

RESEARCH ARTICLE



Diversity, stand and population structure of riparian woody species in two contrasting land use types in the distal Okavango Delta, Northwestern Botswana

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Abstract

Land use change threatens the integrity of riparian woodland vegetation. The aim of this study was to investigate the diversity and population structure of riparian plant species in protected and communal areas. A total of 71 transects were sampled from each of the protected and communal areas. Total species richness recorded was 36 and 38 in communal and protected areas, respectively. Species diversity was significantly ($p < 0.05$) higher in the protected than communal areas. *Vachellia tortilis* (communal areas) and *Croton megalobotrys* (both areas) showed a reverse J shaped pattern with more individuals in the lower diameter size classes than in the large ones. *Dichrostachys cinerea* (both areas), *Ziziphus mucronata* (communal areas), *Combretum imberbe* (protected areas), *C. hereroense* (protected areas), *Berchemia discolor* (protected areas) and *Vachellia erioloba* (communal areas) showed a reverse-J distribution pattern, but with missing size classes. *Philenoptera violacea* (protected areas) was characterized by a bell-shaped distribution with more individuals in the middle size classes than in the lower and upper ones while *Combretum hereroense*, *C. imberbe* and *B. discolor* were characterized by irregular population structure in communal areas. *Croton megalobotrys*, *D. cinerea*, *C. imberbe*, *C. hereroense*, *Z. mucronata*, *B. discolor* and *S. erubescens* had higher Important Value Indices (IVIs) in protected than communal areas. Comparatively, *Vachellia tortilis*, *P. violacea* and *V. erioloba* had higher IVIs in communal than protected areas. We recommended that species with J-shaped population structure and those with only one size class be protected to enable them to attain healthy population structures.

Keywords Conservation · Density · Ecosystem health · Episodic recruitment · Regeneration

Introduction

Despite their importance, riparian forests are globally threatened by anthropogenic fragmentation due to deforestation (Freitas et al. 2021) associated with land use changes

(Miserendino et al. 2011; Díaz-Pascacio et al. 2018). Communal land use is often associated with conversion of land for crop production, livestock rearing and urbanisation/human settlement (Díaz-Pascacio et al. 2018). These land conversions result in reduction in plant canopy cover and selective removal of some species, leading to low species diversity (Moffatt et al. 2004). Furthermore, the anthropogenic disturbances on riparian woodland vegetation may lead to introduction of invasive species, change in microclimate conditions and alteration of hydrologic and nutrient cycles, which will alter ecosystem functioning (Zipperer 2002), such as fluxes of organic matter and energy (McCord et al. 2007). As a result of these progressing anthropogenic activities, the riparian woody vegetation may shrink and degrade (Agbo et al. 2011), resulting in reduction of their capacity to provide ecosystem services (Burton et al. 2009).

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Riparian ecosystems are important for their ecological, biological and hydrological functions (Harting et al. 1997). The interaction of hydrologic gradient, moist conditions and nutrient influx make them rich in biodiversity (Graziano et al. 2022). Riparian vegetation is also important for water purification, provision of freshwater (Pastor et al. 2022), flood regulation, carbon sequestration (Zhu et al. 2022), habitat provision (Rouquette et al. 2013), regulation of water flow (Nunes et al. 2019) and nutrient cycling (La Notta et al. 2017). In the Okavango Delta, riparian woody plant species help to maintain water quality through evapotranspiration. The Okavango Delta loses 98% of its total inflow through evapotranspiration (Gumbrecht and McCarthy 2003) with riparian woodland vegetation being one of the key factors contributing to the loss (Lubinda et al. 2017). This evapotranspiration water loss results in the Okavango Delta being a freshwater system, which supports wildlife and local communities (Zimmermann et al. 2006; Kujinga et al. 2014). This is because the evaporative water losses create a unidirectional gradient of underground water flow from the floodplains such that solutes are sequestered underneath the islands (McCarthy et al. 1993). As a result of this, saline and freshwater do not mix, resulting in a surface freshwater system (Ramberg and Wolski 2008). Therefore, considering how the riparian vegetation is crucial to ecosystem functioning and livelihood support, there is a need to determine how they are influenced by land use.

Most studies in riparian zones were mainly concerned with investigating the effect of physico-chemical environmental factors on species composition and distribution of riparian plant communities at the expense of land use (Ferreira et al. 2005). Therefore, the changes on plant population structure associated with land use indicative of riparian integrity may go unnoticed in some riparian landscapes due to the current dearth of knowledge. Past studies have found that land use in communal areas has negative impacts on population structure and diversity of riparian plant populations (Pennington et al. 2010; Me'ndez-Toribio et al. 2014; Díaz-Pascacio 2018).

In the Okavango Delta, there is currently scarce information on the influence of land use on the population structure of riparian plant species. This is despite the Okavango Delta being an important global habitat for biodiversity conservation (Francis et al. 2021). Past studies on the influence of land use (communal and protected areas) on riparian plant species in the Okavango Delta have been on regeneration status inferred through height class distributions (Tsheboeng et al. 2017), the impact of flood recession farming on selected plant species compared between

three villages of Tubu, Shorobe and Xobe (Neelo et al. 2013), the impact of wine tapping on *Hyphaene petersiana* in Shorobe (Babitseng and Teketay 2013) and the impact of the removal of herbivores in Maun Educational Park (Kashe et al. 2021). These studies had limitations in that they did not investigate the influence of land use on plant population structure based on diameter size class distribution (Tsheboeng et al. 2017), were only limited to communal land use (Neelo et al. 2013) and only focused on one species (Babitseng and Teketay 2013). A recent study by Kashe et al. (2021) on the effect of wildlife removal on plant diversity and population structure was limited in terms of spatial scope as it was only confined to one protected area being Maun Educational Park. Therefore, there still exists a knowledge gap on the influence of land use on riparian plant population structure and species diversity in the Okavango Delta.

The current study aims to address this knowledge gap by comparing plant population structure and diversity between communal and protected areas along Thamalakane river in the distal region of the Okavango Delta. Thamalakane river was chosen as a study site as it is surrounded by fast growing Maun village (from 149 755 in 2011 to 193 725 residents in 2022) (Statistics Botswana 2022) where residential plots are allocated along its river banks. This poses a threat to riparian woodland species due to increased anthropogenic pressure from communal land use. Therefore, assessment of diversity, plant species composition and plant population structure can give insights on the health status of its vegetation (Sop et al. 2011; Kuma and Shibu 2015). The information on plant population structure can be important for making inferences on how activities associated with land use will impact plant population structure (Feeley et al. 2007; Tabuti 2007). It can also indicate species that are threatened by possible local extermination (Addo-Fordjour et al. 2009; Maua et al. 2020). Therefore, such information may have implications on efforts aimed at restoration of degraded riparian woodland habitats (Teketay 2005ab; Tesfaye et al. 2010).

