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Original Research Article

## Vegetation structure and effects of human use of the dambos ecosystem in northern Mozambique

Aires Afonso Mbanze<sup>a, b, c, \*</sup>, Amade Mário Martins<sup>d</sup>, Rui Rivaes<sup>e</sup>,  
Ana I. Ribeiro-Barros<sup>b</sup>, Natasha Sofia Ribeiro<sup>f</sup><sup>a</sup> Universidade Lúrio, Faculty of Agricultural Sciences (FCA), Sanga University Campus, Niassa Province, Mozambique<sup>b</sup> Universidade de Lisboa, Instituto Superior de Agronomia (ISA), Linking Landscape, Environment, Agriculture and Food (LEAF), Plant Stress & Biodiversity Lab, Tapada da Ajuda, P.O.Box, 1349-017, Lisbon, Portugal<sup>c</sup> Universidade Nova de Lisboa, Nova School of Business and Economics, Campus de Carcavelos, Rua da Holanda 1. P.O.Box 2775-405, Lisbon, Portugal<sup>d</sup> Technical Institute of Ecotourism Armando Emílio Guebuza, Marrupa District, Niassa Province, Mozambique<sup>e</sup> Universidade de Lisboa, Instituto Superior de Agronomia (ISA), Forest Research Centre (CEF), Tapada da Ajuda, P.O.Box, 1349-017, Lisbon, Portugal<sup>f</sup> Eduardo Mondlane University, Faculty of Agronomy and Forest Engineering, Av. J. Nyerere 3453/Campus Universitário Principal, Maputo, Mozambique

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## ABSTRACT

The Niassa National Reserve (NNR) is the most extensive conservation area in Mozambique and the third largest in Africa, encompassing 42,000 km<sup>2</sup> of endemic miombo vegetation. Dambos wetlands occur within the wooded grassland and grassland vegetation of NNR and provide a wide range of Ecosystem Services (ES), including life support for animal species, regulation of water flow and prevention of soil erosion. It also generates income for the livelihoods of local communities by providing land for agriculture and harvesting of non-timber products. The dynamics of these ecosystems is poorly understood despite the contribution of the dambos to global biodiversity and ES. This research is the first preliminary assessment of the vegetation structure and composition of six dambos within NNR, selected using Google Earth, MODIS satellite images and an exploratory field visit. Field data collection was performed using a two-stage systematic sampling approach, along transect lines of 100 × 10 m (0.1 ha), perpendicular to the dambos' flow. Square plots of 0.25 m<sup>2</sup> were established for grass survey within the transects where grass vegetation was measured, counted and identified. Data were analyzed with R software. The sociological position of each species was analyzed with regard to the vertical structure while for horizontal structure, the abundance, dominance, frequency and Importance Value Index (IVI) were determined. In order to understand the differences between dambos, evenness (H) and reciprocal of Simpson's heterogeneity index (Hill's N<sub>2</sub>) were calculated. Principal Coordinates Analysis (PCoA) and Cluster Analysis were also used to characterize the surveyed species communities. A total of 58 transects (5.8 ha) and 336 subplots were assessed, recording 110 woody and 73 grass species, respectively. The most common tree species were *Vitex doniana*, *Burkea africana*, *Syzygium cordatum* and *Annona senegalensis*, while for grass vegetation the most abundant species were *Andropogon eucomus* and *Helictotrichon turgidulum*. According to the IVI, the most dominant tree and shrub species were *V. doniana*, *Pseudolachnostylis maprouneifolia*, *A. senegalensis* and *S. cordatum*. Homogeneity (Hill's N<sub>2</sub> = 18.92) and evenness (H = -4.27) were, on average, low in all dambos. Dambo 2 was the most heterogeneous (Hill's N<sub>2</sub> = 18.21) while dambo 1 was the least

\* Corresponding author. Universidade Lúrio, Faculty of Agricultural Science (FCA), Sanga University Campus, Niassa Province, Mozambique  
E-mail addresses: [ambanze@unilurio.ac.mz](mailto:ambanze@unilurio.ac.mz), [aires.banze@gmail.com](mailto:aires.banze@gmail.com) (A.A. Mbanze).

heterogeneous (Hill's  $N_2 = 5.71$ ). Dambo 6 was most equitable ( $H = -1.35$ ) whereas dambo 2 the least equitable ( $H = -3.72$ ). Using species abundance and based on PCoA and cluster analysis, four main groups of dambos were identified based mainly on the water gradient, with data variation captured by the first three axes reaching almost 83%. The p-value (0.42), suggested no significant differences between species communities in the dambos, and thus, human disturbances appear not to be enough to modify dambos microenvironment. Accordingly, the results suggest that human activities, at this level, do not necessarily affect the structure and diversity of dambos in the NNR. The results also suggest that the species *A. senegalensis*, *Combretum psidioides*, *Crossopteryx febrifuga*, *Protea nitida*, *P. maprouneifolia* and *S. cordatum* can be used as indicator dambo species in NNR, with high likelihood of occurrence.

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## 1. Introduction

The miombo woodlands eco-region is among the 35 priority eco-regions identified by the WWF's Global Program Framework (WWF, 2012). It is rich in biodiversity, representing the most predominant ecosystem in Sub-Saharan Africa, covering approximately 3 million hectares in seven countries (Campbell, 1996; Desanker and Prentice, 1994; White, 1983; WWF, 2012), and hosting more than 65 million people (Deweese et al., 2010). The provision of miombo Ecosystem Services (ES) accounts for 7 to 11\$ billion year<sup>-1</sup> for rural livelihoods and 76% of the energy used in the sub-region (Deweese et al., 2010; Ryan et al., 2016). However, with the projected population growth, where the livelihoods are entirely dependent on agriculture, fishing, hunting and fuel wood (Jew et al., 2016), over-exploitation of plant resources and unsustainable harvest practices are likely to continue towards the depletion of ES in the miombo area (Bruschi et al., 2014; Deweese et al., 2010; Strydom and Savage, 2018). Thus, the expansion of Protected Areas (PAs) has been a principal strategy for conservation and sustainable management of natural resources (Vedeld et al., 2012). However, little is known about the effectiveness of PAs in containing deforestation and forest degradation. This expansion led to an exponential increase in studies of forest cover, structure, diversity and species composition in the miombo woodlands PAs (Banda et al., 2008, 2006; Giliba and Boon, 2011; Green et al., 2013; Mwakalukwa et al., 2014; Paul et al., 2013; Ribeiro et al., 2013, 2008). Such studies were conducted either to meet the demand and agenda of different conservation actors (Cobbinah et al., 2014) or to assess whether the best way of conserving natural resources was by restricting access in to PAs (Banda et al., 2006; Hall et al., 2003).

Despite the efforts that have been made, there is still a huge lack of understanding about the vegetation structure of PAs in the region. Improving this understanding is not only important to inform management options and decisions but also to help conservation experts and managers to develop consistent conservation guidelines (Banda et al., 2006; Dewi et al., 2013; Fisher et al., 2014; Kelboro and Stellmacher, 2015). These challenges are situated in the context of global climate change as well as other direct and indirect drivers of biodiversity and ES changes (Green et al., 2013; Naidu and Kumar, 2016; Ribeiro et al., 2015), including population growth, urbanization and industrialization (Newmark, 2008; UNEP et al., 2013; Walker and Desanker, 2004).

