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Full Length Research Paper

Woody species diversity, structure and biomass carbon of parkland agroforestry practices in Gindeberet District, West Shoa Zone, Oromia Regional State, Ethiopia

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Parkland agroforestry woody species are prominent features in many landscapes worldwide, and their ecological, social and economic importance is widely acknowledged. It is the traditional agroforestry systems from different countries and is almost a universal occurrence in Ethiopia. This study was conducted in Gindeberet District, West Shoa Zone, Oromia Regional State, Ethiopia to assess the parkland agroforestry woody species composition, diversity, structure and biomass carbon. Woody species inventory was carried out on 103 plots (each, 50 m x10 0m) in the crop field laid along 7 transects. For woody species ≥ 5 cm DBH, measurements of DBH and tree height were taken. A total of 61 woody species belonging to 35 families were recorded. The study indicated that the woody species Shannon and Simpson diversity indices were higher at lowland than midland agro-ecology. The species richness was significantly different between the two agro-ecological zones ($X^2 = 8.5$, $p = 0.003$). This study showed low carbon storage potential in living biomass of woody species; it is recommended to develop a policy on the woody species management, conservation and regeneration to increase the carbon storage potential in living biomass of woody species.

Key words: Parkland agroforestry, woody species, latitude, diversity index, biomass carbon.

INTRODUCTION

Many useful indigenous plant species are kept within the crop fields and form a prominent component of the farmland. This land use system, commonly known as the agroforestry parkland systems, has been successively described as farmed parkland by Pullan (1974) then,

subsequently, as one of the many agroforestry systems observed all over the world (Nair, 1985). It is characterized by well-grown scattered trees on cultivated and recently fallowed land. These parklands develop when crop cultivation on a piece of land becomes more

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permanent (Verheij, 2003).

Parkland agroforestry woody species are prominent features in many landscapes worldwide, including natural, cultural and recently modified landscapes and their ecological, social and economic importance are widely acknowledged (Munzbergova and Ward, 2002; Plieninger et al., 2003; Manning et al., 2006). Woody plants integrated with the agricultural crops of smallholders characterize various forms of traditional agroforestry systems from different countries and is almost a universal occurrence in Ethiopia (Mohammed and Zemed, 2015). Woody plants of the farmed landscapes in Ethiopia have been part of the farmed commodities as they serve a wide range of economic, socio-cultural and ecological functions within the traditional farming systems (Kassa et al., 2011).

These agroforestry parkland systems have been described as good examples of traditional land use systems and biodiversity management practices (Boffa, 1999; Schreckenber, 1999; Lovett, 2000); regulation of nitrogen dynamics and carbon sequestration (Barton et al., 2016; Hartel et al., 2017). The carbon (C) sequestration potential of agroforestry systems has been shown to vary with species composition, age, geographical location of the system (Jose, 2009), previous land use (Mutuo et al., 2005, Sauer et al., 2007), climate, soil characteristics, crop-tree mixture, and management practices (Dossa et al., 2008; Schulp et al., 2008).

Most of the carbon in trees and shrubs is accumulated in aboveground biomass (AGB) and 50% of the total biomass is taken as carbon stock. Aboveground carbon stock is the amount of carbon that is assumed to be 50% of the total vegetation biomass made up by carbon (Nair et al., 2009; Kumar and Nair, 2011). The belowground biomass of vegetation is considered as a fraction that takes about 25-30% of aboveground biomass depending on the nature of a plant, its root system and ecological conditions (Nair et al., 2009; Kumar and Nair, 2011).

Moreover, understanding of the roles of trees on farms and diversification of the farm in terms of species richness, as well as evenness through increase in number of trees of rare species, or through replacement of more common species are the best options for preventing degradation of agroforest ecosystems on farms (Kindt and Coe, 2005).

Even if the woody plants of parkland agroforestry have many benefits, unfortunately in natural, cultural and recently modified landscapes, it is facing some threats in these environments as well as some threats that are unique to particular ecosystems. The most direct threats to all those plants are clearing by humans, that is most of them are human driven and anthropocentric in origin. For example, the legal and illegal removal of scattered trees is widespread in every landscape worldwide (Gibbons and Boak, 2002; Aguilar and Condit (2001)). Parkland

agroforestry degradation reduces both richness and abundance of useful trees and shrubs leaving the rural poor with fewer options to improve their health, nutrition and income. In addition, it reduces available habitat for other native plants and animals that figure importantly in local diets, medicines, etc.

However, to date there are no data in the literature about the study area which could help to provide the status of the woody species diversity of parkland agroforestry systems. Therefore, this study aims to assess the composition, diversity, structures and biomass carbons of woody species of parkland agroforestry in Gindeberet District, West Shoa Zone, Oromia Regional State, Ethiopia.

MATERIALS AND METHODS

Study area

The study was conducted in Gindeberet District, West Shoa Zone, Oromia Regional State, Ethiopia. Gindeberet District is located between 9° 21' to 9° 50' N Latitude and 37° 37' to 38° 08' E Longitude (Figure 1) and 193 km distance in the West of Addis Ababa, the capital city of Ethiopia (PEDOWS, 1997).

According to WQMBAG (2004), the total area of Gindeberet District is estimated to be about 119,879 km² and it is divided into 31 kebeles. Land is exclusively used for agriculture. The Oromo people of the study area categorize their surroundings by local language, Afan Oromo into different land-use/land-cover systems: home-garden (oddoo), crop field (lafa qonnaa/oyiruu), grazing land (lafa kaloo), forestland (bosona), fallow land (laf-bayii) and shrub lands (miciree). Out of the total area of Gindeberet district, 50,494 km² (42.1%) is used for agricultural purposes, 39,791 km² (33.1%) is used for grassland, 4,248 km² (3.5%) is covered by forest, 10,389 km² (8.7%) is covered by shrubs and water bodies like river, wetland and 6,972 km² (5.8%) is not used for any development purposes, 2,670 km² (2.2%) religious organizations and 5,315 km² (4.4%) residential areas (WQMBAG, 2013).

Two agro-ecological zones can be found in Gindeberet, with 43 and 57% of the land area classified as midland (Weinadega) and lowland (Kola), respectively. The mean monthly minimum and maximum temperature and rainfall for the agro-ecological zones of the study area are shown along with altitudinal variations in Table 1. The variability of the rainfall regime of the study areas affects cultivation, planting and harvesting activities.

Sampling size and sampling techniques

Selection of the study sites

The study district was stratified into two agro-ecological zones: namely Weinadega (midland) and Kola (lowland) based on their altitudinal range. To select representative study sites within each agro-ecological zone, administrative units were used. The smallest administrative unit in the district is locally called ganda or kebele, which means Peasant Associations (PAs). Five PAs were selected purposively from both of the agro-ecology, three from lowland and two from midland based on the woody vegetation coverage. Farmlands (crop fields) were considered to lay down the plots in the parkland agroforestry in each kebele.

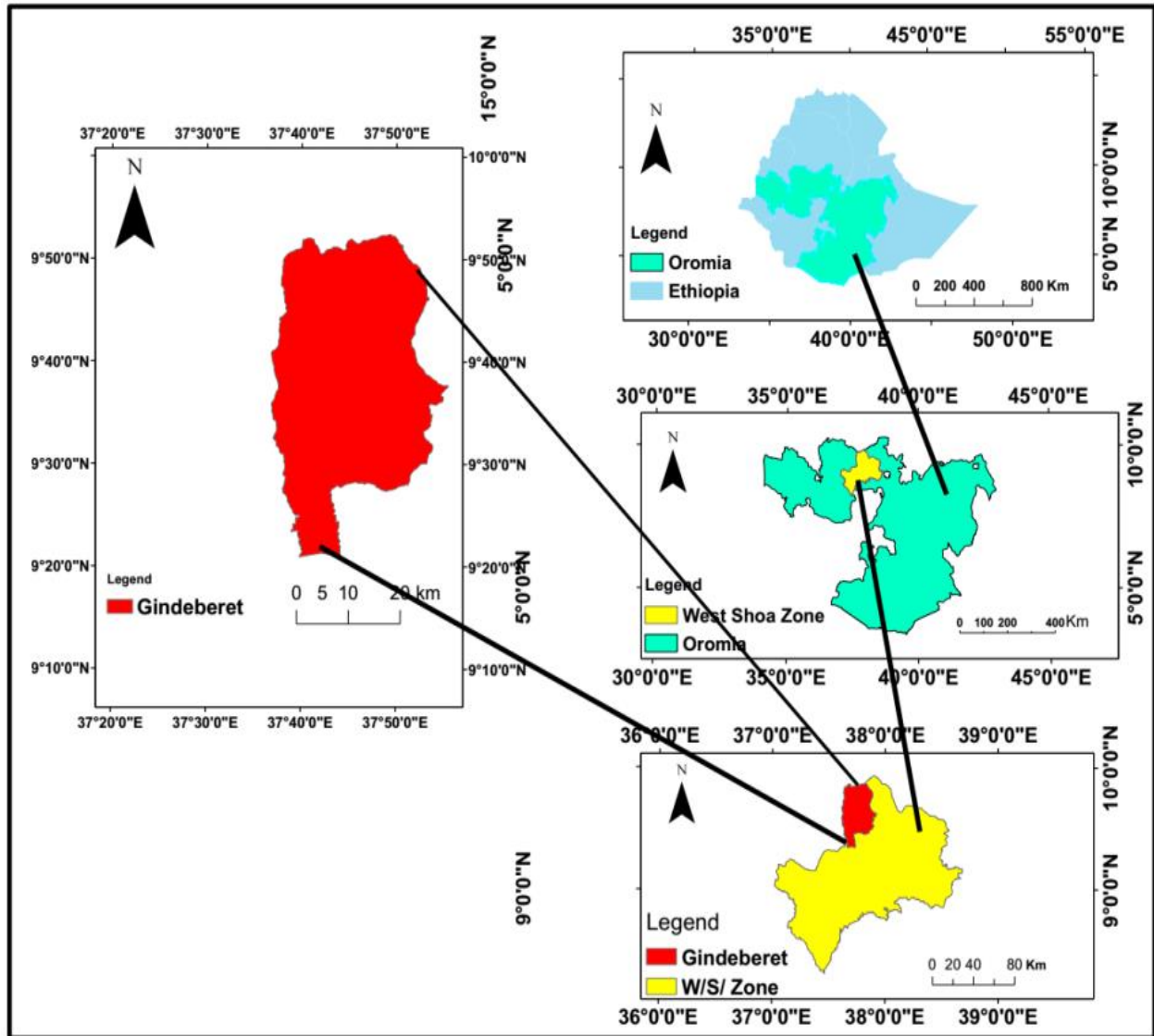


Figure 1. Location of the study area.

Tree inventories

Before starting field survey, reconnaissance was carried out for one week in the selected kebeles to get first-hand information about the study area. A total of 7 transect lines were established for the inventory in the farmland. Along the transect lines 103 plots of 100 m x 50 m (5000 m²) size were laid in the farmland. A systematic sampling method was applied to locate the sample plots to collect woody species structure and composition. The data were collected following the transect line by excluding non-targeted habitats (e.g. rivers, rocky hills, farmers' compounds). The distance between each of the transects and plots was 500 and 400 m, respectively. All woody species found in the plots, with individuals having diameter at breast height (DBH) \geq 5 cm, were recorded at 1.3 m height from ground level. The diameters were measured using tree caliper and diameter tape, and height was measured using a Suunto clinometer and approximately estimated in those cases where the topography and canopy conditions were not suitable to

measure by a Suunto clinometer. Samples of all trees and shrubs species encountered in the plots were recorded by their local names, and specimens were collected for further identification. For specimen identification, Fichtl and Admasu (1994) and Azene (2007) were used, supported by expertise. The geographical position of plots was recorded with a GPS (Global positioning system) allowing their accurate location to allocate the x-y axis of each plot.

Data analysis

Diversity analysis

The species diversity in the parkland agroforestry was estimated using species richness, Shannon diversity index, Simpson diversity index and Shannon evenness (Kent and Coker, 1992). The Species richness is the total number of species in the community (Krebs,

Table 1. Agro-climatic description of the study areas.

Agro-ecology	Temperature range (°C)		Altitude range (m)		Annual rainfall (mm)	
	Min	Max	Min	Max	Min	Max
Weinadega	5	25	1501	2404	700	1400
Kola	10	30	1000	1500	300	850

Source: Gindeberet District Agricultural Office (WQMBAG, 2004).

1999). It was analysed by using Jack knife software version 7.2 (Chorles and Krebs, 2011).

Shannon diversity index is calculated as: $H' = - \sum p_i (\ln p_i)$
Where, H' = Shannon diversity index, P_i = proportion of individuals found in the i^{th} species; or the number of individuals of one species/total number of individuals in the samples.

The evenness of a population was calculated by (Krebs, 1999):

$$E = \frac{H'}{H_{\max}} = \frac{H'}{\ln(S)}$$

with $H_{\max} = \ln(S)$

Where, E = Evenness, H' = Calculated Shannon-Wiener diversity, $H_{\max} = \ln(S)$ [species diversity under maximum equitability conditions]; S = the number of species; Simpson's diversity index (D) was calculated as:

$$D = 1 - \left(\frac{\sum n(n-1)}{N(N-1)} \right)$$

Where, D = Simpson's index, n = The total number of organisms of a particular species, N = The total number of organisms of all species.

At the end, the diversity indexes were converted to true diversity (effective number of species by using the formula $T_D = e^H$
Where T_D = True diversity, e = Base of natural logarithm and H = Shannon diversity index.

To measure the similarity between the vegetation samples, Sorensen's coefficient of similarity (S_s) was used. It is given by the formula of Kent and Coker (1992):

$$S_s = \frac{2a}{2a + b + c}$$

Where, S_s = Sorensen similarity coefficient, a = number of species common to both samples, b = number of species in sample 1 and c = number of species in sample 2.

The coefficient is multiplied by 100 to give a percentage.

Structural analysis

Basal area

Basal area is the cross-sectional area of woody stems at breast height. It measures the relative dominance (the degree of coverage of a species as an expression of the space it occupies) of a species in an area. Basal area was calculated for each woody species with diameter ≥ 5 cm as:

$$BA = \frac{\pi(DBH)^2}{4}$$

BA = basal area (m^2)

Where, $\pi = 3.14$ and DBH = diameter at breast height (cm).

Diameter and height classes were arbitrarily recognized in each of the two agro-ecologies of parkland agroforestry. For this, seven diameter classes (<10, 10-20, 21-30, 31-40, 41-50, 51-60, and >6), and five height classes (<5, 5.1-10, 10.1-15, 15.1-20 and > 20) were classified in each of the agro-ecological zones

Density

Density was calculated by summing up all stems across all area and converting into hectare basis.

$$\text{Density} = \frac{\text{Total number of individual species}}{\text{Sample area (ha)}}$$

Relative density

$$= \frac{\text{Number of individual of species}}{\text{Total number of individuals}} * 100$$

Relative dominance

$$= \frac{\text{Dominance of aspecies}}{\text{Total dominance of all species}} * 100$$

Frequency

$$= \frac{\text{Area of the plot in which species occurs}}{\text{Total number of sample plots}}$$

Relative frequency

$$= \frac{\text{Frequency of a species}}{\text{Frequency of all species}} * 100$$

Importance value index

The importance value index (IVI) indicates the importance of species in the system and it is calculated with three components

(Kent and Coker, 1992).

Importance value for each woody species was calculated by using the formula:

$IVI = \text{Relative frequency} + \text{Relative density} + \text{Relative dominance}$

Trees/shrubs biomass carbon estimation

Woody species carbon was estimated for different woody species available in parkland agroforestry using non-destructive methods. Particularly, biomass carbon estimation was done as per the method adopted by Pandya et al. (2013); where he used the same formula for estimation of biomass carbon for 25 tree species.

Tree bio-volume (T_{BV})

Height and diameter of trees within each species were converted into bio-volume as follows:

$\text{Bio-volume } (T_{BV}) = 0.4 \times (D)^2 \times H$ (Pandya et al., 2013).

Where, H = Height of the tree (m) and D = Diameter (cm)

Aboveground biomass (AGB)

Aboveground biomass was calculated by using the following formula:

$\text{Aboveground biomass} = T_{BV} \times P$

Where, P = Wood density and T_{BV} = Tree bio-volume

In this case for woody density, Global Woody Density Bases of Carsan et al. (2012) and Goldsmith and Carter (1981) were used.

Belowground biomass (BGB)

The belowground biomass was calculated by multiplying the aboveground biomass (AGB) by 0.26; a factor expressing the root: shoot ratio (Hangarge et al., 2012).

$BGB = AGB \times 0.26$

Total biomass

Total biomass is the sum of above and belowground biomass (Sheikh et al., 2011).

In this study, the equation for total biomass was: $(TB) = \text{Aboveground biomass (excluding litter)} + \text{Belowground biomass (Excluding Soil Organic Matter)}$.

Carbon estimation

Generally, for any plant species 50% of its biomass is considered as carbon (Pearson et al., 2005) that is $\text{Carbon Storage} = \text{Biomass} \times 50\%$.

Statistical data analysis

After the data were collected, species composition, species richness, species diversity, structures and biomass carbon estimate were analyzed using SPSS, version 20 and Microsoft Excel version 2010. These data were summarized and discussed using descriptive statistics such as frequencies, percentage and crosstabs.

RESULTS AND DISCUSSION

Woody species composition

Totally, 61 woody species (54 to species level, 6 to genus level and 1 unidentified) were collected from the two agro-ecological zones of the parkland agroforestry of Gindeberet (Appendix 1). Out of this, 31 species were collected from the midland parkland agroforestry; while 53 species were collected from the lowland parkland agroforestry. Twenty-three woody species were common for both agro-ecological parkland agroforestrys. The species richness was significantly different between the two agro-ecological zones ($X^2 = 8.5$, $p = 0.003$).

The collected species belonged to 35 families, excluding unidentified species. Fabaceae, Moraceae and Myrtaceae were the most dominating families. They were diverse in terms of species number being 12 for Fabaceae and 4 for Moraceae and Myrtaceae, each. Bajigo and Tadesse (2015) and Worku et al. (2011) reported that Fabaceae was the family with a higher number of woody species in Gununo Watershed in Wolaita Zone and Debre Zeit, central rift valley of Ethiopia.

The total number of woody species individuals from midland and lowland agro-ecological parkland agroforestrys was 492 and 951, respectively; indicating a significant difference ($p < 0.05$) between the two agro-ecological zones in terms of agroforestry tree and shrub species abundance. In terms of habit classification, 73.8% were trees and 26.2% were shrubs with 93.4% indigenous and 6.6% exotic species. Comparison of the woody species richness of the present study site with other sites indicated that it is higher in most cases. For example, Nikiema (2005) reported 41 in Burkina Faso while Motuma (2006) reported 32 in Arsi Negelle. Likewise, Worku et al. (2011) reported only 7 species in Debre Zeit and Bajigo and Tadesse (2015) reported 11 in Gununo of Woliata District. In all the above cases, we can see that there was a significant difference ($p < 0.05$) between our study site and study sites reviewed in the literature. Such differences in the farmlands could exist as agro-ecological characteristics; or other factors such as: site, socio-economic, culture and management strategy of the farmers.

Diversity of woody species

In order to get a better picture on extent of woody species diversity, the Shannon, Simpson and evenness indices were employed. The values of the indices for evenness, Shannon's and Simpson's, respectively, were: 0.478, 2.96, 0.935 (midland parklands) and 0.467, 3.2, 0.937 (lowland parklands) as shown in Table 2.

Similarly, the value of woody species richness at midland altitude and lowland altitudes parkland agroforestry were 61 and 105, respectively. The values of

diversity indices of woody species (Shannon and Simpson's diversity indexes) in the lowland parkland agroforestry were greater than the midland parkland agroforestry, but the evenness value of lowland parkland agroforestry was lower than the midland parkland agroforestry.

In the present study, the Shannon and Simpson diversity indices showed high value in the lowland agro-ecological parkland agroforestry as compared to the midland parkland agroforestry. This may be due to the high number of species richness in the lowland agro-ecological parkland agroforestry compared to the midland parkland agroforestry. The species richness also showed the variation between the two agro-ecological parkland agroforests. The lowland agro-ecology supported higher numbers of woody species richness than midland agro-ecology. This may be due to agro-ecological or site characteristics, altitudinal variation, socio-cultural and farmer's management strategy.

The study by Getahun (2011) on the diversity and management of woody species in home-garden agroforests in Gimbo District, South west Ethiopia shows that the site, socio-economic, culture and management strategy could be the factors for woody species variation. As the study conducted by Hodel and Gessler (1999) stated, besides altitude and temperature, soil quality is another agro-ecological factor that generates variation of plant diversity. According to Dossa et al. (2013), there is a decline in tree species richness with increasing altitude, because of a greater role of environmental filtering at higher elevations (e.g. cooler temperatures, fog, reduced light incidence and higher relative humidity). Maghembe et al. (1998) also reported the influences of socio-cultural factors on woody species management and diversity. This is demonstrated both as encouraging and discouraging of woody species retention or their planting on farmlands.

The true diversity (effective number of species) of woody species in lowland parkland agroforestry and midland parkland agroforestry estimates were: 24.5 and 19.3, respectively (Table 2). From this, it is also possible to conclude that lowland parkland agroforestry was more diverse than the midland parkland agroforestry.

Similarity index

The similarity in woody species composition between the two agro-ecological parkland agroforests was 35.4% (Table 2). The low similarity could be due to the differences in agro-ecology and species growing requirements. Woody species adapted to midland agro-ecology may not adapt to lowland agro-ecology and vice-versa.

In this study, more numbers of woody species were recorded in lowland agro-ecologies as compared to the

midland agro-ecologies. And also, the presence of a low number of woody species in midland agro-ecologies could be due to the fact that the midland agro-ecologies had relatively more infrastructures like roads and markets as compared to lowland agro-ecologies. According to Tesfaye (2005)'s report there was low woody species diversity and a low number of species richness in farms located near roads and access to markets. Also, as aforementioned agro-ecological or site characteristics, socio-cultural and farmer's management strategy could be the cause for the variation of woody species between the two agro-ecological zones.

Structure of woody species

Basal area

The total basal area of all woody species in the midland and lowland agro-ecologies of the parkland agroforestry were calculated from the diameter at breast height (DBH) of the individual tree/shrub species.

The mean basal area of midland parkland agroforestry (3.62 ± 1.3) was higher than the lowland parkland agroforestry (2.64 ± 0.92) (Table 3). However, there was no statically significant difference between the two means for basal areas of parkland agroforests.

Frequency of woody species

Frequency of woody species is one of the structural parameter which was measured in the two agro-ecological zones, and the top five frequent woody species in the two agro-ecological zones is listed in Table 4.

In the midland parkland agroforestry, the most frequent species were *Maytenus obscura*, *Rhus vulgaris*, *Acacia abyssinica* *Erthyria brucei*, *Prunus africana*, being 47.1%, 38.2%, 26.5%, 26.5% & 23.5%, respectively (Table 4). In the lowland parkland agroforestry, the most frequent woody species were *Croton macrostachyus* (63.8%), *Faidherbia albida* (37.7%), *C. africana* (27.5) and *Albizia schimperiana* (27.5%).

Density of woody species

Overall, 1443 individual woody species were collected from 51.5 ha from the two agro-ecological zones of the parkland agroforestry of Gindeberet. The mean density of midland parkland agroforestry (1.04 ± 0.35) was significantly lower than lowland parkland agroforestry (1.87 ± 0.22) at ($p < 0.05$) (Table 4). In general, the two agro-ecological parkland agroforests have the lower mean density per hectare. This is because of the

Table 2. Diversity indices and species richness of woody species in the parkland agroforestry practices at the two agro-ecological zones.

Agro-ecological altitude	Number of Plot	Species richness	Diversity index value			True diversity	Sorensen Similarity percentage
			Evenness	Shannon diversity	Simpson diversity		
Midland	34	61	0.478	2.96	0.935	19.3	
Lowland	69	105	0.467	3.20	0.937	24.5	35.4

Table 3. Mean \pm Standard Deviation of the two agroforestry parkland structures.

Parameter	Agro-ecology	Mean \pm Standard Deviation	p-value
Diameter at breast height (cm)	Midland	32.91 \pm 4.19	0.153
	Lowland	25.44 \pm 3.11	
Height (m)	Midland	9.79 \pm 0.82	0.883
	Lowland	9.51 \pm 1.40	
Density (ha ⁻¹)	Midland	1.04 \pm 0.35	0.041
	Lowland	1.87 \pm 0.22	
Basal area (m ²)	Midland	3.62 \pm 1.38	0.543
	Lowland	2.64 \pm 0.92	

Table 4. Top five frequent woody species in the two agro-ecological zones of Gindeberet in their descending order.

Agro-ecological zones	Scientific name	% in frequency
Midland parkland agroforestry	<i>Maytenus obscura</i>	47.1
	<i>Rhus vulgaris</i>	38.2
	<i>Acacia abyssinica</i>	29.4
	<i>Erythrina brucei</i>	26.5
	<i>Prunus africana</i>	23.5
Lowland parkland agroforestry	<i>Croton macrostachyus</i>	63.8
	<i>Faidherbia albida</i>	37.7
	<i>Cordia africana</i>	27.5
	<i>Albizia schimperiana</i>	27.5
	<i>Vernonia amygdalina</i>	24.6

continuous cultivation of farmland and low regeneration potential of species in the study area. The research conducted by Worku et al. (2011) in the parkland agroforestry of Debre Zeit also revealed that, due to the continuous cultivation of farmland and no fallow practices that could enable species to regenerate and grow to big size contributes to the low density of species in farmland.

Diameter class distribution

Seven diameter classes were arbitrarily recognized in

each of the two agro-ecologies of parkland agroforestry to see the distribution of diameter classes (Figures 2 and 3). In the midland agro-ecology the higher diameter class (>60 cm) was dominated by *Ficus sur*, *Erythrina brucei* and *Prunus Africana*; whereas, the lowest diameter class (<10 cm) was dominated by *Acacia abyssinica* and *Vernonia auriculifera* species in terms of DBH.

The rest of woody species have low juvenile populations, but this increases at the middle diameter classes and then decreases toward the larger diameter class in the midland parkland agroforestry. The distribution of population structure of these woody species

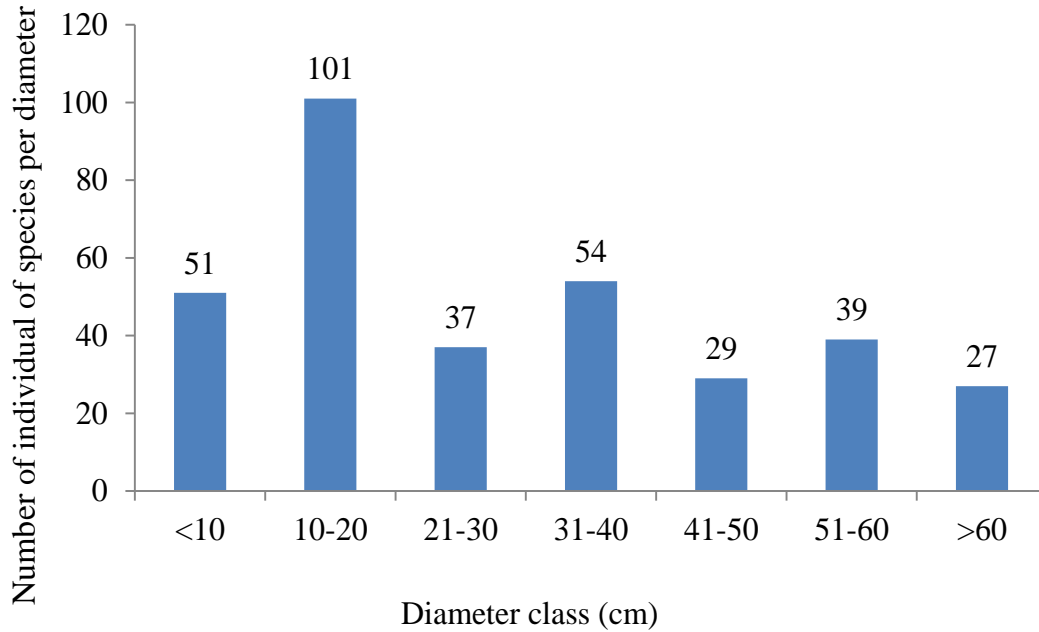


Figure 2. Diameter class distribution in midland parkland agroforestry of Gindeberet.

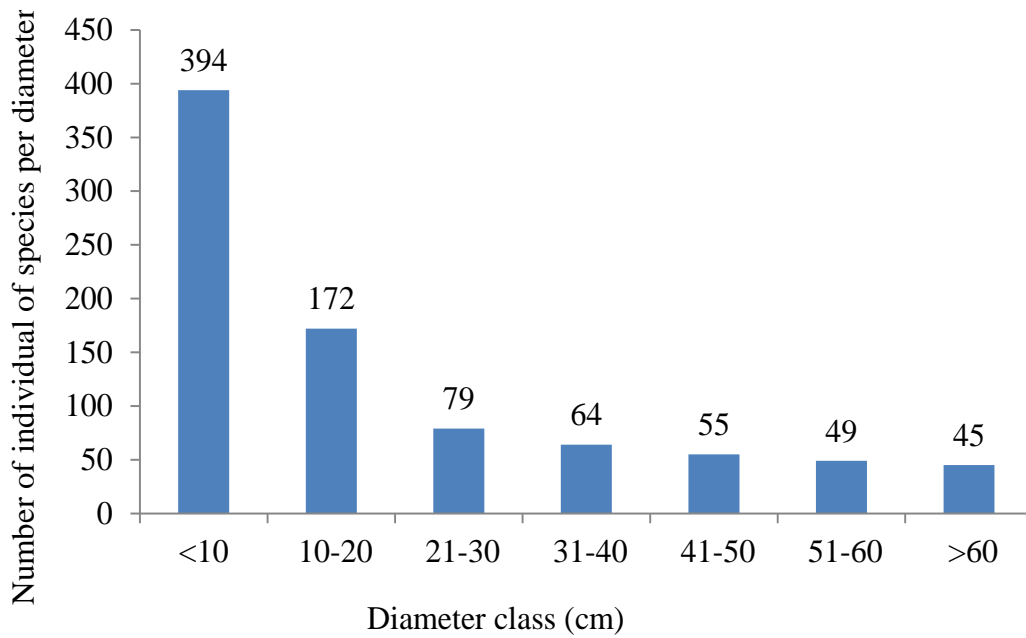


Figure 3. Diameter class distribution in lowland parkland agroforestry of Gindeberet.

species resembles close to a bell shape curve, which shows a high number of intermediate classes, but a very low number in the small and large diameter classes (Figure 2).

In the lowland parkland agroforestry (Figure 3), the total number of woody species in each DBH class decreased

with increasing diameter classes. This was a normal DBH distribution pattern, when viewed from the whole set of plant communities, confirming a reversed J-shape plot (Figure 3). About 45.9% of the total populations were found in the first lower DBH class showing the dominance of small trees in the parkland agroforestry due to some

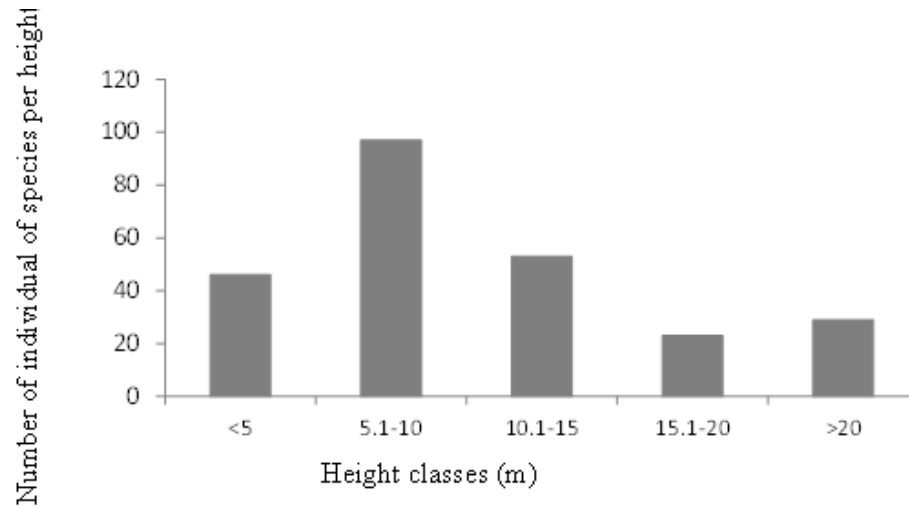


Figure 4. Height class distribution in midland parkland agroforestry of Gindeberet.

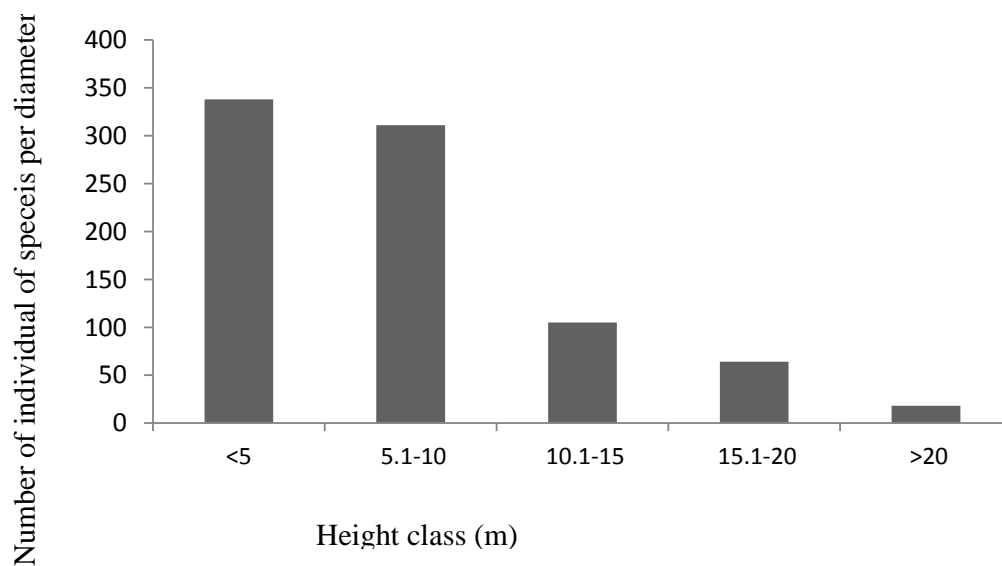


Figure 5. Height class distribution in the lowland parkland agroforestry of Gindeberet.

species were regenerating and some species were sprouting from the old trees that were coppiced, while the rest were distributed in all the remaining DBH classes. This diameter distribution pattern is similar with an earlier report by Yemenzwork (2014).

Height class distribution

Generally, five height classes were identified in each of the agro-ecological zones (Figures 4 and 5). In the midland agro-ecology, the most dominant woody species

with the higher height classes (>20 m) were *Ficus sur*, *Erythrina brucei* and *Prunus africana*; whereas *Acacia abyssinica* was the dominant species in the lowest height classes (<5.1 m).

In the lowest class, *Acacia abyssinica* was naturally regenerating better than the other woody species. This is due to the management practices like coppicing and lopping. The height attained was in the lower height classes. The height distribution structure of woody species in midland looks like a bell-shaped distribution, which shows a high number of intermediate classes, but a very low number in the small and large height classes

Table 5. The top five woody species with the highest importance value index in the two agro-ecological parkland agroforestry of Gindeberet.

Agro-ecology	Scientific name	Relative Frequency %	Relative Density %	Relative Dominance %	Importance Value Index
Midland	<i>F. sur</i>	3.31	2.03	35.18	40.52
	<i>M. obscura</i>	13.22	12.4	7.93	33.55
	<i>R. vulgaris</i>	10.74	10.16	10.04	30.95
	<i>E. brucei</i>	7.44	8.74	12.9	29.08
	<i>A. abyssinica</i>	8.26	10.16	2.63	21.05
Lowland	<i>C. macrostachyus</i>	17.88	15.12	28.39	61.39
	<i>F. albida</i>	5.36	8.93	11.67	25.97
	<i>F. vasta</i>	2.00	5.15	17.03	24.18
	<i>A. schimperiana</i>	7.15	6.53	5.44	19.12
	<i>C. africana</i>	3.68	6.53	7.87	18.08

(Figure 4).

In the lowland agro-ecologies (Figure 5), the total number of woody species in each height class showed a decreasing trend with increasing height classes. This is also similar with the DBH class distribution in lowland agro-ecologies. This is a normal height distribution pattern, when viewed from the whole set of plants in a community, confirming a reversed J-shape plot (Figure 5).

The majority of the populations were found in the first height class showing the dominance of small trees in the parkland agroforestry. This is due to the management practices, i.e. lopping and coppicing. When the average mean height of trees in lowland parkland agroforests (9.79 ± 0.82 m) is compared with the average mean height of midland agroforestry (9.51 ± 1.40 m), there is a slight difference. The difference may be due to the difference in management practices carried out at two locations. However, statistically, the independent t-test value revealed no significant difference (Table 3).

Importance value index (IVI)

In the two agro-ecological zones, the importance value index of all woody species was assessed. However, the top five important woody species were briefly discussed here in terms of their importance value index (Table 5). Accordingly, *F. sur*, *M. obscura*, *R. vulgaris*, *E. brucei* and *A. abyssinica* were the top five ranked woody species, and had mean IVI values of 40.52, 33.55, 30.95, 29.08 and 21.05, respectively, in midland parkland agroforests.

In the lowland parkland agroforests, *C. macrostachyus*, *F. albida*, *F. vasta*, *A. schimperiana* and *C. africana* were the top five ranked woody species with the mean IVI values of: 61.39, 25.97, 24.18, 19.12 and

18.08, respectively. *C. macrostachyus* ranked first at lowland and *F. sur* ranked first at midland agro-ecologies. IVI is used to determine the overall importance of each species in the community structure. Species with the greatest importance value are the primary dominant species of a specified vegetation (Simon and Girma, 2004).

Estimate of the aboveground and belowground biomass and biomass carbon

This study estimated the above and belowground biomass, total biomass and biomass carbon of the woody species in the two agro-ecological zones of parkland agroforests in Gindeberet. The total woody biomass and the biomass carbon of lowland parkland agroforests were considerably higher (38.33 Mg/ha) and (19.17 MgC/ha) than at midland parkland agroforestry (20.28 Mg/ha) and (10.14 MgC/ha), respectively (Table 6). This could be due to the difference in altitude, species richness, and structure of woody species in the area.

Since the aboveground biomass depends on the height and diameter of woody species, the aboveground biomass increases with increasing diameter and height. The structure and composition of vegetation (tree species, density, diameter at breast height size and height, etc.) affects the aboveground biomass carbon (Unruh et al., 1993; Weifeng et al., 2011). According to Leuschner et al. (2013), the aboveground biomass of vegetation decreased with increasing altitude. The relationship between height and diameter is also related to species, climatic, soil characteristics, region and even tree diversity (Imani et al., 2017). With regard to taxonomic characteristics, species richness has been associated with aboveground biomass.

Table 6. Estimate of the above and belowground biomass, total biomass and biomass carbon estimation in the two agro-ecology zones of Gindeberet (Mg/ha).

Agro-ecology	Aboveground biomass	Belowground biomass	Total biomass	Total biomass carbon
Midland	16.09	4.18	20.28	10.14
Lowland	30.42	7.91	38.33	19.17

Environmental parameters, such as climate and soils also affect aboveground biomass (Lewis et al. 2013; Poorter et al., 2015).

Conclusions and Recommendations

Even though Gindeberet District is among the most severely deforested parts of West Shoa Zone in Oromia Regional State, Ethiopia; parkland agroforestry woody species still exist, although within various challenges.

However, the differences exist in the diversity and composition of woody species in the parkland agroforestry among the agro-ecological zones. Lowland parkland agroforestry supports higher number of woody species with higher diversity indices than midland parkland agroforestry. This set of parkland agroforestry practices was less complex structurally and had low storage of woody biomass and biomass carbon as compared to the other parkland agroforestry practices.

In general, even if the diversity of species is better in the study area as compared to the other parkland agroforestries, it needs improvements in management to support socio-economic and environmental sustainability.

To ensure the regeneration and to save the species, even from becoming extinct, direct sowing and preserving the desired species in the parkland agroforestry is the solution to overcome the problems.

Since this study showed low carbon storage potential in living biomass of woody species, it is recommended to develop a policy on the woody species management, conservation and regeneration to increase the carbon storage potential in living biomass of woody species to accomplish the goal of the Climate Resilient Green Economy Policy of the country by considering parkland agroforestry practices as one part for its achievement.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Appendix 1. List of woody species in Gindeberet.

