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The size of topographic depressions in a Sahelian savanna is a driver of woody vegetation diversity

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ABSTRACT

In drylands, water availability is the main limiting factor for plant growth. Topographic depressions in the Sahel that reveal a more favorable water balance display greater tree diversity compared to their surroundings. However, the environmental factors that drive differences in botanical composition between depressions remain unknown. Here, we investigated the depression features, and the landscape and connectivity metrics responsible for woody vegetation composition in a savanna of Senegal. We mapped depressions in a 700 km^2 area and inventoried woody vegetation in 61 depressions varying in area. Simple linear models were applied between (i) indicators of richness and botanical composition and (ii) depression attributes, landscape and connectivity metrics. We found that the area of a depression increased species richness. The number of vegetation strata and the presence of a temporary pond also positively influenced species richness. Yet, while large depressions always had high richness, some small depressions did too. We were not able to identify additional factors to explain this diversity between small depressions. In the context of decreasing richness and composition shift observed in the Sahel over recent decades, depressions, as biodiversity hotspots, are key elements in ecosystem functioning. Further studies are needed to understand other potential drivers of species diversity, such as soil water availability.

1. Introduction

Drylands are defined as lands where potential evapotranspiration largely exceeds annual rainfall, with an aridity index of less than 0.65 according to the U.N. Convention to Combat Desertification (Cherlet et al., 2018). Contrary to the widespread public view that drylands are "useless", they actually support greater biodiversity than usually reported, with organisms that show remarkable strategies to cope with disturbances such as drought, grazing and fire (Maestre et al., 2012b; Pennington et al., 2018). In Africa, 41% of the continent's population occupies these drylands (Reynolds et al., 2007), which are of key importance as they provide numerous ecosystem services.

Open savanna with scattered trees and an annual herbaceous stratum constitutes the typical plant formation of the Sahelian drylands. The bioclimatic zone of the Sahel covers the lands that lie south of the Sahara desert and receives between 100 and 700 mm of annual rainfall in one short rainy season lasting 3–4 months (Nicholson, 1995). As rainfall is low and highly variable on a spatial and temporal scale (Nicholson, 2013), water is a strong limiting factor for plant growth in this area. The soil water balance depends on the rainfall pattern and on the interactions between soil properties (texture, bulk density, organic matter) and slope (Austin et al., 2004; Whitford and Duval, 2020). As a result, Sahelian vegetation often forms a two-phase vegetation mosaic with vegetation patches separated by (almost) bare soil. A well-known and studied example is the "tiger bush" vegetation found in many Sahelian ecosystems (Axelsson and Hanan, 2017; Lefever and Lejeune, 1997).

In the Sahelian sylvo-pastoral zone of Senegal (the Ferlo), woody vegetation differs depending on the toposequence, but does not present the same pattern as tiger bush. Woody vegetation is denser at the bottom of slopes as a result of a more favorable water balance (Dendoncker and Vincke, 2020). These valley bottoms (hereafter referred to as topographic depressions) correspond to low elevation sites of toposequences,

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displaying a difference in elevation of several meters compared to their surroundings. They usually cover areas of approximately a thousand square meters to a few hectares (Fig. 1). These sites are particularly important for the ecosystem. Indeed, although the botanical composition varies between depressions, they host greater species richness than slopes and hilltops (Dendoncker and Vincke, 2020). They can also be a refuge for species during years with longer intervals between rainfall periods, because the soil remains moist for a longer period compared to the upper parts of the relief (Tybirk, 1991). Moreover, the presence of woody vegetation enhances other biological communities, such as soil microbial communities, due to the creation of favorable habitats by accumulating water and nutrients (Ochoa-Hueso et al., 2018). These depressions can therefore be compared to "fertility islands" (Schlesinger William et al., 1990). Such areas have been identified as a key determinant for ecosystem functioning (Ochoa-Hueso et al., 2018) playing, in addition, an important role in the connectivity of vegetation within the landscape.

