

Typology of the woody plant communities of the Ethiopian Nech Sar National Park and an assessment of vegetation-environment relations and human disturbance impacts

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Background and aims – Deforestation and forest degradation have hugely affected the Southern Ethiopian Rift Valley, jeopardizing biodiversity conservation and ecosystem service provisioning. Quantifying the impacts of human activities on the remaining woody plant communities and recognizing vegetation-environment relationships provide the basis for targeted conservation and rehabilitation.

Material and methods – The study was performed in the Nech Sar National Park (NSNP). Based on a large systematic vegetation survey of 104 plots, we quantified the woody vegetation composition, and we provided a vegetation classification based on Non Metric Multidimensional Scaling, cluster analysis and indicator species analysis. Furthermore, we evaluated vegetation – environment relationships and the effects of human disturbance on community composition and woody plant species richness and diversity.

Key results – Our analyses revealed three very distinct woody vegetation types (*Acacia mellifera-Combretum aculeatum*; *Lecaniodiscus fraxinifolius-Deinbollia kilimandscharica* and *Acacia polyacantha-Ficus sycomorus*) which were significantly differentiated by soil pH, electrical conductivity, available soil phosphorus and organic matter, and by elevation. Human disturbance, as quantified by a compound Human Disturbance Index (HDI) significantly affected community composition, species richness and diversity, and was significantly positively correlated with species richness and diversity. The latter is likely due to intermediate levels of disturbance and encroachment of disturbance affiliated shrubs such as *Dichrostachys cinerea*, *Lantana camara*, and *Acalypha fruticosa*. Furthermore, the demographic structure of key woody species such as *Acacia polyacantha*, *Acacia tortilis*, *Balanites aegyptiaca*, *Diospyros abyssinica*, *Lecaniodiscus fraxinifolius* and *Terminalia brownii*, showed impacts of human disturbance.

Conclusion – Our results provide a baseline for further conservation actions in the NSNP which should be differentially targeted on the different plant community types. Overall, human disturbance seems not to have resulted yet in species richness declines, although it has started to affect the integrity of the delineated vegetation types and resulted in small scale succession.

Keywords – Deforestation; forest degradation; human disturbance index; Southern Ethiopian Rift Valley; species diversity; species richness; vegetation – environment relations.

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INTRODUCTION

Understanding vegetation – environment relations and influences of human disturbance on woody vegetation are at the core of forest ecology, as they principally dictate species distribution and community organization (Zuo et al. 2012). Environmental constraints including climate, landscape physiography and soil parent material are considered universal determinants of vegetation composition and distribution at various spatial scales (Maestre et al. 2003; Zuo et al. 2012). Among these different environmental drivers, soil properties overwhelmingly control vegetation characteristics (Iwara et al. 2011), as they reflect an interplay among combinations of pedogenesis factors and underpin habitat heterogeneity (Li et al. 2018). At smaller spatial scales, human disturbances exert pressures that can reconfigure vegetation composition and, eventually, plant community type (Iwara et al. 2011; Shiferaw et al. 2019).

Ethiopia is ecologically diversified and is consequently a hotspot of floristic diversity (6500 to 7000 vascular plants) and a centre of plant endemism (10–12% of the flora) (Kelbessa & Demissew 2014). Ethiopia had a substantial forest cover (35–40%) in the early 1900s, which drastically diminished to less than 3% by 1985 (Yeshitela & Bekele 2002), due to human population growth, agricultural expansion, overgrazing, excessive wood collection, and establishment of settlements (Senbeta & Denich 2006; Yiniger et al. 2008). Many of the remaining forests, including those considered sacred (e.g. Church forests) and legally protected as nature conservation areas, continue to suffer from human disturbances (Wassie et al. 2010; Lemenih & Kassa 2014). For example, many of the forests within the main Ethiopian rift valley system (MERV), which provided important ecosystem services and which protected downstream lakes from sediment deposition, were cleared for agriculture and other land uses (Garedew et al. 2009; Meshesha et al. 2012). Garedew et al. (2009) showed an alarming reduction in the forest cover in the Arsi-Negele district (MERV), from 40% in 1973 to 9% in 2006 while agricultural land increased twofold during the same period. Also the Lake Abaya and Lake Chamo watershed, the southernmost extension of the hydraulically interrelated MERV lake system (Legesse & Ayenew 2006), suffers from severe deforestation and land degradation due to population increase and an exodus of people from the remote rural areas to the fringes of the city of Arba Minch (Assefa & Bork 2014; Utaile & Sulaiman 2016).

This study aimed to classify the woody vegetation of the Nech Sar National Park (NSNP), located within the Lake Abaya and Lake Chamo watershed in the Ethiopian MERV, and to assess the effects of environmental variables and human disturbance on plant community composition. The NSNP was primarily established for wildlife and forest conservation (Kelboro & Stellmacher 2012), and it significantly contributes to the local and national economy through ecotourism (Fetene et al. 2012b) and ethnobotanical use of plants (Alemu et al. 2017). The park consists of a mosaics of woody vegetation types, including groundwater forest, riverine forest, shrublands and woodlands (Fetene et al. 2011), providing important ecosystem services including water provisioning, carbon sequestration and habitat for large mam-

mals such as Waterbuck, Greater kudu, Lesser kudu, Anubis baboon, Black and white colobus monkey, Guenther's dik-dik and Warthog (Fetene et al. 2011; Wolde et al. 2014). Yet, these unique woody vegetation types, and the ecosystem services that they provide, are under anthropogenic pressure due to wood cutting, cattle grazing and the encroachment of disturbance indicating woody species such as *Dichrostachys cinerea* (Fetene et al. 2012a; Y. Utaile pers obs.). Whereas some other studies have been carried out in the park with the aim to describe the occurring plant communities (e.g. Shimelse et al. 2010; Kebebew & Demissie 2017), and to evaluate vegetation – environment relationships (Shetie et al. 2017), previous studies have not been exhaustive in terms of sampling size and geographical extent, and they did not quantitatively evaluate the effects of human disturbance on vegetation composition and species richness. Yet, such a vegetation classification and better understanding of the vegetation – environment relationships and human disturbances impacts could provide the evidence-base for any management plan aiming to conserve and restore the remaining woody vegetation (Sutherland et al. 2004).

