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REGULAR PAPER

Elucidating woody vegetation patterns in relation to soil and topography in tropical Africa: the case of Nech Sar National Park (Ethiopia)

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Background and aims – Although soils and topography are reported to be key factors determining vegetation patterns, there are very few studies on this topic in tropical Africa. Given the young nature of the soils of Nech Sar National park, we hypothesised that the woody vegetation would be related to both topsoil and subsoil characteristics. As topography also determines soil characteristics, we investigated whether soil and topography could be considered independently.
Methods – Abundance of woody plant species was measured in 19 stratified randomly selected plots of 20 m × 20 m. At the centre of each plot a soil profile pit was dug and samples were taken from each horizon. Topographic characteristics were derived from a 30 m × 30 m digital elevation model. TWINSPAN and Detrended Correspondence Analysis (DCA) were used to identify major patterns in species composition. Factor Analysis was used to assess the variability of, and correlation between, the soil characteristics. Differences between the vegetation groups in-terms of stand and environmental characteristics was tested with the Mann-Whitney U test. DCA axes describing the major variation in vegetation patterns were correlated with soil and topographic characteristics.
Results – Forest vegetation was found on Fluvisols and Gleyic Cambisols while bushland was found on Andosols and Vertic Cambisols. The vegetation gradient from forest to bushland (DCA-1) was correlated with both topsoil and subsoil characteristics reflecting parent material and alkalinity; these could however not be dissociated from topography. In contrast, variation both within the forest and the bushland (DCA-2) was not correlated with environmental characteristics. We attribute this variation to disturbances such as collection of firewood or logging, and to the absence of large browser or scarcity of wildfires.
Conclusions – This study calls for giving equal attention to topsoil and subsoil for elucidating woody vegetation patterns. Though vegetation patterns vary with topography, a comprehensive understanding requires insights into soils.

Key words – Riverine forest, Bushland, Fluvisols, Cambisols, Andosols, soil characteristics, topographic characteristics, digital elevation model.

INTRODUCTION

Vegetation patterns, and the relative abundance of plant species, are known to be governed by climate, soil texture, soil depth, soil fertility, drainage, topography (slope, terrain roughness, altitude), and disturbance regimes (fire, grazing, browsing) (Scholes & Archer 1997, Augustine 2003, Demel 2005, Doku et al. 2007). Even in apparently homogeneous landscapes, there are complex mosaics of plant communities, many related to soil variations as well as to the interaction of topography and climate (Furley 1976, Chen et al. 1997). Soil characteristics, such as salinity, acidity and nutrient availability influence vegetation diversity (Chen et al. 1997, Kubota et al. 1998, van Breemen & Finzi 1998). Vegetation, in turn, influences soil characteristics mainly through addition of organic matter to the soil (Finzi et al. 1998). Though

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the relation between environmental factors and forest vegetation has gained interest over the last decades (e.g. Florinsky & Kuryakova 1996, Chen et al. 1997, John et al. 2007), there are only few quantitative field studies from tropical Africa. Some examples are the studies of Parmentier (2003), Dondeyne et al. (2004), Yimer et al. (2006) and Vleminckx et al. (2015). Furley (1976) and Ruggiero et al. (2002) who studied the relation between woody vegetation and soils in tropical America, reported high correlations between vegetation patterns and soil surface characteristics, while they found low correlations with subsoil characteristics. Ruggiero et al. (2002) argued that vegetation influenced the characteristics of the upper soil layers by the transfer of organic matter and nutrients of soils that have very homogenous subsoil characteristics.

Nech Sar National Park, in the rift valley of southern Ethiopia (fig. 1A), is one of the country's major tourist destinations. It was specifically established to protect the Swayne's hartebeest (*Alcelaphus buselaphus swaynei* Sclater, 1892), an endemic antelope (Vymyslická et al. 2011). Vegetation varies from evergreen riverine forest over woodland, shrubland to grassland and swamp (fig. 1B). Climate is rather homogenous within the park and altitude ranges from 1,100 to 1,650 m a.s.l. Previous studies in the park focused on the encroachment of woody species into the grasslands, population dynamics of large mammals and bird species diversity (Duckworth et al. 1992, Aregu & Demeke 2006, Samson 2010, Yusuf et al. 2011, Datiko & Bekele 2011). Recently, Marsboom (2014) and Fetene et al. (2016) analysed land-cover changes of the park using remote sensing data and field observation (fig. 1B).

The potential vegetation map of eastern Africa indicates that Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket vegetation would be the dominant natural vegetation of the rift valley in southern Ethiopia (Lillesø et al. 2011). This vegetation type is the climax vegetation over the greater part of the Somalia-Masai floristic region and characteristically consists of a dense bushland, 3 to 5 m tall with scattered emergent trees up to 9 m (Kindt et al. 2011a). However, vegetation types of Nech Sar National park are more diverse than what the potential vegetation map would suggest. Evergreen riverine forests are prominent in the western part of the park along the Kulfo river (fig. 1B). Besides being tied to the river these forests also depend on shallow groundwater and the numerous springs occuring at the base of the escarpment. According to Duckworth et al. (1992) and Friis et al. (2010), typical forest canopy tree species are *Ficus sycomorus* L., *Garcinia livingstonei* T.Anderson, *Cordia africana* Lam., *Diospyros abyssinica* (Hiern) F.White, *Trichilia emetica* Vahl, *Croton macrostachyus* Hochst. ex Delile, *Celtis africana* Burm. f., *Acacia polyacantha* Willd. and *Lecaniodiscus fraxinifolius* Baker. Woodlands, defined by Kindt et al. (2011b: 1) "as open stands of trees of at least 8 m tall with a canopy cover of 20–40% or more, but never with interlocking crowns and usually with a field layer of heliophilous ('sun-loving') grasses", occur in Nech Sar National Park on footslopes and gentle hill slopes. As described by Duckworth et al. (1992) and Fetene et al. (2016), typical tree species are *Acacia polyacantha*, *A. nilotica* (L.) Willd. ex Delile, *A. mellifera* (Vahl) Benth., *Balanites rotundifolia* (Tiegh.) Blatt., *Boswellia neglecta* S.Moore, *Commiphora africana* (A.Rich.) Engl., *Dobera glabra* (Forssk.) Juss. ex Poir., *Salvadora persica* L., *Sterculia africana* (Lour.) Fiori and *Terminalia brownii* Fresen. On steep slopes the woodlands grade into dense shrublands, forming closed stands of bushes usually 3 to 7 m tall, with *Acacia mellifera*, *A. nilotica*, *Cadaba farinosa* Forssk., *Cordia monoica* Roxb., *C. sinensis* Lam. as typical species. At other places, the woodland grades into open woodland and grassland, with as most common grasses *Chrysopogon aucheri* (Boiss.) Stapf, *Tetrapogon roxburghiana* (Schult.) P.M.Peterson, *Cenchrus ciliaris* L., *Ischaemum afrum* (J.F.Gmel.) Dandy, *Heteropogon contortus* (L.) P.Beauv. ex Roem. & Schult., *Bothriochloa radicans* (Lehm.) A.Camus and *Themeda triandra* Forssk.

Given the above described variation in vegetation, we investigated how soil characteristics and topography relate to vegetation patterns in the western part of the park. Despite the wide interest for the ecology of the East African rift valley, factors that govern the variation in forest vegetation patterns, and particularly soils, have never been studied before in the area. We limited this research to the woody species because herbaceous species under the woody vegetation are easily affected by seasonality, while woody species are obviously persistent. As digging and describing soil profile pits in this environment is time demanding (typically at least one day, for four persons), this research was limited to 19 study sites. Consequently, this research is, to some extent, exploratory in nature. The specific objectives, and related hypotheses, were to investigate to which extent vegetation composition and species diversity are related to variation in both soil and topographic characteristics. In theories on soil genesis, topography is a key factor linked to soil formation (Jenny 1941, Schaetzl & Thompson 2015). We therefore wanted to test whether soil characteristics can be considered independently from topography to explain variation in vegetation composition, or alternatively whether they need to be considered conjunctively. Additionally, we wanted to assess the relative importance of topsoil and subsoil characteristics, particularly as topsoil characteristics are often reported to be more important in relation to vegetation (e.g. Ruggiero et al. 2002, Amorim & Batalha 2008), while subsoil characteristics are considered important in soil classification systems (e.g. Soil Survey Staff 2014, IUSS Working Group WRB 2015).

