarpus falcatus* (Thunb.) C N. Page, usually form seedling banks on the forest floor and lack persistent soil seed reserves (Teketay 1997a; Teketay & Granström 1997; Tekle & Bekele 2000). Thus, if clearing of forests is followed by permanent cultivation or intensive grazing, which is typically the case in northern Ethiopia, regeneration will be seriously hampered (Teketay 1997b). In this type of degraded landscape, natural forest succession will primarily depend on seed dispersal from nearby forest patches into exclosures (Teketay & Granström 1995; Turner & Corlett

1996; Teketay 1997b; Duncan & Duncan 2000). Remnants of the original Afromontane forest vegetation are largely restricted to church yards and other sacred groves. Forest regeneration may become very difficult if these remnants further deteriorate or are eliminated (Teketay 1997b), especially because extinction rates are high and recovery times long for both forest plant species and seed dispersers in fragmented landscapes with prolonged habitat loss (Hames et al. 2001; Vellend 2003; Verheyen et al. 2004). In addition to these recolonisation problems, soil-vegetation feedback cycles may influence forest succession (Guariguata & Ostertag 2001) and restrict the possibilities for natural forest regeneration in exclosures.

In Afromontane dryland forest, the ecological relationships between tree species, forest communities and environmental variables have not been studied in detail. Although the natural forest vegetation is often presumed to be dry mono-dominant Afromontane *J. procera* forest of the Ethiopian highlands (Friis 1992), it is not possible to predict what forest communities will regenerate in exclosures without prior knowledge of the location and the composition of remnant forest communities. Without such knowledge, management guidelines assisting the restoration process can not be devised properly. In this study, therefore, we i) determined the species composition and diversity of small remnant forest communities, and ii) assessed the physical environmental correlates of these communities. In addition, we examined whether forest community composition was spatially correlated to strengthen predictive power about which forest communities may regenerate in a given area.

Methods

Study sites

The study was conducted in the Geba river watershed (13° 37’ N, 39° 21’ E, elevation: 1980-2000 m a.s.l.) in Central Tigray, 20 km NW of the regional capital Mekelle, from July through September 2002. Seven church forests and three other sacred forest fragments were surveyed. These were the only remaining forest patches north of the Tsilme and Gereb Aba Haylu rivers in the study area of approximately 13,000 ha. Each forest was mapped in the field using a GeoExplorer III GPS (Trimble Navigation Limited, Sunnyvale, CA), and later combined in ArcView GIS 3.2a (ESRI, Redlands, CA) with other spatial data digitized from a topographic map (1339-A4 North Mekelle, Ethiopian Mapping Authority, Addis Ababa) (Fig. 1).

The climate of the study area is determined by its mountainous nature and falls within the Sudanese zone (Nyssen et al. 2004). The mean annual temperature is 18 °C and the mean annual precipitation is 625 mm (Meze-Hausken 2004), most of which occurs during the summer rainy season (June-September) in the form of highly erosive rains (65–77% of the rains > 25 mm h^{-1}) brought in by prevailing eastern winds. The winter is hot and dry due to winds from the Sahara (Nyssen et al. 2004).

The soils clearly reflected topography and geology. Between 1800 and 2000 m, near the lower limit of the highlands, the parent material is usually Antalo limestone. This is the most important parent rock in the sampled forest fragments. Over the limestone basement Cambisols with various lower level soil units were formed, while Leptosols and Vertisols formed on shallower or more clayey parent materials, respectively. Forest fragments were embedded in a virtually treeless landscape of cropland and heavily grazed *Acacia* shrubland. The latter was characterized by a discontinuous cover of shrubs in a matrix of herbaceous vegetation and bare soil. It can thus be defined as semiarid degraded savanna (Vetaas 1992).

[Insert Fig. 1]

Data collection

Using a random design and a density of approximately one plot per two hectares in each fragment, thirty-one 20 m × 20 m plots were sampled. Within forest fragments, sample plots were located > 50 m apart to ensure sample independence. The mean distance to the nearest plot within each fragment was 120 m (Fig. 1).

Dry forests on poor site conditions are usually single-storied – approximately 4–12 m in height – and often characterized by a virtually impenetrable (thorn) shrub layer (Lamprecht 1989). Shrubs are generally defined as low-growing woody perennials with several stems no more than 4.5 m in height. But because many trees in semiarid environments may not grow much taller than 5 m or grow as shrubs under unfavourable conditions, an arbitrary division between trees and shrubs was used. Each tree (all single-stemmed woody individuals ≥ 1 m in height and all multi-stemmed individuals ≥ 2 m in height) was identified to species level and its height and circumference of the stem at breast height were measured. Shrubs (all single-stemmed woody individuals < 1 m in height and all multi-stemmed individuals < 2 m in height) were sampled in a random 10 m × 10 m subplot within the 20 m × 20 m plot. Plant nomenclature follows Hedberg & Edwards (1989), Hedberg et al. (2003) and Klopper et al. (2005).

Slope inclination (Suunto inclinometer), grazing intensity (0 no grazing, 1 occasional grazing and 2 regular or heavy grazing) and position of the plot in the landscape along the vertical gradient (1 valley, 2 concavity on the lower slope, 3 convexity on the upper slope and 4 plateau) were recorded. The horizontal distance to the nearest major natural drainage line (seasonal stream or permanent river) was calculated in ArcView GIS using a spatial join operation. Aspect was recorded as the azimuth (θ) measured from true north and transformed to a relative measure for heat load (HL) using the equation $HL = [1-\cos(\theta)]/2$ (McCune & Keon 2002).

To quantify nutrient availability, soil samples were randomly collected inside each plot (three subsamples per plot) from two depths (0–20; 20–70 cm) using an Edelman auger with a diameter of 27 mm and a length of 200 mm. Subsamples from the same depth interval in a plot were combined. The composite samples were air-dried, sieved (< 2 mm) and oven-dried (24 hours at 80°C) in the laboratory. Following standard soil analysis methods (Van Reeuwijk 2002), each sample was analysed for the following chemical variables: soil acidity pH(H_2O) and potential soil acidity pH(KCl) (potentiometric method in soil–water and soil–KCl suspension, respectively), total inorganic carbonate $CaCO_3$ (titrimetrical method with HCl and NaOH), total soil organic carbon SOC and total nitrogen N (Dumas combustion analysis) and total phosphorus P (ammonium lactate extraction and spectrophotometry). Stoniness and mean soil depth were assessed using the rod penetration method (Eriksson & Holmgren 1996) based on 60 systematic steel bar depth measurements per plot. The soil profile observed in each plot was described in the field and classified according to the World Reference Base for Soil Resources (FAO et al. 1998).