Here we provide the first comprehensive and structured survey of the woody vegetation of the NSNP in the Southern part of the Rift valley in Ethiopia. We furthermore quantitatively assess the effects of human disturbance and environmental variables (soil characteristics and elevation) on these woody plant communities and their species richness. Based on a survey of 104 vegetation plots, our specific objectives were: (1) to define and characterize woody vegetation types in terms of plant community composition and soil characteristics; (2) to quantify plant species richness and diversity and identify indicator species for each vegetation type; and (3) to assess the impacts of human disturbance on plant community composition, richness and diversity.

MATERIAL AND METHODS

Study area

The study was performed in the Nech Sar National Park in southern Ethiopia (supplementary file 1). The park was established in 1974 and covers 514 km² in an altitudinal range between 1100 m and 1650 m a.s.l. (Fetene et al. 2019). The park's broad ecological units are terrestrial (85%) and aquatic (15%) ecosystems. The terrestrial vegetation of the park mainly consists of savannah, deciduous woodland, and evergreen riverine and groundwater forests which harbour a wide range of wildlife (Fetene et al. 2011). The woody vegetation (including thorny savanna) accounts for about 59% of the terrestrial part (Schubert 2015). The region has a semiarid climate (tropical savanna, 'Aw' climate by the Köppen-Geiger system), and a bimodal rainfall pattern with average annual precipitation of 906 mm and average monthly temperature of 23.5°C. The driest period occurs between December and March, whereas the long and short wet periods occur between April and June, and between September and November, respectively (supplementary file 2). Its basic geological formations are similar to the main Ethiopia rift valley, and its graben (or rift floor) consists of alluvial and lacustrine deposits, and ignimbrite and basaltic rocks (Shetie et al. 2017),

and its horsts are composed of crystalline basement rocks overlaid with sandstone (Schubert 2015).

Data collection

In May and June 2018, a reconnaissance of the Nech Sar National Park was performed to assess the variation in plant composition and woody vegetation structure. The survey was concluded with the preliminary identification of five physiognomically distinct vegetation types, namely *Acacia* woodland, bushland, groundwater forest, riverine forest and lakeside forest. Following the reconnaissance, the vegetation composition was assessed for 104 systematically established 20 m × 20 m plots stratified across the five preliminary vegetation types, and spaced at least 400 m from each other along line transects, separated by 500 m (supplementary file 1). The number of plots in each vegetation type was approximately related to its area, with 8, 45, 17, 22 and 12 plots in *Acacia* woodland, bushland, groundwater forest, riverine forest and lakeside forest, respectively. In each plot, for all trees and shrubs with diameter at breast height (DBH) ≥ 5 cm, DBH was measured with a tree diameter caliper and diameter tape. Next, the height of all trees and shrubs with a height ≥ 0.5m was measured using a known height pole. Crown cover (%) of individual trees and shrubs was visually estimated, and their stem number was counted. A visual estimation of the crown cover provides a direct and reliable field estimation (Chiarucci et al. 2001). Elevation and geographic coordinates at each plot were recorded with the Garmin GPS-MAP 64s. Verification of all species names was done at the National Herbarium, Addis Ababa University, and nomenclature followed the flora of Ethiopia and Eritrea (Hedberg & Edwards 1989; Edwards et al. 2000). Sample completeness species-accumulation curves were plotted for each preliminary vegetation type. Soil was collected at a depth of 20–25 cm in each plot corner and centre, and thoroughly mixed to make up a composite sample. Total nitrogen (TN), available phosphorus (AP), soil pH, organic matter (OM), electrical conductivity (EC) and cation exchange capacity (CEC) were analysed at the National Soil Testing Center, Addis Ababa, Ethiopia, following standard soil analysis procedures (Pansu & Gautheyrou 2007). Finally, human disturbance in each plot was quantified by assessing the presence or absence (1/0) of (i) wood cutting, (ii) stem debarking (girdling of living trees/shrubs), (iii) cattle grazing, and (iv) human foot trails. Because there are no universally developed methods for estimating disturbance intensities, we subjectively set criteria to rank disturbance intensities (Senbeta & Denich 2006; Sahu et al. 2008; Htun et al. 2011). We then used the aggregate sum of the different disturbance factors as an indicator of total human disturbance per plot, further referred to as the Human Disturbance Index (HDI).

Data analysis

All analyses were performed in R (version 3.5.1). All data were checked for normality and plant crown cover data was Hellinger transformed prior to ordination. Nonmetric Multidimensional Scaling (NMDS) was used to visualize variation in plant community composition. The optimal number of NMDS axes ($k = 2$) was chosen based on a stress plot

using the *dimcheckMDS* function in R. Complementary to the NMDS, an average linkage agglomerative clustering was applied to cluster plots in vegetation types using the *hclust* function in R. The average linkage method was chosen because of its ability to maximize cophenetic correlation between input dissimilarities and dissimilarities from the resulting dendrogram between pairs of species (Gauch Jr & Whittaker 1981). The optimal number of clusters was determined iteratively whilst looking for the one which best represents the vegetation plots, and was further verified with a cophenetic correlation (Kassambara 2017). Based on the NMDS and cluster analysis, we defined the true vegetation types. A multiresponse permutation procedure (MRPP) was carried out with 999 permutations to test for differences in species composition between the newly defined vegetation types (Aerts et al. 2006). Indicator species analysis (*Indval* function in R) was subsequently used to determine species characteristic for each vegetation type (De Cáceres et al. 2010). Woody plants species richness, Shannon diversity and Simpson diversity was then determined for each vegetation type, using standard procedures (Magurran & McGill 2011). Total mean cover (m²/ha) and total mean stem density (number of stems/ha) were computed for each vegetation type as, respectively, the average plot-level (400 m²) total cover and total density across all measured plots of that vegetation type, and then scaled up to 1 ha. Similarly, the total mean basal area was calculated for each vegetation type as the average plot-level total basal area of all individuals with a DBH ≥ 5 cm, across all measured plots of that vegetation type, and then scaled up to 1 ha.