MATERIALS AND METHODS

Study area

Nech Sar National Park covers an area of 450 km^2 of which 85% is terrestrial, the remaining belonging to two lakes. The park is bounded in the west, next to Arba Minch town, by a steep escarpment, in the east by the Amaro mountains, in the north by Lake Abaya and in the south by Lake Chamo (fig. 1B). Two major rivers drain the surrounding areas and flow through the park: in the western part the Kulfo river runs southwards through the evergreen riverine forest (Duckworth et al. 1992, Aregu & Demeke 2006); the eastern part is drained by the Sermele river which runs to the south (fig. 1). Mean annual rainfall in Arba Minch town is around 860 mm and follows a bimodal distribution with a major rainy season

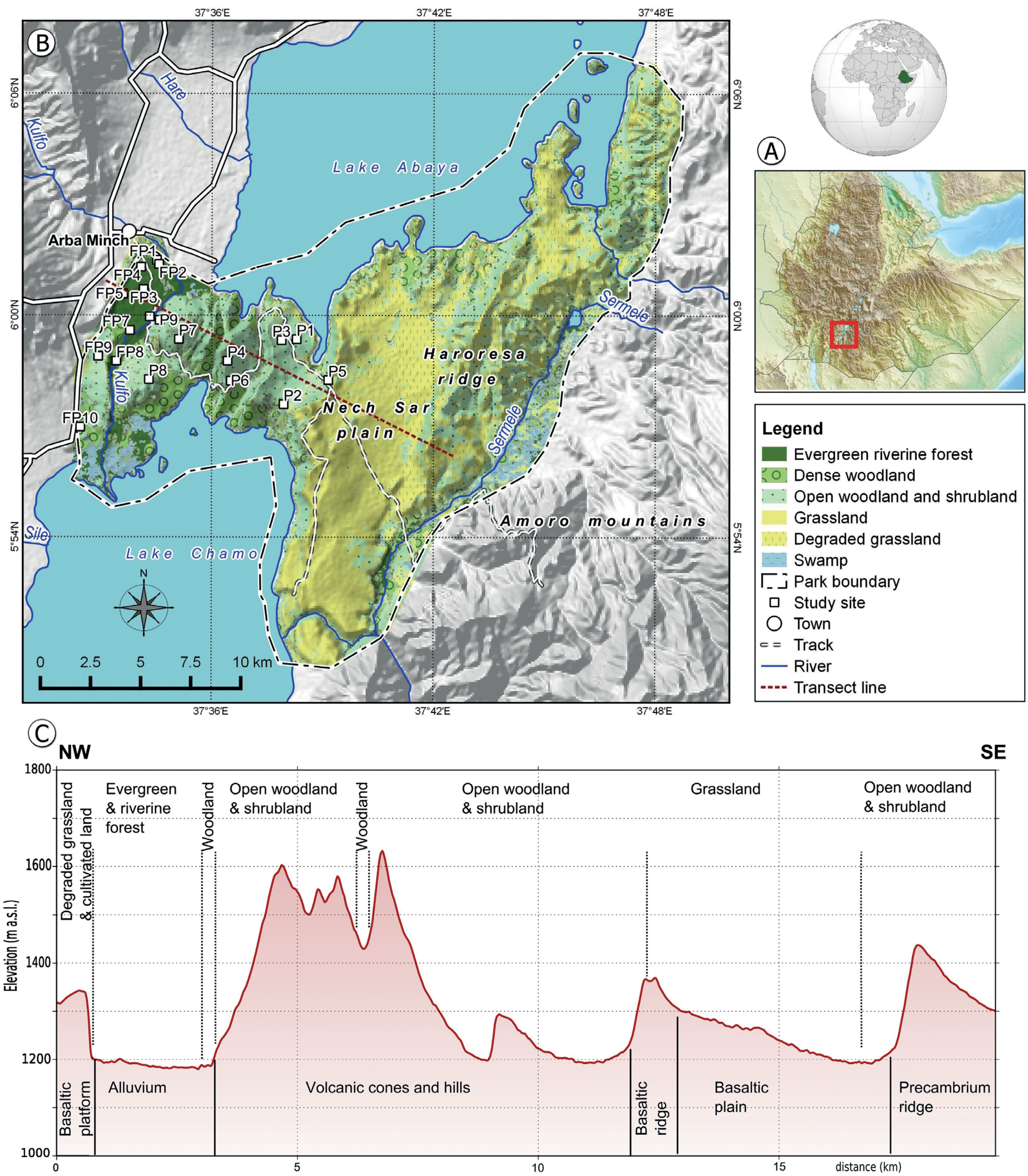

Figure 1 – A, location of Nech Sar National Park in the rift valley of southern Ethiopia (adapted from https://commons.wikimedia.org/); B, vegetation of Nech Sar National Park and location of the study site (adapted from Marsboom 2014), where FP stands for sites in the "forest" and "P" sites in the "bushland"; C, major vegetation and geomorphologic units along a topographic transect (topography based on SRTM data available from http://earthexplorer.usgs.gov; geology based on Makin et al. 1975).

from April to May, and a minor rainy season from September to October. Monthly average temperature ranges from 24 to 28°C.

Evidence from lacustrine deposits shows that Lake Abaya and Lake Chamo were one single lake in the geologic recent past (Ayenew & GebreEgziabher 2015). Volcanic and tectonic activities during the Pliocene formed a strip of land that separated the two lakes. This strip of land, known as 'the God's bridge', consists of volcanic cones and hills (fig. 1C). The bedrocks consist mainly of Tertiary pyroclastic materials and Quaternary basalt. The rift valley floor includes extensive lacustrine, colluvial and alluvial deposits (Makin et al. 1975, Ayenew & GebreEgziabher 2015).

Vegetation data

An exploratory survey was carried out in August 2012 during which as many areas as possible were visited and from which 1200 GPS points were recorded at 400 meter interval. From these points a stratified random sample of 19 sites, spread over 110 km^2, were selected: ten sites from sites taken as forest (sites with code "FP" in fig. 1B) and nine from shrub and woodlands (code "P" in fig. 1B). Height and diameter at breast height (dbh) were measured of the woody species with a height of more than 2 m and a dbh of more than 2 cm in quadrats of 20 m × 20 m; specimens shorter than 2 m and/or with a dbh of less than 2 cm were counted. Plant species which were difficult to identify in the field were collected, pressed and dried and were identified at the National Herbarium of Ethiopia. Nomenclature follows the Flora of Ethiopia and Eritrea (Hedberg & Edwards 1989, Edwards et al. 1995, Hedberg et al. 1995, Edwards et al. 1997, Edwards et al. 2000, Hedberg et al. 2003, Hedberg et al. 2004, Hedberg et al. 2006). The list of recorded species is provided in electronic appendix 1.

Soil data

At the centre of each of the 19 sites (fig. 1), a soil profile pit was dug, up to 2 m where possible, and bulk samples were taken from each horizon. The soil profiles were described following the FAO guidelines (FAO 2006). Soil samples were air dried and sieved (2 mm). The standard analyses consisted of pH-H_2O, electrical conductivity (EC) (both using a 1 : 2.5 ratio of soil : distilled water), bulk density (BD) by gravimetric method using 100 cm^3 Kopecky's rings (van Reeuwijk 2002); organic carbon (OC) and total nitrogen (N) by dry combustion using an elemental analyser after hydrochloric acid treatment (Carlo Erba 1108) (Kirsten 1983). Cation exchange capacity (CEC), and exchangeable Ca^{2+}, Mg^{2+}, K^+, Na^+, were determined using the silver thiourea (AgTU) method and measured by atomic absorption spectrometry (van Reeuwijk 2002). Calcium carbonate ($CaCO_3$) was analysed by a rapid titration method with HCl (van Reeuwijk 2002). Soil texture was measured by Laser diffraction (Beckman Coulter LS 13 320) after hydrochloric acid (HCl) and hydrogen peroxide (H_2O_2) treatment to remove carbonates and organic matter, respectively (van Reeuwijk 2002). Soils were classified according to the international soil classification system 'World Reference Base for soil resources' (IUSS Working Group WRB 2015).

Data analysis

Species association was investigated with Two-Way Indicator Species Analysis (TWINSPAN) based on the abundance of species expressed as the number of stems per plot using PC-ORD 4.0 (McCune & Mefford 1999). The following parameters were used: cut off levels set at 0, 2, 5, 10 and 20; the minimum group size for division 5; the maximum number of indicators per division 5, and 40 as the maximum number of species in the final table – being the 40 most common species – and the maximum level of divisions 5. Subsequently, based on the four groups of the sites identified by TWINSPAN (i.e. at the second level of classification), we further identified species communities by applying the Indicator Species Analysis on the forty most common species. Indicator Species Analysis in PC-Ord involves the computation of indicator value for each species in each group. The indicator value index is derived from the product of relative abundance (specificity) and the relative frequency (fidelity). Plant communities were named after the two species with the highest indicator value. The probability that a given species belongs to a particular community was determined by a Monte Carlo randomisation test with 1,000 permutations. The species richness was expressed as the number of species per site. The species diversity per site was assessed by the Shannon diversity and evenness indices. The differences between the vegetation groups in terms of stand characteristics (basal area, stem density, crown closure, max tree height and diversity indices) and in terms of soil characteristics were assessed with the Mann-Whitney U test using SPSS (Kent 2012, SPSS 2008). Gradients in the floristic composition of the 19 sites was analysed with Detrended Correspondence Analysis (DCA) after log-transforming the number of individuals of species to reduce skewness.