Global PAs are an important focus of environmental regulation and biodiversity conservation worldwide, and are key to understand the factors that are likely to limit conservation potential (Durán et al., 2013). In Mozambique, PAs cover about 25% of national forest (Marzoli, 2007), in which the Niassa National Reserve (NNR) accounts for 5.3% (ANAC, 2016) and 44.9% of conservation areas (Ganzin et al., 2010). NNR is the third largest PA in Africa (Bluwstein and Lund, 2016; Prin et al., 2014; Ribeiro et al., 2008), encompassing approximately 42,000 km<sup>2</sup>, which is more than the area of Switzerland (Ganzin et al., 2010; Prin et al., 2014; Ribeiro et al., 2008). The vegetation in the reserve is divided into nine main classes, where the dry miombo woodland is the more abundant, covering approximately 90% of its area. Within this ecosystem, one can find seasonally saturated and well drained depressions called *dambos* (Beekman et al., 2014; Lupankwa et al., 2000; Mapaure and McCartney, 2001; Timberlake and Chidumayo, 2011; von der Heyden and New, 2010). Dambos occupy in general the lowest topographic positions in African catenae or land systems (Hansen et al., 2009), and are set into the landscape by subduction processes induced by differential weathering and subsurface removal of material by lateral flow of groundwater. Altogether, these wetlands cover up to 40% of the miombo landscape (Whitlow, 1990; Zolho, 2005), and cover approximately 11% of the arable land in Africa (Hansen et al., 2009). Moreover, the functionality of miombo woodlands is highly dependent on dambos, as they capture and retain both rainfall and groundwater (von der Heyden and New, 2010), protect and regulate the water flow, and help to prevent soil erosion (DWAf, 2005; Madebwe and Madebwe, 2005). In conservation areas, dambo wetlands provide life support for a wide variety of terrestrial and aquatic species, mostly relying on it for water, food and reproduction (Fynn et al., 2015; Madebwe and Madebwe, 2005; Matayaya et al., 2017; Timberlake and Chidumayo, 2011). From the human perspective, dambos are a great source of income generation, providing formidable and arable land for agriculture (Kotze, 2011; Lupankwa et al., 2000; Ryan et al., 2016; Whitlow, 1990) and non-timber products such as food and medicines (van Wyk and van Wyk, 1997).

Despite their importance, dambos wetlands are placed amongst the most threatened habitats in the world (DWAF, 2005; Kotze, 2011) and the biodiversity dynamics of these ecosystems is still poorly understood. Furthermore, the sustainability of the human exploitation of this natural resource in conservation areas has never been ascertained before. The existing few studies about vegetation structure, composition and species diversity of dambos in general (Dube and Chitiga, 2011; Matayaya et al., 2017) and of dambos in the NNR in particular, consider the entire miombo ecosystem in general and do not focus on the dambos wetlands in particular (Ribeiro et al., 2015, 2013). Accordingly, the present research was carried out in order to assess the vegetation structure of dambos wetland in the NNR. Particularly, we intend to understand: (i) what are the patterns of the vegetation structures of this ecosystem; (ii) does the vegetation structure of seasonal dambos differ from those that are always wet? (iii) do the human related disturbances have different effects on dambos? The resulting information will not only enhance the scarce existing literature but will also provide relevant information for improving the management of dambo wetlands in conservation areas, as well as in other similar ecosystems elsewhere.

## 2. Methods

### 2.1. The study area location

The NNR is located in northern Mozambique, between coordinates: 12°38′48.67″S and 11°27′05.83″S, and 36°25′21.16″E and 38°30′23.74″E (Fig. 1).

The climate in the region is tropical sub-humid, with a dry and hot period between May and October and a wet season between December and April. The average temperature is between 20 and 26 °C, with an average rainfall of 900 mm. The landscape mostly comprises a gently undulating plateau at an altitude of around 200–600 m above sea level (Ganzin et al., 2010; SRN, 2008). The most common vegetation is characterized as dry Zambezi miombo woodland that is dominated by *Brachystegia spiciformis*, *Bachystegia boehmii* and *Julbernardia globiflora* (White, 1983). According to the last inventory in the NNR, the species density increased from 548 to 587 species/ha, with *J. globiflora* the most important species in the reserve (Ribeiro et al., 2013). Anthropogenic fire is one of the main drivers that influence the dynamics of the NNR ecosystem (Ribeiro et al., 2015; Maquia et al., 2013; Ribeiro et al., 2008). The reserve is one of few intact miombo savannahs remaining in the world (Ribeiro et al., 2013; WWF, 2012), home to 1200 lions, which makes the Reserve one of seven remaining strongholds with more than 1000 lions in the world (NCP, 2015; Riggio et al., 2013). Unfortunately, poaching and illegal ivory and skin trade is a huge threat to conservation, due to the rising demand for ivory in fast-growing Asia economies, particularly China and Thailand (Booth et al., 2014; UNEP et al., 2013).

### 2.2. Sampling procedure

The six dambos sampled in this study were selected using Google Earth and MODIS satellite images. After the identification of the dambos, an exploratory field trip was made to verify whether the dambos were appropriate for the establishment of the plots to be inventoried. The selection was required to offer a representative sample size, close to the Mbatamila Center Office of the Reserve, due to budget constraints and poor road accessibility. A preliminary, basic characterization was conducted in all dambos, which consisted of assessing fire occurrence in the last two years, shifting cultivation (Sc), artisanal fishing (Af), soils and vegetation characteristics, seasonal water (Sw) or permanent water (Pw) and fire occurrence as described in Mbanze et al. (2019). Data were collected using a two-stage systematic sampling procedure. In the first stage, trees and shrub vegetation was collected in the main transects of 100 × 10 m (0.1 ha), established perpendicular to the length of the dambo. In the second stage, grass vegetation was counted, height measured and collected for later identification in the six square subplots of 0.25 m<sup>2</sup> (50 cm × 50 cm) established within the main transects, according to Tito et al. (2009). A total of 336 subplots were established in all transects (See Fig. S1 in Mbanze et al., 2019).

### 2.3. Vegetation survey

Vegetation survey in the transects consisted of species inventory and recording of the tree height (h) and diameter at breast height (dbh) of all trees with a dbh over 5 cm, and the basal diameter (D) for all trees under 5 cm in dbh. Each stem was identified in the field to the species level and data was recorded. For the species that were difficult to identify in the field, samples were collected for later identification by a botanist. Detailed information on vegetation survey is available in Mbanze et al. (2019).

### 2.4. Data analyses

Analyses were performed in R software. In a first step, the aim was to understand the dambo ecosystem of NNR as a whole, and therefore, both vertical and horizontal structures were analyzed without discrimination among dambos, assuming a common dambo plant community. The succession stage of each species in the vertical structure was analyzed according to its sociological position, by dividing the forest canopy in three main strata, namely lower, middle and upper, based on the variable height (h), according to the equation that is provided in Mbanze et al. (2019).



**Fig. 1.** Geographic location of the dambos used for data collection in the Niassa National Reserve (NNR).

In relation to the grass vegetation, only the height of the grass, species richness and absolute dominance were measured and recorded. For better visualization, the three most dominant species of each dambos were presented in a histogram, to serve as simple description, since the main focus of this paper is tree and shrub vegetation survey. Although we recognize grass as the most dominant vegetation of the dambos ecosystem, we were particularly interested in analyzing the effects of multiannual continued human pressures. Research on dambos with a similar approach were also published elsewhere (Dube and Chitiga, 2011; Mapaure and McCartney, 2001; Matayaya et al., 2017). To understand the distribution pattern of grass species between wet and dry dambos, a hierarchically clustered heat map of absolute dominance of each species in the dambos, was plotted, based on Euclidean Distance (ED). The procedure is widely used to group similar objects with different characteristics in different fields of study (Farrelly et al., 2017; Wood et al., 2018).