Relationships between vegetation composition, soil variables and elevation were assessed with the *Envfit* function in the *vegan* R package (LeBlanc et al. 2015; Oksanen et al. 2019). *Envfit* fits environmental factors onto an ordination diagram, and thereby computes the significance of the correlation between the fitted vectors and corresponding environmental variables (Oksanen et al. 2019). We employed the *Adonis* function, a permutational multivariate analysis of variance, to test for differences in species composition among the delineated communities, and to evaluate the effects of HDI on their species composition (Oksanen et al. 2019). *Adonis* partitions dissimilarities in multivariate data for the sources of variation, and uses permutation tests (999 permutations) for determining significances (Oksanen et al. 2019). The differences in species richness and diversity, soil variables, and elevation among the delineated vegetation types were assessed with Kruskal-Wallis tests and Dunn's post hoc tests with Bonferroni correction. Kruskal-Wallis tests were also employed separately for each community to examine for the effects of HDI on their species richness and diversity. Association between HDI and the species richness and diversity indices of each community was additionally evaluated with a Spearman's rank correlation. As an indication for human disturbance-induced shifts in woody community composition, we scrutinized the abundance of the most abundant light demanding species (i.e. *Acalypha fruticosa*, *Dichrostachys cinerea* and *Lantana camara*) in each community by evaluating the relationships between their abundances and HDI, using boxplots. Finally, to further elucidate the effect of human disturbance on tree structure, we

examined population age structure of six tree species which are highly prized and harvested by the local community (Y. Utaile pers. obs.), through simple graphical presentation of the DBH classes vs. the number of individuals.

RESULTS

Wood species composition

All preliminary distinguished physiognomic vegetation types showed typical asymptotic species accumulation curves, thus demonstrating sample completeness (supplementary file 3). A total of 89 woody plant species representing 35 families were identified (supplementary file 4). Fabaceae (17%), Euphorbiaceae (10%), Malvaceae (7.7%) and Capparaceae (5.6%) were the most represented families, whereas the majority of the remaining families were represented by one species. Trees accounted for 55% and shrubs for 45% of the total vegetation survey. The overall average (\pm SD) species richness, Shannon and Simpson diversity per plot were 11.3 ± 4.2 , 1.7 ± 0.5 and 0.7 ± 0.2 , respectively. The overall total mean (\pm SD) cover, stem density, and basal area were 1801 ± 3927 m²/ha, 340 ± 685 stems/ha and 2.1 ± 8.9 m²/ha.

Community classification and characterization

NMDS coupled with cluster analysis resulted in four distinct plant communities (fig. 1, supplementary file 5). Goodness-of-fit between the ordination and the observed dissimilarities at $k = 2$ was very high (non-metric fit $R^2 = 0.98$) indicating

a good representation of the vegetation data by the ordination diagram. Because one of the clusters contained only two sample plots, it was omitted from the dataset, resulting in three distinct, true vegetation types. The MRPP furthermore confirmed significant differences ($\delta = 0.71$, $P = 0.001$) in species composition among these three delineated vegetation types. The homogeneity within groups was 0.1896, which indicates more homogenous communities than would be expected by chance (Aerts et al. 2006). Also, the multivariate analysis of variance using the *Adonis* function revealed that the vegetation types differed significantly ($F = 20.08$, $P = 0.001$) in their species composition. Further analysis with Kruskal-Wallis tests showed significant differences in species richness ($\chi^2 = 27.78$, $P < 0.001$), Shannon diversity ($\chi^2 = 38.05$, $P < 0.001$) and Simpson diversity ($\chi^2 = 31.11$, $P < 0.001$) among the vegetation types. Dunn's post hoc test significantly differentiated species richness and diversity between the *Acacia mellifera-Combretum aculeatum* community (see community descriptions further down) and the other two communities (table 1).

To examine the underlying environmental gradients structuring the delineated vegetation types, we overlaid the soil variables and elevation onto the vegetation NMDS using the *Envfit* function. The analysis showed significant correlations of soil variables and elevation with species composition (fig. 1). Kruskal-Wallis tests further revealed that both elevation ($\chi^2 = 30.01$, $P < 0.001$) and soil variables (specifically, pH ($\chi^2 = 23.97$, $P < 0.001$), EC ($\chi^2 = 19.66$, $P < 0.001$), AP ($\chi^2 = 23.33$, $P < 0.001$), and OM ($\chi^2 = 5.61$, $P = 0.06$)) were significantly different among the communities (table 1).