As the first horizon could be as thin as 3 cm or as thick as 20 cm, values of physico-chemical characteristics of topsoil were calculated as a weighted average of the surface horizons between 0 and 20 cm. For example, for the soil OC content, a weighted average was calculated as

$$OC_{topsoil} = \sum w_i \, OC_i$$

Where w_i is the thickness of horizon i (in cm) divided by 20 cm.

For the subsoil, the characteristics of the horizons at a depth of around 100 cm were taken. The variation of the physico-chemical characteristics of the topsoil and subsoil was assessed with factor analysis after VARIMAX rotation. VARIMAX is an orthogonal rotation of the factor axes minimising the number of factors needed to explain each variable. It is commonly used as it makes the interpretation of the underlying physical factors easier (Abdi 2003). Only the factor axes with loadings of which the absolute values ≥ 0.50 were taken to be significant. In the field, slope inclination was determined with a clinometer and elevation with a handheld GPS. These data were found to be consistent with Digital Elevation Model (DEM) with a 30 m × 30 m resolution available from http://earthexplorer.usgs.gov/. To assure coherence in the data, the topographic characteristics elevation, slope aspect, slope inclination, topographic position index, topographic roughness index, topographic wetness index were derived from the DEM (data in electronic appendix 2)

Table 1 – **Abundance (presence in 19 plots of 20 m × 20 m) of woody species in Nech Sar National Park, southern Ethiopia.**
The species and sites were grouped with TWINSPAN; only the 40 most common species are presented. Significant levels of the species indicator values (IV) per community are indicated with * ($p < 0.05$), or ** ($p < 0.01$); Plant trait code: T = tree, S = Shrub, Z = small tree or shrub, V = vine, e = evergreen, s = semi-deciduous, d = deciduous.

Community / Species	Plant trait	IV (%)	Forest vegetation							Bushland vegetation											
			FP1	FP2	FP5	FP6	FP7	FP8	FP3	FP4	FP10	P1	P2	P4	P5	P6	P3	P7	P8	FP9	P9
***Trichilia emetica - Celtis africana* community**																					
Acacia polyacantha Willd.	T, s	41	12	9	-	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-
Celtis africana Burm.f.	T, d	83*	1	2	8	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
Euclea divinorum Hiern	Z, e	29	72	1	21	-	-	-	17	-	186	-	1	-	-	-	-	-	-	45	1
Ficus sycomorus L.	T, d	52	-	11	7	3	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Syzygium guineense (Willd.) DC.	T, e	57	11	69	49	48	24	35	24	-	-	-	-	-	-	-	-	-	-	-	-
Ziziphus spina-christi (L.) Desf.	T, e	37	-	-	-	-	-	-	2	10	-	-	-	-	-	-	-	2	3	-	1
Trichilia emetica Vahl	T, e	83**	4	4	3	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
***Combretum collinum - Garcinia livingstonei* community**																					
Combretum collinum Fresen.	Z, d	75*	-	-	-	3	11	31	-	-	-	-	-	-	-	-	-	-	-	-	-
Combretum molle R.Br. ex G.Don	T, d	17	-	-	-	-	-	-	6	-	-	-	-	5	-	1	1	-	-	-	-
Garcinia livingstonei T.Anderson	S, e	75*	-	-	-	4	2	116	-	-	-	-	-	-	-	-	-	-	-	-	-
Lecaniodiscus fraxinifolius Baker	T, e	52	82	81	266	153	256	148	116	25	-	-	-	-	-	-	-	-	-	-	-
Tamarindus indica L.	T, e	25	-	-	-	1	1	-	2	3	-	-	-	-	-	-	1	1	3	-	-
Trichilia dregeana Sond.	T, e	65	10	32	73	109	65	24	199	30	2	-	-	-	-	-	-	-	-	-	-
Vepris dainellii (Pic.Serm.) Kokwaro	Z, e	75	1	8	14	3	16	3	80	2	-	-	-	-	-	-	-	-	-	-	-
***Acacia mellifera - Combretum aculeatum* community**																					
Acacia brevispica Harms	S, d	74*	-	-	-	-	-	-	-	1	13	-	-	7	-	-	3	3	6	3	3
Acacia mellifera (Vahl) Benth.	Z, d	68**	-	-	-	-	-	-	-	24	-	14	2	6	5	6	7	3	11	5	13
Acalypha fruticosa Forssk.	S, s	93*	7	8	-	-	-	2	-	139	12	-	-	-	-	-	-	-	1	-	1
Allophylus rubifolius (Hochst. ex A.Rich). Engl.	T, s	38	1	-	-	1	-	-	-	9	-	-	-	-	-	2	3	-	3	1	-
Balanites aegyptiaca (L.) Delile	T, e	55	1	-	-	-	-	-	-	1	1	-	-	-	-	1	1	1	2	-	-
Cadaba farinosa Forssk.	S, e	74*	-	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	1	3	3
Cissus quadrangularis L.	V, d	58	-	-	-	-	-	-	-	1	2	-	1	-	-	1	-	1	3	3	2
Combretum aculeatum Vent.	Z, d	96**	-	-	-	-	-	-	2	18	8	-	-	-	-	-	-	-	-	-	1
Cordia africana Lam.	T, d	30	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Cordia monoica Roxb.	T, d	46	-	-	-	1	-	-	1	15	-	-	1	-	-	-	-	-	-	1	-
Flueggea virosa (Roxb. ex Willd.) Voigt	S, d	59	-	-	-	-	-	-	1	5	1	-	-	-	3	1	-	2	1	11	-
Lantana camara L.	S, e	88*	6	-	-	-	-	-	-	14	16	-	-	-	-	-	-	-	-	-	-
Maytenus senegalensis (Lam.) Exell	T, e	35	9	-	1	8	-	-	15	9	1	-	-	-	-	-	-	-	1	-	-
Rhus natalensis Bernh. ex C.Krauss	S, d	66*	-	-	-	-	-	-	6	63	3	2	5	14	5	6	5	30	37	30	18
Sclerocarya birrea (A.Rich.) Hochst.	T, d	50	-	-	-	-	-	-	18	11	2	-	-	-	-	-	-	3	6	2	8
Ziziphus spina-christi (L.) Desf.	T, e	41	-	-	-	-	-	-	2	10	-	-	-	-	-	-	-	2	3	-	1

Table 1 (continued) – Abundance (presence in 19 plots of 20 m × 20 m) of woody species in Nech Sar National Park, southern Ethiopia.
The species and sites were grouped with TWINSPAN; only the 40 most common species are presented. Significant levels of the species indicator values (IV) per community are indicated with * ($p < 0.05$), or ** ($p < 0.01$); Plant trait code: T = tree, S = Shrub, Z = small tree or shrub, V = vine, e = evergreen, s = semi-deciduous, d = deciduous.

Community / Species	Plant trait	IV (%)	Forest vegetation							Bushland vegetation											
			FP1	FP2	FP5	FP6	FP7	FP8	FP3	FP4	FP10	P1	P2	P4	P5	P6	P3	P7	P8	FP9	P9
***Grewia mollis* - *Acacia nilotica* community**																					
Acacia hockii De Wild.	S, d	60	-	-	-	-	-	-	-	-	-	1	-	-	-	1	15	-	2	12	2
Acacia nilotica (L.) Willd. ex Delile	T, d	78**	3	-	-	-	-	-	-	-	1	6	16	5	-	2	12	4	6	7	37
Acacia senegal (L.) Willd.	Z, d	60	-	-	-	-	-	-	-	-	-	3	3	10	2	1	-	-	1	-	-
Acacia seyal Delile	T, d	50	-	-	-	-	-	-	-	-	-	-	-	2	-	2	-	8	12	-	6
Boswellia neglecta S.Moore	Z, d	60	-	-	-	-	-	-	-	-	-	-	-	2	-	2	2	3	2	-	2
Dichrostachys cinerea (L.) Wight & Arn.	S, d	66	-	-	-	-	-	-	-	-	6	-	5	50	26	3	-	3	14	17	17
Grewia bicolor Juss.	S, d	63**	-	-	-	-	-	-	1	-	4	1	4	5	4	2	5	4	2	4	7
Grewia mollis Juss.	S, s	90**	-	-	-	-	-	-	-	-	-	1	2	3	-	2	1	6	7	2	8
Harrisonia abyssinica Oliv.	S, e	65*	-	-	-	-	-	-	2	3	-	4	4	3	-	1	1	10	10	12	7
Pappea capensis Eckl. & Zeyh.	T, e	18	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	1	2	2
Terminalia brownii Fresen.	T, d	60	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	17	12	4	1

and were processed with QGIS version 2.8 (QGIS Development Team 2014).

The relation between vegetation composition, soil and topographic characteristics was investigated by calculating Spearman's rank correlation coefficients between the DCA axes derived from the vegetation data, the soil physico-chemical and topographic characteristics.

As we considered the underlying environmental gradients at play as unknown, we preferred this indirect approach for investigating the relation between environmental factors and vegetation composition rather than a direct method such as Canonical Correspondence Analysis or Redundancy Analysis (Kent 2012).

