ORIGINAL ARTICLE

Grasses cope with high-contrast ecosystem conditions in the large outflow of the Banhine wetlands, Mozambique

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Abstract

Ecosystems with highly pulsed water supply must be better understood as climate change may increase frequency and severity of intense storms, droughts and floods. Here we collected data over 3 years (2016–2018) in the episodic wetland outflow channel (Aluize), Banhine National Park, in which the system state changed from dry to wet to dry. Field sampling included vegetation records, small-scale vegetation zoning, the seed bank and water and soil quality. The same main plant species were found in both dry and wet conditions across the riverbed of the outflow channel. We found only very few diaspores of plants in the soil after prolonged drought. In the subsequent flooded state, we examined very dense vegetation on the water surface, which was dominated by the gramineous species *Paspalidium obtusifolium*. This species formed a compact floating mat that was rooted to the riverbed. The Cyperaceae *Bolboschoenus glaucus* showed high clonal growth in the form of root tubers, which likely serve as important food reservoir during drought. Soil and water analyses do not indicate a limitation by nutrients. We outline how resident people may change the plant community structure with an increasing practice of setting fire to the meadows in the dried-up riverbed to facilitate plant regrowth as food for their livestock.

KEYWORDS

Aluize, biological soil crusts, Changane, droughts, floating mat, flooded grasslands, multi-year flooding cycle, plant clonality, seed bank, temporary wetland

Résumé

Il est important de mieux comprendre les écosystèmes disposant d'une alimentation en eau à débit élevé, car il est probable que la fréquence et la gravité de violentes tempêtes, sécheresses et inondations causées par les changements climatiques s'intensifient. Dans cette étude, nous avons collecté des données sur trois ans (2016–2018) dans le canal d'écoulement des zones humides épisodiques (Aluize) du parc national de Banhine, dans lequel l'écosystème est passé d'une condition sèche à humide, pour repasser ensuite à une condition sèche. L'échantillonnage effectué sur le site impliquait notamment le répertoriage de la végétation ainsi que le zonage à petite

échelle de celle-ci, la banque de graines et la qualité de l'eau et du sol. La présence des mêmes espèces végétales principales a été constatée dans des conditions sèches et humides sur le lit de rivière du canal d'écoulement. Nous n'avons trouvé que très peu de diaspores de plantes dans le sol après une sécheresse prolongée. Dans les conditions d'inondation qui ont suivi, nous avons examiné une végétation très dense à la surface de l'eau, qui était dominée par l'espèce graminée *Paspalidium obtusifolium*. Cette espèce formait un tapis flottant compact qui était enraciné dans le lit de la rivière. L'espèce de Cypéracées *olboschoenus glaucus* a montré une forte croissance clonale sous forme de tubercules radiculaires, qui servent probablement de réserve alimentaire importante pendant la sécheresse. Les analyses du sol et de l'eau n'indiquent pas de limitation causée par les éléments nutritifs. Nous décrivons la façon dont les résidents peuvent modifier la structure de la communauté végétale avec une pratique de plus en plus fréquente consistant à incendier les prairies dans le lit asséché de la rivière pour faciliter la repousse des plantes qui servent de nourriture pour leur bétail.

1 | INTRODUCTION

Natural systems are essentially dynamic. Alexander von Humboldt and Charles Darwin were among the first to introduce this fact into biological science. Their studies in the 19th century fundamentally changed the way nature was described by emphasising the understanding of dynamics as a core objective in plant and ecological science (Darwin, 1859; Humboldt & Bonpland, 1805). Ecosystems are continuously changing at different temporal scales, and changes can occur gradually or rapidly, as it is the case in systems that alternate between aquatic and terrestrial character. Receiving water and drying up, that is flooding and drawdown (van der Valk, 1981), are key mechanisms driving patterns of biodiversity and determining the functions and services of ecosystems. Little is known in such extremely varying systems, though a thorough understanding of the structuring elements and the development of efficient methods to describe and monitor vegetation dynamics is imperative, for example for the protection of wetlands (Arieira et al., 2011). Studies in floodplain ecosystems can promote our knowledge of structure-forming elements (Bouska et al., 2020; Tabacchi et al., 2019). Wetlands are essential dry-season habitats for wild and domestic herbivore populations throughout Africa (Fynn et al., 2015). Wetlands are often supported by rivers; however, an increase in frequency and intensity of droughts predicted due to climate change (Alcamo et al., 2007; Hirabayashi et al., 2008; Wilcox et al., 2020) may result in many perennial rivers becoming intermittent rivers (Datry et al., 2016; Reid et al., 2019). Changing climates can affect ecological processes that support ecosystem functioning (e.g. Körner et al., 2010; Mariani et al., 2019). For instance, climate change can impair ecological processes, affecting the distribution or phenology of species, and the desynchronisation of interspecific interactions (Scheffers et al., 2016). Scientists working on rivers are urgently asked to collect data in ways that mechanisms can be understood, for example responses of biodiversity to changes in river flow (Tonkin et al., 2019).

Here we aim to make a significant contribution in characterising and understanding vegetation dynamics in an outflow of the Banhine wetlands before its confluence with the Changane River through a descriptive approach. As a tributary of the increasingly intermittent stream Limpopo, the near-pristine Changane River is an episodic river with a short flooded state and several years in a dry condition (Stalmans & Wishart, 2005), distinguishing it from other rivers in Africa that have a regular annual inundation cycle, such as the Okavango, which has been the subject of extensive studies (Mladenov et al., 2005; Murray-Hudson et al., 2014; Wolski & Murray-Hudson, 2008). Since hydrological data are lacking even more for the Banhine National Park and its wetlands, McNamara and Larsen (2006) recommended further investigation to determine year-to-year variability of the wetland filling. Thus, we conducted research at site in the understudied region in order to investigate structural elements relevant for a sufficient understanding of the dynamics in an episodic wetland outflow channel of Banhine by favouring direct access (Pietersen & Pietersen, 2010).