In a second step, data were partitioned among dambos to allow comparisons and to understand whether human-induced factors and other site characteristics affected dambos differently. A sample-based rarefaction curve was plotted for each dambo to see whether the sampling intensity was adequate to embrace conveniently the dambos species richness. Sample-based rarefaction computes the expected number of species from a certain number of samples that are assessed randomly (without replacement) from an assemblage (Chao and Jost, 2012; Letters et al., 2001). The method is useful to identify coverage deficit of samples, which is also the probability that a new, previously unsampled species would be found if the sampling was enlarged by one individual (Chao and Jost, 2012). The coverage deficit can often be judged by looking at the final slope of the rarefaction curve calculated from the species frequency data. The sampling is considered nearly complete if the slope of the curve is small (Olszewski, 2004). These procedures will enhance our understanding in relation to sampling procedures and intensity in order to improve future studies in dambos multiple sites.

The three most important species of each dambos were selected based on the IVI, and their positions in the strata were used to understand the influence of these species in the future vegetation succession in the ecosystem. In addition, we analyzed species richness, (total number of species sampled) and species evenness. This latter variable measured the proportion of abundance of each species in the community and was calculated using the following equation,  $H = n^* \left( \sum_{i=1}^k x_i - \sum_{i=1}^k y_i \right) / \sum_{i=1}^k N_i$ , suggested by Hosokawa et al. (2008), where  $H$  is the species evenness index or equitability,  $n$  is the number classes of frequency,  $x_i$  is the number of species with absolute frequency between 80 and 100% in the plot  $i$ ,  $y_i$  is the number of species with absolute frequency between 0 and 20% in the plot  $i$  and  $N_i$  is the total number of species in the plot  $i$ . A given community is more equitable when  $H$  is closer to 1 ( $H \rightarrow 1$ ). The measurement of diversity by means of heterogeneity was carried out using the reciprocal of Simpson's index (Hill's  $N_2$ ),  $\frac{1}{D} = \sum_{i=1}^k p_i^2 = \text{Hill's } N_2$ , where  $\frac{1}{D}$  is the reciprocal of Simpson's index (=Hill's  $N_2$ ) and  $p_i$  is the proportion of species  $i$  in the community. Hill's  $N_2$  combines species richness and evenness and is widely used to express the degree of homogeneity of a given forest, as in this case, where the goal was to weight the common species in the dambos (Krebs, 2014). Hill's  $N_2$  varies from 1 to  $Sp$ , depending on the recorded number of species in the sample. In this case, Hill's  $N_2 < Sp_{0.25}$  means a lower diversity or heterogeneity,  $Sp_{0.25} \leq \text{Hill's } N_2 < Sp_{0.75}$  a moderate diversity and Hill's  $N_2 \geq Sp_{0.75}$  is higher species diversity.

Principal Coordinates Analysis (PCoA), based on Bray-Curtis dissimilarities, was used to assess the main species communities characterizing the surveyed dambos. PCoA (also known as metric multidimensional scaling), allows for the exploration and visualization of data dissimilarities by condensing and representing them in a lower-dimensional space. A cluster analysis was then performed, using also the Bray-Curtis dissimilarities, by the "average" method, which is widely used in plant ecology. The cluster cophenetic correlation was computed to assess how realistically a dendrogram preserves the pairwise distances between the observed data.

A permutational multivariate analysis of variance (PERMANOVA) was performed to statistically test the differences among dambos, based on its species composition. PERMANOVA was based on Bray-Curtis dissimilarities and assessed the groups arising from the ordination and classification analyses. An indicator species analysis was also performed using the relative abundance of the species. This methodology allows us to determine which species can be used as indicators based on the indicator value (Dufrene and Legendre, 1997). The indicator species analysis was performed using the "indicspecies" package running in the R environment (R Core Team, 2018). Due to the small sample of surveyed dambos, the confidence intervals for the indicator values were bootstrapped ( $n_{boot} = 1000$ ).

### 3. Results

#### 3.1. Grass vegetation

The height of the grass vegetation in the NNR ranged from 0.30 m to 2.30 m, with a mean of 1.32 m. Higher grass heights were observed in the permanent wet dambos, where *Pennisetum macrourum*, *Cymbopogon excavatus* and *Andropogon schirensis* were the dominant species. A total of 73 grass species were identified in all dambos. The number of species per dambo ranged from 10 to 55, with the least number of species identified in dambo 3, whereas the largest number of species was present in dambo 6 (See Fig. 2 and Table S1 in Mbanze et al., 2019). In general, the most abundant species were *Andropogon eucomus* with 1381 individual in all dambos, representing the top three most dominant species in dambos 3, 5, 4 and 1, with 434, 347, 253 and 182 individuals respectively, followed by *Helictotrichon turgidulum* with 997 individuals distributed as: 353, 259 and 178 in the dambos 5, 3 and 1, respectively (see Fig. 2). The less represented species were *Ctenium concinnum* and *Setaria verticillata* with four individuals in dambos 3 and 6, respectively. There were also three most dominant species observed in only one dambo: *Aristida adscensionis* with 141 individuals in dambo 4; *Aristida junciformis* and *Cenchrus ciliaris* with 296 and 156 individuals, both in the dambo 6.

Fig. 3 presents the heat map of dambos and species clusters. The horizontal dendrogram represents the clusters of dambos while in the vertical positions are the clusters of the grass species. The light-yellow colors represent the major number of individuals of that grass species recorded in the dambos, while the dark red, means that almost no individuals of that species were recorded in that dambo. One can observe that, in general, most of the species are absent in all NNR dambos. Regarding to the clusters of the dambos, there are two possible solutions: the first is a two clusters solution, with a subset of sub-clusters in the right side, represented by dambos 2 and 6, and a subset on the left side including all the other dambos. Those two clusters are mostly separated by a solution of three clusters on the vertical side of the species. The first cluster in the top of the vertical position, is represented only by *Hyperthelia dissoluta* which is not so important to divide the dambos in a two cluster solution, since it does not represents a clear separation between both clusters, because the light yellow and dark red are in both subsets. The second cluster is the most important to divide the dambos, being more represented by dark yellow to light-yellow, mostly by *Hyparrhenia filipendula* and *Hyparrhenia hirta*, as well as *Andropogon gayanus* and *Hyparrhenia cymbaria* in the last subset of clusters.

The second solution is composed by five clusters, being the middle subset of the cluster composed by dambos 3 and 5, while in the left and right are subsets of two single dambos. Those clusters are clearly distinguished by the first cluster of a single species (*H. dissoluta*), in the vertical position and in the second tree clusters by the species *H. hirta* and *A. gayanus*.