RESULTS

Vegetation patterns

In total, 105 woody plant species, belonging to forty families, were recorded. The Fabaceae was the largest family (17 species, 16%) followed by the Capparaceae, Tiliaceae, Anacardiaceae and Euphorbiaceae (six species each, 6%), and the Boraginaceae, Burseraceae and Rubiaceae (four species each, 4%). The five most frequent woody plant species were *Acacia mellifera* (58%), *Rhus natalensis* Bernh. ex C.Krauss (52.6%), *Grewia bicolor* Juss. (53%), *Acacia nilotica* (42%) and *Lecaniodiscus fraxinifolius* (42%).

Two major vegetation groups were identified with TWINSPAN and are further referred to as 'forest' and 'bushland' vegetation. The forest harbours predominantly tall evergreen or semi-deciduous tree species while the bushland is dominated by shrubs and small, often deciduous, trees (table 1). As shown in table 2, the stand characteristics of the forest and bushland vegetation are clearly different: basal area, stem density, crown closure and maximum tree height are higher in the forest vegetation than in the bushland. However, Shannon diversity index and evennes index of the forest was lower than that of the bushland. At the second level, TWINSPAN separated the sites FP1, FP2 and FP5 from the other four forest sites, and FP4 and FP10 from the other bushland sites.

The most abundant forest canopy species are *Lecaniodiscus fraxinifolius*, *Trichilia dregeana* Sond., *Syzygium guineense* (Willd.) DC. and *Ficus sycomorus*. These species form tall, mostly evergreen, trees resulting into a closed canopy. The forest vegetation can be subdivided into the *Trichilia emetica* - *Celtis africana* community and the *Combretum collinum* - *Garcinia livingstonei* community. The *Trichilia emetica* - *Celtis africana* community is dominated by tall evergreen trees typically found along the river. The *Combretum collinum* - *Garcinia livingstonei* community consists of tall evergreen and semi-deciduous trees among which the endemic small tree or shrub *Vepris dainellii* (Pic.Serm.) Kokwaro, often occuring in the undergrowth. The bushland vegetation has, as most common species, *Acacia mellifera*, *Acacia nilotica*, *Acacia brevispica* Harms. and *Dichrostachys cinerea* (L.) Wight & Arn. The bushland vegetation can be divided into the *Acacia mellifera* - *Combretum aculeatum* community and the *Grewia mollis* - *Acacia nilotica* commu-

Table 2 – Medians and inter-quartile range of stand and environmental characteristics of forest and bushland vegetation of Nech Sar National Park, southern Ethiopia.

Only soil characteristics with $p \leq 0.35$ are shown; p value according to the Mann-Whitney U test for two independent samples; BS: base saturation, calculated as the ratio between the total exchangeable base cations (Ca, Mg, K, Na) and the soil's cation exchange capacity (CEC) in percent; TPI: Topographic Position Index, calculated as the difference between a cell's elevation and the average elevation of a 100 m radius neighbourhood; TRI, Topographic Roughness Index (or Topographic Ruggedness Index), calculated as the square root of the sum of the deviation of a cell's elevation and an 8-cell neighbourhood; TWI, Topographic Wetness Index, determined by the local slope and size of the upstream catchment area of a cell.

	Forest vegetation (n = 7)	Bushland vegetation (n = 12)	*p*
Stand characteristics			
Basal area (m^2 ha^{-1})	150 ± 192	24 ± 14	< 0.01
Stem density (number of stems ha^{-1})	3250 ± 2525	1200 ± 2594	< 0.03
Crown closure (%)	100 ± 4	71 ± 35	< 0.01
Average max. tree height (m)	50 ± 5	18 ± 11	< 0.01
Species richness (number of species)	15 ± 7	24 ± 11	0.07
Shannon diversity index	1.64 ± 0.56	2.7 ± 0.46	< 0.01
Shannon evenness index	0.28 ± 0.11	0.58 ± 0.11	< 0.01
Topsoil characteristics			
pH-H_2O	7.9 ± 0.5	7.3 ± 1.7	0.22
BD (g cm^{-3})	1.0 ± 0.04	1.0 ± 0.2	< 0.01
$CaCO_3$ (%)	6.6 ±1.9	2.1 ± 3.9	< 0.01
Ca ($cmol_c$ kg^{-1})	25.7 ± 3.5	24.6 ±13.5	0.31
CEC ($cmol_c$ kg^{-1})	40.6 ± 3.0	37.9 ± 15.0	0.31
Silt (%)	41.3 ± 12.0	37.3 ± 11.4	0.09
Subsoil characteristics			
pH-H_2O	8.6 ± 1.2	8.3 ± 0.7	0.11
EC (µS cm^{-1})	224.0 ± 120.6	132.3 ± 124.9	0.02
$CaCO_3$ (%)	7.3 ± 2.1	3.4 ± 5.3	0.04
Mg ($cmol_c$ kg^{-1})	15.9 ± 7.1	11.5 ± 9.4	0.09
Ca ($cmol_c$ kg^{-1})	29.2 ± 13.5	22.2 ± 12.4	0.35
BS (%)	100.0 ± 0.0	99.0 ± 6.0	0.03
Topographic characteristics			
Elevation (m a.s.l.)	1193 ± 17	1252 ± 120	0.01
Slope (%)	3.70 ± 8.3	9.15 ± 23.87	0.21
Aspect (degree)	185 ± 154	144.5 ± 156	0.31
TPI	-0.24 ± 0.92	-0.35 ± 1.90	0.80
TRI	0.94 ± 1.65	2.24 ± 5.29	0.07
TWI	11.00 ± 1.5	10.35 ± 4.75	0.49

nity (table 1); the former typically has more trees, the latter more shrubs.

DCA-1 corresponds to a gradient from forest to bushland (fig. 2). DCA-2 corresponds to a gradient from closed to more open vegetation. For the sites of the forest this corresponds to a gradient from closed crowns of tall trees (sites FP8 and FP7), typically with species of the *Combretum collinum* - *Garcinia livingstonei* community, to more open forest (sites FP1 and FP2) characterised by species from the *Trichilia emetica* - *Celtis africana* community. For the sites of the bushland, this corresponds to a gradient from close stands of *Acacia nilotica* and *Dichrostachys cinerea* shrubs (sites P4 and P5) belonging to the *Grewia mollis* - *Acacia nilotica* community to more open shrubland and woodland of the *Acacia mellifera* - *Combretum aculeatum* community (sites P1, P3, P7 and P8). The sites FP4 and FP10, though grouped by TWINSPAN as 'bushland', have many species in common with the forest vegetation, and hence can be considered an intermediate group.

Table 3 – Soil classification and physico-chemical characteristics of 19 soil profiles under woody vegetation of Nech Sar National Park, southern Ethiopia.
Soil names are following the World Reference base for soil resources (IUSS Working Group WRB 2015); textural classes according to FAO (FAO 2006) with SiC: Silty clay; C: Clay; SiCL: Silty clay loam; CL: Clay loam; L: Loam; C:N, standing for soil organic carbon to nitrogen ratio; BS, base saturation (see full definition in table 2).