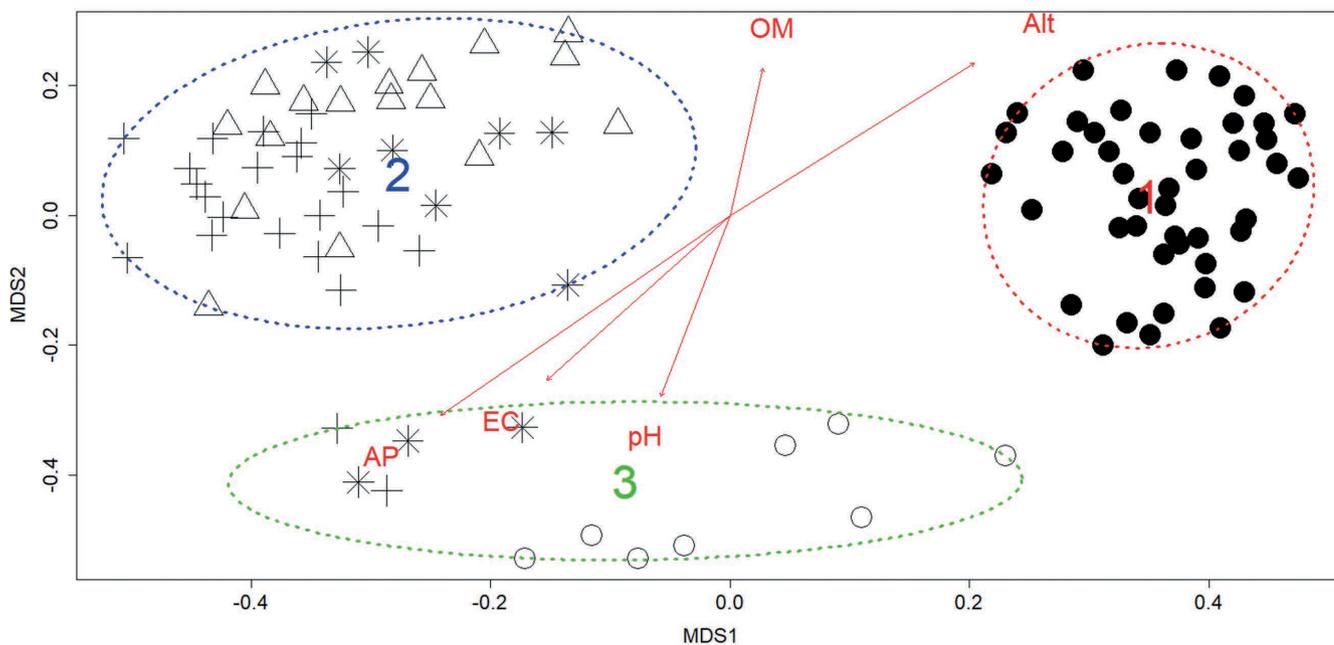


Figure 1 – NMDS ordination of 102 plots based on Bray-Curtis similarities among plots in the Nech Sar National Park, South Ethiopian Rift Valley. The three plant communities are visualized; 1: *Acacia mellifera-Combretum aculeatum* community, 2: *Lecaniodiscus fraxinifolius-Deinbollia kilimandscharica* community, 3: *Acacia polyacantha-Ficus sycomorus* community. Symbols indicate the five preliminary vegetation types used for stratification of the plots. Triangle: groundwater forest, cross: riverine forest, star: lakeside forest, black circle: bushland, white circle: *Acacia* woodland. *Envfit* of significantly correlated soil variables (pH ($P = 0.001$); EC ($P = 0.002$), electrical conductivity; OM, ($P = 0.03$), organic matter; AP ($P = 0.001$), available phosphorus); and Alt, elevation ($P = 0.001$)).

Table 1 – Summary of mean values of soil variables, species richness and diversity, elevation, plant structural attributes, and HDI in the three identified plant communities, Nech Sar National Park, South Ethiopian Rift Valley.

Community 1, 2 and 3 are represented by 44, 45 and 13 plots, respectively. HDI, human disturbance index; EC, electrical conductivity; CEC, cation exchange capacity; OM, organic matter; TN, total nitrogen; AP, available phosphorus. Letters (a, b) in the superscript indicate statistical significance of differences among communities following a Kruskal-Wallis pairwise test. ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; (°): $P < 0.1$.

Environmental and vegetation Variables	Kruskal Wallis statistics (χ^2 and P- values)	<i>Acacia mellifera-Combretum aculeatum</i> (1)	<i>Lecaniodiscus fraxinifolius-Deinbollia kilimandscharica</i> (2)	<i>Acacia polyacantha-Ficus sycomorus</i> (3)
Species richness	$\chi^2 = 27.78^{***}$	(13.8 ± 4.1) ^a	(9.6 ± 2.9) ^b	(8.7 ± 3.9) ^b
Shannon diversity	$\chi^2 = 38.05^{***}$	(2.1 ± 0.4) ^a	(1.6 ± 0.4) ^b	(1.3 ± 0.5) ^b
Simpson diversity	$\chi^2 = 31.11^{***}$	(0.8 ± 0.1) ^a	(0.7 ± 0.1) ^b	(0.6 ± 0.2) ^b
HDI	$\chi^2 = 24.49^{***}$	(2.8 ± 1.1) ^a	(2.2 ± 0.6) ^b	(1.5 ± 1.6) ^b
pH-H2O	$\chi^2 = 23.97^{***}$	(6.98 ± 0.47) ^a	(7.33 ± 0.47) ^b	(7.49 ± 0.45) ^b
EC (ds/m)	$\chi^2 = 19.66^{***}$	(0.19 ± 0.09) ^a	(0.29 ± 0.19) ^b	(0.33 ± 0.07) ^b
CEC (meq/100g)	$\chi^2 = 2.62$	(44.44 ± 11.06)	(45.97 ± 9.77)	(41.85 ± 4.43)
OM (%)	$\chi^2 = 5.61^*$	(2.64 ± 1.01) ^a	(3.08 ± 2.26) ^a	(1.83 ± 0.69) ^b
TN (%)	$\chi^2 = 2.15$	(0.24 ± 0.10)	(0.27 ± 0.20)	(0.24 ± 0.23)
AP (mg/Kg)	$\chi^2 = 23.33^{***}$	(14.45 ± 11.82) ^a	(30.52 ± 28.71) ^b	(43.74 ± 28.24) ^b
Elevation (m)	$\chi^2 = 30.01^{***}$	(1155.5 ± 19.9) ^a	(1190.5 ± 43.2) ^b	(1136 ± 52.1) ^a
Total mean cover (m ² /ha)		736 ± 1060	3242 ± 5694	2028 ± 3716
Total mean basal area (m ² /ha)		0.37 ± 0.66	3.0 ± 11.3	1.7 ± 3.7
Total mean stem density (number of stems/ha)		354 ± 678	352 ± 734	225 ± 498
Canopy height (m)		3.1 ± 1.9	7.1 ± 5.9	6.1 ± 7.5

The *Indval* analysis finally identified diagnostic species characterizing the three vegetation types, and the communities were named after the two species with the highest indicator values (supplementary file 6).

Acacia mellifera-Combretum aculeatum community

The *Acacia mellifera-Combretum aculeatum* community (hereafter community 1) largely corresponds with the bushland vegetation from our preliminary survey (supplementary file 1). In our dataset, it consisted of 54 woody species with an average plot-level species richness of 13.8 ± 4.1, Shannon diversity of 2.1 ± 0.4 and Simpson diversity of 0.8 ± 0.1. A total of 24 indicator species were identified, of which *Acacia mellifera* (indicator value (*indval*) = 0.96, $P = 0.001$) and *Combretum aculeatum* (*indval* = 0.81, $P = 0.001$) were considered community identifiers (supplementary file 6). Trees with the highest average DBH were *Sclerocarya birrea* (25 cm) and *Balanites aegyptiaca* (20 cm). *Acacia mellifera*, *Combretum aculeatum*, *Grewia bicolor*, *Rhus natalensis*, *Acacia brevispica*, *Ximenia americana* and *Cadaba farinosa* were both abundant and widespread in the community, and about 56% of the occurring species were unique to this community. The community did not exhibit clear vertical layering since species mainly occur as scattered individuals. The

total mean (± SD) cover, stem density, basal area, and canopy height of the community were 736 ± 1060 m²/ha, 354 ± 678 stems/ha, 0.37 ± 0.66 m²/ha, and 3.1 ± 1.9 m, respectively (table 1).