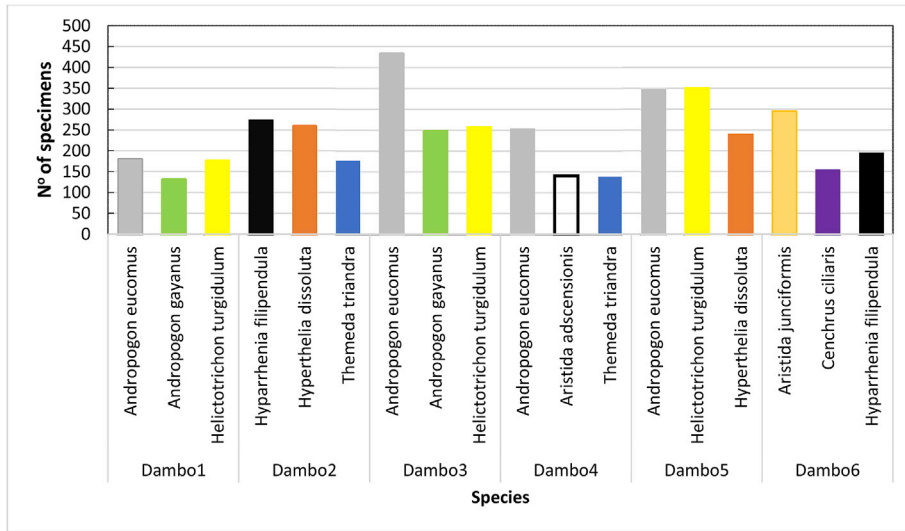


Fig. 2. Representation of the three most dominant grass species per dambo.

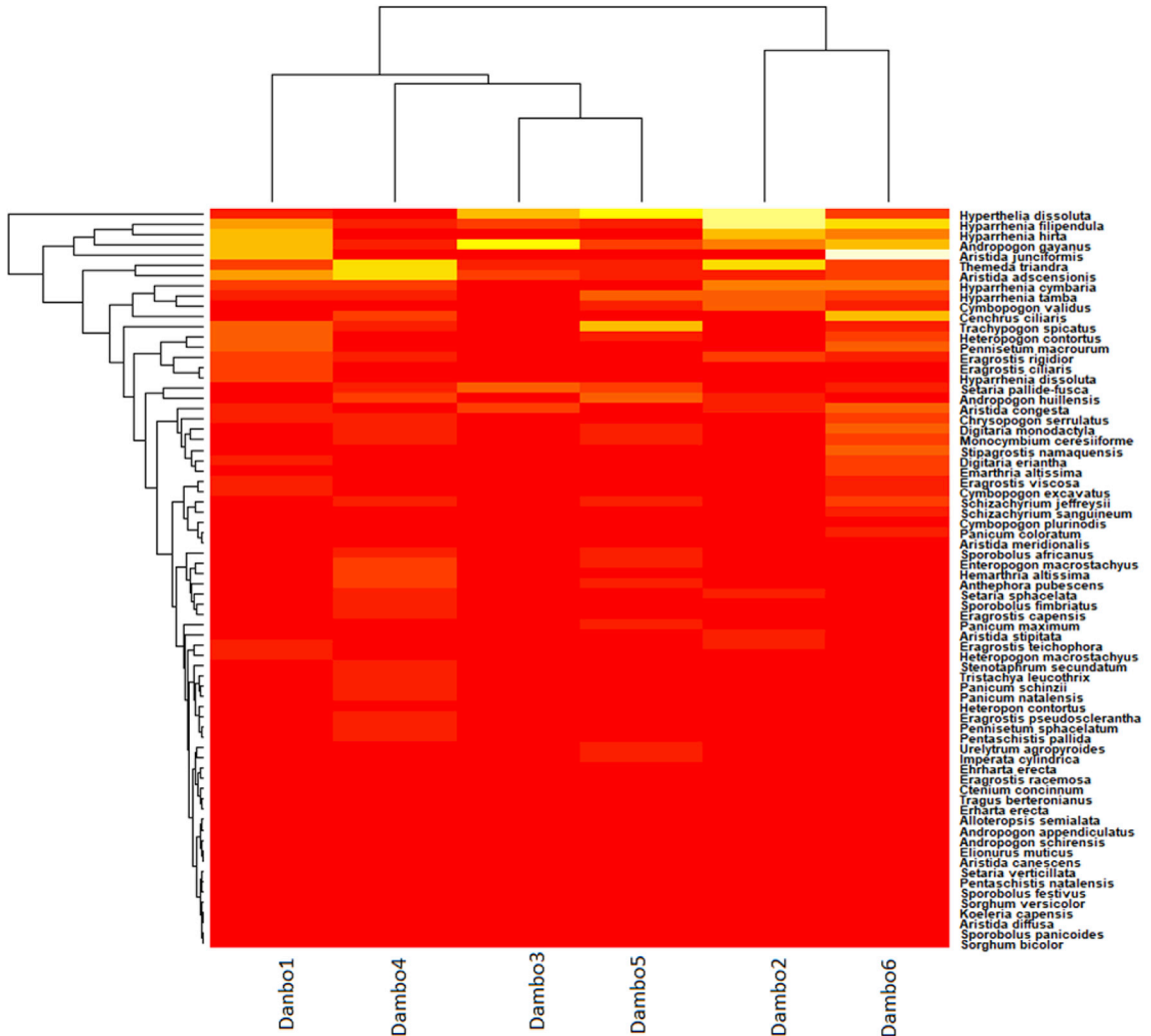


Fig. 3. Heat map clustering the dambos according to species abundance.

### 3.2. Distribution of species diversity across all the dambos

Fig. 4 presents the number and percentage of trees and shrub species per family assessed in all dambos. A total of 110 species representing 32 families was found in the sampled plots. These species were unevenly distributed among families, with Combretaceae having the most species, namely 15 (13.64%), followed by Fabaceae with 12 (11%) and Caesalpiniaceae and Rutaceae each with 10 (9%).

More than half of the families (59.38%) were represented by only one (0.91%) or two (1.82%) species, as is the case of Apocynaceae, Asteraceae, Chrysobalanaceae, Clusiaceae, Dipterocarpaceae, Flacourtiaceae, Loganiaceae, Meliaceae, Mimosaceae, Moraceae, Myrtaceae, Olacaceae, Pittosporaceae, Proteaceae, Rhamnaceae, Rutaceae, Sapindaceae, Sapotaceae and Vitaceae.

The average total mean height of the vegetation dambos was 5.436 m, with a standard deviation (Sd) of 3.519. The IVI ranged from 0.177 (*Gymnosporia senegalensis*) to 60.99 (*Syzygium cordatum*), while most of the tree species had an IVI lower than one ( $IVI < 1$ ). The top three well-represented species in the dambos were *Syzygium cordatum* (Myrtaceae), *Annona senegalensis* (Annonaceae), and *Pseudolachnostylis maprouneifolia* (Euphorbiaceae). *S. cordatum* (Ar = 11.13%, Dr = 44.49%, Fr = 5.38% and IVI = 61.00) was distributed almost equally in the middle (43.66%) and upper (55.35%) strata while *A. senegalensis* (Ar = 9.42%, Dr = 1.84%, Fr = 7.28% and IVI = 18.54) revealed the majority of its individuals in the middle stratum (97.86%), and *P. maprouneifolia* (Ar = 7.19%, Dr = 5.17%, Fr = 5.45%, IVI = 17.89) was well represented in the middle stratum (80.67%) with other considerable representation in the upper stratum (19.39%). More-detailed information about the distribution of species among families, including Ar, Dr, Fr, IVI and the percentage of trees of each species per stratum, can be found in Table S2, Mbanze et al. (2019).