Vegetation groups and sites	Soil names	Depth (cm)	Texture	BD (g cm^{-3})	Sand (%)	Silt (%)	Clay (%)	pH H_2O	EC (µS cm^{-1})	$CaCO_3$ (%)	Mg <----------(cmol$_c$ kg^{-1})---------->	Na	K	Ca	CEC	BS (%)	N (%)	C (%)	C:N	P (mg/100g)
Forest vegetation																				
FP1	Panthofluvic Fluvisol	0–20	SiC	0.99	6.6	40.1	53.3	8.1	109	7.8	7.7	0.39	0.79	25.1	40.1	84	0.05	0.5	10.3	7.2
		60–100	SiCL	-	7.5	57.7	34.8	8.1	224	5.63	11.3	0.36	0.65	35.1	44.6	100	0.12	1.2	9.7	-
FP2	Panthofluvic Fluvisol	0–20	SiCL	1.03	28	52.1	20	7.9	142	6.18	9.5	0.22	1.3	28.4	39.8	99	0.1	1.2	11.7	8
		45–100	SiC	-	2.6	46.9	50.5	7.9	302	6.17	10.1	0.32	0.99	35.7	45.4	100	0.1	1.2	12.2	-
FP3	Panthofluvic Fluvisol	0–20	SiC	1.17	4.6	47.3	48.1	7	66.5	6.64	14.1	0.3	2.84	24.1	41.9	99	0.13	1.5	11.6	28.4
		90–130	SiC	-	6.6	40.1	53.3	8.6	181	6.97	14.0	1.18	0.72	29.4	43.5	100	0.07	0.6	7.9	-
FP5	Gleyic Cambisol	0–20	SiC	1.03	10	40.4	49.6	8.3	226	5.94	15.7	1.14	4.43	24.9	43.1	100	0.31	3.8	11.8	88
		70–105	SiC	-	4.6	47.6	47.8	9.5	300	9.5	27.4	5.12	0.8	9.36	41.5	100	0.03	0.3	11.0	-
FP6	Orthofluvic Fluvisol	0–20	SiC	0.97	3.4	55.3	41.2	7.6	131	5.16	10.8	0.19	1.05	28.1	40.6	99	0.13	1. 3	10.3	7.2
		90–160	C	-	0	35	65.1	8.6	171	7.29	18.4	0.56	3.25	28.0	45.5	100	0.08	0.8	10.0	-
FP7	Panthofluvic Fluvisol	0–20	SiC	1.01	4.8	41.3	53.9	7.8	77.6	6.72	9.4	0.25	2.14	25.7	40.5	92	0.12	1.4	11.3	8.6
		75–130	C	-	3.8	32.2	64	8.6	194	8.18	15.9	0.78	2.97	29.2	47.3	100	0.07	0.8	11.3	-
FP8	Panthofluvic Fluvisol	0–20	C	1.02	12.6	37.4	50	8.2	297	9.11	11.0	0.21	2.73	34.0	46.0	100	0.34	4.0	11.6	14.4
		90–130	C	-	3.9	38.8	57.3	9.4	399	8.23	16.9	6.46	3.79	21.7	44.0	100	0.1	1.0	10.4	
Intermediate group																				
FP4	Fluvic Cambisol	0–20	SiC	1.18	3.4	55.3	41.2	8.2	122	6.69	9.8	0.58	2.34	34.4	46.2	100	0.15	1.7	11.4	13.2
		70–130	SiC	-	1.7	32.3	66	8.3	94.8	7.38	14.1	0.63	0.39	31.7	47.7	98	0.05	0.7	14.0	-
FP10	Andic Cambisol	0–20	C	1.12	1.7	33.9	64.5	7.7	88	6.38	12.3	0.25	1.82	25.9	42.5	95	0.14	1.4	9.9	16.3
		80–150	SiC	-	4.6	41.8	53.7	8.4	250	7.13	15.0	0.98	0.69	31.3	46.5	100	0.04	0.4	10.3	-
Bushland vegetation																				
P1	Silandic Andosol	0–20	SiC	0.93	4.8	41.3	53.9	6.7	93.7	1.62	10.8	0.17	1.74	16.7	31.6	93	0.24	3.4	14.8	24.1
		60-105	SiC	-	3.3	46.1	50.6	8.2	89.1	4.2	10.7	1.46	1.07	22.4	42.8	83	0.12	1.4	11.9	-
P2	Silandic Andosol	0-20	SiC	0.89	3.9	41.4	54.8	7	84	2.58	13.3	0.41	2.62	25.7	44.4	95	0.13	2.1	15.9	36.1
		60–110	C	-	2	36.5	61.5	7.7	82.3	2.65	12.4	2.19	1.55	27.1	44.9	96	0.08	1.7	22.1	-
P3	Silandic Andosol	0–20	C	0.94	4.3	31	64.8	7.6	160	3.74	7.7	0.28	2.05	30.1	34.0	100	0.17	2.5	14.8	4
		80–110	SiCL	-	9.4	54.5	36.1	8.2	181	2.12	6.1	1.97	1.72	29.6	42.0	94	0.06	0.9	14.8	-
P4	Vitric Andosol	0–20	C	1.16	12.6	37.4	50	7.1	89.7	0.76	5.0	0.23	2.34	15.1	28.0	81	0.26	2.9	11.4	9.3
		50–100	CL	-	25	45	30	7.6	79.9	2.04	5.1	0.72	0.38	22	29.0	97	0.08	1.0	12.0	-
P5	Vitric Andosol	0–20	SiCL	1	20.7	43.7	35.6	8.8	114	4.53	14.2	0.55	0.76	25.4	41.4	99	0.06	0.5	9.1	8.6
		80–110	C	-	28.4	30.8	40.8	9.4	258	10.82	26.8	6.09	0.45	22	54.2	100	0.01	0.1	8.0	-

Table 3 (continued) – Soil classification and physico-chemical characteristics of 19 soil profiles under woody vegetation of Nech Sar National Park, southern Ethiopia. Soil names are following the World Reference base for soil resources (IUSS Working Group WRB 2015); textural classes according to FAO (FAO 2006) with SiC: Silty clay; C: Clay; SiCL: Silty clay loam; CL: Clay loam; L: Loam; C:N, standing for soil organic carbon to nitrogen ratio; BS, base saturation (see full definition in table 2).

Vegetation groups and sites	Soil names	Depth	Texture	BD	Sand	Silt	Clay	pH	EC	$CaCO_3$	Mg	Na	K	Ca	CEC	BS	N	C	C:N	P
		(cm)		(g cm^{-3})	(%)	(%)	(%)	H_2O	(µS cm^{-1})	(%)	<-------	-------	(cmolc kg^{-1})	-------	------->	(%)	(%)	(%)		(mg/100g)
Bushland vegetation																				
P6	Vitric Andosol	0–20	C	1.04	3.8	37.1	59.2	7.3	63.6	0.85	8.5	0.11	1.82	21.4	33.7	94	0.13	1.4	10.6	4
		45–100	C	-	19	33.6	47.4	8.7	170	3.57	5.1	4.84	0.9	18.8	34.8	85	0.02	0.2	10.4	-
P7	Vitric Andosol	0–20	C	0.82	6.4	30.7	62.9	7.4	209	2.77	8.3	0.07	3.32	23.8	35.8	99	0.49	5.9	12.1	5.3
		70–100	SiC	-	3.9	41.4	54.8	6.5	43.1	0.96	9.1	0.23	1.04	10.8	20.5	100	0.13	1.5	11.5	-
P8	Vitric Andosol	0–20	C	1	13.2	31.2	55.6	6.9	82.9	0.34	9.1	0.24	1.44	12.2	23.6	97	0.18	2.2	12.7	4
		90–150	CL	-	22.2	38	39.8	8.3	186	3.24	12.8	1.03	0.34	18.4	29.7	100	0.07	0.5	6.2	-
P9	Vitric Andosol	0–20	L	1.44	49.6	32.6	17.8	8.3	103	0	1.5	0.08	0.91	7.74	8.8	100	0.14	1.1	8.0	4
		40–105	L	-	42	38.9	19.2	7.8	53.1	0	1.4	0.21	0.89	2.35	2.3	100	0.02	0.3	10.4	-
FP9	Vertic Cambisol	0–20	SiC	1.05	3.6	43.5	52.9	7.3	74.8	0	17.2	0.17	1.74	32.3	52.6	98	0.23	2.8	12.3	13.4
		60–100	C	-	0	40.1	59.9	8.5	212	7.71	18.1	1.96	1.37	34.9	54.4	100	0.1	1.6	15.6	-

Soil classification and characteristics

Soils under forest are dark, with Munsell colour values and chromas of 3 or less, and with a silty clay texture. They generally have a high chemical fertility status. These soils have high organic carbon, phosphorus and calcium carbonate content and also have a high cation exchange capacity (table 3). The soils that are regularly flooded by the Kulfo river, are classified as Panthofluvic Fluvisols and Orthofluvic Fluvisols; those having shallow groundwater are Gleyic Cambisols (table 3). Soils under bushland are mostly shallow and have a sandy clay texture and have lower silt content than the soils under forest. The soils found on the hills of the 'God's bridge' (fig. 1), which are developed on volcanic ejecta, are Silandic Andosols and Vitric Andosols (table 3). The intermediate vegetation group occurs on soils which have intermediate soil properties: Fluvic Cambisols, i.e. weakly developed soils formed on alluvial deposits and Andic Cambisols, weakly developed soils incorporating volcanic material.

The factor loadings of the physico-chemical characteristics are presented in table 4. For the topsoil, the variation along Factor 1 corresponds to the parent material as it has high loadings for cation exchange capacity (CEC), soil texture (sand) and $CaCO_3$ content. The Factor 2 reflects accumulation of organic matter (OC, N) which occurs on less favourable drained soils. For the subsoil, the variation along Factor 1 is determined by soil reaction and alkalinity (pH, Na^+, EC, $CaCO_3$ and Mg^{2+}). The variation along Factor 2 is again related to the parent material (sand, clay, CEC, Ca^{2+}, $CaCO_3$).

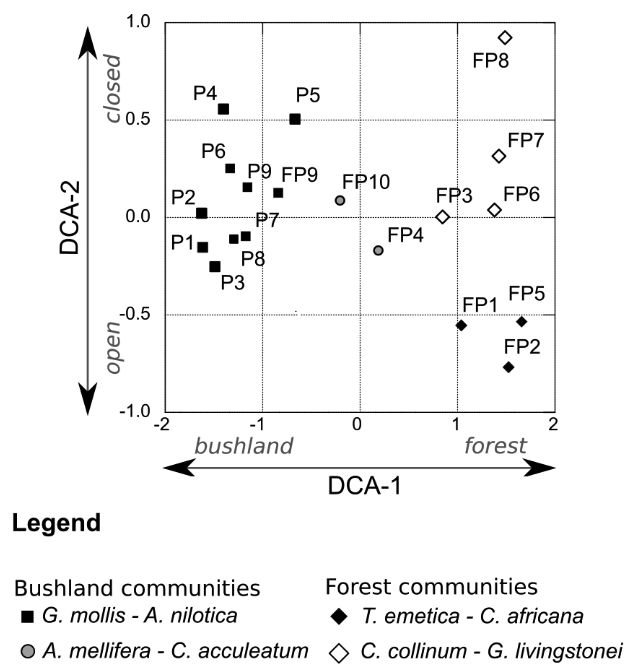

Figure 2 – Ordination (DCA) of vegetation composition of 19 study sites of Nech Sar National Park. DCA-1 corresponds to a gradient from bushland to forest. DCA-2 corresponds to a gradient from relatively 'open' to relatively 'closed' vegetation. FP stands for sites initially regarded as 'forest' and P as 'bushland' – see table 1 for details on the vegetation communities.

