Water SA 51(3) 228–242 / Jul 2025
https://doi.org/10.17159/wsa/2025.v51.i3.4115

Research paper

Spatio-temporal changes in the riparian vegetation associated with the Savanna Biome section of the Olifants River, Mpumalanga, South Africa

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The spatio-temporal changes in plant communities along the macro-channel of the Olifants River in the Central Bushveld were investigated over a 26-year period. A variable belt transect method was used to resurvey selected sites previously assessed approximately 26 years ago. Species richness increased from upstream to downstream, driven by an influx of forbs, dwarf shrubs, and shrubs, with a notable rise in naturalised alien and invasive alien species. Canopy cover changes varied within and between plant communities, increasing in the upstream and downstream sections but decreasing in midstream areas. These shifts in species richness, canopy cover, composition and structure suggest a response to land use and integrated disturbance regimes, including river regulation, commercial and subsistence agriculture, development and conservation efforts, which interact with natural disturbances such as floods amid climate change. This underscores the need for stricter implementation and monitoring of legislation to protect water resources at the land-use level and preserve the natural functionality of riparian systems.

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DATES
Received: 14 December 2023
Accepted: 13 June 2025

KEYWORDS
riparian vegetation
plant communities
disturbances
macro-channel bank
rivers

INTRODUCTION

Riparian vegetation is driven by physical and biological processes at different spatial and temporal scales (Naiman et al., 2010). Physical processes through geomorphic (topography, geology) and hydrologic (discharge, flooding) variables are the primary drivers of change in riparian systems occurring at different hierarchical scales from catchments to riparian microhabitats (Frissell et al., 1986; Bendix, 1998), through three dimensions of lotic ecosystems, namely longitudinal, lateral and vertical dimensions (Ward, 1989). Biological processes are secondary response variables capable of creating, structuring and maintaining river corridors and thus riparian vegetation (Naiman and Rogers, 1997; Tabacchi et al., 1998). Vegetation provides bank stability by increasing macro-channel roughness, reducing erosive power and promoting sediment deposition and therefore altering the macro-channel morphology (Naiman et al., 2010).

Different authors have studied the influence of human activities on riparian ecosystems ranging from river regulation and infrastructure developments to the agricultural and mining sectors (Jansson et al., 2000; Myburgh, 2001; Dabrowski and De Klerk, 2013). Climate change has also been shown to play a role in riparian vegetation dynamics (Stromberg et al., 2010; Rivaes et al., 2013). Therefore, natural drivers of change in riparian systems are no longer acting in isolation within these systems (Naiman et al., 2010). Vegetation dynamics are initiated by different disturbance regimes at various temporal and spatial scales (White, 1979). Thus, the temporal and spatial scale of a disturbance is relative to the community investigated (White, 1979).

A total of 9 plant communities were previously identified and described in the Savanna Biome section of the Olifants River (Myburgh and Bredenkamp, 2004). During this study, various human activities were found to cause floristic variations within these plant communities (Myburgh and Bredenkamp, 2004). Therefore, to obtain insight into possible changes in plant communities over temporal and spatial scales and determine which factors influenced these observed changes, this study aimed to (i) investigate changes in plant community structure, canopy cover and species composition over 26 years and (ii) identify disturbance regimes most associated with changes in plant communities.

STUDY AREA

This study examined riparian vegetation changes along a 250 km stretch of the Olifants River in South Africa (Fig. 1). The region's geological composition includes rocks from the Waterberg, Rooiberg and Pretoria Groups of the Bushveld Complex (Coetsee, 1978). Vegetation falls within the Savanna Biome of the Central Bushveld bioregion (Mucina and Rutherford, 2006). The macro-channel width ranges from 17 to 75 m, with the upstream section characterized by mountainous terrain, pools and riffles/rapids, while the downstream portion features gently sloping banks, alluvial deposits and channel-bed islands (Myburgh and Bredenkamp, 2004).

METHODS

Four of the nine plant communities originally described by Myburgh and Bredenkamp (2004) were resurveyed in this study. The initial floristic data were collected in 1995 (Myburgh, 2001), while the current data were gathered from a subset of the same sites in 2021. Sampling was conducted opportunistically, with access limited to sites where landowners, tenants or residents granted permission.

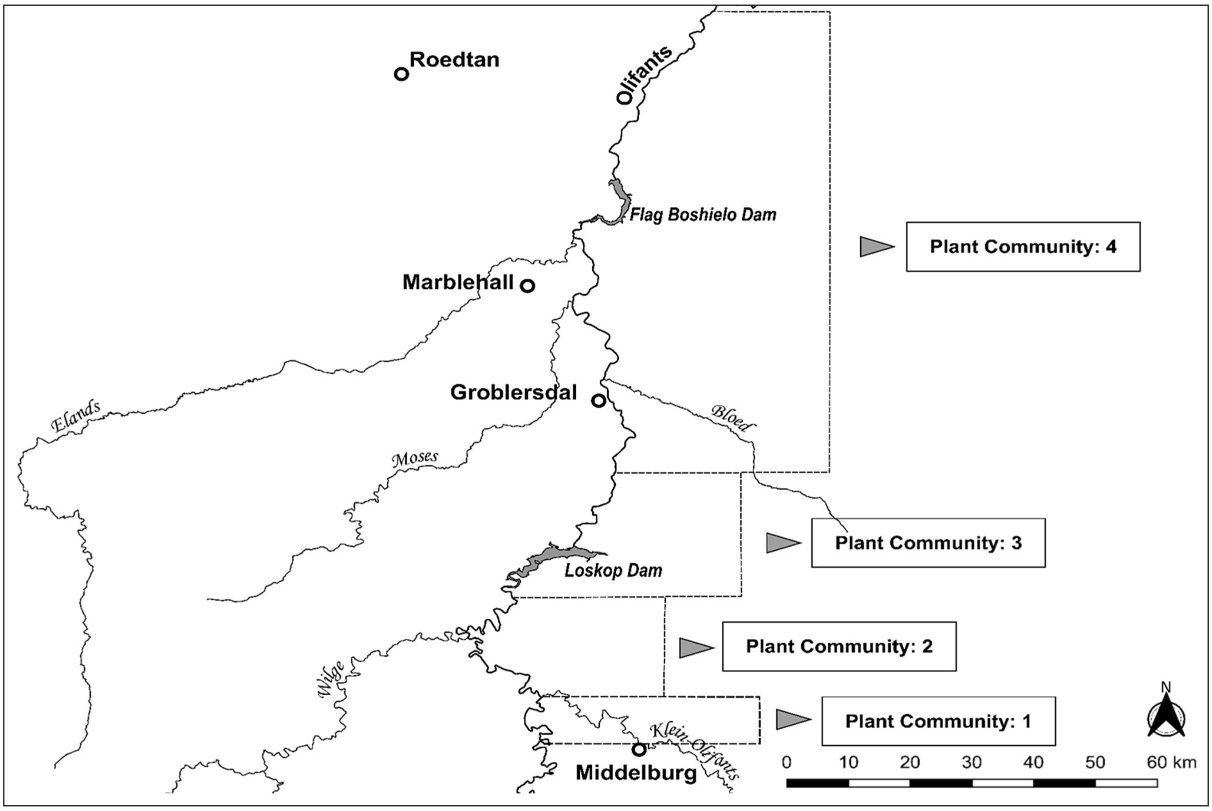

Figure 1. The Olifants River system in the Savanna Biome section with the associated plant communities (adapted from Myburgh and Bredenkamp, 2004)

A total of 18 sampling sites were surveyed, with both riverbanks sampled where possible, resulting in 35 sampling plots. An area-based vegetation sampling method was used to assess the macro-channel of the Olifants River. A variable belt transect with a minimum size of 200 m^2 was placed on a GPS-referenced sampling site on the macro-channel bank of the Olifants River (Myburgh and Bredenkamp, 2004).