The hypotheses for the study were: (i) Plant species diversity will be higher in protected areas than in communal ones and (ii) Riparian plant species in communal areas will exhibit unstable/unhealthy population structure while protected areas will have a healthy population structure. The specific objectives of the study were: (i) To compare riparian plant species diversity between communal and protected areas and (ii) To compare riparian plant population structure between communal and protected areas along Thamalakane river.

Materials and methods

Study area

The study was conducted in the Okavango Delta along the Thamalakane River, which passes through the Maun Village (Fig. 1).

The Okavango Delta is fed by the annual floods that originate from the Angolan highlands. The floods reach the inlet of the Okavango Delta (Mohembo) during March and April and the distal regions, including Thamalakane River, between May and October (McCarthy 2006). The inflow in the Delta shows both intra- and inter-annual variations in terms of its magnitude and areal extent (Wolski et al. 2006), largely influenced by amount of rainfall in the Angolan highlands. In addition to the short flooding variations, the Okavango Delta floods also experience long-term pluri-annual variation, where they experience either high or low flood over a series of years. The hydrology of the Delta is

also influenced by local annual rainfall of approximately 500 mm, which occurs between November and February (Wilson and Dincer 1976).

Vegetation sampling

The Field Survey was carried out between February and April 2016. A total of 71 plots were surveyed between the Boteti junction in the southwest and the Matsaudi crossing in the northeast. These were sampled from both communal and protected areas. Protected area refers to an area with an enclosure to prohibit anthropogenic and animal disturbance. In this study, they were represented by Maun Educational Park, Big Tree Lodge and Island Safari Lodge. From a random starting point at Boteti junction, plots were located on alternating sides of the Thamalakane river, 500 m apart. Plots measured 20 m (along the river's edge) $\times$ 50 m (away from the river's edge) each and were sub-divided into five subplots each, measuring 20 m $\times$ 10 m. In each plot, woody

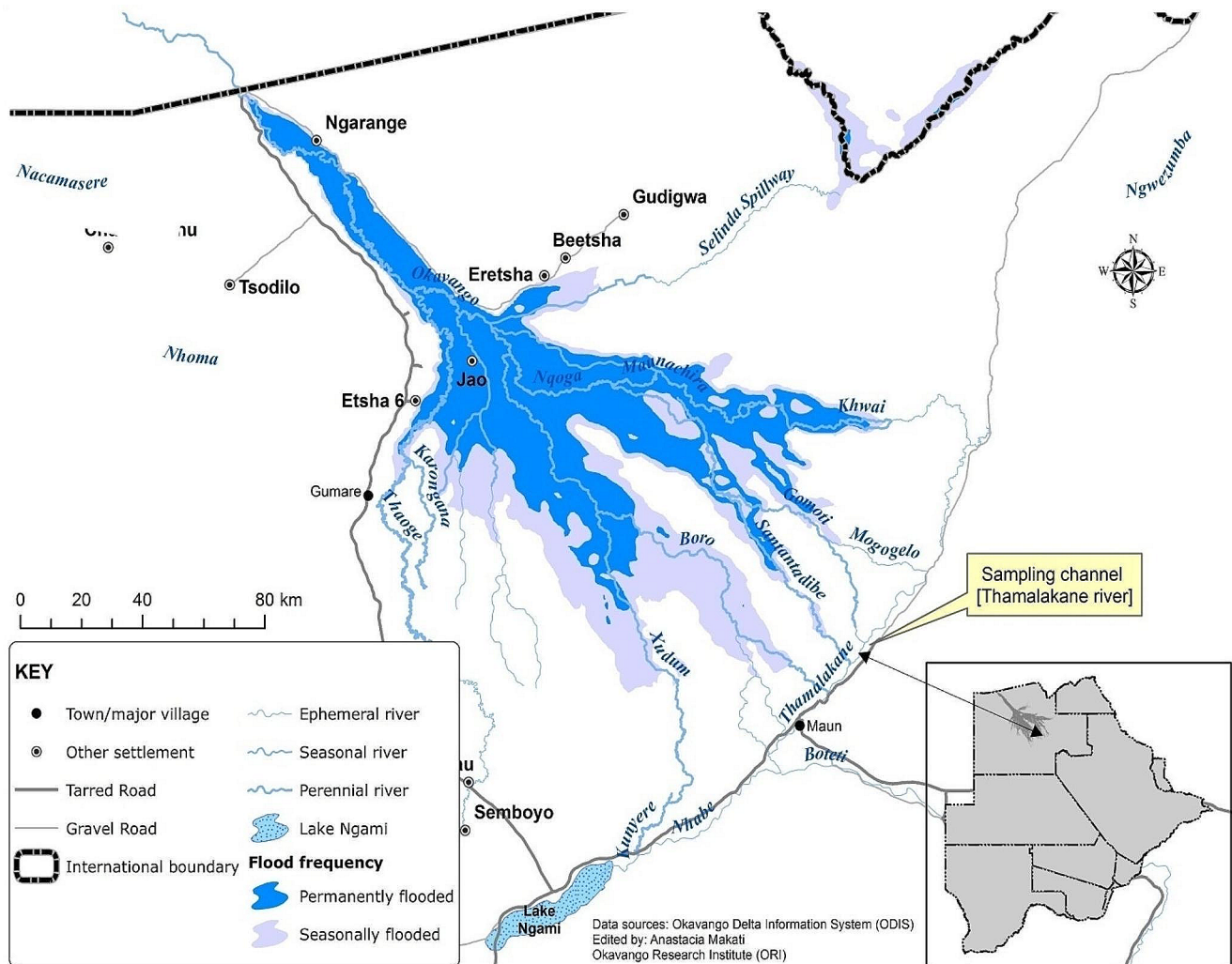


Fig. 1 Map showing the location of the study area

plant species with diameter at breast height (DBH) ≥ 2 cm were identified counted (Teketay et al. 2018). Plants were identified using Van Wyk and Van Wyk (2013) and Setshogo and Venter (2003) references. For species that could not be identified in the field, herbarium specimens were collected, pressed, dried and identified in the Peter Smith University of Botswana Herbarium (PSUB). The plant nomenclature used in this article follows Setshogo and Venter (2003) and Kyalangalilwa et al. (2013). Canopy cover of each plot was determined using the Braun-Blanquet method (Mueller-Dombois and Ellenberg 1974).

Data analyses

Diversity

Mean species diversity, richness, evenness, density and frequency were computed from species composition data using standard formulae. The density, species evenness and diversity were compared between communal and protected areas using paired *t*-test statistical analysis. Species richness was determined from the total number of the different woody species recorded in the study area. The diversity of woody species was represented by Shannon-Wiener Diversity Index (H') (Krebs 1989; Magurran 2004). Evenness or Equitability (E) was calculated by using Shannon-Wiener Equitability Index (E) (Krebs 1989; Magurran 2004).

