

Diversity and production of Ethiopian dry woodlands explained by climate- and soil-stress gradients

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ABSTRACT

Dry woodlands cover about 14% of the total African land surface and represent about 25% of the natural vegetation. They are characterized by a seasonal climate, with a dry season of 4–7 months. Large parts of these ecosystems are degrading due to grazing, fire or exploitation by people. We studied species richness and productivity patterns of dry woodlands in Ethiopia. For such ecosystems, classic productivity and diversity hypotheses predict that species richness and productivity increase as the wet season length increases, and decrease when soil conditions create water stress. We inventoried and measured trees in 18 2-ha plots distributed in two sites, one higher altitude site with a shorter wet season than the lower altitude site. We found that the stand volume per hectare was lower in the site with a shorter wet season. Across all 18 plots we observed that stand volume decreased with soil water stress (estimated from texture and depth). This was in line with the prediction. The species richness was lower in the short-wet-season woodlands, but was unaffected by variation in soil conditions. This suggests that climate driven constraints (wet season length) set the limits to species richness, and not soil conditions. As far as we know, this study is one of the first studies that evaluated these productivity and diversity hypotheses for dry African woodlands.

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1. Introduction

Dry tropical forests or woodlands once covered over 40% of the global tropical forest areas (Mayaux et al., 2005) and 14% of the total African surface. These forests however decline rapidly in area by the expansion of agriculture and pasture lands (Gerhardt, 1993; Janzen, 1988; Miles et al., 2006). About 97% of the remaining dry tropical forests are at the risk of being further fragmented and degraded by fire, fuel wood collection (Lerdau et al., 1991; Miles et al., 2006; Mittermeier et al., 1999) and grazing damage (Yates et al., 2000). Tropical dry forest, defined as frost-free regions with 500–2000 mm annual precipitation and a dry season of four to seven months (Bullock et al., 1995; Walter, 1971), differs significantly from wet tropical forests in structure, diversity, species composition, leafing phenology, and other functional aspects (Bullock et al., 1995). While less rich in species than wet forests, tropical dry forest provides habitats for a large number of tree species (Hegner, 1979; Murphy and Lugo, 1986; Wassie et al., 2010; White, 1983), often

used by local communities for a multitude of products and services. In the present study, we investigate how dry tropical woodlands in Ethiopia vary in the production by woody plants and in woody plant richness and diversity.

The production in tropical dry forest is expected to be greater with a more extensive rainy season and more fertile and deeper soils where texture improves water availability. It is less obvious how species richness will vary along such environmental gradients. The classical theories that have been developed for explaining broad diversity patterns suggest that diversity peaks at intermediate levels of disturbance (Bongers et al., 2009; Connell, 1978) and abiotic stress (Huston, 1979; Michalet et al., 2006). For example, species diversity might be highest at intermediate productivity levels when only few species are able to survive at high stress levels, few rapidly growing competitors dominate at low stress levels, and both groups of species survive at intermediate stress levels. It is however not yet clear how this hypothesis holds for dry tropical woodlands, which have been poorly studied in this respect (but see Bongers et al., 2009). For tropical dry woodlands the long dry season obviously creates stressful conditions, while water shortage generally is inferior in wet tropical forests. Moreover, dry forests are more often disturbed by grazing and fires (Miles et al., 2006; Yates et al., 2000), which remove biomass frequently and hinder the dominance by few competitive species (cf. Grace and Jutila, 1999; Huston, 1979). For the tropical dry woodlands studied here,

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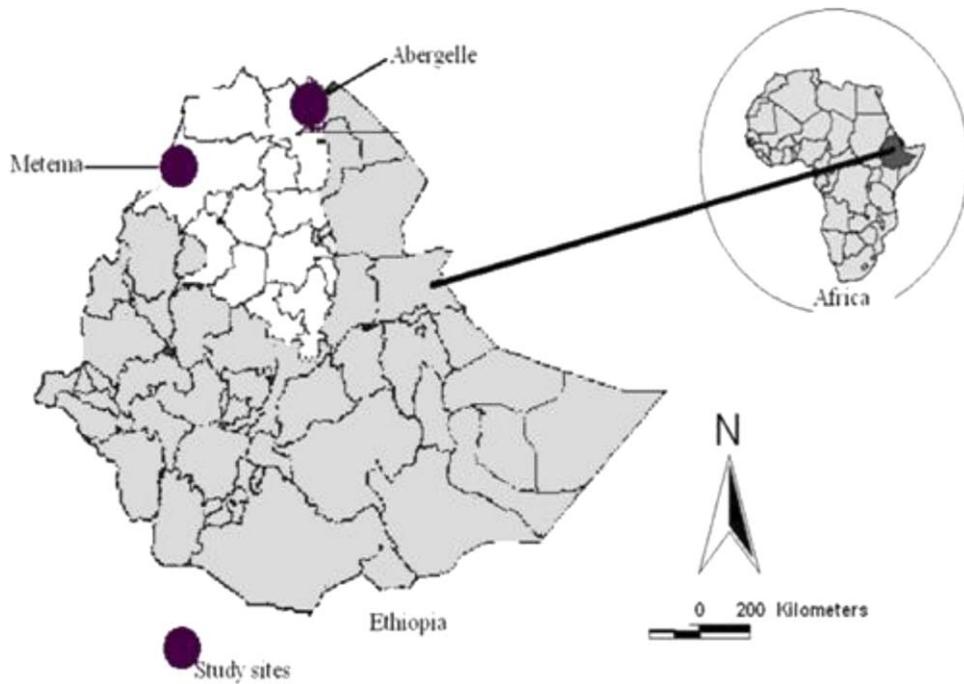


Fig. 1. The locations of the two study sites in Ethiopia: Metema in the Amhara Region and Abergelle in the Tigray Region.

we thus predict a higher species richness with lower abiotic stress, as provided by climatic or soil conditions.

In the present paper, we test these predictions for dry woodlands in northern Ethiopia, co-dominated by the Frankincense tree, *Boswellia papyrifera* (Del.) Hochst. We predicted that productivity (using tree size and stand volume as proxies) and species richness increase with wet season length and for deeper soils with a texture and composition that better supplies nutrients and water to plants. We explore predictions with a correlative field study of dry tropical woodlands in two contrasting areas in Ethiopia, and associated soil and vegetation properties across 18 dry woodland stands. The studied woodlands include the climatic extremes of the “Combretum–Terminalia woodlands”, co-dominated by *B. papyrifera*, in the Horn of Africa.