S/N	Scientific name	Family name	Vernacular name in Afan Oromo	Habit
1	<i>Acacia abyssinica</i> Hochst. ex Benth.	Fabaceae	Laaftoo	T
2	<i>Acacia</i> sp1.	Fabaceae	Laaftoo	T
3	<i>Acacia</i> sp2.	Fabaceae	Doddota	T
4	<i>Acacia tortilis</i> Forsk.	Fabaceae	Laaftoo	T
5	<i>Albizia gummifera</i> J.F.Gmel.	Fabaceae	Muka-arbaa	T
6	<i>Albizia schimperiana</i> Oliv.	Fabaceae	Imalaa	T
7	<i>Albizia</i> sp.	Fabaceae	Gaafatoo	T
8	<i>Allophylus abyssinicus</i> (Hochst) Radlk.	Sapindaceae	Sarara	T
9	<i>Apodytes dimidiata</i> E. Mey ex Arn.	Icacianaceae	Calalaqaa	T
10	<i>Bersama abyssinica</i> Fresen.	Melanthaceae	Lolchiisaa	S
11	<i>Brucea antidysenterica</i> J.F. Mill.	Simarobiaceae	Qomonyoo	S
12	<i>Buddleja polystachya</i> Fresen.	Buddlejaceae	Anfaara adii	T
13	<i>Calpurnia aurea</i> (Lam.) Benth.	Fabaceae	Ceekaa	S
14	<i>Carissa spinarum</i> L.	Apocynaceae	Hagamsa	S
15	<i>Celtis africana</i> Brum. F.	Ulmaceae	Mata qoma	T
16	<i>Coffea arabica</i> L.	Rubiaceae	Buna	S
17	<i>Cordia africana</i> Lam.	Boraginaceae	Waddeessa	T
18	<i>Croton macrostachyus</i> Hochst. Ex.A.Rich.	Euphorbiaceae	Bakkaniisa	T
19	<i>Cussonia arborea</i> A. Rich.	Araliaceae	Gatamaa	T
20	<i>Dombeya torrida</i> D. goetzenii.	Sterculiaceae	Daannisa	T
21	<i>Dovyalis abyssinica</i> A. Rich.	Flacourtiaceae	Koshommii	T
22	<i>Dracaena steudneri</i> Engl.	Dracaenaceae	Merqoo	T
23	<i>Ekebergia capensis</i> Sparrm.	Meliaceae	Somboo	T
24	<i>Erythrina brucei</i> Schweinf.	Fabaceae	Walensuu	T
25	<i>Eucalyptus camaldulensis</i> Dehnh.	Myrtaceae	Baarzaafii Wallaggee	T
26	<i>Eucalyptus globulus</i> Habill.	Myrtaceae	Baarzaafii	T
27	<i>Eucalyptus saligna</i> Smith.	Myrtaceae	Baarzaafii wallagge	T
28	<i>Euclea racemosa</i> L.	Ebenaceae	Miheessaa	S
29	<i>Euclea</i> sp.	Ebenaceae	Jimaa	S
30	<i>Faidherbia albida</i> Del.	Fabaceae	Garbii	T
31	<i>Ficus</i> sp.	Moraceae	Qilinxoo	T
32	<i>Ficus sur</i> Forsk.	Moraceae	Harbuu	T
33	<i>Ficus thonningii</i> Bl.	Moraceae	Dambii	T
34	<i>Ficus vasta</i> Forsk.	Moraceae	Qilxuu	T
35	<i>Grevillea robusta</i> A. Cunn. ex R. Br.	Proteaceae	Giravillaa	T
36	<i>Grewia ferruginea</i> Hochst. Ex. A. Rich.	Tiliaceae	Dhoqonuu	S
37	<i>Justicia schimperiana</i> T.anders.	Acanthaceae	Dhummuugaa	S
38	<i>Maesa lanceolata</i>	Myrsinaceae	Abbayii	S
39	<i>Maytenus obscura</i> (A. rich) Cuf.	Celastraceae	Kombolcha	T
40	<i>Maytenus</i> sp.	Celasteraceae	Kombol biitee	S
41	<i>Millettia ferruginea</i> Hochst.	Fabaceae	Birbirraa	T
42	<i>Nuxia congesta</i> R.Br. ex Fresen.	Loganiaceae	Anfaara gurraacha	T
43	<i>Olea europaea</i> L.	Oleaceae	Ejersa	T
44	<i>Olinia rochetiana</i> A.Juss.	Oliniaceae	Soolee	T
45	<i>Pavetta oliveriana</i> Hiern.	Rubiaceae	Buruurii	S
46	<i>Phoenix reclinata</i> Jack.	Arecaceae	Meexxii	T
47	<i>Podocarpus falcatus</i> (Thunb.) C. N. Page.	Podocarpaceae	Birbirsa	T
48	<i>Premna schimperii</i> Engl.	Verbenaceae	Urgeessa	T
49	<i>Prunus africana</i> (Hook.) Kalkm.	Rosaceae	Gurraa	T
50	<i>Rhamnus prinoides</i> L. Herit.	Rhamnaceae	Geshoo	S

Appendix 1. contd.

51	<i>Rhus glutinosa</i> A.Rich.	Anacardiaceae	Xaaxessaa	T
52	<i>Rhus vulgaris</i> Meikle.	Anacardiaceae	Dabobessaa	T
53	<i>Ricinus communis</i> L.	Euphorbiaceae	Kobboo	S
54	<i>Rumex nervosus</i> Vahl.	Polygonaceae	Dhangaggoo	S
55	<i>Salix subserrata</i>	Salicaceae	Aleltuu	T
56	<i>Sesbania sesban</i> (L.) Merr	Fabaceae	Inchinnii	S
57	<i>Syzygium guineense</i> (Wild) D.C.	Myrtaceae	Baddeessaa	T
58	<i>Teclea nobilis</i> Del.	Rutaceae	Hadheessa	T
59	<i>Vernonia amygdalina</i> Del.	Asteraceae	Dheebicha	T
60	<i>Vernonia auriculifera</i> Heirn.	Asteraceae	Reejjii	S
61	-	-	Coocingaa*	S

*Local name by Afan Oromo.

Full Length Research Paper

Biological diversity of agroforestry species in the socioeconomic context of producers in the Barh-kôh Department, Southern Chad: Case of Kissimi, Mayelé and Badara villages

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This study aims to better understand the woody biodiversity and the relationship between the state of tree cover in the Agroforestry Park and the management units, and also to know the socio-economic role played by the trees of the parks. The study was conducted in 3 villages in Barh-kôh Department, Chad, between May and November 2018. A plot of 2500 m² has been materialized in each management unit and the species found there are inventoried. Average per hectare is 37 feet in the bush fields, 27 feet in the village fields and 23 feet in the box fields. The study showed a cut rate of 87% among the wealthy classes against 82% among the poor. Tree cutting is more important in hut fields where only 5% of trees are spared. This study shows that agroforestry seems to be the technique conducive to the conservation of ligneous diversity. By virtue of its environmental and socio-economic contributions, this traditional agricultural practice could be part of the logic of sustainable agriculture. Also, by building the agroforestry parks, they will endow the agrarian systems with wood production capital with multiple associated functions.

Key words: Biodiversity, conservation, agricultural practice, sustainable agriculture, Chad.

INTRODUCTION

Due to the strong human pressure on natural environments, agroforestry systems around the world are

today both a technique for conserving biodiversity and meeting the socio-economic needs of populations (Gone,

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2013). Biodiversity and more precisely its plant component is recognized as a living heritage common to all humanity (Manfo, 2013). However, it is nowadays subject to erosion and transformations engendered by forms of development that are more and more incompatible with its preservation. In Chad, like most countries in Sudano-Sahelian Africa, the farming land system integrates trees scattered in the fields. This system has always allowed good land use in an environment where the use of mineral fertilizers remains very limited. But this agriculture, and more specifically slash-and-burn agriculture, is considered to be the main factors responsible for more than 70 to 90% of forest cover losses in Chad (ONDR, 2012). This situation challenges everyone to behave more responsibly in the use of the goods that nature offers us and that we must also bequeath to our children (Bambara et al., 2018). It is in this sense and to draw the attention of all to the uncontrolled use of natural resources that can lead to a situation of non-return, that the international community adopted the Convention on Biological Diversity in 1992. In the framework of its implementation, a national strategy and a plan of action on biological diversity has been elaborated at the national level because, it is in the synergy of action that the battle against the degradation of plant resources, the desertification by the deforestation, and for the safeguarding of biological diversity can be won. There is also evidence that today, with population growth and the growing need for agricultural land, biodiversity and the number of trees saved during clearing is decreasing. Agroforests according to Jagoret (2011) are generally characterized by a dominant stand, the main source of income or use (*Vitellaria paradoxa*, *Parkia biglobosa*, *Amblygonocarpus andongensis*, *Tamarindus indica*, etc.). These agroforests, in fact, are conservative of a certain level of biodiversity, up to a level close to that of secondary forest according to the systems of Tayo (2014) cited by Manfo et al. (2015). In the Barkôh Department, agroforestry has several advantages depending on the types of agricultural development. To this end, woody species should be inventoried in the different management units taking into account the socio-economic categories of the park operators and assessing the impacts on the conservation of biodiversity.

MATERIALS AND METHODS

The study material consists of farmers and the fields of some producers to check the density of trees per hectare. Tools such as forms developed for primary data collection were used.

Study site

The study was conducted in the Barh-kôh Department, specifically in 3 villages: Kissimi, Mayélé and Badara. In this area agroforestry seems to play an important role in the dynamics of plant

communities and biodiversity. The Barh-kôh Department covers an area of 17,258 km² in southern Chad, between 8° 30'00 " and 10° 30'00 " North and 17° 30'00" and 18° 30'00' 'East (Figure 1). It includes 5 sub-prefectures, 9 cantons and 435 villages, with a population of about 319,087 inhabitants, largely of sedentary origin (INSEED, 2014). The climate is tropical with alternating rainy season and dry season with an average duration of six months each. Located in the Sudanian zone, it has a rainfall ranging from 900 to 1,200 mm per year and an annual average of 983 mm. The average annual temperature is 27.6°C with extreme of 25 and 32°C. Hydrography is characterized by permanent rivers such as Chari, Bahr-koh, Bahr Sara, Bahr Keita and Bahr Aouk rivers, which are the main suppliers of fish in the region (Guibert and Kakiang, 2011). The vegetation consists of an important forest mass comprising three types of formations: open forests, tree savannas and shrub savannas (WFP, 2012).

Collection of data

Three types of management units were identified based on their position relative to the family enclosures.

Data collection

Three types of management units were identified based on their position relative to the family enclosures (Figure 2). The village field (CDV) is located after the box fields (Figure 3). The bush field (CBD) is completely outside the village (Figure 4), usually between 2 and 15 km from the dwellings.

Identification Operator and units

For each household, data likely to influence the management of the fields with an impact on agricultural production and the use of trees were considered, during our interview with the farmers. These are active or inactive persons (men, women, and children) in the household and the level of education of the head of the household. For each farmer, information on his identity and on the trees of the fields was collected.

Choice of farmers

In each village, the farmers were grouped into 3 classes of prosperity namely the poor, the well-off and the prosperous according to criteria of prosperity defined by themselves. The choice of operators for the woody inventory in the agroforestry parks took into account the prosperity class and the type of management unit. For each village, a sample of 9 farmers was taken; that is, 3 farmers per prosperity class. Each selected operator should have 3 types of management unit.

Inventory

In each management unit (field), a square plot of 50m x 50m has been materialized and the species found there are inventoried. The data are collected on an inventory sheet with measurements made on each species (circumference at 1.30 m or at the base, number of strands) and other information on the condition of the foot considered. The biodiversity of woody species has been determined using the Shannon-Wiener Index, which is used to assess species diversity and abundance in a given area. The index has the formula:

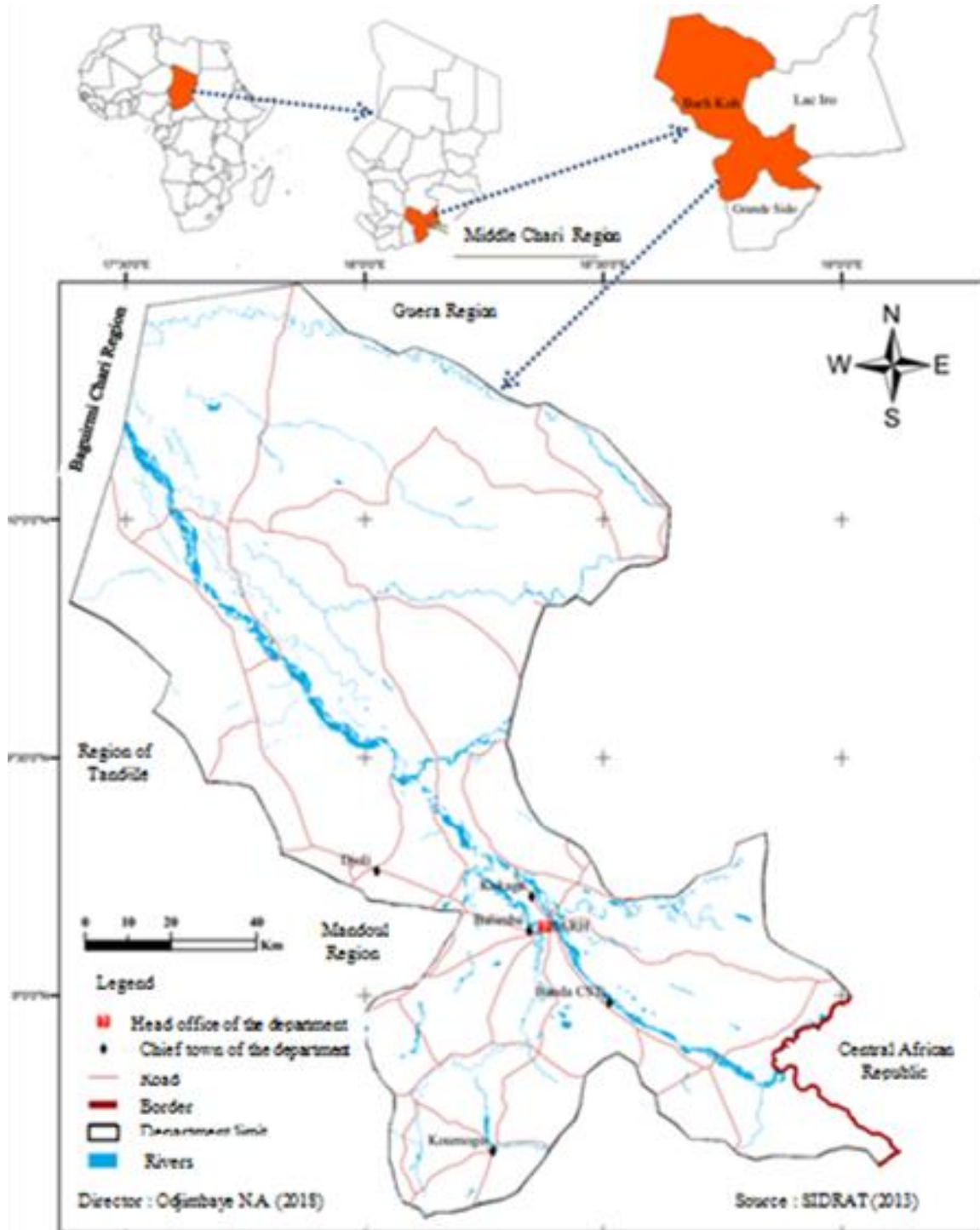


Figure 1. Geographic location of the study environment.

$$H' = \sum_{i=1}^S P_i * \log P_i$$

Where P_i represents the proportional abundance of a species and

is calculated as: $P_i = n_i / N$ where n_i = number of individuals of the species in the sample and N = total number of individuals of all species in the sample; S = total number of species. The statistical analysis was performed using a two-factor ANOVA (factor 1: management unit, factor 2: village). In the presence of a significant difference between different types of management units or between villages, comparisons were made using the test of the



Figure 2. Box field.



Figure 3. Village field.

smallest significant difference.

Non-measurable information is coded as follows: Cut level: 0 = not cut; 1 = <50%; 2 => 50%; 3 = totally cut; Attack level: 0 = not attacked; 1 = <50%; 2 = 50-75%; 3 => 75%. Biological type: GA = large tree, H> 14 m; A = Height tree between 7 and 17 m; PA = Small Tree, individual height H between 4 to 7 m; Ar = shrub, woody individuals of height H <4 m single-celled;

ligeneous individual of height H <4 m polycalle. Sanitary state: S = healthy; M = Death; At = Attacked; Cp = Cut. Origin of the tree: Se = Sowing; R = Rejection; D = Drageon. An observation column made it possible to note for example the nature of the attacks or the cause of the mortality of an observed tree. The 2007 Excel spreadsheet was used to produce graphs illustrating the results of the research.



Figure 4. Bush field.

Table 1. Biodiversity of woody species by management unit in each of the three study cities.

Town	Prosperity level	Management unit		
		CDC	CDV	CDB
Kissimi	Deprived	1.0188±0.0805 ^a	1.0175±0.0839 ^b	1.0502±0.1012 ^a
	Easy	0.1264±0.1036 ^b	1.0306±0.0630 ^b	1.3747±0.1077 ^b
	Prosperous	0.8265±0.0660 ^c	1.0219±0.0775 ^b	1.5048±0.0402 ^b
Mayelé	Deprived	0.1148±0.1056 ^b	1.3278±0.0327 ^a	1.0487±0.0455 ^a
	Easy	0.1317±0.1210 ^b	1.0512±0.0633 ^b	1.0672±0.0711 ^a
	Prosperous	0.7317±0.0786 ^c	1.3013±0.0442 ^a	1.0521±0.0468 ^a
Badara	Deprived	0.0187±0.0712 ^a	1.3415±0.0530 ^a	1.9516±0.0263 ^a
	Easy	0.1326±0.1530 ^b	-	1.9815±0.0512 ^a
	Prosperous	0.7108±0.0526 ^c	-	1.8518±0.0346 ^a

The values associated with the same letter are not statistically different from each other at the 5% threshold. CDC = Box field, DCV = Village field, CDB = Bush field.

RESULTS

Biological diversity of agroforestry species according to the management unit and the prosperity class

The analysis of variance on biodiversity calculated from the Shannon-Wiener Index revealed the existence of statistically significant differences between villages ($p < 0.0001$), as well as between management units. Contrast analysis revealed significant differences between the management units for two villages (Mayelé and Badara) out of three ($p < 0.0001$, $p < 0.0004$ in the case of Badara village) (Table 1). Table 2 gives the result

of the distribution of trees per hectare according to the type of field and the standard of living of the farmer. Figure 5 shows the biological spectra of woody biodiversity in the different management units (Figure 5a: box field, Figure 5b: village field, Figure 5c: bush field).

Specific diversity in parks by level of prosperity and by village

Table 3 shows the distribution of trees by prosperity class. Dynamics of agroforestry species encountered in the different management units. The results on the dynamics of agroforestry species encountered in the

Table 2. Distribution of trees per hectare according to the type of field and the standard of living of the farmer.

Villages	Prosperity levels	Management unit			Average
		CDC	CDV	CDB	
Kissimi	Deprived	0	42	48	45
	Easy	0	42	49	46
	Prosperous	0	0	48	48
Average		0	42	48	
Mayelé	Deprived	7	38	52	32
	Easy	42	20	28	32
	Prosperous	21	24	32	26
Average		23	27	37	
Badara	Deprived	0	0	36	36
	Easy	0	0	19	19
	Prosperous	0	0	30	30
Average		0	0	28	

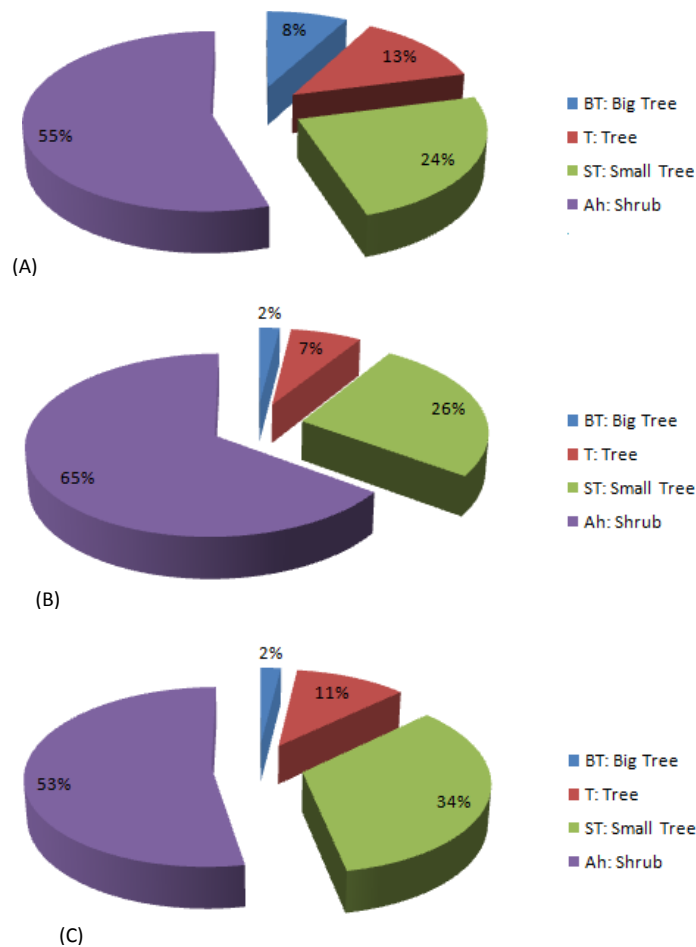


Figure 5. Biological types of trees by management unit (a) Biological types (box field), (b) Biological types (village field) and (c) Biological types (bush field).

Table 3. Distribution of trees encountered.

Village	Prosperity level		
	Deprived	Easy	Prosperous
Kissimi	16	12	10
Mayelé	14	11	8
Badara	6	5	9

Table 4. Distribution of trees by management unit in Kissimi.

N°	Tree species	Management unit					
		CDC		CDV		CDB	
		Adult	Rejection	Adult	Rejection	Adult	Rejection
1	<i>Acacia ataxacantha</i>	0	0	0	1	2	3
2	<i>Acacia senegal</i>	0	0	0	4	3	3
3	<i>Acacia seyal</i>	0	0	4	6	12	6
4	<i>Anogeissus leiocarpa</i>	0	0	0	0	1	0
5	<i>Balanites aegyptiaca</i>	0	0	8	7	9	26
6	<i>Combretum collinum</i>	0	0	1	1	0	0
7	<i>Combretum glutinosum</i>	0	0	1	0	0	0
8	<i>Combretum molle</i>	0	0	0	0	1	1
9	<i>Crateva adansonii</i>	0	0	1	0	0	0
10	<i>Diospyros mespiliformis</i>	0	0	0	0	1	3
11	<i>Guiera senegalensis</i>	0	0	0	1	0	0
12	<i>Lannea barteri</i>	0	0	6	0	2	0
13	<i>Piliostigma reticulatum</i>	0	0	1	1	6	22
14	<i>Sclerocarya bieria</i>	0	0	2	0	0	0
15	<i>Tamarindus indica</i>	0	0	0	0	1	0
16	<i>Vitellaria paradoxa</i>	0	0	0	0	1	0
17	<i>Ziziphus mauritiana</i>	0	0	0	4	1	26
18	<i>Ziziphus mucronata</i>	0	0	0	0	0	1
	Total	0	0	24	25	40	91

different management units are presented in Tables 3 to 6. Cutting level, mortality and tree attack: the tree cutting rate is 87% for the wealthy and 82% for the poor. In the management units, only 5% of the trees are spared. Tree attacks were also observed.

Socio-economic conditions of the farmers

Table 7 establishes the social burden of the farmers in the three villages in relation to the identified prosperity classes.

DISCUSSION

Biological diversity of agroforestry species by management unit and prosperity class

In each of the two villages where significant differences

were observed, it is in the case of fields where the biodiversity is the lowest (Table 1). The diversity of species and abundance of individuals within each species combine to provide biodiversity indices that reveal a clear distinction between the different types of management unit. The distribution of the number of woody species between management units varies significantly between villages ($p < 0.0001$). In general, it is in the fields of box that the arboreal biodiversity is weakest. Thus, depending on the management unit and the prosperity class, it turned out that there is no longer a box office in Kissimi for all farmers and a village field for the prosperous class. The given reason is the subdivision of the land. Through this operation, the box fields have become residential plots that are being serviced. It is only at Mayelé that we are currently meeting all the management units. Depending on the management units, more trees are found in the bush fields than in the village fields, which in turn have more trees than the box fields when all three types exist. In Kissimi, where there are

Table 5. Distribution of trees by management unit in Mayelé.

N°	Tree species	Management unit					
		CDC		CDV		CDB	
		Adult	Rejection	Adult	Rejection	Adult	Rejection
1	<i>Acacia ataxacantha</i>	2	0	2	0	0	0
2	<i>Acacia senegal</i>	0	0	0	0	0	4
3	<i>Acacia seyal</i>	0	0	1	0	2	3
4	<i>Acacia sieberiana</i>	0	4	2	9	6	5
5	<i>Balanites aegyptiaca</i>	1	0	5	8	22	32
6	<i>Combretum collinum</i>	0	0	0	0	1	0
7	<i>Combretum fragrans</i>	0	0	0	0	0	1
8	<i>Combretum glutinosum</i>	0	0	0	0	0	1
9	<i>Faidherbia albida</i>	0	0	8	1	4	1
10	<i>Guiera senegalensis</i>	0	0	1	0	0	1
11	<i>Hyphaene thebeica</i>	3	0	5	2	0	2
12	<i>Maerua crassifolia</i>	0	0	1	0	0	0
13	<i>Piliostigma reticulatum</i>	0	0	0	0	1	0
14	<i>Piliostigma thonningii</i>	0	0	0	1	0	0
15	<i>Sclerocarya bieria</i>	0	0	3	4	3	0
16	<i>Ziziphus mauritiana</i>	0	1	2	17	0	9
	Total	6	5	30	42	39	59

Table 6. Distribution of trees by management unit in Badara.

N°	Tree species	Management unit					
		CDC		CDV		CDB	
		Adult	Rejection	Adult	Rejection	Adult	Rejection
1	<i>Acacia ataxacantha</i>	0	0	0	0	0	1
2	<i>Acacia senegal</i>	0	0	0	0	1	1
3	<i>Acacia sieberiana</i>	0	0	0	0	10	7
4	<i>Balanites aegyptiaca</i>	0	0	0	0	32	6
5	<i>Combretum fragrans</i>	0	0	0	0	0	2
6	<i>Combretum glutinosum</i>	0	0	0	0	2	0
7	<i>Faidherbia albida</i>	0	0	0	0	1	2
8	<i>Maerua crassifolia</i>	0	0	0	0	2	0
9	<i>Prosopis africana</i>	0	0	0	0	1	0
10	<i>Ziziphus mauritiana</i>	0	0	0	0	0	1
	Total	0	0	0	0	49	20

only two types of field, there is an average of 48 hectares in the bush fields and 42 in the village fields. In Mayelé, 37, 27 and 26 trees per hectare were inventoried in the bush fields, village and hut respectively. On the other hand, the work of Abegg et al. (2006), on the socio-economic factors influencing the woody biodiversity of agroforestry parks in two villages of the central plateau in Burkina Faso, showed an increase in biodiversity from village dwellings. However, no significant influence on biodiversity has been observed in relation to a farmer's prosperity class. Considering the standard of living of the

farmers, the woody diversity of the parks differs from village to village. At Kissimi, if the density of trees per hectare is greater among the prosperous and less among the poor, at Mayelé and Badara, it is the contrary phenomenon, they are more ligneous in the fields of the poor than the prosperous ones. Subsequent studies (Pounakoumna, 2017; Madjimbe et al., 2018; Ngoh-allah, 2018) had shown the existence of three types of fields in Kissimi and Mayelé, and only bush fields in Badara because of the extension of the Chari River at the expense of agricultural areas and the importance of lifting

Table 7. Household burden by prosperity class.

Class	Number of people in the family			
	Assets	Inactive	Total charge	Children
Deprived	61	17	78	39
Collateralised	58	16	74	24
Prosperous	57	26	83	39

with the omnipresent animals around the concessions. Figure 5 shows that biological spectra of woody biodiversity in the different management units show only three biological types in the box fields and five types in the village and bush fields. In the box or village fields, the dominant stratum consists of shrubs (Karembe et al., 2014), whose height is generally less than 4 m, and a few large trees (9%) are the authors of the concessions. In the bush fields, it is the individuals between 4 and 7 m high that form the largest stratum.

Specific diversity in parks by level of prosperity and by village

In the majority of cases, the poor have more plant species in their fields than the rich or prosperous, so this is a situation that needs to be encouraged. This is the case in Kissimi with 16 species among the poor, 12 among the rich and 10 among the prosperous. In Mayelé, we find in the same order 14, 11 and 8 species. Although the differences are not so clear as can be seen, the tendency for the poor to keep more plant species is noticeable. The use of different parts of the trees for feeding, especially during the lean season, may explain the option of the poor to diversify the species in their fields (Guibert and Kakiang, 2011). In Badara, the situation is different, as the prosperous keep more species than the other two classes. In this village, livestock is the main activity and forage research for animals can explain the interest in keeping various species.

Dynamic agroforestry species encountered in different management units

In bush fields like those in the village, there is a predominance of discards on adults. In Kissimi, it is especially in the bush fields that the rejection rate is very appreciable compared to that of the village fields. By species, *Balanites aegyptiaca*, *Ziziphus mauritiana* and *Piliostigma reticulatum* have higher rates of regeneration than other species. In Mayelé, however, species such as *Vitellaria paradoxa*, *Tamarindus indica*, *Sclerocarya bieria*, *Anogeissus leiocarpa* or *Lannea barteri* do not show discards to ensure succession. The regeneration

situation according to the management unit is similar to that of Kissimi. There are more rejections in the bush fields than elsewhere. By species, *Balanites aegyptiaca* and *Ziziphus mauritiana* have more discards than other inventoried species. Unlike Kissimi and Mayelé, in Badara there are more adult trees than rejections in the only management unit, the bush field. These results are consistent with the findings of Carriere (2002) who worked on ancestral agricultural practice in the service of forest regeneration. The same author has indicated that for all species, the rate of regeneration is low hence the succession of woody in the parks is very compromised.

Cutting level, mortality and attack of trees

The cutting of trees is observed in all classes, wood being the only source of energy in the village. Even wealthy people do not use gas. Demand for wood is higher among the wealthy classes and explains the high cut rate (87%) compared to the poor (82%). In comparison to the management units, tree cutting is more important in the box fields where only 5% of the trees are spared. It is in the village fields that the cut is less felt. The causes of tree cutting are multiple. Regarding the trees of the fields, the cuts are made for the manufacture of working tools like the house or to make mortars and pestles. At the harvest time, farmers lop some big feet to reduce the volume of their crowns. Indeed, it seems that the trees with big crowns attract the birds pests cereals. According to Bamba et al. (2010), the size of the crowns reduces the number of birds on the trees, which limits the damage. The uprooting of trees by the wind and the intensity of the cuts are the most important cause of tree mortality. The attacks are caused by termites, fungi, locusts, ants or other plants such as *Leptadenia hastata* which sometimes envelops all the host's crown and thus hinder its normal development.

Socio-economic conditions of the farmers

In terms of human capital, we note that the three classes have almost the same potentialities. This complicates the situation for the underprivileged class, faced with feeding the same number of mouths as the wealthy and prosperous, which only widens the gap between the poor

and the rich. We find that the prosperous have more inactive people in their charge and fewer active arms than the other two classes. To agree with Vroh et al. (2010), it can be concluded that the child is considered as a source of wealth and motive for consolation. This explains why the poor have as many children as the prosperous ones to make up for their economic shortfall.

Conclusion

The inventory of woody species in the different management units takes into account the level of prosperity of the farmers. This makes it possible to rule on the relationship that may exist between the ligneous diversity of the agroforestry parks, the level of prosperity of the farmers and the units of management. In terms of species diversity, there is a higher number of species in the fields of the poor in Kissimi and Mayelé. In Badara, a village where livestock is the main activity of the population, the wealthy class keeps more species in the fields than the poor. In terms of the number of individuals, the woody diversity of the parks according to the level of prosperity also differs from village to village. In Kissimi, there are more trees in the fields of the prosperous while in Mayelé and Badara it is the opposite phenomenon. Depending on the management units, there is clearly a predominance of plant biodiversity in bush fields compared to village fields.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Full Length Research Paper

Forest structure and carbon stocks of Osun-Osogbo Sacred Grove, Nigeria

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Forest trees and soil are considered for climate change mitigation. Forest structure of the grove is required to predict its capacity to mitigate climate change. Therefore, the objective of this study was to determine the forest structure and carbon stocks of Osun-Osogbo Sacred grove. Five (30 × 30 m²) plots were demarcated in Old-growth forest (OF) and Re-growth forest (RF). Trees with ≥10 cm diameter-at-breast-height (dbh) were identified to species level and enumerated. Tree height and dbh were measured and stem volumes were converted to carbon stock. Soil samples were collected with cores at three soil depths, oven-dried and carbon content estimated. The tree species diversity and richness indices of OF was higher than OR. Diameter distribution of OF and RF expressed reverse J-shaped and rotated sigmoid curves, respectively. The stem carbon stock ranged from 0.12±0.00 (OF) to 0.02±0.00 Mg/ha (RF). The soil carbon stock ranged from 0.65 (OF) to 0.90 Mg/ha (RF). Stand structure of OF was more develop than RF. The OF and RF contained high stem and soil carbon stocks, respectively. Forest structure enhances stem carbon stock of Old-growth forest while soil of Re-growth forest is also an option for carbon sequestration.

Key words: Carbon sequestration, stem diameter distribution, carbon stock, forest structure, old-growth forest.

INTRODUCTION

Climate change is recognized to be one of the most adverse global environmental problems (Tashi, 2017; Anand, 2013). Climate change is causing unpredictable weather extremes and natural disasters, such as: intense drought, wildfires, wild-winds, irregular rainfall patterns and flooding in most countries. However, one of the inexpensive ameliorative strategies of climate change is the sequestration of carbon dioxide through photosynthesis by forest trees and subsequent deposition in soil. The contribution of tropical forests to carbon sequestration is imperative, because of the magnitude

and capacity of biomass and soil carbon pools that can absorb the sequestered CO₂ (Oades, 1988). Hence, there is a balanced distribution and transfer of carbon between these components of carbon stocks; however, if this flux is disturbed, carbon stocks can become carbon sources.

Sacred groves are forests protected by people for spiritual and cultural practices, and thus completely protected from human interference (Israel et al., 1997). Cultural rites and religious rituals perpetuated in the groves confer protection on it and also help to ensure the

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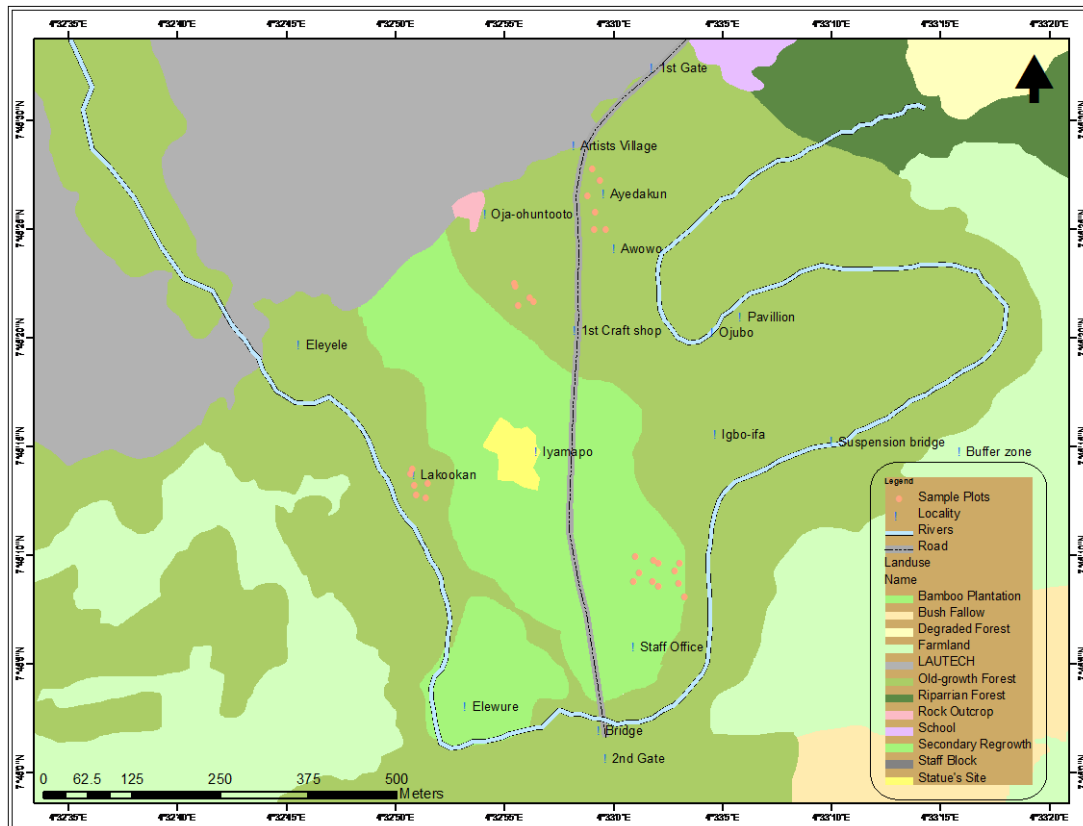


Figure 1. Map of Osun-Osogbo sacred grove and its land use types.

protection of the vegetation of the sacred grove, maintaining it in pristine condition (Sukumaran et al., 2008). According to Baraiah et al. (2003), sacred groves harbour a high diversity of medicinal plants and tree stems than forest reserves.

Forest structure is described as the spatial and vertical distribution of the forest stems and species diversity (Akpata and Okali, 1986; Miren et al., 2004). Structure and canopy of forests provide numerous micro-climatic conditions for diverse ecosystem functions and services. The structure of a forest is a good indicator of its capacity to deliver ecosystem goods and services. Ecosystem services are the benefits people obtain from ecosystem (Chandler, 2016). However, the effect of forest structure on the carbon sequestration capacity of Osun-Osogbo Sacred Grove is yet to be clarified. Moreover, less evidence is available on the effect of forest structure on carbon storage capacity of stem biomass and soil of the Osun-Osogbo Sacred Grove.

There are different views on the carbon sequestration capacity of surface soil and its subsoil layers. Some studies suggested that soil carbon sequestration is restricted to the top soil (<15 cm) (Fang et al., 2015) while others argue that the carbon stock of deep soil layers within a depth of 10 to 35 cm are more stable than top soil, though their process of carbon stabilization may

differ. However, it is imperative to determine the carbon stock of the soil surface, sub-surface and the deep soils, with a view to enhancing soil carbon sequestration capacity of Osun-Osogbo Sacred Grove. The study was conducted to investigate the forest structure and carbon stocks of Osun-Osogbo Sacred Grove with a view to developing a management strategy for optimizing its carbon sequestration capacity.

MATERIALS AND METHODS

The study area

The Osun-Osogbo Sacred Grove is a primary forest and located in lowland rainforest zone of Nigeria. It covers an area of 75 ha on the outskirts of Osogbo city along the Osun River; and it is regarded as the abode of the Yoruba goddess of fertility. The grove is located within Latitudes $7^{\circ}45'0''$ and $7^{\circ}45'30''$ N and Longitudes $4^{\circ}32'35''$ and $4^{\circ}33'30''$ E on the banks of River Osun (Figure 1) in the southern part of Osogbo town, about 2 km from Ataoja's Palace/Oba's market on Adunni Hill slope. It was established during the second settlement of Osogbo in Ohuntoto forest and it is culturally and legally protected by Decree 77 of 1988 (UNESCO-WHC, 2017).

The Osun River drains its basin in a north-south direction and passes out the grove south-east wards. The underlying rocks of the river bed are of Precambrian formation and are exposed in several parts of the grove during the dry season when the river breaks into

pools or lakes. There are deposits of alluvial soils at the banks of the river and at the lower slopes (Aigbe et al., 2014). The grove experiences two seasons, which are the rainy and dry seasons. The rainy season is between March and October and dry season lasts from November to March. The mean annual rainfall is above 1000 mm; while relative humidity is generally high, often greater than 60% during the day, and less than 70% at night. The temperature is generally high 22 to 35°C; and the effects of the Harmattan season is usually mild in the grove (UNESCO-WHC, 2017). The grove has a mature, undisturbed forest canopy, which supports a rich and diverse flora and fauna; and is referred to as an Old-growth forest. Some parts (around Iyamapo shrine and staff office) were reported by local residents to be cleared and used for agricultural purposes, and later abandoned. This portion of the grove is referred to as second re-growth forest, which originated following clearance for agricultural settlement in the 1950s and abandon for over 50 years at the time of sampling.

Data collection

Five sample plots (30x30 m²) were demarcated in each of the identified forest types; Old-growth and Re-growth forests. The boundary of each sample plot was marked with wooden pegs and red twine. Tree stems ≥10 cm diameter-at-breast height (dbh) were identified to species level and enumerated. The stem dbh and height were measured and categorized into diameter and height classes. Also, the diameter-at (-base, -middle and -top) were measured using Spiegel relaskop (Bitterlich model).

Flora of West Tropical Africa (Hutchinson et al., 2014) was used for the identification and authentication of tree species composition on the field with the help of taxonomist. Plant part of those that could not be identified on the field was collected and pressed and compared with collections of reference available in the Herbarium of the Forestry Research Institute of Nigeria (FRIN).

Therefore, forest structure of the grove is described by stem height and diameter class distributions and species diversity. Most matured rainforests are multi-layered with five distinct strata (Whitmore, 1993) and therefore the height of tree stems were categorized into height classes expressed as (Whitmore, 1993):

- (1) Emergence tree stems (≥ 36 m and above)
- (2) Upper Canopy tree stems (26-35 m)
- (3) Middle Canopy tree stems (16-25 m)
- (4) Lower Canopy tree stems (6-15 m)
- (5) Ground Level tree stems (0-5 m).

Tree species diversity in the sampled plot was assessed using the Shannon-Weiner and Simpson diversity indices and Margalef index of species richness (Huang et al., 2003). In addition to Margalef index, number of tree species composition in Old-growth and Re-growth forests was as index of species richness.

Shannon-Weiner diversity index (H'):

$$H = - \sum_{i=1}^s p_i \ln p_i \quad (1)$$

where $p_i = \frac{n_i}{N_i}$, n_i = number of tree species i , N_i = total number of tree species represented.

Simpson's diversity index (D) expressed as:

$$D = 1 - \frac{\sum n(n-1)}{N(N-1)} \quad (2)$$

Where n = number of individual tree species enumerated and N =

total number of individuals of all tree species enumerated.

Margalef index of species richness

$$(M) = \frac{n-1}{\ln N} \quad (3)$$

where n = number of tree species identified, \ln = natural logarithm, and N = number of individual trees enumerated.

Determination of stem biomass and carbon of the grove

Tree stem biomass was estimated to quantify the tree stem carbon stock in the study area. Malhi et al. (2004) indicated that carbon is about 50% of biomass. The stem volume of individual tree species was estimated per plots and sum of the volume of individual tree species in all the plots was multiplied with individual species wood density and converted to stem biomass per hectare.

Newton's formula was used to compute the stem volume for each tree stem (Fonwebau, 1997). Newton's formula is expressed as:

$$\text{Volume} = \frac{Db + 4Dm + Dt}{6} \times h \quad (4)$$

where D_b = Tree diameter at the base, D_m = Tree diameter at the middle, D_t = Tree diameter at the top, and h = Tree height

$$\text{Stem carbon stock/species (Mg/ha)} = WV \times WD \times \text{constant (0.45)} \quad (5)$$

where WV = Wood volume and WD = Wood density.