Total density of woody species was determined by converting the abundance of each woody species encountered in all the quadrats of the study site to an equivalent number per unit of area (ha^{-1}) (Kent and Coker 1992). Frequency of the woody species was determined through the calculation of the proportion (%) of the number of quadrats in which each woody species was recorded from the total number of quadrats assessed in the study site. The mean dominance/basal area of the woody species, with diameter at breast height (DBH) of > 2 cm, was determined from the sum of the space it covers on the ground, i.e. its basal areas ($\text{m}^2 \text{ha}^{-1}$), occupied by all individuals of each woody species (Kent and Coker 1992). Basal area (BA) was calculated using the following formula: $\text{BA} (\text{m}^2) = \pi \times [\text{DBH} (\text{cm})]^2 / 40,000$, where, $\pi = 3.14$.

Similarity in Species Composition

The similarity in species composition was determined using Jaccard's Similarity Index (S_j) (Kent and Coker 1992).

Importance value index

The importance value index (IVI), which indicates the relative ecological importance of a woody species in a given

study site (Lamprecht 1989), was determined from the summation of the relative values of density, frequency and dominance of each woody species (Kent and Coker 1992). Relative density was calculated as the percentage of the density of each species by total density of all species. Relative frequency was computed as the ratio of the frequency of the species to the sum total of the frequency of all species. Relative dominance was calculated as the percentage of the total basal area of a species out of the total basal area of all species.

Regeneration status

To assess the regeneration status of woody species, histograms were prepared using the DBH of all individuals of each woody species categorized into the following diameter classes: < 10 , 10–20, 20–30, 30–40, 40–50, 50–60, 60–70 and > 70 cm and their corresponding densities. We assessed the regeneration status of each species and categorized it as good, fair, poor and none (Carmona et al. 2013; Gebeyehu et al. 2019). Good regeneration occurred when seedling density was greater than sapling density and sapling density greater than adult tree density. Regeneration was considered fair when seedling density was more than sapling density, which was less than adult tree density (Jayakumar and Nair 2013; Neelo et al. 2015; Storch et al. 2018). In terms of poor regeneration, the plant is only represented in the sapling and adult growth stages without the seedlings, while those with none regeneration have the adult stage only without the seedlings and saplings (Carmona et al. 2013; Gebeyehu et al. 2019; Maua et al. 2020).

Ordination of sites by species composition

Ordination of sites by plant species composition was done through Non-metric multi-dimensional scaling (NMDS) (Tsheboeng et al. 2016; Lukhele et al. 2021) in PC-ORD version 6. The similarities in species composition between the communities in communal and protected areas were assessed using Multi-response permutation procedures (MRPP) (Tsheboeng et al. 2016).

Results

Species, genera and family richness of riparian woodland species

A total of 45 species, representing 16 families and 29 genera were recorded in both communal and protected areas along Thamalakane River (Tables 1 and 2). Of these, 36 species, 14 families and 24 genera were found in the communal areas

(Table 1). In terms of family species richness, Fabaceae exhibited the highest number with 11 species followed by Combretaceae (5 species), Euphorbiaceae (3 species), Tiliaceae (3 species) and Ebenaceae (2 species) in communal areas. Other families had one species each (Table 1). Genera *Vachellia* (4), *Combretum* (4), *Senegalia* (3) and *Grewia* (3) had the highest richness in communal areas. The other genera were represented by either two or one species (Table 1).

A total of 38 species, belonging to 28 genera and 16 families were recorded in the protected areas (Table 2). Just like in communal areas, family richness in protected areas was dominated by Fabaceae (11 species). This was followed by Combretaceae (5 species), Euphorbiaceae (3 species) and Ebenaceae (3 species). Other families had one species each (Table 2). In terms of Genera, the most common genus in

protected areas was *Vachellia* (5 species) followed by *Combretum* (4 species). Other genera either had one or two species (Table 2).

Similarities in richness of riparian woody species, families and genera

Of all the 45 species that were encountered, 31 were common to both communal and protected areas, representing Jaccard's similarity (S_j) index of 72% (Table 3). Five species were found only in communal areas. Comparatively, 7 species were found only in the protected areas. Of the 16 families encountered, 14 were shared between communal and protected areas representing Jaccard's similarity index (S_j) of 88% (Table 3). Only 2 families of Rubiaceae and

Table 1 List of riparian woody species in communal areas along Thamalakane River

Species	Family	Total Density	RD	%Frequency	RF	Dominance	RDO	IVI
<i>Croton megalobotrys</i> Müll. Arg	Euphorbiaceae	4370.0±14.4	13.2	81.4	7.0	522.0	34.3	73.4
<i>Vachellia tortilis</i> (Forssk) Galasso & Banfi	Fabaceae	7470.0±17.0	23.0	100.0	9.0	176.0	12.0	60.0
<i>Philenoptera violacea</i> (Klotzsch) Schrire	Fabaceae	3590.0±13.0	11	85.2	7.3	195.0	13.0	25.4
<i>Dichrostachys cinerea</i> (L) Wight & Arn	Fabaceae	3090.0±10.1	9.4	81.4	7.0	39.2	3.0	18.2
<i>Combretum imberbe</i> Wawra	Combretaceae	330.0±2.2	1.0	46.3	4.0	158.0	10.4	17.2
<i>Albizia harveyi</i> E. Fourn	Fabaceae	50.0±1.0	0.2	11.1	1.0	171.0	11.2	12.4
<i>Phyllanthus reticulatus</i> Poir	Euphorbiaceae	1620.0±8.0	5.0	52.0	4.4	-	-	9.4
<i>Vachellia erioloba</i> (E. Mey.) P. J. H. Hurter	Fabaceae	1370.0±6.0	4.2	46.3	4.0	34.1	2.2	8.2
<i>Terminalia prunioides</i> M. A. Lawson	Combretaceae	320.0±2.0	1.0	41.0	4.0	27.0	2.0	7.3
<i>Ficus sycomorus</i> L	Moraceae	50.0±1.0	0.2	20.4	2.0	77.0	5.0	7.3
<i>Hyphaene petersiana</i> (Klotzsch ex Mart	Arecaceae	3320.0±27.0	10.1	39.0	3.3	24.0	2.0	7.0
<i>Grewia retinervis</i> Burret	Tiliaceae	260.0±1.2	1.0	54.0	5.0	-	-	6.0
<i>Ziziphus mucronata</i> Willd	Rhamnaceae	220.0±2.0	1.0	37.0	3.2	20.0	1.3	6.0
<i>Combretum hereroense</i> Schinz	Combretaceae	50.0±1.0	0.2	19.0	2.0	26.0	2.0	5.0
<i>Diospyros mespiliformis</i> Hochst. Ex. A. DC	Ebenaceae	20.0±0.2	0.1	19.0	2.0	42.0	3.0	5.0
<i>Senegalia mellifera</i> (Vahl) Seigler & Ebinger	Fabaceae	440.0±3.4	1.3	26.0	2.2	-	-	4.0
<i>Berchemia discolor</i> (Klotzsch) Engl	Rhamnaceae	200.0±1.2	1.0	26.0	2.2	10.4	1.0	3.4
<i>Gymnosporia senegalensis</i> (Lam) Loes	Celastraceae	990.0±7.2	3.0	39.0	3.3	-	-	3.3
<i>Capparis tomentosa</i> Lam	Capparaceae	210.0±1.2	1.0	26.0	2.2	-	-	3.3
<i>Combretum mossambicense</i> (Klotzsch) Engl	Combretaceae	80.0±1.0	0.2	27.0	3.0	-	-	3.2
<i>Grewia bicolor</i> Juss	Tiliaceae	130.0±1.0	0.4	26.0	2.2	-	-	3.0
<i>Colophospermum mopane</i> (J. Kirk ex Benth)	Fabaceae	20.0±0.2	0.1	24.1	2.1	-	-	2.1
<i>Garcinia livingstonei</i> T. Anderson	Guttiferae	80.0±1.0	0.2	17.0	1.4	0.2	0.01	2.0
<i>Combretum albopunctatum</i> Suess	Combretaceae	80.0±1.0	0.2	17.0	1.4	-	-	2.0
<i>Vachellia luederitzii</i> (Engl.) Kyal. & Boatwr	Fabaceae	70.0±1.0	0.2	17.0	1.4	-	-	2.0
<i>Grewia villosa</i> Willd	Tiliaceae	60.0±0.4	0.2	17.0	1.4	-	-	2.0
<i>Senegalia erubescens</i> (Welw. Ex Oliv.) Kyal. & Boatwr	Fabaceae	10.0±0.1	0.03	46.3	4.0	1.0	0.1	2.0
<i>Senegalia nigrescens</i> (Oliv.) P. J. H. Hurter	Fabaceae	1.3	0.1	20.4	2.0	0.3	0.02	2.0
<i>Diospyros lycioides</i> Desf	Ebenaceae	4070.0±23.0	12.3	17.0	1.4	-	-	1.4
<i>Vachellia hebeclada</i> (DC) Kyal. & Boatwr	Fabaceae	300.0±2.4	1.0	15.0	1.3	-	-	1.3
<i>Flueggea virosa</i> (Roxb. Ex Willd) Voigt	Euphorbiaceae	100.0±1.1	0.30	11.1	1.0	-	-	1.3
<i>Ximenia americana</i> Welw. Ex Oliv	Olcaceae	30.0±0.3	0.1	13.0	1.1	-	-	1.2
<i>Markhamia zanzibarica</i> (Bojer ex DC) K. Schum	Bignoniaceae	30.0±0.4	0.1	7.4	1.0	-	-	1.1
<i>Searsia tenuinervis</i> (Engl.) Moffett	Anacardiaceae	20.0±0.3	0.1	9.3	1.0	-	-	1.0
<i>Maerua angolensis</i> DC	Capparaceae	20.0±0.2	0.1	6.0	0.4	-	-	1.0
Total		33 010						