2. Materials and methods

2.1. Study areas

This study focuses on dry woodlands that are known as the Combretum–Terminalia or Acacia–Commiphora woodland vegetation (Teketay, 2000). Such woodlands are often encountered in degraded sites with shallow soils, steep rocky slopes, lava flows or sandy river valleys (Fichtl and Admasu, 1994; Teketay, 2000). These woodlands are co-dominated by one or more tree species that produce gum or resin (Lemenih et al., 2003; Ogbazghi et al., 2006a). The selected sites of this study were co-dominated by the Frankincense producing tree, *B. papyrifera*. These woodlands have been classified under “undifferentiated woodlands in Ethiopia and Sudan Republic” by White (1983). In Ethiopia, about half of the country's land area is located in such dry areas and associated tropical dry forest (NCSS, 1993). Moreover, these woodlands extend in large areas in other parts of Africa, including Nigeria, Cameroon, Central African Republic, Chad, Uganda, Sudan and Eritrea (White, 1983). The forests consist of many species providing timber and non-timber products to local communities (FAO, 1995). Owing to high human pressure and migration programs, they are currently rapidly turned into permanent agricultural or pastoral lands and

thus losing their potential role for producing their traditional non timber forest products.

We established plots in the climate extremes for *B. papyrifera* dominated Combretum–Terminalia woodland types in northern Ethiopia (Fig. 1). The plots at Metema (North Gondar Zone of Amhara Regional State) were situated at an altitudinal range of 600–1200 m.a.s.l., and plots at Abergelle (central Tigray) between 1400 and 1650 m.a.s.l. At Metema, the annual rainfall ranged from 870 to 1390 mm (between 1988 and 2007) with mean annual rainfall of 965 mm and the rainy season (>100 mm/month) lasts for 4 months from June till September (Fig. 2). Diurnal minimum and maximum temperature per month are 19.6 and 35.7 °C, respectively. At Abergelle, the annual rainfall ranged from 400 to 1059 mm for the period from 1980 to 2008 and mean annual rainfall was 800 mm. The rainy season (>100 mm/month) lasts for 3 wet months from June to August. The diurnal minimum and maximum temperature per month are 14.2 and 29.3 °C, respectively (Fig. 2). The Abergelle site is inhabited since long and woodlands are considered heavily disturbed (Gebrehiwot et al., 2003). The Metema site is inhabited only for a few decades and their woodlands are considered one of the least affected wooded vegetations in Ethiopia (Teketay, 2000), but this situation is rapidly changing (Lemenih et al., 2007).

2.2. Plot establishment and sampling

A total of eighteen plots were established in August, 2007: 12 plots at Metema and 6 plots at Abergelle. The distance between plots ranged from 2.5 km to 30 km within a study site. At Metema more plots were established because dry woodlands covered a larger area and greater heterogeneity in soil and tree physiognomy. Both at Abergelle and Metema, the Combretum–Terminalia woodlands are dominated by *B. papyrifera* and are fragmented within a landscape of other dry woodland types and, in some cases, surrounded by agricultural lands. While we aimed at the establishment of 2 ha plots, some fragments were too small for a full 2 ha plot (Appendix A). Taking a minimum distance of 2.5 km between plots, we consider different plots as independent, approx-

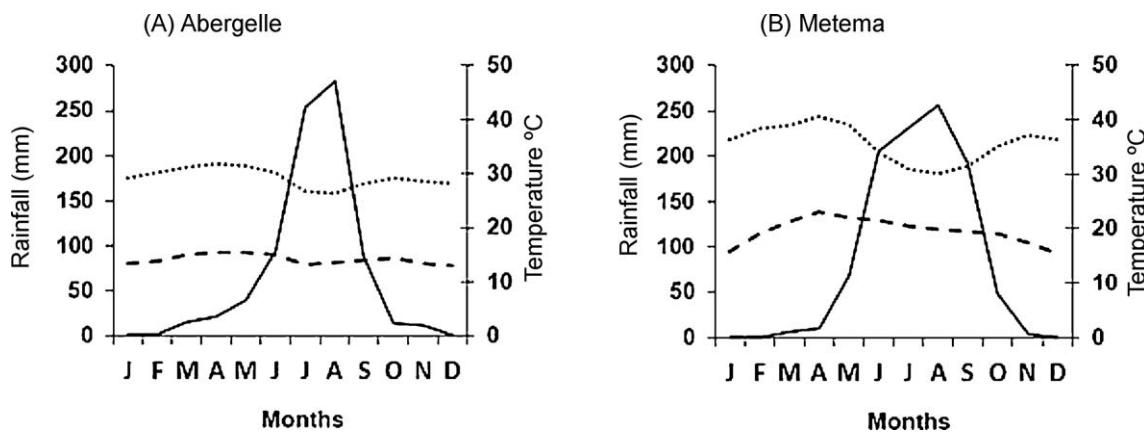


Fig. 2. Climate variation over the year for the two study sites Abergelle (A) and Metema (B) in Ethiopia. Monthly rainfall (mm month^{-1}) is indicated by the solid line, mean diurnal maximum temperature per month ($^{\circ}\text{C}$) by the dotted line, and mean diurnal minimum temperature per month by the dashed line. The climatic data of Metema was obtained at the Gendwuha meteorological station (~25 km away from the study plots) for the period from 1988 to 2007. The annual rainfall ranged from 870 to 1390 mm. Data for Abergelle was obtained at the Abi-adi station (~20 km away from the study plots) for the period from 1980 to 2007. The annual rainfall ranged from 400 to 1050 mm.

imate randomly selected replicates of the selected woodland types in both areas. However, since selected plots were at walking distance (<5 km) from existent roads and relatively easy to reach by people, we cannot exclude some bias to more disturbed conditions by, for example, grazing and fire or tapping regime. For Abergelle, such disturbances have a longer history (>50 years) than at Metema (<20 years), but at Metema the same disturbances are rapidly becoming more frequent and intense, owing to new settlements and new roads providing access to people. From that perspective, we expect that the historical effects of disturbance on Abergelle woodlands are nowadays acting in many areas of Metema woodlands, and certainly in the selected plots since they were accessible from the current road and walk track system.

Each permanent plot was divided into $20\text{ m} \times 20\text{ m}$ subplots where all $\geq 1.5\text{ m}$ tall trees and shrubs were systematically surveyed by identifying, measuring and coding them. For all stems, also for different stems of the few multiple-stemmed shrubs, we measured the stem diameter, using a diameter tape at breast height (1.3 m above the ground). Stem height (to the top of the crown) was measured using a telescopic pole up to 12 m, and with a Suunto clinometer for taller trees. Local names for tree and shrub species were recorded and individuals were identified to species level at the site according to The Flora of Ethiopia (Edwards et al., 1995, 1997, 2000; Hedberg and Edwards, 1989; Hedberg et al., 2003). Individuals that could not be identified in the field were collected and identified at the National Herbarium in Addis Ababa University. Altitude of all plots was also recorded.