Indeed, numerous ecological processes can be explained by connectivity in drylands (Okin et al., 2015). Connectivity is defined by Peters et al. (2008) as the "redistribution of material, energy, and information flow within and among spatial units". The landscape can be seen as a network with depressions representing the nodes and hilltops being the links between nodes. Each depression acts as a biodiversity reservoir with species dispersion being ensured by dispersal agents, such as animals and wind, toward the nearby/connected depressions (Messier et al., 2019). Furthermore, a recolonization of hilltops may occur during periods with sufficient rainfall. In addition to landscape features, environmental filters that favor or hinder the establishment of certain woody species from the regional species pool also influence the assembly of local communities. In African savannas, such abiotic and biotic filters are livestock grazing, fire and selective tree cutting (Breman and Kessler, 1995; Sankaran et al., 2005).

In the West African Sahel, specifically in Senegal, many studies have reported a decrease in plant species diversity since the great drought of the 1970s–1980s (Gonzalez, 2001; Gonzalez et al., 2012; Vincke et al., 2010; Wezel and Lykke, 2006). Some research has also reported a decrease in tree density (Gonzalez et al., 2012; Vincke et al., 2010), sometimes followed by a recovery (Dendoncker et al., 2020; Hiernaux et al., 2009). As species richness is a major driver of dryland multifunctionality (Maestre et al., 2012a), it is crucial to preserve this biodiversity to mitigate the negative impacts that increasing aridity (induced by climate change) will have on ecosystem processes (Berdugo et al., 2020). By identifying drivers of botanical composition and species richness between depressions, it will be possible to more effectively account for these depressions in restoration and management plans.

Here, we investigated some environmental factors that drive the botanical composition and species richness of woody communities in topographic depressions located within a 700 km^2 area in the Sahelian sylvo-pastoral zone of Senegal. First, we put forward the hypothesis that the surface area of the depressions is the main driver explaining species richness and we conducted botanical surveys in depressions of different sizes. Second, we studied the impact of other drivers that might explain the difference in species richness and botanical composition observed between depressions. The factors considered here were (i) depression attributes (area, number of woody vegetation strata, mean woody density, position in the landscape, presence of a temporary pond), (ii) landscape metrics (distance from pastoral camps) and (iii) connectivity metrics (distance between depressions, number of nearby depressions, average areas of the nearby depressions).

2. Materials and methods

2.1. Study area

Our study area is located in the sylvo-pastoral zone of Senegal, the Ferlo, in a 15 km-radius circle around the borehole of Widou Thiengoly (15.99° N, 15.32° W). The area has a typical Sahelian climate with a short rainy season from July to September (the mean annual rainfall in Widou between 1940 and 2015 was 297 ± 87.5 mm) followed by a long dry season. The land use is mainly sylvo-pastoral, as low rainfall hinders agriculture. To cope with the highly variables resources, pastoralists mainly rely on livestock mobility.

The major landform is composed of an alternation of sand dunes and plains. The dunes measure 10–30 m in height, 20–50 km in length and 0.5–5 km in width. They are separated by longitudinal plains of 1–5 km in width (Le Houérou, 1989). Soils are predominantly sandy. Ferruginous tropical soils (in the French classification) or ferralic arenosols (in the World Reference Base for Soil Resources) are found on the dunes, while subarid red and brown red soils (Brunic arenosols) are predominant in the plains (Jones et al., 2013). These two types of soils have a low organic matter content, but slightly higher in the subarid brown soils (1–4%) than in the ferruginous tropical soils (0.2–0.5%; Charreau and Fauck, 1965).

In each relief element (dunes and plains), local topography variations form toposequences (hilltops, slopes, valley bottoms). The different topographic positions along a toposequence present a contrasting water balance, due to the difference in soil fine element contents (such as clay and fine silt) and run-off inflows. Available water is greater

Fig. 1. A depression near Widou Thiengoly in which a temporary pond is formed during the rainy season. The right-hand photo shows the extent of the temporary pond (white dashed line).

downslope (in depressions) because of the soil texture (more clay and silts), water input from run-off (Cornet, 1976) and a better soil water retention capacity due to greater litter input, which increases soil organic carbon content (Ellison and Speranza, 2020). Depressions are encountered in both relief elements (dunes and plains) but are more frequent in plains. Moreover, during the rainy season, temporary ponds form inside some depressions of the plains as the soils contain more clay. These ponds do not occupy the whole area of a depression, only the lower part (Fig. 1).