Data analysis

Because most species occurred both in the tree and the shrub layer, vegetation data were pooled to give species abundance at plot level (individuals/400 m^2) by the formula $T + 4S$ where T is the species abundance calculated from individuals in the tree layer (20 m × 20 m plot) and S the species abundance based on the individuals recorded in the shrub layer (10 m × 10 m subplot). Descriptive statistics and outlier analysis were first calculated for plant abundance data. The plant data (58 species) formed a sparse matrix with 82% of the cells containing zero values. Species abundance data was log-transformed by the formula $\log_{10}$(abundance+1) to reduce skewness. After deleting rare species (present in < 2 plots), leaving 40 species and 75% zero values, no more species were recognized as outliers given a cut-off point of two standard deviations from the grand mean Sørensen distance measure. Spearman rank correlation showed a high degree of correlation between top- and subsoil values of the six measured soil-chemical variables ($0.77 \leq r_s \leq 0.97$, $p < 0.001$, n = 31); therefore, only topsoil variables were included. Classification, ordination and statistical tests were conducted using PCord 4.0 for Windows (McCune & Mefford 1999) and SPSS 12.0 for Windows (SPSS Inc., Chicago, IL).

Cluster analysis

Indicator species analysis (Dufrêne & Legendre 1997) was used to determine the optimal number of groups in the cluster analysis. The 31 sample plots were repeatedly clustered into 2–8 groups using a Sørensen distance measurement and flexible beta linkage ($\beta = -0.25$) (McCune & Mefford 1999). For each run, indicator values for each species and the overall average p-value were calculated. To avoid creating additional groups that only marginally improved the overall significance, the last cluster step adding > 0.05 significance to the average p-value was selected as the most informative number of clusters. Differences in community composition between groups (clusters) and between individual forest fragments were tested with a multiresponse permutation procedure (MRPP) test using the Sørensen distance measure and a natural group weighting factor $n_i/\Sigma n_i$ (where n_i is the number of sample plots in each group). MRPP is a nonparametric method for testing multivariate differences among pre-defined groups. The test statistic (T) describes the separation between groups and the chance-corrected within-group agreement (A) describes within-group homogeneity compared to random expectation. $A = 1$ when all items are identical within groups. If heterogeneity within groups equals or exceeds expectation by chance, then $A = 0$ and $A < 0$, respectively. If there is more homogeneity within groups than expected by chance, then $1 > A > 0$. In community ecology values for A are commonly below 0.1 (McCune & Mefford 1999).

To avoid Type I errors induced by testing the same null hypothesis many times, the independent environmental and habitat variables (stem densities, basal area, heights) were tested for differences between groups simultaneously using MANOVA and Tukey’s HSD. Nonparametric Kruskal-Wallis ANOVA and pair-wise comparison (Siegel & Castellan 1988) were used to test for differences between groups in diversity measures and variables lacking homogeneity of variance (Levene’s test $p < 0.05$).

Ordination

Nonmetric multidimensional scaling (NMDS) was used to investigate indirect gradients influencing species distribution. NMDS was run on the log-transformed abundance data using the Sørensen distance measure, six starting dimensions, 40 iterations and an instability criterion of 10^{-5} (McCune & Mefford 1999).

The main environmental gradients were identified using PCA on the environmental data. To test for concordance between environmental variables and the NMDS dimensions, Spearman rank correlation coefficients were calculated and evaluated after Bonferroni correction for multiple tests. Also the PCA axes were explained using this procedure. The Bonferroni correction provides a corrected level of significance (α_{corr}) by dividing the upper limit of the significance level of the individual tests ($\alpha = 0.05$) by the number of coefficients tested in the experiment (in this case $\alpha_{\text{corr}} = 0.05/13 = 0.004$).

Habitat groups were related to the Yangambi nomenclature of tropical vegetation (Conseil Scientifique pour l'Afrique au Sud du Sahara 1959 in Lamprecht 1989) and the forest typology of Africa as proposed by Friis (1992) and Menaut et al. (1995) using results from the gradient and indicator species analysis.

Diversity of fragments

Alpha (α, average species richness per plot), beta (β, total richness/average richness) and gamma (γ, total species) richness, Shannon's diversity (H') and evenness (J and J') and Simpson's diversity (D) indices were calculated for each fragment. Hill's diversity numbers (Hill 1973) were derived from these indices because they are relatively unaffected by species richness and tend to be independent of sample size. N_0 (= γ), N_1 (= $e^{H'}$) and N_2 (= D^{-1}) were used as measures of species richness and diversity, and E_1 (= $e^{J'} = N_1/N_0$) as an index of species evenness. These measures were also calculated for each habitat group and for all plots pooled together.

Fragment shape was quantified using a complex perimeter/area ratio, which compares the total external perimeter of a fragment to the circumference of a circle having the same area and which is not dependent on patch size (Hill & Curran 2005). Multiple linear regression models were run separately for each species richness and diversity number as the dependent variable and the $\log_{10}$-transformed fragment size and the shape index as the independent variables.

Results

The forest fragments were very small (mean size = 6.56 ha) and had a species-poor tree and shrub community (low γ richness), in which plots were rather homogeneous (low β) and most species abundant (high α) (Table 1). Abundant and widespread species included *Acacia etbaica* Schweinf., *Euclea racemosa* ssp. *schimperi* (A. DC.) White., *Justicia schimperiana* T. Anders, *Leucas abyssinica* (Benth.) Briq., *Pavetta gardeniifolia* A. Rich and *Acokanthera schimperi* Benth. & Hook., accounting for 54% of all individuals.

[Insert Table 1]

Clustering the sample plots in five groups provided the maximum separation between groups (T), and a within-group level of homogeneity of 0.275 (A) (Table 2). Five plant communities were identified (Table 3), containing 14–31 species (N_0, Table 6). Only one forest fragment contained sample plots grouped in two different communities (Minta, Fig. 1). Individual forest fragments were internally more homogeneous than the communities ($A_{\text{fragments}} > A_{\text{communities}}$) but were less separated from each other ($|T_{\text{fragments}}| < |T_{\text{communities}}|$) (Table 2).

[Insert Table 2 and Table 3]

For the NMDS ordination, the greatest reduction in 'stress' (McCune & Mefford 1999) was achieved with a three-dimensional solution. The proportions of variance (coefficients of determination R^2 for the correlations between ordination distances and Sørensen distances in the original 40-dimensional space) represented by the three axes were 0.525, 0.264 and 0.116 respectively (cumulative $R^2 = 0.905$). The NMDS ordination unambiguously partitioned the five communities (Fig. 2).