By considering the framework of disparate drivers of vegetation dynamics (Pickett et al., 1987), we studied a river basin section over three consecutive years, during which it changed from dry to wet to dry conditions, or between a seed bank and vital wetlands. We took site conditions, species availability and species performance into account and also considered current direct and longer-term indirect processes that have the potential to drastically change the community at ecosystem-level. Our empirical research focuses in particular on (a) whether there are system states in which different grasses dominate the plant community, (b) how a zonation of vegetation types may be maintained under high variability of abiotic conditions and (c) what are possible consequences of human intervention.

2 | MATERIAL AND METHODS

2.1 | Study area

We conducted this study within Banhine National Park in Gaza Province, southern Mozambique (Figure 1). The environment is semi-arid, and the potential annual evaporation far outweighs precipitation (even the maximum precipitation in a several year observation period) (McNamara & Larsen, 2006). The study region is dependent on water which comes from a large catchment area in the north-west close to the border with Zimbabwe. The most immediate expression of this dependence is the Changane River, which contains water only temporarily and to which Ramsar wetlands (Ramsar Convention on Wetlands of International Importance especially as Waterfowl Habitat) are linked.

The Changane catchment area is a Mozambican sub-basin of the Limpopo basin with an average annual precipitation that varies between years by a factor of 7.5 (from 200 to 1,500 mm; FAO, 2004). Draining 43,000 km^2, the overall nonregulated Changane River has a very low discharge coefficient and long periods without any discharge (FAO, 2004). The Changane River valley is unusual in that it is situated along an old beach line and flows intermittently (FAO, 2004). Related to this, the potential to use groundwater in the Limpopo catchment area is limited or the groundwater is not suitable for human consumption as it is highly mineralised (GOM-DNA, 1999). Nevertheless, resident people dig deep into the riverbed to find water when the riverbed dries out.

The study area is located in the ecoregion 'Zambezian and mopane forests' (Goldberg, 2020) or belongs to the mopane vegetation of the Sudano-Zambezi region (Werger & Coetzee, 1978). Mopane (*Colophospermum mopane* (J.Kirk ex Benth.) J.Léonard) is the most common tree species on the sands of the adjacent plateau. There are also finer sediments than sand in the fluvial plain. The soil can have saline-alkaline properties, as indicated by the presence of the fever tree (*Vachellia xanthophloea* (Benth.) P.J.H.Hurter) that grows in temporary flooded areas along the riverbanks.

McNamara and Larsen (2006) coined the term 'Banhine cyclic wetlands' and differentiate an important wetland landscape that covers about 1%, and a grassland landscape surrounding the wetlands that covers about 14% of Banhine National Park. The grassland landscape consists of open grasslands with scattered trees and clumps of brushy
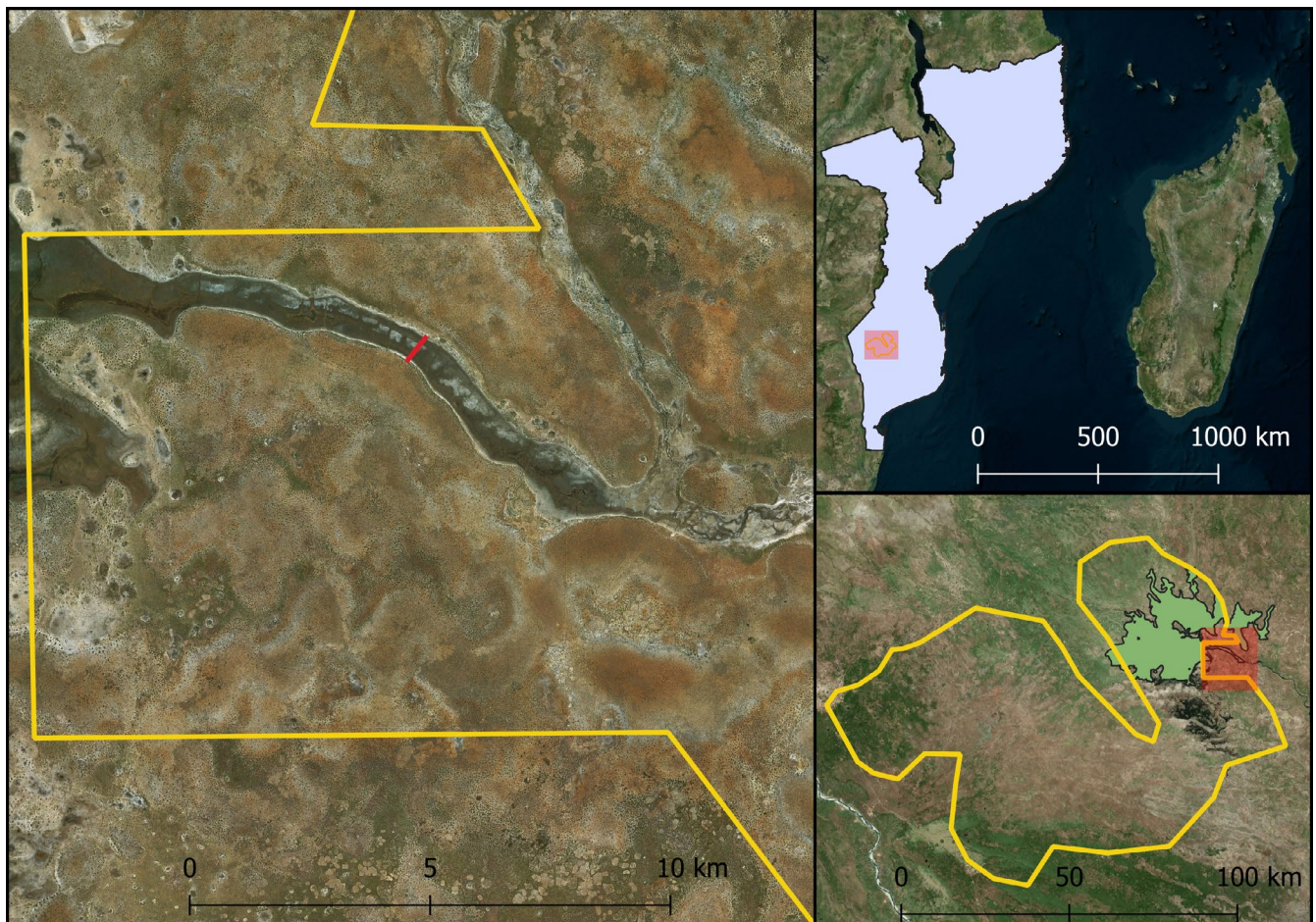

FIGURE 1 Location of the Banhine National Park within Mozambique (pink quadrat in top right panel), Banhine National Park (yellow border) and its wetlands (green-coloured area, down right), as well as transect location (red-marked, left panel) in the wetland outflow and confluence with the Changane River approximately 5 km to the east of the study transect. The images were created using QGIS based on Bing maps

vegetation. Both areas can be flooded. Stalmans and Wishart (2005) pointed out that difficult access, limited resources and a lack of previously published information have severely limited sampling intensity, extent of descriptions and details of the vegetation mapping. Additionally, vegetation records may never have been made before when the river channel had water due to the unpredictability of this event.