### 3.3. Comparison of species diversity among dambos

In Fig. 5 are presented rarefaction curves of the 6 dambos in the different sites where the species were collected. The results reveal that the sampling effort might somewhat have fallen short from the necessary sampling intensity, as the mean richness curves did not reach stability regardless of sample intensity (Fig. 5a). The slopes of the mean rarefaction curves after the totality of the transects being surveyed were 0.26, 0.56, 0.77, 0.30, 1.48 and 0.36, respectively for dambos 1, 2, 3, 4, 5 and 6 revealing that coverage deficit was even higher in the dambos 2 and 6. Notwithstanding, in many cases the confidence intervals appear to be near of reaching asymptotic levels. According to the dambos richness estimation based on the sampling effort, Northern Mozambique dambos are expected to present nearly 110 of tree and shrubby vegetation species (Fig. 5b).

The number of plots sampled in each dambo was proportional to its size (see Table 1). The largest area sampled was in dambo 1 (1.3ha), and the number of individual trees measured was 1012, with lower density (2.27 m<sup>2</sup>/ha), diversity Hill's

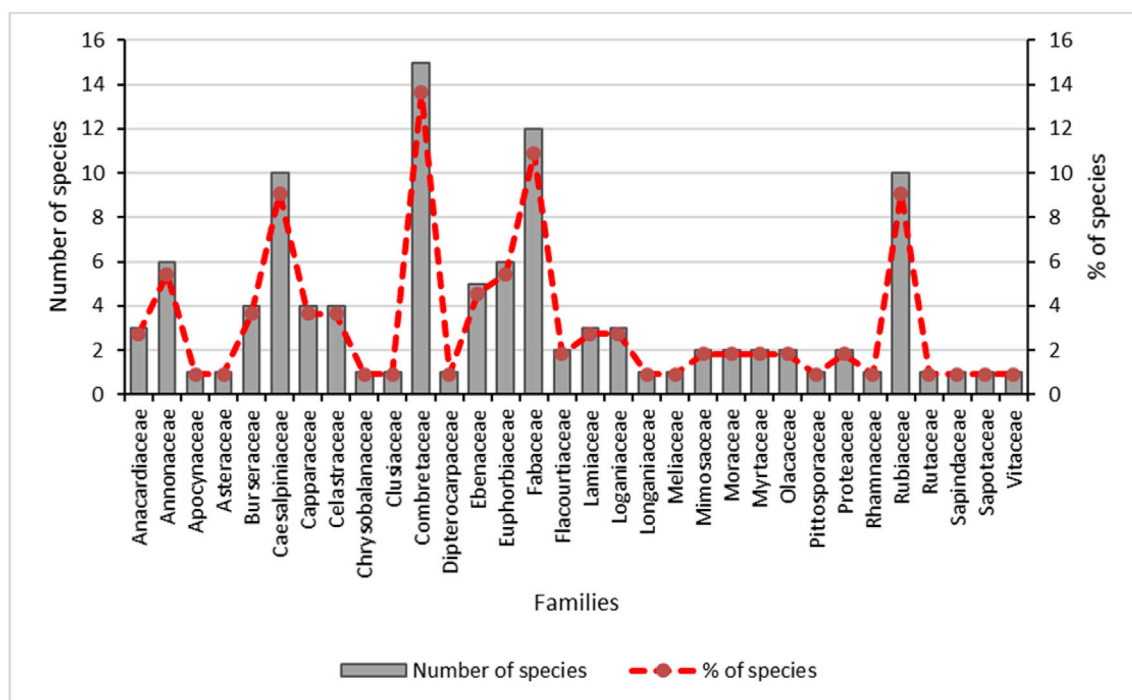
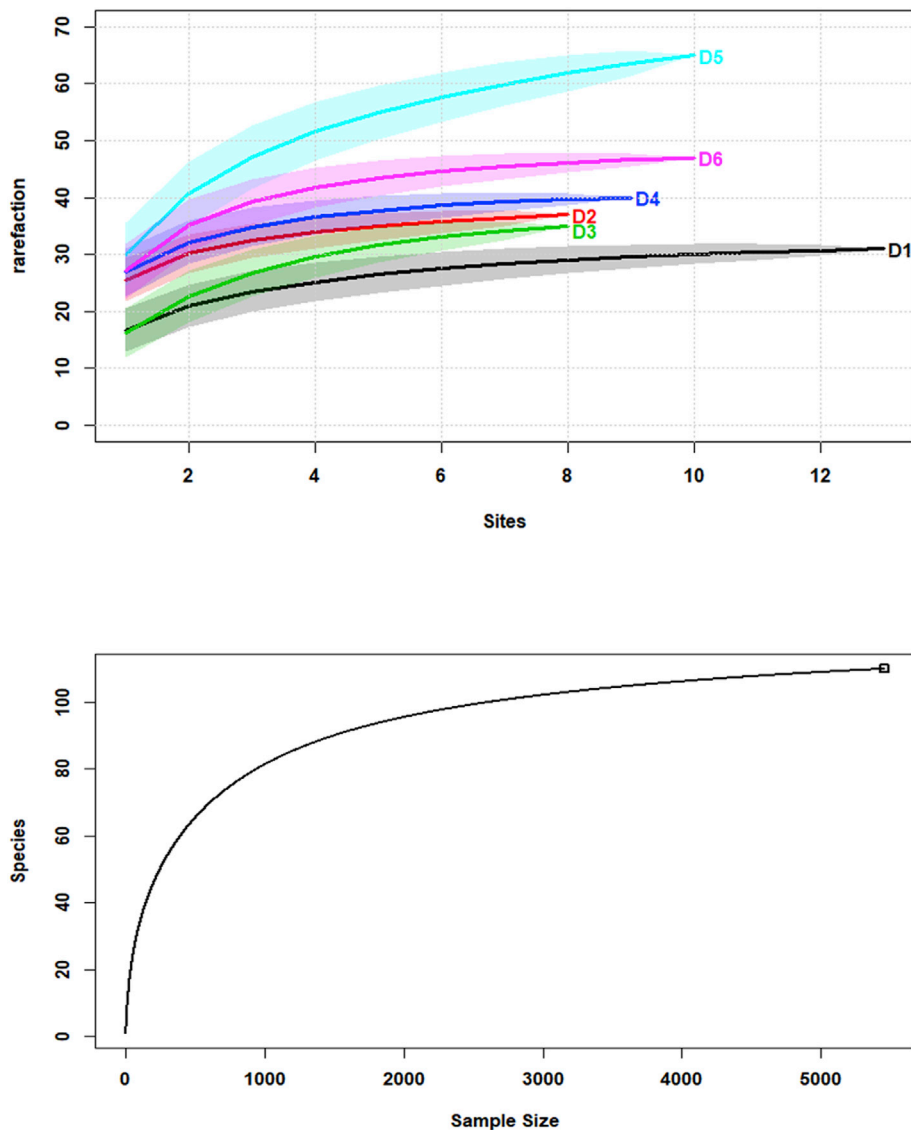


Fig. 4. – Number and percentage of species per family assessed in the set of 6 dambos.



**Fig. 5.** Relationship between species accumulation (rarefaction) and number of plots in each dambo (a), and expected species richness of Northern Mozambican dambos (b).