[Insert Fig. 2]

A soil fertility component (PCA 1, $R^2 = 0.304$), represented by soil organic carbon ($r_s = 0.908$), nitrogen ($r_s = 0.944$) and acidity ($r_s = -0.783$), accounted for the largest fraction of the variance among the environmental data (all $p < 0.001$). Species distributions along the NMDS axes, on the other hand, chiefly responded to a topographical gradient defined by the plot position along the altitudinal gradient and the distance to the nearest drainage line (NMDS 1, Table 4). Soil depth and soil available phosphorus were negatively correlated to this gradient (Table 4). These variables also defined the second component of the PCA (PCA 2, $R^2 = 0.193$) and typically separated plots on deep valley soils (Fig. 2, left) from plots on shallow soils higher on the slopes and on plateaus (Fig. 2, right). The plots were further partitioned along the second NMDS dimension following an increasing grazing intensity gradient (Table 4, Fig. 2). The third NMDS dimension was not significantly related to the environmental variables measured in this study.

[Insert Table 4]

The environmental correlates of the NMDS axes were the only variables showing significant differences between groups (Table 5). Differences between groups were also reflected in the mean stand characteristics (Table 6). *Faidherbia–Achyranthes* and *Celtis–Pterolobium* had less, but significantly larger trees in terms of heights and basal area than any of the other groups (Table 6). Both were communities of deep valley soils with high phosphorus content, but were separated from each other by a higher grazing intensity and a higher shrub density, respectively (Tables 5, 6). The other three communities had high tree and shrub densities, but occurred on different sites with different grazing intensities. *Acacia–Olea* and *Pavetta–Combretum* were communities of poor, shallow soils and occurred on grazed plateaus and ungrazed steep upper slopes, respectively. The *Acacia–Echinops* community was found on deep valley soils and was heavily grazed.

[Insert Table 5 and Table 6]

Plant species richness (N_0) and diversity (N_1) was greater in the *Pavetta–Combretum* community than in the other groups. All groups were characterized by low species evenness (E_1) (Table 6). At the fragment scale, the multiple linear regression models using each species richness and diversity number as a dependent variable and $\log_{10}$(area) and shape index as the independent variables, were significant for N_0 ($F_{2,7} = 6.54$, $p = 0.025$, $R^2 = 0.81$) and for N_2 ($F_{2,7} = 5.52$, $p = 0.036$, $R^2 = 0.78$). The number of species in a forest fragment (N_0) increased with patch area ($\log_{10}$(area): standardized coefficient $\beta = 0.63$, $p = 0.026$). The diversity of abundant species (N_2) increased with increasing shape irregularity (shape index: standardized coefficient $\beta = 0.70$, $p = 0.020$) (Fig. 3).

[Insert Fig. 3]

Discussion

Forest classification

Faidherbia albida (Del.) A. Chev., *Celtis africana* Burm. f. and *Justicia schimperiana* T. Anders are species of riparian forests and river banks (Fichtl & Admasu 1992; Stave et al. 2005). Indicator values for these species reached their maximum values in the communities of deep valley soils, *Faidherbia*–*Achyranthes* and *Celtis*–*Pterolobium* (Table 3), suggesting that both communities may be classified as moist Afromontane forest or a localized phase of the undifferentiated Afromontane forest of the Ethiopian highlands *sensu* Friis (1992). High grazing pressure in the former explains the high indicator value of *Achyranthes aspera* L., a troublesome epizoochorously dispersed weed and true disturbance indicator if abundant in moist, shaded habitats (Fichtl & Admasu 1992). *Pterolobium stellatum* (Forssk.) Brenan occurred in these communities as a large hooking liana and probably proliferated after logging of the original host trees (see Gerwing & Uhl 2002). Under normal conditions, lianas increase the canopy connectedness and fulfill important structural and ecosystem-level functions in tropical forests (Schnitzer & Bongers 2002; Senbeta et al. 2005), but in secondary forests such as the forests sampled in this study, large vine tangles are a potential cause of arrested succession (Chapman et al. 1999; Schnitzer et al. 2000). The species commonly forms dense thickets in exclosures in the region, smothering pioneer shrubs and suppressing tree regeneration.

The *Acacia–Echinops* community may be defined as shrub savanna, an open community dominated by thorny species (*Acacia abyssinica* Benth., *A. etbaica*, *Maytenus senegalensis* (Lam.) Excell) (Table 3). Small trees and a high dominance of *Acacia* typically characterize dry scrub communities of the valley floors of East Africa (Menaut et al. 1995). The prevalence of thistles (*Echinops* sp.) and unpalatable succulents (*Aloe macrocarpa* Tod.) with high indicator value, as well as the structure of this community, may be attributed to heavy grazing pressure. Overgrazing is an ecological threat to woodlands which induces and maintains dominance of short, thorny species.

The remaining two communities may be defined as dry Afromontane forest or the dry mono-dominant Afromontane forest of the Ethiopian highlands *sensu* Friis (1992). The *Acacia–Olea* community is a relatively open forest on shallow soils in plateau situations with a high dominance of *A. etbaica* and disturbance indicators with a high indicator value, for example *Leucas abyssinica* (Table 3). The other shrubs in the understorey are often suppressed trees such as *Rhus natalensis* Bernh. ex Krauss. Large grassy patches existed between the small shrubs and trees, which render this forest into an extremely attractive grazing ground for cattle. Afromontane savanna woodland would therefore be a more appropriate name for this phase of dry Afromontane forest. The vegetation in the grazed matrix areas and the exclosures, which have shallow soils as well, is similar to this forest type, but the woody species, including *Olea*, are usually only present as shrubs as a result of heavy browsing and cutting (see Mengistu et al. 2005).

The *Pavetta–Combretum* community had the highest species richness and diversity (N_0, N_1, Table 6) despite its poor soil conditions (shallow soils on steep slopes; Table 5). *Olea* is an important component in this phase of dry Afromontane forest, and is under these conditions usually associated with *J. procera*. The high relative importance of *Combretum* may indicate that the fragments in this group are intermediate forms along an altitudinal gradient between true dry Afromontane forest and combretaceous woodland, one of the most widespread vegetation types of Ethiopia (Fichtl & Admasu 1992), particularly in the lowlands and lower highlands.