Data base of wood densities of forest tree species was gotten from the Wood Density Database (Zanne, 2009).

Determination of the soil carbon stock of the grove

Five sub-plots (8 cm × 8 cm) were demarcated at the four corners and at the centre of each plot. Steel soil cores (diameter = 7.5 cm and height = 15.0 cm) were used to collect soil samples at the four corners and the centre of each plot at three depths: 0-15 (surface soil), 15-30 (subsurface soil), 30-45 cm (deep soil). The initial weights of the soil core samples were taken in the laboratory before oven drying at 105°C to constant weights and the final weights were taken immediately. The soil bulk density was computed as:

$$\text{Soil bulk density} \left(\frac{g}{cm^3} \right) = \frac{\text{mass of oven dried soil}}{\text{volume of the cylindrical core}} \quad (6)$$

Soil total carbon was determined (Soil and Plant Analysis Council, 1999; Schumacher, 2002) and briefly explained. 10 g of a bulk soil sample from each depth was placed in a ceramic crucible and heated in a Muffle furnace at 440°C for a minimum of 4 h of constant heat. The heated samples were allowed to cool in a desiccator and final weights were taken. Soil total carbon (%) was calculated as:

$$\text{Soil carbon concentration (\%)} = \frac{\text{initial soil weight} - \text{final soil weight}}{\text{initial soil weight}} \times 100 \quad (7)$$

Soil carbon stock estimation

The soil carbon stock was calculated and expressed (Mg/ha) as

Table 1. Forest structural attributes of Old-growth and Re-growth forests.

Attribute	Old-growth forest	Re-growth forest
Tree species richness	55.0	35.0
Tree density (stems/ha)	360.0	224.0
Basal area (m ² /ha)	3.74±0.62	1.39±0.23
Tree height (m)	12.28±6.87	11.98±5.27
Stand volume (cm ³)	253838.69±4568.26	150569.84±3169.00
Tree stem carbon (Mg/ha)	0.12±0.00	0.02±0.00
Dominant tree species	<i>Funtumia elastuca</i> , <i>Cola millenii</i> , <i>Brachystegia eurycoma</i>	<i>Cola millenii</i> , <i>Albizia zygia</i> , <i>Funtumia elastuca</i>

follows (Turner and Lambert, 2000):

Soil carbon (%) × Soil bulk density (g/cm³) × Depth (20 cm) × α × gravel content (8)

α = Correction factor for units ($\frac{10^4 \text{ cm}^3}{\text{ha}} \times \frac{\text{Mg}}{10^6}$)

Gravel content = Correction factor for gravel content (proportion of aggregate >2 mm size).

Data analysis

Descriptive statistics were used to describe the carbon stock per soil depth. Analysis of variance (ANOVA) was used to compare data means and determine whether the soil carbon stock was significantly different among soil depths and between forest types.

RESULTS

Forest structural attributes

A total of 75 tree species representing 30 families was found in the Osun-Osogbo Sacred Grove. A total of 55 tree species (species richness) was recorded in Old-growth forest while 35 tree species (species richness) was found in Re-growth forest (Table 1). The mean basal area of Old-growth forest (3.74 m²/ha) was higher than that of Re-growth forest (1.39 m²/ha). Also, Old-growth forest contained more stem carbon (0.12±0.00 Mg/ha) than Re-growth forest (0.02±0.00 Mg/ha). *Funtumia elastica* had the highest stem density, followed by *Cola millenii* in Old-growth and Re-growth forests.

Tree stem height class distribution

For this study, forest structure of the grove was described by stem height and diameter class distributions and species diversity. In this way, stem heights were classified into five distinct height classes in each identified forest. Lower canopy layer (6-15 m) had the highest stem density of 258 and 217 stems/ha in Old-growth and Re-growth forests, respectively, followed by

Middle canopy (16-25 m) while the least stem density was in emergent (≥ 36 m). There was no tree stem in the emergent height class of Re-growth forest (Figure 2). However, the stem density of Old-growth at ground level was approximately five times the Re-growth forest. Stem density of the Old-growth forest was higher than the Re-growth forest at the identified five distinct height classes. Therefore, there was a difference in stem density between Old-growth and Re-growth forests at ground level, middle canopy, upper canopy and emergent layer. Also, there was a significant difference in stem density within the height classes of Old-growth and Re-growth forests. The ground level and lower canopy of Old-growth forest contained mostly ingrowths or newly-recruited, young tree stems.

Diameter distribution of the tree stems

There was a difference in diameter distribution of Old-growth and Re-growth forests, if the larger dbh trees are considered in the comparison. The class (10-20 cm dbh) contained the highest stem density in Old-growth forest (29.6% of stems) and Re-growth forest (36.0% of stems) while the least stem density occurred at diameter class of 200 to 210 cm of Old-growth and 100-110 and 140-150 cm of Re-growth forest (Figures 3 and 4). Although diameter classes of 90-100, 110-120, 140-170, and 180-200 cm dbh were not represented in Old-growth forest because no stem was found in these classes (Figure 3). The dbh distribution of Old-growth forest was extended to 200 to 210 cm dbh and therefore expressed extended reverse J-shaped curve. Similarly, the dbh distribution of Re-growth forest was extended to 140 to 150 cm dbh and therefore expressed rotated sigmoid curve.

The values of Shannon-Weiner diversity index for the Old-growth and Re-growth forests were 3.22 and 2.85, respectively (Table 2). Also, the values of Simpson diversity index for Old-growth and Re-growth forests were 0.95 and 0.93, respectively; while the species evenness for the Old-growth and Re-growth forest types were 0.91 and 0.88, respectively. The mean values of Margalef index of species richness were 6.46 and 5.15 for the Old growth and Re-growth forests, respectively. The values of

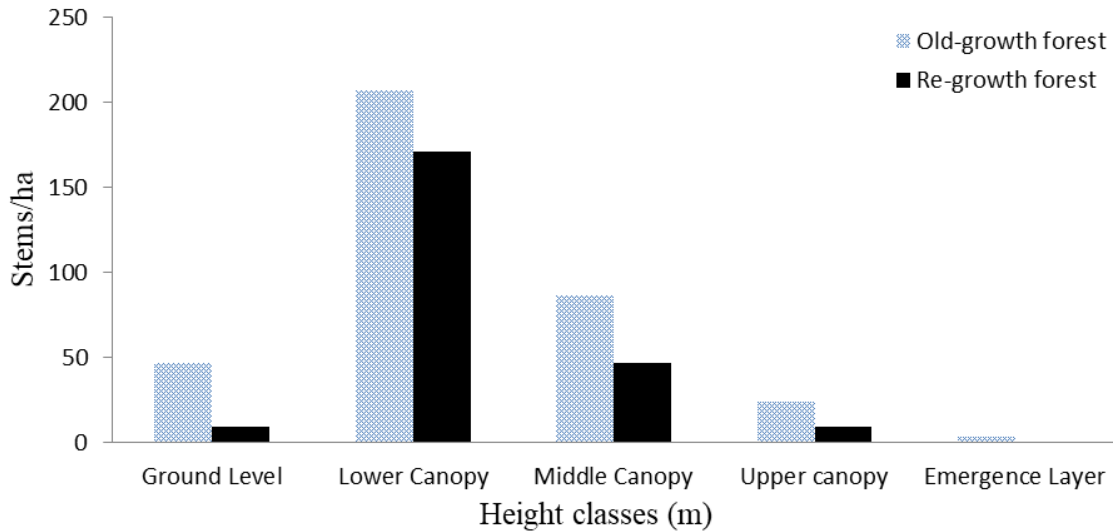


Figure 2. Stem height distribution of trees in the Old-growth and Re-growth forests of Osun-Osogbo Sacred Grove.

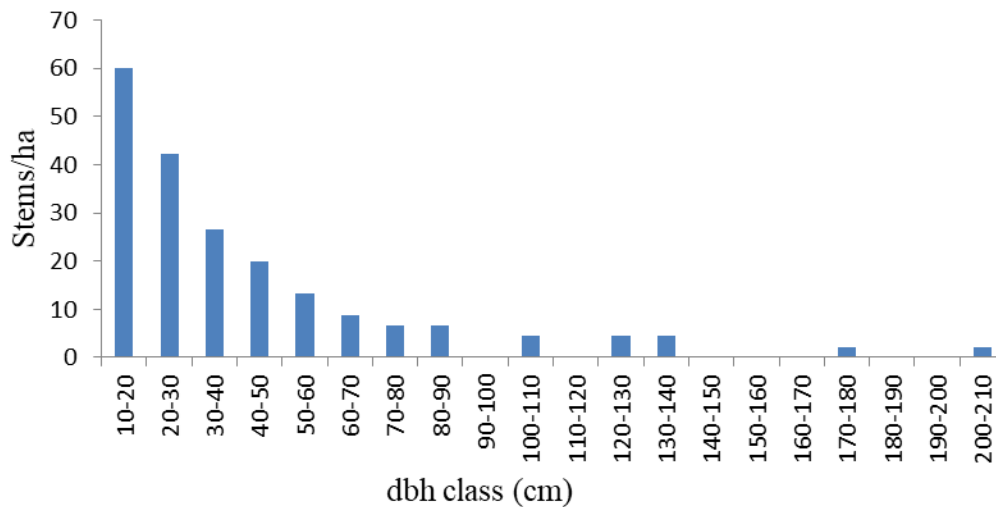


Figure 3. Diameter distribution of tree stems of Old-growth forest in Osun-Osogbo Sacred Grove.

tree species diversity were higher in Old-growth forest than Re-growth forest. These indicated that Old-growth forest has a stable structure.

Soil physical properties at different depths of Osun-Osogbo Sacred Grove

The value of soil bulk density of Old-growth forest ranged from 1.40 ± 0.16 to 1.71 ± 0.11 g/cm^3 with a mean of 1.60 ± 0.132 g/cm^3 (Table 3). Also, soil bulk density of the Re-growth forest ranged from 1.41 ± 0.09 to 1.70 ± 0.10 g/cm^3 with a mean of 1.65 ± 0.10 g/cm^3 (Tables 3 and 4). These indicate that value of bulk density increased with

increase in soil depth in both forest types. However, the Re-growth forest had higher value of soil bulk density than Old-growth forest at the surface and deep soil depth. The least and highest values were obtained in surface and deep soil of Old-growth forest, respectively. The surface soil of the Old-growth forest, with the least soil bulk density, had the highest and least proportions of sand and clay, respectively. There was no difference in the soil textural classes among soil depths but showed variation in the proportion of sand, silt and clay. Hence, high proportion of sand may be attributed to bulk density at the surface soil depth of the Old-growth.

The carbon stock of the Re-growth forest decreased with increase in soil depth. The surface, subsoil and deep

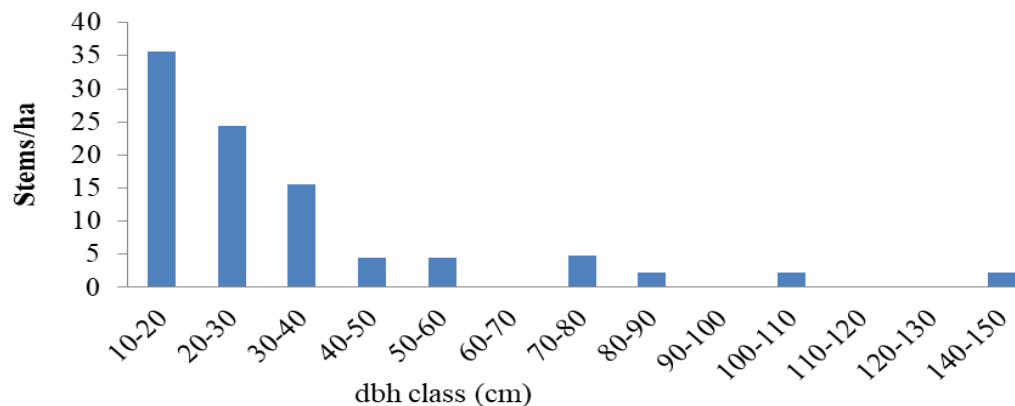


Figure 4. Diameter distribution of tree stems of Re-growth forest in Osun-Osogbo Sacred Grove.

Table 2. The Values of diversity indices of Old-growth and Re-growth forests.

Variable	Old-growth forest	Re-growth forest
Shannon-Weiner (H^1)	3.22	2.85
Simpson diversity index	0.95	0.93
Species evenness	0.91	0.88
Species richness (Margalef index)	6.46	5.15

Table 3. The values of soil physical properties at different depths of the Old-growth forest.

Depth (cm)	Soil bulk density (g/cm^3)	Soil carbon stock (Mg/ha)	Clay (%)	Silt (%)	Sand (%)	Textural class
0-15	1.40±0.16	0.58±0.45	5.38±0.48	4.68±0.57	89.94±0.81	Loamy sand
15-30	1.68±0.12	0.65±0.29	6.32±0.45	4.34±0.64	89.34±1.00	Loamy sand
30-45	1.71±0.11	0.49±0.24	7.04±1.56	4.84±0.82	88.12±2.30	Loamy sand

Table 4. The values of soil physical properties at different depths of the Re-growth forest.

Depth (cm)	Soil bulk density (g/cm^3)	Soil carbon stock (Mg/ha)	Clay (%)	Silt (%)	Sand (%)	Textural class
0-15	1.41±0.09	0.90±0.34	5.34±0.25	3.36±0.43	91.30±0.49	Sand
15-30	1.76±0.10	0.71±0.40	5.60±0.49	4.66±0.29	89.74±0.49	Loamy sand
30-45	1.70±0.10	0.63±0.17	6.00±0.49	4.54±0.89	89.46±1.03	Loamy sand

soil of the Re-growth forest contributed 40.17, 31.69 and 28.12% of the total soil carbon stock across three depths down to 45 cm, respectively (Table 4). The proportion of sand decreased and clay increased with increase in soil depth. Soil carbon stock of the Re-growth forest decreased from surface to subsoil (22.2%) and subsoil to deep soil (11.26%). The surface soil of the Re-growth forest, with the least bulk density, had the highest proportions of carbon stock and sand. The surface, sandy soil is more coarse in texture than the underlying loamy

soil layers in the Re-growth forest.

DISCUSSION

Funtumia elastica and *Cola millenii* are dominant species in the two forest types. Dominant species are species that had wide adaptation and tolerance capability to most micro-sites in the grove. The high value of species diversity and richness in the Old-growth forest was

probably due to the presence of numerous micro-climatic conditions and differences in habitat preference among the species, which enhances the high association of various resident tree species. The high richness and diversity of tree species within a forest is caused by numerous micro-sites and niches for various tree species. This is because tree species vary in their ecological requirements (Huang et al., 2003; Whitmore, 1993). Therefore, it implied that the Old-growth forest presented more micro-sites than the Re-growth forest. According to the value of the Shannon-Weiner and Simpson diversity indices, the Old-growth forest was more stable and resilient than the Re-growth forest. Also, it indicates that abundance and stem density of trees were relatively high in the Old-growth forest, which suggests stability and a balanced ecosystem. An ecosystem is stable if its structure and function remain almost the same or that it quickly returns to equilibrium after disturbance. The Old-growth forest can be described as a primary Old-growth forest, because important attributes of Old-growth include the presence of large diameter trees (Figure 2) and noticeable abundance of dead wood (snags and logs) that were observed during the field work. These attributes characterize Old-growth forests and were confirmed by studies of Piovesan et al. (2005). According to Maguran et al. (2013), the species evenness is a key measure of the community structure and it shows closeness in abundance of resident plant species. Although both forests have a high value of species evenness, the species evenness of the Old-growth forest was higher than the Re-growth forest. High species evenness implies that there was little or no rare species in the grove.

The stem density at five canopy layers of the Old-growth was higher than the Re-growth forests. The lower canopy stratum was well developed in the grove and contained closely growing plant stems. The suppressive effect of this layer probably led to extreme reduction of stem density at ground level in the grove. The stem size distribution of both Old-growth forests expressed an extended reverse J-shaped curve; while Re-growth forests expressed a rotated sigmoid curve. A rotated sigmoid stem size distribution is characterized by a steep decrease in tree density in smallest and largest diameter classes and a plateau or no representation in the middle diameter classes (Piovesan et al., 2010). Westphal et al. (2006) confirmed that forests lacking large stems are more likely to show a rotated sigmoid form of diameter distribution. This indicated that few trees were available at higher dbh classes but many small dbh stems were available in the forest.

The Old-growth forest showed high stem density in the lower stem dbh class (10-20 cm) followed by a gradual decrease and few representatives in the middle classes. This indicates numerous ingrowths and good reproduction, but low recruitment in intermediate classes. The intermediate classes were poorly represented, but

the upper limit class (200-210 cm dbh) was represented.

However, the Re-growth forest showed high stem density in the lower dbh class followed by a rapid decrease and a few representatives in the middle class. This suggests good reproduction but discontinuous recruitment. Lack of middle class in the population clearly indicates that there were few stems of reproductive size, and this can retard the regeneration rate. Re-growth forests lack trees of size 60-70 and 90-100 cm dbh. It suggests good reproduction but bad recruitment. Therefore, the distribution of stem size classes in Old-growth was significantly different from that in the Re-growth forests at large dbh classes. However, there was high stem density of smaller dbh stems in Old-growth and Re-growth forests. High stem density at lower canopy and small dbh classes in the grove suggest intense competition for light and space among recruits and ingrowths of Old-growth and Re-growth forests. Old-growth forests had high values of tree diversity indices and height distribution. This confirmed the study of Huang et al. (2003) that forest structure and species composition influence species diversity and also high species diversity is often related to more complex vertical structure.

Soil carbon stock of the Old-growth forest initially increased from surface (0-15 cm) depth to subsurface (15-30 cm) layer and decreased to the deep (30-45 cm) layer. Therefore, subsurface (15-30 cm) depth had the highest soil carbon stock in the Old-growth forest. However, soil carbon stock of Re-growth forest decreased with increase in soil depth. Hence, highest and least soil carbon stocks of the Re-growth forest occurred in surface (0-15 cm) and deep (30-45 cm) layers, respectively. This indicates that there are different factors responsible for the accumulation of carbon in the two forest types. Movement of dissolved organic carbon derived from litter decomposition and high proportion of sand may be responsible for carbon accumulation in the Old-growth forest. Overall, the amount of soil carbon stock of the Re-growth forest was higher than Old-growth forest. This is probably because of its close proximity to the Osun-Osogbo water body, which passes through the Re-growth forest. Manns et al. (2016) revealed that soil that remains moistened for most times of the year has potential for carbon accumulation and stabilization. Hence, a developed forest structure of the Old-growth forest may have influenced tree stem carbon; but was unable to enhance soil carbon stock. This confirmed the study of Hobbey and Wilson (2016) that high soil carbon stock at soil surface may be controlled by water availability above field capacity, which limits plant growth and favours soil carbon accumulation. Hu et al. (2015) also reported that different mechanisms may be responsible for the accumulation of stand biomass carbon and soil organic carbon in tropical forests. Therefore, forest structure may not determine the amount of soil carbon stock of the grove.

CONCLUSIONS AND RECOMMENDATIONS

Forest structure of the Old-growth forest showed five distinct height strata and sustained high tree species diversity with negative exponential diameter distribution. Therefore, the structural attributes of the Old-growth forest were more developed than the Re-growth forest. Old-growth and Re-growth forests showed large tree stem carbon and soil carbon stock, respectively. Therefore, structural attributes of the Old-growth forest may have influence its tree-stem carbon and not the soil carbon. Hence, Old-growth forests can be considered advantageous for tree stem carbon reservoir, and Re-growth forest for soil carbon reservoir. The tree stems and soil components of Osun-Osogbo sacred grove are important carbon reservoirs for climate change mitigation. The grove is rich in vascular species diversity but diameter distribution indicated there is poor growth and inadequate self-replacement of adult and emergent tree stems. Gap creation and appropriate cultural practices should be undertaken to improve the regeneration of the emergent species.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Review

Wild potatoes of series *Circaeifolia* (*Solanum* section *Petota*) in the Bolivian Andean region, a new evaluation of its distribution

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The *Circaeifolia* series species are only from Bolivia. They are species that have particular morphological characteristics different from any other within the *Petota* section. The taxa of the series *Circaeifolia*, *Solanum circaeifolium*, *Solanum capsicibaccatum* and *Solanum soestii* (recently grouped as *Solanum stipuloideum* Rusby) have been distinguished by morphological characteristics and molecular analysis, however, they are not completely elucidated. Until 1994, some taxa, *S. circaeifolium* and *S. soestii*, had been considered "rare" because of their restricted geographic distribution. However, with recent data a new situation can be inferred for these *Circaeifolia* species. *S. soestii*, may be considered "rare" because it is confined to its type of locality or have restricted geographic distribution; conversely, *S. circaeifolium* and *S. capsicibaccatum* have a greater known distribution until 1994. Besides, several factors, such as anthropogenic activities (forest plantation, urbanization and agriculture expansion) and others related to climate change, like drought and forest fires, are threatening their extinction.

Key words: Section *petota*, rare species, climate change.

INTRODUCTION

Crop wild relatives have a long history of use in potato breeding, particularly for pest and disease resistance (Castañeda-Álvarez et al., 2015). The members of series *Circaeifolia* (*Solanum* section *Petota*) (2n) are solely endemic to Bolivia (Ochoa, 1990), and can be found growing wild in the Yungas region of the Department of La Paz, the Choro-Ayopaya localities of the highlands and Caine River areas in the Cochabamba Department, and up to Valle Grande in the Department of Santa Cruz

(Hawkes and Hjerting, 1989; Ochoa, 1990). The series have three-member species: *Solanum circaeifolium* Bitt. (Hawkes, 1994), *Solanum capsicibaccatum* Cárdenas and *Solanum soestii* Hawkes and Hjerting (Hawkes and Hjerting, 1989), although Ochoa (1990) proposed that the infraspecific category *S. circaeifolium* var. *capsicibaccatum* (Cárd.) Ochoa should also be included. Amplified fragment length polymorphism (AFLP) analysis has confirmed the three accepted species to be distinct

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(Spooner and Salas, 2006), although all have a whitish, stellate flower (Figure 1C) and elliptical or lanceolate fruits (Figure 1F) that distinguish them morphologically from the other species of *Solanum* section Petota (Hawkes and Hjerting, 1989; Ochoa, 1990; Spooner and Salas, 2006). Recently, these species of Circaeifolia series were regrouped in the taxa *Solanum stipuloideum* Rusby (Spooner and Knapp, 2013; Spooner et al., 2014). Hawkes (1994) indicated that *S. circaeifolium* and *S. soestii*, are among the eleven wild species "rare" potatoes of Bolivia (Table 1). However, subsequent prospecting studies have shown that some of the species in the Circaeifolia series have greater distribution (Figure 2) and others may still be considered "rare", but some anthropogenic activities are threatening their survival. For the current review, we consider each species separately taking into account the morphological characteristics described by Hawkes and Hjerting (1989) and Ochoa (1990). This paper records their presently known distributions and some factors related with anthropogenic activities and probable genetic erosion.

S. CIRCAEIFOLIUM

S. circaeifolium was collected in 1855-1861 (although Cárdenas (1973) indicates a date of 1864) by Gilbert Mandon in the Cerro Iminapi locality at an altitude of 2930 m about 6 km from the town of Sorata (Larecaja Province, Department of La Paz) (Ochoa, 1990) on the Sorata-Tacacoma road. It was not described, however, until 1912, by George Bitter. After collecting the species in 1944, Cárdenas (1973) wrote that "around the bottom of the hill there were some shacks and cultivated areas with different crops. Ascending the slope, we found this curious wild potato in loose sandy ground...".

The aforementioned name 'Cerro Iminapi' alludes to a mountain, the peak of which is visible from all around the Sorata area (Figure 1A). Now known as Laripata, this small rural town is in the process of urbanization. The mountain above it has been almost completely cleared of its natural vegetation and is dominated by traditional agricultural land (Figure 1B). *S. circaeifolium* grows among the bushes on the borders dividing the plots. New areas of distribution for the species have been reported in the area of influence of the Sorata Valley, including Cotaña locality near to Viacha (Figure 1D), Condorpata and San Pedro, and in the localities of Italaque and Cotusi-Mocomoco in the Province Camacho in the north of the Department of La Paz (Coca Morante and Castillo, 2007) (Figure 2). In the area of Cotaña, there is also a remarkable process of urbanization and agricultural exploitation with the loss of the original coverage (Figure 1D and E); but, in the other localities due to their geographical remoteness, they are less affected by the anthropogenic

activities. Among the local farmers, this well-known wild species goes by the Aymarian (a native Bolivian language) names of "Monte Ch'ogue" (forest potato) and "Monte Phureja" (phureja potato). The first refers to its being found in the forests that once covered the Sorata Valley, of which now only remnants are left. The second refers to the color and shape of the flower, which is reminiscent of certain varieties of phureja potatoes (*Solanum phureja*) traditionally grown in this area. *S. circaeifolium* is tolerant to potato late blight, caused by *Phytophthora infestans* (Simko et al., 2007), and known to local farmers as "Llejti" (Aymarian for 'leaf burn'), the latter is one of the most destructive of all potato disease. In summary, *S. circaeifolium* is endemic to the temperate and humid micro regions of the North Department of La Paz and, these areas are threatened by the deforestation for agriculture expansion and urbanization process. It also grows in other Departments of Bolivia, but in a very isolated manner and they are threatened by the urbanization process, expansion of agriculture and prolonged droughts of recent years.

S. CAPSICIBACCATUM

S. capsicibaccatum was collected in 1942 by Gandarillas in the Huayrapata and Molle Pujru localities, in the watershed of the Rio Caine (altitude 2800 m) in Tarata Province, Department of Cochabamba (Cárdenas, 1973) (Figure 2). It was described by Martín Cárdenas in 1944 (Cardenas, 1944). The distribution data provided by Hawkes and Hjerting (1989) and Ochoa (1990) suggest the species is endemic to the latter Department. Tunari National Park, an area of potential distribution in the Department of Cochabamba (2700-3300 m) has not been surveyed for the species (Coca Morante and Coca Salazar, 2014) (Figure 2). It is found in both dry and damp, temperate microclimates, but in the latter, where it can be found in greater numbers in the Liriuni, Iscaypata, Taquiña and Chaqhomayu localities (Figure 2), but it is often threatened by some fungal plant pathogens (*Septoria lycopersici*) (Figure 1G) and anthropogenic factors such as deforestation, forest fires, prolonged droughts and expansion of agriculture. Recently, new information has identified *P. infestans* resistance genes originating from *S. verrucosum*, *S. schenckii*, and *S. capsicibaccatum* that could be mapped to potato chromosomes 6, 4, and 11, respectively (Jacobs et al., 2010). According to Guzman and Rodriguez (2008), forest fires in the Tunari National Park (PNT) have been considered as the factor of disturbance that has been causing the most damage to the ecosystem. In this area, due to frequent forest fires, urbanization expansion, and intensive agriculture, this wild species, is in the process of extinction. New potential areas of distribution for *S. capsicibaccatum*

Table 1. Rare Bolivian wild potato species according to Hawkes (1994).

Series	Specie	Ploidy	Distribution area (Department)	Reference
Tuberosa	<i>Solanum achacachense</i>	2x	La Paz	Hawkes and Hjerting (1989)
	<i>Solanum avilesii</i>	2x	Santa Cruz	Hawkes and Hjerting (1989)
	<i>Solanum neocardenasii</i>	2x	Santa Cruz	Hawkes and Hjerting (1989)
	<i>Solanum okadae</i>	2x	La Paz y Chuquisaca	Hawkes and Hjerting (1989)
Megistacroloba	<i>Solanum astleyi</i>	2x	Potosí y Chuquisaca	Hawkes and Hjerting (1989)
Conicibaccata	<i>Solanum violaceimarmoratum</i>	2x	La Paz y Cochabamba	Hawkes and Hjerting (1989)
	<i>Solanum bombycinum</i>	4x	La Paz	Ochoa (1990)
Circaeifolia	<i>Solanum circaeifolium</i> spp <i>circaeifolium</i>	2x	La Paz	Hawkes and Hjerting (1989)
	<i>Solanum soestii</i>	2x	La Paz	Hawkes and Hjerting (1989)
Commersoniana	<i>Solanum arnesii</i>	2x	Chuquisaca	Hawkes and Hjerting (1989)
	<i>Solanum flavoviridens</i>	3x	La Paz	Hawkes and Hjerting (1989)

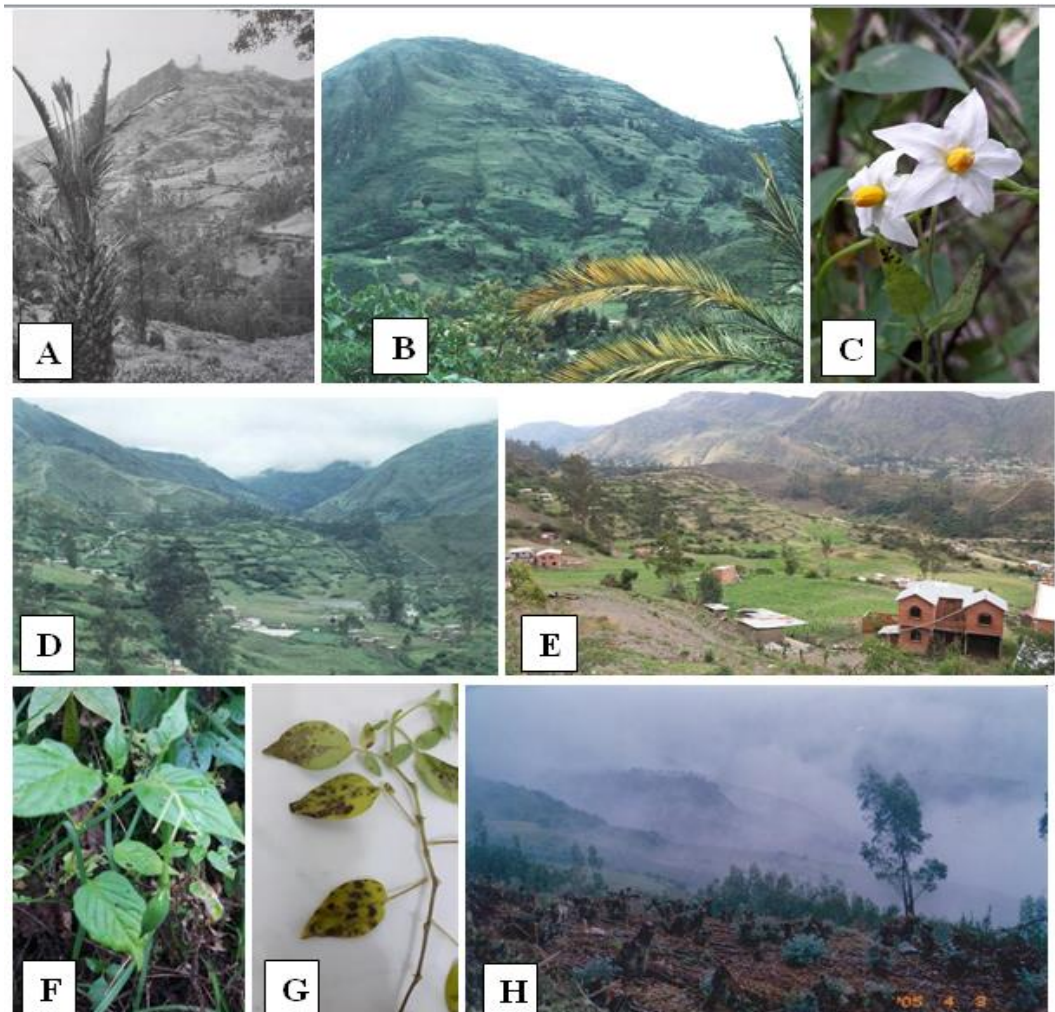


Figure 1. A. Historical photo from book “The Potatoes of South America: Bolivia” of Carlos Ochoa (1990): mountain slope (Cerro Iminapi) near Sorata habitat of *Solanum circaeifolium*; B. Actual photo (year 2018) of cerro Iminapi; C. Stellate flower of *Circaeifolia* species; D. Photo of Cotaña locality, year 2002; E. Actual photo of Cotaña locality, year 2018; F. Capsicum fruit of *S. circaeifolium*; G. Leaves of *S. capsicibaccatum* affected by *S. lycopersici*; H. Forest plantation on Quime locality, type locality of *S. circaeifolium*, *S. soestii* and *S. okadae* (year 2018).

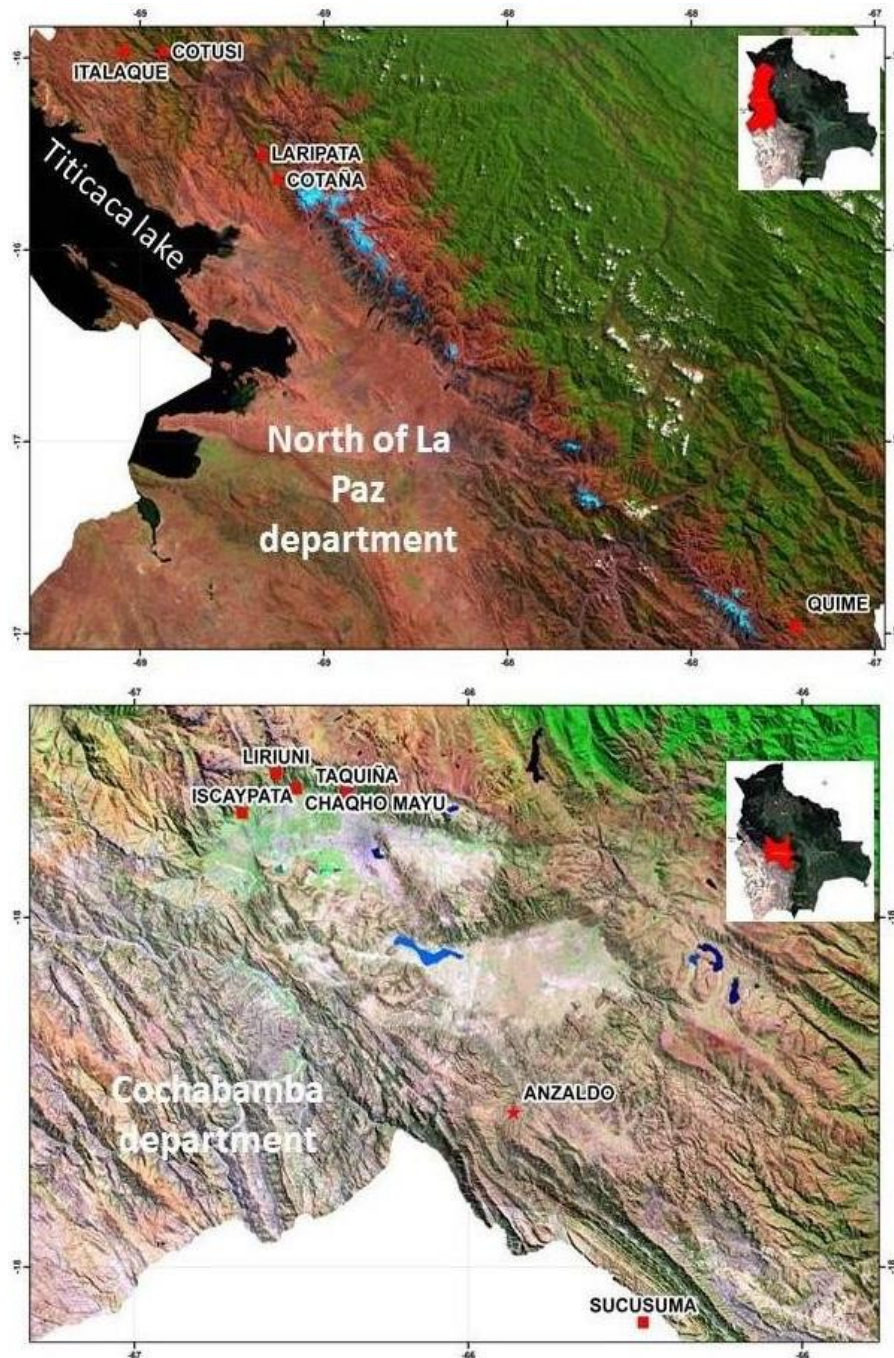


Figure 2. (Top map) New records areas of *S. circaeifolia*, North of La Paz Department localities: Italaque, Cotusi and Cotaña and (Bottom map) *S. capsibaccatum*, Cochabamba Department localities: Iscaypata, Liriuni, Taquiña, Chaqhomayu. Source: Map elaborated by Javier Burgos Villegas, CISTEL, FCAyP, UMSS.

mainly fall within the Department of Cochabamba. Generally, this species is associated with *Solanum brevicaule* in its distribution, and is known to farmers as the "Apharuma" potato. It is generally considered to be a weed, and is commonly eliminated from the borders of farm plots.

S. SOESTII

S. soestii was collected by Lock van Soest on an expedition to the region of Inquisivi, near 4.5 m on the road from Inquisivi to Quime (Inquisivi Province, Department of La Paz) (Hawkes and Hjerting, 1989)

(Figure 2). The species was described, however, by Hawkes and Hjerting (1989), using material collected on an expedition undertaken by Hawkes, Avilés and Hoopes in 1981 (Hawkes and Hjerting, 1989). An assessment of rare species conducted in 2004-2005 showed *S. soestii* to grow in a place known as Rosasani, midway between Quime and Inquisivi in the Department of La Paz (Coca Morante and Castillo, 2007). No other reports are known. These reports confirm the Hawkes (1994) hypothesis, which indicated that *S. soestii*, is among the eleven wild species "rare" potatoes of Bolivia. This species is, therefore, rare from the viewpoint of its distribution. In this locality it is threatened with extinction due to the drastic change in vegetation from natural coverage to forest plantations of *Eucalyptus* species (Figure 1H).

In conclusion, regarding the series *Circaeifolia* species, *S. circaeifolium*, it is evident that it has a greater geographical distribution in the north of the La Paz department, but is affected by rural urbanization and the agriculture expansion; *S. capsicibaccatum*, has greater distribution in the Tunari Mountain of the Cochabamba Department, but is affected by frequent forest fires, urbanization and the agriculture expansion; finally, *S. soestii*, has evident restricted distribution in the Quime and Inquisivi locality, Department of La Paz, and is mainly affected by the forest plantations expansion with *Eucalyptus* spp.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Full Length Research Paper

Woody fodder species in three agro-ecological Parklands of Arba Minch Zuria Woreda, Gamo Gofa Zone, Southern Ethiopia

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This study was conducted in Arba Minch Zuria Woreda of SNNPR, Ethiopia on Parkland agroforestry practices in three agro-ecological zones. The objective of the study was to investigate the fodder tree and shrub species composition, richness, diversity and structure. Key Informant Interviews and Focus Group Discussions were held. In total, ninety 50 m × 20 m plots were laid and standard procedures were followed. Forty nine woody species belonging to 43 genera and 31 families were identified as fodder species. Fabaceae represented by 7 species and Combretaceae and Moraceae (3 species each) were the most diverse families. Mid altitude ($H'=2.98$) is more diverse followed by High altitude ($H'=2.23$) and Low altitude agro-ecology ($H'=1.94$). Species in the low altitude were densely populated and have large basal area followed by mid altitude and high altitude. The top most important species with highest Importance Value Index (IVI) were *Ficus sur* (51.90), *Ficus sycomorus* (46.484) and *Mangifera indica* (60.161) High altitude, middle altitude and lower altitude, respectively. Generally, in the study area, there were diverse fodder trees and shrubs, all likely sources for farmers to feed livestock. So, there should be strong management and conservation practices to ensure future availability, continuous awareness raising efforts, and further study should be conducted for nutritional evaluation.

Key words: Fodder, diversity, Parkland, Arbaminch Zuria Woreda, agroforestry practices.

INTRODUCTION

It has been reported that status of animal protein deficiency in developing world is caused by shortage of forage (Azim et al., 2011; Gaikwad et al., 2017). This constraint mainly limits the realization for exploitation of the full potential of the livestock resources. If animals are not properly fed, they cannot express their genetic

potential for production and reproduction (Adugna et al., 2012).

Fodder tree and shrub are increasingly recognized as an important component of animal feeding; especially as available supplies of protein in many parts of world. Different scholars (Chakeredza et al., 2007; Abebe et al.,

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2008; Aynalem and Taye, 2008) studied and published reviews about the importance of these fodder trees and shrubs in different areas at different times.

Livestock production provides smallholders with a number of benefits, but it also possesses real threats to the environment, which can be mitigated through agroforestry interventions (Dawson et al., 2014). The production of livestock in East Africa has to date mostly focused on these interventions (Cecchi et al., 2010; Dawson et al., 2014; Baudron et al., 2015).

The fodder obtained from trees or shrubs, containing high levels of crude protein, mineral matter and digestibility, are acceptable by the livestock, because of their deep root system; they continue to produce well into the dry season (Dicko and Sikena, 1992; Paterson et al., 1998). They are also considered to be an important contributor to grazing livestock nutrition in rainy areas (Lefroy et al., 1992; Devendra, 1997; Abebe et al., 2008). During the prolonged dry and crop fallow season, farmers traditionally use leaves of indigenous fodder tree species to meet nutritional requirement of grazing or browsing livestock (Lefroy et al., 1992; Otsyina et al., 1999; Gaikwad et al., 2017).

Traditional agroforestry practices are common in various parts of Ethiopia like coffee shade tree systems, scattered trees on the farmland (Parkland agroforestry), homegarden, woodlots, farm boundary practices, and trees on grazing land (Endale, 2019).

The southern region of Ethiopia is endowed with indigenous agroforestry practices that have evolved over years, and which have enabled maintenance of the region's greenery, with its magnificent ecological and socio-economic benefits (Tesfaye, 2005; Molla, 2016). The region is known for its diverse and immense biodiversity of resources in different natural and agroforestry settings (Tesfaye, 2005; Mengistu and Asfaw, 2016; Aklilu and Melaku, 2016; Molla, 2016).

Tree and shrub resources from natural forests are lost due to agricultural expansion and high human and livestock pressure associated with land degradation and feed shortage (Geist and Lambin, 2002; Feddema et al., 2005; FAO, 2010; DeFries et al., 2010, Chakravarty et al., 2012; Kissinger et al., 2012; Hosonuma et al., 2012; Tadesse and Solomon, 2014). This holds true also for fodder tree and shrub species despite high demand of these species for feeding livestock in the community to get increased products.