$N_2(5.71) < Sp_{0.25}$  and evenness ( $H = -3.06$ ). The highest number of trees were assessed in dambo 4, with 1541 individual trees and the highest density of  $17.75 \text{ m}^2/\text{ha}$ , with moderate diversity  $Sp_{0.25} \leq \text{Hill's } N_2(13.42) < SP_{0.75}$ , and relatively high evenness ( $H = -1.75$ ). Diversity and evenness were relatively high in dambo 2, if compared to the rest (Hill's  $N_2 = 18.12$  and  $H = -1.35$ ). Dambo 3 had the second-highest density ( $11.87 \text{ m}^2/\text{ha}$ ). Evenness was low in dambos 3 ( $H = -3.14$ ), 5 ( $H = -3.62$ ), and 6 ( $H = -3.72$ ). Diversity was low in dambo 3,  $N_2(8.22) < Sp_{0.25}$ , but moderate in dambos 5 and 6  $Sp_{0.25} \leq \text{Hill's } N_2(16.58) < SP_{0.75}$  and  $Sp_{0.25} \leq \text{Hill's } N_2(13.18) < SP_{0.75}$  respectively. Dambo 5 had more species than the rest, so it was more diverse than all dambos, but 2 and 4.

Table 2 presents the three most important species in the six dambos that were sampled. The selection was based on IVI, which varies substantially among the species with higher and lower IVI. It can be observed that a total of 10 species representing eight families were found. Myrtaceae and Annonaceae were the two most common families. Species from the Myrtaceae family occurred in all dambos except 2, whereas species from the Annonaceae family were present only in dambos 2 and 5. These two most predominant families also held the dominant species in the dambos, namely *S. guineense*, *S. cordatum* and *A. senegalensis*. The relative abundance (Ar) of the three most important species made up 30% of all individuals, even in dambo 5, where the highest number of species was found (see Fig. 5a), with the exception of dambo 2 ( $Ar = 28.73\%$ ). The most important species covered more than 45% of relative dominance (Dr) in the dambos, except in the dambo 2, where *P. aprouneifolia* was the most dominant species, covering 10.65% of the area. With regard to the relative frequency (Fr), *P. nitida*



**Table 1**

Plot size, density, species richness evenness and heterogeneity for each of the dambo sampled in the Niassa National Reserve.

Dambos	Sampling Size (ha)	N <sup>o</sup> of Plot Sampled	Species Richness	N <sup>o</sup> of Trees	D_m <sup>2</sup> m <sup>2</sup> /ha	Hill's N <sub>2</sub>	H
1	1.3	13	31	1012	2.75	5.71	-3.06
2	0.8	8	37	769	6.22	18.12	-1.35
3	0.8	8	36	421	11.87	8.22	-3.14
4	0.9	9	40	1541	17.75	13.42	-1.75
5	1	10	65	859	9.72	16.58	-3.62
6	1	10	47	852	6.68	13.18	-3.72
TOTAL	5.8	58	110	5454	9.17	18.92	-4.27

Hill's N<sub>2</sub> = Reciprocal of Simpson's index of heterogeneity.

H = Hosokawa et al. (2008) evenness index.

**Table - 2**

Vertical and horizontal profile of the three most important species of each dambo sampled in the Niassa National Reserve.

Dambo	Family	Species	Abundance		Dominance		Frequency		% of Tree/Strata			Volume	
			Ab (n)	Ar (%)	Da (m <sup>2</sup> /ha)	Dr (%)	Fb (%)	Fr (%)	Lower	Middle	Upper	m <sup>3</sup> /ha	IVI
1	Proteaceae	<i>Protea nitida</i>	375	37.06	0.17	6.23	77.95	12.36	10.13	89.87	0.00	0.73	55.65
	Myrtaceae	<i>Syzygium guineense</i>	115	11.36	1.31	47.74	46.15	7.32	3.48	79.13	17.39	31.04	66.42
	Annonaceae	<i>Annona senegalensis</i>	104	10.28	0.15	5.28	53.85	8.54	1.85	98.15	0.00	0.37	24.09
2	Apocynaceae	<i>Diplorhynchus condylocarpon</i>	83	10.79	0.14	2.31	87.50	5.98	3.61	96.39	0.00	0.76	19.09
	Euphorbiaceae	<i>Pseudolachnostylis maprouneifolia</i>	77	10.01	0.66	10.63	87.50	5.98	0.00	87.01	12.99	6.10	26.63
	Lamiaceae	<i>Vitex obovata</i>	61	7.93	0.13	2.09	12.50	0.85	0.00	100.00	0.00	0.66	10.88
3	Myrtaceae	<i>Syzygium cordatum</i>	89	21.14	7.87	66.31	62.50	7.35	0.00	51.69	48.31	110.77	94.81
	Annonaceae	<i>Annona senegalensis</i>	82	19.48	0.37	3.09	87.50	10.29	0.00	97.56	2.44	2.57	32.86
	Combretaceae	<i>Combretum psidioides</i>	63	14.96	0.60	5.07	75.00	8.82	0.00	87.30	12.70	0.62	28.86
4	Myrtaceae	<i>Syzygium cordatum</i>	227	14.73	8.56	48.21	77.78	6.36	1.32	32.60	66.08	119.39	69.31
	Euphorbiaceae	<i>Pseudolachnostylis maprouneifolia</i>	161	10.45	0.64	3.63	88.89	6.36	0.00	81.97	18.03	5.98	20.44
	Annonaceae	<i>Annona senegalensis</i>	150	9.73	0.40	2.23	100.00	7.27	0.00	99.33	0.67	4.07	19.24
5	Proteaceae	<i>Protea nitida</i>	118	13.74	0.06	0.58	20.00	1.52	100.00	0.00	0.00	0.22	15.83
	Rubiaceae	<i>Crossopteryx febrifuga</i>	86	10.01	0.26	2.63	60.00	4.55	4.65	89.53	5.81	1.71	17.18
	Myrtaceae	<i>Syzygium cordatum</i>	86	10.01	4.51	46.43	80.00	6.06	0.00	24.42	75.58	62.90	62.50
6	Myrtaceae	<i>Syzygium cordatum</i>	158	18.54	3.73	55.86	90.00	8.91	0.63	50.63	48.73	49.41	83.32
	Annonaceae	<i>Annona senegalensis</i>	108	12.68	0.07	1.11	90.00	8.91	1.85	98.15	0.00	0.36	22.69
	Euphorbiaceae	<i>Margaritaria discoidea</i>	75	8.80	0.34	5.02	10.00	0.99	8.00	90.67	1.33	2.07	14.81
MEAN/TOTAL	8	10	2218	NA	1.67	NA	67.06	NA	7.53	75.24	17.23	22.21	684.61

Note: Absolute (Ab) and relative (Ar) Abundance, Absolute (Ad) and Relative (Dr) Dominance, Absolute (Fa) and Relative (Fr) Frequency, Importance Value. Index (IVI).

was the most frequent species in dambo 1, occurring in 12.36% of the plots assessed, while *V. obovata* in dambo 2, and *Margaritaria discoidea* in dambo 6, were the lowest frequent species, with Fr = 0.85 and Fr = 0.99, respectively. Dambos 1, 2, 3 and 6 presented more than half of all tree species in the middle stratum. In dambo 4, the most important species (*S. cordatum*) represented 66.08% and 32.60% of the trees in the upper and middle strata, respectively. In dambo 5, *P. nitida* corresponded to 100% of the scored individuals in the lower stratum, while *S. cordatum* corresponded to 24.42% in the middle, and 75.58% in the upper stratum. *S. cordatum* presented the highest density of the dambos ecosystem, with 110.77 m<sup>2</sup>/ha, 119.39 m<sup>2</sup>/ha, 62.9 m<sup>2</sup>/ha and 49.41 m<sup>2</sup>/ha in dambos 3, 4, 5 and 6 respectively.