Our main study site is located around the wetland outflow channel between the Banhine wetlands in the west and its confluence with the Changane River to the east (Figure 1). The outflow, also called Aluize, has a river-like appearance when it contains water, has a greater width than the Changane river and has a more recognisable zoning of its banks (Figure 1).

2.2 | Study transect

In November 2016, we established one 530 m transect across the riverbed of the wetland outflow closely located to the Fish Eagle Research Camp (solid red line in Figures 1 and 2); located between the terminal points (latitude, longitude in decimal notation): −22.629, 33.272 (north-east) and −22.633, 33.269 (south-west; in Figures 1 and 2). The study site is located approximately midway between the Banhine wetlands to the west and the confluence with the Changane River to the east (Figure 1). In contrast to most surrounding landscapes, the study site including the transect (Figure 2) is permanently accessible from land. This conscious choice of location is intended to facilitate continuous research in the Banhine National Park as it is imperative to have efficiency in monitoring wetlands to improve

their protection (Arieira et al., 2011). Our descriptive approach anticipates and responds to the current call by Tonkin et al. (2019) for a new global campaign to collect natural history data on biodiversity responses to river change, explicitly including monitoring.

2.3 | Analysis of the soil seed bank

A total of 50 soil samples were taken with a soil core sampler (8 cm in diameter, 5 cm in height, 251.3 cm^3 in volume) on 18 November 2016, along the study transect and in its extension into the dry forest. Samples were sieved and examined with regard to propagules. The examination was carried out immediately and entirely on site using a magnifying glass and was not designed to detect so-called 'dust seeds'. In addition, tubers of Tuberous Bulrush (*Bolboschoenus glaucus* (Lam.) S.G.Sm.) were excavated in late November 2018. They were washed, air dried, weighed and individually stored for later experimental use.

2.4 | Vegetation records

Six plots of 1 m × 1 m each were established along the study transect in 2017, when the wetland outflow contained water (Figures 1–3; Table 1); the water level along the transect was up to 1.7 m. Total vegetation cover and the cover of each species were estimated per plot, by wading through the river. All species were counted as vertical structures rising above the water surface. The
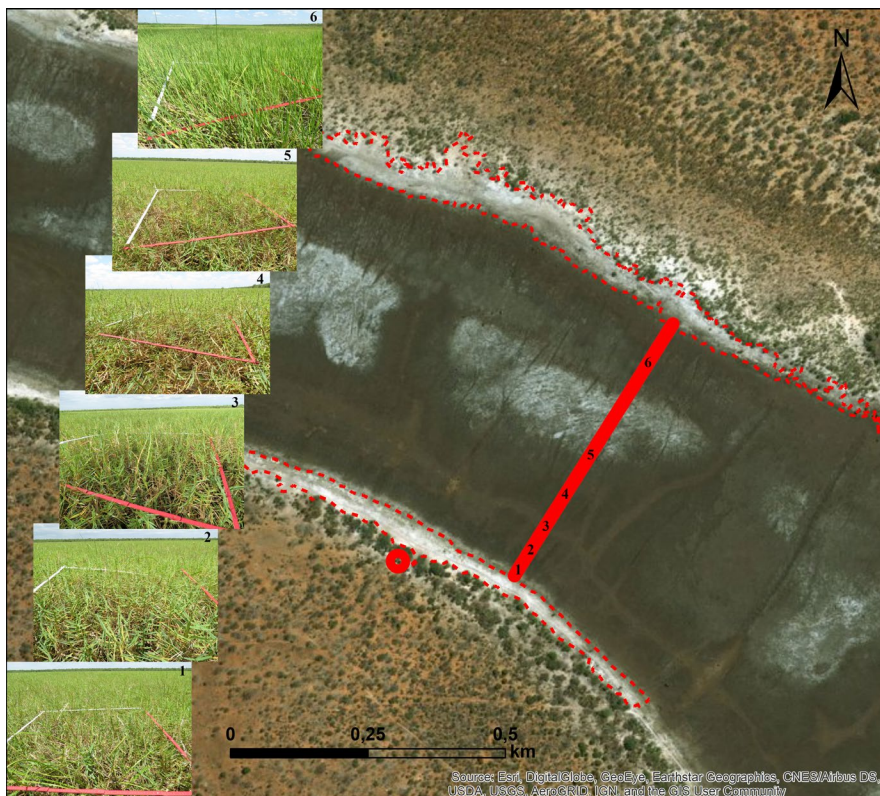

FIGURE 2 Location of the study transect across the Banhine wetland outflow (Aluize). The high-spatial resolution true colour satellite image obtained from Esri represents the dry state. The red-dashed lines are empirically recorded tracks representing the edge of the outflow channel during both 2016 and 2017 (inner lines) as well as the edges of dry forests (outer lines). The photograph inlets show the six vegetation plots along the transect in 2017 with their approximate positions indicated by numbers. The location of the main building of the Fish Eagle Research Camp is indicated by a red circle