A Garmin Etrex 30 GPS was used to locate the sampling sites, which were surveyed in 1995 and the same sampling strategy and methodology were applied as in the previous study (Myburgh, 2001; Myburgh and Bredenkamp, 2004). This enabled direct comparisons of floristic data per sampling plot and plant community.

The length and width of the variable belt transect, placed parallel and perpendicular to the river, respectively, varied on different sampling plots based on the width of the macro-channel bank and floristic parameters of the riparian vegetation (Myburgh and Bredenkamp, 2004). In each sampling plot all rooted plants were recorded and canopy cover was assigned using the 'plant number scale' (Westfall and Panagos, 1988). Each recorded plant species was assigned a growth form following Westfall et al. (1996). Nomenclature followed Germishuizen and Meyer (2003).

The environmental data for this study included land cover information and on-site disturbances recorded during field surveys. Land cover data from the South African National Land-Cover dataset (DEFF, 2021) were used to represent 2021 data and the National Land-Cover dataset (ARC and CSIR, 1998) as a proxy for 1995. Recognising the change in institution responsible for land cover mapping over 26 years, a land cover spatial similarity analysis was done. This involved overlaying the land cover dataset of both years on sampling points in QGIS (v. 3.34.7), followed by simplification of the 1995 classification based on the 2020 group classes, to ensure similarity and consistency across both the 1995 and 2020 datasets. This process resulted in the identification of 8 land-cover classes along with 7 on-site disturbances within the Olifants River macro-channel (Table A1, Appendix).

A phytosociological classification approach, as in the study by Myburgh and Bredenkamp (2004), was used. However, in this study, a variation in the form of a forced phytosociological classification (Panagos, 2019) was employed with the use of the PHYTOTAB-PC program (Westfall et al., 1997) to allow for comparison between sampling periods.

A forced classification involves a classification of species presence/absence using a predetermined grouping of sampling plots so that temporal changes of species within these groupings can be ascertained. A constancy value, an output of PHYTOTAB-PC program, was assigned per plant species, which refers to the proportional presence of the plant species in the plant community as a function of the number of sampling plots in which a specific plant species was recorded in relation to the total number of sampling plots in that plant community. Floristic parameter results from the PHYTOTAB-PC software were tested statistically using Pearson's chi-squared test of association with the p-value set at 0.05. The use of Pearson's chi-squared was due to the asymmetrical distribution of the count data collected using the plant number scale (Westfall and Panagos, 1988).

Plant community and environmental data were analysed with detrended correspondence analysis (DCA) to determine the variation in species composition over 26 years as a response to land cover and on-site disturbances. DCA is an indirect gradient analysis method and was chosen due to its robustness in addressing the arch and edge affects, as well as its ability to handle heterogeneous data and thus estimate heterogeneity in community composition (Peet et al., 1988; Lepš and Šmilauer, 2003). All statistical analyses were performed with R version 4.4.2 (The R Foundation for Statistical Computing Platform, 2024) using vegan 2.6-8 (for DCA; Oksanen et. al., 2024) and base R functions for chi-squared.

RESULTS AND DISCUSSION

Species richness increased across the Savanna Biome section of the Olifants River over 26 years. Sub-Communities 2.1, 4.6, 4.5, and Plant Community 3 showed the highest species richness gains (Table 1). Total species richness rose from 237 species in 1995 to 341 in 2021. The forb layer exhibited the greatest species richness increase across the macro-channel, except in Plant Community 1 and Sub-Community 2.1 (Table 1).

The results from DCA for the first two axes are shown in Fig. 2, explaining approximately 20.7% of the variation. The most statistically significant environmental variables ($p < 0.05$) influencing species composition across the two sampling periods were commercial livestock grazing, open woodland, communal land (subsistence crop and livestock agriculture) and river regulation (dams), of which all were associated with Axis 2. The variable 'artificial dam' moderately influenced species composition but this was not statistically significant at $p = 0.05$.

The gradient length for Axis 1 was 7.6377 standard deviations (SD), exceeding the 4.0 SD threshold, indicating highly heterogeneous species composition (Table 2). This high SD supports the use of unimodal models, as suggested by Lepš and Šmilauer (2003). Further supporting this, the lowest mean floristic affinity between plant communities across both sampling periods was observed, with Plant Community 3 in 2021 recording the highest mean floristic affinity at just 11% (Table A2, Appendix).

The sampling periods, 1995 and 2021, were separated along DCA1 and DCA2, implying some form of variation in species composition across the observed temporal scale (Table 3). However, the goodness-of-fit test indicated that this variation was not statistically significant ($r^2 = 0.1235$, $p = 0.0696$) suggesting limited evidence for temporal shifts in species composition.

The macro-channel riparian vegetation of the Olifants River in the Savanna Biome section is a product of multiple physical environmental factors that resulted in 9 plant communities (Myburgh and Bredenkamp, 2004). The diverse landscape through which the Olifants River traverses, in conjunction with hydrological processes (Tabacchi et al., 1998) and human-induced disturbances (Myburgh, 2001; Shafroth et al., 2016) will have an integrated influence on the riparian vegetation of the Olifants River. It is also important to note that a 1:100-year flood event occurred in the Olifants River system in 1996, in which the macro-channel was significantly impacted (Myburgh, 2001). Therefore, the observed spatio-temporal changes will be strongly influenced by previous flooding, as was observed in the Sabie River (Parsons et al., 2006).

The overall increase in species richness could be ascribed to the interplay between natural and human-induced disturbance regimes as a result of observed land uses creating suitable conditions for the establishment of pioneer plant species such as forbs and enabling competitive woody species to establish.

Table 1. Plant species richness of the Savanna Biome section of the Olifants River system (*represents statistical significance at $p = 0.05$)

1995								
Plant community number	**1**	**2.1**	**2.3**	**3**	**4.2**	**4.3**	**4.5**	**4.6**
Mean no. of species	33	32	23	42	46	35	25	34
Forb	28	16	3	35	34	17	15	24
Graminoids	24	30	6	51	20	8	18	12
Dwarf shrub	4	9	1	9	8	7	6	11
Shrub	7	17	9	7	10	6	5	6
Tree	10	12	4	11	10	7	6	7
2021								
Plant community number	**1**	**2.1**	**2.3**	**3**	**4.2**	**4.3**	**4.5**	**4.6**
Mean no. of species	49	57	65	59	51	50	50	53
Forb	31	44	19	68	54	32	43	53
Graminoids	37	51	18	52	29	14	34	33
Dwarf shrub	7	10	8	18	11	9	7	15
Shrub	11	30	11	13	13	10	8	11
Tree	7	18	9	15	9	9	13	8
Total no. of species (1995)	**73**	**84**	**23**	**113**	**82**	**45**	**50**	**60**
Total no. of species (2021)	**93**	**153**	**65**	**166**	**116**	**74**	**105**	**120**

Table 2. Numerical summary of the DCA ordination analysis showing eigenvalues, decorona values, axis length and total variance (inertia)

Calculated DCA variables	**Axis**				**Total inertia**
	DCA1	**DCA2**	**DCA3**	**DCA4**	
Eigenvalues	0.6509	0.4919	0.3021	0.2818	
Additive eigenvalues	0.6509	0.4955	0.3056	0.2811	
Decorana values	0.7494	0.4539	0.3042	0.1634	
Axis lengths	7.6377	4.7006	2.5476	1.0275	
Total inertia (scaled chi-square)					5.5269