Species abundance was plotted in Principal Component Analysis (PCoA), to assess the main species communities characterizing the surveyed dambos (Fig. 6). One can see that species abundance had a clear influence in the dambos dissimilarities, with roughly four species groups clearly differentiating the surveyed dambos.

The first two axis of the PCoA captured approximately 65% of dambos variation. The data variation captured by the first three axes reached almost 83%. These results indicate that the total variation of the dambos in the NNR can be adequately explained in a two to three-dimensional space. Furthermore, the first PCoA axis appears to represent a humidity gradient, as the permanently humid dambos (3, 4 and 6) are located on the right side of the plot while the temporarily humid dambos are grouped more to the left.

The cluster analysis confirmed the PCoA results. Using species abundance, there were four main groups of dambos, in which dambos 3, 4 and 6 (permanently humid) can be gathered into a single group. The cophenetic correlation was 0.85, revealing the good quality of the cluster analysis. From both ordination and classification analyses one can infer four different groups of dambos, based on species composition and abundance. The PERMANOVA test of the abundance data for the four considered dambos groups, namely group 1 (dambo 1), group 2 (dambo 2), group 3 (dambo 5) and group 4 (dambos 3, 4, and 6), yielded a pseudo-F statistic of 1.0876, with an R<sup>2</sup> of 0.21 and a p-value of 0.42. This means that the difference in dambos represents only 21% of the species composition variation, and the H<sub>0</sub>: no difference between dambos, cannot be rejected due to a non-significant p-value. Accordingly, there was no evidence that species communities are significantly different among dambos.

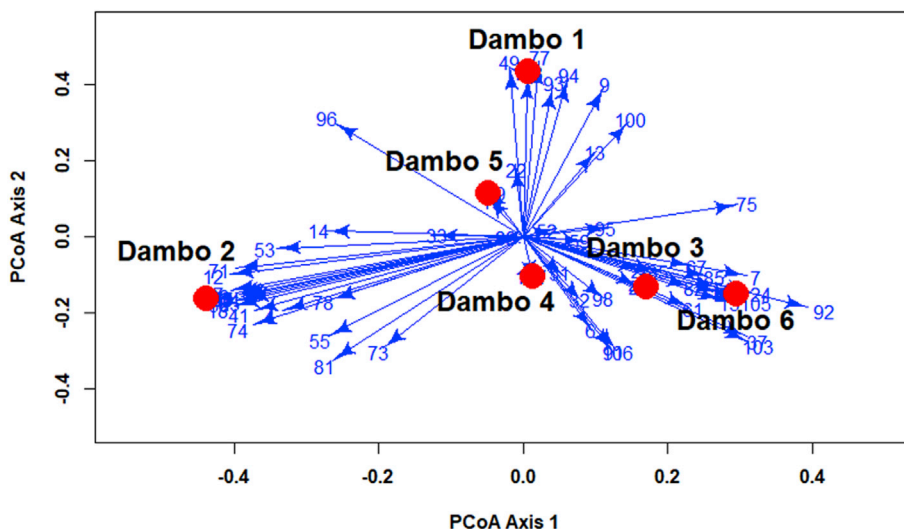


Fig. 6. Principal Coordinates Analysis of the surveyed dambos based on species abundance.

In fact, no indicator species were found for any dambo in particular, as none of the observed species were significantly associated with a specific dambo or combination of dambos (defined by the cluster analysis). Notwithstanding, we did find some indicator species of dambos in general. According to the indicator species analysis, the species *A. senegalensis*, *C. psidioides*, *C. febrifuga*, *D. condylorcarpon*, *P. nitida*, *P. maprouneifolia*, *S. cordatum* and *S. guinensis* presented an indicator value of about 0.67 (95% confidence interval ranges from 0.33 to 1). The species *A. senegalensis*, *C. psidioides*, *C. febrifuga*, *P. nitida*, *P. maprouneifolia* and *S. cordatum* in particular, had an occurrence probability of approximately 83% (95% confidence interval ranges from 0.5 to 1). From these, the species *A. senegalensis*, *C. psidioides*, *C. febrifuga*, *D. condylorcarpon* and *P. maprouneifolia* were expected to be always present in any dambo (occurrence probability of 1 with a 95% confidence level).

#### 4. Discussion

Research on grass vegetation in Mozambican wetland ecosystems are very scarce, which can be either related to the lack of expertise or even resources constraints. However, for the few existing studies, we have observed that, all grass species found in our work were previously reported to occur in Mozambique (Oudtshoorn, 2018). The nine most dominant grass species belonging to the family Poaceae, as well as the soil and climatic conditions where they were reported to occur, are similar to those from the NNR (Oudtshoorn, 2018). Most of those species were also reported to occur in the wetlands of NNR, excluding *Cenchrus ciliaris* and *Aristida junciformis* (Ganzin et al., 2010) and in other related dambo wetland studied elsewhere (Fynn et al., 2015; Mapaure and McCartney, 2001). The average height is also in accordance to previous studies on dambo grasslands (Mapaure and McCartney, 2001; Nyamadzawo et al., 2014; Oudtshoorn, 2018). Most of the dominant species were also important to distinguish the two and five groups of dambos in the heat map. The less dominant grass species (<120 individuals) were evenly distributed in all dambos, and hence did not play an important role to cluster different dambos. Most of the studies conducted in dambos, reported different effects of the grass burning and others related anthropogenic effects in soils, environment and microflora (Nyamadzawo et al., 2015, 2014), but not necessarily on the structure and diversity of the grass species. However, Matayaya et al. (2017), reported a positive correlation between species richness and fire frequency. Although in this study we did not record the burning frequencies and intensity of the different dambos assessed, due to lack of data, we postulate that the same pattern is likely to occur.

The vegetation of NNR is generally described as dry miombo woodland (Ribeiro et al., 2013, 2008), characterized by the dominance of woody species from Fabaceae family (e.g. *Brachystegia spp* and *Julbernardia globiflora*). The dominant vegetation classes vary from dense to open miombo woodlands, with a canopy cover ranging from 80% to 30% (Ganzin et al., 2010). Within these, dambos are particular enclave systems usually found at the bottom of slopes in more humid and more fertile places. They are characterized by wooded grassland to grassland with low trees densities up to 10–20%, dominated by permanent high grass and dispersed small trees, where typical miombo species (e.g. *B. africana*, *P. angolensis* and *S. mada-gascariensis*) are usually present but not mandatory. In fact, dry miombo woodland species are not always dominant and under particular circumstances can even be totally replaced by *Acacia* or *Combretum* species (Ganzin et al., 2010).

Notwithstanding, most of the research concerning species composition in miombo woodland has been conducted as a general overview of this ecosystem, without focusing on specific habitats or vegetation types. As a result, the existing studies present a mixture of all miombo vegetation types, including riparian and wetland vegetation (Banda et al., 2006; Ribeiro et al.,

2013). This study was therefore focused on the dambos system, and the methodology used was adapted to its particularities. The transect procedure employed was focused on the wetland areas, established in a way that could comprise also the gradual transition from grassland to woodland, which enabled understanding of the horizontal structure of the dambo wetlands. The use of transects is considered one of most robust sampling procedures for vegetation communities (Krebs, 2016). The number of plots established in each dambo was proportional to the dambo's dimension. This procedure is commonly used and highly recommended in ecology to find the optimal sampling intensity, before plot establishment, especially for variable counts (Krebs, 2016). In fact, the results show that a more intensive sampling effort would be necessary in further surveys in order to perform a more complete vegetation assessment, especially in dambos 5 and 6 where the species richness appears to be higher, but the slope of rarefaction curves has proved otherwise. In addition, coverage deficit was also higher in the permanent water dambos, where higher species richness is preserved. That is probably related to the fact that the estimated richness is strongly dependent on both sample size and the relative abundances (Olszewski, 2004).