FIGURE 3 Aerial views on the flooded Aluize towards the west. (upper panel) In the middle, a flooded ford/dam on which vehicles can cross at low water levels. The study transect is situated close to the location shown in the figure (slightly below the lower edge of the image). (lower panel) The vegetation showed high spatial autocorrelation. The studied transect is located in the foreground. The photographs were taken with an unmanned aerial vehicle on 23 November 2017 (by Stefan Schwill)

vegetation surveys were carried out always by the same person (M. K. Zaplata, hereafter MKZ), thereby avoiding biases potentially arising by different investigators. For each plot and species separately, MKZ estimated the degree of plant cover according to a modified Londo scale (Londo, 1976; 0.1: ≤0.1%; 0.5: >0.1%–0.5%; 1: >0.5%–1%; 2: >1%–2%, in 1% steps up to 100). Each 1-m^2 plot was subdivided with the help of pens to simplify the overview for the estimation. Vegetation cover estimates were made from different angles of each plot. This was done by first estimating the species cover from one side of the plot and then from at least one other plot side. If the cover estimates differed between the two angles (if they did, then mostly slightly), estimates were iteratively repeated until equal cover estimates were obtained for both angles. The procedure ensured a more consistent estimate of cover for each plant species. The same plot-based survey along the study transect was planned for the following year, but execution was too dangerous due to randomly distributed sloughs, that were still filled with mud and partly also water. This situation might be similar to the *Paspalidium obtusifolium* open grasslands of the nearby Zinave National Park (Stalmans & Peel, 2010) and has limited the direct inspection of transect vegetation in 2018. Nevertheless, surveys in this year were more than absence/presence records of the vegetation; MKZ crossed the dried out riverbed at several places with special attention to the re-sprouting pattern of *B. glaucus* and *P. obtusifolium*.

A one square metre sample of the vegetation of the Aluize vegetation near the southern riverbank was cut out with a machete on 30 November 2017 (Figure A1). This vegetation sample was dried

TABLE 1 Plant cover, number and above water level height of floating mat species

Plant species	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Mean	SE
Paspalidium obtusifolium (Delile) Simpson ↭	90% (352)	99% (398)	98% (325) ⚥	92% (293) ⚥⚥⚥	100% (489) ⚥	1% (6)	80.0% (310.5)	15.9 (67.0)
Utricularia gibba L.	75% (−)	60% (−)	15% (−)	100% (−)	20% (−)	95% (−)	60.8% (−)	14.9 (−)
Poaceae: furrowed, rigid, sharp leaves	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	99% (137)	16.5% (22.8)	16.5 (22.8)
Cyperaceae: thin, long-stemmed ↭	5% (80)	1% (11)	1% (25)	1% (5)	0% (0)	0% (0)	1.3% (20.2)	0.8 (12.6)
Bolboschoenus glaucus (Lam.) S.G.Sm	3% (28)	1% (2)	0% (0)	0% (0)	0% (0)	0% (0)	0.7% (5)	0.5 (4.6)
Neptunia oleracea Lour.	0% (0)	1% (1)	0% (0)	0% (0)	0% (0)	0% (0)	0.2% (0.2)	0.2 (0.2)
cf. *Cyperus articulatus*	0% (0)	0% (0)	0% (0)	0% (0)	0% (0)	0.5% (2)	0.1% (0.3)	0.1 (0.3)
Total	98% (460)	100% (412)	99% (350)	100% (298)	100% (489)	100% (145)	99.5% (359)	0.3 (51.5)
Maximum height (cm) of vegetation above water level	50	55	50	50	45	98		

Note: This was recorded November 2017 in the study transect plots (Figure 2). The number of vertical structures per square metre is given in brackets, except for *Utricularia gibba* that was not counted, because only flowers protruded from the water. The ↭ sign indicates pronounced clonality, the ⚥ sign indicates plots where *Paspalidium* inflorescences have been observed.

outdoors for 24 hr on porous concrete of the camp facility and then weighed with a simple scale.

The shoreline and the tree line along the outflow channel were both recorded in 2016 and 2017 by walking along with a handheld GPS device (Garmin etrex 20×). The tree line on both sides of the outflow channel was followed where the *C. mopane*-dominated dry forest adjacent to the river basin began (Figure 2). Remains of large Cyperaceae and differences in soil colour were used as indicators of the shoreline in 2016, whereas in 2017, the shoreline was indicated by the waterline.

2.5 | Biological soil crusts

Biological soil crusts (BSCs) were examined on both sides of the wetland outflow into the dry forest (in 2016 also along the transect, especially in the area of blown sand). They were identified based on the existence of lateral networking and recognisable filaments and their level of development was visually assessed according to Belnap et al. (2008) and Zellman (2014). The thickness of the BSCs was measured in 2016 with a calliper gauge, and the penetration resistance was measured in 2017 with a digital penetrometer (PCE-PTR 200, Taiwan) equipped with a round head adapter (area = 1 cm^2).

2.6 | Nutrients in soil and water

No water sample could be taken near the transect in the extremely dry year 2016. There was one residual water hole closer to the confluence with the Changane (Lumula), which was sampled on 20 November 2016 and repeated on 30 November 2017. The samples (0.5 L each) were transported to Germany (dark, but not cooled) and analysed photometrically at the BTU Cottbus-Senftenberg using LANGE cuvette tests.

A soil sample (~1.5 kg) was taken in the middle of the riverbed of the wetland outflow near the transect (slightly upstream) on 29 November 2018 (when the river was dried out) and examined at the Forschungsinstitut für Bergbaufolgelandschaften e.V. in Finsterwalde (Germany). Plant available phosphorus (P) and potassium (K) were analysed using double lactate extraction according to VDLUFA Bd. I, A 6.2.1.2 (1991). Plant available magnesium (Mg) was analysed using calcium chloride extraction according to VDLUFA Bd. I, A 6.2.4.1 (1991). Concentrations of cadmium (Cd), iron (Fe) and lead (Pb) were measured using aqua regia digestion. The air-dry sample was dried at 105°C to remove residual moisture for referring analytical values to dry matter.

2.7 | Faunistic observations

The importance of Banhine as resting place for thousands of migratory birds becomes increasingly apparent (PPF, 2020). Visitors of the park are often particularly interested in the birdlife and other wildlife. With the use of binoculars, we observed fauna regularly during the study periods (late November/early December) in all 3 years. Here we report about observations at the Aluize section captured in Figure 2.