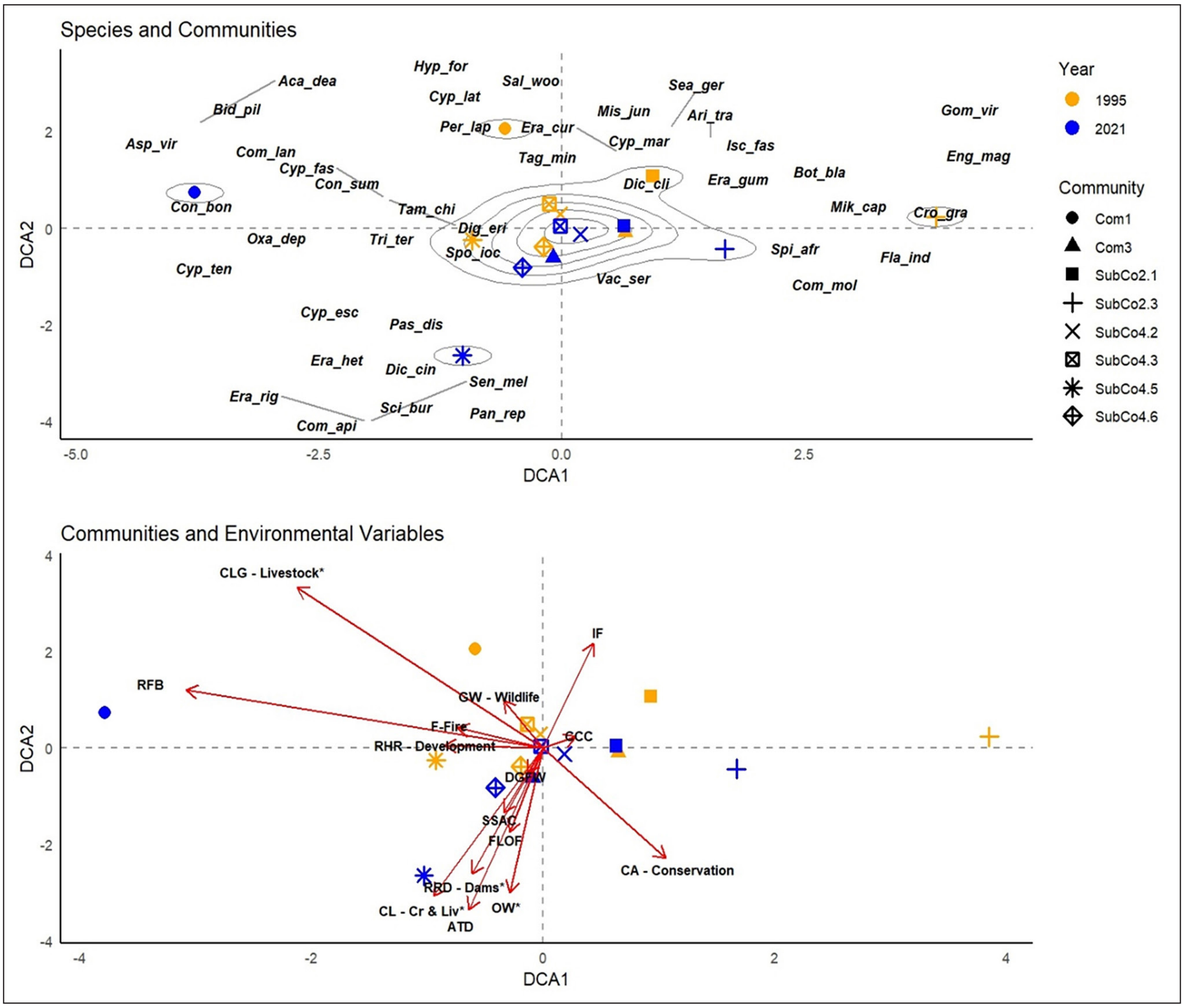

Figure 2. DCA ordination diagram of species, plant communities and environmental variables. Plant communities are represented by different shapes. Com = plant community; SubCo = sub-community; 1995 = orange; 2021 = blue; *represents statistical significance at $p = 0.05$.

Table 3. Temporal change analysis in plant communities based on DCA ordination centroids

	Centroids	
	DCA1	DCA2
Year 1995	0.2662	0.4214
Year 2021	−0.3065	−0.4853
	Goodness of fit	
	r^2	*Pr*(>*r*)
Year	0.1235	0.0696

Plant Communities 2 to 4 are associated with land uses such as commercial and subsistence agriculture, fallow lands and old fields, degraded forests and woodlands, and on-site disturbances ranging from wildlife and livestock grazing areas to fire adjacent to the macro-channel, all of which are associated with human activities (Fig. 2). These findings concur with the results of Sunil et al. (2011) and Mligo (2016), where human-induced disturbances were found to facilitate the establishment of new pioneer plant species in riparian areas. Additionally, the increases can be noted as a function of river systems as agents of propagule and seed dispersal (Merritt and Wohl, 2006). The woody component's species richness remained fairly stable although compositional changes were more pronounced in the dwarf shrub and shrub layers as a result of the high influx of new plant species post-1995 (Tables 4–11). The notable presence of the understorey woody layer could be explained by a range of factors, notably the accelerated increase in atmospheric CO_2 and warming temperatures (Russell and Ward, 2014; O'Connor et al., 2014), as well as disturbance regimes (Sunil et al., 2011; Mligo, 2016;), which facilitate its establishment and increase across a disturbance gradient (Bendix, 1997). Another external control basin for riparian systems linked to atmospheric CO_2 and warm temperature is climate change (Charlton, 2008). Climate change has been identified as one of the four human-induced disturbances to influence riparian systems, along with land use, pollution and river regulation (Naiman et al., 2010).

Plant Community 1: *Salix mucronata* subsp. *woodii–Hyparrhenia hirta* shrubland

The *Salix mucronata* subsp. *woodii–Hyparrhenia hirta* shrubland is located 10 km downstream of the confluence of the Olifants River and the Klein-Olifants River. The macro-channel is characterised by active and seasonal channels with pools and rapids. There was a slight increase in total average canopy cover between 1995 (58%) and 2021 (62%) (Fig. 3). Although the herbaceous layer growth forms increased in average canopy cover while the shrub layer's canopy cover halved, these trends were not statistically significant ($p > 0.05$).

The invasive alien tree *Acacia dealbata* dominated the community at both sampling times, while *Salix mucronata* subsp. *woodii* declined during the same period (Table 4). There were changes in species composition in the herbaceous layer. The graminoids, namely, *Phragmites australis*, *Cyperus longus* var. *longus*, and the forbs, *Richardia brasiliensis* (naturalised alien) and the invasive *Verbena bonariensis*, dominated the herbaceous layer in 2021 (Table 4).

Overall, canopy cover in Plant Community 1 remained largely unchanged between 1995 and 2021. However, the shrub layer declined by 50%, primarily due to the loss of *Salix mucronata* subsp. *woodii*. This decline created an opportunity for the invasive tree *Acacia dealbata* to expand, leading to a shift in community structure from shrubland to woodland, as per Edward's (1983) classification system. The macro-channel of this community is subject to various human disturbances, including residential developments, low-water bridges, grazing and fire (Fig. 2), all of which have been shown to influence riparian vegetation composition, cover and structure (Kauffman et al., 1983; Oneal and Rotenberry, 2008; Douglas et al., 2015). Species composition changes occurred in the herbaceous layer. These observed spatial and temporal changes could also be explained by lack of channel expansion (narrowing) as a result of walls built to protect properties. Channel narrowing has been shown to cause changes in species composition and the extent of riparian vegetation (Merritt and Copper, 2000; Shafroth et al., 2002).

Plant Community 2: *Heteropyxis natalensis–Bothriochloa bladhii* shrubland

This plant community comprised of 3 sub-communities (Myburgh and Bredenkamp, 2004); however, only 2 were resurveyed. The community stretches from the confluence of the Klein-Olifants and Olifants Rivers up to Loskop Dam. The macro-channel's fluvial geomorphology is associated with long stretches of rocks of variable sizes creating riffles and deep pools. The total average canopy cover for the whole community increased from 39% (1995) to 55% (2021) but this was not significant ($p > 0.05$).