This study showed that the particular habitat characteristics of dambos, such as permanent soils humidity, determine a greater richness in typical wetland species, such as those of the Combretaceae. This pattern is revealed by the importance value of the species present, where the two most important ones, as determined by the species IVI, were *S. cordatum* and *A. senegalensis*, species that are typically found along riverbanks. Moreover, the species *A. senegalensis*, *C. psidioides*, *C. febrifuga*, *P. maprouneifolia* and *D. condylocarpon* are expected, with a high level of confidence, to be present in all dambos and therefore can be considered as indicator species of the dambos ecosystem in general. These species, particularly the first four plus *P. nitida*, are species mostly described to occur in lower land, riverine and wetland areas of the miombo ecoregion (van Wyk and van Wyk, 1997).

Nevertheless, these species are not necessarily common in all areas. For instance, the Combretaceae family is represented by only one species in dambo 3, being the least important in that dambo, while a species of Rubeaceae was sampled in dambo 5 and ranked as the second most important species in that dambo. Ribeiro et al. (2013), sampled a total of 1990 individuals (587 trees ha<sup>-1</sup>) in permanent plots established in the entire NNR, and the 6 most important species, as expressed by IVI, were *Julbernardia globiflora* (IVI = 54), *Diplorhynchus condylocarpon* (IVI = 23), *B. boehmii* (IVI = 22), *P. maprouneifolia* (IVI = 17), *S. birrea* (IVI = 17) and *B. africana* (IVI = 13). As can be seen, only two of these species (*D. condylocarpon* and *P. maprouneifolia*) were found in the dambos surveyed but were considered not very important. Species richness in the northern Mozambican dambos appear also to be higher than in other dambos regions (Dube and Chitiga, 2011; Matayaya et al., 2017).

Regarding the vertical structure of dambos, almost all indicator species were in the middle to upper strata. This result was not surprising, not only because dambos are normally characterized by shrub and small deciduous trees, but also because the tallest trees from other miombo forest sub-types in the plot gradient influence the height and standard deviation of our sample.

The results suggest that human activities do not necessarily affect the structure and diversity of dambos trees and shrub vegetation in the NNR, neither evidences were found on species and richness of grass vegetation. Although dambos 2 and 3 were disturbed by anthropogenic activities such as shifting cultivation, they nonetheless preserved higher diversity and homogeneity. Dambo 2 presents the highest heterogeneity and evenness, while dambo 3 preserves other important characteristics of dambos, such as permanent water and dambo-specific indicator species. This suggestion can also be highlighted by the PERMANOVA results, which, while explaining only 21% of species variation, revealed a non-significant difference among dambos. These results are contrary to what has been reported in other studies, either conducted in dambos (Dube and Chitiga, 2011; Matayaya et al., 2017) or others miombo vegetation types (Madebwe and Madebwe, 2005). Nevertheless, there are also other studies in line with our results. For instance, Banda et al. (2006) analyzed vegetation structure and composition along a protected gradient in miombo woodland and found no difference between protected and non-protected areas. The authors commented that intact protected areas such as National Parks do not necessarily conserve the greatest diversity of tree species or rare species, suggesting that a suite of different types of protection strategies may be the key to conservation of trees in these African dry tropical forests. It is important to highlight that these dambos are located in the most remote protected areas in Africa, far from villages, which hampers their access by local people. As a consequence, disturbance is minimal and likely not enough to affect the structure and composition of dambos. Notwithstanding, fire occurrence in our plots may be a key factor that may have influenced the existence of dry fire-tolerant miombo species, including Fabaceae family, as fires increases the likelihood of shifts from fire intolerant species (e.g. wetland and riparian forest, such as *A. senegalensis* and *C. psidioides*) to more tolerant species (Timberlake and Chidumayo, 2011).

Although we employed a commonly used sampling procedure that is highly recommended, and furthermore considered one of most robust for vegetation communities, according to Fig. 5, sample size appears to have been insufficient. In future studies, sample size should be increased in order to guarantee that, for all the surveyed dambos, the curves of species richness versus sample size approach asymptotic values. However, our study was more focused on continuous variables, where normal distributions can reasonably be expected, and the required sample size is established, based on sample procedures that highlight means and variances quite precisely, which is the case of systematic transect samples. Not surprisingly, this sampling technique shows that patterns found in this study for count variables appear not to have reached the representative sample size, in the case of dambos with high species richness. In the end, sample size can be estimated by knowing the underlying multinomial statistical distribution (Maurer and McGill, 2011), but this is not yet completely ascertained for dambos and reveals the novelty of studying these systems, where methodology is still not yet totally established and requires further investigation.

Furthermore, despite the non-significant results from the PERMANOVA test, the PCoA and cluster results suggest a humidity gradient among dambos, where more humid dambos with permanent water present the most similar vegetation communities. On the contrary, for grass vegetation no consistent patterns can be claimed. In the end, these findings call for a thorough investigation of these ecosystems, in order to ascertain the main factors driving the structure and function of these vegetation communities.

## 5. Conclusions

The conclusions drawn in this research were supported by field data from 6 dambos, representative of the NNR, and subjected to diverse anthropic pressures. Nevertheless, anthropogenic disturbance did not significantly affect the structure and diversity of dambos in the NNR. Therefore, the results of the present study indicate that anthropic pressures are not still significantly influencing the floristic composition of dambos in this region. However, the fairly steep slope of the rarefaction curves suggests that other in-depth sample intensity especially for permanent wet dambos is required in further assessments.

However, patterns of trees and shrub species abundance seem to respond to a humidity gradient among dambos, although there was no statistical support for this difference among dambos. Notwithstanding, the indicator species are quite similar for all dambos: *P. nitida* and *V. obovata* appear to be more frequent in the seasonal water dambos. Furthermore, species richness and tree density were higher in the permanently humid dambos, while heterogeneity and evenness were not different between permanent and seasonal dambos. Overall, evenness and heterogeneity are lower in the dambos ecosystems.

Most of the dominant species, such as *A. senegalensis*, *C. psidioides*, *D. condylocarpon*, *P. nitida*, *S. guineense*, *S. cordatum*, *C. febrifuga* and *P. maprouneifolia*, were more abundant in the lower and middle strata, which may negatively affect the future succession of dambos wetland in the NNR.

Some species are likely to occur in all dambos with a greater probability, therefore may be considered dambos indicator species, namely, *A. senegalensis*, *C. psidioides*, *C. febrifuga*, *P. nitida*, *P. maprouneifolia* and *S. cordatum*.

This research, which was a first approach to dambos ecological assessment in the NNR region, exposes a serious lack of research on the dambos ecosystem, as shown by the absence of survey methodology for these wetlands. Further investigation is needed to better understand the ecology of dambos, the effects of anthropogenic disturbances on these ecosystems and the real effect of protected areas on their conservation.

## Conflicts of interest

Authors declare no competing interests with this manuscript.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00704>.

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