Table 2 List of woody species in protected areas along Thamalakane River

Species	Family	Total Density	RD	Frequency	RF	Dominance	RDO	IVI
<i>Croton megalobotrys</i> Müll. Arg	Euphorbiaceae	4890.0 ± 33.0	12.4	100.0	0.05	73.4	36.0	48.2
<i>Philenoptera violacea</i> (Klotzch) Schrire	Fabaceae	5310.0 ± 40.0	14.0	88.0	0.04	30.0	15.0	29.0
<i>Diospyros mespiliformis</i> Hochst. Ex. A. DC	Ebenaceae	6880.0 ± 111.0	18.0	50.0	0.03	20.3	10.0	28.0
<i>Combretum imberbe</i> Wawra	Combretaceae	590.0 ± 7.0	2.0	75.0	0.04	28.0	14.0	16.0
<i>Vachellia tortilis</i> (Forssk) Galasso & Banfi	Fabaceae	1180.0 ± 12.0	3.0	100.0	0.05	24.0	12.0	15.0
<i>Phyllanthus reticulatus</i> Poir	Euphorbiaceae	5140.0 ± 62.4	13.1	50.0	0.03	-	-	13.1
<i>Dichrostachys cinerea</i> (L) Wight & Arn	Fabaceae	3680.0 ± 24.0	10.0	100.0	0.05	-	-	10.1
<i>Combretum hereroense</i> Schinz	Combretaceae	340.0 ± 4.0	1.0	63.0	0.03	14.0	7.0	8.0
<i>Diospyros lycioides</i> Desf	Ebenaceae	2890.0 ± 46.0	7.4	38.0	0.02	-	-	7.4
<i>Ziziphus mucronata</i> Willd	Rhamnaceae	160.0 ± 2.0	0.4	63.0	0.03	3.0	1.4	5.0
<i>Hyphaene petersiana</i> Klotzsch ex Mart	Arecaceae	700.0 ± 10.0	2.0	50.0	0.03	4.2	2.0	4.1
<i>Combretum mossambicense</i> (Klotzsch) Engl.	Combretaceae	1200 ± 13.0	3.0	100.0	0.03	-	-	3.1
<i>Flueggea virosa</i> (Roxb. Ex Willd) Voigt	Euphorbiaceae	880.0 ± 10.4	2.2	88.0	0.04	-	-	2.2
<i>Garcinia livingstonei</i> T. Anderson	Guttiferae	630.0 ± 7.1	2.0	38.0	0.02	-	-	2.0
<i>Gymnosporia senegalensis</i> (Lam) Loes	Celastraceae	590.0 ± 8.0	2.0	75.0	0.04	-	-	2.0
<i>Terminalia prunioides</i> M. A. Lawson	Combretaceae	400.0 ± 8.0	1.0	75	0.04	2.0	1.0	2.0
<i>Berchemia discolor</i> (Klotzsch) Engl	Rhamnaceae	350.0 ± 4.0	1.0	100.0	0.05	2	1.0	2.0
<i>Vachellia erioloba</i> (E. Mey.) P.J.H.Hurter	Fabaceae	120.0 ± 3.0	0.3	13.0	0.006	3.0	1.4	2.0
<i>Grewia retinervis</i> Burret	Tiliaceae	470.0 ± 5.0	1.2	88.0	0.04	-	-	1.2
<i>Capparis tomentosa</i> Lam	Capparaceae	280.0 ± 4.0	1.0	88.0	0.04	-	-	1.1
<i>Ximenia americana</i> Welw. Ex Oliv	Olcaceae	230.0 ± 3.4	1.0	63.0	0.03	-	-	1.0
<i>Kigelia africana</i> (Lam) Benth	Bignoniaceae	10.0 ± 0.3	0.03	13.0	0.006	1.0	1.0	0.7
<i>Senegalia erubescens</i> (Welw. Ex Oliv.) Kyal. & Boatwr	Fabaceae	180.0 ± 3.3	0.4	25.0	0.01	-	-	0.4
<i>Grewia bicolor</i> Juss	Tiliaceae	180.0 ± 3.0	0.4	75.0	0.04	-	-	0.4
<i>Searsia tenuinervis</i> (Engl.) Moffett	Anacardiaceae	120.0 ± 2.1	0.3	50.0	0.03	-	-	0.3
<i>Albizia harveyi</i> E. Fourn	Fabaceae	100.0 ± 2.0	0.3	25.0	0.01	-	-	0.3
<i>Cordia sinensis</i> Lam	Cordiaceae	10.0 ± 0.3	0.03	13.0	0.006	-	-	0.3
<i>Senegalia mellifera</i> (Vahl) Seigler & Ebinger	Fabaceae	1330.0 ± 16.3	3.4	63.0	0.03	-	-	0.1
<i>Vachellia sieberiana</i> (DC.) Kyal. & Boatwr.	Fabaceae	50.0 ± 1.1	0.1	38.0	0.02	-	-	0.1
<i>Euclea divinorum</i> Hiern	Ebenaceae	40.0 ± 1.0	0.1	25.0	0.01	-	-	0.1
<i>Combretum albopunctatum</i> Suess	Combretaceae	30.0 ± 1.0	0.08	13.0	0.006	-	-	0.1
<i>Gardenia volkensii</i> K. Schum	Rubiaceae	30.0 ± 1.0	0.1	100.0	0.02	-	-	0.1
<i>Boscia albitrunca</i> (Burch) Gilg & Gilg-Ben	Capparaceae	30.0 ± 0.8	0.1	25.0	0.01	-	-	0.1
<i>Markhamia zanzibarica</i> (Bojer ex DC) K. Schum	Bignoniaceae	20.0 ± 1.0	0.1	13.0	0.006	-	-	0.1
<i>Vachellia nilotica</i> (L.) P.J.H. Hurter & Mabb	Fabaceae	20.0 ± 0.5	0.05	13.0	0.006	-	-	0.1
<i>Vachellia luederitzii</i> (Engl.) Kyal. & Boatwr	Fabaceae	10.0 ± 0.3	0.03	13.0	0.006	-	-	0.04
<i>Colophospermum mopane</i> (J. Kirk ex Benth)	Fabaceae	10.0 ± 0.3	0.03	13.0	0.006	-	-	0.04
<i>Ficus sycomorus</i> L	Moraceae	180.0 ± 3.0	0.4	50.0	0.03	-	-	0.03
<i>Grewia flavescens</i> Juss	Tiliaceae	10.0 ± 0.3	0.03			-	-	
Total		39 270						