Plant Sub-Community 2.1: *Heteropyxis natalensis–Eragrostis gummiflua* sub-community

The *Heteropyxis natalensis–Eragrostis gummiflua* sub-community is more widely distributed than Sub-Communities 2.2 and 2.3 (Myburgh and Bredenkamp, 2004). The macro-channel of this sub-community is characterised by a rock percentage cover of between 10% and 60% and shallow soils ranging from 300 mm to 450 mm (Myburgh, 2001). A total of 30 shrub species were recorded in 2021, the highest in the woody component across both sampling periods (Table 1).

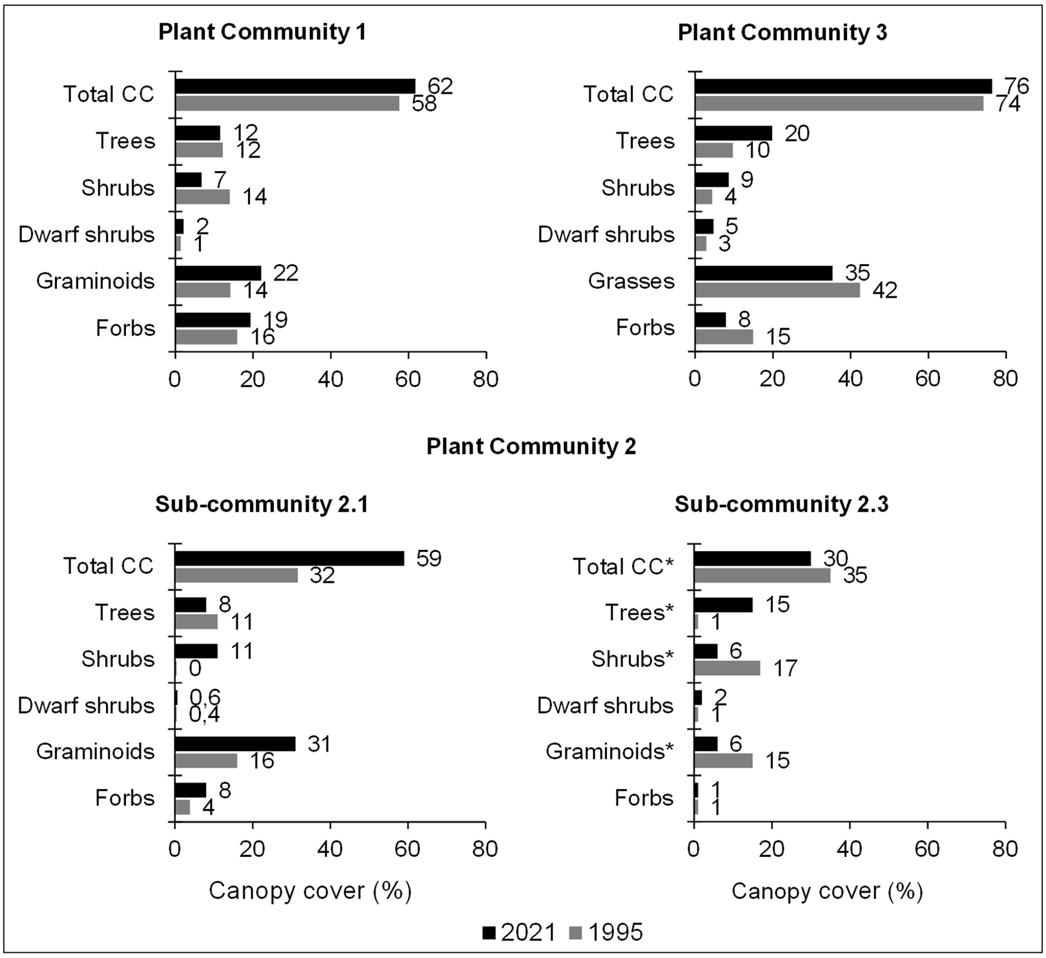

Figure 3. Comparison of growth forms and canopy cover between sampling periods (*represents statistical significance at $p = 0.05$); total CC = total average canopy cover

Table 4. Dominant species of the *Salix mucronata* subsp. *woodii*–*Hyparrhenia hirta* shrubland between 1995 and 2021

Plant species	Sampling period			
	1995		2021	
	C (%)	AC (%)	C (%)	AC (%)
Trees:				
Acacia dealbata	75	7	100	10
Combretum erythrophyllum	50	2	-	-
Searsia gerrardii	100	2	-	-
Shrubs:				
Salix mucronata subsp. *woodii*	100	10	75	3
Gymnosporia buxifolia	50	1	-	-
Dwarf shrubs:				
Asparagus virgatus	-	-	50	1
Graminoids:				
Miscanthus junceus	50	3	-	-
Panicum maximum	50	2	100	2
Ischaemum fasciculatum	50	2	-	-
Cyperus latifolius	50	1	-	-
Cyperus marginatus	100	1	-	-
Hemarthria altissima	75	1	50	1
Phragmites australis	-	-	75	5
Cyperus longus var. *tenuiflorus*	-	-	100	4
Cynodon dactylon	-	-	75	1
Forbs:				
Hypoestes forskaolii	50	8	-	-
Tagetes minuta	75	3	-	-
Richardia brasiliensis	-	-	100	4
Verbena bonariensis	-	-	75	2
Selago densiflora	-	-	25	2
Conyza bonariensis	-	-	50	2
Salvia tiliifolia	-	-	25	1

C = constancy; AC = average canopy cover

All growth forms exhibited an increase in average canopy cover, except for the tree layer which declined from 11% (1995) to 8% (2021). The total canopy cover increased from 32% to 59% (Fig. 3). Observed canopy cover trends between the sampling periods were not statistically significant at $p = 0.05$.

The tree *Combretum erythrophyllum* remained the dominant woody species despite a reduced canopy cover (Table 5). *Salix mucronata* subsp. *woodii* was replaced as the dominant shrub species by *Diospyros lycioides* subsp. *sericea*, *Searsia gerrardii* and *Pappea capensis*. *Cynodon dactylon* dominated the herbaceous layer in 2021 followed by the *sedge Cyperus marginatus*, the reed *Phragmites australis* and the invasive forb *Datura stramonium* (Table 5).

Plant Sub-Community 2.3: *Heteropyxis natalensis*–*Bauhinia galpinii* sub-community

The *Heteropyxis natalensis*–*Bauhinia galpinii* sub-community is located inside the Loskop Dam Nature Reserve (Myburgh, 2001). The macro-channel is characterised by large boulders with a percentage rock cover of >60% and shallow soils with a sandy texture (Myburgh and Bredenkamp, 2004). The trees *Spirostachys africana* and *Combretum molle* characterise the rocky sections of the macro-channel bank.

This sub-community underwent significant structural changes between 1995 and 2021. The shrub layer's average canopy cover declined sharply from 17% to 6% ($p < 0.05$), while the tree layer increased significantly over the same period ($p < 0.05$) (Fig. 3). Similarly, the graminoid layer decreased from 15% to 6% ($p < 0.05$), contributing to an overall reduction in total canopy cover from 35% in 1995 to 30% in 2021 ($p < 0.05$) (Fig. 3).

Several shrubs, including *Bauhinia galpinii*, *Ficus ingens* var. *ingens*, *Elephantorrhiza burkei*, *Croton gratissimus* var. *gratissimus*, and *Ochna* sp., were replaced by trees such as *Spirostachys africana*, *Combretum erythrophyllum*, and *Combretum molle*, which became the dominant woody species (Table 6). Meanwhile, *Phragmites australis* maintained its dominance in the herbaceous layer. The grasses *Hyperthelia dissoluta* and *Diandrochloa namaquensis* were largely phased-out over 26 years (Table 6). The floristic affinity of 1% and the positions of the sub-community on the DCA diagram further suggest evidence of shifts in species composition (Fig. 2; Table A2, Appendix).