Lecaniodiscus fraxinifolius-Deinbollia kilimandscharica community

Forest vegetation preliminary designated as riverine, groundwater and lakeside forest (supplementary file 1) clustered to form the *Lecaniodiscus fraxinifolius-Deinbollia kilimandscharica* community (hereafter community 2). It contained 55 woody species in our dataset, with an average species richness of 9.6 ± 2.9, Shannon diversity of 1.6 ± 0.4 and Simpson diversity of 0.7 ± 0.1 per plot. A total of ten indicator species were identified, of which *L. fraxinifolius* (*indval* = 0.99, $P = 0.001$) and *D. kilimandscharica* (*indval* = 0.87, $P = 0.001$) were considered community identifiers (supplementary file 6). The most abundant tree in the community was *L. fraxinifolius* (44%) followed by *Diospyros abyssinica* (10%) and *D. kilimandscharica* (8%). Trees with the highest average DBH were *Ficus sycomorus* (98 cm) and *Acacia polyacantha* (64 cm). *Lecaniodiscus fraxinifolius*, *Deinbollia kilimandscharica*, *Diospyros abyssinica*, *Mimusops kummel*, *Teclea nobilis*, *Maytenus senegalensis*, *Trichilia emetica* and

Table 2 – Effects of human disturbance (HDI) on community composition and species richness and diversity for the vegetation types of the Nech Sar National Park, South Ethiopian Rift Valley.

Spearman rank correlation indicates tests of significance for association between HDI and plant community characteristics. Adonis test shows test of significance for the effect of HDI on species composition of communities. Whereas Kruskal – Wallis rank sum test shows the effect of HDI on measures of species richness and diversity. ***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$; (°): $P < 0.1$.

Community types	Community characteristics	Spearman rank correlation (rho)	Adonis test (F)	Kruskal-Wallis rank sum test (χ^2)
		HDI	HDI	HDI
<i>Acacia mellifera</i> - <i>Combretum aculeatum</i> (1)	Species richness	0.46***		9.78*
	Shannon diversity	0.45***		9.58*
	Simpson diversity	0.44***		8.60(°)
<i>Lecaniodiscus fraxinifolius</i> - <i>Deinbollia kilimandscharica</i> (2)	Species composition (NMDS)		2.98**	
	Species richness	0.21		3.03
	Shannon diversity	0.01		3.10
	Simpson diversity	-0.06		4.16
<i>Acacia polyacantha</i> - <i>Ficus sycomorus</i> (3)	Species composition (NMDS)		2.54*	
	Species richness	0.74***		8.99(°)
	Shannon diversity	0.66**		10.70**
	Simpson diversity	0.60**		11.14**
	Species composition (NMDS)		2.35*	

Ficus sycomorus were furthermore both abundant and wide-spread species in the community. The vegetation showed typical vertical layering, with the canopy layer mainly consisting of *Acacia polyacantha*, *Celtis africana*, *Deinbollia kilimandscharica*, *Diospyros abyssinica*, *Ficus sycomorus*, *Lecaniodiscus fraxinifolius*, *Mimusops kummel* and *Trichilia emetica*. The subcanopy layer consisted mainly of *Acokanthera schimperi*, *Allophylus rubifolius*, *Bridelia micrantha*, *Cordia africana*, *Cordia myxa*, *Crateva adansonii*, *Euclea divinorum* and *Teclea nobilis*, and the shrub layer consisted of *Canthium pseudosetiflorum*, *Carisa edulis*, *Erythrococca trichogyne*, *Flacourtia indica*, *Flueggea virosa*, *Maytenus senegalensis* and *Phyllanthus ovalifolius*. The total mean (\pm SD) cover, stem density, basal area, and canopy height of the community were 3242 ± 5694 m²/ha, 352 ± 734 stems/ha and 3.0 m²/ha, and 7.1 ± 5.9 m, respectively (table 1).

***Acacia polyacantha*-*Ficus sycomorus* community**

The *Acacia polyacantha*-*Ficus sycomorus* community (hereafter community 3) emerged from vegetation in both *Acacia* woodland and the transitional zones of the riverine and lake-side forests from the preliminary survey (supplementary file 1), which was also reflected by *Pterolobium stellatum* being the only species unique to the community. It was composed of 40 woody species with an average species richness, Shannon and Simpson diversity of 8.7 ± 3.9 , 1.3 ± 0.5 , 0.6 ± 0.2 per plot, respectively. A total of ten woody species diagnostic to the community were identified, of which *Acacia polyacantha* ($indval = 0.70$, $P = 0.001$) and *Ficus sycomorus* ($indval = 0.34$, $P = 0.005$) were considered community identifiers (supplementary file 6). Due to its non-native nature, *Lantana*

camara was not considered as community identifier. *Ficus sycomorus* (DBH = 54 cm) and *Acacia polyacantha* (DBH = 34 cm) were the dominant trees with the highest DBH. This community did not show vertical stratification, but is characterized by scattered trees such as *Acacia polyacantha*, *Acacia seyal*, *Acacia tortilis*, *Balanites aegyptiaca* and *Ficus sycomorus*, with an understory consisting of the exotic invasive shrub *Lantana camara* and light demanding species such as *Acalypha fruticosa*, *Abutilon* sp., *Ricinus communis* and *Solanum incanum*. The total mean (\pm SD) cover, stem density, basal area, and canopy height of the community were 2028 ± 3716 m²/ha, 225 ± 498 stems/ha and 1.71 m²/ha, 6.1 ± 7.5 m, respectively (table 1).

Plant communities and human disturbance

Multivariate analysis of variance based on *Adonis* revealed that the HDI had a significant effect on species composition in all three identified plant communities (table 2). Further analysis with the Kruskal-Wallis tests, however, showed mixed effects of HDI on species richness and diversity. Species richness ($\chi^2 = 9.78$, $P = 0.044$) and Shannon diversity ($\chi^2 = 9.58$, $P = 0.048$) of community 1, and Shannon ($\chi^2 = 10.70$, $P = 0.030$) and Simpson ($\chi^2 = 11.14$, $P = 0.025$) diversity of community 3 were significantly affected by HDI. There was no evidence that species richness ($\chi^2 = 3.03$, $P = 0.39$), Shannon diversity ($\chi^2 = 3.01$, $P = 0.38$) or Simpson diversity ($\chi^2 = 4.16$, $P = 0.25$) of community 2 was affected by HDI. The Spearman rank correlation confirmed a significantly positive correlation between species richness, Shannon and Simpson diversity on the one hand, and HDI on the other, in community 1 and community 3, but not in community 2 (table 2).