To quantify the soil variables per plot, soil samples were collected in three randomly selected $20\text{ m} \times 20\text{ m}$ subplots as replicates per plot. In each of these subplots, three pits measuring $1\text{ m} \times 1\text{ m}$ were dug, one at the center and two at diagonal corners. From each pit, soil samples were collected from the top 20 cm, or from a shallower soil volume when the bed rock was encountered at a depth <20 cm, and mixed to form a soil composite. This composite soil sample was divided into three equal parts and randomly one was selected as a working sample for further analysis. A total of 54 working soil samples, i.e. 36 from Metema woodlands and 24 from Abergelle woodlands were collected. The soil samples were then transported to Water Works Design and Construction Enterprise (WWDCE) soil fertility lab, Addis Ababa, Ethiopia for soil physical and chemical analysis. The soil parameters determined were the percentage mass of sand, silt and clay (%), using a hydrometer. The soil pH was measured using a 1:2.5 soil to water suspension. Cation exchange capacity (CEC) was determined, as well as the amount of exchangeable calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^{+})

and sodium (Na^{+}) in meq/100 g of soil. For this purpose, the cations were extracted from 2.5 g of soil sample in 50 ml of a molar solution of ammonium acetate (Thomas, 1982). The amount of organic C (%) was measured using the Walkley–Black method. The available P (in meq/100 g of soil) was measured using the Olsen method, and the amount of N (%) using the Kjeldahl method. Holes were dug to measure the soil depth as the vertical distance between the surface soil and the solid rocky parent material.

2.3. Data analysis

Differences in textural and chemical soil conditions and tree and stand structure and productivity measures between Abergelle and Metema were tested using a *t*-test, using the plots as replicates. Prior to each *t*-test available P and total cations were transformed using natural logarithm to meet the assumption of normal distribution. The proxies used for tree productivity included the median and maximum height (the 95 percentile) and the median and maximum stem diameter (the 95 percentile). The proxies used for the stand structure and productivity included the tree density (number of stems per hectare), the total basal area per hectare ($\text{m}^2 \text{ ha}^{-1}$), and the stand stem volume per hectare, assuming a cone stem shape (sum of stem volumes, with each tree volume equal to the product of the stem basal area, tree height and a form factor of 1/3). In addition to the community analysis, we also compared all those traits for the *B. papyrifera* populations separately. Vegetation structures are presented for Metema and Abergelle woodlands as frequency diagrams for different diameter classes, both for the whole plant community and for *B. papyrifera* populations separately. The Kolmogorov–Smirnov test was used to determine whether the distributions differed between sites.

For all 18 plots the floristic composition, species richness and species diversity were determined. We calculated individual density per species (where multiple-stem individuals count for one), basal area, stand volume, frequency (number of $20\text{ m} \times 20\text{ m}$ subplots in which a species is present) and importance value index (IVI) of each species per plot. IVI of a species is defined as the sum of its relative abundance (number of individuals per hectare of a species divided by total number of individuals per hectare of all species), its relative dominance (total basal area for a species divided by total basal area for all species), and its relative frequency (frequency of a species divided by the sum of all frequencies of all species) (Kent and Coker, 1992).

To estimate the species richness and diversity of both sites, Rarefaction, Fisher's and Shannon' diversity indices and Shannon

Table 1Soil properties at 0–20 cm depth in dry woodlands at Metema ($N=12$) and Abergelle ($N=6$) in Northern Ethiopia.

Variable	Unit	Metema	Abergelle	t-value	P-value
<i>Physical</i>					
Sand	%	39.22 ± 3.91	40.27 ± 7.24	0.141	0.890
Silt	%	23.91 ± 0.90	29.72 ± 3.18	1.755	0.131
Clay	%	36.86 ± 4.42	30.0 ± 4.28	0.982	0.341
Soil depth	cm	27.73 ± 3.58	15.30 ± 2.97	2.250	0.039
<i>Chemicals</i>					
^a Ca ²⁺	meq/100 g soil	27.95 ± 1.90	31.90 ± 2.46	1.236	0.234
^a Mg ²⁺	meq/100 g soil	17.85 ± 1.23	8.17 ± 0.68	5.310	<0.001
^a Na ⁺	meq/100 g soil	0.26 ± 0.02	0.19 ± 0.01	5.672	0.002
^a K ⁺	meq/100 g soil	0.43 ± 0.11	0.29 ± 0.03	0.745	0.467
Total cations	meq/100 g soil	46.54 ± 2.31	40.58 ± 2.82	1.669	0.115
^b CEC	meq/100 g soil	48.27 ± 2.18	39.26 ± 2.86	2.440	0.027
C	%	2.58 ± 0.35	2.58 ± 0.32	0.008	0.994
N	%	0.19 ± 0.02	0.29 ± 0.04	2.241	0.040
P	mg/kg soil	13.86 ± 4.59	5.29 ± 0.85	1.303	0.211
pH		6.59 ± 0.09	8.28 ± 0.06	12.937	<0.001

^a Exchanges rates.^b Cation exchange capacity.**Table 2**Species diversity and structural characteristics of dry woodlands in Metema ($N=12$) and Abergelle ($N=6$) sites in Northern Ethiopia.

Stand traits	Units	Metema	Abergelle	t-value	P-value
<i>Diversity</i>					
Rarefaction		16.96 ± 0.48	10.84 ± 1.28	5.5	<0.001
Fisher's alpha		3.47 ± 0.16	1.93 ± 0.30	5.1	<0.001
Shannon		1.79 ± 0.07	1.26 ± 0.06	4.6	<0.001
Evenness		0.61 ± 0.02	0.52 ± 0.01	2.4	0.030
<i>Productivity</i>					
Community					
Median diameter	cm	15.86 ± 0.72	9.77 ± 1.55	4.1	0.001
Maximum diameter	cm	30.91 ± 1.3	24.86 ± 0.74	4.0	0.001
Median height	m	7.65 ± 0.37	3.26 ± 0.21	10.3	<0.001
Maximum height	m	11.96 ± 0.50	6.1 ± 0.13	11.5	<0.001
Abundance	ha ⁻¹	438.93 ± 28.08	628.7 ± 76.29	2.9	0.011
Basal area	m ² ha ⁻¹	12.19 ± 0.87	9.54 ± 1.2	1.8	0.095
Stand volume	m ³ ha ⁻¹	38.6 ± 3.79	15.38 ± 1.85	4.2	0.001
Boswellia populations					
Median diameter (cm)	cm	20.17 ± 1.14	18.56 ± 0.55	1.3	0.223
Maximum diameter (cm)	cm	31.33 ± 1.57	27.55 ± 0.9	2.1	0.054
Median height (m)	m	9.09 ± 0.4	4.94 ± 0.12	9.9	<0.001
Maximum height (m)	m	11.66 ± 0.47	6.47 ± 0.14	10.5	<0.001
Abundance		192.2 ± 20.48	281.29 ± 50.66	1.6	0.149
Basal area	m ² ha ⁻¹	7.02 ± 0.92	7.38 ± 1.65	0.2	0.839
Stand volume (m ³ h ⁻¹)	m ³ ha ⁻¹	22.60 ± 3.47	13.79 ± 1.91	1.7	0.107

evenness were calculated on a plot basis. Since species richness and diversity are plot size and abundance dependent (Magurran, 2004), we calculated species richness estimates and species diversity indices based on values from a random selection of twenty five 20 m × 20 m subplots, which is the lowest number of subplots encountered in any plot, using EstimateS software version 8.2 (Colwell, 2006). The difference in species richness and diversity between Metema and Abergelle woodlands was tested using a t-test. We also constructed randomized species accumulation curves against number of individuals for each of the 18 plots and species rank-abundance curves based on logarithmic (base 10) transformed number of individuals for the two woodlands.