Table 3 Jaccard's coefficient of similarity for different taxa in the two sites

Taxa	% Similarity
Family	88
Genera	79
Species	72

Cordiaceae were found exclusively in the protected areas. In terms of genera, of the 29 encountered, 23 were found in both sites while 1 was found exclusively in communal areas, and 5 were found only in protected areas (Tables 1 and 2). The Jaccard's similarity index (S_j) for the genera recorded in the study sites was 79% (Table 3).

Diversity and evenness

There was no significant ($p < 0.05$) difference in evenness between communal and protected areas (Table 4).

Table 4 Comparison of Shannon-Weiner diversity and evenness indices between communal and protected areas along Thamalakane River

Diversity and Equitability indices	Communal	Protected
Evenness($\pm$ SE)	0.48 $\pm$ 0.02	0.48 $\pm$ 0.03
Shannon-Wiener index($\pm$ SE)	0.83 $\pm$ 0.05	1.40 $\pm$ 0.08*

*Significantly different ($p < 0.05$)

Conversely, species diversity (H') was significantly ($p < 0.05$) higher in protected areas than in communal ones (Table 4).

Density of seedlings

Croton megalobotrys, *Philenoptera violacea* and *Diospyros mespiliformis* had significantly ($p < 0.05$) higher seedling densities in protected areas than in communal ones (Table 5). Conversely, *H. petersiana*, *Vachellia tortilis* and

Dichrostachys cinerea showed significantly higher seedling densities in communal areas than in protected ones (Table 5). *Vachellia tortilis* and *Diospyros lycioides* had significantly ($p < 0.05$) higher sapling densities in communal areas than in protected ones while *C. megalobotrys*, *D. cinerea* and *Phyllanthus reticulatus* had significantly higher densities in protected areas than in communal ones (Table 5).

Importance value index (IVI)

The IVI of riparian woody species in communal areas ranged between 73.0 and 1.0% (Table 1) while in protected areas it was between 48.2 and 0.03% (Table 2). The five riparian woody species with the highest IVIs were *C. megalobotrys* (73.4%), *V. tortilis* (60.0%), *P. violacea* (25.4%), *D. cinerea* (18.2%) and *C. imberbe* (17.2%) (Table 1). In protected areas, the five species with the highest IVIs were

Table 5 Comparison of seedlings and saplings densities between communal and protected areas along Thamalakane river