Abundances of the disturbance-tolerant and light demanding shrubs *Acalypha fruticosa*, *Dichrostachys cinerea* and *Lantana camara* increased with increasing HDI in all communities where they were the most abundant (fig. 2). Furthermore, graphical elucidation of six selected, highly harvested tree species highlighted effects of human disturbance on stand structure, with the density of lower and/or higher age groups partially reduced (fig. 3).

DISCUSSION

Woody plant species composition

Establishing protected areas is generally considered among the most effective strategies for biodiversity conservation (Chape et al. 2005). However, concerns over the effectiveness of protected areas in achieving their management objectives have been growing (Geldmann et al. 2019). The Nech Sar National Park has been considered to be among both the most biodiverse and the most degraded protected areas in Ethiopia (Kelboro & Stellmacher 2012). Our results show that the NSNP still has relatively high small-scale woody plant species richness (11.3 ± 4.2 overall mean species richness/plot) and diversity (1.7 ± 0.5 overall mean species/plot) and is dominated primarily by the Fabaceae (17%) and Euphorbiaceae (10%). The dominance of both families is not uncommon in the Paleotropics and is likely the result of their diverse lifeforms and widespread adaptation to these dry tropical ecosystems (Siraj et al. 2016; Lemessa & Teka 2017). The Malvaceae (7.6%) and Capparaceae (5.6%) were the next well represented families. That the majority of the remaining plant families were represented by only one species is a rather typical feature of tropical forests (Gole et al. 2008; Yam & Tripathi 2016).

Community classification and characterization

Defining plant communities based on multivariate analysis offers valuable information on species distributions and the underlying gradients shaping their distribution (Gole et al. 2008). We found three clearly distinct woody plant com-

munities for the NSNP, each containing a distinct species composition and characterized by a set of non-overlapping indicator species. Such a high degree of dissimilarity in species composition suggests inherent differences in factors that determine their formation (Phillips et al. 2003; Valencia et al. 2004). Our results indeed indicate that inherent soil conditions and elevation acted as key determinants of the spatial assortment of species among the identified communities. Although plant community composition changes ultimately through succession (Larkin et al. 2012), the distinguished communities could be assigned to the established overarching Ethiopian potential vegetation types (Friis et al. 2010). Large scale intensive disturbances such as fire, inducing succession, are indeed absent in our study area because the use of fire by farmers is legally prohibited. In view of this, our community 1 (*Acacia mellifera-Combretum aculeatum*) corresponds to the “*Acacia-Commiphora* woodland and bushland” in terms of both its floristic composition and physiognomy. Physiognomically, the community typically lacks vertical layering of vegetation since species mainly occur as scattered individuals. Exceptions were scattered pockets where slightly denser tree stands form a closed canopy. The potential characteristic species which occur in this type of vegetation include *Acacia tortilis*, *Balanites aegyptiaca*, *Balanites rotundifolia*, *Cadaba farinosa*, *Combretum aculeatum*, *Commiphora habessinica*, *Commiphora mildbraedii*, *Rhus natalensis*, *Terminalia brownii* and *Zanthoxylum chalybeum* (Friis et al. 2010). The “*Acacia-Commiphora* woodland and bushland” vegetation type has furthermore been characterized as the most biodiverse vegetation type in Ethiopia and East Africa (Friis et al. 2010; Lemessa & Teka 2017). Our results agree with this assessment as our community 1 also had the highest species richness and diversity, and the highest number of diagnostic species relative to the other two communities. As already pointed out by Lemessa & Teka (2017) and confirmed in this study, the “*Acacia-Commiphora* woodland and bushland” vegetation type also experiences the highest degree of human disturbance impact, which is likely due to its large spatial extent in the Ethiopian lowlands, where extensive cattle husbandry occurs (Friis et al. 2010). Community 2 (*Lecaniodiscus fraxinifolius-Deinbollia*

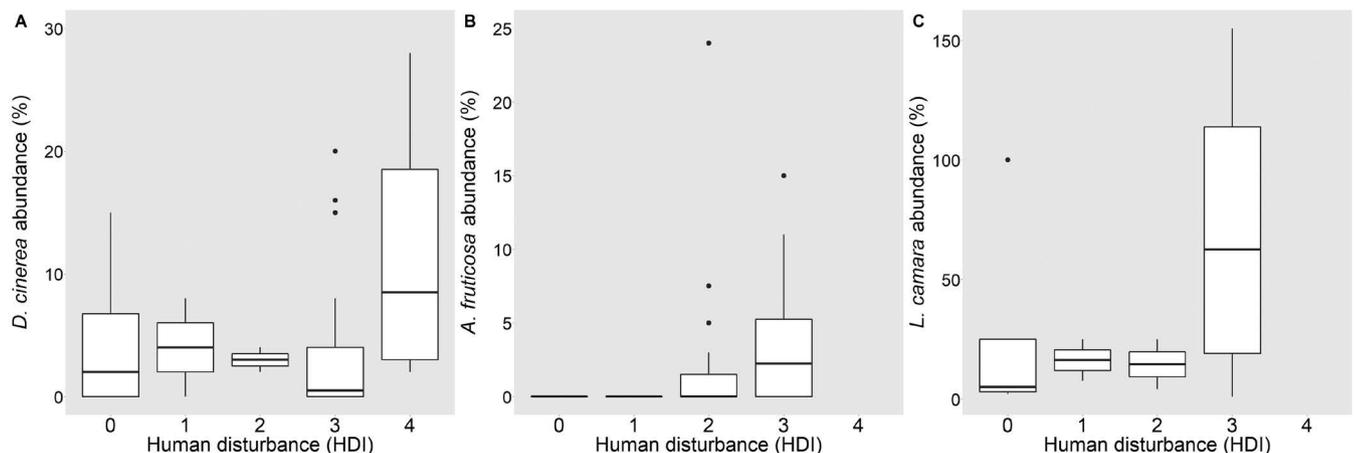


Figure 2 – Boxplots of abundances (%) of light demanding species showing the relationships with the HDI (Human Disturbance Index). For each community the most abundant species is presented: **A.** *Dichrostachys cinerea* in community 1. **B.** *Acalypha fruticosa* in community 2. **C.** *Lantana camara* in community 3.