We computed the principal components (PCs) of the soil variables, and tested for soil-species richness and soil-productivity associations for the first two components. Stand volume of the community and of the *B. papyrifera* population and species richness (dependent variables) were related to soil PCs (independent variables), using a linear regression. We also used linear regression to explore whether individual soil characteristics determined stand species richness and our proxies for stand productivity and *B. papyrifera* productivity, using the stand volume as the best proxy for this. PASW Statistics 17 statistical software was used for these analyses.

3. Results

3.1. Soils

The soils of the Metema woodlands differed from those at Abergelle in some but not all traits (Table 1). At Metema, woodlands occurred on deeper and more clayey soils than at Abergelle, but texture did not differ significantly. The cations Mg²⁺ and Na⁺ and the cation exchange capacity CEC were higher at Metema than at Abergelle, but N supply and soil pH were lower at Metema. P and K supply did not differ between sites. Thus, except for N, the soils at Metema are generally more fertile in terms of nutrients.

The first two PCs of the soil variables from all plots described 56% of the variance (results not shown). The first axis is a fertility and acidity axis which shows a gradient from basic and less fertile to almost neutral and more fertile soils. The second axis is a textural and organic carbon content axis. These two PCs, clay content and soil depth affected community tree volume and *B. papyrifera* volume (Table 3). When each soil variable was tested separately, altitude, CEC, nitrogen and soil pH did not affect the stand volume of the community or of *B. papyrifera* alone (Fig. 5 and Table 3). Site had an effect on the following soil variables: PC2, clay, soil depth and CEC for community tree volume, and only PC1 and PC2 for

Table 3

Testing for the effects of soil conditions on stand volume ($\text{m}^3 \text{ ha}^{-1}$) and *Boswellia* population volume ($\text{m}^3 \text{ ha}^{-1}$), while controlling for site (Abergelle and Metema) and site interaction effects. For unit of soil traits, see Table 1. Interactions are not shown since they were not significant. PCA-1 and PCA-2 are the major multivariate factors that result from a principal component analysis of all soil factors. Results are based on linear relation in relation to listed soil variables; test and significance (ns: $P \geq 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Variable	Intercept	Slope	Site	F	P	R^2
<i>Community</i>						
PCA-1	31.81	13.75**	ns	18.14	<0.001	0.67
PCA-2	14.81	ns	24.10***	12.78	<0.001	0.58
Clay	-0.81	0.54**	19.55***	21.13	<0.001	0.70
Soil depth	4.31	0.72**	14.26**	24.43	<0.001	0.73
CEC	-3.37	ns	18.95**	9.84	0.002	0.51
<i>Boswellia</i> ^a						
PCA-1	30.83	14.26**	-16.76*	10.07	0.002	0.52
PCA-2	13.18	5.56*	9.71*	5.31	0.018	0.34
Clay	-2.01	0.53**	ns	10.58	0.001	0.53
Soil depth	2.96	0.71***	ns	13.41	<0.001	0.59

^a Altitude, N and pH did not show significant trends for the whole community and *Boswellia* population, and CEC did not show a trend for *Boswellia*.

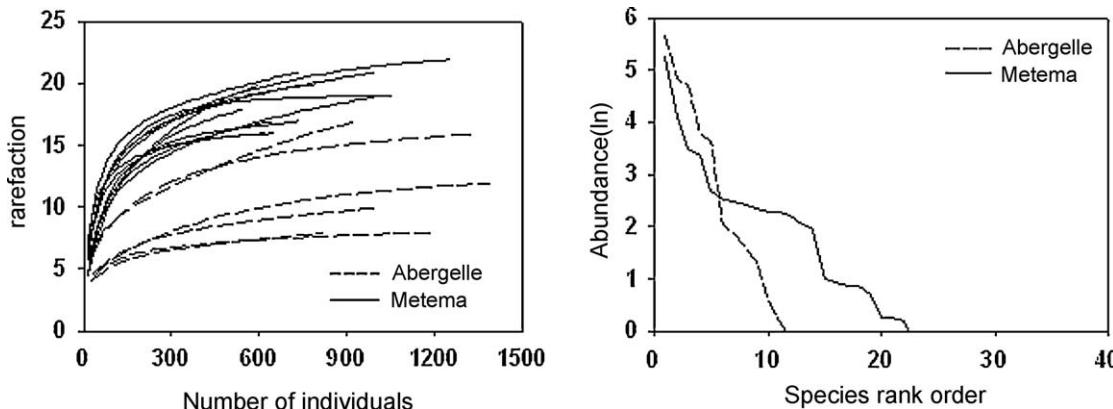


Fig. 3. Species richness and diversity patterns of dry woodlands at Abergelle and Metema in Northern Ethiopia. (A) Rarefied species-effort curves, with accumulating amount of individuals per plot on the x-axis and (B) species dominance rank curves showing the relative abundance of species versus rank order for both sites.

B. papyrifera volume (Table 3). In all cases Metema had the higher tree volumes when controlling for the independent variable (Fig. 5). None of the soil variables significantly affected species richness (data not shown).

3.2. Population structure

At the community level, trees and shrubs were taller and had greater stem diameters at Metema than at Abergelle (Table 2). The mean abundance of trees and shrubs in Abergelle (range: 364–858 ha^{-1}) was higher than in Metema (range: 329–646 ha^{-1} , t -test, $P=0.011$), but mean basal area (range: 5.8–12.4 $\text{m}^2 \text{ ha}^{-1}$ for Abergelle and 7.6–16.4 $\text{m}^2 \text{ ha}^{-1}$ for Metema) did not differ significantly ($P=0.095$). Because trees were taller in Metema (Table 2), stand volume was significantly higher at Metema (range: 21–57 $\text{m}^3 \text{ ha}^{-1}$) compared to Abergelle (range: 9–20 $\text{m}^3 \text{ ha}^{-1}$).

B. papyrifera populations did not significantly differ in abundance and basal area between Abergelle (ranges: 117–401 ha^{-1} and 5.8–12.4 $\text{m}^2 \text{ ha}^{-1}$, respectively) and Metema (ranges: 89–301 ha^{-1} and 7.6–16.4 $\text{m}^2 \text{ ha}^{-1}$, respectively, Table 2). Because trees at Metema were taller than at Abergelle (Table 2), the *Boswellia* stand volumes tended to be larger at Metema (range: 7–38 $\text{m}^3 \text{ ha}^{-1}$) than at Abergelle (range: 7–19 $\text{m}^3 \text{ ha}^{-1}$), but this was not significant.