2.8 | Human-caused fires

The administration of the Banhine National Park pays attention to fires. Fires in the wide plain are set with the goals of rejuvenating pasture for livestock and facilitating poaching of wildlife. Records of fires are supported by a growing number of National Park rangers (46 rangers in 2018) which enhances the pool of employees who can record fires and increases the chance that GIS-trained personnel are available. The fire statistics in this study are based on data from the National Park Authority.

TABLE 2 Seeds and root tubers found in soil samples of the study transect

Features	Sampling location					
	#1: 25m to the Camp at the southern riverside	#2: 50 m to the Camp at the southern riverside	#3: 200 m to the dry forest at the north, 400 m to the Camp	#4: 125 m to the dry forest at the northern riverside	#5: 50 m to the dry forest at the northern riverside	#6: 5 m inside dry forest above the northern riverside
Dark alluvial soils	No	No	Yes, but topped by wind-blown sand	Yes	No	No
No. of soil samples	8	7	5	10	10	10
No. of seeds	0	1 (fruit of cf. Asteraceae)	0	3 (2 cf. Asteraceae, 1 *Hibiscus panduriformis*)	0	0
No. of root tubers	0	0	Several	Several	0	0
Topping by BSCs	No	No	No	No	Yes (1.2 mm thickness)	Yes (4 mm thickness)

Note: The samples were in taken in November 2016. The thickness of biological soil crusts (BSCs) was measured in 2017.

3 | RESULTS

3.1 | Temporal variability in system state

Our results show that the riverbed-like outflow of the Banhine wetland (Aluize), which appeared dry and largely devoid of vegetation in 2016, with only an inconspicuous seed bank and tubers, some of them exposed (Table 2), turned into dense floating mats dominated by gramineous plants in 2017 (Figure 3; Table 1). The outflow channel began to fill with water in January 2017, and only isolated water holes were found in this channel in November 2018. In this last year of the investigation period, grass species (e.g. *P. obtusifolium* (Delile) Simpson and *B. glaucus*), which had dominated the floating mats in the previous year, were found to be still widespread. The same grass species that had a floating habitus in 2017 showed a terrestrial appearance in 2018, while water lilies (*Nymphaea nouchali* Burm.f.) had almost completely disappeared. Herbaceous species found only in the flooded condition (2017) were *Utricularia gibba* L. (Lentibulariaceae), *N. nouchali* (Nymphaeaceae) and *Neptunia oleracea* Lour. (Fabaceae). *Hibiscus panduriformis* Burm.f. (Malvaceae) was found only during the drawdown condition in 2016. Inundation events in the riverbed led to the death of young mopane trees.

3.2 | Vegetation composition and structural attributes

In November 2017, plants covered the outflow channel in high densities and formed a dense floating mat on top of the water column (up to 1.7 m depth) in large parts along the transect. The vegetation cover in the six plots was nearly 100 per cent (when all species were estimated together—see 'total' value in Table 1) and largely dominated by species from the Poaceae (e.g. *P. obtusifolium*) and Cyperaceae (e.g. *B. glaucus*) families. Plant cover is area-related and indicates how much vertical light is incident on plant structures. The plant cover can be up to 100% for one plant species or for several plant species considered together. If the cover of individual species was initially estimated separately, the total value can then exceed 100% when added up. Values >100% obtained in this way always indicate a multi-layered vegetation. This was the case for all plots, especially as *U. gibba* showed high covers in a deeper layer (mostly below the water surface).

In the six investigated plots, 145–489 vertical vegetation structures per square metre (359 ± 51 shoots/m², mean value with standard error, Table 1) formed a dense vegetation above the water surface (total cover ranging from 98% to 100%) and were dominated by the perennial *P. obtusifolium*. Water lily (*N. nouchali*) occurred in shallow areas. The high cover was based rather on lateral sections of the culms located at the water surface than on high numbers of individuals. Out of these lateral plant sections, vertical shoots grew into the air frequently, indicating pseudovivipary/clonality (Figure 4). The 1-m² floating mat sample harvested in 2017 consisted primarily of *P. obtusifolium* and illustrates its massiveness and the achievement of integration via lateral structures (Figure A1); the fresh and

FIGURE 4 Pseudovivipary (clonal growth) in Cyperaceae in the floating mat (November 2017). (three upper panels) Arches indicate clonal growth. (lowest panel) Subterranean tubers of *Bolboschoenus glaucus* serving as endurance organs of mostly clonal origin (cross section through tubers in 5–10 cm soil depth, November 2018)

dry mass of the sample weighed 22 and 2.7 kg, respectively, and could be compressed to a volume of 80.000 cm³. In addition to the pronounced lateral growth at the water surface, the subdominant Cyperaceae *B. glaucus* had subterranean tubers (Figure 4, see also soil seed bank section further below).

In 2017, *B. glaucus* was detected only in the southern part of the transect (plot 1 & 2, Figure 2, Table 1), near the research camp. Occurrence of *B. glaucus*, another Cyperaceae species, and Cyperaceae in general showed a decreasing trend towards the north

along the transect, that is from plot 1 to plot 6 (Table 1). Compared to Cyperaceae, the overall dominating grass, *P. obtusifolium*, apparently showed a higher presence in fire affected areas in 2018. This species showed inflorescences only in the middle of the Aluize during the flooded conditions in 2017 (Table 1), whereas inflorescences were more widely distributed under dry conditions in 2018. However, sexual reproduction has rarely been observed during periods of our stays (mid-November to early December). Two grass species that were nonflowering could only be identified to the family level (Table 1). In 2018, thick bulges of *P. obtusifolium*, probably the remains of a previous floating mat from 2017, were widespread across the dried out riverbed. It was evident that fires had occurred in several sites and those dominated by *P. obtusifolium* re-sprouted and have grown vigorously. Fire obviously did not harm *P. obtusifolium* in the inside of the bulges. According to the park rangers, all fires were set intentional. Their arbitrary distribution, even on the transect at this time, was an additional reason not to carry out detailed plot surveys in 2018, besides the occasional extreme danger due to sloughs. Qualitative examinations on the regrowth of *B. glaucus* and *P. obtusifolium* on larger areas resulted in maximum regrowth of *P. obtusifolium* and limited or at least delayed regrowth of *B. glaucus*.