Species	Seedling density (Individuals/ha)		Sapling density (Individuals/ha)	
	Communal	Protected	Communal	Protected
<i>Vachellia tortilis</i>	4280.0 $\pm$ 8.0	600.0 $\pm$ 6.0*	950.0 $\pm$ 3.0	180.0 $\pm$ 2.4
<i>Croton megalobotrys</i>	1400.0 $\pm$ 5.0	3250.0 $\pm$ 21.0*	230.0 $\pm$ 1.0	500.0 $\pm$ 4.0*
<i>Diospyros lycioides</i>	1310.0 $\pm$ 7.0	1360.0 $\pm$ 23.0	1090.0 $\pm$ 7.0	760.0 $\pm$ 11.0
<i>Philenoptera violacea</i>	2780.0 $\pm$ 8.0	4960.0 $\pm$ 35.3*	190.0 $\pm$ 1.0	150.0 $\pm$ 2.0
<i>Hyphaene petersiana</i>	2160.0 $\pm$ 17.0	380.0 $\pm$ 5.0	760.0 $\pm$ 6.2	140.0 $\pm$ 2.3
<i>Dichrostachys cinerea</i>	2100.0 $\pm$ 5.0	1900.0 $\pm$ 10.0*	310.0 $\pm$ 1.1	690.0 $\pm$ 4.4*
<i>Phyllanthus reticulatus</i>	1280.0 $\pm$ 6.0	3180.0 $\pm$ 35.0*	220.0 $\pm$ 1.3	920.0 $\pm$ 12.0*
<i>Vachellia erioloba</i>	1090.0 $\pm$ 4.0	100.0 $\pm$ 2.4*	80.0 $\pm$ 0.4	0.0 $\pm$ 0.0
<i>Gymnosporia senegalensis</i>	550.0 $\pm$ 4.1	250.0 $\pm$ 2.1	170.0 $\pm$ 1.0	100.0 $\pm$ 1.4
<i>Senegalia mellifera</i>	310.0 $\pm$ 2.2	900.0 $\pm$ 9.1*	20.0 $\pm$ 0.2	200.0 $\pm$ 3.0*
<i>Combretum imberbe</i>	160.0 $\pm$ 1.2	110.0 $\pm$ 1.1	30.0 $\pm$ 0.2	0.0 $\pm$ 0.0
<i>Terminalia prunioides</i>	60.0 $\pm$ 0.3	40.0 $\pm$ 1.0	10.0 $\pm$ 0.1	50.0 $\pm$ 1.0
<i>Grewia retinervis</i>	120.0 $\pm$ 1.0	290.0 $\pm$ 3.0	0.0 $\pm$ 0.0	40.0 $\pm$ 1.0
<i>Ziziphus mucronata</i>	40.0 $\pm$ 0.3	0.0 $\pm$ 0.0**	10.0 $\pm$ 0.1	10.0 $\pm$ 0.3
<i>Capparis tomentosa</i>	60.0 $\pm$ 0.3	100 $\pm$ 1.0*	40.0 $\pm$ 0.3	80.0 $\pm$ 1.0*
<i>Berchemia discolor</i>	150.0 $\pm$ 1.0	210.0 $\pm$ 2.0*	30.0 $\pm$ 0.2	60.0 $\pm$ 1.0*
<i>Grewia bicolor</i>	40.0 $\pm$ 0.2	50.0 $\pm$ 1.0	10.0 $\pm$ 0.1	30.0 $\pm$ 0.4
<i>Flueggea virosa</i>	30.0 $\pm$ 0.3	380.0 $\pm$ 4.2*	10.0 $\pm$ 0.1	170.0 $\pm$ 2.0*
<i>Combretum mossambicense</i>	60.0 $\pm$ 0.3	900.0 $\pm$ 9.4*	0.0 $\pm$ 0.0	60.0 $\pm$ 1.0
<i>Garcinia livingstonei</i>	30.0 $\pm$ 0.2	610.0 $\pm$ 7.0*	0.0 $\pm$ 0.0	10.0 $\pm$ 0.3
<i>Combretum albopunctatum</i>	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0**	0.0 $\pm$ 0.0	20.0 $\pm$ 1.0
<i>Vachellia luederitzii</i>	50.0 $\pm$ 1.0	0.0 $\pm$ 0.0**	10.0 $\pm$ 0.1	0.0 $\pm$ 0.0
<i>Combretum hereroense</i>	0.0 $\pm$ 0.0	10.0 $\pm$ 0.3**	0.0 $\pm$ 0.0	40.0 $\pm$ 1.0
<i>Ficus sycomorus</i>	10.0 $\pm$ 0.1	90.0 $\pm$ 1.2*	10.0 $\pm$ 0.1	60.0 $\pm$ 1.0*
<i>Albizia harveyi</i>	40.0 $\pm$ 1.0	80.0 $\pm$ 2.0	10.0 $\pm$ 0.1	20.0 $\pm$ 0.4
<i>Markhamia zanzibarica</i>	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0**	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
<i>Ximenia americana</i>	0.0 $\pm$ 0.0	80.0 $\pm$ 1.1**	0.0 $\pm$ 0.0	10.0 $\pm$ 0.3
<i>Searsia tenuinervis</i>	10.0 $\pm$ 0.1	10.0 $\pm$ 0.3	0.0 $\pm$ 0.0	10.0 $\pm$ 0.3
<i>Diospyros mespiliformis</i>	20.0 $\pm$ 0.2	6730.0 $\pm$ 108.1*	0.0 $\pm$ 0.0	20.0 $\pm$ 0.4
<i>Colophospermum mopane</i>	20.0 $\pm$ 0.2	10.0 $\pm$ 0.3	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
<i>Senegalia erubescens</i>	0.0 $\pm$ 0.0	20.0 $\pm$ 0.4**	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
<i>Vachellia sieberiana</i>	10.0 $\pm$ 0.1	30.0 $\pm$ 1.0	0.0 $\pm$ 0.0	10.0 $\pm$ 0.3

*Significantly different from each other ($p < 0.05$)

**Not compared statistically since they had “0” mean(s) either in one site or both sites

C. megalobotrys (48.2%), *P. violacea* (29.0%), *D. mespili-formis* (28.0%), *C. imberbe* (16.0%) and *V. tortilis* (15.0%) (Table 2).

Population structure

Vachellia tortilis (communal areas) and *C. megalobotrys* (both areas) showed a reverse J- shaped pattern with more individuals in the lower diameter size classes than in the large ones (Fig. 2), which indicates stable regeneration status. *Dichrostachys cinerea* (both sites), *Ziziphus mucronata* (communal areas), *C. imberbe* (protected areas), *C. hereroense* (protected areas), *Berchemia discolor* (protected areas) and *Vachellia erioloba* (communal areas) showed a reverse-J distribution pattern, but with missing size classes (Fig. 2), suggesting hampered regeneration status. *Philenoptera violacea* (protected areas) was characterized by a bell-shaped distribution with more individuals in the middle size classes than in the lower and upper ones while *Combretum hereroense*, *C. imberbe* and *B. discolor* were characterized by irregular population structure in communal areas (Fig. 2), suggesting hampered regeneration status.

Ordination of sites by species composition

The ordinated sites fall into two discrete classes corresponding to protected and communal areas (Fig. 3). Multi-response permutation procedures comparison of the two sites showed that they differed significantly ($p=0.00001$) in terms of species composition.

Discussion

The results of our study showed that there were more species, families and genera in protected areas than in communal areas. Furthermore, species diversity was higher in protected areas than in communal ones. This was in support of our first hypothesis that protected areas will have higher species diversity than in communal areas. Therefore, this demonstrates that protected areas along Thamalakane river are important for enhancing riparian plant species diversity and conservation as they serve as refugia against anthropogenic impacts. Consequently, the protected areas along Thamalakane river may enhance the gene pool of riparian woody species by promoting optimal recruitment and regeneration while severe disturbance in communal areas could reduce diversity through curtailing recruitment and regeneration of sensitive species (Bongers et al. 2009). Ecologically, this