The macro-channel of Plant Community 2 is associated with mountainous terrain and a rocky channel bed. Human-induced disturbances are minimal within this community, except for the occurrence of veld fires, observed from burned vegetation. Indigenous forests are the dominant land cover associated with this community whereas conservation is the main land use (Fig. 2). The woody component's canopy cover remained stable over 26 years, while that of the graminoid layer was responsible for the increases in the total average canopy cover over the same period resulting in temporal changes.

Table 5. Dominant species of the *Heteropyxis natalensis–Eragrostis gummiflua* sub-community between 1995 and 2021

Plant species	Sampling period			
	1995		2021	
	C (%)	AC (%)	C (%)	AC (%)
Trees:				
Combretum erythrophyllum	100	7	100	4
Searsia gerrardii	100	3	-	-
Mimusops zeyheri	-	-	50	2
Croton gratissimus var. *gratissimus*	-	-	50	1
Shrubs:				
Salix mucronata subsp. *woodii*	83	3	-	-
Diospyros lycioides subsp. *sericea*	100	2	100	2
Searsia gerrardii	-	-	67	2
Pappea capensis	-	-	33	2
Vepris reflexa	-	-	33	1
Gymnosporia buxifolia	-	-	50	1
Graminoids:				
Cyperus marginatus	64	5	33	5
Phragmites australis	83	1	100	3
Paspalum scrobiculatum	67	2	-	-
Bothriochloa bladhii	83	1	-	-
Cynodon dactylon	-	-	100	6
Panicum maximum	-	-	100	2
Juncus effusus	-	-	83	2
Eragrostis curvula	-	-	50	1
Themeda triandra	-	-	100	1
Forbs:				
Datura stramonium	-	-	50	2

Table 6. Dominant species of the *Heteropyxis natalensis–Bauhinia galpinii* sub-community between 1995 and 2021

Plant species	Sampling period			
	1995		2021	
	C (%)	AC (%)	C (%)	AC (%)
Trees:				
Spirostachys africana	-	-	100	8
Combretum erythrophyllum	-	-	100	4
Combretum molle	-	-	100	2
Shrubs:				
Bauhinia galpinii	100	4	-	-
Ficus ingens var. *ingens*	100	4	-	-
Flacourtia indica	100	3	-	-
Ochna sp.	100	2	-	-
Elephantorrhiza burkei	100	2	-	-
Croton gratissimus var. *gratissimus*	100	2	-	-
Pappea capensis			100	3
Dwarf shrubs:				
Flacourtia indica	-	-	100	2
Graminoids:				
Phragmites australis	100	3	100	4
Hyperthelia dissoluta	100	8	-	-
Diandrochloa namaquensis	100	2	-	-

Within Sub-Community 2.1, the tree *Combretum erythrophyllum* declined in canopy cover which could be attributed to fire and subsequent intermediate flood disturbances, as this species was observed burnt, broken and bending towards the downstream of the river. By contrast, the shrub species, namely, *Searsia gerrardii* and *Pappea capensis*, associated with rocky sections increased in canopy cover. Disturbances from fires and floods have been shown to alter the composition and cover of riparian vegetation (Pettit and Naiman, 2007; Bendix, 1998). However, in this section, the high rock cover appeared to buffer the understorey woody layer. This buffering role has been observed by Myburgh (2001) to protect riparian vegetation against flood impacts.

Sub-Community 2.3 occurs within a protected area; the lack of human-induced disturbances can explain the vegetation structural change from shrubland to woodland over 26 years as a result of a decline in the canopy cover of the shrub layer and an increase in the tree layer (Table 6). The increase of the tree layer's cover can be linked to a decline of the graminoid layer due to the shade effect imposed by the tree layer, as was previously observed by Myburgh and Bredenkamp (2004), which was exacerbated by grazing wild herbivores (Naiman and Rogers, 1997).

Plant Community 3: *Vachellia sieberiana* var. *woodii*–*Ischaemum fasciculatum* woodland

The *Vachellia sieberiana* var. *woodii*–*Ischaemum fasciculatum* woodland is located between Loskop Dam and the farm Kameeldoorn 71 JS. The river is characterised by dense stands of the reed *Phragmites australis*, resulting in multiple active channels and depositional bars.

The woody component increased in average canopy cover. The increase was mostly via the tree layer, from 10% (1995) to 20% (2021), although this change was not significant ($p > 0.05$) (Fig. 3). By contrast, the herbaceous layer displayed a downward trend in canopy over the same period ($p > 0.05$). The total canopy cover was not significantly different between 1995 and 2021 ($p > 0.05$) (Fig. 3).

The invasive alien trees largely absent in 1995, *Morus alba* var. *alba* and *Populus canescens*, were recorded in 2021 with constancies of 62% and 12%, respectively (Table 7). The shrub layer had compositional and dominance changes over 26 years, including the addition of the invasive *Lantana camara*, with an average canopy cover of 3% (Table 7). Within the graminoid layer there were no changes in terms of dominant species; however,

Table 7. Dominant species of the *Vachellia sieberiana* var. *woodii*–*Ischaemum fasciculatum* woodland between 1995 and 2021

Plant species	Sampling period			
	1995		2021	
	C (%)	AC (%)	C (%)	AC (%)
Trees:				
Combretum erythrophyllum	87	2	87	6
Vachellia sieberiana var. *woodii*	87	2	87	4
Melia azedarach	50	2	87	2
Vachellia karroo	87	2	100	1
Populus canescens	-	-	12	1
Morus alba var. *alba*	-	-	62	3
Terminalia sericea	-	-	25	2
Shrubs:				
Salix mucronata subsp. *woodii*	87	1	-	-
Diospyros lycioides subsp. *sericea*	-	-	87	3
Dichrostachys cinerea	-	-	62	2
Gymnosporia buxifolia	-	-	100	2
Dwarf shrubs:				
Lantana camara			75	3
Graminoids:				
Phragmites australis	100	16	100	7
Cynodon dactylon	75	5	100	7
Ischaemum fasciculatum	75	5	51	1
Panicum repens	37	1	-	-
Bothriochloa bladhii	62	1	-	-
Typha capensis	62	1	-	-
Panicum maximum	100	2	100	4
Imperata cylindrica	-	-	75	2
Paspalum scrobiculatum	-	-	75	2
Cyperus sexangularis	-	-	75	1
Cyperus longus var. *tenuiflorus*	-	-	50	1
Ischaemum fasciculatum	-	-	50	1
Forbs:				
Verbena bonariensis	100	3	-	-
Tagetes minuta	100	2	-	-
Ceratotheca triloba	50	1	-	-

grasses *Imperata cylindrica, Paspalum scrobiculatum* and the sedge *Cyperus sexangularis* were recorded in 2021 with high constancies (Table 7).

Plant Community 3 is located within the commercial farming area of the Loskop Dam Irrigation Scheme (Tlou and Joubert, 2013) (Fig. 2). The broad farming enterprises within this area are a potential source of non-point pollutants leaching into the macro-channel, which could explain the general increasing trend in canopy cover of the woody component. Riparian vegetation acts as a filter of terrestrial agriculture–supplied nutrients, which aid riparian woodland's primary production rates and biomass accumulation (Lowrance et al., 1984; Fail et al., 1987). The increase in canopy cover of invasive alien species in this community can also be explained by this land use type.

There was a notable influx of plant species in Plant Community 3 (Table 7). Storage dams have been linked to changes in riparian vegetation's species composition and increases in canopy cover, especially alien plant species (Merritt and Cooper, 2000; Shafroth et al., 2002; Bejarano and Sordo-Ward, 2011).