Biological soil crusts were found on sandy soil in the wood-free margins directly next to the riverbed. BSCs are more common in mopane-dominated forests. The crusts were dominated by cyanobacteria. The level of BSC development was a maximum of 4 (out of 6) according to the classification by Belnap et al. (2008) and Zellman (2014). Such BSCs are characterised by their colouration and smooth surface. Penetration resistances of two BSC developmental levels and substrate without BSC (undisturbed and disturbed nearby ant lions) showed significant differences ($p < 0.001$). Darker BSCs (high level of development) had the highest penetration resistance (42.5 ± 2.6 Newton/cm^2, mean value with standard error), followed by bright BSCs (lower level of development, 17.3 ± 1.6 Newton/cm^2, Tukey's HSD post hoc test following ANOVA, $p < 0.001$). Substrate without BSCs and substrate close to ant lion funnels showed similar penetration resistance (11.2 ± 1.8 and 9.9 ± 0.7 Newton/cm^2, respectively, Tukey's HSD test, $p = 0.96$). Substrate close to ant lion funnels showed significantly lower penetration resistance than darker and bright BSCs (Tukey's HSD test, $p < 0.001$ and $p = 0.002$, respectively), whereas penetration resistance for substrate without BSCs was not significantly different from resistance for bright BSCs (Tukey's HSD test, $p = 0.095$).

3.3 | Soil seed bank in the last year of a long drought

Few diaspores (three seeds and one fruit) were found in the seed bank, and only from the plant families cf. Asteraceae and Malvaceae that did not play a role during flooded conditions. These plants can only be found at drawdown conditions when the site is free of surface water. The diaspores were found in two out of 17 soil samples (with a total volume of 4,272 cm^3) from the dry riverbed (sampling location 2 & 4 in Table 2, the latter indicated by dark floodplain soil). No seeds or fruits were found in soil samples of the adjacent mopane dry forest where BSCs with considerable penetration resistance existed. Other propagules such as underground storage tubers were found in the river basin. Tubers were often cut by the sampling cylinder. This is an indication of their frequency (there were about 7, and thus more than the number of seeds) and their size (2.8 ± 0.08 cm, mean value with standard error, max: 3.9 cm, min: 1.5 cm, $n = 50$, average weight 6.25 g). The tubers were found in two of the 15 riverbed soil samples (Table 2, location 3 & 4) and belonged either to the water lily *N. nouchali* or to the Cyperaceae *B. glaucus*.

3.4 | Faunistic observations near the study site

The floating vegetation mat on the water surface appeared to create a micro habitat for some terrestrial insects: especially praying mantises and wasps, with wasp nests attached to the vegetation (Zaplata, 2020). Other animal species found in the wetland included lungfish (*Protopterus annectens*), catfish, larvae of flukes (cercaria) and a large number of water birds, for example African Openbill (*Anastomus lamelligerus*), African Sacred Ibis (*Threskiornis aethiopicus*), African Spoonbill (*Platalea alba*) and Goliath Heron (*Ardea goliath*). Most herons, storks, flamingos and pelicans only visited larger areas of open water. The African Jacana (*Actophilornis africana*) was the bird most often observed moving on the floating vegetation. Patches of open water were dominated by a variety of ducks: for example White-faced Whistling Duck (*Dendrocygna viduata*), African Pygmy Goose (*Nettapus auritus*), Knob-billed Duck (*Sarkidiornis melanotos*), Red-billed Teal (*Anas erythrorhyncha*) and Hottentot Teal (*Anas hottentota*). The Spur-winged Goose (*Plectropterus gambensis*) was the only Anatidae occurring both under wet and dry conditions. The Rufous-naped Lark (*Mirafra africana*) was very common during the dry periods, but was also present during the flooded state. The most abundant migrant from the Palearctic, during dry and wet states of the area, was the Barn Swallow (*Hirundo rustica*).

3.5 | Nutrients in soil and water

Neither the soil of the riverbed nor the river water showed potentially nutrient limiting conditions for the investigated substances. The drought and wet years of 2016 and 2017, respectively, showed immense differences in water-dissolved substance concentrations; for example, sulphate and chloride in particular were highly concentrated in 2016 (Table A1). However, the results should be treated with caution, because water samples in 2016 were obtained from residual water in the only remaining waterhole, which was also available for use by livestock. This may have had an impact on water quality. Due to the long period of time between sampling and analysis, particular caution is required when assessing the nitrogen carriers

with regard to microbial transformation processes such as nitrification (ISO 2006, 2006).

3.6 | Human-caused fires in Banhine National Park

There were numerous fires in Banhine National Park during the dry conditions in 2016 and 2018, and about 45 fires in 2017 when the wetland outflow contained water. In 2016, about 105 ignitions that developed into wildfires were recorded. The situation was dramatic in 2018, with fires recorded in half of the park's area (all data are based on the National Park Authority). In November 2018, we also observed several fires directly in the Aluize outflow section shortly after the wetlands (west of the transect). Fires always covered a limited area and then ceased by themselves, especially in 2016 when there was less combustible vegetation available than in 2018. According to the park rangers, the fires were set by local residents in order to clear out dead vegetation matter from previous growth, and rejuvenate grasses for livestock.

Both main grass species coped differently with the fires. *Paspalidium obtusifolium* had formed very dense agglomerations and therefore fires could burn only exposed shoots. This species sprouted regularly again at burned sites and showed high cover (also again up to almost 100%). The above-ground parts of *B. glaucus*, however, were all burned by these fires, and almost no new shoots of this species were observed, suggesting that tubers were damaged by fire.

4 | DISCUSSION

The year of our first investigation, 2016, was the last year of the most extraordinary drought period observed to date in Banhine National Park (Blamey et al., 2018). Very different environmental states occurred during two subsequent years in the study area, where the system changed from drought conditions to flooded conditions with almost standing water and back to a dry drawdown state with residual moisture only at specific places. Vegetation under dry and wet conditions was dominated by grasses, and even the same plant species that was dominant in the year with flooded conditions (2017) formed a grassland during the dry conditions in 2018. Thus, despite fundamentally different environmental conditions in 2017 and 2018, hardly any alternative vegetation regimes could be distinguished with regard to the gramineous species dominating the plant community of the riverbed.