kilimandscharica) floristically corresponds to the “Riverine vegetation” *sensu* Friis et al. (2010), and is primarily dominated by tree species such as *Celtis africana*, *Diospyros abyssinica*, *Ficus sycomorus*, *Mimusops kummel* and *Teclea nobilis*, which establish along river banks, and in areas with a high groundwater table (Friis et al. 2010). This vegetation type forms a vertical stratification of the woody vegetation, thus providing habitat for a range of arboreal animals (Fetene et al. 2011) and playing a key role in microclimate regulation, water provisioning, and carbon storage (Wolde et al. 2014; Nakamura et al. 2017). Our third community (*Acacia polyacantha-Ficus sycomorus*) can be considered as an intermediate between the two former vegetation types *sensu* Friis et al. (2010), both in vegetation structure and species composition. On one hand, it contains tree species such as *Acacia polyacantha* and *Ficus sycomorus*, which are typical for the “Riverine vegetation” type, and on the other hand it also contains tree species typical for the “*Acacia-Commiphora* woodland and bushland” vegetation type, such as *Acacia tortilis* and *Balanites aegyptiaca*. Overall, the species which are occurring in community 3 are all shared with either community 1 or community 2, except for *Pterolobium stellatum* which is both unique and rare. In spite of this, our community 3 was not characterized by soil variables that were intermediate between communities 1 and 2.

Community-environment relationships

Vegetation, soil characteristics and topography are inherently interlinked (Wang et al. 2015; Li et al. 2018). Our results show spatial variability in soil characteristics and elevation across the NSNP, which were found to significantly affect the distribution of woody plant species among the identi-

fied communities. The variation in soil properties across our study area can be primarily linked to the parent material and landscape hydrology influenced by topography. Specifically, our communities 2 and 3 occur on alluvial and lacustrine deposits whilst community 1 occurs on andosols (Shetie et al. 2017). This is reflected by the higher soil pH, electrical conductivity, and available phosphorus in communities 2 and 3 than in community 1. Our results also indicate limited availability of soil phosphorus in community 1 due to its adsorption onto mineral surfaces under conditions of low pH and electrical conductivity (Gonzalez-Rodriguez & Fernandez-Marcos 2018; Nobile et al. 2020). On the other hand, total nitrogen content did not differ among the communities, whereas organic matter was only marginally significantly different. Whereas elevation is known to influence species distribution through its direct effects on climate (Jafari et al. 2004), the elevation variation between sites was relatively limited in this study. The fact that it was a key factor in separating our communities is likely due to its co-variation with the type of parental material (Zebire et al. 2019), and its effects on the sites’ hydrological regimes which exerts strong influence on species composition (Clilverd et al. 2013). For example, our community 2 in particular, is strongly influenced by seasonal flash floods and overflows from the streams discharging into Lake Chamo (Jury 2014). By contrast, community 1 is typically characterized by water stress due to its location away from waterbodies (supplementary file 1) and underlying andosols on the community is established (Shetie et al. 2017).

Community composition and human disturbance

Human-environment interactions often have deleterious effects on forest ecosystems and their potential to provide

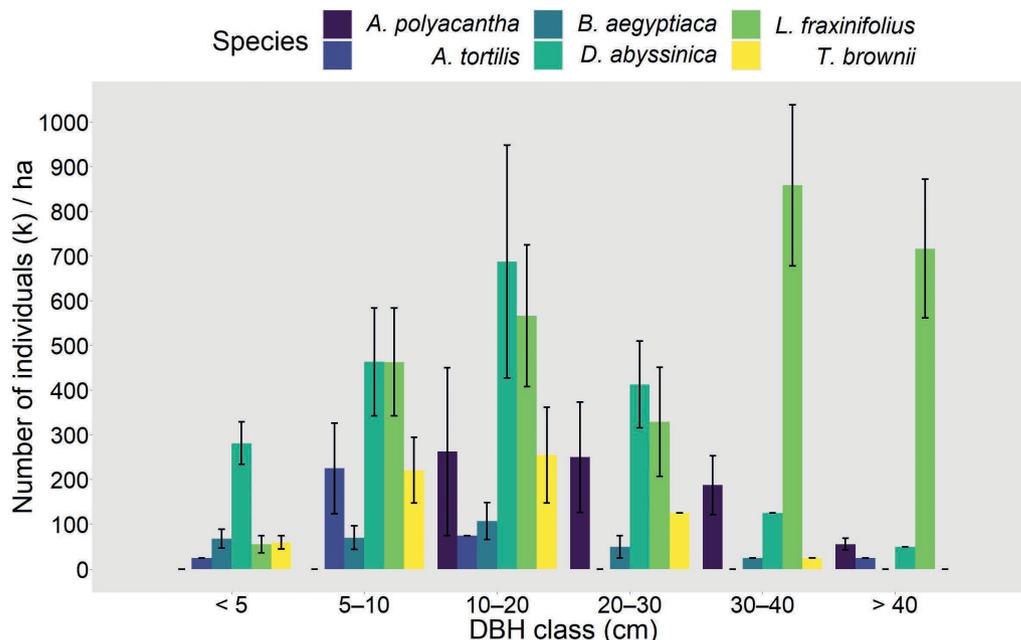


Figure 3 – Summary of population structure of six abundant and highly harvested tree species across all surveyed plots (*Acacia polyacantha*, *Acacia tortilis*, *Balanites aegyptiaca*, *Diospyros abyssinica*, *Lecaniodiscus fraxinifolius*, *Terminalia brownii*). DBH class distribution presented per species as the number of individuals (k) per hectare (\pm standard error). For *L. fraxinifolius* real values of k were divided by 3 for visualization reasons.