Plant Community 4: *Combretum erythrophyllum–Cynodon dactylon* woodland

The *Combretum erythrophyllum–Cynodon dactylon* woodland occupies the section of the Olifants River from the farm Kameeldoorn 71 JS to the R37 road (Burgersfort/Polokwane Road) (Myburgh, 2001). Six sub-communities originally represented the community (Myburgh and Bredenkamp, 2004). However, during this study, only 4 sub-communities were resurveyed. The riparian vegetation in 2021 was characterised by trees *Vachellia tortillis* subsp. *tortillis, Senegalia galpinii* and *Melia azedarach* (invasive alien), as well as stands of the reed *Phragmites australis*. The total average canopy cover for the community declined slightly between 1995 (64%) and 2021 (58%) but this was not significant ($p > 0.05$).

Plant Sub-Community 4.2: *Combretum erythrophyllum–Teramnus labialis* subsp. *labialis* sub-community

The *Combretum erythrophyllum–Teramnus labialis* subsp. *labialis* sub-community is located between the farms Loskop Suid 53 JS and Krokodildrif 25 JS. This section of the Olifants River is associated with intensive commercial crop farming of citrus, maize and grapes on both sides of the river (Fig. 2). All of the growth forms displayed a downward trend in canopy cover over 26 years, except the graminoid layer which displayed no changes (Fig. 4). However, only the forb layer significantly ($p < 0.05$) declined in canopy cover from 33% (1995) to 9% (2021). As a result, the total canopy cover significantly decreased between 1995 (105%) and 2021 (54%) ($p < 0.05$) (Fig 4).

The invasive alien tree *Melia azedarach* declined in average canopy cover from 10% to 3% between 1995 and 2021, respectively, and was replaced by *Senegalia galpinii* as the most dominant tree in the sub-community. *Flueggea virosa* subsp. *virosa* dominated the shrub layer in 2021 following the decline of the previously dominant species such as *Diospyros lycioides* subsp. *sericea* and *Sesbania punicea* (invasive alien) (Table 8).

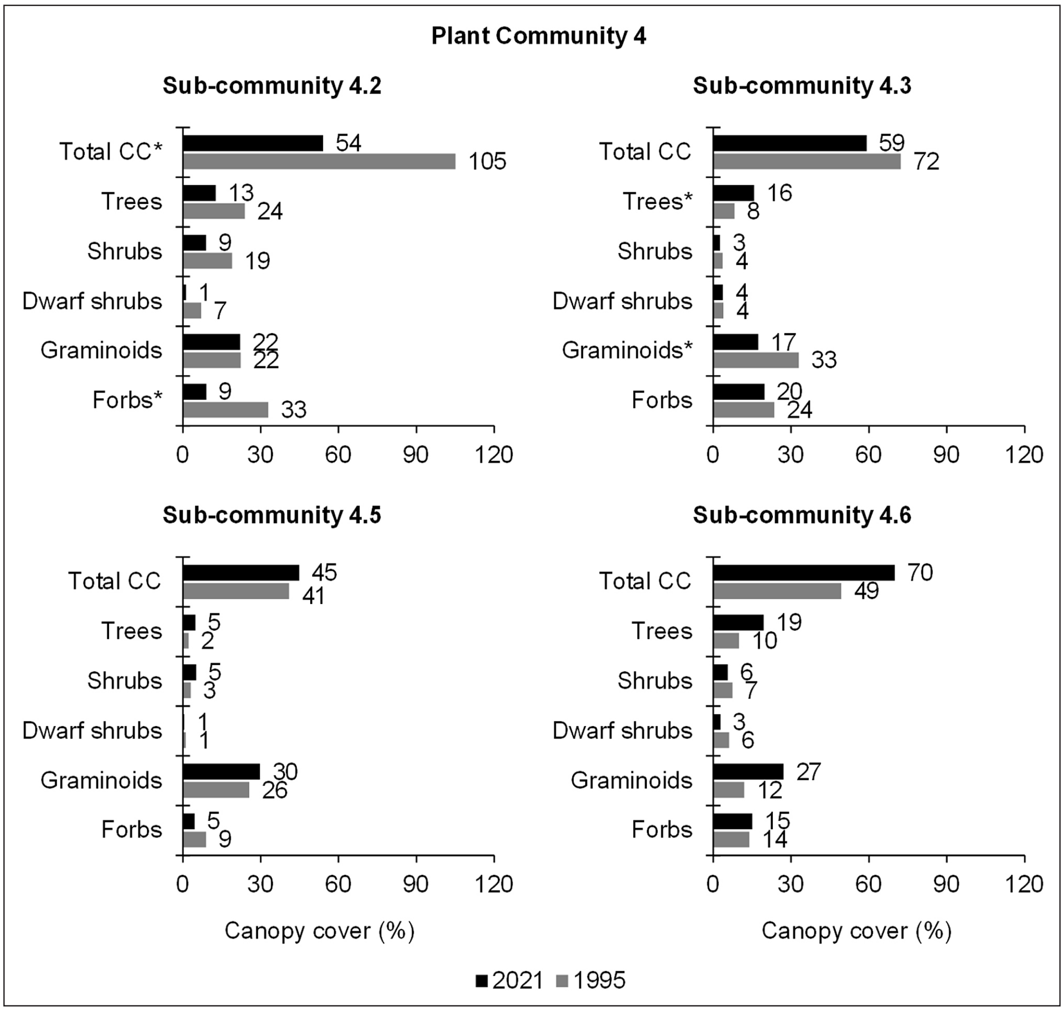

Figure 4. Comparison of growth forms and canopy cover between sampling periods (*represents statistical significance at $p = 0.05$); total CC = total average canopy cover

Table 8. Dominant species of the *Combretum erythrophyllum–Teramnus labialis* subsp. *labialis* sub-community between 1995 and 2021

Plant species	Sampling period			
	1995		2021	
	C (%)	AC (%)	C (%)	AC (%)
Trees:				
Melia azedarach	100	10	4	3
Senegalia galpinii	75	4	50	5
Combretum erythrophyllum	75	3	100	2
Ziziphus mucronata subsp. *mucronata*	100	4	-	-
Vachellia karroo	75	2	-	-
Spirostachys africana			50	2
Shrubs:				
Diospyros lycioides subsp. *sericea*	100	6	-	-
Sesbania punicea	100	3	-	-
Pavetta lanceolata	100	3	-	-
Gymnosporia buxifolia	50	2	50	2
Carissa bispinosa subsp. *zambesiensis*	25	1	-	-
Vachellia tortillis subsp. *woodii*	50	1	-	-
Searsia pyroides var. *pyroides*	75	1	-	-
Flueggea virosa subsp. *virosa*			100	5
Dwarf shrubs:				
Lantana camara	75	2	-	-
Flueggea virosa subsp. *virosa*	75	1	-	-
Sida rhombifolia	100	1	-	-
Graminoids:				
Phragmites australis	100	14	100	12
Panicum maximum	100	3	50	2
Hemarthria altissima	75	1	-	-
Cynodon dactylon	-	-	75	3
Forbs:				
Rivina humilis	100	6	50	2
Teramnus labialis subsp. *labialis*	100	4	-	-
Cissampelos mucronata	100	3	-	-
Equisetum ramosissimum subsp. *ramosissimum*	50	2	-	-
Riocreuxia torulosa	100	2	-	-
Hydrocotyle sp.	100	1	25	1
Achyranthes aspera var. *aspera*	75	1	-	-
Neonotonia wightii	50	1	-	-

Plant Sub-Community 4.3: *Combretum erythrophyllum–Schistostephium heptalobum* sub-community

The *Combretum erythrophyllum–Schistostephium heptalobum* sub-community is surrounded by commercial crop farming on either side of the river bank where the only natural vegetation left is the narrow riparian vegetation (Fig. 2). The active channel is characterised by deep pools. The tree layer canopy cover was significantly increased ($p < 0.05$) from 8% to 16% cover over 26 years (Fig. 4). All other growth forms declined in canopy cover but only the graminoid layer showed a significant ($p < 0.05$) decline in cover over the same period.