Light and nutrients are abundant and constantly present in the investigated habitat. Water, however, only sporadically enters the system and is therefore a pulsed resource. The outflow of the Banhine wetland has an episodic water supply that is efficiently used by the vegetation, that is by the gramineous wetland and terrestrial grassland found successively at the same place. Our findings may be of general relevance, since the water supply in many ecosystems worldwide becomes more pulsed due to climate change or human-caused alterations in hydrology (Junk, 2002; Wilcox et al., 2020).

4.1 | Vegetation zonation

The investigations mostly revealed asexually reproducing perennial species with a potentially indefinite lifespan, which, according to Van der Valk (1981), occur most frequently among aquatic species. These species can endure drought periods, but range expansion into neighbouring dry vegetation types is very unlikely. In turn, plant species with high dispersal abilities and adapted to dry conditions can spread into the riverbed-like Banhine wetland outflow after drying up, but die-off when it is flooded.

The poikilohydric life form of BSCs survive even under water shortage and can fix the substrate by their laterally cross-linked filaments, thereby limiting the transfer of sand from the surroundings into the riverbed during the dry conditions. BSCs may also act as a physical barrier that prevents seeds from becoming seedlings. These two features may help to maintain some distinct spatial separation of adjacent vegetation assemblages with their own characteristics, despite the marginal vertical differentiation of the terrain, a feature typical for floodplains (Ahan et al., 2017; Burkart et al., 1998; King, 2003; Leyer, 2005). We interpret the existence of BSCs between the edge of the outflow channel and the woodlands at as a sign of a rather orderly overall situation at this section of the wetland outflow. The large wetland that fills the outflow (west to the transect, Figure 1) may act as a buffer by releasing the water in a rather controlled manner. In contrast, water flow in the Changane River may be more forceful and variable during water-bearing conditions, which presumably does not allow for a sharp zoning of vegetation along its banks.

The observed pseudovivipary in gramineous species may provide information about environmental heterogeneity and dispersal risks. According to Elmqvist and Cox (1996), pseudovivipary is confined to terrestrial habitats characterised by large spatial and temporal heterogeneity. Pseudovivipary also tends to occur in species that otherwise have only marginal vegetative spread through creeping rhizomes or stolons (Lee & Harmer, 1980). The risk of death during dispersal or the chance of reaching a worse habitat appears to exceed the chance of reaching a better site than the one presently inhabited (Gadgil, 1971). Therefore, the river basin seems to be a reliably good site for these grass species, despite the severe droughts.

4.2 | Key species of the ecosystem

Bolboschoenus glaucus and *N. nouchali* produce subterranean tubers that are full of reserves and serve as resting stages to overcome the long dry periods. The reserves are likely to be of particular importance in the harsh environment of poorly predicable periodicity, where new biomass, reproduction and tubers can only emerge when water is supplied anew. High vegetative propagation rates are known in the congeneric species *Bolboschoenus laticarpus* Marhold, Hroudová, Ducháček & Zákr. and *Bolboschoenus planiculmis* (F.Schmidt) T.V.Egorova, allowing to compensate for a lack of

generative reproduction (Brennenstuhl, 2009). The inconspicuous Cyperaceae *B. glaucus* in our study region may play a key role for the whole ecosystem by being an important food resource. The bottleneck situation for wildlife survival is drought, and during such times, there is not much food except of root tubers, suggesting *B. glaucus* being a system-relevant plant species. Ethnobotany repeatedly states that root tubers of other Cyperaceae species are also eaten (Piepenbring, 2000). Another key species is *P. obtusifolium* (Poaceae) due to its high biomass both at drawdown and flooded conditions. However, after a prolonged drought situation, this grass species is a poor food source for the wildlife as it does not develop starch-rich tubers.

4.3 | Comparisons to globally well-known flooded grasslands and savannahs of Africa

Comparisons are possible between the Banhine region and the ecoregion 'Zambezian flooded grasslands' or the biome 'Flooded grasslands and savannahs'. Ellenbroek (1987) describes a *P. obtusifolium* water meadow in the Kafue Flats (Zambia), which differs in habitus from the Aluize floating mats in that *P. obtusifolium* in our system did not grow that strictly upright. Due to this difference in growth habitus, we classify our system as a floating mat in comparison to a water meadow as observed in Zambia. *Paspalidium obtusifolium* in the Aluize floating mats showed few underwater shoots and very high numbers of upright vegetation shoots above the water surface. Similar ecosystems in Africa are the Inner Niger Delta (Republic of Mali), Lake Bangweulu (Zambia), the Okavango Delta (Botswana) and the Sudd (South Sudan). Regarding the flood level, vegetation distribution was described for the Sudd (Petersen et al., 2007; Sutcliffe, 1974). There were 'free-floating beds' and also species that were anchored like our grasses in the wetland outflow channel, suggesting that their distribution depends on the flood level. The anchored species described in the previous studies dominated only in areas where the flood level did not exceed 1.30 m over a period of 10 years or 1.18 m for 1 month in the year. The little-known vegetation of the Banhine wetland outflow could therefore be exceptional in terms of the underwater caulome length of a rooted floating mat which occurred at water levels up to 1.7 m.

Because of its saline groundwater and dependence on fresh water coming from outside through the Changane, the FAO has some doubts that the Banhine region is permanently inhabitable by humans. The fact that the salt content in the village wells is in many cases too high for the drinking water standard was confirmed by our own measurements in 2016. Some kilometres downstream of the transect, salt indicator plants were present in the Lumula salt pan. Except for such special locations, there is a high growth potential in the river basin, and bare soil is occupied by BSCs.

Favourable years with lush vegetation may attract large herbivores to Banhine National Park, for example wildebeest and zebra, which previously occurred permanently in Banhine, while elephant and eland had been observed seasonally in the area

(Anderson, 2002). Nowadays, their appearance would be a positive example of distance migration of large animals against the global trend (Tucker et al., 2018). Banhine was formerly called the 'Serengeti of Mozambique' (Stalmans & Wishart, 2005). Unfortunately, it is no longer clear whether the 'extensive seasonal pans and wetlands' actually overlap to a certain extent with 'open grasslands' (Briggs, 2017). They may partly alternate over time as this study suggests. The wetlands or grasslands have not been observed regularly in the past, because the Banhine region in general and the sites concerned in particular have been very difficult to reach and still have very limited facilities (Briggs, 2017). It goes back to Stalmans and Wishart (2005), who defined '*P. obtusifolium* open grassland' as one of 11 vegetation communities for the Banhine National Park. Here we propose an overarching characterisation as 'flooded savannah' or 'flooded grassland' for the area concerned in Banhine National Park as long as the system alternates between rarely occurring wetlands and grassland.