To cope with such problems, agroforestry is considered as the best solution (Nair, 1993; Bhagwat et al., 2008; Alao and Shuaibu, 2013; Atangana et al., 2013; Atangana et al., 2014).

Livestock in the Ethiopian rift valley mainly depend on grazing of natural grasses and crop residues (Belete et al., 2012; Yisehak et al., 2014). As a result, there are issues of sustainability of natural forests and other reservoirs. The Gamo Gofa zone, generally, and Arba Minch Zuria Woreda, particularly, is not exceptional. Traditionally, there are fodder trees and shrubs grown in

and around farm lands that the livestock can utilize as fodder in the agroforestry practices.

The land use systems where there is scattered tree and shrubs in a farmer's crop field are commonly called Parklands; and agroforestry practice is most traditional in these areas. Despite these convenient tree- and shrub-based agricultural systems, there are no previous reports on fodder tree and shrub species in the Arba Minch Zuria Woreda of the Gamo Gofa zone. So the current study investigated the composition, richness, diversity and structure of woody species, which serve as animal feed, in the three main agro-ecological zones of Ethiopia: highland (2300-3200masl), midland (1500-2300masl) and lowland (500-1500masl).

MATERIALS AND METHODS

Description of study area

Location and topography

The study was conducted in three kebeles namely Chano Mile representing lowland, Dega Ocholo representing midland and Zigiti Merche representing highland of Arba Minch zuria woreda of Gamo, Southern Ethiopia (Figure 1).

Arba Minch Zuria is one of the woredas in the Southern Nations, Nationalities, and Peoples' Region of Ethiopia. A part from the Gamo Gofa Zone located in the Great Rift Valley, Arba Minch Zuria is located roughly between 5°70" -6°21" N latitude and 37° 31"- 37° 67" E longitude. The woreda is found at about 500 km south of Addis Ababa, capital city of Ethiopia.

Topography of the *woreda* is characterized by escarpment and narrow valleys. The slope ranges between 20 and 70% which has resulted in massive soil erosion. The altitude of the woreda lies between 1150 and 3300 masl.

The drainage patterns follow the general topographic orientation, so that small rivers rising from Gamo highlands drain to Lake Abaya and Lake Chamo. Among these, Hare and Baso drain to Lake Abaya; whereas Kulfo, Sile and Sego Rivers drain to Lake Chamo (AZWANaRDO, 2016/2017).

Climate and soil

Out of 29 kebeles in Arba Minch Zuria Woreda, 10 kebeles (33%) are in lowland, 15 kebeles (53%) are in midland and the remaining 4 kebeles (14%) are in highland agro-ecology (AZWANaRDO, 2017).

The average annual temperature of the woreda ranges from 16 to 37°C, varying between July and March. Rainfall distribution in the woreda is bimodal with a long rainy season from the beginning of March to the end of May with maximum rainfall around the month of April (228 mm), and a short rainy season from mid-August to mid-October. The minimum rainfall is recorded in January (18 mm) (AZWANaRDO, 2017).

As Mateos (2003) stated, the soils under the forest and the state farm are composed of three main types: Fluvisols, Gleysols and Vertisols. Fluvisols consist of soil materials developed in alluvial deposits and flood plains. Accordingly, it is mainly quaternary volcanic alluvial deposits and lacustrine clay.

According to AZWANaRDO (2017), the total land area of the woreda is about 168,172 ha from which 60,605 ha are occupied by settlements, roads, and others, 45,916 ha are arable land, 34,137 ha are cropland, 15,163 ha are forest land, 8,450 ha are water

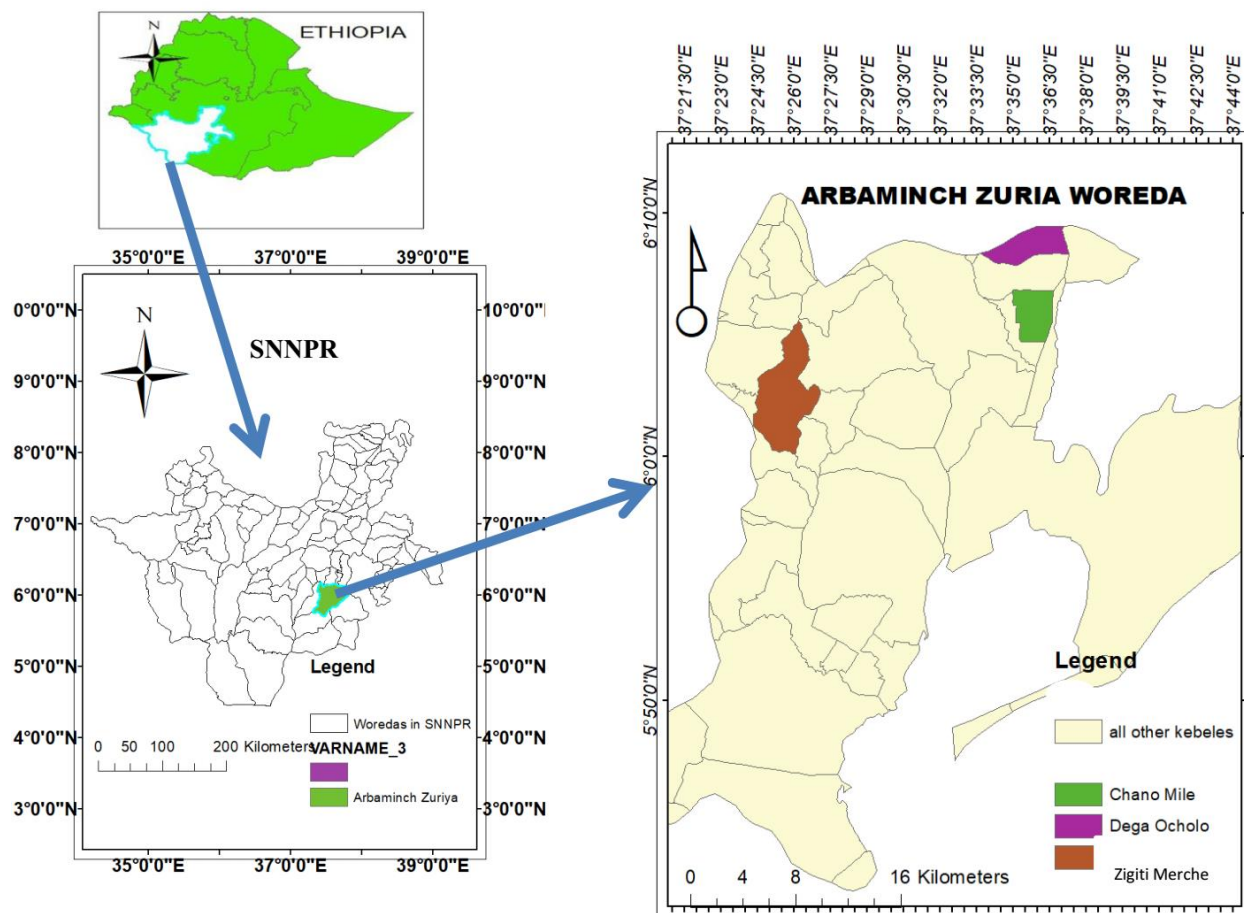


Figure 1. Map of the study area.

bodies, 3,563 ha are grazing land, and 338 ha are non-arable land.

Sampling and data collection

Site selection and sampling techniques

The study was conducted in three selected kebeles of Arba Minch Zuria Woreda, that is, Chano Mille (1,178-1,233 masl), Dega Ocholo (1,600-2,200 masl) and Zigiti Merche (2,220-2,682 masl), each from lowland, midland and highland agro-ecology, respectively. The study kebeles were selected purposively based on their suitability and accessibility for the researcher. Reconnaissance was carried out to get firsthand information about the landuse/land cover types of the area so that sampling plots could be established in appropriate way.

To ascertain the Parkland agroforestry practice of each *kebele*, an inventory was conducted using a transect walk. Thus, along each transect line, the available identified fodder tree and shrub species were inventoried in each of the 50 m × 20 m (1000 m²) sample plots. In total ninety, sample plots (that is, 30 from each *kebele*) were laid. The distance between each of the transects and plots was 500 and 400 m, respectively. But, areas like roads, stone gorges, and natural forests were not considered. The first plot was selected randomly and subsequent plots were systematically selected. In addition to these, an agricultural development expert

(DA), focus group discussant (FGD), and key informants (KII) were selected. As a result, one agricultural development expert and four key informants were purposively selected from each *kebele*. The key informants were the model farmers who were knowledgeable about animal production and fodder tree feeding/farming as an agroforestry practice by adapting techniques used by den Biggelaar (1996). The participants of group discussion were selected by the help of experts (DAs). Specifically, they were drawn from elder farmers and village leaders in each *kebele*.

Data collection method

Key informants (knowledgeable model cattle breeders), personal experiences and observation were deployed to identify fodder tree/shrub species in the study area. For the identified fodder trees/shrub species, the local name, part edible by the animals and the type of animals that mostly prefer the species were identified and further confirmed by the FGDs as well. Species identification for common species was done in the field using different plant identification keys as references (Azene, 2007). But for others species, identification was done by an expert botanist in the discipline.

All identified fodder tree and shrub species in each plot of the Parkland agroforestry were counted and recorded. For those tree and shrub species with DBH ≥ 2.5 cm, DBH and height

measurements were taken using tree caliper and clinometer, respectively. Where topography made the height measurement difficult, height was estimated using a graded 5-m tree pole. The altitude of each plot and garden was recorded using GPS. Particular events like experience of planting the fodder species, and fodder foliages collected by farmers were also photographed to complement observations on the ground.

Data analysis

Diversity, richness and structure

Fodder tree and shrub species diversity of parkland agroforestry practices was calculated using Shannon diversity index (H') (Kent and Coker, 1992). Each of the Shannon diversity index was converted to effective number of species (True diversity) for comparison. The Shannon diversity index is calculated as follows:

$$H' = -\sum_{i=1}^s (P_i * \ln P_i) \quad (1)$$

where H' is the Shannon-Wiener index of species diversity, s is the number of species in community, P_i is the proportion of total abundance represented by the i^{th} species, and \ln is natural log. True diversity was calculated and expressed in terms of number.

$$\text{True diversity} = e^{H'} \quad (2)$$

where e is the base of the natural logarithm and H' is Shannon-Wiener index.

Structure

The structure of fodder trees and shrubs were characterized in terms of Density, Basal Area, Frequency and Importance Value Index (IVI) as recommended by Newton (2007) and Leul et al. (2010). The structural parameters for fodder trees and shrub species, including Density, Basal Area, Dominance, Frequency and Importance Value Index were analyzed and calculated using the relative standard equation as the following.

Density

This is the most important structural parameters to be considered during vegetation data analysis calculated as:

$$\text{Density} = \frac{\text{total No of individual species}}{\text{sample area in hectare}} \quad (3)$$

$$\text{Relative density} = \frac{\text{total number of individuals of aspecies}}{\text{total number of all species}} \times 100 \quad (4)$$

Basal area

It is the cross-sectional area of woody stems at breast height or at 1.37 m. It is calculated as:

$$BA = \frac{\pi (DBH)^2}{4} \quad (5)$$

where $\pi = 3.1416$, BA = basal area (m^2), DBH = diameter at breast height (cm).

Dominance of species

This is calculated as follows:

$$\text{Dominance} = \frac{\text{area covered by species}}{\text{sum of all plot areas in Ha}} \quad (6)$$

$$\text{Relative dominance} = \frac{\text{basal area of single species}}{\text{total basal area of all species}} \times 100 \quad (7)$$

Frequency

It is defined as the probability of finding a species in a given sample area or quadrat (Mata et al., 2011). Two frequency values were computed for each woody species encountered within the study plots:

$$F = \frac{\text{Number Of Plots In Which Species Occured}}{\text{total number of sample plots}} \times 100 \quad (8)$$

$$RF = \frac{\text{Frequency of a species}}{\text{Frequency of all species}} \times 100 \quad (9)$$

where F is frequency and RF is relative frequency.

Important value index (IVI)

This is used to express the relative ecological significance of the species in the ecosystem. It was calculated by summing up the relative dominance, relative density and relative frequency of the species (Kent and Coker, 1992) calculated as follows:

$$IVI = RF + Rd + RD \quad (10)$$

where IVI stands for importance value index, RF for relative frequency and Rd for relative density and RD for relative dominance. The species floristic and structural data were analyzed using Microsoft excels version 10 software.

RESULTS AND DISCUSSION

Species composition

A total of 49 species belonging to 43 genera and 31 families were identified as fodder trees and shrubs from the three agro-ecologies. The species were also distributed among different families in different proportions. Accordingly, Fabaceae was represented by 7 species; both Combretaceae and Moraceae were represented by 3 species; Anacardiaceae, Boraginaceae, Buddlejaceae, Meliaceae, Myrtaceae, Rubiaceae, Verbenaceae, and Oleaceae were represented by 2 species each; and the rest of the families were represented by one species each. The species reported in this study were in agreement with the previous

literature in other areas. For instance, species such as *Acanthus pubescens*, *Buddleja polystachya*, *Celtis africana*, *Combretum molle*, *Milletia ferruginea*, and *Terminalia schimperiana* were reported as fodder species from Wolaita zone by Takele et al. (2014). *Annona senegalensis*, *Acacia albida*, *Kigelia africana* and *Terminalia brownii* were also reported as important browse species in improvement of livestock feeds in western Bahr El Ghazal State of Sudan by Gaiballa and Lee (2012). *Cordia africana*, *Ehretia cymosa* and *Vernonia amygdalina* were reported as multipurpose fodder trees in Ethiopia by Abebe et al. (2008). *Leucaena leucocephala*, *Azadirachta indica* and *Psidium guajava* were reported as fodder species from the scarcity zone of Maharashtra in India (Gaikwad et al., 2017). *Grevillea robusta*, *Persea americana*, *Mangifera indica* and *Carica papaya* were reported from Kenya as fodder species by Gachuiiri et al. (2017). Most of the species identified in this study were also reported as fodder in different parts of Ethiopia by Azene (2007).

Richness

The species richness of the fodder tree and shrub were 19, 32 and 19 in lowland, midland and highland, respectively. This shows species richness is higher at midland with an irregular pattern at increasing altitudes. This could be because of suitability of the mid agro-ecology for different species. Besides, this can be explained in terms of fewer disturbances in midland.

Diversity

In terms of fodder tree and shrub species, Parkland agroforestry of midland ($H' = 2.98$, 20 species) is more diverse followed by highland ($H' = 2.23$, 9 species) and lowland agro-ecology ($H' = 1.94$, 7 species). This report is in disagreement with the report by Tesfaye (2005) and Shimono et al. (2010), who reported that species diversity and richness decrease with increasing altitude in a regular trend. However, species richness and diversity were higher in midland followed by Highland and Kola. This could be because species in lowland were dominated by uniform fruit plantations (homogenization) and other fodder species (e.g., *M. indica* and *Cordia africana*) unlike that of different remnant and natural regenerating species in addition to suitability of agro-ecology of midland and highland.

Structure

The structure of Fodder tree and shrub species was analyzed (Appendix 1). Accordingly, fodder tree and shrub species in the Parklands of Lowland (140

individuals ha^{-1}) were densely populated followed by Midland (114.3 individuals ha^{-1}) and Highland (88.7 individuals ha^{-1}). This result is in agreement with Yirefu et al. (2016). The authors reported that woody species density and richness decreases from lowland to highland. This could be due to the fact that to get maximum benefit of desired product (e.g., fruit) farmers might have accommodated a higher number of tree and shrubs species in Lowland.

The species such as *V. amygdalina* (25.0 individuals ha^{-1} , 28.2%), *B. polystachya* (20.67 individuals ha^{-1} , 23.3%) and *Erythrina brucei* (13 individuals ha^{-1} , 14.7%) were abundant fodder tree and shrub species in Highland (Zigit Merche). In Midland (Dega Ocholo) species such as *C. africana* (16 individuals ha^{-1} , 14%), *T. brownii* (15.3 individuals ha^{-1} , 13.4%), *Rhus vulgaris* (12.7 individuals ha^{-1} , 11.08%), and *Ficus sur* (11.3 individuals ha^{-1} , 9.9%) contributed for more of the total density of the fodder trees and shrub species. Whereas, *M. indica* (individuals ha^{-1} , 36.43%), *C. africana* (26. individuals ha^{-1} , 19.05%), and *Trichillia emetica* (11.7 individuals ha^{-1} , 8.33%) were the most abundant species in Lowland (Chano Mile).

The basal areas of the species in Parkland of the respective agro-ecology regions varies from 0.320 $m^2 ha^{-1}$ in Highland, 0.893 $m^2 ha^{-1}$ in Midland to 1.005 $m^2 ha^{-1}$ in Lowland, respectively. The fodder tree and shrub species with the highest basal area in Parkland agroforestry practice of Highland were *Ficus sur* (0.110 $m^2 ha^{-1}$, 34.45%), *C. africana* (0.09 $m^2 ha^{-1}$, 28.09%), *E. brucei* (0.031 $m^2 ha^{-1}$, 9.55%) and *Dombeya torrida* (0.018 $m^2 ha^{-1}$, 5.68%). *Ficus sycomorus* (0.385 $m^2 ha^{-1}$, 43.06%), *Ficus vasta* (0.145 $m^2 ha^{-1}$, 16.25%), *P. americana* (0.077 $m^2 ha^{-1}$, 8.93%) and *F. sur* (0.053 $m^2 ha^{-1}$, 5.96%) were the species that contribute highest percent of the total basal area of the species in the Parkland agroforestry of Midland. While *F. sycomorus* (0.502 $m^2 ha^{-1}$, 50%), *K. africana* (0.161 $m^2 ha^{-1}$, 16%), *A. albida* (0.093 $m^2 ha^{-1}$, 9.3%) and *Moringa stenopetala* (0.047 $m^2 ha^{-1}$, 6.68%) were species that accounted for largest share of total basal area of species in Lowland.

The most frequent species in Parkland agroforestry of Highland were *V. amygdalina* (67%), *B. polystachya*, *E. brucei* (50%), *F. sur* (37%), *Galiniara saxifraga* and *Hibiscus calyphyllus* (20%).

In Midland, frequent species in Parkland agroforestry were *F. sur* (56.7%), *C. africana* (50%), *R. vulgaris* (40%), *T. brownii* (30%), *Acacia tortilis* and *H. calyphyllus* (23%).

The species such as *M. indica* (90%), *C. africana* (73%) *A. indica* (53%), *T. emetica* (47%), and *Moringa stenopetala* (40%) were most frequent species in Parkland of lowland.

The top most important fodder woody species with highest IVI were *F. sur* (51.90), *F. sycomorus* (46.484) and *M. indica* (60.161) in highland, midland and lowland agroecologies, respectively and species with least value of IVI were *L. leucocephala*, *Caesalpinia decapetala* nd

A. senegalensis, respectively in Highland, Midland and Lowland. As Whittaker and Niering, (1975) puts forward, the IVI is an important index for summarizing vegetation characteristics and ranking species for management. Accordingly, species with lower IVI value (more sparse or among least dense) need high conservation effort, while those with higher IVI value require less management attention.

Conclusion

The results of the present study showed that, the Parkland agroforestry practices in Arba Minch Zuria Woreda is rich in woody species, which animals prefer for food (so-called fodder tree and shrubs). About 49 fodder tree and shrub species that belong to 43 genera and 31 families were identified from the aforementioned practice. The midland (Woina dega) had higher species richness and diversity than other agro-ecologies. Density, basal area and abundance of individuals of species decreased lowland (Kola) to highland (Dega) agroecology. This could be due to human interferences and management practices, suitability of agro-ecology and nature of the species. The species with highest values of IVI (e.g., *F. sur*, *F. sycomorus* and *M. indica*) require less conservation effort than species with lower value of IVI (e.g., *L. leucocephala*, *C. decapetala* and *A. senegalensis*). Generally, in the study area, there were diverse fodder trees and shrubs that may be promising for farmers to feed to livestock, while obtaining ecological and socioeconomic merits. Thus, further actions and topics for research are recommended as following. The awareness of the farmers on the utilization and management of this potential species should be continuously advocated, open traditional systems particularly open grazing could significantly result in severe land degradation. Farmers should adopt and feed cut carry feeding system of available species from their crop field. The woreda agriculture and livestock sector should integrate agroforestry in their annual extension plan in general and silvopastoral system, in particular. The role of agroforestry systems and practices for livestock farmers should be acknowledged at the national, regional and even at woreda levels. Further research on nutritional value, propagation, management and interaction of fodder species with annual crops and economic analysis of the species is highly recommended for the study area.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Appendix 1. The structure of fodder trees and shrub species in Parkland agroforestry in three agro-ecologies of Arba Minch zuria woreda.

Scientific name	Density (individuals ha ⁻¹)	Basal area (m ² ha ⁻¹)	Frequency (%)	IVI	AE
<i>Buddleja polystachya</i> Fresen.	20.667	0.004	50.00	39.011	
<i>Erythrina brucei</i> Schweinf.	13.000	0.031	50.00	38.772	
<i>Galiniera saxifraga</i> Hochst.	4.667	0.003	20.00	12.130	
<i>Psydrax schimperiana</i> (A.Rich.)	0.667	0.001	3.33	2.086	
<i>Ficus sur</i> Forsik.	6.000	0.110	36.67	51.901	
<i>Nuxia congesta</i>	0.333	0.017	3.33	6.506	
<i>Vernonia amygdalina</i>	25.000	0.005	66.67	49.327	
<i>Grevillea robusta</i>	1.333	0.009	6.67	6.281	
<i>Acanthus pubescens</i>	1.333	0.001	16.67	6.526	
<i>Hibiscus calyphyllus</i>	1.333	0.001	20.00	7.508	High altitude
<i>Dombeya torrida</i>	2.333	0.018	6.67	10.253	
<i>Leucaena leucocephala</i>	0.333	0.001	3.33	1.568	
<i>Cordia africana</i>	1.000	0.090	6.67	31.157	
<i>Syzygium guineense</i>	6.333	0.007	13.33	13.236	
<i>Schrebera alata</i>	1.000	0.013	3.33	6.036	
<i>Caesalpinia decapetala</i>	0.333	0.001	6.67	2.539	
<i>Lippia adoensis</i>	1.000	0.001	10.00	4.206	
<i>Pittosporum viridiflorum</i>	1.000	0.009	3.33	4.787	
<i>Rubus sanctus</i>	1.000	0.001	16.67	6.170	
Total in High altitude	88.667	0.320	343.33	300	
<i>Terminalia schimperiana</i> Hohst	0.667	0.013	6.67	3.572	
<i>Persea americana</i> Mill.	1.000	0.077	3.33	10.254	
<i>Ficus vasta</i> Forsik	1.667	0.145	10.00	19.963	
<i>Acacia seyal</i> Delile var.	2.000	0.001	6.67	3.413	
<i>Millettia ferruginea</i> (Hochst.)	3.667	0.014	20.00	9.288	
<i>Erythrina brucei</i> Schweinf.	3.000	0.049	16.67	11.925	
<i>Solanum incanum</i> L.	3.333	0.001	20.00	7.506	
<i>Acacia tortilis</i> Forsk.	5.000	0.024	23.33	12.328	Mid altitude
<i>Psydrax schimperiana</i> (A.Rich.)	1.000	0.002	3.33	1.876	
<i>Ficus sur</i> Forsik	11.333	0.053	56.67	28.653	
<i>Terminalia brownii</i>	15.333	0.010	30.00	21.340	
<i>Vernonia amygdalina</i>	3.333	0.008	16.67	7.625	
<i>Grevillea robusta</i>	1.000	0.005	3.33	2.237	
<i>Dovyalis abyssinica</i>	2.333	0.004	13.33	5.488	
<i>Moringa stenopetala</i>	0.667	0.012	3.33	2.708	

Appendix 1. Contd.

<i>Acanthus pubescens</i>	1.333	0.001	3.33	1.979	
<i>Lippia javanica</i>	3.000	0.001	10.00	4.959	
<i>Ficus sycomorus</i>	1.333	0.385	10.00	46.484	
<i>Dombeya torrida</i>	1.667	0.003	6.67	3.344	
<i>Hibiscus calyphyllus</i>	5.667	0.000	23.33	10.275	
<i>Mangifera indica</i>	1.667	0.005	6.67	3.524	
<i>Rhus vulgaris</i>	12.667	0.002	40.00	20.337	
<i>Cordia africana</i>	16.000	0.022	50.00	27.692	
<i>Syzygium guineense</i>	0.667	0.004	3.33	1.829	
<i>Schrebera alata</i>	0.333	0.031	10.00	6.062	
<i>Hypericum quartinianum</i>	3.667	0.001	3.33	4.037	
<i>Caesalpinia decapetala</i>	0.333	0.000	3.33	1.098	
<i>Dodonaea viscosa</i>	1.000	0.001	3.33	1.767	
<i>Nuxia congesta</i>	2.667	0.003	6.67	4.166	
<i>Combretum molle</i>	1.000	0.011	6.67	3.575	
<i>Lippia adoensis</i>	4.000	0.001	13.33	6.563	
<i>Maytenus sp.</i>	2.000	0.001	10.00	4.134	
Total in Mid Altitude	114.333	0.893	443.33	300	
<i>Persea americana</i>	1.333	0.009	10.00	4.010	
<i>Annona senegalensis</i>	0.667	0.006	6.67	2.517	
<i>Trichilia emetic</i>	11.667	0.022	46.67	20.349	
<i>Kigelia africana</i>	3.667	0.161	26.67	24.267	
<i>Terminalia brownii</i>	6.333	0.011	13.33	8.398	
<i>Acacia albida</i>	3.333	0.093	16.67	15.202	
<i>Grevillea robusta</i>	2.667	0.021	13.33	6.785	
<i>Moringa stenopetala</i>	10.000	0.067	40.00	22.271	
<i>Ehretia cymosa</i>	2.000	0.004	13.33	4.628	
<i>Citrus aurantifolia</i>	3.333	0.004	10.00	4.866	Low altitude
<i>Leucaena leucocephala</i>	1.000	0.003	10.00	3.093	
<i>Mangifera indica</i>	51.000	0.047	90.00	60.161	
<i>Cordia Africana</i>	26.667	0.029	73.33	37.413	
<i>Azadirachta indica</i>	7.667	0.002	53.33	16.949	
<i>Carica papaya L</i>	4.667	0.008	20.00	8.351	
<i>Acacia seyal</i>	0.333	0.008	6.67	2.428	
<i>Caesalpinia decapetala</i>	1.667	0.001	10.00	3.358	
<i>Ficus sycomorus</i>	0.333	0.502	6.67	51.650	

Appendix 1. Contd.

<i>Psidium guajava</i>	1.667	0.007	6.67	3.304
Total in Low altitude	140.000	1.005	473.33	300
Total in all agro-ecology categories	343.000	2.218	1260.00	900

Note : AE for agroecology and IVI for important value index

Full Length Research Paper

Analysis of socio-economic contribution of agroforestry systems to smallholder farmers around Jimma town, Southwestern Ethiopia

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Integration of trees into land use practices is an old-aged experience of smallholder farmers in Southwest Ethiopia. The contribution of this practice is much undermined. The objective of this study was to assess socio-economic contributions of agroforestry system to smallholder farmers around Jimma town, Southwest Ethiopia. A total of 199 households were proportionally sampled from the three selected sites (Mazora, Waro kolobo, and Merawa). A semi-structured questionnaire was used to collect data from sampled households. Data collected were analyzed using descriptive statistics and an econometric model. The results show that tree-based agroforestry, land-use practice is an integral part of smallholder farmers' livelihoods in the study sites, and furthermore a tree has socio-economic benefits. An average household income from trees was estimated to be 2592, 4652 and 1922 ETB in Mazora, Waro kolobo, and Merawa sites, respectively. Smallholder farmers appreciated trees more importantly from the socio-economic points of view in home garden, pasture land and woodlot, across sites. Education level, tree planting experience, and major livelihood positively and significantly influenced income derived from tree products, while livestock possession was negatively and significantly affecting income in the study sites. In general, tree-based agroforestry land use practice is the most crucial for improving smallholder farmer's livelihoods. Therefore, tree-based agroforestry land use practice should be encouraged in the study sites.

Key words: Agroforestry system, income, livelihoods, socio-economic.

INTRODUCTION

Agroforestry system is an integrated approach to solving land use problems. According to FAO (2013), it is a form of sustainable land use systems that combine tree with

crop or animal husbandry simultaneously and sequentially. Literature has shown that due to its economic and social benefits, agroforestry is the common

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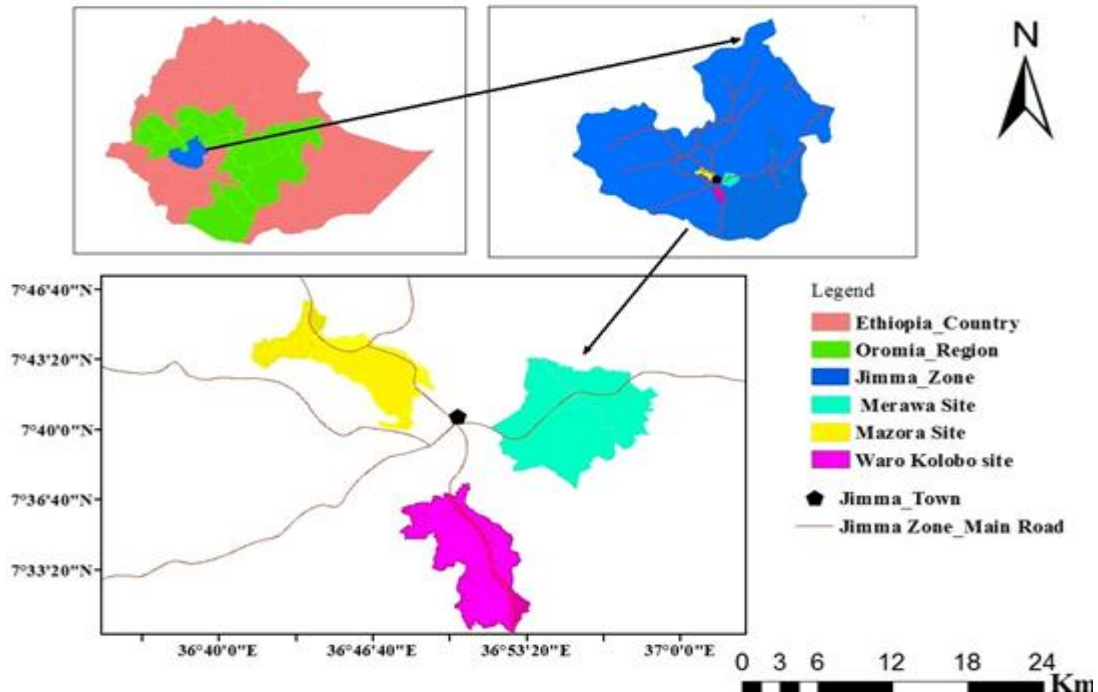


Figure 1. Map of the study sites.

experience that has been promoted throughout Africa (Mbow et al., 2014).

The Federal Government of Ethiopia has strengthened the agroforestry extension package as one of the rural development strategies in the country Ministry of Agriculture and Rural Development (MOARD, 2005). As a result, the agroforestry practice has been expanded throughout the country to maximizing production and maintaining livelihoods of farmers from fixed land use. For example, in Sidama, South Nations, Nationalities and People Regional State (SNNPRS), there are different types of agroforestry practices such as tree-enset-coffee, tree-enset, woodlot, scattered trees on farmland and pasture land, and boundary planting (Asfaw and Agren, 2007; Madalcho and Tefera, 2016). Smallholder farmers are more habituated with enset-coffee home garden agroforestry system in Sidama zone (Abebe et al., 2010). This is due to the fact that its contribution in providing income is well known (Kebebew and Urgessa, 2011), including sources of firewood, coffee shade and timber (Muleta et al., 2007). Given this, many studies have been conducted on agroforestry systems (AFS) in Southwestern Ethiopia; however, most of them have given little or no emphasis on the socio-economy of AFS. As a result, there is a gap of information to policymakers, to the government and to smallholder farmers because they do not have an equal understanding about the socio-economy of the AFS. These show that there is an inadequate study of research in the study sites. Therefore,

this research was conducted to fill a gap in the study sites.

The aims of this study were to: (1) assess the socio-economic benefits of agroforestry for smallholder farmers, (2) investigate and estimate the income contribution of tree products of AFS to smallholder farmer's annual income, and (3) determine factors that influence income derived from tree products of AFS in the study sites.

MATERIALS AND METHODS

Study sites

The study was conducted around Jimma town of Oromia Regional State within a 20-km radius, at Mazora, Waro kolobo, and Merawa sites, in Southwest Ethiopia. Jimma town is located at 352 km distance to Southwest from Addis Ababa, the capital city of Ethiopia (Tefera et al., 2014). Geographically, it lies between latitude 7°40' N and 36°50' E longitude with an average elevation of 1750 m above sea level (Figure 1).

The temperature fluctuates between 6 and 31°C. An average annual rainfall ranges from 1138 to 1690 mm (Alemu et al., 2011). Table 1 shows a detailed description of the study sites. The Oromo are the dominant inhabitants in the area; because of this, Afan Oromo language is the most commonly spoken language.

Socio-economic activity

The livelihood of smallholder farmers depends on the mixed crop-livestock system on a subsistence scale. Teff, maize, sorghum,

Table 1. Description of the study site.

Variable	Mazora site	Waro Kolobo site	Merawa site
Total population size	9540	15281	18665
Male	4660	7616	10262
Female	4880	7665	8403
Household head	2360	2646	3094
Area (Ha)	3403.5	3516.5	7932
Elevation	2029	1814	1459

Source: Woreda Agriculture and Natural Resource Management Offices (WANRMO) (2016).

Table 2. Number of households and sample size proportional determined across the study sites.

Site	Numbers of households	Sample size determined proportional
Mazora	2360	58
Waro Kolobo	2646	65
Merawa	3094	76
Total	8100	199

coffee, fruit crops, vegetables, potato, pulse, and enset are the dominant crops grown in the study sites (Kechero et al., 2013). Maize is the most staple food crop in the study sites. Cows, oxen, goats, sheep, and poultry are a livestock commonly known in the study sites. Tree-based agroforestry land use practice is commonly known in the sites. Smallholder farmers have experience in the use of the home garden, farmland, coffee farm, and woodlot land uses agroforestry practices (Kebebew and Urgessa, 2011). Among them, coffee-based agroforestry practice is the main one in the sites.

Smallholder farmers obtain their annual income from crops, livestock, trees products, and off-farming activity. Coffee and khat are the most important cash crops in the study sites.

Study site selection

A reconnaissance survey was conducted before the actual survey to capture information about the agroforestry practice and coverage surrounding of Jimma town within a 20 km radius. During this, the intensity and extent of tree-based agroforestry practice and accessibility of roads were identified. Consequently, four districts were chosen: Mana, Seka chekorsa, Dedo and Kersa of Jimma Zone; including eight sites, namely Mazora, Yabu, Somoddo, Doyyo, Waro kolobo, Bore, Kachama, and Merawa.

Multistage sampling techniques were applied to select sampled households. At the first stage, Jimma zone was selected purposively. In the second stage, three districts Mana, Dedo, and Kersa were purposively selected based on reconnaissance results. In the third stage, three sites, namely Mazora from Mana, Waro kolobo from Dedo and Merawa from Kersa districts were selected purposively. On the final stage, a total of 199 household heads were randomly sampled, which were determined by using the Yemane (1967) Equation 1.

$$n = \frac{N}{1+N(e^2)} \quad (1)$$

where n is sample size, N is the size of population and e is the desired level of precision.

According to Yemane (1967), the margin of error varies between 5 and 10%. The marginal error of 7%, the confidence level of 95% and tabulated $Z_{0.25} = 1.96$ were used. Then the proportional size samples in each kebele were determined by Equation 2, and finally by summing up the total sample size of each site; which defines the entire sample of the study sites as well.

$$n_i = \frac{N_i \cdot n}{N} \quad (2)$$

where n_i is the determined proportional sample size, N_i represents the household (HHs) size of the i^{th} strata, n is the sample size determined in Equation 1 and N is the total number of HHs (Table 2).

Data collection

Both primary and secondary data were collected and used. Primary data was collected from sampled households through semi-structured and structured questionnaires, key informant interview, focus group discussion (FGD) and field observation. Secondary data was collected from a different source such as books, reports, journal articles and websites, and unpublished sources. The questionnaire was initially written in English, and then translated into the local language 'Afan Oromo' for the purpose of avoiding an information impurity during data collection and enhancing the validity of the data. Before using it in the main survey, the questionnaire was pre-tested using 30 farmers from the three sites. Then, a questionnaire was modified by incorporating the results obtained in order to collect accurate data for this study site.

Information about socio-economic and demographic characteristics of household (HHs); name, age, family size, level of education, numbers of livestock, total land size and major livelihood activity were collected from the sampled HHs.

Table 3. Description of dependent and independent variables with their expectation.

Independent variable	Unit	Description	Hypothesis
Sites (X1)	Categorical	0=Mazora site 1=Waro kolobo site 2=Merawa site	Positive relationship
Sex (X2)	Dummy, takes the value of 1 if female and 0 otherwise		Male head HHs positive relationship and other negative
Age (X3)	Year	Continuous	Negative relationship
Family size (X4)	Number	Continuous	Negative relationship
Education level (X5)	Grade	Continuous	Positive relationship
Total land size (X6)	Hectare	Continuous	Positive relationship
Experience of tree planting (X7)	Year	Continuous	Positive relationship
Livestock (X8)	TLU	Continuous	Positive relationship
Livelihoods activities (X9)	Dummy, takes the value of 1 if agriculture and 0 otherwise (agriculture and off-farm)		Agriculture and off-farm activity is negative relationship

The total annual HHs income was quantitatively collected from individual HHs in the study sites. In this case, any products (tree, livestock, and crop) used for house consumption was not included in cash. The amount of income estimated was only for one year (January 1, 2016-December 31, 2016). Data about annual household income from tree products (timber, fruit, firewood, pole, and charcoal) was collected from individual farmers by asking the amount of actual cash they obtained. An annual household income from crop products (coffee, khat, maize, teff) and from livestock products (egg and milk) and animal sales (cattle, donkey, mule, horse, sheep, goats and poultry) was collected from individual households. The qualitative information about the benefit (socio-economic) of tree-based agroforestry land use practice was collected from sampled HHs.

Data analysis

Both quantitative and qualitative data were first summarized, categorized and coded, then entered into Microsoft Excel 2007, and finally copied into Statistical Package for the Social Science (SPSS) Version 20. Socio-economic and demographic characteristics of HHs such as ages, family size, level of education, land holding size, wealth status and the contribution of AFS to HHs were analyzed through descriptive statistics such as frequency, percentage, mean, maximum and minimum then presented in the form of a table. Finally, a Chi-square test was used to test the significance of some categorical variables while mean comparisons were tested by one-way analysis of variance (ANOVA). The data obtained from FGD, key information and field observations were expressed in narrative forms.

Factors affecting income derived from tree products were analyzed by using multiple linear regression models. It was developed to visualize whether or not the dependent and independent variables were significantly related or not. The general model used in multiple linear regressions was as follows:

$$Y_i = B_0 + B_1X_1 + B_2X_2 + \dots + B_9X_9 + \epsilon_i \quad (3)$$

where Y_i is the i^{th} total annual income obtained from tree products,

B_0 =intercept, B_1 to B_9 are coefficients of an independent variable. X_1 to X_9 are explanatory variables (age, sex, family size, land holding size, sites, livestock holding, tree planting experience, level of education, and livelihood activity) which influence (Y_i); and ϵ_i is an error term.

The study hypotheses indicated that these independent variables have an effect on the amount of income derived from tree products in the study sites. The pretesting of explanatory variables were explained in Table 3. The assumption for SPSS and Multiple regression was tested through normality (predicted probability (P-P) plot), linearity (Histogram and scatterplots), homoscedasticity, and multicollinearity (Variance Inflation Factor (VIF) and tolerance).

RESULTS AND DISCUSSION

Socio-economic and demographic characteristics of household

The results for socio-economic and demographic characteristics showed that among the sampled households 86.2% were male heads of households in Mazora and Waro kolobo, whereas 88.2% were male-headed households in Merawa site (Table 4). The range in ages of respondents in Mazora site was a minimum of 20 and a maximum of 70 and in Waro Kobolo, a minimum of 22 and maximum of 75; while in Merawa site the minimum was 21 and maximum was 75. The average age of respondents was 43.40, 47.77 and 42.63 years in Mazora, Waro Kobolo, and Meraw sites, respectively. The difference in average age of members of HHs was statistically significant ($p < 0.05$) among the study sites. The minimum and maximum education levels of respondents were estimated to be zero and ten (10), with a mean of 3.9, 2.74 and 2.66 in Mazora, Waro Kobolo, and Merawa sites, respectively. There was a statistically

Table 4. Socio-economic and demographic characteristics of household farmer per the study site.

Household characteristic		Mazora (%)	Waro Kolobo (%)	Merawa (%)	Average (%)	(χ^2)
Sex	Female	13.8	13.8	11.8	13.1	0.922
	Male	86.2	86.2	88.2	86.9	
Major sources of livelihoods						
Agriculture only	-	93.1	92.3	94.7	93	0.837
Agriculture and off-farm	-	6.9	7.7	5.3	7	
Wealth status	Rich	22.4	38.5	11.8	24	0.006*
	Medium	37.9	29.2	47.4	38	
	Poor	39.7	32.3	40.8	38	
P-value						
Age (years)	Minimum	20.0	22.0	21.0	21	0.012*
	Maximum	70.0	75.0	75.0	73	
	Mean	43.40	47.77	42.6	44.6	
Family size (Numbers)	Minimum	3.0	3.0	3.0	3	0.325
	Maximum	10.0	10.0	10.0	10	
	Mean	6.6	6.2	6.1	6.3	
Education level (Years)	Minimum	0.0	0.0	0.0	0	0.032*
	Maximum	10.0	10.0	10.0	10	
	Mean	3.9	2.74	2.66	3.1	
Tree planting experience (years)	Minimum	2.0	2.0	3.0	2	0.003*
	Maximum	32.0	39.0	32.0	34	
	Mean	13.26	14.92	12.9	14	

*The mean difference is significant at the 0.05.
Source: Field Survey (2016).

significant difference in education levels ($p < 0.05$) among the study sites.