2.2. Depression mapping and field inventory

We manually mapped the depressions (more than 8000 in total) in the study area using Bing map images (Fig. 2). Depressions were identified based on their high woody cover (Dendoncker and Vincke, 2020) and not on their difference in elevation. Two densely covered spots were considered as two different depressions if the distance between the outer limits was more than 50 m. We classed these depressions in five categories. First, we split them into three groups based on their area (small <1 ha, average from 1 to 3 ha and large >3 ha, Fig. 2) using a Jenks Natural Breaks Classification in ArcGIS (ESRI Inc., Version 10.6). Then, within each group, we differentiated between depressions according to the landform, i.e. their location on dunes or in plains. As large depressions were only found in plains, we eventually formed five groups: small depressions in plains, small on dunes, average in plains, average on dunes, and large in plains. Within each category, we randomly sampled 10 to 20 depressions to be inventoried. However, due to time constraints we could not visit all of them. In May 2021, we inventoried woody vegetation in 61 depressions, varying in area from 0.1 ha to 5.3 ha: 8 large depressions (in plains), 25 average (19 in plains, 6 on dunes) and 28 small (17 in plains, 11 on dunes).

In each depression, species of adult individuals were recorded along a transect that crossed the depression lengthwise. A Braun-Blanquet cover score was attributed to each species according to its percentage of cover (Braun-Blanquet, 1932). We also counted all the individuals in one to three circular plots 14.1 m in radius (0.062 ha), one plot in small depressions, two and three plots for average and large depressions, respectively. We also recorded the number and types of vegetation strata present within the depression (shrub, bush and tree strata, based on morphology) and whether a temporary pond was formed during the rainy season.

2.3. Explaining species composition, species richness and density

2.3.1. Botanical composition

Based on the Braun-Blanquet cover scores, we obtained a matrix of species relative abundances in the inventoried depressions. A Bray-Curtis botanical dissimilarity matrix was calculated from the matrix of species abundances. We then proceeded with non-metric multidimensional scaling (NMDS) to visualize surveys within a two-dimensional space according to their botanical composition.

Three additional types of information were gathered to characterize the ecology of the inventoried species. First, we classified species based on their exclusive presence in depressions, as opposed to a presence in all local topography positions. To determine this feature, we retrieved species frequencies in 43 plots located in depressions from the inventory of Dendoncker and Vincke (2020) carried out in 2015 in the same area, which included hilltops and depressions. Based on these inventories, we specified for each species whether it was exclusively encountered in depressions in 2015. These species are hereafter referred to as "depression-specific". Second, we retrieved species frequencies from a subset of 278 surveys from the Flotrop database (Taugourdeau et al., 2019) located in the same area and dating from the 1970s–1980s (see Dendoncker et al., 2020 for details about these surveys) to see whether the inventoried species were abundant in the study area at that time. Third, using Arbonnier (2019), we noted the species biogeographical affinity. These affinities were converted into mean annual rainfall requirements based on the climatic zones of West Africa (Sahelian zone: 250–500 mm; Sudano-sahelian: 500–900 mm; Sudanian: 900–1100 mm; Guinean: above 1100 mm). The plant nomenclature followed the World Checklist of Vascular Plants (WCVP; POWO, 2022).