[Insert Fig. 4]

A theoretical transect through the study area oriented along an altitudinal gradient with reference to potential forest vegetation, key species and soil groups is presented in Figure 4. The classification of communities into moist and dry Afromontane forests is in agreement with the simplified classification of tropical forests according to temperature (temperate tropics, mean annual temperature 14–22 °C, elevation 800–2100 m) and precipitation regime (alternating wet and dry seasons) (Lamprecht 1989). Most of the Afromontane forests described in the central and southern highlands of Ethiopia (Bekele 1994; Michelsen et al. 1996; Lemenih & Teketay 2005) belong to the humid and alpine Afromontane forest and rainforest formations. The fragments described in this study differed considerably in species composition from these forests, despite similar soil nutrient levels (Michelsen et al. 1996; Lemenih et al. 2005). The location of the study area near the lower limit of the highlands may partially explain their differences from the Afromontane forests of central and southern Ethiopia and their greater similarity to dry forests and savannas of East Africa. Results are comparable to those of Menaut et al. (1995) for African dry forests and savanna under mesic climatic conditions, where savanna and forest showed similar associations to landscape position and soil depth. In a study of the woody vegetation of Ol Choro Oiroua in the Masai Mara region in south-western Kenya, similar diagnostic species were found (Van Essen et al. 2002). *A. etbaica*, *E. racemosa* and *R. natalensis* were diagnostic for low closed woodland, whereas *O. europaea* was characteristic for short forest, with a comparable stem number of 3150 individuals ha^{-1}. Hovestadt et al. (1999) described analogous vegetation types in West African forest-savanna mosaics in Ivory Coast, where forest islands were either humid forests, dry undisturbed forest or dry disturbed forests, with an increase in savanna and disturbance-tolerant forest species in the disturbed forests.

Diversity of fragments

The total species richness was lower compared to the richness recorded in larger Afromontane forests in the central and southern highlands of Ethiopia (Bekele 1994; Lemenih & Teketay 2005). All forest fragments studied must be considered degraded to a certain degree. But despite the low total species richness, all remaining fragments are true islands of forest biodiversity considering the surrounding matrix of semiarid degraded savanna. They are important for their role in the landscape ecology of the region (as refuges and species pools) and for their contribution in producing seeds and should thus be protected and managed accordingly (Turner & Corlett 1996; Lawes et al. 2005).

Species-area relationships and the island effect are often used to explain the relation between forest fragmentation and declining species richness. These approaches assume that populations are distributed uniformly before fragmentation and that local extinctions are due to the effects of small population sizes (Wilsey et al. 2005). Beta diversity (among plots) increased with increasing fragment size (Fig.

3), indicating that populations may not be distributed uniformly. Plant populations of some species may be abundant locally but rare elsewhere. This could result in species-specific effects of fragmentation on plant demography (Wilsey et al. 2005).

Larger fragments exhibited higher total species richness (Fig. 3), which could be attributed to ecological processes (island effect, e.g. Hill & Curran 2003) but equally to sampling effects, whereby larger forest fragments contained more plots that sampled more of the community (Hill & Curran 2001). More irregularly shaped remnants (with a higher shape index) showed lower levels of woody species diversity (α, N_0, N_1), which agrees with established forest core/edge theories stating that habitat fragmentation and the subsequent negative implications for biodiversity conservation are primarily problems of edge effects (e.g. Turner 1996; Hill & Curran 2003). In irregular fragments, more common and abundant species occurred (higher N_2). Invasion of light-demanding woody pioneer species through the edge may also be explained as an effect of the degraded matrix on the forest fragments (Sizer & Tanner 1999; Honnay et al. 2002).

The historical ecology of the communities

Pollen data from two lakes in the highlands of northern Ethiopia provide evidence that the natural, pre-disturbance vegetation of the area was undifferentiated Afromontane *Afrocarpus–Juniperus* forest (Darbyshire et al. 2003). At about 500 BC this primary mixed conifer forest was cleared and replaced by a secondary vegetation of *Dodonaea* scrub and grassland that persisted for 1800 years. Mono-dominant dry Afromontane *Juniperus* forest with increasingly important secondary forest species such as *Olea* and *Celtis*, then expanded from 1400 to 1700 CE throughout East-Africa, caused by either increased rainfall or reduced human impact

(Darbyshire et al. 2003). Clearing of forests and land degradation during the last 300 years probably explain the dominance of thorny savanna species at present, while the traditional protection of church yard vegetation explains the survival of dry forest and secondary woodland species in the fragments. The strong correlation between present tree associations and the environment on the other hand, suggests that the secondary climax forest in the study area may have been patchy and diverse depending on the soil and topography, and not a continuous, mono-dominant *Juniperus* forest as is often presumed. Dry Afromontane forest interlaced by broad strips of moist Afromontane forest along rivers and streams seems a more realistic pattern.

Churches were built on strategic or symbolic locations such as commanding plateau situations (Giorgis Sesemat, Endagaber Mheni and Medhane Alem Geramesagu) or travertine dams near permanent rivers or seasonal streams (Enda Maryam Chenferes and Giorgis Romanat) (Fig. 1). The present spatial configuration of forest remnants is therefore caused by active protection of forest near church yards or other sacred places, not purely by topography or pedological variables. Fire shadow effects described for South Africa's southern Cape landscape (Geldenhuys 1994) were probably not important here. For Africa, similar examples of *in situ* conservation of earlier forest ecosystems in sacred groves are described in the context of Ghanaian savannas (Campbell 2004) and miombo woodland in Tanzania (Mgumia & Oba 2003).

Application to forest rehabilitation

Woodland recovery in Sub-Saharan Africa has been associated with decreasing intensities of browser pressure (Walpole et al. 2004). The establishment of exclosures where domestic grazing and browsing is no longer permitted may therefore contribute to forest regeneration. However, we cannot expect existing plant communities in forest fragments to be identical to those several hundred years ago, nor can we expect future communities in exclosures to be identical to those sampled in fragments today. Given the current state of desiccation and land degradation (Nyssen et al. 2004) and the absence of essential Afromontane species such as *Afrocarpus falcatus* and *Juniperus procera*, it is most unlikely that moist Afromontane forest will regenerate in exclosures in the near future. Mature trees of species which are explicitly linked to moist Afromontane forest may persist in small fragments, but with little or no possibility to regenerate *in situ*, these species are virtually extinct locally (Turner & Corlett 1996; Hill & Curran 2005).

Acacia shrubs do regenerate readily in the area, mostly through resprouting from pre-established individuals. For many other tree species, the success of natural regeneration in exclosures will greatly depend on the quality of the physical environment and the vicinity to forest remnants. If seed dispersal from forest fragments into exclosures and subsequent tree recruitment are both successful, the vegetation type most likely to establish in degraded semiarid savanna of northern Ethiopia is Afromontane savanna woodland. If exclosures are managed properly, eventually dry Afromontane forest may arise. Increasing the size of small patches and placing forest plantations and exclosures in the vicinity of small forest fragments may increase the likelihood of patch colonization by forest birds (Wethered & Lawes 2005) and thus foster the regeneration of native woody species.

O. europaea has a wide ecological range, is present as a seed source in forest fragments and villages, has fleshy fruits which are attractive for avian seed dispersers, and its natural regeneration in degraded areas is facilitated by pioneer shrubs (Aerts et al., in press). Therefore, *O. europaea* may be one of the key precursor species for natural forest regeneration in the study area.