The Banhine region and its wetland outflow (Aluize) are not yet included in a list of the ecoregion 'Zambezian flooded grasslands', although it is described as a 'constantly changing mosaic of edaphic grasslands, interspersed with permanent swamp vegetation' (Goldberg, 2020). Based on our study, we support such a classification.

4.4 | Fires and risk to the ecosystem

The ecosystem of the Aluize and the spatially connected episodic wetlands of Banhine as well as the Changane River basin are at risk from human-caused fires. These fires may alter functional ecosystem processes such as vegetation regeneration (for more information see Keeley, 2009) and possibly reduce the ecosystems' resilience (defined as grazed dry-land ecosystem's ability to buffer drought effects on forage provision; McAllister et al., 2006, cited in Linstädter et al., 2016). According to our observations, fire may reduce long-term food availability for animals and humans by devitalising root tubers. Vital tubers could not be found at burned sites, even though *B. glaucus* tubers were located up to some decimetre in the soil. A loss of tuber abundance and quality could be detrimental for the entire ecosystem, because the root tubers are a presumably important food source for fauna during drought periods. Cape Porcupine (*Hystrix africaeaustralis*), Southern African Springhare (*Pedetes capensis*) and Common Warthog (*Phacochoerus africanus*) can certainly dig out the tubers by themselves, thereby making the tubers also accessible to other animal species. On the other hand, man-made fires have led to regrowth of *P. obtusifolium*, supplying herbivores including cattle with fresh grass biomass. A study in six wetlands of northern Ghana suggested that the shift in the distribution range of plant species may be caused rather by human-led activities than by climatic variability factors (Nsor et al., 2014). Vegetation modelling in the neighbouring Limpopo Province, South Africa, suggests that the probability of critical biome shifts is highest in more open ecosystems (Scheiter et al., 2018).

4.5 | Plots are representative of surrounding vegetation

Previous studies in the system by Stalmans and Wishart (2005) and McNamara and Larsen (2006) operated at different scales and differed also in their objectives. The vegetation records of plots along our study transect are representative of their surroundings, because the vegetation showed very high spatial autocorrelation, that is the same plant taxa occurred with similar cover near a plot, even at distances of up to hundreds of metres (Figure 3b). Several factors may favour such an extensive spatial autocorrelation: (a) fluvial processes can homogenise nutrient availability and the aquatic state provides homogeneous water availability; (b) clonal growth of the plant species favours homogeneous cover formation in adjacent areas; (c) the previous prolonged drought may have shifted the system to a more initial state, and initial landscapes offer strong potential for plant cover with a high degree of spatial autocorrelation (Zaplata et al., 2013). The vegetation in the study area along the more than 1 km long section of the wetland outflow (Figure 2) was largely similar in terms of plant taxa and cover. Recordings of additional plots, close to each of the six investigated here (i.e. replicates), would probably not have gained more insights. Given the resources available, our aim was rather to apply a nonreplicated approach in order to capture potential nonlinear responses in plant occurrence across the riverbed. Little is known about vegetation dynamics in this region, and our study will hopefully stimulate interest in continuing transect surveys at the site.

5 | CONCLUSIONS

This study gives first insights into basic relationships of vegetation dynamics in the Banhine wetland outflow, Mozambique. The transect survey revealed a poor seed bank after a prolonged drought period and a fast and dense vegetation growth shortly after the river filled with water. During the water-filled state, some heterogeneity in plant community composition could be observed across the transect. Dominant grass species that grew in dense floating mats on the water surface were also found in the subsequent year, when water was present only in remaining water holes. Vegetation zonation may be maintained by die-off of nonadapted plant species when the basin is filled with water and by some physical impedance of BSCs outside the river basin. Terrestrial fauna (mainly insects) could proliferate during the flooded condition by using the floating mats of grasses as habitat. We identified key plant species of the system and potential threats by man-made fires that may reduce the ecosystem's resilience. Future studies could use the transect established here. We encourage continuing basic research, for instance, on questions of the stability of this ecosystem to management measures or climate change impacts.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available in the article itself and the Appendix of this article.

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APPENDIX A

TABLE A1 Soil and water analyses in the Banhine wetland outflow (Aluize)

Parameter	Riverbed substrate	River water 2017 (2016)
pH (CaCl$_2$)	6.8	5.96 (6.72)
Electrical conductivity	2.00 mS/cm	0.76 (11.24) mS/cm
Dry matter	99.0 (%)	–
		0.27 (0.15) nitrite, mg/L
N$_{total}$	0.126% dry matter	3.30 (4.72) nitrate, mg/L
		2.11 (b.d.) ammonium, mg/L
K	779 mg/kg dry matter	n.a.
P	10.1 mg/kg dry matter	2.03 (0.30) phosphate, mg/L
Mg	967 mg/kg dry matter	n.a.
Cd	<1.5 mg/kg dry matter	b.d. (b.d.)
Fe	20.4 g/kg dry matter	2.11 (0.39) mg/L
Pb	6.03 mg/kg dry matter	0.17 (0.11) mg/L
Phenol	n.a.	3.98 (8.72) mg/L
Sulphate	n.a.	22.50 (254) mg/L
Chloride	n.a.	23.88 (2,482) mg/L

Note: The soil substrate sampling site (2018) was close to the investigated transect. The water sampling site was the location nearest downstream in 2016 (the year of the extraordinary drought) and at the same location in 2017. Note, the values of the Aluize water in year 2016 are given in brackets.

Abbreviations: b.d., below detection limit, n.a., not analysed.

FIGURE A1 Square metre of floating mat sampled in the study transect to illustrate its anchorage (see culms remaining in the sampling square, upper panel) and massiveness (lower panel)