Table 4 – Factor loadings after VARIMAX rotation of the topsoil (0–20 cm) and the subsoil (c. 100 cm) characteristics.
Loadings with an absolute value > 0.5 are shown in bold.

Soil characteristics	Topsoil		Subsoil	
	Factor 1	**Factor 2**	**Factor 1**	**Factor 2**
BD (g cm^{-3})	**-0.57**	-0.36	-	-
Silt (%)	0.47	**-0.51**	-0.09	0.06
Clay (%)	0.37	0.39	0.10	**0.63**
Silt:Clay ratio	-0.11	-0.27	-0.29	-0.07
Sand (%)	**-0.72**	-0.10	-0.05	**-0.73**
CEC ($cmol_c$ kg^{-1})	**0.96**	0.02	0.48	**0.85**
$CaCO_3$ (%)	**0.59**	-0.03	**0.73**	**0.52**
EC (µS cm^{-1})	0.20	**0.75**	**0.83**	0.19
BS (%)	0.15	0.23	0.01	0.06
Mg^{2+} ($cmol_c$ kg^{-1})	**0.68**	-0.04	**0.67**	0.38
Ca^{2+} ($cmol_c$ kg^{-1})	**0.93**	0.08	-0.01	**0.88**
Na^+ ($cmol_c$ kg^{-1})	0.21	-0.02	**0.86**	-0.18
pH-H_2O	0.07	-0.08	**0.94**	0.11
OC (%)	0.03	**0.94**	-0.43	0.38
N (%)	-0.04	**0.94**	-0.37	0.29
C:N ratio	0.31	0.30	-0.32	0.34
K^+ ($cmol_c$ kg^{-1})	0.18	**0.66**	0.31	-0.04
P (mg/100g)	0.10	0.19	-	-
% var	31.1	22.2	33.4	26.1
Cum Var%	31.1	53.3	33.4	59.5

Table 5 – Spearman's rank correlations between DCA axes of the vegetation and soil and topographic characteristics.
Only the soil characteristics which are significant in at least the topsoil or the subsoil are presented, n = 19; BS, base saturation; TPI: Topographic Position Index; TRI, Topographic Roughness Index; TWI, Topographic Wetness Index (see full definitions in table 2). * Correlation is significant at the 0.05 level (2-tailed). ** Correlation is significant at the 0.01 level (2-tailed).

Characteristics	DCA1	DCA2
Topsoil		
Silt (%)	0.41	-0.10
Clay (%)	-0.51*	-0.06
CEC ($cmol_c$ kg^{-1})	0.43	0.04
$CaCO_3$ (%)	0.71**	-0.16
EC (µS cm^{-1})	0.36	-0.30
BS (%)	0.32	-0.18
Mg^{2+} ($cmol_c$ kg^{-1})	0.30	0.06
pH-H_2O	0.63**	0.04
Subsoil		
Silt (%)	0.01	-0.58**
Clay (%)	0.27	0.07
CEC ($cmol_c$ kg^{-1})	0.36	0.06
$CaCO_3$ (%)	0.69**	0.14
EC (µS cm^{-1})	0.69**	-0.08
BS (%)	0.71**	0.05
Mg^{2+} ($cmol_c$ kg^{-1})	0.58**	0.10
pH-H_2O	0.51*	0.27
Topography		
Elevation (m)	-0.60**	-0.04
Slope aspect (degrees)	0.40	0.20
Slope inclination (%)	-0.20	0.20
TPI	0.11	-0.15
TRI	0.51*	-0.06
TWI	-0.49*	-0.11

Vegetation patterns in relation to soils and topography

Soils under forest and bushland are both moderately to slightly alkaline, i.e. relatively high pH, $CaCO_3$ (%), EC, exchangeable Ca and Mg content. The alkalinity is more pronounced under the forest than under the bushland; CEC and silt content are also higher under the forest than under the bushland (table 2). Elevation of the forest, being located on alluvium in the lowest part of the rift valley is lower than that of the bushland vegetation (table 2, fig. 1). Likewise, slope inclination and topographic roughness index are higher under the bushland.

As shown in table 5, DCA-1 of the vegetation, which corresponds to the gradient from forest to bushland, is correlated to both topsoil and subsoil characteristics which can be related to parent material (Clay %, $CaCO_3$ %) and alkalinity (EC, BS %, Mg^{2+}, pH-H_2O). This vegetation gradient is however also correlated to topography, particularly elevation, topographic roughness and local convexities as expressed by the topographic wetness indices. DCA-2 of the vegetation, which corresponds to a gradient from closed to more open vegetation, is not meaningfully correlated with the environmental variables (table 5).

DISCUSSION

Vegetation composition and soil classification

Based on the species abundance, forest and bushland could be identified as two major vegetation groups, though many species were found across these groups (table 1). The forest vegetation corresponds to the 'Somali-Masai riverine forest' as described by White (1983) and has been named 'groundwater forest' by Duckworth et al. (1992) and Fetene et al. (2016).

The soil names of the international soil classification system 'World Reference Base' (IUSS Working Group 2015), which hinges on subsoil characeteristics, reflect well ecological relevant properties such as the parent material (Andosols vs. Fluvisols or Cambisols) as well as the water regime expressed as Fluvic, Vertic and Gleyic properties (table 3). The forest vegetation occurs on alluvial deposits where groundwater is relatively shallow and on soils classified as Panthofluvic Fluvisols, Orthofluvic Fluvisols and Gleyic Cambisols (table 3). The bushland vegetation corresponds to '*Acacia-Commiphora* deciduous bushland' as described by White (1983), Duckworth et al. (1992) and Soromessa et al. (2004). It also corresponds to the 'Somalia-Masai *Acacia-Commiphora* deciduous bushland and thicket vegetation' of the potential vegetation map of Ethiopia (Lillesø et al. 2011). The bushland occurs on shallow, rocky soils of the 'God's bridge' that are Vitric Andosols and Silandic Andosols or on Vertic Cambisols on the basaltic platform (FP9) (fig. 1, table 3).

Vegetation patterns and environmental factors

Using multivariate analysis (TWINSPAN, DCA, Indicator Species Analysis, Factor Analysis) and Spearman rank' correlation cofficient, it is possible to elucidate the patterns of the woody vegetation of Nech Sar National park in terms of soil and topographic characteristics. The gradient from forest to bushland – as expressed by the DCA-1 (fig. 2) – could be explained by soil characteristics reflecting the parent material (table 5). As the topography is also determined by the parent material, the major vegetation gradient is also significantly correlated with topographic characteristics (table 5). Clearly, soil characteristics and topography cannot be dissociated from each other. Florinsky & Kuryakova (1996) advocated using digital elevation models (DEM) for vegetation studies. DEMs have, for example, been used to explain the relative abundance of montane forests and herbaceous communities in the Lassen Volcanic National Park in the USA (Pinder et al. 1997), to explain grass-nutrient patterns in savanna rangelands in southern Africa (Mutanga et al. 2004), and to delineate land components (Mashimbye et al. 2014). Our data however shows that though topography can be a useful covariate to explore vegetation patterns, to fully understand the variation in vegetation patterns both topsoil and subsoil characteristics need to be taken into account. Concerning the subsoil, our results constrast with the findings of Furley (1976) and of Ruggiero et al. (2002), who reported only high correlations between vegetation patterns and topsoil characteristics and weak correlation with the subsoil. Ruggiero et al. (2002) argued that vegetation influenced the characteristics of the upper soil layers by the transfer of organic matter and nutrients of soils with very homogenous subsoil characteristics. The topsoil characteristics in our study area, of the relatively young soils (Fluvisols, Andosols and Cambisols), seem to be more determined by the parent material than by the vegetation. As parent material has a strong bearing on the topsoil characteristics, we would argue that vegetation composition is determined by topsoil characteristics rather than the other way around. It could be argued that the high correlation we found between subsoil and the vegetation groups, could be due to the heterogenous nature of the subsoil as it concerns relatively young, weakly developed soils. Our findings are however in-line with the findings of Dondeyne et al. (2004) who also found a clear correlation between woodland vegetation composition and the subsoil of more weathered soils in southeastern Tanzania. As studies on tropical vegetation are often restricted to topsoil characterestics (e.g. de Lima Dantas & Batalha 2011, Vleminckx et al. 2015) on the argument that these are most correlated to vegetation structure, this topic deserves more research.