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Figure 1. Location of Afromontane forest fragments (stars on central inset) and sample plots in Central Tigray, northern Ethiopia (bottom inset). Sample plots are labeled according to five habitat groups produced by cluster and indicator species analysis: moist Afromontane forest: ● grazed and ○ not grazed; △ shrub savanna; dry Afromontane forest: ▲ savanna woodland and ■ closed-canopy forest. Crosses indicate Ethiopian Orthodox churches.

Figure 2. Nonmetric multidimensional scaling (NMDS) ordination of the 31 plots sampled in ten Afromontane forest fragments in northern Ethiopia. Sample plots are labeled according to five habitat groups produced by cluster and indicator species analysis: moist Afromontane forest: ● grazed and ○ not grazed; △ shrub savanna; dry Afromontane forest: ▲ savanna woodland and ■ closed-canopy forest.

Figure 3. Species richness and Hill's diversity numbers in relation to fragment size ($\log_{10}$-scale) and shape index for ten Afromontane forest fragments in northern Ethiopia: α, average number of species per plot; β, among-plot diversity; $\gamma = N_0$, total species richness; N_1, Hill's species diversity; N_2, Hill's diversity of abundant species; E_1, Hill's evenness. *p*-values are the factor significance levels of multiple linear regression models run separately for each species richness and diversity number as the dependent variable, using $\log_{10}$(area) and shape index as independent variables.

Figure 4. Hypothetical transect near the lower limit of the highlands of northern Ethiopia (1800 – 2000 m) with associated potential forest vegetation: MF, moist Afromontane forest; DF, dry Afromontane forest; SW, Afromontane savanna

woodland; SS, shrub savanna. Key tree species: *Aab*, *Acacia abyssinica* Benth.; *Aet*, *Acacia etbaica* Schweinf.; *Ase*, *Acacia seyal* Del.; *Asc, Acokanthera schimperi* (DC.) Benth.; *Asi*, *Acacia sieberiana* DC. ssp. *woodii* (Burtt Davy) Keay & Brenan; *Asp*, *Aloe* sp.; *Caf*, *Celtis africana* Burm. f.; *Cau*, *Calpurnia aurea* (Ait.) Benth.; *Cco*, *Combretum collinum* Fresen.; *Cof*, *Cordia africana* Lam.;*Csi*, *Cassia singueana* Del.; *Eab*, *Euphorbia abyssinica* Gmel.; *Era*, *Euclea racemosa* ssp. *schimperi* (A. DC.); *Fal*, *Faidherbia albida* (Del.) A. Chev.; *Fsp*, *Ficus* spp.; *Oeu*, *Olea europaea* ssp. *cuspidata* (Wall. ex G. Don) Cif.; Jsc, *Justicia schimperiana* T. Anders; *Psc*, *Psydrax schimperiana* (A. Rich.) Bridson; *Rna*, *Rhus natalensis* Bernh. ex Krauss. Soil groups according to FAO et al. (1998): CM, Cambisol; LP, Leptosol; VR, Vertisol; ca, calcaric; vr, vertic; sk, skeletic.