The whole tree community showed a bi-modal distribution with relatively large numbers of individuals in the lowest and middle diameter size classes (Fig. 4). Abergelle had a large proportion of individuals in the lowest classes (DBH $\leq 5 \text{ cm}$); while in Metema the middle classes had the highest values. Abergelle had hardly any tree bigger than 33 cm while Metema showed higher numbers of such trees. In contrast to the bi-modal distribution of the community, the

diameter distribution of *B. papyrifera* showed a hump or uni-modal distribution in both woodlands without individuals in the lowest classes (Fig. 4). Larger *B. papyrifera* individuals were encountered at Metema than at Abergelle (Table 2). The frequency distributions of both the whole tree community and *B. papyrifera* populations were statistically different between the two sites, both for shape ($P < 0.001$) and location of the DBH size distribution ($P < 0.001$).

3.3. Species composition, richness and diversity

A total of 36 and 22 tree and shrub species representing 20 and 9 families were recorded in Metema and Abergelle woodlands, respectively. The most dominant plant families included the Bursaraceae, Fabaceae, Combretaceae and Anacardiaceae (Appendix B). Vegetation at both sites were dominated by *B. papyrifera* and, in some cases, co-dominated by *L. fruticosa*, *Combretum collinum*, *Pterocarpus lucens* or *Lonchocarpus laxiflorus* (Appendix B). The species that occurred at both sites were *B. papyrifera*, *L. fruticosa*, *Stereospermum kunthianum* and *Dichrostachys cinerea*. The total number of observed species and also the estimated species richness was significantly higher for Metema than Abergelle (Table 2). At Metema, woodlands were also more diverse and species were more evenly distributed than at Abergelle (Table 2 and Fig. 3).

4. Discussion

4.1. Species composition and structure

In the present study we found that the species composition differed between the high altitude site Abergelle and the lower alti-

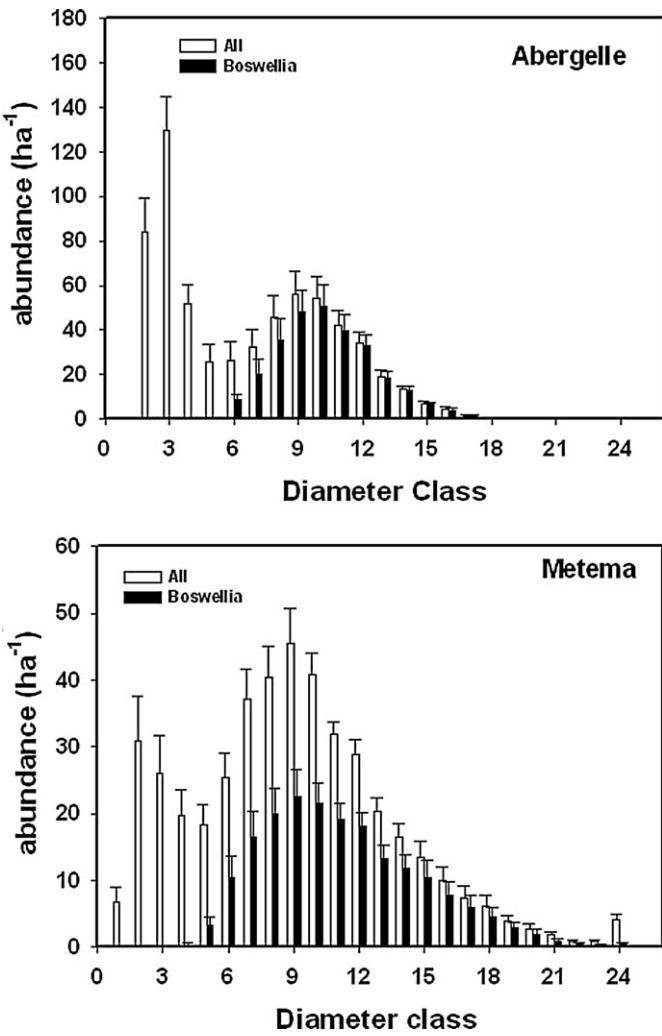


Fig. 4. Size frequency distributions of dry woodlands at Abergelle ($N=6$) and Metema ($N=12$) in Northern Ethiopia. Results are shown for the whole tree community (white bars) and the populations of the most dominant species, *Boswellia papyrifera* (black bars). Abundance is the number of individuals per size class per hectare. Errors indicate ± 2 standard errors. DBH class 1 = 0–<1, 2 = 1–<3, 3 = 3–<5, 4 = 5–<7, ..., 23 = 41–<43 and 24 = 43 cm. Errors bars indicate ± 1 standard errors.

tude site Metema. This difference in species composition might be associated with differences in precipitation and other climate conditions and soil characteristics between the two sites (Clark et al., 1998; John et al., 2007). Awas (2007) had also found similar results where soil variables significantly affect the species composition in lowland woodlands of western Ethiopia. Our woodlands were dominated by *B. papyrifera*, as were large areas in Ethiopia and Eritrea (Abiyu et al., 2010; Gebrehiwot, 2003; Ogbazghi et al., 2006b) and Sudan (Chikamai, 2002). This dominant species largely differed in population structure from the rest of the community. While the general community showed juvenile trees, this was not the case for the *B. papyrifera*. A lack of juvenile trees was also observed for *B. papyrifera* elsewhere in Ethiopia and Eritrea (Abiyu et al., 2010), and for other dry forest species, both in Ethiopia (Gebrehiwot, 2003; Sterck et al., 2010; Tesfaye et al., 2010) as elsewhere (Metcalfe et al., 2007). Population structures that lack juveniles are also found in other forest areas, notably in Ethiopian Afromontane systems, including Ethiopian church forest areas—small woodland remnants around churches and protected by church owners (Wassie et al., 2010). The lack of regeneration in our case and those other cases is driven by land use changes, and increasing grazing intensity, fire frequency and clearing for agricultural purpose in particular

(Belsky and Blumenthal, 1997; Fischer et al., 2009; Sagar et al., 2003; Shorrocks, 2007; Staver et al., 2009; Tesfaye et al., 2004; Wassie et al., 2010). Our results suggest that the currently very dominant *B. papyrifera* will gradually be replaced by other species. Such changes in species composition have also been observed elsewhere, particular in relation to uncontrolled grazing (Yates et al., 2000).

4.2. Productivity

We predicted larger trees and higher stand volumes as proxies for stand productivity at lower abiotic stress levels. We indeed found that the wetter – lower altitude site – had larger tree and larger stand volumes than the drier – higher altitude – site, suggesting that wet season length and annual rainfall limit tree and stand productivity. At Metema, a longer wet season allows for longer leaf life spans and, in turn, for a greater potential for resource acquisition over a year. Probably, trees were therefore taller and had greater stem diameters and stand volumes were larger at Metema. Across all 18 plots, tree sizes and stand volumes increased with soil depth and soil clay content, but no trend was observed with nutrient supply. Since water stress becomes less with increasing soil depth as well as with increasing clay content, we expected that soil water stress drove the major variation in tree size and stand volume within the studied woodlands systems. This trend was observed for both whole tree communities and for *B. papyrifera* populations separately.