Species diversity and enviromental factors

Though soil characteristics and topography clearly affect species composition between the forest and bushland vegetation, the diversity across these groups expressed in terms of species richness does not differ significantly (table 4). However, as indicated by the higher Shannon evenness index (table 2), the vegetation of the bushland is more heterogeneous than of the forest vegetation and which may be related to the higher variability of soil characteristics and topography on the 'God's bridge' (fig. 1, table 4). The typical response of species richness in relation to nutrient availability has been described as a 'humped-back curve' whereby species richness is low at low nutrient levels, increases to a peak at intermediate levels and declines more gradually at high nutrient levels (Pausas & Austin 2001). The lack of significant difference in species richness between the forest and bushland vegetation in our study could be due to the relative high soil fertility under both vegetation groups eventhough the soils belong to different Reference Soil Groups. However, the differences in disturbance regimes between the forest and the bushland should also be taken into account, and therefore should further be investigated.

Vegetation patterns and disturbance factors

Variation within the forest as well as within the bushland – as reflected by DCA-2 – is not meaningfully correlated with neither soil characteristics nor with topography (table 5). For the forest vegetation, the *Combretum collinum - Garcinia livingstonei* community represents the least disturbed parts of the forest. It is also in this community that *Vepris dainellii* is found, which is an endemic species of southern Ethiopia and listed as threatened but of "least concern" (Vivero et al. 2005). *Prunus africana* (Hook.f.) Kalkman and *Cordia africana* are also found in this community and are considered threatened species within Ethiopia. Based on our vegetation records this community may be considered as the most valuable for conservation particularly given that evergreen forest has since long been under pressure from illegal firewood collectors and some timber logging (Duckworth et al. 1992, Aregu & Demeke 2006). Hence, human disturbance of the forest seems to be the most likely factor to explain the differentiation between the two forest communities, resulting into the occurrence of species like *Acalypha fruticosa* Forssk. and the invasive *Lantana camara* L. into the forest (table 1). For the bushland it is harder to identify a root cause. Firewood is also collected from the bushland but much less so than from the forest. In contrast to the grasslands of the Nech Sar plain (fig. 1), cattle is not being grazed in the bushland (Doku et al. 2007, Yusuf et al. 2011) so grazing by cattle is unlikely to be a factor of disturbance. The lack of large browsers over the last decades – such as black rhinoceros [*Diceros bicornis* (Linnaeus, 1758)] and elephants [*Loxodonta africana* (Blumenbach, 1797)] – could be a factor, as their absence will favour the spread of thorny shrubs such as *Acacia* spp. and *Dichrostachys cinerea* (Mukinya 1977, Owen-Smith & Chafota 2012). Another factor could be the very low incidence of wildfires as, based on remote sensing data, Marsboom (2014) demonstrated that only 68 wildfires were recorded within the park between 2001 to 2013.

CONCLUSIONS

Our case study shows that the major pattern in the woody vegetation of Nech Sar National Park is correlated to soil characteristics and topography. The major variation of the soil characteristics reflects variation in parent material and which in turn is strongly related to the topography. Though topographic characteristics turn out to provide useful covariates to explain vegetation patterns, and have the advantage to be easily available as digital elevation models, our case study illustrates the importance of soil data of both the topsoil and the subsoil. The floristic variation within the forest as well as within the bushland is neither related to soils nor to topography but can at least in part, be attributed to disturbances, such as collection of firewood, logging, an to the absence of large browser and wildfires.

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data) and consists of: (1) list of woody plant species recorded in 19 study sites in Nech Sar National Park; and (2) topographic characteristics of the 19 study sites in Nech Sar National Park as derived from DEM data.

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REFERENCES

Abdi H. (2003) Factor rotations in factor analyses. In: Lewis-Beck M., Bryman A., Futing T. (eds) Encyclopedia of social sciences research methods. Thousand Oaks, Sage. Available from https://www.utdallas.edu/~herve/Abdi-rotations-pretty.pdf [accessed 27 Aug. 2015].

Amorim P.K., Batalha M.A. (2008) Soil chemical factors and grassland species density in Emas National Park (central Brazil). Brazilian Journal of Biology 68: 279–285. https://doi.org/10.1590/S1519-69842008000200008

Aregu L., Demeke F. (2006) Socio-economic survey of Arba-Minch riverine forest and woodland. Journal of the Drylands 1: 194–205.

Augustine D.J. (2003) Long-term, livestock-mediated redistribution on nitrogen and phosphorus in an East African savanna. Journal of Applied Ecology 40: 137–149. https://doi.org/10.1046/j.1365-2664.2003.00778.x

Ayenew T, GebreEgziabher M. (2015) Morphometric characteristics and hydrology of selected Ethiopian rift lakes. In: Billi P. (ed.) Landscapes and landforms of Ethiopia, world geomorphological landscapes: 275–287. Berlin, Springer Science. https://doi.org/10.1007/978-94-017-8026-1_16

Chen Z.-S., Hsieh C.-F., Jiang F.-Y., Hsieh T.-H., Sun I.-F. (1997) Relationships of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan. Plant Ecology 132: 229–241. https://doi.org/10.1023/A:1009762704553

Datiko D., Bekele A. (2011) Population status and human impact on the endangered Swayne's hartebeest (Alcelaphus buselaphus swaynei) in Nechisar plains, Nechisar National park, Ethiopia. African Journal of Ecology 49: 311–319. https://doi.org/10.1111/j.1365-2028.2011.01266.x

de Lima Dantas V., Batalha M.A. (2011) Vegetation structure: fine scale relationships with soil in a cerrado site. Flora-Morphology, Distribution, Functional Ecology of Plants 206: 341–346. https://doi.org/10.1016/j.flora.2010.11.003

Demel T. (2005) Seed and regeneration ecology in dry Afromontane forests of Ethiopia: I. Seed production-population structures. Tropical Ecology 46: 29–44.

Doku Y., Bekele A., Balakrishnan M. (2007) Population status of plains zebra (Equus quagga) in Nechisar plains, Nechisar National park, Ethiopia. Tropical Ecology 48: 79–86.

Dondeyne S., Wijffels A., Emmanuel L.B., Deckers J., Hermy M. (2004) Soils and vegetation of Angai forest: ecological insights from a participatory survey in South Eastern Tanzania. African Journal of Ecology 42: 198–207. https://doi.org/10.1111/j.1365-2028.2004.00513.x

Duckworth J.W., Evans M.I., Safford R.J., Telfer M.G., Timmins R.J., Chemere Z. (1992) A survey of Nech Sar National Park, Ethiopia: Report of the Cambridge Ethiopia ground-water forest expedition 1990. International Council for Bird Preservation Study Report No. 50. Cambridge, U.K., International Council for Bird Preservation.

Edwards S., Mesfin T., Hedberg I. (1995) Flora of Ethiopia and Eritrea. Vol. 2, Part 2. Addis Ababa, National Herbarium, Addis Ababa University, & Uppsala, Department of systematic Botany, Uppsala University, Uppsala.

Edwards S., Sebsebe D., Hedberg I. (1997) Flora of Ethiopia and Eritrea. Vol. 6. Addis Ababa, National Herbarium, Addis Ababa University, & Uppsala, Department of systematic Botany, Uppsala University.

Edwards S., Mesfin T., Sebsebe D., Hedberg I. (2000) Flora of Ethiopia and Eritrea. Vol. 2, Part 1. Addis Ababa, National Herbarium, Addis Ababa University, & Uppsala, Department of systematic Botany, Uppsala University.

FAO (2006) Guidelines for soil description. 4th Ed. Rome, Food and Agriculture Organization of United Nations.

Fetene A., Hilker T., Yeshitela K., Prasse R., Cohen W., Yang Z. (2016) Detecting trends in landuse and landcover change of Nech Sar National park, Ethiopia. Environmental Management 57: 137–147. https://doi.org/10.1007/s00267-015-0603-0

Finzi A.C., van Breemen N., Canham C.D. (1998) Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. Ecological Applications 8: 440–446.

Florinsky I.V., Kuryakova G.A. (1996) Influence of topography on some vegetation cover properties. Catena 27: 123–141. https://doi.org/10.1016/0341-8162(96)00005-7

Friis I., Demissew S., van Breugel P. (2010) Atlas of the potential vegetation of Ethiopia. Copenhagen, Det Kongelige Danske Videnskabernes Selskab.

Furley P.A. (1976) Soil-slope-plant relationships in the northern Maya mountains, Belize, Central America. III. Variations in the Properties of Soil Profiles. Journal of Biogeography 3: 303–319. https://doi.org/10.2307/3038020

Hedberg I., Edwards S. (1989) Flora of Ethiopia and Eritrea. Vol. 3. Addis Ababa, National Herbarium, Addis Ababa University, & Uppsala, Department of systematic Botany, Uppsala University.

Hedberg I., Edwards S., Phillips S. (1995) Flora of Ethiopia and Eritrea. Vol. 7. Addis Ababa, National Herbarium, Addis Ababa University, & Uppsala, Department of systematic Botany, Uppsala University.