Figures

Fig. 1

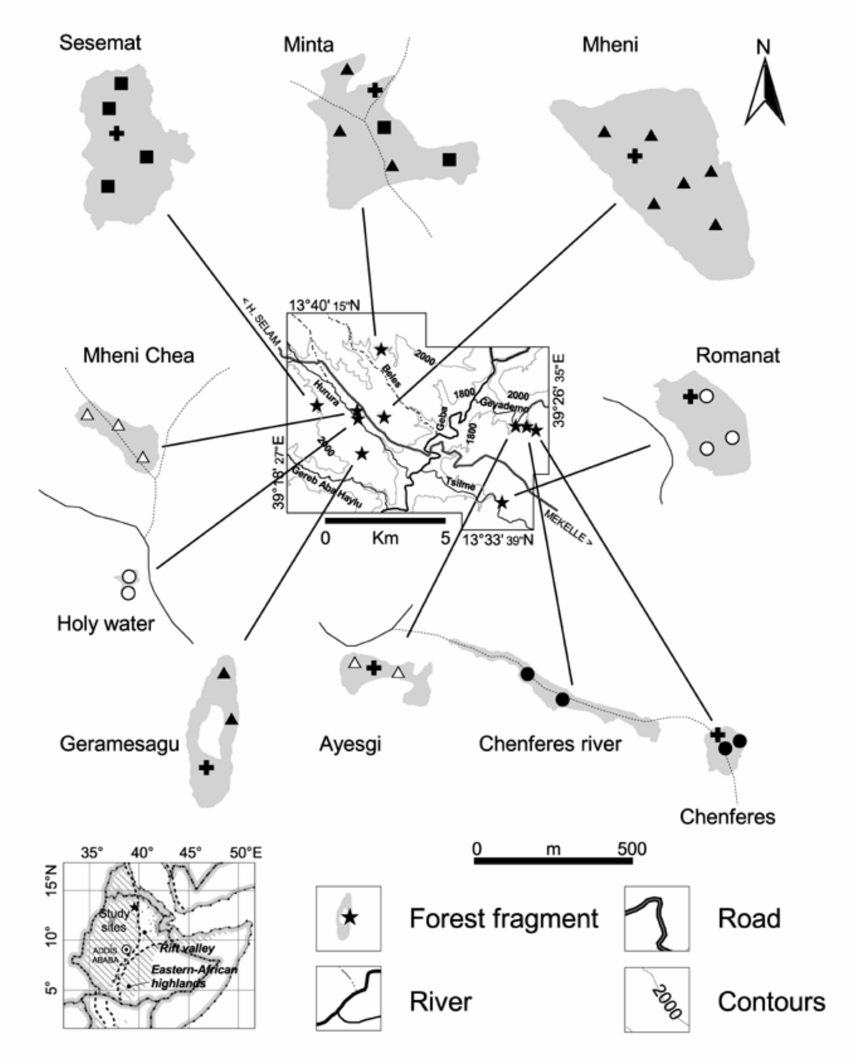


Fig. 2

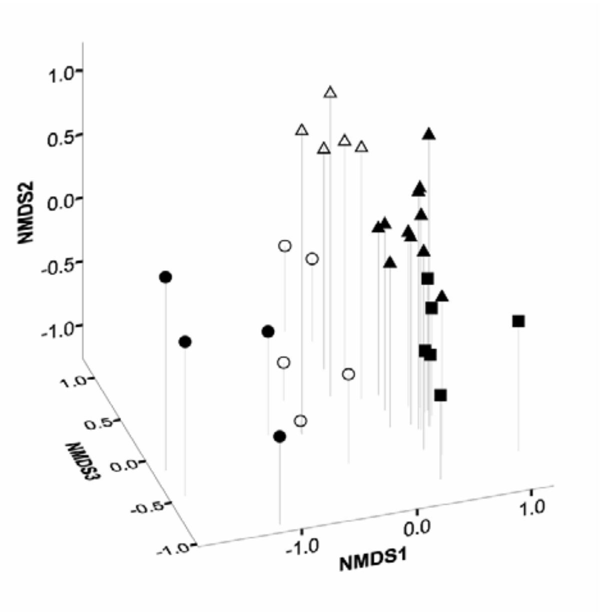
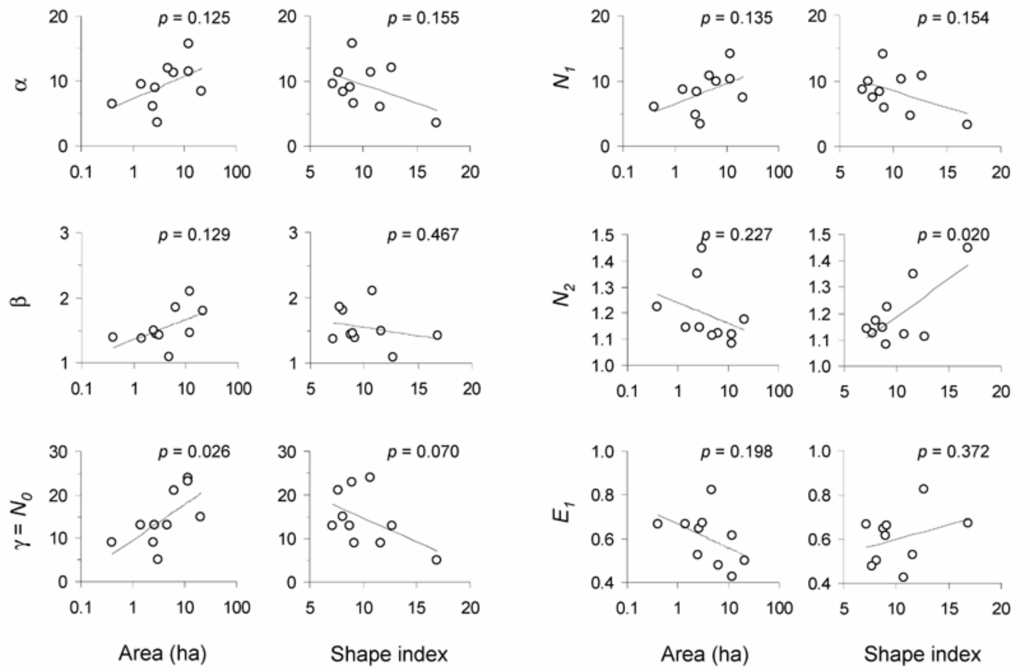


Fig. 3



p = 0.125
p = 0.155
p = 0.135
p = 0.154
p = 0.129
p = 0.467
p = 0.227
p = 0.020
p = 0.026
p = 0.070
p = 0.198
p = 0.372
α
β
γ = N0
N1
N2
E1
0.1
1
10
100
5
10
15
20
Area (ha)
Shape index
Area (ha)
Shape index

Fig. 4

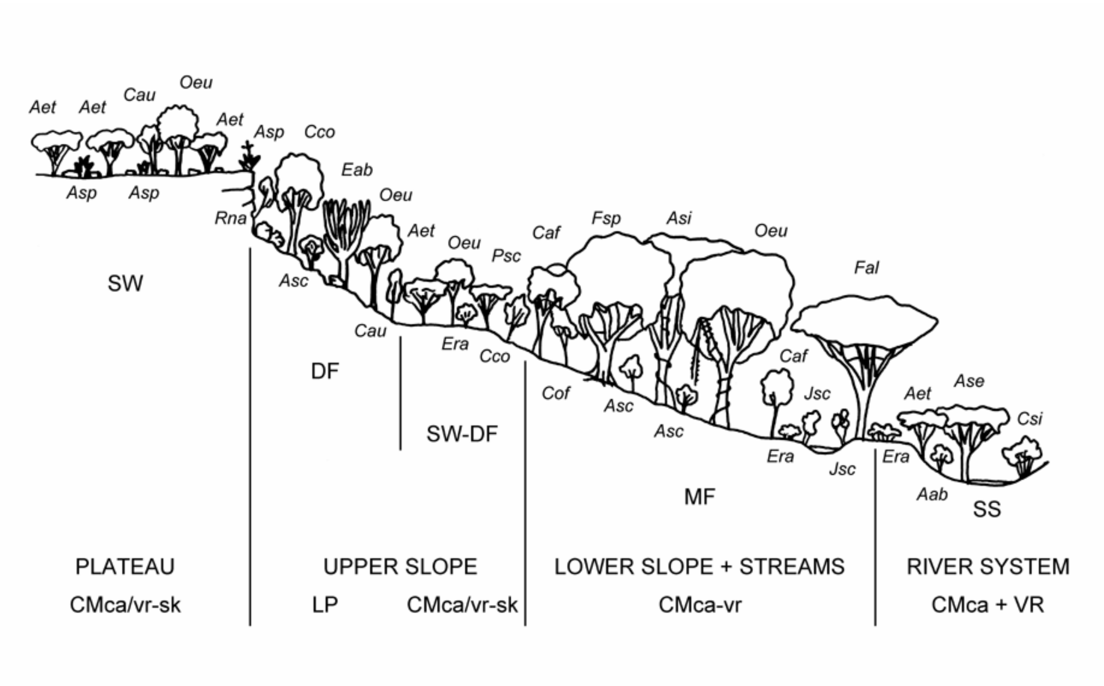

Aet
Aet
Cau
Oeu
Aet
Asp
Cco
Asp
Asp
Eab
Oeu
Rna
Aet
Oeu
Psc
Caf
Fsp
Asi
Oeu
Fal
SW
Asc
Cau
DF
Era
Cco
Caf
Cof
Asc
Jsc
Aet
Ase
Csi
SW-DF
Asc
Era
Jsc
Era
Aab
MF
SS
PLATEAU
CMca/vr-sk
UPPER SLOPE
LP
CMca/vr-sk
LOWER SLOPE + STREAMS
CMca-vr
RIVER SYSTEM
CMca + VR

Table 1. Area and diversity summary statistics of ten Afromontane forest fragments sampled in a study area of 13,000 ha in northern Ethiopia.

Total forest area (ha)	65.62
Mean fragment size ± SE (ha)	6.56 ± 2.04
Fragment size range (ha)	0.40–20.95
Relative forest area (%)	0.50
α (average number of species per plot)	9.87
β (among-plot diversity)	4.05
γ (Hill's N_0, total species richness)	40
Hill's N_1	8.35
Hill's N_2 (richness of abundant species)	1.17
Hill's E_1 (evenness)	0.21

Table 2. Summary statistics for MRPP analyses.