For *B. papyrifera*, we did not observe any difference in tree size or stand volume between the drier and wetter area at a given clay or soil depth content. In other words, annual rainfall and wet season length do apparently not explain the observed variation between those sites. From this observation, we suggest that production differences of *B. papyrifera* populations between the two studied geographic regions are driven by differences in texture (clay content) and soil depth, which drive soil water availability. In contrast, the productivity of the other species is much lower (Fig. 5) in the drier – high altitude – site at a given soil depth and clay content. Thus, the overall community productivity seems suppressed by low annual rainfall or a shorter wet season length.

4.3. Species richness

For the studied dry Ethiopian woodlands, we expected higher species richness with decreasing water stress (cf. Gentry, 1982, 1988; Hawkins et al., 2007; Holdridge et al., 1971). Despite considerable variation in soil properties, significant relationships between species richness and soil properties were not encountered. In line with our prediction, we did observe a higher species richness, diversity and evenness at the site that was characterized by a longer wet season (Metema). We cannot exclude other potential factors influencing species richness, such as for example altitude differing between the wetter (800 m) and drier site (1600 m). The decline in species richness is thus also associated with increasing altitude, as was observed for church forests in the same region (Wassie et al., 2010). These church forests however varied in altitude over a larger range (1800–3300 m) and, remarkably, consisted of far more species, possibly owing to the forest policy of the church owners (Bongers et al., 2006; Wassie et al., 2010). Qualitatively, our results and those of Wassie et al. (2010) confirm those on other tropical forests showing that species richness and diversity generally decrease with altitude (Aiba and Kitayama, 1999; Hemp, 2006; Lieberman et al., 1996; Stevens, 1992; Vázquez and Givnish, 1998). For our expectation that species richness decreases with higher soil water stress (explained in terms of soil clay content and soil depth), we thus found no proof either. The tree size and stand volume analysis showed however that soil depth and clay content largely

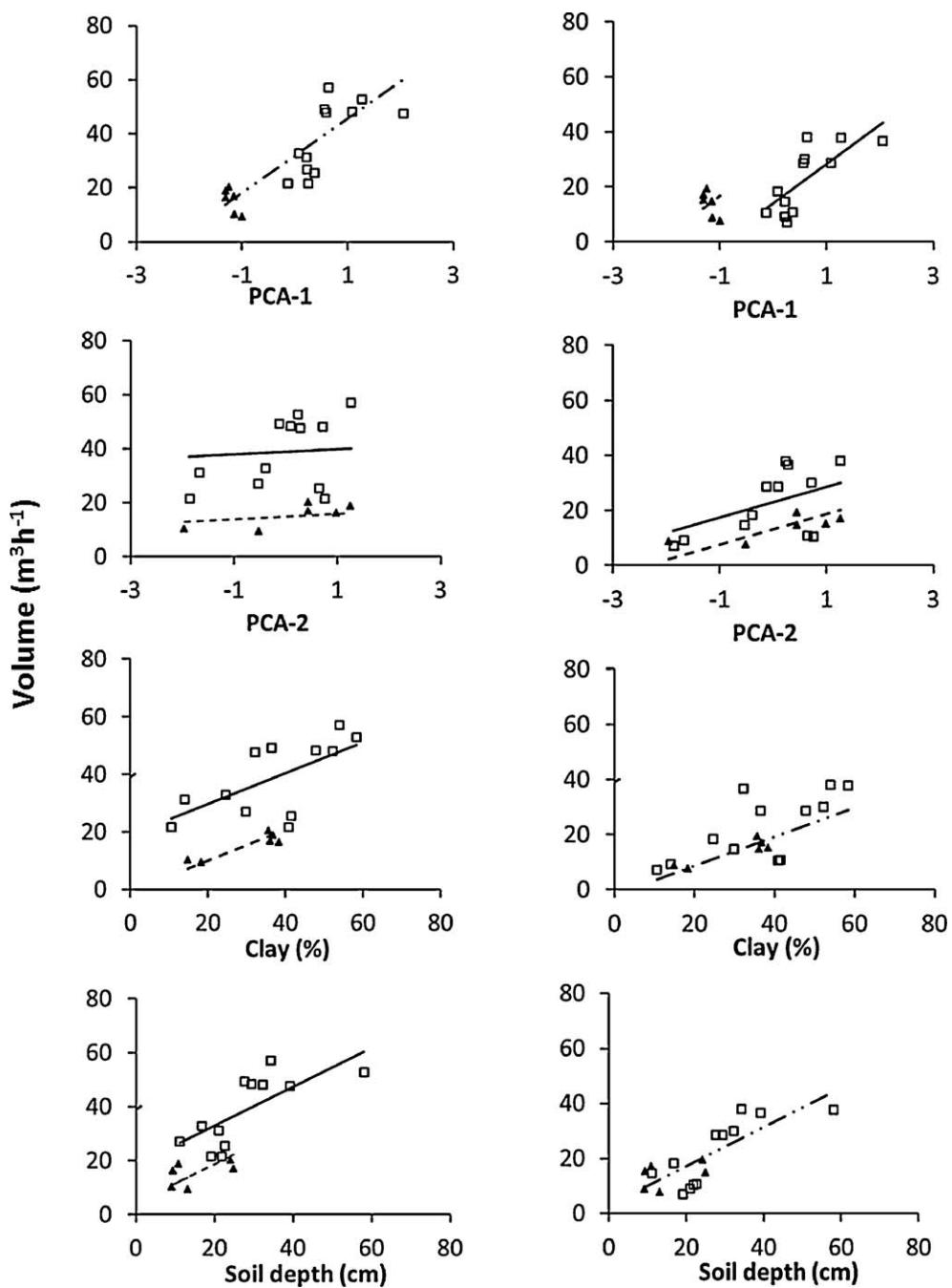


Fig. 5. Significant trends between stand volume and soil properties for the community (left side) and the *Boswellia papyrifera* populations (right side). Solid lines show a fitted line for Metema plots; dashed lines are fitted lines for plots in Abergelle, and dashed-dotted lines for both areas (no site effect). For statistics, see Table 3.

contributed to the productivity of sites. Knowing that these factors reduce water stress and possibly nutrient stress (Fernandez-Illescas et al., 2001; Knoop & Walker, 1985), we conclude that soil water stress did not contribute to variation in species richness in our study sites.

Both the study sites are exposed to anthropogenic disturbances, such as burning, grazing, and wood collection, which may also affect plant species richness and productivity of forests (Sabogal, 1992; Swaine, 1992; Maass, 1995). These effects would depend on the type and severity of the disturbance and the response of plant species to disturbances. Plant species richness is often hypothesized to be higher at intermediate disturbance level (Connell, 1978; Huston, 1979; Bongers et al., 2009). The argument is that species richness should be maximized under intermediate levels of dis-

turbance because at low levels of disturbance superior competitor species monopolize resources and exclude other species, whereas at high disturbance levels only the most resistant species survive. The longer occupation of Abergelle site could actually result in a high disturbance in the dry forests compared to the recently inhabited Metema forests. Thus, in addition to the wet season length and soil variables, the longer and more intense disturbance history at Abergelle might also contribute to the observed variation in species richness and productivity between the two studied sites.