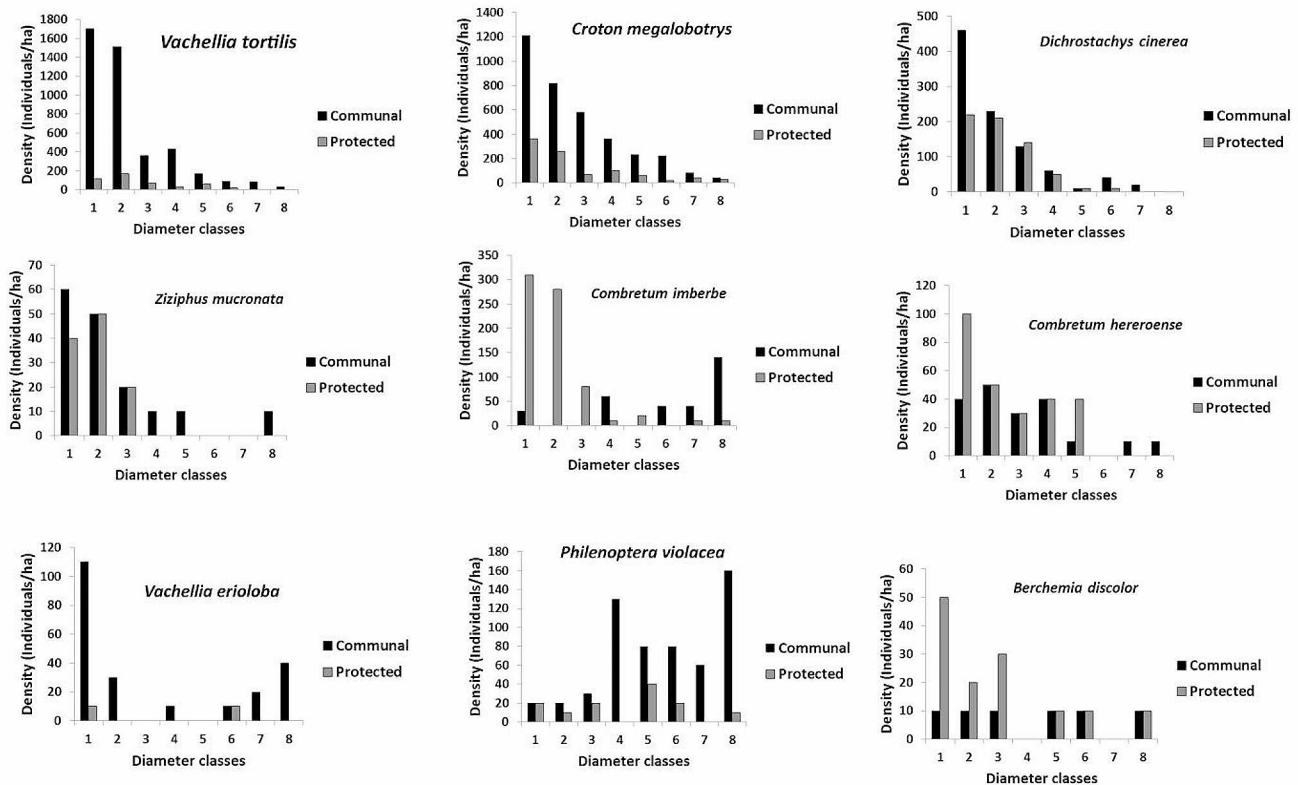


Fig. 2 Population structure of riparian woody plants in different land use types along Thamalakane river

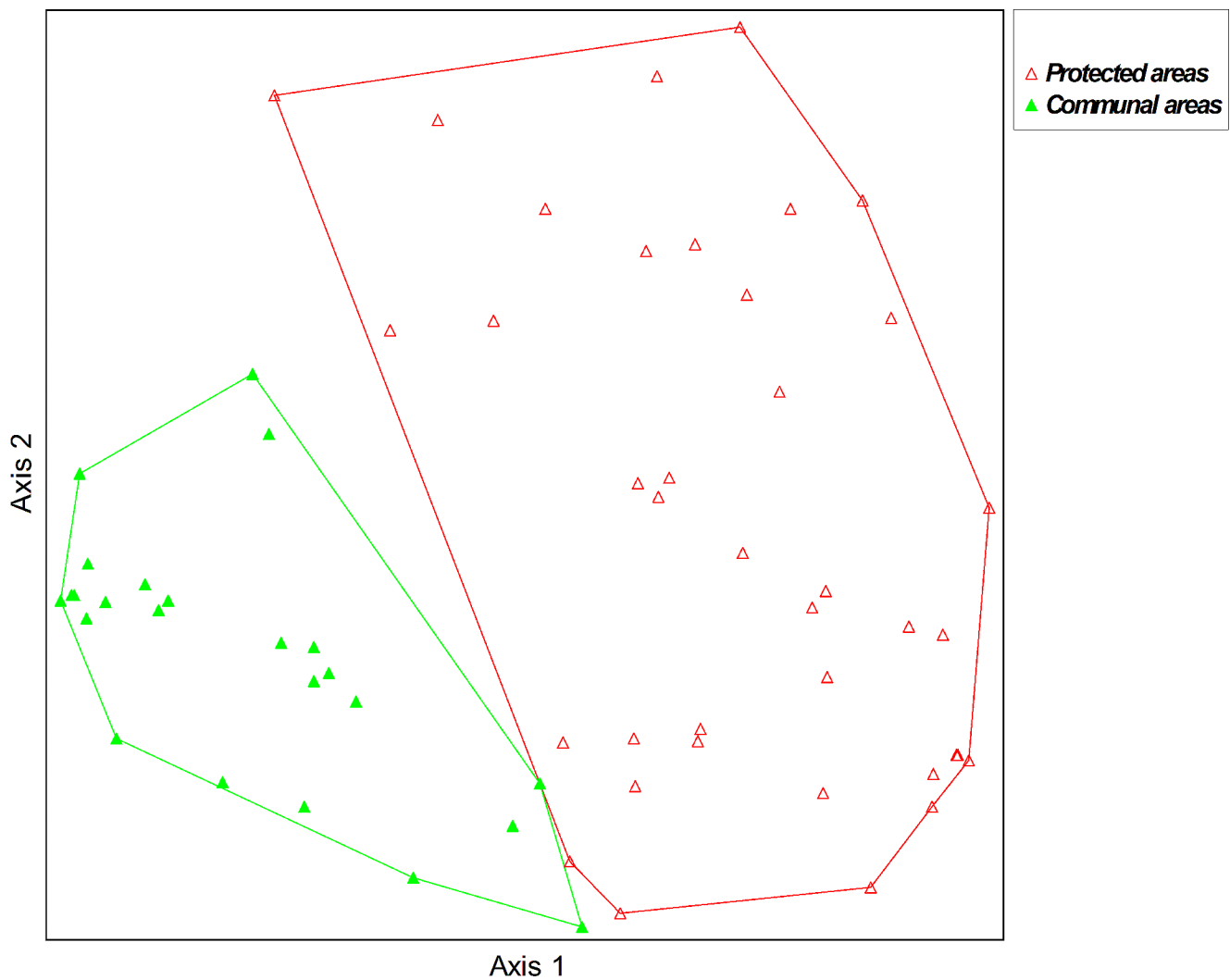


Fig. 3 Non-metric multidimensional scaling ordination of sites by plant species composition between communal and protected areas

serves a critical role of maintaining the ecosystem functioning of woody plant species, such as water purification, provision of freshwater (Pastor et al. 2022), flood regulation, carbon sequestration (Zhu et al. 2022), habitat provision (Rouquette et al. 2013), regulation of water flow (Nunes et al. 2019) and nutrient cycling (La Notte et al. 2017). This is specifically vital in the fragile Thamalakane river and by extension, Okavango Delta ecosystem, which is faced with multiple anthropogenic threats, such as over-exploitation of woody species, which have the potential to reduce its overall ecosystem functioning and integrity.