Alternative hypothesis	*T*	*p*	*A*
Plant communities, determined by cluster and indicator species analysis, differ in species composition.	– 14.29	< 0.001	0.27
Individual forest fragments differ in species composition.	– 10.60	< 0.001	0.36

The test statistic (*T*) describes the separation between groups and the chance-corrected within-group agreement (*A*) describes within-group homogeneity compared to random expectation.

Table 3. Five communities of woody species in ten forest fragments in northern Ethiopia determined by indicator species analysis.

Moist Afromontane forest		Shrub savanna	Dry Afromontane forest	
Apple-ring thorn–Horsewhip	Stinkwood–Redwing	Umbrella thorn–thistle	Thorn–Olive	Bride's bush–Bushwillow
Faidherbia–Achyranthes	*Celtis–Pterolobium*	*Acacia–Echinops*	*Acacia–Olea*	*Pavetta–Combretum*
Faidherbia albida **0.61** (0.003) ^{T}	*Celtis africana* **0.41** (0.027) ^{T}	*Acacia abyssinica* **0.60** (0.005) ^{TS}	*Leucas abyssinica* **0.77** (0.001) ^{SH}	*Pavetta gardeniifolia* **0.79** (0.002) ^{TS}
Achyranthes aspera **0.57** (0.006) ^{SH}	*Pterolobium stellatum* **0.40** (0.059) ^{C}	*Echinops* sp. **0.60** (0.005) ^{SH}	*Psiadia punctulata* **0.55** (0.006) ^{SH}	*Combretum collinum* **0.78** (0.002) ^{T}
Justicia schimperiana **0.49** (0.019) ^{S}	*Teclea nobilis* **0.35** (0.091) ^{T}	*Acacia etbaica* **0.48** (0.001) ^{TS}	*Acacia etbaica* 0.39 ^{TS}	*Clerodendron cordifolium* **0.77** (0.001) ^{SH}
Ehretia cymosa **0.42** (0.018) ^{T}	*Euclea racemosa* **0.34** (0.001) ^{S}	*Cassia singueana* **0.47** (0.025) ^{TS}	*Rhus natalensis* **0.32** (0.131) ^{TS}	*Psydrax schimperiana* **0.50** (0.013) ^{TS}
Capparis tomentosa **0.25** (0.175) ^{CS}	*Justicia schimperiana* 0.30 ^{S}	*Maytenus senegalensis* **0.40** (0.037) ^{TS}	*Olea europaea* **0.30** (0.209) ^{TS}	*Acokanthera schimperi* **0.50** (0.013) ^{TS}
Ficus spp. **0.22** (0.303) ^{T}	*Carissa edulis* **0.29** (0.161) ^{S}	*Aloe macrocarpa* **0.36** (0.067) ^{S}	*Euclea racemosa* 0.25 ^{S}	*Hibiscus micranthus* **0.50** (0.019) ^{S}
Celtis africana 0.16 ^{T}	*Calpurnia aurea* 0.26 ^{TS}	*Euclea racemosa* 0.13 ^{S}	*Aloe macrocarpa* 0.18 ^{S}	*Steganotaenia araliacea* **0.50** (0.008) ^{TS}
Olea europaea 0.07 ^{TS}	*Ficus* spp. 0.18 ^{T}	*Capparis tomentosa* 0.12 ^{CS}	*Jasminum abyssinicum* 0.16 ^{CSH}	*Grewia ferruginea* **0.32** (0.077) ^{TS}
	Maytenus senegalensis 0.14 ^{TS}	*Acacia seyal* **0.12** (0.823) ^{T}	*Combretum collinum* 0.10 ^{T}	*Jasminum abyssinicum* **0.32** (0.097) ^{CSH}
	Olea europaea 0.14 ^{TS}	*Rhus natalensis* 0.10 ^{TS}	*Ocimum forskolei* 0.10 ^{SH}	*Ocimum forskolei* **0.32** (0.101) ^{SH}
	Acacia seyal 0.08 ^{TS}	*Achyranthes aspera* 0.05 ^{SH}	*Dodonaea viscosa* **0.09** (0.912) ^{S}	*Rhus natalensis* 0.31 ^{TS}
	Grewia ferruginea 0.07 ^{TS}		*Clerodendron cordifolium* 0.08 ^{SH}	*Calpurnia aurea* **0.31** (0.156) ^{TS}
	Psydrax schimperiana 0.06 ^{TS}		*Justicia cordata* 0.08 ^{S}	*Olea europaea* 0.25 ^{TS}
	Euphorbia abyssinica 0.06 ^{TS}		*Calpurnia aurea* 0.07 ^{TS}	*Euphorbia abyssinica* **0.24** (0.188) ^{TS}
			Acokanthera schimperi 0.06 ^{TS}	*Euclea racemosa* 0.17 ^{S}
			Cassia singueana 0.06 ^{TS}	*Carissa edulis* 0.13 ^{S}
				Teclea nobilis 0.12 ^{T}
				Acacia etbaica 0.11 ^{TS}
				Justicia cordata **0.09** (0.824) ^{S}
				Cassia singueana 0.08 ^{TS}
				Dodonaea viscosa 0.08 ^{S}

Only species with an indicator value > 0.05 are shown. The indicator values range from zero (no indication) to 1 (perfect indication). For observed maximum indicator values (bold), *p*-values (in parantheses) are calculated from a Monte Carlo permutation test for each species. Superscripts indicate life forms: trees (T), shrubs (S), climbers (C) and herbs (H).

Table 4. Spearman rank correlations between NMDS plot scores and significant[1] environmental variables for 31 plots from ten Afromontane forest fragments in northern Ethiopia.

	NMDS 1		NMDS 2		NMDS 3	
	r_s	*p*	r_s	*p*	r_s	*p*
Soil available phosporus (mg/100g)	– 0.80	< 0.001	– 0.25	0.182	0.11	0.551
Soil depth (m)	– 0.60	< 0.001	– 0.05	0.808	0.50	0.004
Stoniness (%)	0.74	< 0.001	0.04	0.851	– 0.29	0.117
Distance to nearest drainage line (m)	0.62	< 0.001	– 0.05	0.806	0.02	0.897
Position along the vertical gradient	0.69	< 0.001	0.09	0.632	– 0.22	0.235
Grazing intensity	– 0.05	0.778	0.82	< 0.001	0.05	0.803

[1] Only environmental variables that were significantly correlated to at least one NMDS axis are shown. Correlations need to be evaluated against a corrected $\alpha_{corr} = 0.004$ to assure an overall significance of $\alpha = 0.05$ (Bonferroni correction for 13 tests).