Land use types

Land-use types identified in the study sites were: home garden, farmland, coffee farm, pasture land and woodlot (Table 5). The total average of home garden landholding size per HHs was 0.19, 0.34 and 0.76 ha in Mazora, Waro Kolobo, and Merawa sites, respectively. Kebebew et al. (2011) reported that the size of each home garden ranged from 0.01 to 1 ha, with an average of 0.15 ha from Southwestern, Ethiopia. Differences in the size of home gardens were statistically significant different ($p < 0.05$) among the study sites.

The size of land classified in the category of coffee farm estimated in descending order for Mazora and Waro kolobo and Merawa sites was 26.9, 14.7, and 19.1 ha.

Coffee land size was statistically significant different ($p < 0.05$) among the study sites. Around 4.3, 14.1 and 3.3 ha of land was allocated as woodlots in Mazora, Waro kolobo, and Merawa sites, respectively. Generally, an average landholding size per HHs was 1.46 ha, 1.84 ha and 1.73 ha in Mazora, Waro kolobo, and Merawa sites, respectively. Correspondingly, Kechero et al. (2013) also reported that the size of land holding per HHs varied, generally from 0.25 to 2.5 in Jimma, Southwestern Ethiopia.

Socio-economic contribution of tree-based agroforestry practice to smallholder farmer

In the study sites, tree-based agroforestry practices contribute various socio-economic benefits, which enabled smallholder farmers to fulfill their livelihood requirements. Those tree products are firewood, charcoal,

Table 5. Land use types across Mazora, Waro Kolobo, and Merawa sites.

Land use types	Mazora site		W/kolobo ste		Merawa site		Average values (ha)	P- value
	Area (ha)	%	Area (ha)	%	Area (ha)	%		
Home garden	10.8	13	21.8	18	25.9	20	19.5	0.000*
Farmland	34.6	41	52.4	44	60.3	46	49.1	0.026*
Coffee farm	26.9	32	14.7	12	19.1	14	20.2	0.000*
Pasture land	8.1	10	16.6	14	23.2	18	16.0	0.014*
Woodlot	4.3	5	14.1	12	3.3	3	7.2	0.000*
Average of land size per HHS	1.46		1.84	-	1.73	-	1.19	-
Total land size	84.7	100	119.6	100	131.8	100	112.0	0.051*

*The mean difference is significant at the 0.05.

Source: Field Survey (2016).

Table 6. Socio-economic benefits of tree-based agroforestry land uses across the study sites.

Site		Socio-economic benefits						
		Income (%)	Charcoal (%)	Construction (%)	Firewood (%)	Fodder (%)	Timber (%)	Fruit (%)
Mazora	HG	60	6.9	46.6	46.6	13.8	34.5	62.1
	FL	41.4	15.5	15.5	46.6	25.9	20.7	-
	CF	46.6	20.7	15.5	25.9	10.3	15.5	-
	PL	20.7	10.3	25.9	41.4	36.2	10.3	-
	WL	82.8	-	51.7	48.3	-	-	-
Waro kolobo	HG	62.1	-	41.5	32.3	18.5	36.9	55.4
	FL	32.3	9.2	13.8	41.5	9.2	46.2	-
	CF	32.3	4.6	18	18.5	23.1	9.2	-
	PL	41.5	4.6	41.5	36.9	32.3	13.8	-
	WL	85.6	-	55.4	46.2	-	-	-
Merawa	HG	59.2	-	43.4	27.6	15.8	35.5	71.1
	FL	39.5	3.9	63.2	35.5	15.8	43.4	-
	CF	51.3	19.7	7.9	23.7	7.9	15.8	-
	PL	43.4	3.9	15.8	15.8	26.3	32.9	-
	WL	68.4	-	71.1	63.2	-	-	-

HG: Home garden, FL: farm land, CF: coffee farm, PL: pasture land, WL: woodlot.

Source: Field Survey (2016).

construction materials, timber, fruit, animal fodder and income (Table 6). These tree-based agroforestry products help the farmer as a source of income and also for household consumption. The integration of trees into different forms of land uses assists the farmer by providing multiple benefits. For instance, 62.1, 55.4 and 71.1% of the sampled households reported that the trees planted in the home garden provide fruit products in Mazora, Waro Kolobo, and Merawa sites, respectively. This finding concurs with Emukule et al. (2013) who reported that agroforestry practice provides fruit in Northern Rwanda. Agize et al. (2016) also reported that

farmers obtain fruit from home garden trees in Wolaita Zone, Southern Ethiopia. Similarly, Emukule et al. (2013) and Gideon and Verinumbe (2013), also reported that trees growing on farmland provide various benefits such as fodder, fuelwood, and building equipment. About 48.3, 46.2, and 63.2% of farmers were collecting their firewood from woodlot in Mazora, Waro kolobo, and Merawa sites, respectively. Therefore, household source of energy is one advantage of tree-based agroforestry products, which save many farmers from the problems that arise from shortages of energy; because, there are no alternative energy sources. This is in line with Missanjo et

Table 7. Mean annual source of household income across in the study sites.

Sources of HHs annual income (ETB)	Sites						Average values	P-values
	Mazora		Waro kolobo		Merawa			
	Mean	%	Mean	%	Mean	%		
Annual income from crop	6382.1	60.15	2409.9	26.3	3817.6	49.45	4203.2	0.000*
Annual income from trees products	2592.6	24.43	4652.2	50.8	1922.1	24.90	3055.6	0.006*
Annual income from livestock	1204.8	11.36	1399.9	15.3	1592.7	20.63	1399.1	0.784
Annual income from off-farm activity	431.0	4.06	691.5	7.6	388.2	5.03	503.6	0.632
Mean annual income	10,610	-	9154	-	7721	-	9162	-

1USD= 22.0799 Ethiopia Birr (ETB) in 2016 year. *The mean difference is significant at the 0.05. Source: Field Survey (2016).

al. (2015) and Ndalama (2015) who reported that in the rural area, farmers obtained their primary energy from tree products in Malawi. On the other hand, the value of tree products that the farmer used for house consumption, or provided as a gift to neighbors, is called subsistence income. About 51.7, 55, and 71.1% of respondents responded that they obtained construction materials from woodlot tree products in Mazora, Waro kolobo, and Merawa sites, respectively. Relatively smallholder farmers appreciate trees more importantly from the socio-economic points of view in the home garden; pasture land and woodlot across sites.

Source of households' annual income

Data in Table 7 shows that the farmers earn their annual income from a crop, tree products, livestock, and off-farm activities in the study sites. The average income from sales of crops was estimated to be 6382 (60.15%), 2409 (26.33%) and 3817 (49.46%) Ethiopian birr (ETB) in Mazora, Waro kolobo, and Merawa sites, respectively. In Mazora and Merawa sites, a crop accounted as a major source of income, because this area is mostly known by cash crop production like coffee and khat rather than other uses recorded in the Waro kolobo site. This is in agreement with Woldemariam (2003) and Megerssa et al. (2013) who reported that coffee and khat are a cash crop in Southwestern Ethiopia. The mean annual sources of household income from the agricultural crop were statistically significantly different among the study sites ($F(2,196) = 8.82, p = 0.000$).

Tree products contribute an average income of 2592 (24.43%), 4652 (50.82%) and 1922 (24.90%) ETB to annual household incomes in Mazora, Waro kolobo, and Merawa sites, respectively. This coincides with Safa (2005) who also reported from Yemen, that AFS contributes extra income for farmers who incorporate the practices of AFS compared to those who do not adopt the practice. The mean annual income from tree products was statistically significant between the study sites (F

[2,196] = 5.31, $p = 0.006$).

Mean annual income from tree-based agroforestry products

Table 8 shows the relative mean annual income from differently integrated tree products across land use types. In general, tree products help the farmer as an extra source of income through sales of timber, wooden poles, fruit, charcoal, and firewood. However, the amount of income received from tree products differs from land use types to land use across the study sites. As the sampled HHs responded that they have been getting an average annual income of 1197, 1452 and 898 ETB from home garden tree products in Mazora, Waro kolobo and Merawa sites, respectively. This concurs with Agize et al. (2016) who reported that a home garden provides an average annual income from 800 to 1500 ETB in Wolaita Zone, Southwestern Ethiopia. But it is less than findings reported by Kebebew and Urgessa (2011). They reported that home garden tree products contribute an average income of 1683 ETB to household income in Jimma zone, Southwest Ethiopia. This may be due to a different location of the study sites. The income contributed from home garden tree products (e.g., poles) to total annual household income was statistically significant ($p < 0.05$) among the study sites; whereas it is not significant for timber and fruit tree products. This may be due to the extent of *Grevillea robusta* and *Cupressus lusitanica* trees around the home garden, which the farmers used for fencing purposes in the study sites.

The average annual income contributed from woodlot tree products was estimated to be 1257, 2917 and 644 ETB in Mazora, Waro kolobo and Merawa sites, respectively. Average income obtained from woodlot products was relatively higher in Waro kolobo than other sites. This is due to the extent of woodlot cultivation in Waro kolobo site. The average annual income obtained from woodlot was statistically significantly different ($P < 0.05$) among the study sites.

Table 8. Mean annual income of tree products per land use across the study sites.

Mean annual HHs income of tree products (ETB)		Mazora Site	Waro kolobo Site	Merawa site	Average values	P-value
Home garden	Timber	38.17	41.85	177.12	85.7	0.087
	Poles	220.08	320.62	109.54	216.7	0.038*
	Fruit	939.03	1089.23	610.85	879.7	0.437
	Sub-total	1197.28	1451.7	897.51	1182.2	0.368
Farm land	Timber	14.03	33.08	103.32	50.1	0.03*
	Charcoal	11.88	32.85	00	14.9	0.372
	Sub-total	25.91	65.93	103.32	65.1	0.177
Coffee farm	Timber	20.93	31.61	67.39	40.0	0.143
	Charcoal	11.88	36.85	62.60	37.1	0.843
	Firewood	27.48	35.61	21.50	28.2	0.05*
	Sub-total	60.29	104.07	151.49	105.3	0.260
Pasture land	Timber	10.58	31.61	67.38	36.5	0.039*
	Charcoal	28.26	46.46	34.44	36.4	0.684
	Firewood	13.21	34.96	24.11	24.1	0.018*
	Sub-total	52.05	113.03	125.94	97.0	0.15
Woodlot	Poles	1239.09	2885.16	620.72	1581.7	0.000*
	Firewood	17.97	32.26	23.10	24.4	0.018*
	Sub-total	1257.06	2917.42	643.82	1606.1	0.001*

*The mean difference is significant at the 0.05.
Source: Field Survey (2016).

Data collected during FGD, farmers mentioned that they accrued extra income from integrated tree-based agroforestry products. They also confidently reported that the income they earned from agricultural crop products like maize, teff; sorghum and coffee were not regular because of some problems. These problems include crop disease, climate changes (rainfall variation) and land degradation, which in turn brings low crop production. However, the income obtained from tree products is helping them as a supplement (to regular income), which empowers the farmers to cope with such situations by enhancing the capacity to purchase household materials, inputs, cereal crops, cover some costs like fees of school and festivals. This agrees with Kebebew and Urgessa (2011) who reported that agroforestry contributes an average of 4148 ETB per household, which in turn helps them to purchase food crops.

Factors affecting income derived from tree products

The linear regression model analysis showed that out of the nine variable hypotheses, five of them were found to be significantly affecting income derived from tree products ($p < 0.05$). Three of these that positively

affected income are: total land holding size, level of education and experience of tree planting. However, the other two (numbers of livestock holding and the source of livelihood activities) were negative in effect ($p < 0.05$). The multiple coefficients of determination, R^2 was above the moderate level of fitness, which showed that 76.1% of the variation of income could be explained by the explanatory variables (Table 9). As predicted, the education level of the household head was positively and significantly ($p < 0.01$) related to the amount of income earned from tree products. This implies that educated farmers are relatively planting more trees than less-educated ones, as a means of income. For that reason when the farmer education level is increased by one grade, it would lead to increases in the income of farmers by 294.203 factors, when other variables are held constants. This coincides with Oyewole et al. (2015) who reported that educated farmer participated more in agroforestry adoption than a less educated farmer in Nigeria. Moreover, educated farmers are more interested in planting tree species than uneducated ones in Tigray, Northern Ethiopia (Gebreegziabher et al., 2010).

The total land size positively, statistically ($p < 0.01$) affected the income that farmers earned from tree products as predicted. With other factors held constant,

Table 9. Multiple linear regression results in the study sites.

Determinant factor	Unstandardized coefficients		Standardized coefficients	T	p-value
	B	St. Error	Beta		
(Constant)	7870.833	1696.894	-	4.638	0.000
Sites	25.789	239.526	0.004	0.108	0.914
Sex	133.903	541.128	0.009	0.247	0.805
Age	40.528	21.049	0.096	1.925	0.150
Family size	-32.643	95.133	-0.013	-0.343	0.732
Level of education	294.203	82.567	0.167	3.563	0.000***
Total holding land size	627.952	220.213	0.111	2.852	0.005***
Tree planting experience	80.527	29.025	0.144	2.774	0.006***
Livestock numbers	-160.772	68.674	-0.099	-2.341	0.020**
Livelihoods activities	-9687.782	871.791	-0.536	-11.113	0.000***
R ² =0.761	-		Adjusted R ² =0.750		F =66.99

** ,*** statistically significance at 5 and 1%, respectively.

when total land holding size was increased by 1 ha, the amount of income the farmer obtained from tree products also increase by 627.927 factors. This suggests that the farmers who have a large size of land participated more in retaining or planting of different tree species on their land, which in turn provided more income. This agrees with Oyewole et al. (2015) from Ekiti State, Nigeria, and Gebreegziabher et al. (2010) and Abiyu et al. (2012) from Ethiopia, who reported that farmers who have large land size participated more in tree planting than farmers with a relatively smaller size of land.

The experience of tree planting by HHs head, as predicted, was positively and significantly ($p < 0.01$) affecting income obtained from trees. This suggests that the income of households should increase by a coefficient of 80.527 when the experience of the farmer in tree planting increased by one year. This result agrees with Oyewole et al. (2015) who reported that more experienced farmers are purposively planting/retaining trees on their land compared to less experienced farmers.

Dissimilarly to the predicted results, the numbers of livestock held by HHs was negatively and statistically significant ($p < 0.05$) affecting income derived from tree products. This implies that farmers who have large numbers of livestock allocated larger portions of land for pasture than tree planting in order to feed their livestock. This is due to traditional ways of keeping livestock through free grazing. Therefore, the farmer's income from tree products is decrease by 160.772 coefficients as the farmer's numbers of livestock increased by one TLU, keeping all other variables constant. Gebreegziabher et al. (2010) reported that when the number of cattle increased, the farmers paid more attention to the livestock, and comparatively they gave less attention to tree planting in Tigray, Northern Ethiopia.

As a prior assumption forecasted, the farmer's livelihood

activity (source) negatively affected the income obtained from tree products ($p < 0.01$). This implies that a farmer who has additional livelihood source, excluding agriculture activity, they have an opportunity of getting additional income. Due to this reason, the farmers' livelihood sources were diversified. Particularly, farmers who have additional income from off-farm activity is less likely to be retaining/planting a tree, compared to farmers who have livelihood activity (crop production), because trees may take a long period to mature and return the income. Therefore, as the livelihood activity is diversified (crop production + off-farm) the amount of income obtained from trees decreases by 9687.782 factors, assuming all other factors remain constant.

CONCLUSIONS AND RECOMMENDATION

Smallholder farmers are familiar with the benefits of tree-based agroforestry land use practices in Southwestern Ethiopia. This is because farmers obtain multiple benefits from tree-based agroforestry land use under different forms of arrangements. Accordingly, farmers substantially appreciated the value of trees from a socio-economic point of view in a home garden, pasture land, and woodlot. In Mazora, Waro kolobo and Merawa, the amount of an average annual income obtained from tree products was 2592, 4652, and 1922 ETB, respectively. Respondent farmers obtained an annual cash income of 22 to 55 ETB per hectare from tree products in the study sites. Woodlot agroforestry practices provide more income than other practices. This helps them as a supplementary source of income, which enables the farmers to fulfill their family needs.

From the total of nine (9) independent variables hypothesized to affect income from tree products, five variables were found to significantly affect income derived

from tree products. Among the significant variables contributing to income are: education level, tree planting experience and total land size positively; while livestock possession and livelihood activity negatively influenced income in the study sites. Generally, integrating tree in land use practice accounted as substantially as a keystone in improving the livelihoods of the households through providing socio-economic benefits in the study sites. Based on the study findings, the following recommendations are made:

- (1) Educated farmers participated relatively more in retaining/planting tree on their own land. So more education should be encouraged.
- (2) More experienced farmers participated relatively more in tree-based agroforestry land use practice. Therefore, empowering and inspiring more experienced farmers to engage in retaining/ planting trees should be increased.
- (3) The extent of retaining/planting tree increased as land size increased; this should be modified through integrating of the trees into land use intensively rather than extensively.
- (4) High numbers of livestock need large areas of land to graze, and consumes an excessive amount of land resources, because livestock has been traditionally kept in the study sites. This adversely affects the planting/regenerating of tree species. Therefore, intervention should be implemented through training farmers on how trees can be integrated with livestock on fixed land units and thus improve fodder without affecting planted/regenerated trees.
- (5) Further research is needed on the management system, cost-benefit analysis of AFS and market availability to tree products in the study sites.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Full Length Research Paper

Assessment of avifaunal assemblage and their distribution pattern across different habitat types of Gibe Sheleko National Park, South-western Ethiopia

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This study was conducted in Gibe Sheleko National Park from March to August 2015 covering wet and dry seasons. Sampling sites were taken based on the habitat characteristics and a transect line of 1 or less km with a distance of 250 to 300 m in between the transect lines was taken in the woodland habitat and point count was used in the riverine forest habitat. A total of 116 bird species consisting of 2 endemics to both Ethiopia and Eritrea were recorded. The riverine habitat had higher species number (100 species, $H' = 3.00$) and diversity during both seasons than the woodland habitat (84 species). The number of species during the dry season (111) was higher than during the wet season (105). The variation in avifauna species number between the two habitats was not significant. However, there was a significant variation in abundance of birds between habitats ($t = 1.418$, $P < 0.05$ and $df = 1$) during both seasons. The relative abundance of each species in the two habitat types was different, where the number of rare and frequent birds is somewhat higher than the other abundance ranks. Generally, avifauna species richness, diversity and relative abundance including their distribution between habitats were determined by the availability of food, vegetation structure and season. Moreover, the area is under severe pressure exacerbated by human-induced factors such as the expansion of agricultural investments, illegal settlement as well as deforestation. Therefore, significant conservation and management undertakings are very essential to maintain the biodiversity of the Park for present and future.

Key words: Avifauna, Gibe Sheleko National Park, deforestation, habitat characteristics, relative abundance.

INTRODUCTION

Birds are often common denizens of the ecosystems and they have been considered as an indicator species of inhabited areas and hence were studied by scientists for

centuries unlike other terrestrial animals (Blair, 1999). The abundance and diversity of birds are becoming an excellent indicator of ecosystem health for both terrestrial

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and aquatic ecosystem including the impact of climate change (Gaston, 1975; Hardy et al., 1987; Mikusiński et al., 2001). The estimation of local densities of avifauna helps to understand the abundance of various species of other organisms (Turner, 2003). One of the major priorities in conserving animals is monitoring their populations to find methods for their long term survival (Caughley, 1982). Although most birds occupy a wide range of habitats of the earth, there are some range-restricted species found only in particular regions and habitats of the globe. The vegetative structure is frequently assumed to be the primary proximate factor determining where and how species use resources (Collins et al., 2018). It has the highest ecological importance to birds, goes beyond as a source of food but also for nesting materials, nesting sites, lookout posts, singing stations and protective cover (Welty, 1975).

Ethiopia has set aside more than 17% of its total landmass for conservation undertakings (UNEP-WCMC, IUCN and NGS, 2018). The biodiversity endowment in Ethiopia deserves regional and global attention since the country is blessed with a very diverse set of ecosystems ranging from humid forest and extensive wetlands in the west to the desert of Afar depression on the northeast (EWNHS, 1996; Pol, 2001) and outstanding landscapes. The protected areas (PAs) network in the country includes nearly all habitat types found in the country. However, the ornithological investigation of the country is yet underdeveloped and it is in its infancy stage (Hiwot, 2007). Lack of sufficient knowledge towards birds has been hampering the effort of bird's study and conservation endeavours. The EWNHS (1996) reported that the avifauna in Ethiopia is largely negligible when compared to other counterpart countries in the region. Few researchers have conducted studies on the diversity and ecology of avifauna species in some parts of Ethiopia (Ash and Gullick, 1989).

The Gibe Sheleko National Park (GSNP) is well known for its avifauna blessings and remarkable landscape. Given the greatly abundant avifauna species occurrence and proximate location of the park to the capital Addis Ababa, the Park can be among the prime birding destination in Ethiopia and at large. Thus, understanding of avifaunal assemblage and their distribution pattern is key for robust avifauna conservation and management strategies development that will enhance avitourism practices as a driver of ecotourism development to the GSNP.

The main purpose of the present study was to provide brief and well-structured primary information on the diversity, distribution, relative abundance and habitat association of the avifauna of the GSNP to provide vigorous information for the improvement of biodiversity conservation in the area. The foremost aim of this study was to determine the avifaunal endowment of the area particularly species richness and diversity, distribution and composition of birds across various habitat types.

METHODS

The study area description

The GSNP where this study was conducted is among the exceptionally blessed natural heritages in Ethiopia. It is the nearest National Park to the continent's political centre and Ethiopia's capital Addis Ababa, located only 170 km southwest on the edge of the Ethiopian highland massif. The park geographically located between 7°57'0"-8°21'0" N and 37°27'0"-37°45'0" E found in Gurage zone of the Southern National Nationalities and People's Region (SNNPR) adjoining four districts of Gurage zone: these are Abeshege, Cheha, Enemore and Ener districts (Figure 1). It was established in 2009 and gazetted in 2011 covering an area of 360 km² of the upland plateau, parts of the Gibe River gorge area and patches of endemic forest. The park has remarkable landscape mainly characterized by varied terrain peaks, a larger proportion is hilly undulating interspersed with the different valley floor. Besides, some flatlands and undulating to rolling plains with incised river and perennial streams, valley and gorges occur in the area. This Park is unique due to its high bird species diversity and woodland ecosystem, including its magnificent gorges and rivers.

Sampling design and data collection

The study was conducted during both the wet and dry seasons from March to August 2015 where data was collected twice a day early in the morning and late in the afternoon (Sutherland, 1996; Sutherland et al., 2004). Stratified random sampling technique was employed for multi-species surveys and diversity studies which help to extrapolate the results for estimating species diversities on the two main habitat types (woodland and riverine habitats) in the study area (Bibby et al., 1998; Krebs, 1989). A number of sampling units representing each habitat type were selected based on a random sampling method. The technique involves dividing each habitat by point stations (open habitats) and line transects (forest habitat) and choosing representative sample units randomly (Bibby et al., 1998).

Line and point transect methods which are suitable for the area were used by moving along a fixed route and recording the birds seen or heard on either side of the route. Point and transects were selected randomly with respect to birds distribution to obtain unbiased data (Bibby et al., 1998).

Line transect

This was applied in a habitat with good visibility and with less dense forest or woodland, generally with an open uniform habitat (open woodland) and open riverine habitats (Bibby et al., 1998). It was employed by moving across a randomly selected transect to record the observed birds in either side of the transect line. In an open area, the sighting distance was extended to 150 m on either side of the transect, but in an area where visibility is limited or being a bushy habitat, the distance was contracted to 100 m. Walking at a rate of 2 km per hour in open habitat and 1 km per hour in bushy habitat was employed for standardized data collection (Sutherland, 1996).

During transect count, the transect route(s) was chosen at random which is crucial to produce unbiased density estimates which can be extrapolated to other areas of the same habitat type (Sutherland, 1996; Bibby et al., 1998). Each transect line was partitioned into distance intervals along its length by putting markers every 50 m along a transect line which helps to follow the correct track and also allows habitat information to be collected for specific sections of the transect (Bibby et al., 1998). In general, a total of 11.5 km transect length was sampled to count birds in the study area.

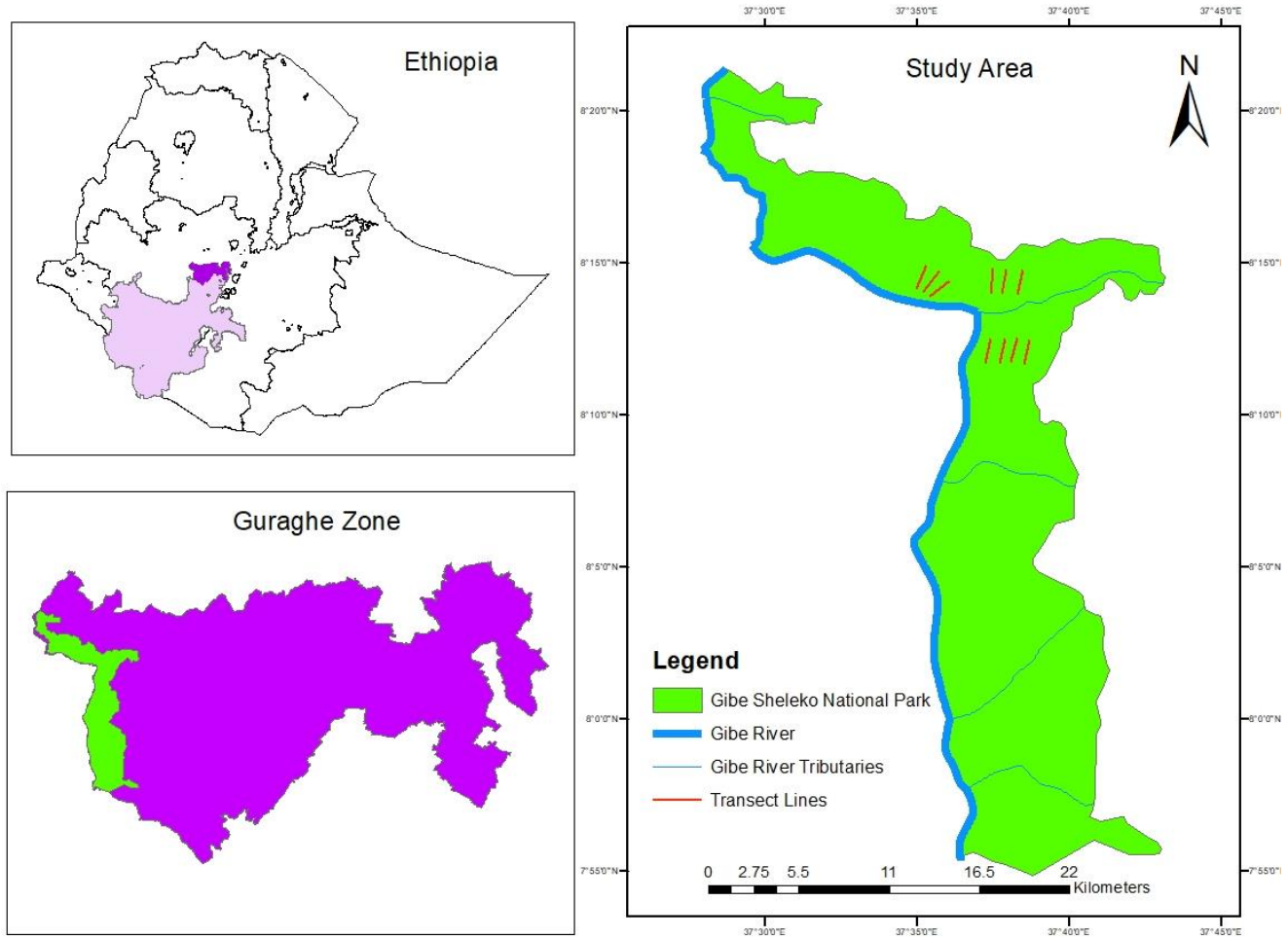


Figure 1. Location map of the study area.

Point transect

This was conducted by walking into and locating a particular spot and recording all bird contacts by observation and hearing within a radius of 25 m for a predetermined period of time 10 min before moving to the next point depending on how conspicuous the birds are. The first minute for flushing birds to settle (settling period) and the remaining 9 min for counting and recording birds heard or seen. This method was employed in the forest and riverine habitat where birds are difficult to observe. For the point count method, counting was carried out as quickly as possible to reduce the risk of double counting and allow more points to be covered (Sutherland, 2000), and the distance between the points was at least 200 m to reduce the probability of double counting. In general, a total of 25 points were sampled to count birds in the sampled study area.

Data analysis

Data were analyzed using the Shannon-Weaver Index to determine the species diversity and evenness in the study area (Shannon and Wiener, 1949). The relative abundance of different avifauna species within a site and of the same species across different habitat types was also compared.

The diversity of bird species in the habitats was expressed by means of Shannon-Weaver Index by the formula:

$$(H' = -\sum P_i \ln P_i) \tag{1}$$

Where, H' = Shannon-Wiener Index, P_i = Proportion of i^{th} species; \ln = Natural Logarithm

To see the degree of similarity of bird species between the two habitats with respect to the composition of species was compared by applying Simpson's Similarity Index:

$$(SI = 2C / A+B) \tag{2}$$

Where, SI = Simpson's Similarity Index; A = Number of species in habitat A; B = Number of species in habitat B; C = Common number of species in habitats A and B.

Species evenness, which measures the pattern of distribution of the bird populations present in the area, was evaluated using the Shannon-Wiener evenness Index (E):

$$E = H' / H'_{\max} \tag{3}$$

Where, H'_{\max} = $\ln s$; E = Shannon-Wiener Evenness Index; H' = Shannon-Wiener Diversity Index; S = Total number of species and \ln = Natural logarithm.

The relative abundance of avifauna species was determined using encounter rates that give crude ordinal scales of abundance as abundant, common, frequent, uncommon and rare (Bibby et al., 1998).

$$\text{Encounter rate} = \frac{\text{Total number of individual Avifauna observed}}{\text{period of observation in hour}} * 100 \quad (4)$$

Encounter rate was calculated for each species by dividing the number of hours spent searching the species, for having the figure of birds per hour per each species. The abundance category (the number of individuals per 100 field hour) was: < 0.1, 0.1-2.0, 2.1-10.0, 10.1-40.0 and 40+. The following abundance score was given as 1 (rare), 2 (uncommon), 3 (frequent), 4 (common) and 5 (abundant), respectively. Data were also analysed using other appropriate statistical tools like SPSS where ANOVA was used to analyze the effect of variables namely season and habitat on avifauna abundance and diversity.

RESULTS

Species composition

In total, 116 bird species belonging to 89 genes, 49 families and 17 orders were recorded during the study period from the two different habitat types of the study area (Table 1). The records of the birds in the National Park and their distribution in the riverine and woodland habitats are presented in Table 1

Of the total 116 species recorded, 104 and 112 bird species were recorded during wet and dry season counts, respectively. During the wet season, 92 species were recorded in the riverine habitat while 81 were recorded in the woodland habitat whereas during the dry season 94 and 78 birds were recorded in the riverine and woodland habitats, respectively. In addition, of the total recorded birds, 16 were migratory species, of which 5 were northern (Palearctic) migrants and 11 were inter-African (Table 1). Passeriformes constituted the predominant group, representing 52% (n= 61) of the recorded species followed by Columbiformes (10.3%) (n=12) and Accipitriformes (6.8%) (n= 8) (Table 2). The dominant families with the largest number of species were *Columbidae* (10.3%) (n= 12) and *Muscicapidae* (9.4%) (n=11). Order Passeriformes had the highest number of families, 26 (51 %) (Table 2). The White-collared pigeon (*Columba albitorques*) and Brown-rumped Seed Eater (*Serinus tristriatus*) are endemic to the highlands of Ethiopia and Eritrea. In addition, one critically endangered bird, White-backed vulture (*Gyps africanus*) was recorded.

The highest species number was recorded in the riverine habitat 100 (85.5%), followed by woodland habitat 84 (71.8%). The highest bird abundance was also recorded in the woodland habitat with 2,895 individuals (85.3%) and the lowest was recorded in the riverine habitat with 500 individuals (14.7%). The abundance of bird species during the dry season is higher than that of wet season with number of individuals of 1,788 (52.7%)

and 1,607 (47.3%), respectively. The number of species recorded during the wet season was higher than the dry season record. The dry season record shows the occurrence of 112 (95.7%) while wet season records were slightly lower with 105 (89.7%).

Species abundance and diversity

The species diversity was higher ($H'=3.00$) in the riverine habitat than the diversity in the woodland habitat ($H'=2.96$) (Table 3). During the dry season, regardless of higher species diversity in the riverine habitat (3.13), it was the woodland habitat that had the higher bird abundance (1517) (Table 5). In terms of species abundance, there was a significant variation ($t= 1.418$, $P<0.05$ and $df= 1$) between the two habitats, however the variation in species richness showed no significant variation ($t=11.5$, $P>0.05$ and $df= 1$). In addition, the riverine habitat had more evenly distributed species in the habitat ($E= 0.68$) than the woodland habitat ($E= 0.64$) (Table 3).

During the wet season, higher avifauna diversity was recorded in the riverine habitat ($H'= 2.71$) than the woodland habitat ($H'= 2.58$) (Table 4). Higher even distribution was also recorded in the riverine habitat than woodland habitat with ($E= 0.9$) and ($E= 0.8$), respectively. In terms of abundance, a total of 1378 and 229 individual birds were recorded from the woodland and riverine habitats, respectively (Table 4). As a result, the variation in abundance between these two habitats during the wet season was significant ($t= 1.34$, $P>0.05$, $df= 1$).

During the dry season, avifauna diversity in the riverine and woodland habitats was $H'= 3.13$ and $H'= 3.07$, respectively (Table 5). Furthermore, the even distribution in the riverine and woodland habitats was also $E= 0.69$ and $E= 0.71$, respectively. During the same season, a total of 1517 and 271 individual birds were recorded from the woodland and riverine habitats, respectively (Table 5). The variation in abundance between the riverine and woodland habitats during the dry season was significant ($t= 1.42$, $P>0.05$ and $df= 1$).

In the woodland habitat, the abundance of Village weaver (*Ploceus Cucullatus*) was the highest individuals, 1092 (37.7%) followed by White-rumped babbler (*Turdoides leucopygia*), 176 (6.1%) individuals and Common bulbul (*Pycnonotus barbatus*) 147 (5.1) (Figure 2). The variation in abundance within the woodland habitat of the top ten bird species show significant difference ($t=2.02$, $P>0.05$ and $df=9$).

In the riverine habitat, the same as in the woodland habitat Village weaver (*P. Cucullatus*) and Common bulbul (*P. barbatus*) were the most abundant species in the habitat with 92 (18.4) and 60 (12) number of individuals respectively (Figure 3). However, unlike the woodland habitat, there is a no significant difference in the abundance of individuals among the top ten abundant species ($t =4.76$, $P<0.05$ and $df =9$).

Table 1. Bird species recorded during the study period in the two habitat types (LC, Least concern; IAM, Intra-African migrant; PM, Palearctic migrant; R, Resident).

Family	Species Name	Scientific Name	Status
Order Passeriformes			
Hirundinidae	Red-rumped swallow ^{IAM}	<i>Ceropsis daurica</i>	LC
	Rock martin ^{PM}	<i>Ptyonoprogne fuligula</i>	LC
Pycnonotidae	Common bulbul ^R	<i>Pycnonotus barbatus</i>	LC
	Ruppell's robin-chat ^R	<i>Cossypha semirufa</i>	LC
	Mocking cliff chat ^R	<i>Thamnolaea cinnamomeiventris</i>	LC
	African gery flycatcher ^R	<i>Bradornis microrhynchus</i>	LC
	Little rock thrush ^R	<i>Monticola rufocinereus</i>	LC
	Familiar chat ^R	<i>Cercomela familiaris</i>	LC
	Muscicapidae	African dusky flycatcher ^R	<i>Muscicapa adusta</i>
Little rock thrush ^R		<i>Monticola rufocinereus</i>	LC
Pale flycatcher ^R		<i>Bradornis pallidus</i>	LC
Rufous-tailed scrub robin ^R		<i>Cercotrichas galactotes</i>	LC
Northern black flycatcher ^R		<i>Melaenornis edolioides</i>	LC
Blue rock thrush ^R		<i>Monticola solitarius</i>	LC
Turdidae	Mountain thrush ^R	<i>Turdus (olivaceus) abyssinicus</i>	LC
Monarchidae	African paradise flycatcher ^{IAM}	<i>Terpsiphone viridis</i>	LC
	Scarlet-chested sunbird ^R	<i>Chalcomitra senegalensis</i>	LC
Nectariniidae	Olive-bellied sunbird ^R	<i>Cinnyris chloropygia</i>	LC
	Copper sunbird ^R	<i>Cinnyris cupreus</i>	LC
	Corvidae	Cape rook ^R	<i>Corvus capensis</i>
Pied crow ^R		<i>Corvus albus</i>	LC
Sturnidae	Red-winged starling ^R	<i>Onychognathus morio</i>	LC
	Greater blue-eared starling ^R	<i>Lamprotornis chalybaeus</i>	LC
Passeridae	Swainson's sparrow ^R	<i>Passer swainsonii</i>	LC
	Baglafaecht weaver ^R	<i>Ploceus baglafaecht</i>	LC
	Red-headed weaver ^R	<i>Anaplectes rubriceps</i>	LC
	Village weaver ^{IAM}	<i>Ploceus cucullatus</i>	LC
Ploceidae	Red-billed quelea ^R	<i>Quelea quelea</i>	LC
	Yellow bishop ^R	<i>Euplectes franciscanus</i>	LC
	Black bishop ^R	<i>Euplectes gierowii</i>	LC
	Spectacled weaver ^R	<i>Ploceus ocularis</i>	LC
	Red-cheeked cordon-bleu ^R	<i>Uraeginthus bengalus</i>	LC
Estrildidae	Red-billed firefinch ^R	<i>Lagonosticta senegala</i>	LC
	Abyssinian waxbill ^R	<i>Paludicola ochrogaster</i>	LC
	Brown-rumped seedeater ^R	<i>Serinus tristriatus</i>	LC
	Yellow-fronted canary ^R	<i>Serinus mozambicus</i>	LC
Fringillidae	Streaky seedeater ^R	<i>Serinus striolatus</i>	LC
	African citril ^R	<i>Crithagra citrinelloides</i>	LC
	Yellow-throated seedeater ^R	<i>Crithagra flavigula</i>	LC
Zosteropidae	Abyssinian white-eye ^R	<i>Zosterops abyssinicus</i>	LC
Leiothrichidae	White-rumped babbler ^R	<i>Turdoides leucopygia</i>	LC
Platysteiridae	Black-headed batis ^R	<i>Batis minor</i>	LC
	Black-crowned tchagra ^R	<i>Tchagra senegalus</i>	LC
	Northern puffback ^R	<i>Dryoscopus gambensis</i>	LC
Malaconotidae	Orange-breasted bushshrike ^R	<i>Telophorus sulfureopectus</i>	LC
	Ethiopian Boubou ^R	<i>Laniarius aethiopicus</i>	LC
Motacillidae	African pied wagtail ^R	<i>Motacilla aguimp</i>	LC
	Mountain wagtail ^R	<i>Motacilla clara</i>	LC

Table 1. Contd.

Dicruridae	Fork-tailed drongo ^R	<i>Dicrurus adsimilis</i>	LC	
Cisticolidae	Pectoral-patch cisticola ^R	<i>Cisticola brunnescens</i>	LC	
	Grey-backed camaroptera ^R	<i>Camaroptera brachyura</i>	LC	
	Red-fronted warbler ^R	<i>Urorhipis rufifrons</i>	LC	
	Green-backed eremomela ^R	<i>Eremomela canescens</i>	LC	
	Abyssinian oriole ^R	<i>Oriolus monacha</i>	LC	
Oriolidae				
Campephagidae	Red-shouldered cuckooshrike ^{IAM}	<i>Campephaga phoenicea</i>	LC	
Macrosphenidae	Northern crombec ^R	<i>Sylvietta brachyura</i>	LC	
Laniidae	Common fiscal ^R	<i>Lanius humeralis</i>	LC	
Sturnidae	Rüppell's starling ^R	<i>Lamprotornis purpuroptera</i>	LC	
	Violet-backed starling ^{IAM}	<i>Cinnyricinclus leucogaster</i>	LC	
Viduidae	Pin-tailed whydah ^R	<i>Vidua macroura</i>	LC	
Platysteiridae	Brown-throated wattle-eye ^R	<i>Platysteira cyanea</i>	LC	
Order Columbiformes				
Columbidae	Speckled pigeon ^R	<i>Columba guinea</i>	LC	
	White-collared pigeon ^R	<i>Columba albitorques</i>	LC	
	Namaqua dove ^{IAM}	<i>Oena capensis</i>	LC	
	Ring-necked dove ^R	<i>Streptopelia capicola</i>	LC	
	Red-eyed dove ^R	<i>Streptopelia semitorquata</i>	LC	
	Laughing dove ^R	<i>Streptopelia senegalensis</i>	LC	
	Dusky turtle dove ^R	<i>Streptopelia lugens</i>	LC	
	Bruce's green pigeon ^R	<i>Treron calvus</i>	LC	
	African mourning dove ^R	<i>Streptopella roseogrisea</i>	LC	
	African collared dove ^R	<i>Streptopelia roseogrisea</i>	LC	
	Blue-spotted wood dove ^R	<i>Turtur afer</i>	LC	
	Black-billed wood dove ^R	<i>Turtur abyssinicus</i>	LC	
	Order Accipitriformes			
	Accipitridae	Yellow-billed kite ^{PM}	<i>Milvus (migrans) aegypticus</i>	LC
Hooded vulture ^R		<i>Necrosyrtes monachus</i>	LC	
African fish eagle ^R		<i>Haliaeetus vocifer</i>	LC	
Augur buzzard ^R		<i>Buteo augur</i>	LC	
White-backed vulture ^R		<i>Gyps africanus</i>	CR	
Short-toed snake eagle ^{PM}		<i>Circaetus gallicus</i>	LC	
Western banded snake eagle ^R		<i>Circaetus cinerascens</i>	LC	
Long-crested eagle ^R		<i>Lophaelus occipitalis</i>	LC	
Order Cuculiformes				
Musophagidae	White-cheeked Turaco ^R	<i>Tauraco leucotis</i>	LC	
	Klaas's cuckoo ^{IAM}	<i>Chrysococcyx Cupreus</i>	LC	
Cuculidae	Blue-headed coucal ^R	<i>Centropus monachus</i>	LC	
	Red-chested cuckoo ^{IAM}	<i>Cuculus solitarius</i>	LC	
Order Bucerotiformes				
Bucerotidae	Abyssinian ground-hornbill ^R	<i>Bucorvus abyssinicus</i>	LC	
	Eastern yellow-billed hornbill ^R	<i>Tockus flavirostris</i>	LC	
	African grey hornbill ^R	<i>Tockus nasutus</i>	LC	
Order Piciformes				
Lybiidae	Double-toothed barbet ^R	<i>Lybius bidentatus</i>	LC	
	Banded barbet ^R	<i>Lybius undatus</i>	LC	
	Yellow-fronted tinkerbird ^R	<i>Pogoniulus chrysoconus</i>	LC	
	Black-billed barbet ^R	<i>Lybius guifsobalito</i>	LC	
Order Apodiformes				
Apodidae	African palm swift ^R	<i>Cypsiurus parvus</i>	LC	
	Little swift ^R	<i>Apus affinis</i>	LC	

Table 1. Contd.