5. Conclusions

We found that the stand volume was lower if annual rainfall was lower and the wet season was shorter, and decreased with

stronger soil water stress (estimated from texture and depth). This was in line with the prediction. The species richness was lower in the short-wet-season woodlands, but was unaffected by variation in soil conditions. This suggests that climate driven constraints such as wet-season length or factors related to altitude set the major limits to species richness, while soil conditions do not. Dry woodlands like the ones we studied are threatened by increasing pressure by local communities and, with them, increasing disturbances by grazing, fire and exploitation (e.g. Abiyu et al., 2010; Eshete et al., 2005; Miles et al., 2006). The increasing disturbance levels will probably negatively affect the species richness and productivity of these woodlands. In response to disturbance, changes are expected in species composition, such as the decline in the currently dominant *B. papyrifera* populations. Our results suggest that this latter species is particularly well adapted, or acclimated, to climate stressed conditions and that the loss of this species might result in a serious decline of the productivity at the most climate stressed sites.

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Appendix A.

Plot information. The number of families and observed species, the abundance is given as the density (number of >1.5 m tall individuals ha^{-1}) and basal area of the plots studied in the *Boswellia papyrifera* dominated woodlands in northern Ethiopia.

Site	Plot no.	Altitude (m)	Plot size (ha)	No. family	Observed no. species	Abundance No. ha^{-1}	Basal area ($\text{m}^2 \text{ha}^{-1}$)
Metema	1	793	2	10	19	540	14.6
	2	883	1.6	12	20	381.9	9.5
	3	880	2	13	21	329	8.0
	4	852	2	11	19	509	16.24
	5	851	2	10	20	407	14.2
	6	875	2	9	17	507.5	11.9
	7	593	2	10	16	332	7.6
	8	597	2	13	21	423	9.6
	9	782	1.8	8	16	354.4	13.7
	10	881	2	13	22	646	11.0
	11	823	1.8	11	18	366.7	14.6
	12	825	1.6	9	17	470.6	15.4
Abergelle	1	1636	1.8	5	8	682.8	10.6
	2	1635	1.8	6	12	789.4	11.9
	3	1660	1.6	7	16	858.8	12.4
	4	1656	1.6	9	17	596.3	10.7
	5	1580	1	7	10	481	5.8
	6	1575	1	5	8	364	5.9

A.1. Appendix B.1.

Scientific names of species, family names, abundance (number of individuals per hectare), basal area, frequency, and IVI (important value index) of species found in the plots in the Metema site.

No.	Scientific names	Family name	Abundance	Basal area/ha	Frequency	IVI
1	<i>Acacia polyacantha</i> Willd. subsp. (unidentified)	Fabaceae	1.3 ± 0.6	0.05 ± 0.02	2.0 ± 0.8	1.7 ± 0.6
2	<i>Acacia polyacantha</i> Willd. subsp. <i>campylacantha</i> (Hochst. ex A.Rich.) Brenan	Fabaceae	0.7 ± 0.4	0.02 ± 0.02	0.9 ± 0.5	0.8 ± 0.5
3	<i>Acacia seyal</i> (Del.) Var. <i>Seyal</i>	Fabaceae	2.0 ± 1.1	0.005 ± 0.002	2.6 ± 1.2	1.7 ± 0.8
4	<i>Acacia seyal</i> Del. var. <i>fistula</i>	Fabaceae	0.1 ± 0.1	0.002 ± 0.001	0.3 ± 0.3	0.2 ± 0.2
5	<i>Accaia spp3.</i>	Fabaceae	0.5 ± 0.4	0.001 ± 0.001	0.4 ± 0.3	0.4 ± 0.3
6	<i>Albizia malacophylla</i> (A.Rich.) Walp.	Fabaceae	0.1 ± 0.1	0.004 ± 0.003	0.2 ± 0.1	0.2 ± 0.1
7	<i>Anogeissus leiocarpa</i> (DC.) Guill. & Perr.	Combretaceae	9.9 ± 5.7	0.32 ± 0.2	5.9 ± 2.7	8.3 ± 4.4
8	<i>Balanites aegyptiaca</i> Del.	Balanitaceae	0.1 ± 0.1	0.001 ± 0.001	0.2 ± 0.2	0.1 ± 0.1
9	<i>Boswellia papyrifera</i> (Del.) Hochst.	Burseraceae	192.2 ± 20.5	7.0 ± 0.9	43.6 ± 1.7	92.9 ± 15.8
10	<i>Boswellia pirottiae</i> Chiov.	Burseraceae	0.4 ± 0.3	0.01 ± 0.01	0.6 ± 0.4	0.6 ± 0.4
11	<i>Chimlikie/Dimeto</i>	Unidentified	0.8 ± 0.3	0.02 ± 0.01	1.5 ± 0.5	1.2 ± 0.4
12	<i>Combretum aculeatum</i> Vent.	Combretaceae	1.3 ± 0.4	0.02 ± 0.01	2.0 ± 0.7	1.4 ± 0.5
13	<i>Combretum adenogonium</i> Steud. ex A.Rich.	Combretaceae	7.7 ± 2.2	0.08 ± 0.02	8.6 ± 1.9	6.2 ± 1.4
14	<i>Combretum collinum</i> Fres.	Combretaceae	32. ± 12.9	0.2 ± 0.1	15.0 ± 3.8	14.1 ± 4.2
15	<i>Combretum molle</i> R.Br. ex G.Don	Combretaceae	9.8 ± 4.2	0.1 ± 0.04	9.6 ± 3.1	7.5 ± 2.4
16	<i>Cordia africana</i> Lam.	Boraginaceae	0.1 ± 0.1	0.001 ± 0.001	0.1 ± 0.1	0.1 ± 0.1
17	<i>Dalbergia melanoxylon</i> Guill. & Perr.	Leguminosae	6.9 ± 4.1	0.03 ± 0.01	3.8 ± 1.9	2.0 ± 1.0
18	<i>Dichrostachys cinerea</i> (L.) Wight & Arn	Fabaceae	10.6 ± 3.8	0.03 ± 0.01	4.4 ± 1.2	3.7 ± 1.1
19	<i>Diospyros mespiliformis</i> Hochst. ex A.DC.	Ebenaceae	0.2 ± 0.2	0.001 ± 0.001	0.1 ± 0.1	0.1 ± 0.1
20	<i>Ficus glomosa</i> Del.	Moraceae	0.4 ± 0.4	0.01 ± 0.01	0.3 ± 0.3	0.3 ± 0.3
21	<i>Flueggea virosa</i> (Roxb. ex Willd.) Voigt	Euphorbiaceae	12.4 ± 8.4	0.01 ± 0.01	3.2 ± 2.4	3.4 ± 2.3
22	<i>Gardenia ternifolia</i> Schumach. & Thonn.	Rubiaceae	0.3 ± 0.2	0.001 ± 0.001	0.3 ± 0.1	0.2 ± 0.1
23	<i>Grewia bicolor</i> Juss.	Tiliaceae	0.1 ± 0.1	0.001 ± 0.001	0.2 ± 0.1	0.1 ± 0.1
24	<i>Lannea fruticosa</i> (A.Rich.) Engl.	Anacardiaceae	60.1 ± 5.5	1.3 ± 0.2	39.3 ± 1.8	35.3 ± 4.7
25	<i>Lonchocarpus laxiflorus</i> Guill. & Perr.	Fabaceae	14.6 ± 3.1	0.3 ± 0.04	16.3 ± 2.0	13.3 ± 2.3
26	<i>Maytenus senegalensis</i> (Lam.) Exell	Celastraceae	2.5 ± 1.6	0.01 ± 0.01	1.9 ± 1.2	1.3 ± 0.8
27	<i>Mebrat Zaf</i>	Unidentified	0.1 ± 0.1	0.003 ± 0.002	0.2 ± 0.1	0.1 ± 0.1
28	<i>Ochna leucophloeos</i> Hochst. ex A.Rich.	Ochnaceae	0.8 ± 0.4	0.01 ± 0.01	1.4 ± 0.6	1.1 ± 0.6
29	<i>Pterocarpus lucens</i> Guill & Perr.	Fabaceae	28.8 ± 12.3	1.0 ± 0.	19.5 ± 3.4	18.9 ± 5.2
30	<i>Sterculia setigera</i> Del.	Sterculiaceae	9.1 ± 2.0	1.2 ± 0.2	11.5 ± 2.3	12.8 ± 3.3
31	<i>Stereospermum kunthianum</i> (Cham, Sandrine. Petit)	Bignoniaceae	2.8 ± 0.7	0.05 ± 0.01	4.4 ± 0.9	2.8 ± 0.6
32	<i>Strychnos innocua</i> Del.	Loganiaceae	2.4 ± 0.8	0.1 ± 0.02	2.4 ± 0.7	2.21 ± 0.8
33	<i>Terminalia laxiflora</i> Engl. Ex Diels	Combretaceae	2.4 ± 0.8	0.2 ± 0.05	3.5 ± 1.1	3.8 ± 1.3
34	<i>Ximenia americana</i> L.	Olaceae	11.3 ± 5.1	0.04 ± 0.01	4.8 ± 1.	4.7 ± 1.6
35	<i>Ziziphus abyssinica</i> Hochst. ex A.Rich.	Rhamnaceae	12.0 ± 3.8	0.05 ± 0.02	8.1 ± 2.2	6.2 ± 1.8
36	<i>Ziziphus spina-christi</i> (L.) Willd.	Rhamnaceae	1.2 ± 1.0	0.002 ± 0.002	1.1 ± 0.9	2.1 ± 1.5