The disparity between the two land use systems, in terms of species diversity and composition, could be due to progressive anthropogenic activities in the communal areas (Mohammed et al. 2021). These include overexploitation of woodland species for utilization in fencing fields, kraals and homesteads and deforestation for establishment of settlements (Tesfaye et al. 2010; Neelo et al. 2015; Kashe et

al. 2021). Fire might have played a role as recurrent fires are common in semi-arid Botswana (Maabong and Mphale 2021). Additional factors that could lead to the variation in species composition between protected areas and communal ones could be browsing by livestock (Augustine and McNaughton 1998). Research has shown that areas closer to water points are, usually, degraded by overgrazing either by livestock or wild animals (Moleele and Perkins 1998; Mukwashi 2012; Averett et al. 2017). Therefore, in this study with riparian woodlands found on the margins of the river, it could be that they are exposed to detrimental effects of heavy browsing by ungulates (Teren and Owen-Smith 2010; Kashe et al. 2021).

Our results suggest that protected areas along Thamalakane river serve as refuge to woodland species, which promotes their conservation and regeneration (Teketay et al. 2018; Balemi et al. 2022). This is because in these areas there is no human disturbance. Even in protected areas,

such as Maun educational park and Big tree lodge, woody species are exposed to browsing by wild animals, although their impact could be lower compared to unprotected areas. In Maun educational park most of the large herbivores were removed in 2012 (Kashe et al. 2021). This has resulted in reduced browsing intensity leading to low impact of herbivory on the diversity of riparian plant species (Kashe et al. 2021). Other protected areas, such as Island safari lodge were completely excluded from any impact either anthropogenic or by wildlife. This promoted establishment of woody species and regeneration (Teketay et al. 2018; Balemi et al. 2022). The establishment of woody species could be from soil seedbanks, coppicing and seedlings that survived disturbance (Teketay 2005a, b). As a result, in the long term, plant community structure increases in protected areas compared with their communal counterparts (Teketay et al. 2018).

Croton megalobotrys, *V. tortilis*, *P. violacea*, *D. cinerea* and *C. imberbe* exhibited the highest five IVIs in communal and protected areas, suggesting that they are the most ecologically important species (Lamprecht 1989). For *C. megalobotrys* and *V. tortilis*, their high IVI could be an indication of disturbance along Thamalakane river since they usually colonize disturbed sites. Thamalakane river could be disturbed by cattle grazing and deforestation. *Vachellia tortilis* could also be an indicator of dry condition along the seasonally flooded Thamalakane river (Oba et al. 2001). The seasonality in flooding opens colonization window for dry tolerant species, such as *V. tortilis* and *D. cinerea* (Ringrose et al. 2007; Murray-Hudson et al. 2014). Furthermore, the high IVI of species in both areas could be an indication that they are ubiquitous, not site-specific and have wide niche breadth. In terms of human use, the high IVI of these species could suggest that they are not the preferred species; hence, they are able to proliferate. However, considering that *V. tortilis* and *D. cinerea* are used to fence fields along Thamalakane river (Neelo et al. 2013), their high IVIs could suggest that their utilization is low.

The population structure of riparian tree species in the distal regions of the Delta were characterized by six patterns being; Reverse-J, Reverse-J with missing size classes, Bell shaped, irregular shaped with all classes and irregularly shaped with missing size classes. The species with a reverse J-shaped regeneration pattern were *V. tortilis* in communal areas and *C. megalobotrys* in both areas. Reverse J-shaped structure shows a healthy population since the species will naturally replace themselves through good recruitment (Kuma and Shibru 2015). It shows on-going recruitment of individuals across different diameter classes (Mwavu and Witkowski 2009). This is true for our study since the seedlings and saplings of *V. tortilis* were higher in communal areas than in protected ones. Therefore, this is an indication of higher ongoing recruitment for this species in the

communal areas than in protected areas. The reverse-J structure of *V. tortilis* in communal areas could be an indication of its ability to survive in prevailing disturbances. *Vachellia tortilis* is an early colonizer of disturbed sites (Skarpe 1990; Hottman and O'Connor 1999; Neelo et al. 2013; Neelo et al. 2015). Therefore, the anthropogenic clearing of riparian zones along Thamalakane river creates space for colonization by *V. tortilis* in the early stages of succession.

Other species, being *Z. mucronata* (communal areas), *C. imberbe* (protected areas), *C. hereroense* (protected areas), *B. discolor* (protected areas), *V. erioloba* (communal areas) and *T. prunioides* (protected areas) exhibited reverse-J population structure with missing size classes. Furthermore, *C. hereroense*, *V. erioloba* and *Z. mucronata* were characterized by irregular population structure with missing size classes. These patterns may result from the selective removal of individuals in some diameter classes either for human use or from mortality due to destruction by elephants (Gurmessa et al. 2012). Therefore, their long-term persistence may result in the concerned species being threatened by local extermination since they cannot replace themselves due to poor recruitment (Tsheboeng 2016). In the current study area, the removal of individuals could be for human use (Belayneh and Demissew 2011). The distal region of the Okavango Delta along the Thamalakane river is primarily used for human settlement. Therefore, the individuals in the missing size classes could have been cut for use as poles for constructing the fences of homesteads, fields and kraals.

In terms of regeneration, species such as *V. tortilis*, *D. cinerea* and *V. erioloba* had significantly ($p < 0.05$) higher seedling densities in communal areas than in protected areas. Likewise, except for *D. cinerea*, they also had higher sapling densities in communal areas than in protected areas. Overall, their seedling densities were greater than those of the saplings. This shows that these species have ongoing regeneration in communal areas than protected ones (Senbeta and Denich 2006; Tesfaye et al. 2010). The three species are indicators of bush encroachment. Their leaves are nutritious fodder, but presence of thorns limit browsing by herbivores, resulting in thickets of shrubs and trees (Moleele and Perkins 1998). Conversely, other species had higher densities of seedlings and saplings in protected areas, also indicating an ongoing recruitment. These included *P. violacea*, *C. megalobotrys*, *P. reticulatus* and *S. mellifera*.

Conclusions and recommendations

The results of this study revealed that woody species exhibited contrasting population structure influenced by the land use type. The influence is linked to the difference in anthropogenic disturbance between the land use types. Generally, more plants in the protected areas showed reverse-J

population structure, which is theoretically a healthy pattern. In terms of land use, the missing size classes could be an indication of the past effects of human uses on the vegetation. It could be suggesting that the missing size classes were preferentially targeted in the past. These species should be prioritized for conservation. Mature individuals will serve as a source for propagation materials (seed/cuttings).

Ecologically and economically important species with J-shaped pattern and those with one diameter class should be protected from possible future exploitations to allow them to re-establish. There could also be consideration of creating exclosures and plantations that are aimed at promoting the regeneration of these species and minimizing the impact of human use and livestock grazing/browsing. Future studies should investigate the environmental factors that influence the population of riparian woody plant communities along the Thamalakane river. There should also be research on the extent of human use of the riparian woodland resources along the Thamalakane river.

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Data availability Data for this manuscript is available upon request through the first author.

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