Order Coliiformes			
Coliidae	Blue-naped mousebird ^R	<i>Urocolius macrourus</i>	LC
	Speckled mousebird ^R	<i>Colius striatus</i>	LC
Order Caprimulgiformes			
Caprimulgidae	Montane nightjar ^R	<i>Caprimulgus poliocephalus</i>	LC
Order Galliformes			
Phasianidae	Common quail ^{PM}	<i>Coturnix coturnix</i>	LC
Numididae	Helmeted guineafowl ^R	<i>Numida meleagris</i>	LC
Order Strigiformes			
Strigidae	Greyish eagle-owl ^R	<i>Bubo cinerascens</i>	LC
Order Coraciiformes			
Alcedinidae	African pygmy kingfisher ^{IAM}	<i>Ceyx pictus</i>	LC
Halcyonidae	Grey-headed kingfisher ^{IAM}	<i>Halcyon leucocephala</i>	LC
Cerylidae	Pied kingfisher ^R	<i>Ceryle rudis</i>	LC
Meropidae	Little bee-eater ^R	<i>Merops pusillus</i>	LC
Order Pelecaniformes			
Threskiornithidae	Hadada ibis ^R	<i>Bostrychia hagedash</i>	LC
	Glossy ibis ^{PM}	<i>Plegadis falcinellus</i>	LC
	Sacred ibis ^R	<i>Threskiornis aethiopicus</i>	LC
Scopidae	Hamerkop ^R	<i>Scopus umbretta</i>	LC
Ardeidae	Black-headed heron ^R	<i>Ardea purpurea</i>	LC
Order Ciconiiformes			
Ciconiidae	Yellow-billed stork ^R	<i>Mycteria ibis</i>	LC
	Abdim's stork ^{IAM}	<i>Ciconia abdimii</i>	LC
Order Charadriiformes			
Pluvianidae	Egyptian plover ^R	<i>Pluvianus aegypticus</i>	LC
Burhinidae	Senegal thick-knee ^R	<i>Burhinus senegalensis</i>	LC
Charadriidae	African wattled plover ^R	<i>Vanellus senegallus</i>	LC
Order Anseriformes			
Anatidae	Egyptian goose ^R	<i>Alopochen aegypticus</i>	LC
Suliformes			
Phalacrocoracidae	Long-tailed Cormorant ^R	<i>Phalacrocorax nigrogularis</i>	LC

Seasonal and habitat wise bird species similarity

In the woodland habitat, 0.97 (97%) of the avifauna species were common during the wet and dry seasons, whereas low species similarity was recorded in the riverine habitat with 0.93 (93%) common species during the two seasons (Table 6).

During the wet season, species similarity between the woodland and riverine habitat was SI=0.8. During the dry season, the species similarity index between the two habitat types was SI=0.7. During both seasons, the species similarity between the woodland and riverine habitats was SI=0.8.

Relative abundance of bird species

Abundance rank score using encounter showed that, in

the woodland habitat, there were more rare (26, 26%) and frequent (25, 25%) bird species followed by (17, 17%) common and (13, 13%) abundant species. On the other in the riverine habitat where were more rare (50, 59.5%) and frequent (19, 22.6%) species of birds followed by common and uncommon birds species with abundance rank of 17 (20.2%) and 15 (17.8%), respectively (Table 7).

DISCUSSION

The record of 116 species of birds during the study period in both the riverine and woodland habitats of the National Park shows that the diversity of birds had high both migratory and resident species. At the same time, the occurrence of winter birds in the area indicates that the area is important for migratory birds which were

Table 2. Composition of birds in the study area.

Order	Number of family	No. of species
Accipitriformes	1	8
Cuculiformes	2	4
Passeriformes	26	61
Bucerotiformes	1	3
Piciformes	1	4
Apodiformes	1	2
Coliiformes	1	2
Columbiformes	1	12
Caprimulgiformes	1	1
Galliformes	2	2
Strigiformes	1	1
Coraciiformes	4	4
Pelecaniformes	3	6
Ciconiiformes	1	2
Charadriiformes	3	3
Anseriformes	1	1
Suliformes	1	1
Total	51	117

Table 3. Species diversity between woodland and riverine habitats during both wet and dry seasons.

Habitat	Species richness	Abundance	H'	H _{max}	E	D
Woodland	84	2895	2.96	4.61	0.64	0.84
Riverine	100	500	3.00	4.43	0.68	0.92

Table 4. Species diversity between the woodland and riverine habitats during the wet season.

Habitat	Species richness	Abundance	H'	H' _{max}	E	D'
Woodland	81	1378	2.58	4.39	0.59	0.8
Riverine	92	229	2.71	4.52	0.6	0.9

Table 5. Species diversity between the woodland and riverine habitats during the dry season.

Habitat	Species richness	Abundance	H'	H' _{max}	E	D'
Woodland	78	1517	3.07	4.35	0.71	0.9
Riverine	94	271	3.13	4.54	0.69	0.9

observed from November to early March. Most of the birds (103, 88%) were resident whereas 14 species (12%) were regular visitors. The avifauna community composition in the woodland habitat has a slight difference with the composition of bird species in the

nearby habitat (riverine). Woodland habitat supports a smaller number of species of the total species recorded than the riverine habitat, which accounts for 85.5% of the total avifauna species recorded in the study area. This might be due to the vegetative structure difference in the

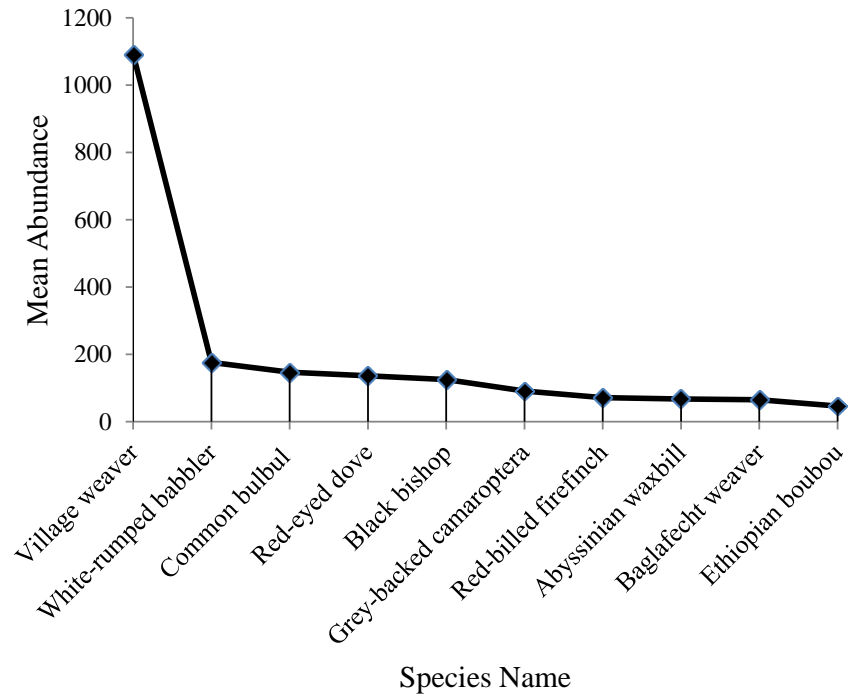


Figure 2. Top ten most abundant species of the woodland habitat.

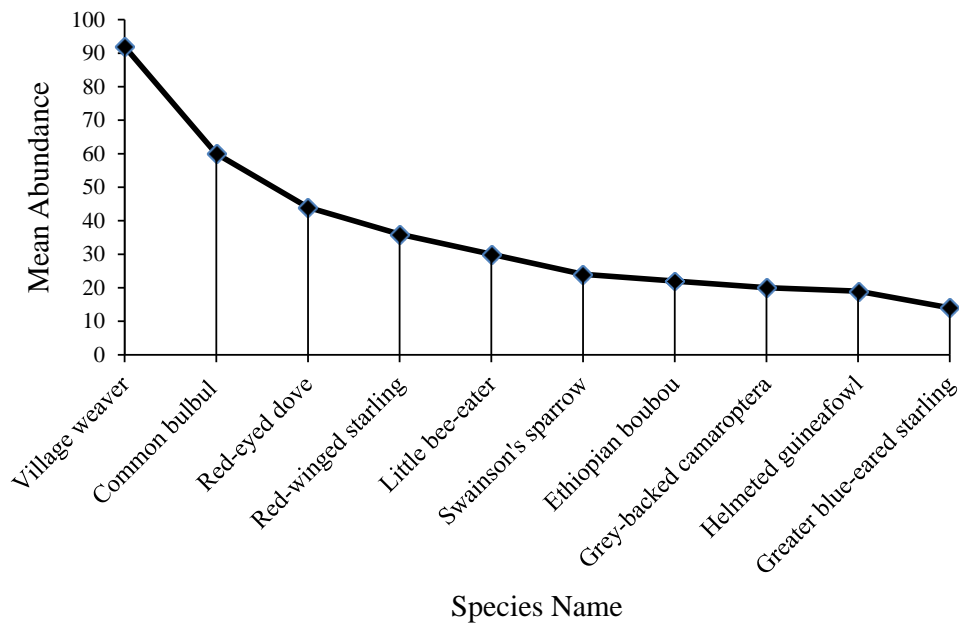


Figure 3. Top ten most abundant species in the riverine habitat.

two habitats influencing their distribution. The difference of bird species preference is influenced by the individual species-specific requirement to each specified habitat since organization and composition of bird species is

clearly related to the complexity of vegetation they inhabit (Manual, 1978). In this regard, some may require inhabiting and feeding in riverine habitats while others may need completely woodland habitats. However, some

Table 6. Species similarity (SI) within habitats during wet and dry seasons.

Habitat	Wet	Dry	Common species	SI	SI%
Woodland	81	78	77	0.97	97
Riverine	92	94	86	0.93	93

Table 7. Relative abundance of bird species in the two habitats.

Habitat	Abundance rank				
	Rare	Uncommon	Frequent	Common	Abundant
Woodland	26	11	25	17	13
Riverine	50	15	19	17	7

species can be generalists being associated with more habitat types (Isacch et al., 2003). On the other hand, this might be associated with their feeding behaviour, in which some species might be carnivores, insectivores, granivorous and others may be generalists. Therefore, the presence of enormous number of fish species in the major rivers and riverine habitat composed diverse riverine forests have a profound impact for the occurrence of abundant bird species in the riverine habitat. Moreover, the presence of wading birds such as Cattle egret (*Bubulcus ibis*), Black-headed heron (*Ardea melanocephala*) and others in the riverine habitat was associated with the presence of ephemeral ponds, which had abundant food source. This may have contributed to the presence of more bird species in the riverine habitat.

The abundance of bird species in the study area was distributed differently between the two habitats because the change in habitat characteristics and level of disturbance can influence avifauna abundance. The reason for the difference might be due to the difference in habitat characteristics (such as availability of food, water and shelter) of the two habitats. In addition, birds can respond to changes in vegetation composition and structure, which in turn affects their food resources. Food abundance, availability, variety and preferences could be the reason for the differences in the relative abundance of bird species between habitats (Girma Mengesha et al., 2011). Lee and Kand (2019) also suggested that local bird abundance varied annually due to many factors such as weather patterns and regional fluctuations in population size. Morris et al. (2008) also reported that the abundance of doves was best associated with moderate grazing and the presence of green grass, which provide them with good foraging opportunities.

Species diversity index and evenness were higher in the riverine habitat than in the woodland habitat during the entire study period. This might be due to the abundance of food resource in the riverine habitat. However, Think (2006) reported that habitat heterogeneity and vegetation structure determine bird species diversity.

There was no significant difference in the number of avifauna species in the study area in both habitats between the wet and dry seasons. The evergreen riverine forest ecosystem around the Gibe River crossing the Park during both seasons could contribute to the insignificant effect of seasons on bird species composition in the studied habitats. Similarly, Shimelis and Bekele (2008) have reported no significant variation in avifaunal composition between the wet and dry season in the riverine and wetland habitats of Infranz and Yiganda at the southern tip of Lake Tana, Ethiopia, due to extended time of inundation of the area during the wet and dry seasons. However, the record showed a slight difference in the number of species between seasons both in the woodland and riverine habitats. Malizia (2001) reported similar results where the composition of the entire bird community fluctuated seasonally. Seasonal variation in the temperature and rainfall, as well as the level in the water availability in Gibe River, was observed, where during the mid-dry season the water was lower than in the mid wet season. George et al. (1992) found a temperature-related drought and great decline of birds in population and community structure in western North Dakota.

The variation in avifauna composition in the riverine and woodland habitat was different between the wet and dry seasons. In the riverine habitat, there was an increase of 2.2% (n=2) bird species of the total species recorded whereas a decrease by 3.7% (n=3) bird species was recorded during the wet season in the woodland habitat. The observed seasonal reduction in avifauna species could be due to seasonal irregularity in the availability of food resources especially during the dry season where birds could move to the evergreen riverine forest ecosystem to access forest food. Karr and Roth (1976) and Machado and Fonseca (2000) have reported food resources availability have significantly affected the seasonal reduction of avifauna species may force avifauna species to either shift their feeding behaviour or move to another area where the original food resource is

available.

Seasonal bird species similarity was higher in the woodland habitat than in the riverine habitat. This might be due to better habitat stability of the woodland habitat. This agrees with the work of Karr and Roth (1976) wherein areas where there is a minimal seasonal irregularity in food availability and other factors are held constant, a species can maintain itself throughout the year. As the volume decreased during the dry season, instantly small ephemeral ponds have emerged, these help the wading birds and kingfishers to feed and nest during the dry season then disappearing during the wet season (Dorn and Cook, 2015). This may reduce the stability of the habitat and bird species similarity in between seasons of the riverine habitat.

Across habitats, bird species similarity was higher during the wet season than the dry season. This might be due to the greater increase of the wading and water birds in the riverine habitats during the dry season and disappearance of some birds along from the woodland habitats due to seasonal movements. In addition, habitat characteristics between these two habitats were relatively more similar during the wet season than the dry season. Power (1975) found that avifaunal similarity between habitats was associated with habitat similarity or habitat characteristics particularly vegetation and degree of isolation in between habitats. Gottschalk et al., (2007) in their finding pointed out that low similarities of the bird communities on the 'Kirawija' and 'Musabi Plains' in Serengeti plots to those of other plots of the same vegetation class, i.e. short grass and long grass, respectively. There was a variation in the relative abundance of bird species (common, frequent, abundant and uncommon) across habitats. This might be due to the difference in response to avifauna species to many habitat parameters such as vegetation. In the riverine and woodland habitats, the high number of rare bird species was recorded during the study period.

Livestock grazing and deforestation is the most prominent threat in the area, which could affect the conservation of both the woodland and riverine birds. In line with this, to Yenenesh Hailu *et al.* (2018) reported that in the Park forest land was declined by 66.8%, bushland and shrubland was increased by 20% as well as the grazingland was increased by 134.6 ha/year from 1990 to 2016. In addition, intensified grazing by livestock can have a profound impact on the widespread population decline of many birds in a habitat (Soderstro et al., 2001). However, livestock grazing could not have the same effect on all birds in one habitat because many birds respond to this pressure differently. This coincides with the findings of Soderstro et al., (2001) in which ground-feeding insectivorous bird species are affected by yearly changes in grazing pressure, but there was no effect of grazing on ground-feeding species that fed on a mixed diet or on species that foraged in trees and shrubs. In general, large insectivorous (>30 g) preferred

moderately grazed pastures and small insectivorous (<30 g) preferred pastures with intensive grazing pressure.

As it was confirmed by researcher's field observation and other related researches undertaken in the area, the park has been severely affected by human-induced pressures such as the expansion of farmlands, logging of forest and expansion of settlements around the Park. Similarly, Yenenesh et al. (2018) have disclosed that 66.8% of forest land of the park was diminished for the last 27 years due to anthropogenic factors (that is Agricultural expansion, illegal settlement and deforestation for fuelwood). All these may affect avifauna species richness, abundance and distribution in the study area. Miller et al. (2003) also found a decline in species richness as urbanization increases in the surrounding landscape in the lowland riparian areas of Colorado. Brenna and Kuvlesk (2005) examined cumulative factors such as afforestation, in the eastern United States, fragmentation and replacement of prairie vegetation with agricultural landscape and large deterioration of western United States rangelands were the major causes for avifauna decline in these areas.

However, human-induced factors do not affect all avifauna species in one habitat rather it may sometimes favour other species. According to Miller et al. (2003), migrant and low nesting species were associated with lower levels of development in the habitat, whereas resident and cavity-nesting species tended to increase with urbanization in a habitat.

Conclusion

The GSNP is the most notable habitat for birds of both migratory and residents for nesting, breeding, sheltering and feeding and can serve as the main National Parks in Ethiopia to promote avitourism. A total of 116 species of birds were recorded in the study area within the two habitats and during both wet and dry seasons. The study claimed that there was a variation of species diversity parameters between the two habitats and the dry and wet seasons. Habitat wise, higher species richness was recorded in the riverine ecosystem while higher species abundance was recorded during the dry season. However, the overall species composition, diversity, abundance and distribution varied both seasonally and habitat wise. This was associated with the individual species response to vegetation characteristics and the availability of water in a river. In general, the results suggest that the evergreen riverine forest is important during the dry season for migratory birds. The study also revealed that seasonality and habitat types are important determinant factors to both the migrant and non-migrant bird species abundance and distribution in the Park indicating specific habitat use by some of the species. Human pressure from the surrounding area such as an expansion of agriculture inside the Park and nearby

sloppy habitats, an increase of livestock and its pressure on the wildlife habitat and forest logging for the wood and construction are becoming threats to this important habitat. Therefore, significant conservation strategies and management plans should be put in place by making the Park more economically viable to farmers around by promoting the area for tourists and participatory wildlife management should be implemented.

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CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Full Length Research Paper

Tree community structure and recruitment dynamics in savanna woodlands

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Climate, fire and herbivory rank among the key factors and processes shaping savanna woodland community composition and diversity. We analyzed recruitment dynamics, community biomass, diversity, stability and composition and their relationships with rainfall fluctuations and herbivory in a savanna woodland community in the Masai Mara National Reserve of Kenya. Seedling and sapling recruitment varied differentially over time among the five commonest tree species. Rainfall exerted both positive and negative effects on recruitment dynamics, with saplings responding to longer rainfall lags than seedlings. The proportion of trees damaged by browsers peaked at intermediate rainfall levels and was higher for adults than seedlings or saplings. Community biomass, species richness and evenness increased with increasing rainfall. Biomass decreased, whereas richness and evenness hardly varied over time. Both rare and common species occurred in more diverse communities, prevalent at high rainfall locations, suggesting strong nestedness in community composition. Moreover, community stability and diversity appeared unrelated. Protection from browsers and lower per capita browsing pressure at high rainfall apparently enable rare species to successfully establish and elevate species diversity. If climate change makes droughts more frequent and intense and lowers soil moisture, browsing intensity could increase, reducing diversity and recruitment, especially of rare, stress-sensitive species.

Key words: Masai Mara, species diversity, habitat filtering, rainfall, browsing, fire, competition, stochastic processes, tree biomass.

INTRODUCTION

A central goal in ecology is understanding the operation of processes that shape the structure and dynamics of vegetation communities (Diamond, 1975; Weiher et al., 1998; McGill et al., 2006). Three generic ecological

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processes that contribute to structuring of plant communities include competition, habitat filtering, and stochastic processes. Processes proposed as key drivers of vegetation community structure and dynamics therefore fall into three broad categories that: (1) emphasize the fundamental role of competitive interactions (Tilman, 1982), (2) focus on habitat filtering and thus restrict species numbers (O'Connor, 1995; Shipley et al., 2011), and (3) focus on the balance between colonization and extinction processes, commonly designated as stochasticity (Hubbell, 2001; Chase and Leibold, 2003; Hubbell, 2005). Although the relative importance of these processes in shaping vegetation communities and modulating the relationship between rainfall and plant community biomass, diversity, stability and composition is likely to vary in space and time; relatively little work has examined this variation in tropical African savannas using long-term monitoring data (Ozinga et al., 2005; Adler and Levine, 2007).

Tropical savannas rank among the most widespread terrestrial biomes, covering some 20% of the earth's land surface area (Ozinga et al., 2005; Adler and Levine, 2007; Chape et al., 2008). African savannas are typified by a continuous grass layer, scattered closed thickets of a diverse range of shrubs and *Acacia* woodlands and occur in climates with strongly seasonal rainfall patterns (Walker, 1987). As with many African savanna habitat types, closed thickets often occur in riparian areas and on hilltops and consist of diverse and dense patches of woody species. They add spatial heterogeneity to the ecosystem by producing taller and longer-lived landscape elements (Belsky, 1994). These woody thickets represent important and reliable habitats for many browsing herbivores, especially during dry periods (Oloo et al., 1994; Dublin, 1995).

Rainfall is the primary climatic component controlling the recruitment dynamics of savanna vegetation communities (Harper, 1977; Holmgren et al., 2006; Zimmermann et al., 2009). Increasing rainfall generally leads to longer periods with high soil moisture necessary for successful germination of tree seedlings, their establishment and recruitment into sapling and adult stages (O'Connor, 1995), and hence to the long-term survival and establishment of plant populations. Furthermore, high rainfall leads to higher biomass production with profound consequences for plant species diversity (Hutchinson, 1959; Rosenzweig, 1995), stability (McNaughton, 1977; Tilman, 1994) and composition (Ozinga et al., 2005; Silvertown et al., 1994). The trend of rising temperatures, recurrent severe droughts and other environmental stresses (e.g., frequent fires, intense herbivory and habitat deterioration) in African savannas imply that the survival prospects of species in particular communities depend most strongly upon their relative recruitment and competitive abilities, resistance and resilience to the environmental changes (Virginia and

Wall, 2001).

Seedling and sapling recruitment rates should be correlated with variation in rainfall, the major source of soil moisture for plants in African savannas (O'Connor, 1995). To establish the functional forms of the relationships between seedling and sapling recruitment and the rainfall components most strongly correlated with the recruitment rates, we explore if seedling and sapling recruitment rates: (1) increase (or decrease) linearly with increasing rainfall, or 2) peak at intermediate levels of rainfall, if rainfall extremes reduce habitat suitability for juvenile recruitment. As saplings are older and have roots able to access deeper underground soil moisture than seedlings, sapling recruitment should be influenced less by short-term rainfall and should respond to past rainfall accumulated over longer periods than seedling recruitment due to carryover (or delayed) effects of prior habitat conditions. As well, if increasing rainfall is associated with increased vegetation biomass for mixed grazer/browsers (Coe et al., 1976; Deshmukh, 1986), such as elephants (*Loxodonta africana*) and impala (*Aepyceros melampus*), then the proportion of young plants damaged by browsers should decrease with increasing rainfall. However, the amount of this decrease should be higher for seedlings than saplings or adults because of the high palatability of seedlings (Sharam et al., 2006). Increasing rainfall generally leads to higher biomass and dominance of particular species, resulting in differential competitive exclusion, if competition for resources enables species with stronger competitive abilities to outperform (e.g., become taller than) less competitive species (Zimmermann et al., 2009). This would result in low species richness and evenness in wetter areas (Figure 1a). Alternatively, if species richness increases with increasing rainfall, then competition is less likely to be important in structuring plant communities and alternative processes are more likely to be at play. If species are limited by stress or disturbances (e.g., drought, herbivory, or fire) then richness and evenness should increase with increasing rainfall (Figure 1b) (Augustine and McNaughton, 1998; Walker et al., 2006). Stochastic processes may also lead to a positive relationship between species richness and rainfall. If the total abundance of all trees is likely to increase with rainfall, so are the abundances of the individual constituent species, thus reducing the chances of random extinctions because any dying individual could be randomly replaced by an immigrant from the community (Alonso et al., 2006). Hence, a positive relationship between rainfall and richness (Figure 1c) may imply an important role for stochastic processes. Furthermore, a decrease in evenness can be expected if stochastic processes are more important in determining community structure because, as biomass is likely to increase at higher rainfall, so is the dominance of more productive species (Huston, 1997).

If the stability of communities increases with diversity, this could be interpreted as suggesting an important role for competition (Figure 1a) (Tilman, 1994; Tilman et al., 2006). Under changing environmental conditions or disturbances the loss of one species can be compensated for by other co-existing species (Tilman, 1996) independently of the abiotic conditions. Alternatively, if diversity and stability are unrelated, this can be viewed as signalling habitat filtering or stochastic processes (Figure 1a and b).

Furthermore, community composition, expressed in terms of nestedness (Wright and Reeves, 1992; Wright et al., 1997), measures whether relatively rare species tend to be confined to areas where common species are also present. If low rainfall areas are the most species rich, with both common and rare species, while wet areas only allow common, competitively superior species, then a nested pattern could be viewed as a sign of reduced competition in dry areas, but high competition in wet areas (Figure 1a) (Hutchinson, 1959; Grime, 1997). Alternatively, high nestedness may result from habitat filtering, with only favourable, wet areas allowing both common, drought tolerant, and rare, drought intolerant species (Figure 1b) (Adler and Levine, 2007; Keddy, 1992). Nestedness could also be the outcome of the dynamics of random extinction and colonization processes, where most diverse communities are those with the highest biomass (Figure 1c).

Here, we analyze the influences of rainfall and large browsing herbivores on woodland (*Croton* thickets) community structure and recruitment dynamics using long-term monitoring data on tree recruitment, biomass, diversity, composition and stability patterns in woodlands arranged along a rainfall gradient in a premier African savanna, namely the Mara-Serengeti ecosystem. Specifically, we analyze the dynamics of tree seedling and sapling recruitment and tree damage by large browsing herbivores and the spatial relationships between rainfall and (i) tree community biomass, (ii) species richness, (iii) evenness, (iv) stability and (v) composition. We use the resultant insights to infer and interpret savanna woodland community structure and recruitment dynamics.

MATERIALS AND METHODS

Study area

The study was conducted in the Masai Mara National Reserve (MMNR), a premier protected area covering some 1530 km² in south-western Kenya and the northernmost section of the Greater Mara-Serengeti ecosystem covering some 40,000 km². The ecosystem is delineated by annual migratory movements of wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga burchelli*), Thomson's gazelle (*Gazella thomsoni*) and eland (*Taurotragus oryx*) from the Serengeti plains in the south and Masai pastoral ranches to the north-east. The reserve is a dry season refuge for both migratory and resident herbivores (Dublin et al.,

1990a); whereas, the adjoining pastoral ranches and wildlife conservancies support vast herds of livestock and a diverse assemblage of resident large wild herbivores (Stellfox et al., 1986). The MMNR and its neighbouring pastoral ranches and wildlife conservancies constitute the Mara region. Rainfall in the Mara region is bimodal with "short" rains falling during November–December and "long" rains during March–June. The dry season spans July–October, but January–February is also often dry. Rainfall in the Mara-Serengeti ecosystem increases along a southeast-northwest gradient and with increasing altitude; and averages less than 600 mm in the southeast in Tanzania and over 1200 mm in the northwest of the Mara region (Pennycuik and Norton-Griffiths, 1976). Mean temperature levels have been rising in the Mara region in recent decades, a trend associated with progressive habitat desiccation (Ogutu et al., 2008a). The MMNR also experiences recurrent severe droughts, the most noteworthy during the study period (1989–2003) being in 1993 and 1999–2000 (Ogutu et al., 2008a).

Rainfall measurements

Monthly rainfall data were collected from a network of 58 rain gauges distributed over the entire Mara-Serengeti ecosystem by the Serengeti Ecological Monitoring Program and the Masai Mara Ecological Monitoring Program during 1985–2003 (Coughenour, 2006). Of these 58 gauges, 43 were located in the Serengeti; whereas, the remaining 15 were located in the Mara Reserve. We used spatially interpolated monthly mean and annual precipitation over the entire ecosystem at a spatial resolution of 1 × 1 km² using the PPTMAP computer program described in detail by (Reed et al., 2009). We associated each vegetation sampling plot in the MMNR with the interpolated monthly rainfall for the grid cell in which the plot fell based on the 1985–2003 rainfall measurements. Rainfall was summarized into wet (November–June) and dry (July–October) season and annual (November–October) components because the climatic year begins in November of the current year and ends in October of the following year. We derived seasonal and annual rainfall lags and moving averages spanning periods of 1 to 5 years before the sampling year to evaluate the influence of delayed and cumulative past rainfall on seedling and sapling recruitment dynamics. The 5-year period was selected to match the 5-year quasi-periodic oscillation evident in the regional rainfall and the associated changes in vegetation state (Ogutu et al., 2008a). Table 1 summarizes the specific rainfall components, lagged and moving averages considered.

Sampling design and monitoring

The study is based on biennial vegetation monitoring data collected by the Masai Mara Ecological Monitoring Program over a 15-year period spanning 1989–2003 in Kenya's Masai Mara National Reserve. The Masai Mara Ecological Monitoring Program (MMEMP) established four pairs of *Croton* thicket plots at four sites in the MMNR in 1989 (Dublin, 1991). Each site had two replicate plots running parallel to each other and located 100 m apart. Hence, there were a total of 8 croton thicket plots in the entire MMNR. Each of the 8 plots was 100 m long and 20 m wide (2000 m²) and was subdivided into 10 subplots each measuring 10 m by 20 m or 200 m². Records from all the 10 subplots per plot were combined into one set of plot data for analysis. The 8 plots were selected to represent the dominant croton woodland habitats and were oriented along a southeast-northwest gradient. The plots were arrayed along a rainfall gradient covering the full length and breadth of the MMNR (Figure 2). Metal rods driven into the ground were used to mark the boundaries of each plot. The dominant species in

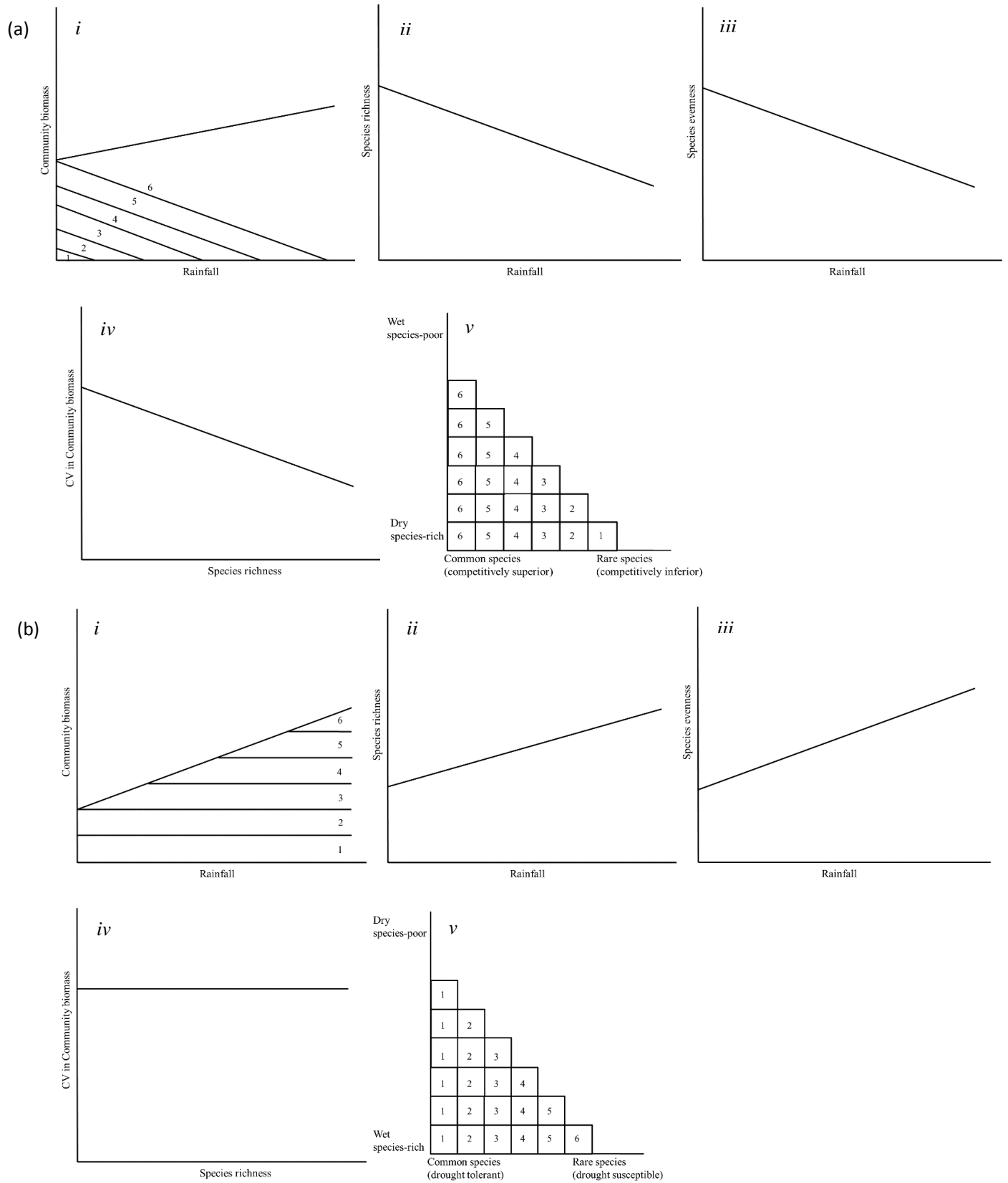


Figure 1. Theoretical predictions of the relative importance of (a) competition, (b) habitat filtering and (c) stochastic processes in structuring woodland communities in savannas.

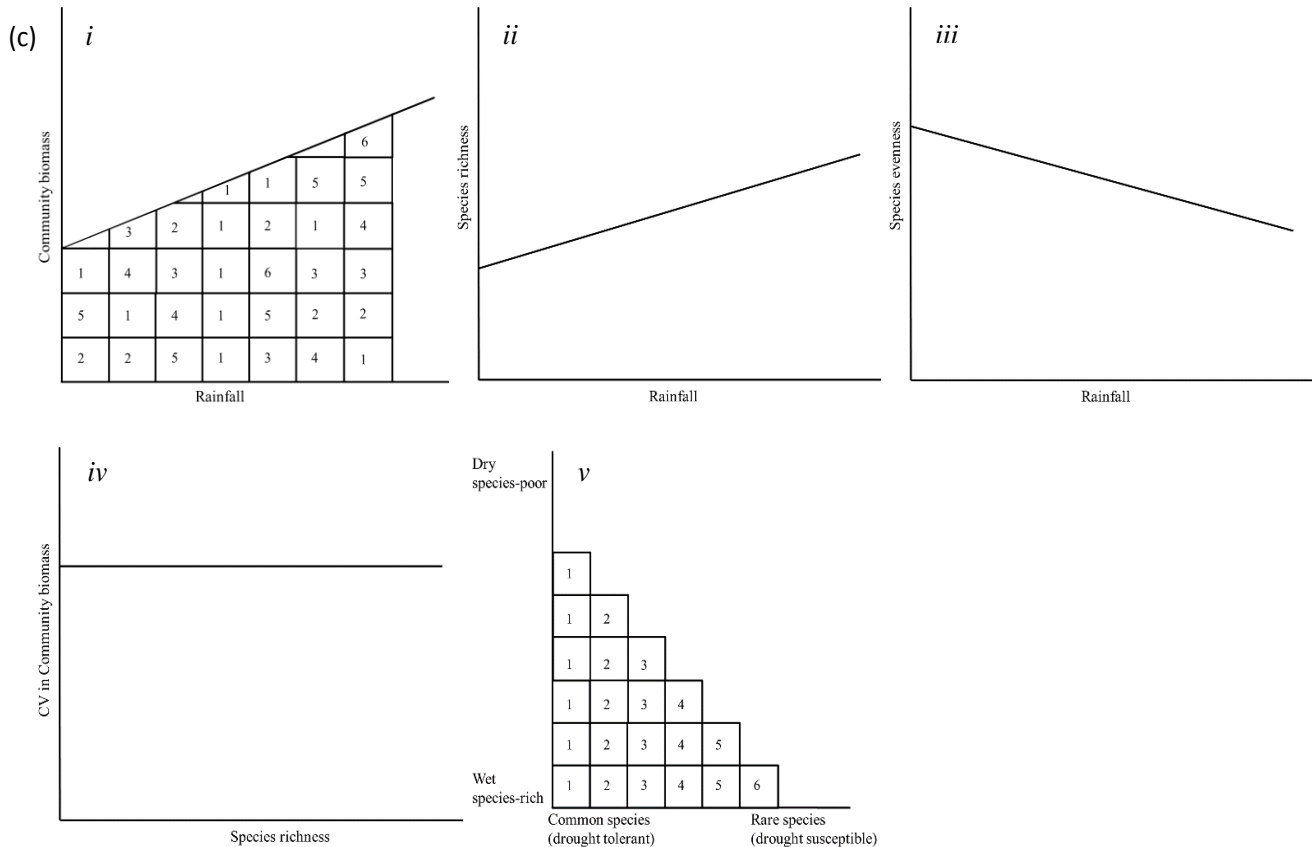


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Croton thickets consist of the fire-tolerant shrubs *Croton dichogamus*, *Euclea divinorum*, *Grewia similis* and *Tarenna graveolens* interspersed with *Acacia* species such as *A. gerradii* and 53 relatively rare species (S1 Data). Each of the eight plots was sampled eight times during the 1989-2003 monitoring period, specifically in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003, when the monitoring program ended. Sampling a single plot took two people one week to complete, on average; with a sampling day starting at 0700-0730 h and ending at 1700 h. The total of 8 plots thus took a total of 40 days to sample. The plots were accessed by vehicle, or on foot, using a global positioning system (GPS; S2 Data). Plots were not fenced and hence were open to all grazers and browsers because of the high risk of fence damage by elephants. Over the course of the monitoring period, a total of four field staff carried out the same sampling procedure in each plot to ensure comparability of the long-term vegetation samples. All the field staff were thoroughly trained in vegetation sampling, identification of plant species and data recording before carrying out field sampling to ensure consistency. All trees and shrubs with stem diameters 10 cm or larger were measured using a standard diameter tape and identified following Beentje (1994). Measurements of stem diameter were taken at 10 cm above the ground, rather than at breast height because of the diminutive stature of most of the trees in the woodland communities and to take care of the seedlings, saplings and natural regeneration. Additional measurements recorded for each tree were height, degree of browsing and extent of fire damage as detailed below for each attribute.

Most savanna tree species are strong resprouters and therefore poor recruiters, making size an imperfect indicator of tree age in savannas; a short individual may be ancient and may have survived many bouts of drought, herbivory or fire. Therefore, we carefully examined all saplings to accurately determine whether they were new or transitioning seedlings. Similarly, we used knowledge of tree growth rates to determine whether seedlings were regressed saplings (after drought or herbivory).

As a result, the monitoring program devised and implemented an elaborate procedure to accurately distinguish resprouters from seedlings and saplings and new saplings from transitioning seedlings in the field. Resprouters were distinguished from seedlings or saplings in the field as follows. Resprouts have browsing (e.g., from bark stripping) or fire scars on the leading shoot or its branches. Resprouters have a mature stem with a thick and mature bark particularly at the base, just above the ground level, which is lacking in seedlings or saplings. Resprouters also have high branching of the tree stem, particularly from the area it was browsed compared to new seedlings or saplings. Moreover, virtually all the tree species are indigenous and grow very slowly in terms of the mean annual increment (MAI). We thus used knowledge of the tree species' MAI, to help differentiate resprouters from seedlings and saplings. Lastly, we checked earlier records for each of the subplots, typically from the last sampling session, to establish if a particular tree had appeared in the earlier records to help distinguish resprouters from seedlings or saplings. Resprouters but not seedlings or saplings should appear in the past records. If a tree belonged to the same species that had dominated

Table 1. Rainfall components, the months covered by each component, moving averages and lags computed for each component.