ecosystem services (Keenan et al. 2015; Ge et al. 2019). Although large scale disturbances such as fire were absent, our results indicate that human disturbance (HDI) significantly impacted species composition, species richness and diversity of the delineated plant communities, and resulted in small-scale successional patterns. Community 1 was the most disturbed, i.e. having the highest mean HDI, likely due to proximity to adjacent agricultural activities (supplementary file 1). Human disturbances can cause various impacts on forest communities (Htun et al. 2011). Surprisingly, our results showed a concurrent increase in species richness and diversity with increasing human disturbance. This was partly due to the emergence of disturbance tolerant, light demanding and fast-growing ruderal species. For example, the abundances of *Acalypha fruticosa*, *Dichrostachys cinerea* and *Lantana camara* showed generally increasing trends with increasing human disturbance. One of the most important effects of human disturbance on forest communities is the facilitation of invasion by non-native species (Jauni et al. 2015). We observed that the most disturbed parts of, in particular, community 3 were invaded by the invasive shrub *Lantana camara* (see also Serawit 2010). It is well known that *Lantana camara* performs well in human disturbed canopy gaps across the tropics (Totland et al. 2005) and negatively impacts the establishment of native plants through shading, jeopardizing regeneration of the native flora (Sharma & Raghubanshi 2007). Also studies conducted elsewhere have found that species richness and diversity can increase with human disturbances due to influx of shrubs following disturbance (Sahu et al. 2008; Asefa et al. 2015). In the long term, increasing cover of such disturbance affiliated species may jeopardize recovery and establishment of native species (Asefa et al. 2015). Our results may also fit into the 'Intermediate Disturbance Hypothesis' (IDH), which asserts that species richness peaks at intermediate levels of disturbance (Catford et al. 2012) due to coexistence of both competitors and colonizers (Roxburgh et al. 2004). Overall, our findings may indicate that currently, ecosystem integrity rather than species diversity *per se* is suffering from human disturbance, but that species diversity as well may become negatively affected in the longer term when human disturbance increases further.

Community structure and human disturbance

Stand structure of a forest is commonly evaluated in terms of structural attributes such as tree diameter, canopy cover, stem density and basal area (McElhinny et al. 2005), which are considered as an alternative approach to compositional measurements of plant communities (Lindenmayer et al. 2000). We examined the relation between total stand density (stem counts/ha) and average tree diameter (DBH) as a measure of population structure change for six frequently harvested tree species, as proxies for effects of human disturbances on the communities' stand structure (Okuda et al. 2003). The overall consensus is that a forest with healthy stand dynamics shows a *reverse-J* structure, highlighting continuous natural regeneration and stand replacement (McElhinny et al. 2005). By contrast, our results show that, although the overall trend seems to suggest natural replacement, the densities of lower and higher age groups were underrepresented for

some species. For example, closer inspection of abundances of selected species (e.g. *Terminalia brownii*, *Diospyros abyssinica* and *Acacia tortilis*) reveal that older age classes were represented by less individuals than would be expected in natural population dynamics (fig. 3). Human disturbances (in this case wood cutting and cattle grazing) are most likely attributable to these undesirable changes in the tree population structure. Shiferaw et al. (2019) also reported severe disruptions in the demographic structure of woody species in the Debrelibanos monastery forest in central Ethiopia, due to human induced constraints on its natural regeneration potential. It is also possible that sediment deposition has hindered recruitment of trees, and especially the natural regeneration of *Diospyros abyssinica* and *Lecaniodiscus fraxinifolius* in our community 2 (Cavalcanti & Lockaby 2006).

Basal area is a substantive structural attribute that is often used as a measure of stand productivity (McElhinny et al. 2005). Both basal area and crown cover demonstrate stand biophysical conditions and they co-vary with plant community types (McElhinny et al. 2005). In that sense, our results coincided with the expected quantitative measures for the structural attributes in the identified communities. The total mean crown cover (3242 ± 5694 m²/ha) and basal area (3.0 ± 11.3 m²/ha) were highest for community 2, and lowest (736 ± 1060 , 0.37 ± 0.66 m²/ha) for community 1. Nevertheless, in the field, we observed random felling of larger trees such as *Acacia* species, *Balanites aegyptiaca*, *Deinbollia kilimandscharica*, *Diospyros abyssinica*, *Lecaniodiscus fraxinifolius*, *Pappea capensis* and *Terminalia brownii* in various parts of the park, corroborating our examination of disturbance factors in the communities. Disturbance types also vary among communities. For example, wood cutting and cattle grazing were problematic in community 1 (*Acacia mellifera-Combretum aculeatum*), whereas stem debarking on the one side and cattle grazing on the other were mainly affecting community 2 (*Lecaniodiscus fraxinifolius-Deinbollia kilimandscharica*) and community 3 (*Acacia polyacantha-Ficus sycomorus*), respectively. Although community 2 has previously been reported to be affected by anthropogenic wood collection (Fetene et al. 2012a), our data does not support that wood collection was problematic.

Conclusion

Our comprehensive vegetation survey of the woody vegetation of the Nech Sar National Park allowed the delineation of three distinct plant communities. These emergent communities varied in their soil characteristics, elevation and degree of human disturbance. HDI significantly influenced community composition, and positively correlated with species richness and diversity. We argue that the positive correlation between HDI and species richness (and diversity) implicated the expansion of disturbance tolerant and ruderal shrubs and may also be explained by the Intermediate Disturbance Hypothesis. We conclude that (1) further community level studies should be carried out to clarify which species leave and enter the communities through time, and (2) conservation management of the Nech Sar National Park should consider management actions at plant community level, taking into consideration site conditions and human impact.

SUPPLEMENTARY FILES

Six supplementary files are associated to this paper:

- (1) Location of the preliminary distinguished vegetation types and the true community types in the Nech Sar National Park, South Ethiopian Rift Valley:
<https://doi.org/10.5091/plecevo.2020.1698.2019>
- (2) Climate diagram of the study area showing average (monthly) temperature (23.5°C) and annual rainfall (906 mm):
<https://doi.org/10.5091/plecevo.2020.1698.2021>
- (3) Species accumulation curves for all vegetation plots, lakeside forest, *Acacia* woodland, bushland, groundwater forest, and riverine forest indicating sample completeness:
<https://doi.org/10.5091/plecevo.2020.1698.2023>
- (4) List of woody plant species as identified from 104 plots across Nech Sar National Park, South Ethiopian Rift Valley:
<https://doi.org/10.5091/plecevo.2020.1698.2025>
- (5) Dendrogram or tree diagram showing four preliminary plant communities as identified by the agglomerative cluster analysis:
<https://doi.org/10.5091/plecevo.2020.1698.2027>
- (6) List of indicator species of the three identified communities in the Nech Sar National Park, South Ethiopian Rift Valley, as determined by indicator species analysis:
<https://doi.org/10.5091/plecevo.2020.1698.2029>

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