The invasive alien tree *Melia azedarach* replaced the tree *Combretum erythrophyllum* as the most dominant woody plant in the sub-community. Similarly, the forb *Cissampelos mucronata* replaced the invasive alien forb *Rivina humilis* as the most dominant forb species (Table 9). Additional invasive alien plants, *Morus alba* var. *alba* (tree) and *Solanum nigrum* (forb) were also dominant in the sub-community in 2021 (Table 9).

Plant Sub-Community 4.5: *Combretum erythrophyllum–Tamarix chinensis* sub-community

The *Combretum erythrophyllum–Tamarix chinensis* sub-community is located upstream of the Flag Boshielo Dam. The macro-channel is divided into two types of land uses. The southern river bank is on communal land used for subsistence livestock farming, whereas the northern river bank is inside Schuinsdraai Nature Reserve (Fig. 2). The macro-channel is characterised by high water levels encompassing the riparian vegetation.

There was no significant change in total canopy cover between 1995 (41%) and 2021 (45%) ($p > 0.05$) (Fig. 4). The graminoid, shrub and tree strata increased slightly in canopy cover while forbs declined in canopy cover, but these differences were not significant ($p > 0.05$). The woody plants, *Senegalia mellifera* (2% cover) and *Dichrostachys cinerea* (5% cover) were not recorded in the 1995 survey but dominated the woody component during the 2021 sampling period. *Cynodon dactylon* dominated the herbaceous layer during both sampling periods while *Panicum repens* co-dominated in 2021 (Table 10).

Table 9. Dominant species of the *Combretum erythrophyllum–Schistostephium heptalobum* sub-community between 1995 and 2021

Plant species	Sampling period			
	1995		2021	
	C (%)	AC (%)	C (%)	AC (%)
Trees:				
Combretum erythrophyllum	100	4	50	1
Melia azedarach	100	3	100	7
Vachellia karroo	-	-	100	4
Morus alba var. *alba*	-	-	100	2
Shrubs:				
Gymnosporia buxifolia	100	1	-	-
Dwarf shrubs:				
Asparagus setaceus	100	1	-	-
Cardiospermum halicacabum var. *microcarpum*	50	1	-	-
Graminoids:				
Phragmites australis	100	12	100	11
Panicum maximum	100	5	100	3
Forbs:				
Rivina humilis	100	7	50	1
Pergularia daemia var. *daemia*	100	3	-	-
Schistostephium heptalobum	100	3	-	-
Tagetes minuta	100	3	100	2
Persicaria lapathifolia	100	2	-	-
Ludwigia octovalvis subsp. *octovalvis*	100	2	-	-
Cissampelos mucronata	-	-	100	6
Commelina erecta	-	-	100	4
Solanum nigrum	-	-	50	2
Bidens bipinnata	-	-	50	1

Table 10. Dominant species of the *Combretum erythrophyllum–Tamarix chinensis* sub-community between 1995 and 2021

Plant species	Sampling period			
	1995		2021	
	C (%)	AC (%)	C (%)	AC (%)
Trees:				
Vachellia karroo	100	1	-	-
Senegalia mellifera	-	-	75	2
Shrubs:				
Sesbania punicea	100	1	-	-
Tamarix chinensis	50	1	-	-
Dichrostachys cinerea			100	5
Graminoids:				
Cynodon dactylon	100	9	100	17
Hemarthria altissima	50	6	-	-
Typha capensis	50	2	-	-
Cyperus fastigiatus	50	2	-	-
Panicum repens	-	-	100	5
Eragrostis heteromera	-	-	75	1
Forbs:				
Conyza sumatrensis var. *sumatrensis*	25	3	-	-
Tribulus terrestris	50	2	-	-
Tagetes minuta	75	1	-	-

Plant Sub-Community 4.6: *Combretum erythrophyllum–Gymnosporia tenuispina* sub-community

The *Combretum erythrophyllum–Gymnosporia tenuispina* sub-community is located downstream of the Flag Boshielo Dam. The river morphology is characterised by multiple channels as a result of alluvium deposits creating islands and channel bars on the channel bed.

There were slight but insignificant increases in tree and graminoid canopy cover over 26 years (p > 0.05) (Fig. 4). There was no significant change in total average canopy cover between sampling times (p > 0.05) (Fig. 4). The trees *Combretum erythrophyllum* and *Vachellia karroo* remained the dominant woody species in the sub-community over 26 years despite the latter's reduced constancy to 17% (Table 11). *Diospyros lycioides* subsp. *sericea* (2021) replaced *Gymnosporia buxifolia* (1995) as the most dominant shrub species. The grass *Panicum maximum* increased from 2% (1995) to 5% (2021) cover to co-dominate with *Cynodon dactylon*. The invasive alien forbs *Flaveria bidentis* and *Xanthium strumarium* were among the dominant species in the forb layer in 2021 (Table 11).

Plant Community 4 overall average canopy cover declined over 26 years. Although temporal shifts in species composition between 1995 and 2021 were not significant (Table 3), the low floristic affinity of between 6% and 10% obtained by sub-communities provides evidence of both temporal and spatial changes in species composition (Table A2, Appendix).

The sub-communities displayed variability in their respective average canopy covers. Sub-Communities 4.2 and 4.3 are located between Loskop and Flag Boshielo Dams. Loskop Dam is a regulated storage dam servicing the Loskop Dam Irrigation Scheme and various municipalities (Tlou and Joubert, 2013). This might explain the increased canopy cover of the tree layer in Sub-Community 4.3 and the increase of indigenous trees in Sub-Community 4.2 which can be ascribed to reduced natural base flow. Merritt and Copper (2000) and Shafroth et al. (2002) found that reduced natural base flow due to river regulation led to increases in the woody component in riparian systems.

By contrast, Sub-Community 4.2 had a decline in the canopy cover of invasive alien species. This sub-community traverses both commercial farms and residential areas (Fig. 2). The Loskop Dam Irrigation Scheme made the control of invasive alien species one of their main management objectives (Tlou and Joubert, 2013), which could explain the drastic decline in these problem plants. The control of invasive alien plants was patchily observed across this sub-community. Surprisingly, the shade-loving grass *Panicum maximum* declined in canopy cover in Sub-Community 4.3 post-1995. This can be attributed to densification of the canopy of the woody layer by the forb species *Cissampelos mucronata* (Table 9). The riparian vegetation of Sub-Community 4.2 showed signs of structural transitioning from a thicket to a woodland-type vegetation whereas Sub-Community 4.3 changed from an open woodland to a closed woodland, thus resulting in spatial changes.