Table 5. Environmental variables (mean ± SE) and five habitat groups in ten Afromontane forest fragments in northern Ethiopia.

	Habitat types (sample size per habitat group)						
	Moist Afromontane forest		Shrub savanna	Dry Afromontane forest			
	grazed	not grazed		savanna woodland	closed-canopy forest		
	Faidherbia–Achyranthes	*Celtis–Pterolobium*	*Acacia–Echinops*	*Acacia–Olea*	*Pavetta–Combretum*		
	(n = 4)	(n = 5)	(n = 5)	(n = 11)	(n = 6)		
MANOVA[1]						$F_{4,26}$	*p*
P (mg kg^{-1})	9.25 (1.49)^{bc}	9.66 (1.34)^{c}	4.32 (1.34)^{ab}	3.14 (0.90)^{a}	2.52 (1.22)^{a}	7.24	< 0.001
$CaCO_3$ (mass %)	29.5 (8.3)	21.0 (7.4)	27.8 (7.4)	19.2 (5.0)	11.2 (6.7)	1.03	0.409
Soil organic C (mass %)	2.3 (0.6)	3.6 (0.5)	2.3 (0.5)	3.4 (0.3)	3.0 (0.5)	1.64	0.195
N (mass %)	0.26 (0.05)	0.30 (0.04)	0.20 (0.04)	0.30 (0.03)	0.26 (0.04)	1.17	0.348
pH (H_2O)	8.30 (0.08)	8.20 (0.07)	8.24 (0.07)	8.14 (0.05)	8.17 (0.07)	0.93	0.460
pH (KCl)	7.35 (0.08)	7.18 (0.07)	7.24 (0.07)	7.24 (0.05)	7.20 (0.07)	0.75	0.568
Soil depth (m)	0.75 (0.17)^{b}	0.88 (0.10)^{b}	0.79 (0.17)^{b}	0.32 (0.03)^{a}	0.25 (0.03)^{a}	11.23	< 0.001
Slope angle (°)	9.8 (4.3)	20.2 (3.9)	8.6 (3.9)	8.0 (2.6)	23.0 (3.5)	4.27	0.009
Slope heat load (aspect)	0.45 (0.19)	0.75 (0.17)	0.47 (0.17)	0.29 (0.12)	0.40 (0.16)	1.28	0.304
Distance to nearest drainage line (m)	20 (12)^{a}	127 (27)^{bc}	50 (21)^{ab}	345 (57)^{c}	301 (67)^{c}	10.58	< 0.001
KW[2]						χ^2	*p*
Stoniness (%)	6.3 (6.3)^{a}	0.0 (no variance)^{a}	12.0 (7.3)^{a}	23.4 (3.7)^{ab}	47.0 (3.8)^{b}	21.56	< 0.001
Grazing intensity[3]	occasional to regular ^{ab}	no or occasional ^{a}	heavy ^{b}	heavy ^{b}	no or occasional^{a}	20.95	< 0.001
Position along the vertical gradient[3]	valley ^{a}	concave lower slope ^{a}	valley ^{a}	plateau ^{b}	convex upper slope ^{ab}	27.06	< 0.001

[1] MANOVA: Wilk's λ = 0.007, $F_{40,66}$ = 4.51, $p < 0.001$. Letters indicate significant differences between groups according to Tukey's HSD test.

[2] Kruskal-Wallis ANOVA by ranks. Letters indicate significant differences between groups according to nonparametric Kruskal-Wallis multiple comparison.

[3] Ordinal variable. Values are medians.

Table 6. Stand characteristics (mean ± SE) and diversity indices for five habitat groups in ten Afromontane forest fragments in northern Ethiopia.

	Habitat types (sample size per habitat group)						
	Moist Afromontane forest		Shrub savanna	Dry Afromontane forest			
	grazed	not grazed		savanna woodland	closed-canopy forest		
	Faidherbia–Achyranthes	*Celtis–Pterolobium*	*Acacia–Echinops*	*Acacia–Olea*	*Pavetta–Combretum*		
	(n = 4)	(n = 5)	(n = 5)	(n = 11)	(n = 6)		
MANOVA^{1}						$F_{4,26}$	*p*
Tree density (stems ha^{-1})	225 (25)^{a}	285 (84)^{a}	692 (159)^{b}	570 (42)^{b}	618 (82)^{b}	5.64	0.002
Shrub density (stems ha^{-1})	567 (167)^{a}	3620 (1023)^{b}	1583 (359)^{ab}	3050 (479)^{b}	2700 (417)^{b}	6.28	0.001
Total stem density (stems ha^{-1})	792 (156)^{a}	3905 (1043)^{b}	2275 (349)^{b}	3620 (486)^{b}	3318 (427)^{b}	8.60	< 0.001
Basal area of trees (m^{2} ha^{-1})	68.2 (15.7)^{b}	45.9 (13.2)^{b}	11.0 (3.2)^{a}	9.4 (1.5)^{a}	13.2 (2.1)^{a}	10.44	< 0.001
Mean tree height (m)	9.5 (1.8)^{c}	11.5 (0.6)^{c}	4.2 (0.3)^{ab}	3.7 (0.2)^{a}	5.5 (0.4)^{b}	41.13	< 0.001
KW^{2}						χ^{2}	*p*
Mean maximum tree height (m)	15.2 (3.8)^{b}	17.9 (0.5)^{b}	6.8 (0.9)^{ab}	5.9 (0.3)^{a}	9.4 (1.1)^{ab}	18.63	0.001
Hill's N_0 (= total number of species γ)^{3}	16	29	14	26	31	–	–
Hill's N_1 (= $e^{\text{Shannon } H'}$)	4.47 (1.11)^{a}	8.40 (1.24)^{ab}	6.55 (0.90)^{ab}	9.51 (0.73)^{ab}	12.94 (0.84)^{b}	19.06	0.001
Hill's N_2 (= Simpson D^{-1})	1.37 (0.11)^{b}	1.17 (0.03)^{ab}	1.24 (0.05)^{ab}	1.13 (0.01)^{ab}	1.10 (0.01)^{a}	17.31	0.002
Hill's E_1 (=$e^{\text{Shannon } J'}$)	0.28 (0.07)	0.29 (0.04)	0.47 (0.06)	0.37 (0.03)	0.42 (0.03)	6.41	0.170

[1] MANOVA: Wilk's $\lambda = 0.023$, $F_{20,74} = 7.83$, $p < 0.001$. Letters indicate significant differences between groups according to Tukey's HSD test.

[2] Kruskal-Wallis ANOVA by ranks. Letters indicate significant differences between groups according to nonparametric Kruskal-Wallis multiple comparison.

[3] Hill's N_0 is the total number of species observed in a group and has no variance.