Rainfall component	Months	Moving averages	Lagged rainfall
Wet season	Nov-Jun	Mavwet1-Mavwet5	Lagwet1-Lagwet5
Dry season	Jul-Oct	Mavdry1-Mavdry5	Lagdry1-Lagdry5
Annual	Nov-Oct	Mavannual1- Mavannual5	Lagannual1-Lagannual5

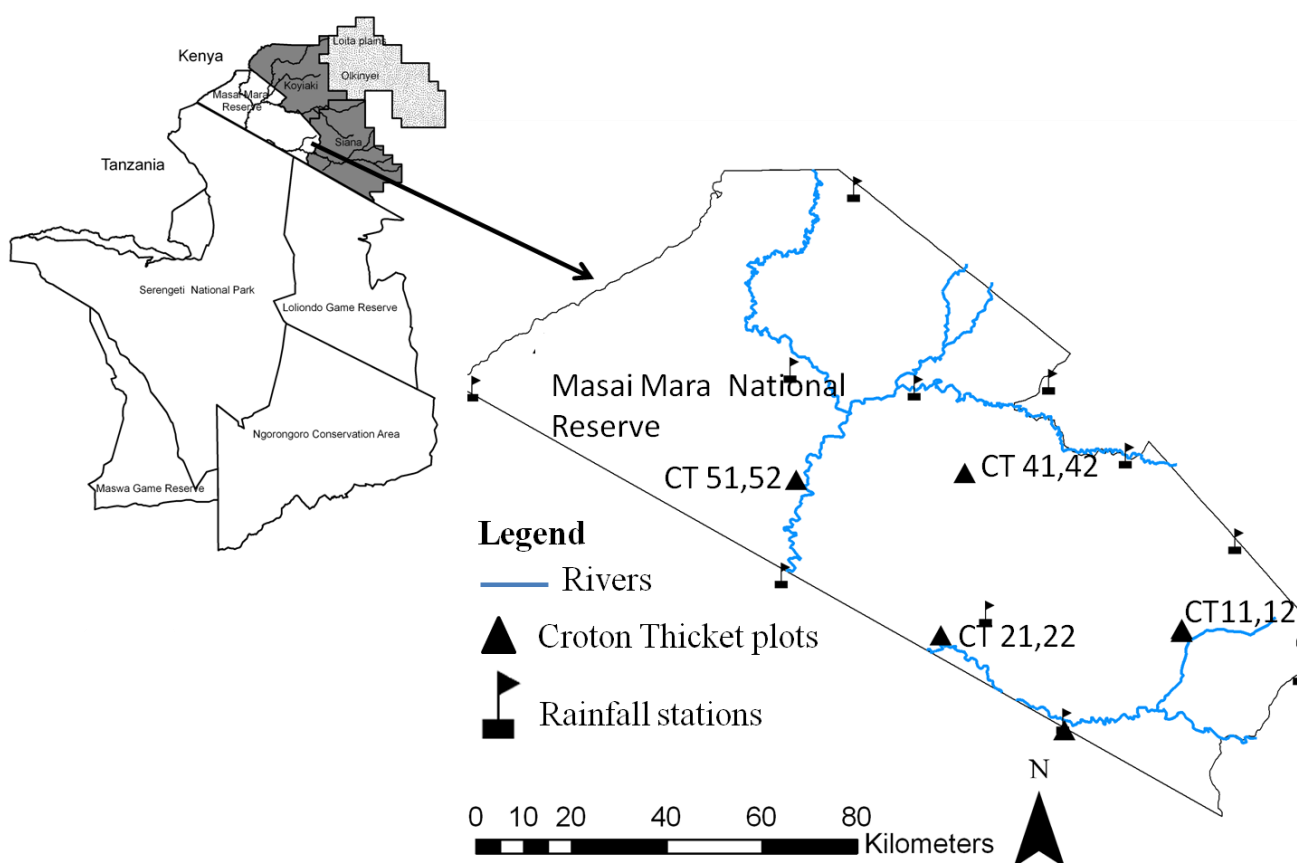


Figure 2. Distribution of eight *Croton* thicket plots, each composed of 10 subplots, across the Masai Mara National Reserve.

a subplot in the previous records, then we used its size to determine if it is a resprouting tree, seedling or sapling.

Height

Tree height (in cm) was assumed to be the height of the main tree crown and was measured using a regular measuring tape. Individual plants of the five major dominant species within each plot were measured and assigned to one of three height classes: seedlings < 0.6 m, saplings > 0.6 but < 1.50 m and adults > 1.50 m. These height classes overlap the mean browsing heights for the common large browsing species in the study area (Dublin et al., 1990b). The sapling height category represents the mean browsing height of resident antelope browsers primarily involved in woodland dynamics in the Mara-Serengeti, including dik dik (*Rhynchotragus*

kiriki), Grant's gazelle (*Gazella granti*) and impala (Dublin, 1991). Elephant and giraffe (*Giraffa camelopardalis*) largely browse on trees taller than 1.5 m in both *Croton* thickets and *Acacia* woodlands; whereas, fires affect all trees shorter than 3 m (Dublin et al., 1990a).

Browsing and fire damage

Individual trees were categorized into either "damaged" or "not damaged" classes. Trees were classified as damaged using combinations of browsing characteristics, such as bark stripping, branch clipping, branch breakage and branch toppling. Elephants and other browsers promote seed dispersal (Dublin, 1986), but elephants also destroy trees. An average of about 1000 elephants used the Mara Reserve and this number varied little during the

monitoring period (Dublin and Douglas-Hamilton, 1987; Ogotu et al., 2011). Fires were frequent in the MMNR during the monitoring period that spanned the longest El Niño episode on instrumental record up to 2003 (Ogotu et al., 2008a; Green et al., 2015). The fires reduce seed germination and increase seedling death but can also break dormancy and improve seed germination for some species. Trees damaged by fire were categorized using fire scars on the barks, or branches. From 1991 to 2003, the MMNR management restricted burning largely to the short dry season (January-February), when grass biomass and combustibility is low due to high moisture content, making fires less damaging. Fire scars, therefore, became extremely rare in both *Croton* and *Acacia* woodlands and had little influence on recruitment. The number of trees damaged by elephants and fire were summed together for each age class prior to analysis.

Community biomass index

We estimated the basal area (in m^2) as $\pi d^2/4$, where d is the stem diameter. We then estimated the parabolic volume (in m^3) of the individual trees as the basal area x height / 2. We then averaged the parabolic volume over all individuals within each plot in each sampling year to obtain an index for total community biomass. We also calculated a community-level stability index (S), as the standard deviation divided by the mean community biomass (coefficient of variation) for each plot over the entire monitoring period as well as for each year across all the plots. A community is regarded as “stable” if S is equal to 1 and unstable if S is equal to 0 (Pimm, 1984).

Species’ richness, evenness and nestedness

Species richness was determined by the total number of different species; whereas, species evenness (Pielou, 1977) was calculated as diversity/ \ln (richness), where diversity is calculated using the Shannon-Weaver Diversity index (Shannon and Weaver, 1949). We estimated an index of nestedness for the species presence/absence matrix as a measure of community composition (Wright and Reeves, 1992).

Statistical analysis

We first describe temporal patterns in recruitment rates for the five woody species constituting major dominants in *Croton* thickets and then relate the patterns to temporal fluctuations in rainfall and herbivory. More precisely, we analyze the seedling (number of saplings /number of seedlings) and sapling (number of adults /number of saplings) recruitment dynamics and evaluate the relative influence of past rainfall accumulated over periods spanning 1 to 5 years. We also analyze relationships between plant community biomass, diversity, stability and composition and spatial variation in rainfall and use them as proxies for inferring the relative importance of the three generic processes structuring savanna woodland communities along the rainfall gradient.

Modeling temporal trends in recruitment

Statistical analysis aimed to establish whether climate, herbivores, antecedent conditions indexed by rainfall lags or cumulative past rainfall or their interactions were primarily responsible for the patterns we uncovered. Modeling temporal changes in the seedling

and sapling recruitment rates for individual species requires a model able to accommodate non-normality, non-constant variance of the counts, missing values and many zero counts. We thus analyzed temporal trends in the seedling and sapling recruitment rates using a generalized linear model assuming a negative binomial error distribution for the counts and a log link function to satisfy these requirements. The model incorporated year as a categorical fixed effect. The expected seedling recruitment rate was calculated as the number of saplings summed across all plots, which we used as the response variable, offset by the logarithm of the number of seedlings summed across all the eight plots. Similarly, the expected sapling recruitment rate was calculated as the number of adults summed across all plots (response variable) offset by the logarithm of the number of saplings. The model assumed that missing counts were missing at random (Ozinga et al., 2005) and hence ignorable. The models were fit using the package MASS version 7.3-8 in the R Software (R Development Core Team, 2010). The scale and overdispersion parameters of the negative binomial model were estimated automatically by the procedure.

Modeling relationship between recruitment and rainfall

We regressed recruitment rates for each of the four dominant species on each of the 30 derived rainfall components to identify the components most strongly correlated with the rates and the functional forms of the relationships. To establish the functional form of the relationship between recruitment and rainfall, each expected recruitment rate was related to each of the 30 rainfall components r using the following three generalized linear models (Ogotu et al., 2008b):

$$\mu = \exp(\alpha + \beta r) \quad (1)$$

$$\mu = \exp(\alpha + \beta_1 r + \beta_2 \ln(r)) \quad (2)$$

$$\mu = \exp(\alpha + \beta_1 r + \beta_2 r^2 + \beta_3 \ln(r)) \quad (3)$$

where α is the intercept and β_1 to β_3 are regression slopes. We use these models to test if seedling and sapling recruitment rates (1) increase or decrease linearly with increasing rainfall or (2) peak at intermediate levels of rainfall. We also test if sapling recruitment rates are influenced less by rainfall and respond to rainfall accumulated over longer periods than seedling recruitment due to carryover effects of prior rainfall. We use the corrected Akaike Information Criterion (AICc) (Burnham and Anderson, 2002), to select both the best model and rainfall component most strongly correlated with recruitment rates for each species (S1 Table). The models were also fitted using negative binomial regression in the package MASS version 7.3-8 of the R Software (R Development Core Team, 2010).

Modeling trends in, and relationships between, browsing damage and rainfall

We first modelled temporal trends in the age class-specific proportions of individual trees of each species damaged by browsers across all plots. We then related these proportions to each of the 30 seasonal and annual rainfall components and their lagged and moving average components to identify the components

most strongly correlated with the rates for each species using AICc (S2 Table). We modelled the proportion of damaged seedlings by specifying the number of damaged seedlings as the response variable and the logarithm of the total number of seedlings as the offset variable in the negative binomial regressions. We similarly modelled the proportion of damaged saplings and adults. The models were also fitted in the MASS package version 7.3-8 in the R Software (R Development Core Team, 2010). Differences in the expected proportion damaged between years were tested using the Wald chi-squared test (Draper and Smith, 1998).

Temporal variation in community biomass

We calculated the total community biomass of all trees averaged over all plots in each year. We then analyzed temporal trends in community biomass using linear regression analyses. The biomass was the response variable; whereas, the year of vegetation sampling was incorporated in the models as a fixed effect. To assess changes in community biomass in response to rainfall, we regressed the total community biomass of all trees over all plots on each of the 30 rainfall components assuming normal errors and an identity link. We used AICc in R version 2.12.0 (R Development Core Team, 2010), to select both the best model and rainfall component most strongly correlated with biomass (S3 Table). We tested for temporal trends in species richness and evenness using the same statistical approach as for biomass and regressed these against the various rainfall components.

Spatial variation in species diversity, stability and nestedness

To characterize the spatial patterns in species richness and evenness we summed the total number of different coexisting species and calculated the relative abundance of each species to the total abundance in each plot and averaged them over the monitoring period. We evaluated spatial patterns in species richness (the number of species) and evenness (a measure of the equitability of the proportional abundances of species) in each plot by averaging them over the monitoring period. The relationships between species richness and evenness and rainfall were analyzed using the standard normal-theory linear regressions. Again, AICc was used to identify the best model and the rainfall component having the strongest correlation with richness and evenness (S3 Table). The models were also fit using a linear regression assuming normality of errors and an identity link. We determined community stability using all the data collected biennially on woody vegetation biomass within each plot during 1989-2003. To evaluate the relationship between community stability and richness, we calculated stability in community biomass (S) as $S = j/m$ (i.e., coefficient of variation) where j is the standard deviation and m is the mean biomass in a given plot during 1989-2003. We used linear regression analyses to evaluate temporal variation in community-level stability between plots of varying richness. The models, incorporating richness as a continuous covariate, were also fit assuming normality and an identity link.

We estimated an index of nestedness of the species presence/absence matrix using the 'binmatnest' algorithm of (Rodríguez-Gironés and Santamaría, 2006), implemented in the 'bipartite' R package (Dormann et al., 2008) to characterize how species are distributed among all the plots. The tree data from all the survey years (1989-2003) were used to construct a species presence-absence matrix. This procedure followed a three-step process: first, the matrix is reorganized by arranging rows (plots) and columns (species) from full (species presence) to empty (species absence) cells. Second, to maximize nestedness the full cells are mainly located in the upper-left corner and empty cells are

mainly located in the lower right corner. An isocline for this matrix of perfect nestedness is calculated. Third, for the reorganized, presence-absence matrix, full cells above the isocline and empty cells below the isocline were identified and a normalized sum of their distances to the isocline calculated, in such a way that it ranged from 0 (no deviation and therefore perfect nestedness) to 100 (maximum deviation and therefore perfect 'un-nestedness'). This normalized deviation measure of an observed matrix from a perfectly nested matrix is called the 'nestedness temperature' with low values indicating high nestedness. More details on this procedure can be found in Rodríguez-Gironés and Santamaría (2006). To test whether the observed nestedness was higher or lower than that expected by chance, we used a null model developed for a permutation test by (Bascompte et al., 2003). The test involves creating new random matrices of the same size as the observed matrix. The probability of each cell in these matrices being filled is the average of the probability of filling each of its associated rows ($n = 8$ plots) and columns ($n = 70$ species). This type of null model is relatively conservative, but is less vulnerable to type II errors (Rodríguez-Gironés and Santamaría, 2006; Cottenie, 2005). We ran the null model with 1000 permutations as implemented in the 'bipartite' package.

RESULTS

Temporal trends in rainfall and temperature

The period 1989–2003 was one of the hottest recorded since the 1960s (Ogutu et al., 2008a), implying that climatic variation was likely a major factor in vegetation recruitment dynamics. In particular, the study period was characterized by recurrent severe (1993, 1997 and 1999-2000) and mild (1991 and 1994) droughts and exceptional floods (1997-1998) associated with the longest (1990-1995) and strongest (1997-1998) El Niño Southern-Oscillation (ENSO) episodes on instrumental record up to 2003. The cumulative dry season rainfall component was largely below average from 1980s to 2003 implying reduced vegetation production and quality in the savanna grasslands (Ogutu et al., 2008a). More detailed descriptions of the temporal climatic patterns are presented elsewhere (Ogutu et al., 2008a).

Trends in recruitment rates

The seedling recruitment rate for all species but *T. graveolens* varied significantly across years. Recruitment rates for *E. divinorum* and *G. similis* increased exponentially; whereas, the rates for *A. brevispica* and *C. dichogamus* increased from 1990 to a peak during the El Niño floods of 1997/98 and then declined consistently soon after (Figure 3A-E, Table 2). These recruitment rates were low at the onset of the longest recorded ENSO episode (1990-1995) and the 1999-2000 ENSO drought (Ogutu et al., 2008a), revealing the adverse effect of low rainfall conditions on seedling recruitment. The sapling recruitment rates for all the species but *A. brevispica* and *T. graveolens* decreased significantly

Seedling recruitment

Sapling recruitment

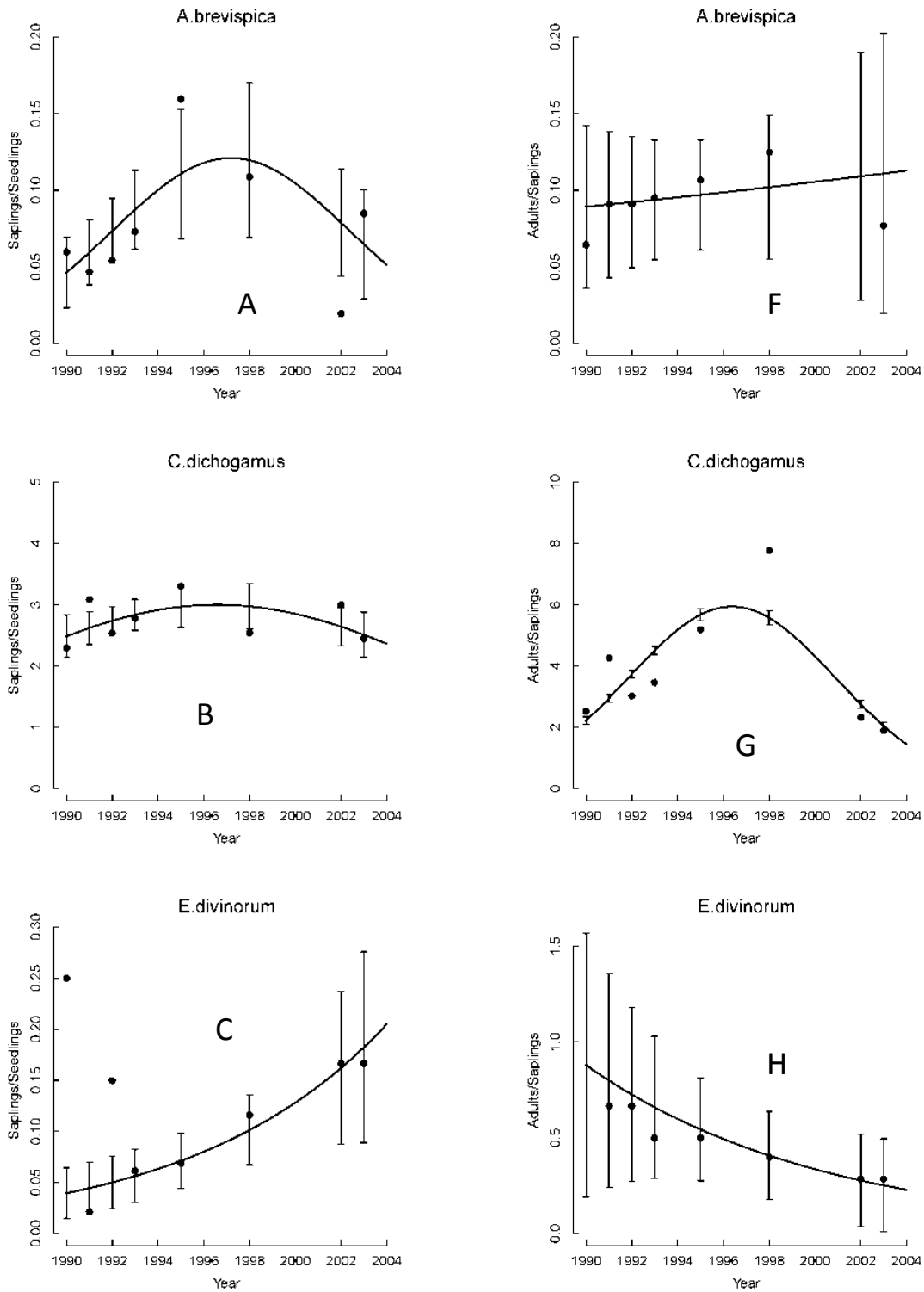


Figure 3. The changes in the expected (a-e) seedling and (f-j) sapling recruitment rates for the most common *Croton* species and the associated 95% confidence intervals for the trend lines across 8 plots, each consisting of 10 subplots, monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003.

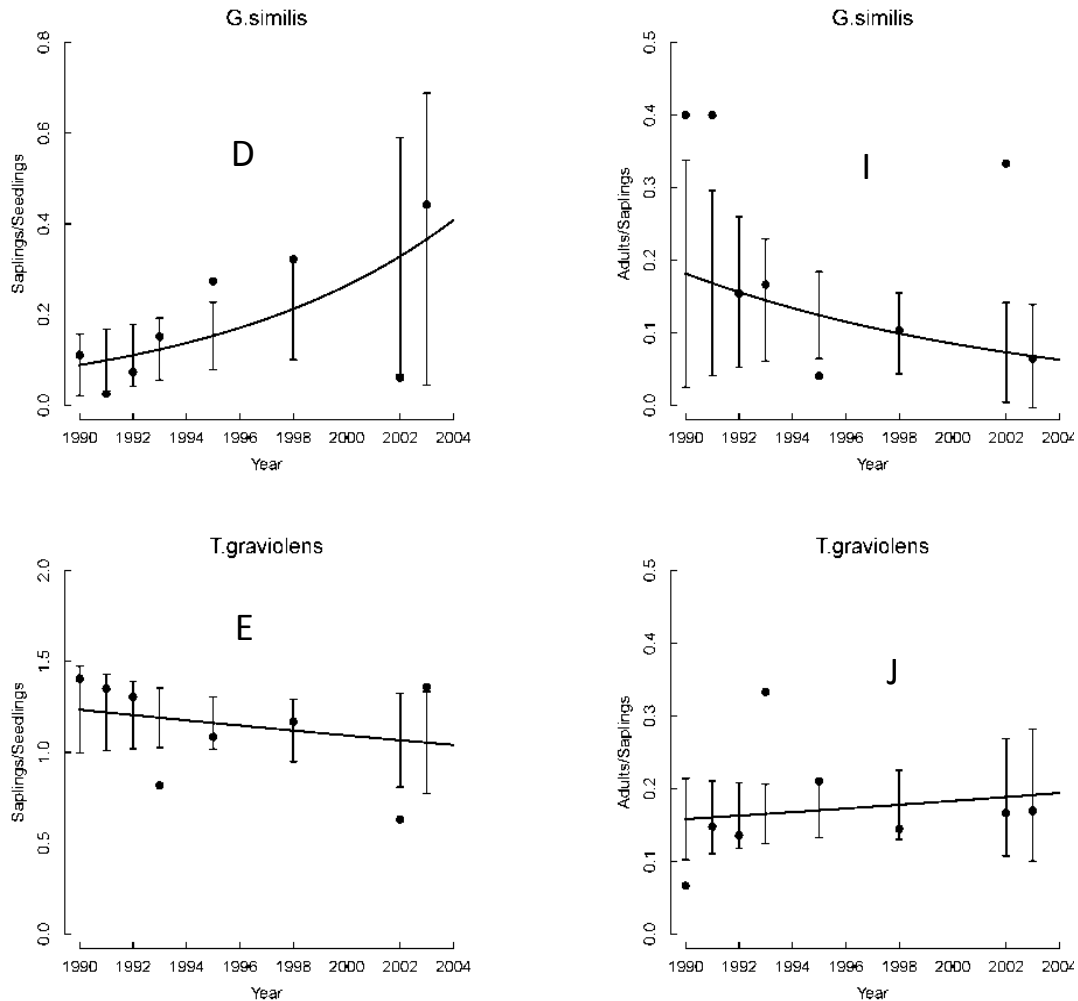


Figure 3. Contd.

across years (Figure 3F-J, Table 2). Sapling recruitment rates for *C. dichogamus* showed a similar trend to that of the seedlings.

Relationships between recruitment rate and rainfall

The recruitment rates for seedlings of all species varied significantly with rainfall. In particular, the rates for all the five dominant species but *A. brevispica* increased exponentially with increasing rainfall. Seedling recruitment rates for *E. divinorum* and *G. similis* increased with increasing 2-year running mean of the wet season rainfall component; whereas, the rates for *C. dichogamus* and *T. graveolens* increased with the 2-year running mean of the dry season and annual rainfall components (Figure 4A-E, Table 3). In contrast, the recruitment rates for saplings of all the dominant species but *C. dichogamus* and *G. similis* did not vary significantly

with increasing rainfall. The recruitment rate for *C. dichogamus* saplings showed a humped relationship with the 3-year running mean of the dry season rainfall, increasing initially up to a peak at about 150 mm of rainfall and then decreasing with further increase in rainfall (Figure 4F-J, Table 3).

Trends in the proportion of trees damaged by browsers

Trends in the proportion of damaged trees in the *Croton* habitats for all the five dominant species but *C. dichogamus* varied significantly between years (Table 4). The proportion of damaged trees in all height classes was highest during the early 1990s, decreased steeply until the exceptional El Niño rains of 1997/1998 and then increased sharply thereafter (Figure 5A-E). The proportions of damaged trees were highest at the early

Table 2. Negative binomial regression coefficients (estimate), their standard errors (SE), Z and P values for changes in expected seedling and recruitment rates for the most common *Croton* species across 8 plots, each consisting of 10 subplots, and monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003.

Height class	Species	Effect	Estimate	SE	Z	P> Z
Seedlings	<i>A. brevispica</i>	year	70.429	25.717	2.739	0.006
		year x year	-0.018	0.006	-2.737	0.006
	<i>C. dichogamus</i>	year	17.356	8.968	1.935	0.053
		year x year	-0.004	0.002	-1.935	0.053
	<i>E. divinorum</i>	year	0.125	0.042	3.013	0.003
	<i>G. similis</i>	year	0.120	0.060	2.006	0.045
Saplings	<i>T. graveolens</i>	year	-0.012	0.015	-0.809	0.419
		<i>A. brevispica</i>	year	3.779	4.950	-0.759
	<i>C. dichogamus</i>	year x year	-0.092	0.012	-0.752	0.452
		year	96.923	3.238	29.931	0.000
	<i>E. divinorum</i>	year x year	-0.024	0.001	-29.938	0.000
		year	-0.070	0.071	-0.985	0.032
	<i>G. similis</i>	year	-0.043	0.069	-0.624	0.053
	<i>T. graveolens</i>	year	0.015	0.027	0.532	0.594

stages of the longest recorded ENSO episode (1990-1995) and following the extreme 1999-2000 La Niña drought. The proportions of damaged adult *A. brevispica* and *C. dichogamus* trees were significantly higher than the corresponding proportions for their saplings and seedlings throughout 1989-2003 (Figure 5A-E, Table 4). For *E. divinorum* and *T. graveolens*, in contrast, saplings and seedlings suffered significantly greater damage than the adults did; whereas, for *G. similis* the proportions of damaged trees were comparable across all the three age classes during the monitoring period (Figure 5A-E, Table 4).

Relationships between browsing damage and rainfall

The proportions of damaged trees showed humped relationships with the annual rainfall component for all the five dominant species and peaked at intermediate values of rainfall before decreasing with further increase in rainfall except for *T. graveolens* for which the proportion of damaged individuals decreased exponentially with increasing rainfall (Figure 5F-4J, Table 5).

Temporal variation in community biomass, richness, evenness and stability

Community biomass over the entire landscape declined consistently over the monitoring period (Figure 6A) but increased linearly with the 2-year cumulative moving average of the dry season rainfall (Figure 6B, Table 6). However, species richness and evenness and community stability were apparently temporally stable (Table 6).

Spatial variation in community biomass, richness, evenness, stability and nestedness

Average woody biomass per plot did not vary significantly with any rainfall component. However, species richness per plot increased up the rainfall gradient and also increased strongly with the 2-year cumulative moving average of the dry season rainfall (Figure 6C, Table 6). In contrast, the average species evenness per plot was not significantly related to rainfall (Table 6). The coefficient of variation of biomass (stability index) for each plot was not significantly correlated with richness (Table 6). The average (\pm 1SE) "nestedness temperature" of the randomized communities was 49.254 ± 11.325 . The observed nestedness temperature was 34.50 and was significantly ($P < 0.05$) lower than that expected for randomly assembled communities, indicating that species composition was significantly more nested than expected by chance alone (Figure 7).

DISCUSSION

We examined variation in a range of structural and demographic variables (tree recruitment, damage, species diversity, community biomass) over time and in relation to rainfall and community nestedness.

Recruitment trends and relationship with rainfall

We found significant year-to-year variation in recruitment patterns during 1989-2003. Specifically, seedling and sapling recruitment rates for the dominant species varied

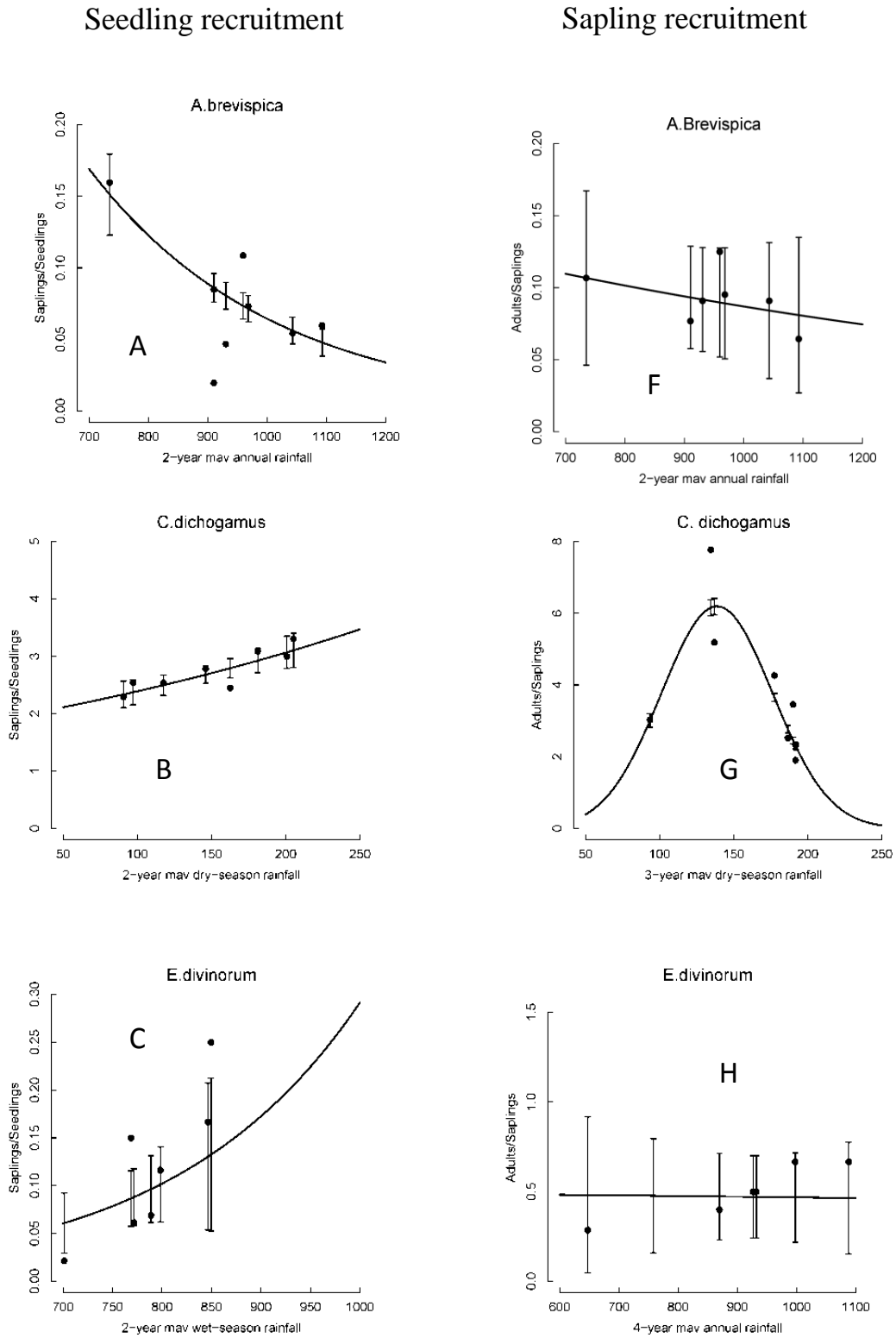


Figure 4. The relationships between cumulative past rainfall and the expected (a-e) seedling and (f-j) sapling recruitment rates for the most common *Croton* species and the associated 95% confidence intervals for the trend lines across 8 plots, each consisting of 10 subplots, monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003. Mav means moving (running) average of rainfall.

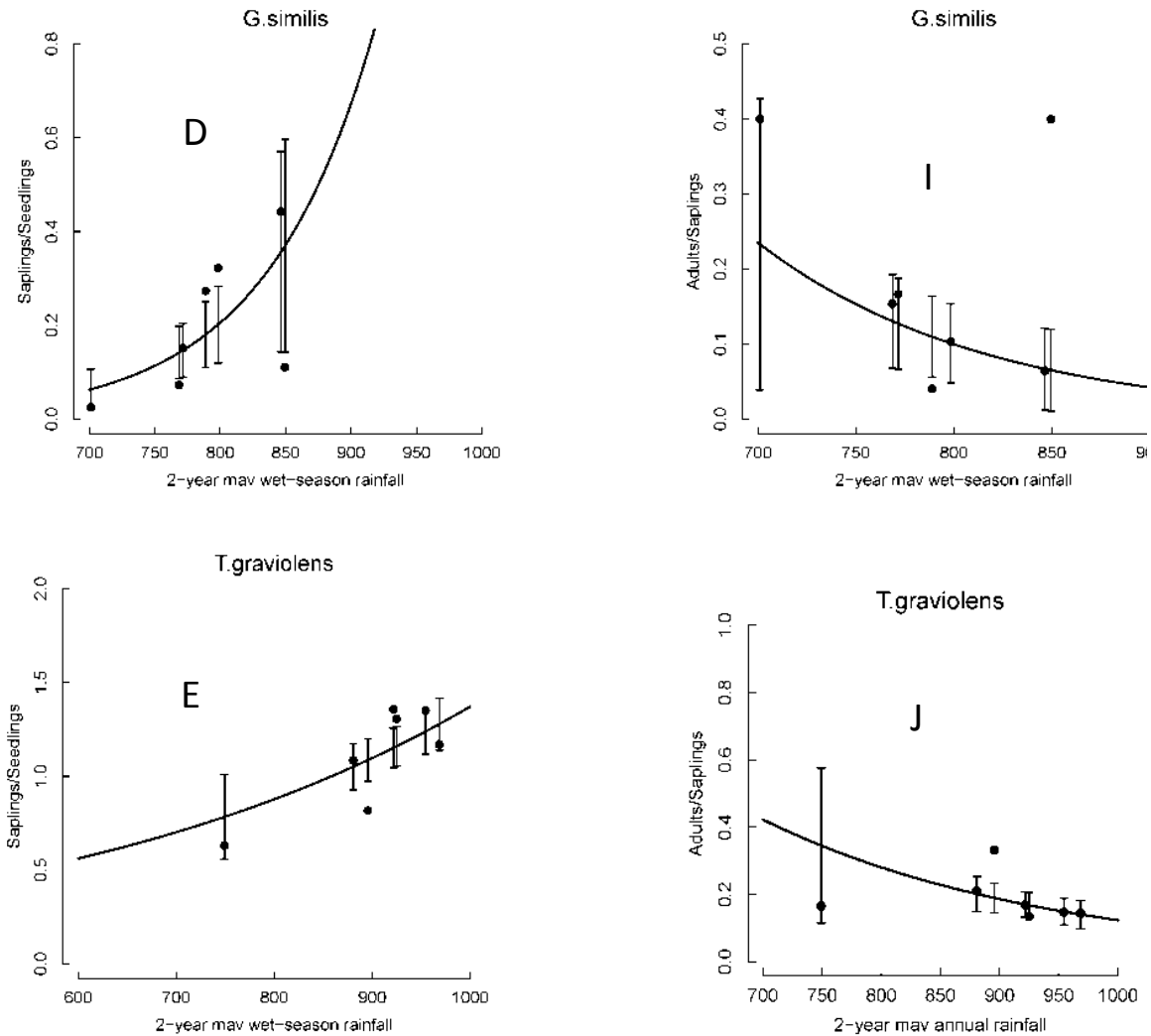


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Table 3. Negative binomial regression coefficients (estimate), their standard errors (SE), Z and P values for the influences of cumulative past rainfall on the seedling and sapling recruitment rates for the most common *Croton* and *Acacia* species across 8 plots, each consisting of 10 subplots, and monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003.

Height class	Species	Effect	Estimate	SE	Z	P> Z	R ²
Seedlings	<i>A. brevispica</i>	Mavannual2	-0.003	0.000	-7.351	<0.0001	0.670
	<i>C. dichogamus</i>	Mavdry2	0.002	0.001	3.489	<0.0001	0.698
	<i>E. divinorum</i>	Mavwet2	0.013	0.004	3.153	0.002	0.445
	<i>G. similis</i>	Mavwet2	0.015	0.003	4.774	<0.0001	0.823
	<i>T. graveolens</i>	Mavannual2	0.002	0.001	2.884	0.004	0.823
Saplings	<i>A. brevispica</i>	Mavannual2	-0.001	0.001	-0.556	0.578	0.044
	<i>C. dichogamus</i>	Mavdry3	0.098	0.004	27.551	<0.0001	0.783
		Mavdry3 × Mavdry3	0.000	0.000	-29.361	<0.0001	
	<i>E. divinorum</i>	Mavannual4	0.002	0.002	0.979	0.327	0.881
	<i>G. similis</i>	Mavwet2	-0.012	0.005	-2.455	0.014	0.698
	<i>T. graveolens</i>	Mavannual3	0.004	0.038	1.240	0.215	0.478

Table 4. Negative binomial regression coefficients (estimate), their standard errors (SE), Z and P values for changes in the expected proportion of trees damaged in each height class for the most common Croton species across 8 plots, each consisting of 10 subplots, and monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003.

Species	Effect	Estimate	SE	Z	P> Z
<i>A. brevispica</i>	Intercept	78307.82	38856.11	2.015	0.040
	saplings	-0.435	0.441	-0.986	0.324
	seedlings	-0.676	0.429	-1.575	0.115
	year	-78.434	38.923	-2.015	0.044
	year x year	0.02	0.01	2.015	0.044
<i>C. dichogamus</i>	Intercept	6865.278	41319.86	0.166	0.868
	saplings	-0.306	0.378	-0.81	0.418
	seedlings	-0.654	0.386	-1.695	0.090
	year	-6.929	41.389	-0.167	0.867
	year x year	0.002	0.01	0.169	0.866
<i>E. divinorum</i>	Intercept	128652.5	62634.36	2.054	0.040
	saplings	0.801	0.733	1.093	0.274
	seedlings	0.124	0.687	0.18	0.857
	year	-128.858	62.724	-2.054	0.040
	year x year	0.032	0.016	2.055	0.040
<i>G. similis</i>	Intercept	178242.2	54180.27	3.29	0.001
	saplings	0.068	0.551	0.123	0.902
	seedlings	0.037	0.535	0.069	0.945
	year	-178.506	54.259	-3.29	0.001
	year x year	0.045	0.014	3.29	0.001
<i>T. graveolens</i>	Intercept	90745.83	36228.38	2.505	0.012
	saplings	0.096	0.357	0.269	0.788
	seedlings	0.074	0.357	0.208	0.835
	year	-90.89	36.289	-2.505	0.012
	year x year	0.023	0.009	2.504	0.012

over time following contrasting patterns, with some species first increasing up to a peak in 1997/1998 and then decreasing thereafter (*A. brevispica*, *C. dichogamus*); whereas other species, particularly for seedlings, either increased (*E. divinorum*, *G. similis*), or for saplings, decreased (*E. divinorum*, *G. similis*), persistently over time. The humped relationship with rainfall implies that recruitment rates would reduce if climate change moved rainfall in either direction away from the optimum. The contemporaneous increase in seedling recruitment and decrease in sapling recruitment over time as well as with increasing rainfall, for *E. divinorum* and *G. similis*, for example, suggests the contribution of other factors beyond fire, browsing and rainfall to the removal of saplings.

Recruitment rates for all species were most strongly correlated with the 2- to 4-year moving average of either the annual, dry, or wet season rainfall components. Specifically, the recruitment rates for saplings of *C. dichogamus* and *E. divinorum* were more strongly influenced by longer rainfall lags; whereas, their seedling

recruitment responded to shorter rainfall lags, as expected. Longer lags in rainfall effects arise from the time needed for vegetation to recover from past extreme rainfall events or heavy browsing pressure. Prior rainfall can affect current habitat conditions by exerting a lagged influence on the vegetation state and, therefore, plants need to invest in allocating and storing resources in underground parts. This would promote above-ground plant growth at the onset of rainfall in the following rainfall season.

The proportion of trees damaged by browsers first increased with rainfall up to a peak between 850-900 mm of rainfall and then decreased with further increase in rainfall. This quadratic relationship reflects the fact that under dry conditions, especially where soils are fertile, plant parts tend to be more palatable and browsers to be more dependent on tree foliage because of limited production of herbaceous forage (Lavorel, 1999). Dry conditions also tend to support high densities of many herbivore species; e.g., in East African savannas (Olf and Ritchie, 1998). Thus, under arid conditions the

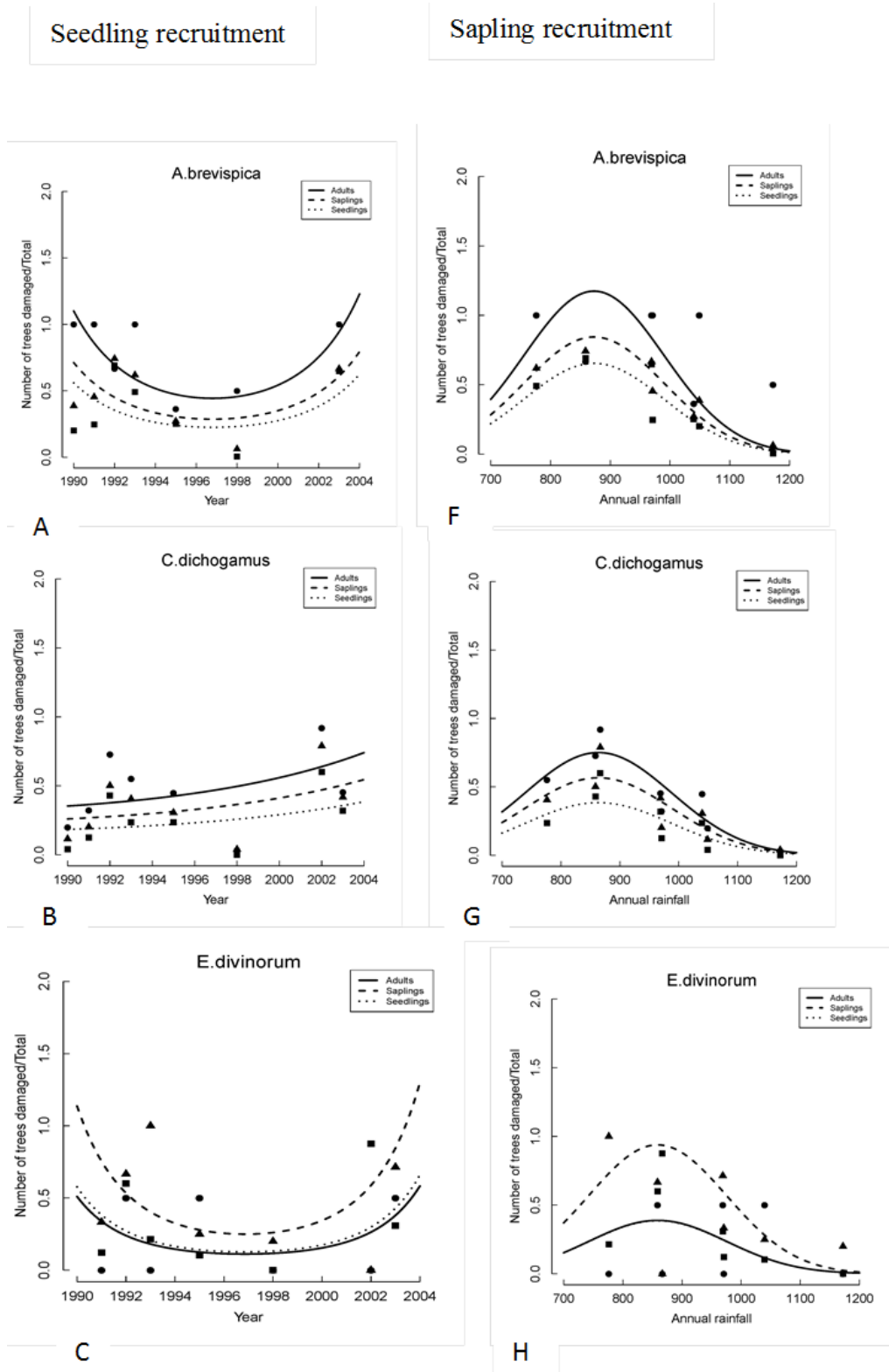


Figure 5. (a-e) The changes in the expected proportion of trees damaged in each height class and (f-j) the relationships between annual rainfall and the expected proportion of trees damaged in each height class for the most common *Croton* species across 8 plots, each consisting of 10 subplots, monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003.