Table 11. Dominant species of the *Combretum erythrophyllum–Gymnosporia tenuispina* sub-community between 1995 and 2021

Plant species	Sampling period			
	1995		2021	
	C (%)	AC (%)	C (%)	AC (%)
Trees:				
Combretum erythrophyllum	100	6	100	9
Vachellia karroo	83	3	17	3
Vachellia tortillis subsp. *woodii*	-	-	100	2
Eucalyptus camaldulensis	-	-	17	2
Faidherbia albida	-	-	33	1
Shrubs:				
Gymnosporia buxifolia	67	4	100	1
Diospyros lycioides subsp. *sericea*	83	2	83	2
Searsia pyroides var. *pyroides*	100	2	-	-
Dwarf shrubs:				
Malvastrum coromandelianum	33	1	-	-
Sida rhombifolia	-	-	83	2
Graminoids:				
Cynodon dactylon	100	4	100	5
Phragmites australis	100	3	100	4
Panicum maximum	100	2	100	5
Urochloa mosambicensis	-	-	100	3
Hemarthria altissima	-	-	50	3
Paspalum scrobiculatum	-	-	33	1
Cyperus esculentus var. *esculentus*	-	-	17	1
Forbs:				
Achyranthes aspera var. *aspera*	100	3	-	-
Solanum campylacanthum subsp. *panduriforme*	100	1	83	1
Flaveria bidentis	-	-	33	3
Xanthium strumarium	-	-	100	2
Ruellia patula	-	-	67	1

Sub-Community 4.5 is located upstream of the Flag Boshielo Dam. This sub-community is characterised by a lack of a clear riparian zone because of a deep pool active channel attributed to a backwater effect. Myburgh and Bredenkamp (2004) observed a similar impact associated with the backwater effect within this sub-community, resulting in dead standing woody riparian species. Contrasting land uses occur on either side of the macro-channel, where one bank is within communal land while the other bank is inside a protected area, resulting in contrasting disturbance regimes which might explain the overall increase in canopy cover and changes in species composition and dominance (Fig. 2, Table 10). The tree *Senegalia mellifera* and shrub *Dichrostachys cinerea*, predominantly occurring on the communal land side of the macro-channel, were responsible for the slight increase in the woody component. The observed grazing and browsing by cattle and horses on the macro-channel bank might have facilitated the establishment of these encroachers.

On the lightly grazed macro-channel banks within Schuinsdraai Nature Reserve, the high-grazing-value *Panicum repens* and the lawn-forming grass *Cynodon dactylon* were established and increased in canopy cover post-1995, and thus contributed to an increase in canopy cover of the graminoid layer. A combination of human-induced disturbances resulted in spatio-temporal changes in Sub-Community 4.5 (Fig 2). Integrated disturbance regimes were found to cause changes in the species composition of riparian systems (Patten, 1998).

The macro-channel banks of Sub-Community 4.6, located downstream of Flag Boshielo Dam and in communal areas, varied from vertical to gently sloping, which could be attributed to bank scouring and basal undercutting because of increased river flow related to river regulation following periods of reduced base flows. The influence of variable river flows has been shown to impact bank slope due to scouring and basal undercutting (Rowntree, 1991). Additionally, variability in river flow due to river regulation (Jansson et al., 2000; Merritt and Copper 2000; Mallik and Richardson, 2009) can be ascribed to the increase in canopy cover of the tree layer and the invasion of invasive alien species, as was observed in this sub-community. River regulation has been related to channel narrowing and the establishment of alien plant species in the USA (Friedman et al., 1998; Shafroth et al., 2002).

Over 26 years, the understorey woody layer declined, primarily due to harvesting for communal agricultural practices near riparian banks and firewood collection. Similar impacts have been documented in the Olifants River (Myburgh, 2001) and the riparian systems of Tanzania (Mligo, 2016) and Cameroon (Egbe et al., 2021). This decline led to structural vegetation changes, shifting from a thicket to a woodland, as per Edward's (1983) classification systems, which in turn favoured the graminoid layer, resulting in spatio-temporal changes.

CONCLUSION

The biotic and abiotic templates of river systems are exposed to varying degrees of disturbances and the plant communities of the Olifants River in the Savanna Biome section are no exception. The plant communities of the Olifants River are fragmented by two dams as part of river regulation, which has been shown to facilitate both upstream and downstream changes in species composition, structure and variability in canopy cover trends in the Olifants River system. These changes have further been facilitated by different land uses and on-site disturbance regimes, such as commercial and subsistence agriculture, developments, river regulation and conservation areas. The current riparian vegetation state could also be a legacy of historic floods, such as the 1:100-year flood that occurred in 1996. The riparian vegetation of the Olifants River system in the Savanna Biome is thus influenced by a myriad of land uses, human-induced disturbances and natural disturbances in the face of climate change, all of which are linked to the observed spatio-temporal changes and shifts in species composition, richness and canopy cover. In view of the observed changes, some of which may detrimentally affect riparian ecosystem functionality and biodiversity conservation, we call for stricter and more rigorous implementation and monitoring of legislation and guidelines aimed at the protection and conservation of water resources and associated ecological support areas at a land-use level, as well as capacitation of communal land communities in the sustainable use of riparian system natural resources.

ACKNOWLEDGEMENTS

This project was supported by funds from the Lapalala Wilderness Foundation, Tshwane University of Technology and Prof. WJ Myburgh.

AUTHOR CONTRIBUTIONS

PNM collected and analysed the data, conducted data analysis and prepared the manuscript. WJM and MDP critically reviewed the analysed data and the final manuscript.

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APPENDIX

Table A1. Environmental variables used in the DCA ordination analysis

Land cover	Code
Indigenous forest	IF
Open woodland	OW
Cultivated commercial crops	CCC
Fallow land & old fields	FLOF
Degraded forest and woodland	DGFW
Residential formal (bare)	RFB
Artificial dam	ATD
Subsistence – small-scale annual crops	SSAC
On-site disturbance	**Code**
Commercial livestock grazing	CLG – Livestock
Grazing – wildlife	GW – Wildlife
Conservation area	CA – Conservation
River regulation (dams)	RRD – Dams
Residential houses and recreational resorts	RHR – Development
Communal land (subsistence crops and livestock)	CL – Cr and Liv
Fire	F – Fire

Table A2. Affinity matrix showing proportion of co-occurring species as a percentage of the total of all species for each set of two sampling points/communities were Com represent a Community and SubCo represents a Sub-community. The _95 and _21 represents the 1995 and 2021 sampling periods respectively.

Plant communities	Plant Community 1		Plant Community 2				Plant Community 3		Plant Community 4								Means
	Com 1_95	Com 1_21	SubCo 2.1_95	SubCo 2.1_21	SubCo 2.3_95	SubCo 2.3_21	Com 3_95	Com 3_21	SubCo 4.2_95	SubCo 4.2_21	SubCo 4.3_95	SubCo 4.3_21	SubCo 4.5_95	SubCo 4.5_21	SubCo 4.6_95	SubCo 4.6_21	
Com 1_95	0	9	9	10	2	3	9	10	6	7	4	3	3	3	4	5	5%
Com 1_21	9	0	10	17	1	6	10	16	6	10	4	6	6	7	5	9	8%
SubCo 2.1_95	9	10	0	15	3	3	10	10	7	7	3	3	3	4	3	6	6%
SubCo 2.1_21	10	17	15	0	4	9	12	21	7	12	5	7	5	9	6	11	9%
SubCo 2.3_95	2	1	3	4	0	1	3	3	1	1	1	1	0	1	0	1	1%
SubCo 2.3_21	3	6	3	9	1	0	4	10	4	8	3	5	2	6	4	7	5%
Com 3_95	9	10	10	12	3	4	0	16	13	12	7	7	7	7	8	10	8%
Com 3_21	10	16	10	21	3	10	16	0	11	19	6	10	7	14	7	16	11%
SubCo 4.2_95	6	6	7	7	1	4	13	11	0	10	8	7	6	5	8	8	7%
SubCo 4.2_21	7	10	7	12	1	8	12	19	10	0	6	12	6	11	8	16	9%
SubCo 4.3_95	4	4	3	5	1	3	7	6	8	6	0	6	5	3	6	5	4%
SubCo 4.3_21	3	6	3	7	1	5	7	10	7	12	6	0	4	7	6	12	6%
SubCo 4.5_95	3	6	3	5	0	2	7	7	6	6	5	4	0	6	7	7	5%
SubCo 4.5_21	3	7	4	9	1	6	7	14	5	11	3	7	6	0	5	14	6%
SubCo 4.6_95	4	5	3	6	0	4	8	7	8	8	6	6	7	5	0	7	5%
SubCo 4.6_21	5	9	6	11	1	7	10	16	8	16	5	12	7	14	7	0	8%