Hedberg I., Edwards S., Sileshi N. (2003) Flora of Ethiopia and Eritrea. Vol. 4, Part 1. Addis Ababa, National Herbarium, Addis Ababa University, & Uppsala, Department of systematic Botany, Uppsala University.

Hedberg I., Friis I., Edwards S. (2004) Flora of Ethiopia and Eritrea. Vol. 4, Part 2. Addis Ababa, National Herbarium, Addis Ababa University, & Uppsala, Department of systematic Botany, Uppsala University.

Hedberg I., Ensermu K., Edwards S., Sebsebe D., Persson V. (2006) Flora of Ethiopia and Eritrea. Vol. 5. Addis Ababa, National Herbarium, Addis Ababa University, & Uppsala, Department of systematic Botany, Uppsala University.

IUSS Working Group WRB (2015) World reference base for soil resources 2014. International soil classification system for naming soils and creating legends for soil maps. Update 2015. World Soil Resources Reports 106. Rome, FAO.

Jenny H. (1941) Factors of soil formation. New York, McGraw-Hill.

John R., Dalling J.W., Harms K.E., Yavitt J.B., Stallard R.F., Mirabello M., Hubbell S.P., Valencia R., Navarrete H., Vallejo M., Foster R.B. (2007) Soil nutrients influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences 104: 864–869. https://doi.org/10.1073/pnas.0604666104

Kent M. (2012) Vegetation description and data analysis: a practical approach. 2nd Ed. Oxford, Wiley-Blackwell.

Kindt R., Van Breugel P., Lillesø J.B., Bingham M., Demissew S., Dudley C., Friis I., Gachathi F., Kalema J., Mbago F., Minani V., Moshi H., Mulumba J., Namaganda M., Ndangalasi H., Ruffo C., Jamnadass R., Graudal L.O.V. (2011a) Potential natural vegetation of eastern Africa. Volume 4. Description and tree species composition for bushland and thicket potential natural vegetation types. Forest & Landscape Working Paper, no. 64. Copenhagen, University of Copenhagen.

Kindt R., van Breugel P., Lillesø J.B., Bingham M., Demissew S., Dudley C., Friis I., Gachathi, F., Kalema J., Mbago F., Minani V., Moshi H., Mulumba J., Namaganda M., Ndangalasi H., Ruffo C., Jamnadass R., Graudal L.O.V. (2011b) Potential natural vegetation of Eastern Africa (Ethiopia, Kenya, Malawi, Rwanda, Tanzania, Uganda and Zambia). Volume 3. Description and tree species composition for woodland and wooded grassland potential natural vegetation types. Forest & Landscape, University of Copenhagen. Forest & Landscape Working Papers, no. 63. Copenhagen, University of Copenhagen.

Kirsten W. (1983) Organic elemental analysis: Ultramicro, Micro and Trace Method. New York & London, Academic press.

Kubota D., Masunaga T., Hermansah, Rasyidin A., Hotta M., Shinmura Y., Wakatsuki T. (1998) Soil environment and tree species diversity in tropical rain forest, West Sumatra, Indonesia. In: Schulte A., Ruhiyat D. (eds) Soil of tropical forest ecosystems: 159–167. Berlin, Springer. https://doi.org/10.1007/978-3-662-03649-5_18

Lillesø J.-P.B., van Breugel P., Kindt R., Bingham M., Demissew S., Dudley C., Friis I., Gachathi F., Kalema J., Mbago F., Minani V., Moshi H.N., Mulumba J., Namaganda M., Ndangalasi H.J., Ruffo C., Jamnadass R., Graudal L.O.V. (2011) Potential natural vegetation of Eastern Africa (Ethiopia, Kenya, Malawi, Rwanda, Tanzania, Uganda and Zambia). Volume 1. The atlas. Forest & Landscape Working Papers, no. 61. Copenhagen, University of Copenhagen.

Makin M.J., Kingham T.J., Waddams A.E., Birchall C.J., Teferra T. (1975) Development prospects in the southern rift valley, Ethiopia. Land Resource Study 21. London, Land Resources Division, Ministry of Overseas Development.

Marsboom C. (2014) Vegetation dynamics in Nech Sar National park, Ethiopia: analyzing land use/land cover changes with satellite images, remote sensing and GIS. Master thesis, Faculty of Biosciences, Agriculture and Horticulture, KU Leuven, Geel, Belgium.

Mashimbye Z.E., de Clercq W.P., Van Niekerk A. (2014) An evaluation of digital elevation models (DEMs) for delineating land components. Geoderma 213: 312–319. https://doi.org/10.1016/j.geoderma.2013.08.023

McCune B., Mefford M.J. (1999) PC-ORD. Multivariate analysis of ecological data. Version 4. Gleneden Beach, MjM software.

Mukinya J.G. (1977) Feeding and drinking habits of the black rhinoceros in Masai Mara Game Reserve. African Journal of Ecology 15: 125–138. https://doi.org/10.1111/j.1365-2028.1977.tb00386.x

Mutanga O., Prins H.T.P., Skidmore A.K., van Wieren S., Huizing H., Grant R., Peel M., Biggs H. (2004) Explaining grass-nutrient patterns in a savanna rangeland of southern Africa. Journal of Biogeography 31: 819–829. https://doi.org/10.1111/j.1365-2699.2004.01072.x

Owen-Smith N., Chafota J. (2012) Selective feeding by a mega herbivore, the African elephant (Loxodonta africana). Journal of Mammalogy 93: 698–705. https://doi.org/10.1644/11-MAMM-A-350.1

Parmentier I. (2003) Study of the vegetation composition in three inselbergs from Continental Equatorial Guinea (Western Central Africa): effects of site, soil factors and position relative to forest fringe. Belgian Journal of Botany 136: 63–72.

Pausas J.G., Austin M.P. (2001) Patterns of plant species richness in relation to different environments: an appraisal. Journal of Vegetation Science 12: 153–166. https://doi.org/10.2307/3236601

Pinder J.E., Kroh G.C., White J.D., Basham May A.B. (1997) The relationships between vegetation type and topography in Lassen Volcanic National Park. Plant Ecology 131: 17–29. https://doi.org/10.1023/A:1009792123571

QGIS Development Team (2014) QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from http://qgis.osgeo.org [accessed 4 July 2014].

Ruggiero P.G.C., Batalha M.A., Pivello V.R., Meirelles S.T. (2002) Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil. Plant Ecology 160: 1–16. https://doi.org/10.1023/A:1015819219386

Samson S. (2010) Vegetation ecology, forage biomass and evaluation of nutritive value of selected browse species in Nech Sar National park. MSc Thesis, Addis Ababa University, Addis Ababa, Ethiopia.

Schaetzl R.J., Thompson M.L. (2015) Soils: genesis and geomorphology. New York, Cambridge University Press.

Scholes R.J., Archer S.R. (1997) Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28: 517–544. https://doi.org/10.1146/annurev.ecolsys.28.1.517

Soil Survey Staff (2014) Keys to Soil Taxonomy. 12th Ed. Washington, DC, USDA-Natural Resources Conservation Service.

Soromessa T., Teketay D., Demissew S. (2004) Ecological study of the vegetation in Gamo Gofa zone, southern Ethiopia. Tropical Ecology 45: 209–221.

SPSS (2008) SPSS Statistics for Windows, Version 17.0. Chicago, SPSS Inc.

van Breemen N., Finzi A.C. (1998) Plant-soil interactions: ecological aspects and evolutionary implications. Biogeochemistry 42: 1–19.

van Reeuwijk L.P. (2002) Procedure for soil analysis. Technical Paper 9. 6th Ed. Wageningen, ISRlC.

Vivero J.L., Demissew S., Kelbessa E. (2005) The red list of endemic trees and shrubs of Ethiopia and Eritrea. Cambridge, UK, Fauna & Flora International.

Vleminckx J., Drouet T., Amani C., Lisingo J., Lejoly J., Hardy O.J. (2015) Impact of fine-scale edaphic heterogeneity on tree species assembly in a central African rainforest. Journal of Vegetation Science 26: 134–144. https://doi.org/10.1111/jvs.12209

Vymyslická P., Hejcmanová P., Antonínová M., Stejskalová M., Svitálek J. (2011) Daily activity pattern of the endangered Swayne's Hartebeest (Alcelaphus buselaphus swaynei Sclater, 1892) in the Nechisar National park, Ethiopia. African Journal of Ecology 49: 246–249. https://doi.org/10.1111/j.1365-2028.2010.01243.x

White F. (1983) The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. Paris, UNESCO.

Yimer F., Ledin S., Abdelkadir A. (2006) Soil property variations in relation to topographic aspect and vegetation community in the south-eastern highlands of Ethiopia. Forest Ecology and Management 232: 90–99. https://doi.org/10.1016/j.foreco.2006.05.055

Yusuf H., Treydte A.C., Demissew S., Woldu Z. (2011) Assessment of woody species encroachment on the grasslands of Nech Sar National Park, Ethiopia. African Journal of Ecology 49: 397–409. https://doi.org/10.1111/j.1365-2028.2011.01271.x

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