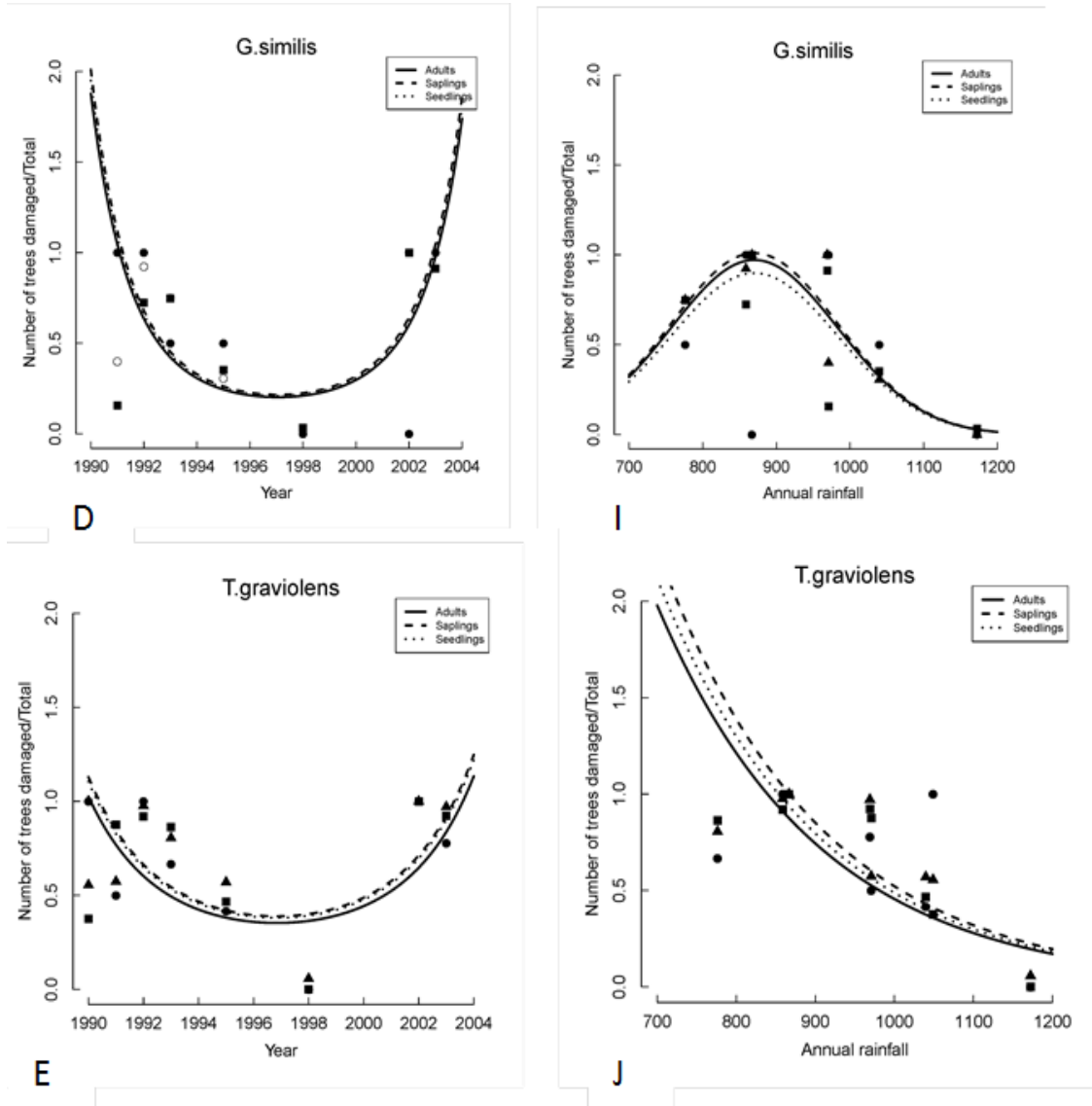


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dominant plant species are likely to be those able to better tolerate herbivory because of the good opportunities for regrowth owing to relatively higher nutrient availability in the soils (McNaughton, 1985; Anderson and Briske, 1995). At high rainfall, plants are likely to have lower tissue nutrient concentrations than in the drier areas. As a result, these plants will probably only be used by fewer, large browsers, which can tolerate low plant tissue quality (Owen-Smith, 1988). Moreover, during the wet season, most browsers forage on grasses in open grasslands (Owen-Smith, 1988) where grass and water are ubiquitous and plentiful; therefore, the proportion of damaged trees is reduced at high rainfall. Furthermore, the proportion of adult trees damaged by

browsers was significantly higher than that of saplings or seedlings, suggesting three possible explanations. First, adult trees are more detectable by browsers than saplings or seedlings. Second, adult trees may be selected by large browsers requiring bulk biomass in preference to saplings and seedlings with higher quality but low biomass. Third, large herbivores sometimes uproot seedlings or saplings thus precluding estimation of the proportion of damaged trees. These findings accord with those of other studies showing that greater proportions of adult trees than sapling or seedlings are damaged by large mammalian browsers, such as elephants and giraffes, in African savannas (Van Die Vijver et al., 1999).

Table 5. Negative binomial regression coefficients (estimate), their standard errors (SE), Z and P values for the combined influences of height class and annual rainfall on the expected proportion of trees damaged for the most common Croton and Acacia species across 8 plots, each consisting of 10 subplots, and monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003.

Species	Effect	Estimate	SE	Z	P> Z	R ²
<i>A. brevispica</i>	Intercept	-27.616	6.071	-4.549	<0.0001	0.509
	saplings	-0.330	0.296	-1.114	0.265	
	seedlings	-0.584	0.282	-2.070	0.038	
	annual	0.064	0.013	4.855	<0.0001	
	annual × annual	0.002	0.000	-5.179	<0.0001	
<i>C. dichogamus</i>	Intercept	-24.276	4.846	-5.010	<0.0001	0.777
	saplings	-0.281	0.165	-1.708	0.088	
	seedlings	-0.668	0.183	-3.653	<0.0001	
	annual	0.056	0.010	5.415	<0.0001	
	annual × annual	0.001	0.000	-5.982	<0.0001	
<i>E. divinorum</i>	Intercept	-28.088	12.814	-2.192	0.028	0.143
	saplings	0.881	0.663	1.328	0.184	
	seedlings	-0.008	0.618	-0.014	0.989	
	annual	0.063	0.028	2.238	0.025	
	annual × annual	0.002	0.000	-2.375	0.018	
<i>G. similis</i>	Intercept	-29.154	8.511	-3.426	0.001	0.413
	saplings	0.038	0.457	0.084	0.933	
	seedlings	-0.078	0.440	-0.178	0.859	
	annual	0.067	0.018	3.674	<0.0001	
	annual × annual	0.003	0.000	-3.969	<0.0001	
<i>T. graveolens</i>	Intercept	4.105	0.884	4.645	<0.0001	0.342
	saplings	0.135	0.288	0.469	0.639	
	seedlings	0.068	0.289	0.235	0.814	
	annual	-0.005	0.001	-5.367	<0.0001	

Spatial relationships between rainfall and community biomass, diversity, stability and nestedness

As predicted, community biomass for the entire landscape was influenced most strongly by the 2-year cumulative moving average of the dry season rainfall. The relationship reflects tree responses to delayed or carry-over effects of prior dry-season conditions rather than to immediate habitat conditions alone. Furthermore, the greater importance of the dry season rainfall relative to the other rainfall components suggests that woody vegetation biomass is limited more strongly by variation in the dry-season rainfall. The significant effect of cumulative past rainfall on woody vegetation biomass suggests that woody species allocate and store more resources in their deep taproots and re-use the stored resources to increase biomass in years of high rainfall.

If competition for light were the main process governing the structural organization of the woodland communities, then species richness should decrease with increasing rainfall. However, species richness in each plot increased with increasing rainfall. This suggests that competition for

light is apparently not the main mechanism controlling the structure of these woodland communities. The patterns suggest that the presence of more species may increase the functional diversity of the communities and thus allow a more differentiated and more complete exploitation of the available niche space, thereby enhancing resource use (Hooper, 1998). For example, species that are deeply rooted have access to water and nutrients not available to more shallowly rooted species, especially in drier areas (Chapin et al., 1996), which are therefore more likely to be found in wetter areas, where water is less limiting. Furthermore, the distribution of browsing pressure over more plants and better protection of rare plants from browsers at high rainfall could enable more species to successfully establish, leading to higher diversity. This suggests an important role for habitat filtering in drier areas, where only a few species are able to establish and/or survive under the stressful conditions, and the potential for interspecific differentiation in resource exploitation in wetter areas, enabling different species to jointly utilize relatively abundant resources. However, it is also possible that the number of species

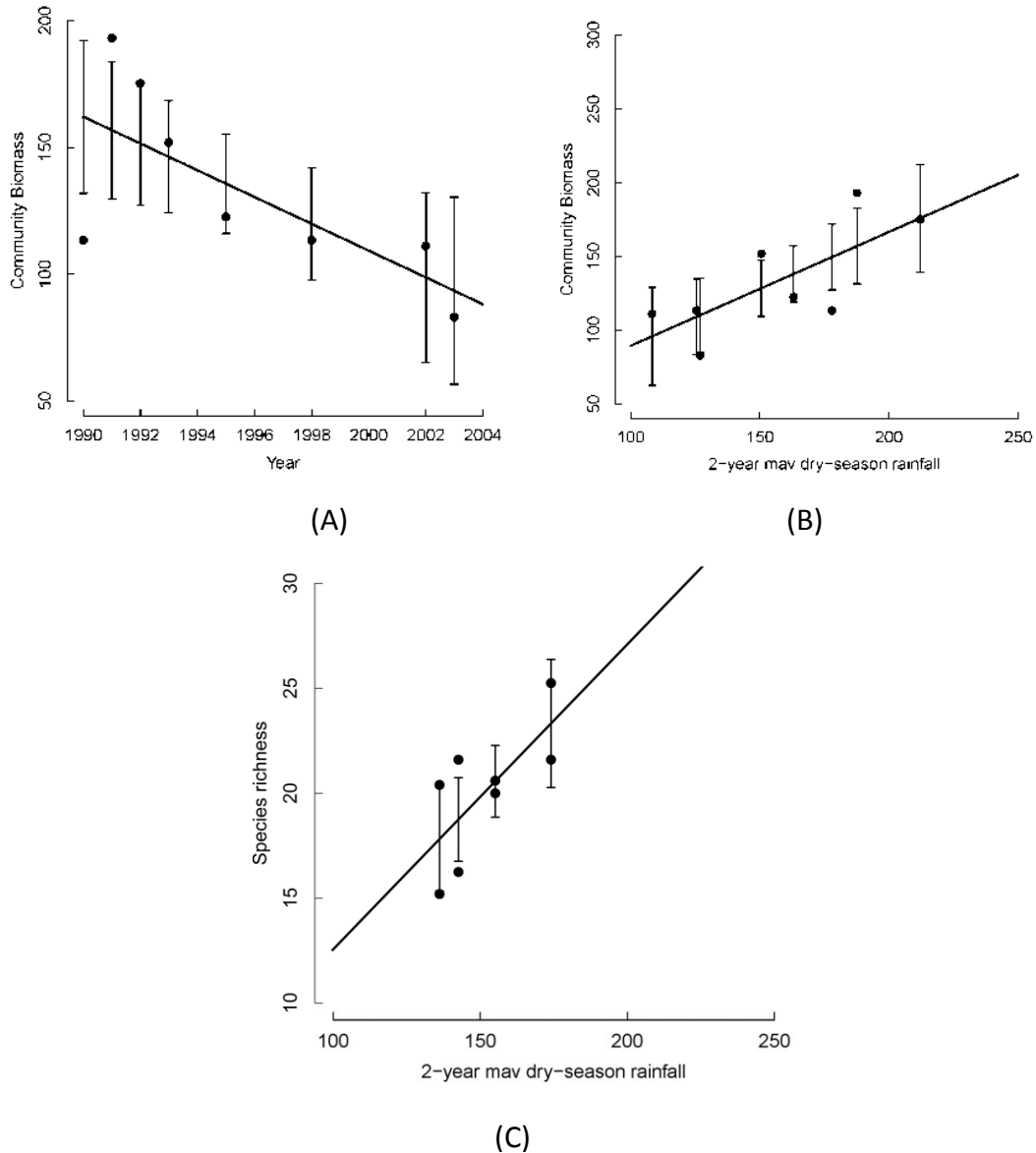


Figure 6. (a) Year-to-year changes in woody biomass averaged over the 8 plots, each consisting of 10 subplots, (b) the relationships between 2-year cumulative dry season rainfall and woody biomass averaged over the 4 plots and (c) the relationships between 2-year cumulative dry season rainfall and species richness for each plot averaged across all years (1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003) in the Masai Mara National Reserve during 1989-2003. Mav (running) means moving average of rainfall.

could increase simply by chance such that if a species is lost from the community, it is replaced randomly by another species from the larger species pool (Alonso et al., 2006). However, such subtle processes are difficult to definitively establish using the data and relationships we examined.

If competition were the main process governing community structuring, we would expect to find a negative relationship between species evenness and

rainfall in which only a few species are competitively dominant and relatively abundant in wetter areas (Nijs and Roy, 2000). In contrast, we found a positive, albeit insignificant relationship between evenness and rainfall, thus providing no evidence for increasing importance of competition for light in wetter areas. Also, we found consistently high values of evenness along the rainfall gradient (0.8) suggesting a more important role for habitat filtering or stochastic processes in community

Table 6. Linear regression coefficients for the relationships between community biomass, richness, evenness and stability averaged across all the 8 plots, each composed of 10 subplots, in each sampling year (1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003) and across all years for each plot. R^2 is the proportion of variance explained by each model.

Variable	Scale	Effect	Estimate	SE	T	P> T	R ²
Community biomass	Temporal	Intercept	10669.080	4256.537	2.507	0.046	0.420
		Year	-5.206	2.103	-2.475	0.048	
Community biomass	Temporal	Intercept	12.324	46.193	0.267	0.799	0.460
		Mavdry2	0.770	0.289	2.671	0.037	
Richness	Temporal	Intercept	-698.955	426.140	-1.640	0.152	0.210
		Year	0.360	0.214	1.687	0.142	
Evenness	Temporal	Intercept	1.441	4.531	0.318	0.761	0.160
		Year	0.000	0.002	-0.179	0.864	
Stability	Temporal	Intercept	32.522	26.067	1.248	0.259	0.068
		Year	-0.016	0.013	-1.230	0.265	
Community biomass	Spatial	Intercept	425.240	392.590	1.083	0.320	0.060
		Dry4	-1.924	2.518	-0.764	0.474	
Richness	Spatial	Intercept	-177.832	80.353	-2.213	0.069	0.420
		Mavdry2	0.272	0.110	2.464	0.049	
Evenness	Spatial	Intercept	0.326	0.188	1.736	0.133	0.180
		Mavdry2	0.002	0.001	1.614	0.158	
Community stability	Spatial	Intercept	-0.168	0.653	-0.258	0.805	-0.040
		Richness	0.027	0.032	0.847	0.430	

structuring or assembly (Walker et al., 2006).

Our results suggest a strong nested pattern in community structure such that common species are present in both low and high rainfall areas; whereas, rare species are present only in the wetter areas. Bastolla et al. (2009) also showed that nestedness reduces effective interspecific competition and enhances the number of coexisting species, providing evidence that competition is not likely the main process shaping these communities. Our results suggest that community composition is apparently constrained by filters allowing only those species with certain properties to persist in stressful or disturbed areas in the community (Weiher et al., 1998). Differential selective environmental tolerances imposed by environmental harshness on particular species likely resulted in nested subsets (Wright et al., 1997). However, besides habitat filtering, such nested patterns may also result from facilitation or the co-dominance of both common and rare species (Aarssen, 1983; Loreau and Hector, 2001). It is possible that some species can aid the growth of others, either through provision of

resources or amelioration of disturbances (Bertness and Callaway, 1994). In other cases, canopy shrubs can facilitate growth of understory species by their positive effects on soil moisture and nutrients (Bertness and Callaway, 1994). Another possible explanation for this nestedness pattern is that it is the outcome of stochastic processes (Bastolla et al., 2009; Sasaki et al., 2012). Wetter areas contain, on average, a higher community biomass, increasing the probability that a particular species occurs in such areas merely by chance. Therefore, we suggest that both habitat filtering and stochastic processes potentially play important roles in structuring savanna tree communities.

A fundamental yet unresolved question is whether diverse ecological systems are more or less stable than those with fewer species (McNaughton, 1977; Tilman, 1996; Bezemer and van der Putten, 2007). We expected to find a negative relationship between community stability and species richness if competitive mechanisms were the main force structuring community assembly, since in diverse communities the loss of one species can

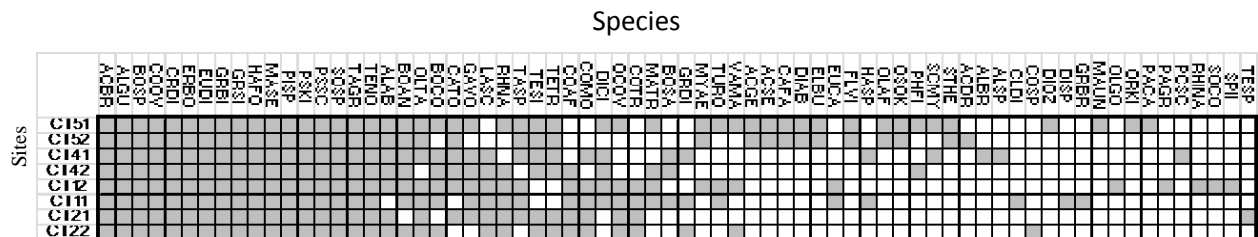


Figure 7. Maximally packed species presence–absence matrix (where species and sites are ordered according to incidence and species richness) for samples from woody vegetation plant communities arrayed across the Masai Mara National Reserve, Kenya. Filled cells indicate presences, white cells indicate absences. The measure of nestedness varies from 0 (no nestedness) to 100 (perfect nestedness). Nrows and Ncolumns are the sum of the nestedness introduced by rows (sites) and columns (species), representing the independent contributions of sites and species to total nestedness. The matrix is significantly nested under the constrained null model ($P < 0.05$).

be compensated for by the gain of a competing species (Tilman, 1994). These predictions were however not supported. Instead, we did not find a significant relationship between stability and richness along the rainfall gradient implying that the loss of a particular species harmed by disturbance may not necessarily be compensated for by a superior competitor. Hence, this further supports the evidence for limited competition and a more important role for habitat filtering or stochastic processes in explaining compositional patterns across the woodland communities of the Mara-Serengeti ecosystem.

Relative dominance of processes structuring the woodland communities

The drier areas were more species poor, and therefore likely to be structured by habitat filtering. Protracted droughts or extended periods of below average rainfall conditions prevent seedling establishment and recruitment into saplings, leading to dominance of certain drought-tolerant species in low rainfall areas (Midgley and Bond, 2001; Fensham et al., 2009), thereby limiting diversity and abundance. Secondly, herbivory might also account for increased habitat filtering in low rainfall areas. Drier areas have more soil nutrients due to less leaching than wet areas. Combined with adjustments in the plant carbon/nutrient balance, dry areas support some of the richest assemblages of herbivores (Sinclair, 1995; Ritchie and Olff, 1999). Herbivores likely have a greater impact on trees in drier areas because they consist of highly palatable species (Anderson and Briske, 1995; Owen-Smith, 1988), compared to trees in wetter areas. Consequently, available browse biomass reduces by 80% during the dry season for woodland communities in the Serengeti (Owen-Smith, 1988). Furthermore, the higher root-to-shoot ratio below ground makes these plant species tolerant to herbivory, because more

resources are stored underground. As a result, the few grazing-tolerant plant species that persist in such areas allocate more nitrogen to their leaves, making them more palatable but able to regrow quickly (Bond et al., 2001). This has been observed in South African savannas (Owen-Smith and Cooper, 1987). In contrast, in the wetter areas, tree seedling germination and establishment is high, enabling recruitment to adulthood (Sankaran et al., 2004). Trees suffer less due to herbivory in wetter areas because they store relatively more carbohydrates above ground so that the above ground green leaves are high in indigestible carbon (Loreau and Hector, 2001). Consequently, low densities of herbivores potentially allow the rare and common species to co-exist in high rainfall areas.

We did not find evidence that competition is the main factor structuring the tree communities in the high rainfall areas. Yet, competition is considered a major structuring force in many plant communities. In savannas, in particular, competition occurs between grass and tree seedlings because the grass layer shades the establishing woody seedlings and both grasses and tree seedlings compete for water and nutrients (Knoop and Walker, 1985; Skarpe, 1992; Scholes and Archer, 1997). However, we focus here on competition between tree species and not between trees and grasses. Except near certain landscape elements, such as rivers or termite mounds, most places in the savannas, even relatively wetter areas, are very open so that light competition between trees could be very limited (Knoop and Walker, 1985; Brenes-Arguedas et al., 2011; Van der Plas et al., 2012). Trees are assumed to be limited by light at the seedling stage, albeit mostly though competition with grasses rather than with other trees (Sankaran et al., 2004). At higher rainfall, better recruitment and dispersal opportunities and reduced stress caused by drought and herbivory enable both rare and common species to establish, recruit and coexist, leading to a higher diversity. These results suggest that tree communities

might therefore be mostly structured by stochastic processes in wetter areas, rather than by habitat filtering, which is more important in drier areas.

In conclusion, our results suggest strong effects of climate change on tree recruitment dynamics. A trend of rising temperatures and recurrent severe droughts could alter the composition of the woodland communities, particularly in wetter areas, where water-stress is typically minimal. If droughts become more frequent and severe, then only a few common species that are better adapted to drought and herbivory may dominate large sections of savanna woodlands, reducing the potential for the woodlands to support rare, stress-sensitive species. This would reduce their overall diversity and stability.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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S1 Table. Selection of the best supported rainfall components and models for seedling and sapling recruitment for the most common species in the *Croton* thickets across the 8 plots, each composed of 10 subplots, and monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003 based on AICc values.

Cohort	Species	†Rainfall component	Linear model		Quadratic model		
			#Parameters	AIC	#Parameters	AIC	
Seedlings	<i>Acacia brevispica</i>	annual	3	60.384	4	62.308	
		annual1	3	59.433	4	61.311	
		annual2	2	61.981	2	61.029	
		annual3	3	61.861	3	61.861	
		annual4	3	61.970	4	61.949	
		dry	3	60.233	4	59.418	
		dry1	3	60.925	4	62.411	
		dry2	3	61.473	4	62.883	
		dry3	3	61.001	4	55.566	
		dry4	3	59.931	3	59.931	
		mavannual2	3	48.830	4	48.930	
		mavannual3	3	60.019	4	60.048	
		mavannual4	3	60.642	4	62.445	
		mavdry2	3	62.069	4	62.146	
		mavdry3	3	61.848	4	58.150	
		mavdry4	3	62.153	4	59.774	
		mavwet2	3	61.704	4	60.918	
		mavwet3	3	62.061	4	60.799	
		mavwet4	3	62.109	4	61.239	
		wet	3	61.309	4	61.464	
	wet1	3	61.308	4	61.463		
	wet2	3	62.150	4	60.479		
	wet3	3	61.692	4	63.215		
	wet4	3	60.510	4	62.433		
		<i>Croton dichogamus</i>	annual	3	80.218	4	82.059
			annual1	3	80.214	4	80.494
			annual2	3	75.350	4	75.561
			annual3	3	80.265	4	77.548
			annual4	3	77.924	4	79.035
			dry	3	80.228	4	82.113
			dry1	3	78.837	4	80.713
			dry2	3	79.222	4	81.099
	dry3		3	76.666	3	76.666	
	dry4		3	79.188	4	72.521	
	mavannual2		3	80.063	4	79.873	

S1 Table. Contd.

	mavannual3	3	76.914	4	78.428
	mavannual4	3	79.444	4	80.553
	mavdry2	3	72.074	4	80.610
	mavdry3	3	80.284	4	79.978
	mavdry4	3	80.050	4	81.082
	mavwet2	3	76.220	4	77.326
	mavwet3	3	78.773	4	77.217
	mavwet4	3	79.683	4	75.595
	wet	3	78.672	4	80.606
	wet1	3	78.673	4	80.607
	wet2	3	80.309	4	80.498
	wet3	3	80.309	4	75.928
	wet4	3	80.231	4	80.373
<i>Euclea divinatorum</i>	annual	2	36.555	3	37.743
	annual1	2	31.206	3	29.584
	annual2	2	36.731	3	37.729
	annual3	2	31.923	3	33.923
	annual4	2	31.380	3	33.073
	dry	2	36.167	3	36.031
	dry1	2	28.202	3	27.140
	dry2	2	36.809	3	31.951
	dry3	2	34.572	3	36.276
	dry4	2	33.424	3	35.422
	mavannual2	2	35.766	3	34.260
	mavannual3	2	36.411	3	37.409
	mavannual4	2	32.452	3	33.829
	mavdry2	2	31.432	3	31.363
	mavdry3	2	35.597	3	35.738
	mavdry4	2	34.782	3	35.611
	mavwet2	2	26.016	3	27.734
	mavwet3	2	34.635	3	29.423
	mavwet4	2	36.857	3	32.555
	wet	2	29.228	3	29.932
	wet1	2	29.228	3	29.932
	wet2	2	32.858	3	33.966
	wet3	2	35.653	3	34.460
	wet4	2	36.768	3	35.147
<i>Grewia similis</i>	annual	3	61.537	4	63.529

S1 Table. Contd.

	annual1	3	61.272	4	62.305
	annual2	3	63.148	4	62.055
	annual3	3	62.496	4	64.220
	annual4	3	56.428	4	57.982
	dry	3	63.088	4	58.431
	dry1	3	58.110	4	57.154
	dry2	3	62.721	4	63.738
	dry3	3	63.291	4	64.956
	dry4	3	63.147	4	65.138
	mavannual2	3	62.113	4	63.253
	mavannual3	3	62.494	4	63.934
	mavannual4	3	63.290	4	64.074
	mavdry2	3	62.305	4	63.310
	mavdry3	3	63.296	4	64.399
	mavdry4	3	63.322	4	64.177
	mavwet2	3	53.216	4	54.883
	mavwet3	3	58.716	4	58.948
	mavwet4	3	62.487	4	64.487
	wet	3	57.567	4	58.122
	wet1	3	57.567	4	58.122
	wet2	3	63.244	4	61.168
	wet3	3	63.301	4	64.158
	wet4	3	59.804	4	61.804
<i>Tarenn</i>	annual	3	65.586	4	65.044
<i>graveolens</i>	annual1	3	66.899	4	68.116
	annual2	3	62.339	4	63.572
	annual3	3	66.890	4	63.539
	annual4	3	65.316	4	67.298
	dry	3	60.177	3	60.177
	dry1	3	67.053	4	68.743
	dry2	3	66.720	4	67.133
	dry3	3	65.244	3	65.244
	dry4	3	65.623	4	67.617
	mavannual2	3	57.632	4	66.424
	mavannual3	2	64.424	2	57.732
	mavannual4	3	63.773	4	65.705
	mavdry2	2	59.764	2	59.764
	mavdry3	3	66.604	4	68.568
	mavdry4	3	66.007	4	67.504

S1 Table. Contd.

		mavwet2	3	64.840	4	66.797
		mavwet3	3	67.044	3	67.044
		mavwet4	3	67.084	3	67.084
		wet	3	65.020	4	66.794
		wet1	3	65.021	4	66.794
		wet2	3	66.310	4	68.145
		wet3	3	67.002	4	68.748
		wet4	3	66.801	4	67.982
Saplings	<i>Acacia brevispica</i>	annual	2	25.452	3	27.321
		annual1	2	25.246	3	27.046
		annual2	2	25.511	3	27.199
		annual3	2	25.454	3	27.264
		annual4	2	25.375	3	27.123
		dry	2	25.465	3	27.463
		dry1	2	25.441	3	27.423
		dry2	2	25.243	3	27.241
		dry3	2	25.483	3	26.813
		dry4	2	25.334	3	27.306
		mavannual2	2	25.012	3	27.235
		mavannual3	2	25.178	3	27.176
		mavannual4	2	25.489	3	27.053
		mavdry2	2	25.519	3	27.439
		mavdry3	2	25.365	3	26.970
		mavdry4	2	25.469	3	27.167
		mavwet2	2	25.316	3	27.040
		mavwet3	2	25.437	3	27.099
		mavwet4	2	25.331	3	26.865
		wet	2	25.426	3	27.367
		wet1	2	25.426	3	27.367
		wet2	2	25.499	3	27.231
		wet3	2	25.224	3	27.129
		wet4	2	25.507	3	27.489
	<i>Croton dichogamus</i>	annual	2	927.82	3	627.69
		annual1	2	967.33	3	739.93
		annual2	2	1340.38	3	1216.74
		annual3	2	868.83	3	842.54
		annual4	2	1247.89	3	453.23
		dry	2	1258.81	3	1259.84

S1 Table. Contd.

	dry1	2	1265.58	3	842.42
	dry2	2	990.25	3	791.76
	dry3	2	1346.39	3	384.43
	dry4	2	1375.44	3	1041.91
	mavannual2	2	1292.52	3	1186.12
	mavannual3	2	1375.59	3	1312.91
	mavannual4	2	1178.15	3	987.00
	mavdry2	2	1371.63	3	1168.78
	mavdry3	2	1157.52	3	292.48
	mavdry4	2	1198.52	3	520.56
	mavwet2	2	1286.50	3	847.12
	mavwet3	2	1371.23	3	1251.77
	mavwet4	2	1163.13	3	812.15
	wet	2	1112.68	3	841.36
	wet1	2	1112.73	3	841.46
	wet2	2	1356.47	3	1253.47
	wet3	2	750.17	3	742.03
	wet4	2	1181.91	3	946.80
<i>Euclea divinatorum</i>	annual	2	20.657	3	22.655
	annual1	2	20.624	3	22.552
	annual2	2	20.733	3	22.348
	annual3	2	20.091	3	22.058
	annual4	2	20.313	3	21.747
	dry	2	20.690	3	22.175
	dry1	2	20.396	3	22.355
	dry2	2	20.267	3	22.200
	dry3	2	20.773	3	22.753
	dry4	2	20.770	3	22.744
	mavannual2	2	20.720	3	22.365
	mavannual3	2	20.773	3	22.755
	mavannual4	2	19.748	3	21.959
	mavdry2	2	20.712	3	22.668
	mavdry3	2	20.519	3	22.511
	mavdry4	2	20.645	3	22.624
	mavwet2	2	19.908	3	21.795
	mavwet3	2	20.100	3	21.972
	mavwet4	2	20.335	3	22.296
	wet	2	20.036	3	22.030
	wet1	2	20.036	3	22.030
	wet2	2	20.728	3	22.298
	wet3	2	20.704	3	22.105

S1 Table. Contd.

	wet4	2	20.393	3	22.382
<i>Grewia similis</i>	annual	2	29.041	3	30.540
	annual1	2	29.532	3	29.120
	annual2	2	30.589	3	28.595
	annual3	2	30.363	3	32.033
	annual4	2	27.974	3	29.317
	dry	2	30.627	3	27.909
	dry1	2	29.344	3	28.664
	dry2	2	30.577	3	29.141
	dry3	2	30.231	3	30.765
	dry4	2	30.327	3	31.856
	mavannual2	2	29.238	3	29.949
	mavannual3	2	30.458	3	29.644
	mavannual4	2	30.626	3	29.202
	mavdry2	2	30.163	3	29.770
	mavdry3	2	30.200	3	31.145
	mavdry4	2	30.617	3	30.233
	mavwet2	2	25.581	3	27.555
	mavwet3	2	29.815	3	31.807
	mavwet4	2	30.529	3	32.485
	wet	2	25.685	3	26.069
wet1	2	25.685	3	26.069	
wet2	2	29.517	3	27.976	
wet3	2	30.602	3	32.394	
wet4	2	29.380	3	31.305	
<i>Tarenna graveolens</i>	annual	2	44.036	3	45.161
	annual1	2	45.396	3	44.699
	annual2	2	43.481	3	43.705
	annual3	2	45.234	3	44.384
	annual4	2	45.401	3	46.420
	dry	2	43.583	3	44.742
	dry1	2	45.458	3	46.648
	dry2	2	45.417	3	47.416
	dry3	2	41.944	3	42.617
	dry4	2	42.649	3	43.375
	mavannual2	2	43.128	3	43.389
	mavannual3	2	40.931	3	41.113
	mavannual4	2	43.086	3	41.439
mavdry2	2	43.746	3	45.593	

S1 Table. Contd.

mavdry3	2	45.252	3	46.926
mavdry4	2	44.187	3	46.109
mavwet2	2	45.173	3	45.138
mavwet3	2	45.276	3	41.589
mavwet4	2	45.498	3	43.236
wet	2	45.483	3	47.478
wet1	2	45.483	3	47.478
wet2	2	45.458	3	42.971
wet3	2	45.228	3	46.072
wet4	2	45.419	3	45.112

[†]Numeric suffixes after rainfall component names denote the time window over which the rainfall component was averaged or by which the component was lagged. For example, mavannual3 means that the annual rainfall component was averaged over a three-year time window whereas annual3 means that the annual component was lagged by three years.

S2 Table. Selection of the best supported rainfall components for the proportion of trees damaged in each height class for the most common *Croton* species across the 8 plots, each consisting of 10 subplots, monitored in 1990, 1991, 1992, 1993, 1995, 1998, 2002 and 2003 in the Masai Mara National Reserve from 1989 to 2003.

Species	†Rainfall component	Linear model		Quadratic model	
		#Parameters	AIC	# Parameters	AIC
<i>Acacia brevispica</i>	annual	5	157.749	6	141.360
	annual1	3	165.347	4	151.917
	annual2	3	165.730	4	167.366
	annual3	3	164.989	4	166.988
	annual4	3	166.515	4	162.593
	dry	3	166.288	4	167.917
	dry1	3	166.151	4	167.131
	dry2	3	166.339	4	168.297
	dry3	3	164.896	4	166.896
	dry4	3	165.896	4	167.373
	mavannual2	3	162.619	4	164.283
	mavannual3	3	165.887	4	167.836
	mavannual4	3	164.724	4	166.722
	mavdry2	3	165.859	4	167.518
	mavdry3	3	165.911	4	167.354
	mavdry4	3	165.461	4	166.439
	mavwet2	3	166.497	4	168.471
	mavwet3	3	166.507	4	168.312
	mavwet4	3	166.250	4	168.085
	wet	3	166.478	4	168.179
wet1	3	166.478	4	168.179	
wet2	3	166.515	4	168.434	
wet3	3	165.429	4	167.250	
wet4	3	166.139	4	166.755	
<i>Croton dichogamus</i>	annual	5	243.274	6	224.887
	annual1	3	262.022	4	227.977
	annual2	3	257.830	4	259.304

S2 Table. Contd.

	annual3	3	257.536	4	255.068
	annual4	3	258.075	4	252.801
	dry	3	261.451	4	263.171
	dry1	3	261.750	4	263.743
	dry2	3	261.610	4	263.486
	dry3	3	262.023	4	264.023
	dry4	3	261.108	4	263.107
	mavannual2	3	247.260	4	249.166
	mavannual3	3	249.827	4	250.985
	mavannual4	3	251.263	4	251.502
	mavdry2	3	261.954	4	263.862
	mavdry3	3	261.632	4	263.605
	mavdry4	3	261.828	4	263.823
	mavwet2	3	260.680	4	262.617
	mavwet3	3	260.017	4	262.007
	mavwet4	3	260.822	4	262.647
	wet	3	261.552	4	263.406
	wet1	3	261.553	4	263.406
	wet2	3	261.660	4	263.596
	wet3	3	261.914	4	262.710
	wet4	3	261.265	4	263.264
<i>Euclea divinatorum</i>	annual	5	87.027	6	82.846
	annual1	3	91.583	4	84.384
	annual2	3	92.357	4	92.240
	annual3	3	90.792	4	92.403
	annual4	3	92.281	4	89.311
	dry	3	92.226	4	93.663
	dry1	3	92.352	4	93.944
	dry2	3	90.810	4	92.796
	dry3	3	92.393	4	94.048
	dry4	3	92.275	3	92.275
	mavannual2	3	85.681	4	81.127
	mavannual3	3	90.904	4	90.868
	mavannual4	3	90.088	4	91.077
	mavdry2	3	92.363	4	94.358
	mavdry3	3	91.733	4	93.435
	mavdry4	3	92.022	4	92.626
	mavwet2	3	92.388	4	94.172
	mavwet3	3	92.393	4	94.135
	mavwet4	3	92.323	4	94.158
	wet	3	92.394	4	94.079
	wet1	3	92.394	4	94.079
	wet2	3	92.382	4	93.647
	wet3	3	92.106	4	93.672
	wet4	3	92.392	4	94.241
<i>Grewia similis</i>	annual	5	136.305	6	123.501
	annual1	3	138.518	4	118.700
	annual2	3	143.350	4	144.152
	annual3	3	140.338	4	141.888
	annual4	3	143.436	4	140.088
	dry	3	142.612	4	144.587

S2 Table. Contd.

	dry1	3	143.440	4	144.438
	dry2	3	142.279	4	144.137
	dry3	3	143.189	4	144.952
	dry4	3	143.366	4	145.012
	mavannual2	3	142.612	4	144.952
	mavannual3	3	143.189	4	144.587
	mavannual4	3	143.607	4	143.418
	mavdry2	4	144.633	4	144.633
	mavdry3	4	143.354	4	143.354
	mavdry4	4	143.239	4	143.239
	mavwet2	4	143.607	4	143.239
	mavwet3	4	144.322	4	144.322
	mavwet4	4	143.418	4	143.418
	wet	3	142.273	4	143.993
	wet1	3	142.273	4	143.994
	wet2	3	143.230	4	145.223
	wet3	3	142.201	4	143.054
	wet4	3	143.447	4	145.084
<i>Tarennia graveolens</i>	annual	5	177.804	5	178.804
	annual1	3	184.981	4	148.808
	annual2	3	188.500	3	188.500
	annual3	3	186.611	4	188.074
	annual4	3	188.257	4	185.111
	dry	3	187.558	4	189.399
	dry1	3	188.720	4	190.583
	dry2	3	188.722	4	190.319
	dry3	3	188.431	4	190.321
	dry4	3	188.713	4	190.709
	mavannual2	3	184.530	4	186.109
	mavannual3	3	186.913	4	188.913
	mavannual4	3	186.028	4	187.966
	mavdry2	3	187.844	4	189.771
	mavdry3	3	188.397	4	190.397
	mavdry4	3	188.330	4	190.231
	mavwet2	3	188.702	4	188.913
	mavwet3	3	188.376	4	190.316
	mavwet4	3	188.348	4	190.320
	wet	3	188.701	4	190.631
	wet1	3	188.701	4	190.631
	wet2	3	188.376	4	190.365
	wet3	3	188.562	4	190.538
	wet4	3	188.717	3	188.717

¹Numeric suffixes after rainfall component names denote the time window over which the rainfall component was averaged or by which the component was lagged. For example, mavannual3 means that the annual rainfall component was averaged over a three-year time window whereas annual3 means that the annual component was lagged by three years.

S3 Table. Selection of the best supported rainfall components for total community biomass, species richness and evenness of all trees over all the 8 plots, each consisting of 10 subplots, in each sampling year (1990, 1992, 1993, 1995, 1998, 2002 and 2003) in the Masai Mara National Reserve based on AICc values.

‡Rainfall component	Tree biomass		Tree species richness		Tree species evenness	
	#Parameters	AIC	#Parameters	AIC	#Parameters	AIC
annual	3	84.809	3	41.923	3	-29.700
annual1	3	84.793	3	45.953	3	-31.850
annual2	3	83.689	3	41.742	3	-29.701
annual3	3	81.695	3	46.026	3	-31.319
annual4	3	81.310	3	45.650	3	-30.915
mavannual2	3	83.033	3	41.734	3	-30.487
mavannual3	3	84.863	3	41.454	3	-30.293
mavannual4	3	83.991	3	43.671	3	-30.999
dry	3	84.361	3	44.922	3	-30.079
dry1	3	79.893	3	45.435	3	-30.258
dry2	3	85.312	3	45.515	3	-33.501
dry3	3	80.083	3	44.700	3	-29.912
dry4	3	82.580	3	46.075	3	-30.404
mavdry2	3	73.878	3	40.487	3	-28.380
mavdry3	3	82.468	3	44.777	3	-32.572
mavdry4	3	80.575	3	43.398	3	-30.486
wet	3	83.025	3	46.046	3	-31.446
wet1	3	82.458	3	46.034	3	-31.441
wet2	3	85.414	3	43.930	3	-30.018
wet3	3	84.358	3	46.026	3	-31.808
wet4	3	81.851	3	45.736	3	-31.894
mavwet2	3	79.156	3	41.619	3	-30.710
mavwet3	3	80.270	3	41.300	3	-30.570
mavwet4	3	85.186	3	44.067	3	-31.575

‡Numeric suffixes after rainfall component names denote the time window over which the rainfall component was averaged or by which the component was lagged. For example, mavannual3 means that the annual rainfall component was averaged over a three-year time window whereas annual3 means that the annual component was lagged by three years.

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