A.2. Appendix B.2.

Scientific names of species, family names, abundance (number of individuals per hectare), basal area, frequency, and IVI (important value index) of species found in the plots at the Abergelle site.

No.	Scientific names	Family name	Abundance	Basal area	Frequency	IVI
1	<i>Acacia abyssinica</i> Hochst. ex Benth	Fabaceae	3.8 ± 1.4	0.2 ± 0.1	3.7 ± 1.4	4.1 ± 1.7
2	<i>Acacia etaica</i> Schweinf.	Fabaceae	125.3 ± 47.5	0.7 ± 0.3	22.8 ± 7.3	37.2 ± 12.9
3	<i>Acacia mellifera</i> (Vahl) Benth.	Fabaceae	0.4 ± 0.3	<0.01	0.5 ± 0.3	0.4 ± 0.2
4	<i>Acacia oerfota</i> (Forsskal) Schweinf	Fabaceae	37.1 ± 13.6	0.3 ± 0.1	15.3 ± 3.3	21.7 ± 5.9
5	<i>Acacia spp1.</i>	Fabaceae	0.2 ± 0.1	<0.01	0.3 ± 0.2	0.2 ± 0.1
6	<i>Acacia spp2.</i>	Fabaceae	7.7 ± 7.4	0.01 ± 0.01	1.7 ± 1.3	2.0 ± 1.7
7	<i>Boswellia papyrifera</i> (Del.) Hochst.	Burseraceae	281.3 ± 50.7	8.1 ± 1.2	33.3 ± 3.9	150.3 ± 7.7
8	<i>Capparis decidua</i> (Forssk.) Edgew.	Capparidaceae	0.9 ± 0.8	<0.01	0.3 ± 0.2	0.5 ± 0.4
9	<i>Combretum hartmannianum</i> Schweinf.	Combretaceae	1.20 ± 0.7	0.02 ± 0.01	1.5 ± 0.8	1.2 ± 0.6
10	<i>Combretum spp</i>	Combretaceae	0.1 ± 0.1	<0.01	0.2 ± 0.2	0.1 ± 0.1
11	<i>Commiphora africana</i> (A.Rich.) Engl.	Burseraceae	0.3 ± 0.2	<0.01	0.5 ± 0.3	0.4 ± 0.2
12	<i>Dichrostachys cinerea</i> (L.) Wight & Arn	Fabaceae	1.9 ± 1.2	<0.01	1.7 ± 1.2	1.3 ± 0.9
13	<i>Grewia erythraea</i> Schweinf.	Tiliaceae	0.2 ± 0.2	<0.01	0.2 ± 0.2	0.2 ± 0.2
14	<i>Grewia villosa</i> Willd.	Tiliaceae	0.1 ± 0.1	<0.01	0.2 ± 0.2	0.1 ± 0.1
15	<i>Ipomoea spp.</i>	Convolvulaceae	45.4 ± 10.1	0.03 ± 0.01	21.3 ± 1.9	24.8 ± 5.0
16	<i>Lannea fruticosa</i> (A.Rich.) Engl.	Anacardiaceae	5.1 ± 2.5	0.1 ± 0.04	5.2 ± 2.4	4.9 ± 2.2
17	<i>Lannea triphylla</i> (A.Rich.) Engl.	Anacardiaceae	0.1 ± 0.1	<0.01	0.2 ± 0.2	0.1 ± 0.1
18	<i>Maerua angolensis</i> DC.	Capparidaceae	0.8 ± 0.6	<0.01	1.00 ± 0.7	0.7 ± 0.5
19	<i>Salvadora persica</i> L.	Salvadoraceae	0.1 ± 0.1	<0.01	0.2 ± 0.2	0.1 ± 0.1
20	<i>Senna singueana</i> (Del.) Lock.	Fabaceae	109.4 ± 29.1	0.2 ± 0.1	24.7 ± 3.3	41.6 ± 10.5
21	<i>Stereospermum kunthianum</i> (Cham, Sandrine. Petit)	Bignoniaceae	0.9 ± 0.5	0.01 ± 0.01	1.3 ± 0.8	1.0 ± 0.6
22	<i>Terminalia brownii</i> Fresen	Combretaceae	6.6 ± 2.0	0.1 ± 0.04	6.0 ± 1.8	7.1 ± 2.1

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