To explain species positions on the NMDS, we tested species axis coordinates according to (i) their exclusive presence in depressions using the Wilcoxon rank test and (ii) their Flotrop frequencies using

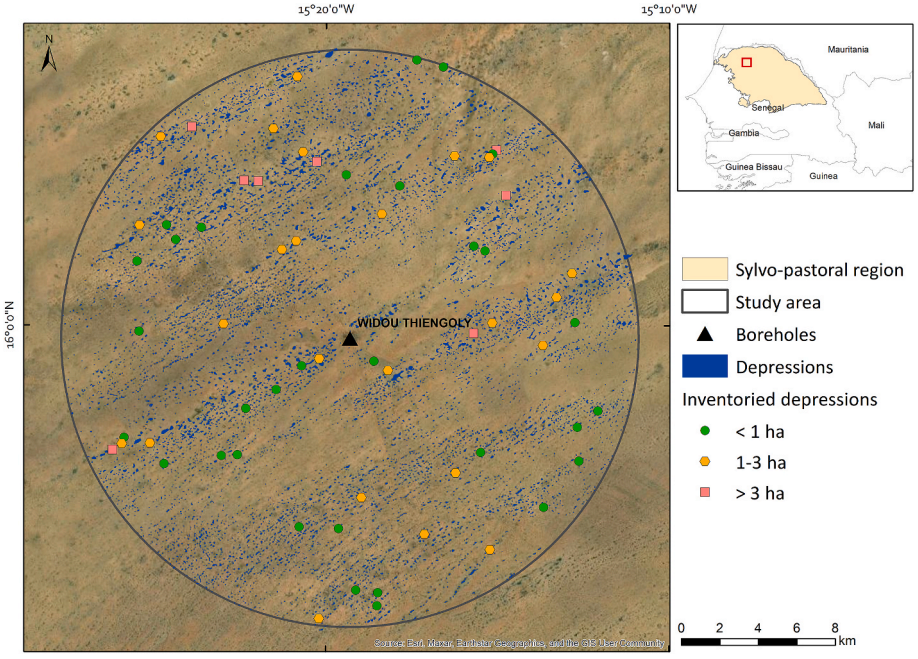

Fig. 2. Depressions in the study area and location of the 61 inventory sites.

linear regression. To further characterize the "depression-specific" species compared to other species, we looked at their mean annual rainfall requirements, their frequencies in our surveys (2021) and in the Flotrop database (1970–1980).

2.3.2. Depression attributes and landscape metrics

From the inventory and mapping, we directly derived the following attributes for each depression inventoried: (i) its area, (ii) the number of woody vegetation strata, (iii) the mean density of woody individuals derived from the circular plots, (iv) its position on a dune versus in a plain, (v) the presence of a temporary pond.

The immediate neighborhood of the inventoried depressions was also characterized using six metrics. The first two were "landscape metrics": (i) the distance from the nearest pastoral camp (Dendoncker and Vincke, 2020) and (ii) the distance from the nearest borehole. These two metrics are proxy for human (pastoral) activity assuming that livestock impacts are more intense near large water points (boreholes) and that wood and other non-woody product collection is more frequent near pastoral camps.

The other four metrics were "connectivity metrics", which characterized the structural connectivity of the inventoried depressions. Indeed, in fragmented habitats the connectivity between the different habitats is a major process in the dispersion and the survival of species (Kindlmann and Burel, 2008). We considered: (iii) the distance from the nearest depression; (iv) the number of depressions located within a 500 m radius; (v) the mean distance between all the depressions in a 500 m radius; (vi) the average area of all the depressions located within this 500 m radius. The 500 m distance was chosen based on expert knowledge to represent an average distance for seed dispersal. We considered that two depressions less than 500 m from each other had the capacity to exchange seeds and were therefore susceptible to influence each other's botanical composition.

2.3.3. Finding drivers of botanical composition and species richness

Depression attributes, landscape metrics and connectivity metrics were tested as explanatory factors for botanical composition, species richness and density. The botanical composition of each inventoried depression was expressed as the coordinates of the depressions on both NMDS axes. Species richness was considered through four indicators: number of species, number of "depression-specific" species, the residuals of a linear regression between the number of species and depression area, and the rarefied species richness. Rarefied species richness represents the expected number of species based on the number of individuals in each sample (i.e. the inventoried depressions; Cayuela et al., 2015). A rarefaction curve was computed using the mobr R package (McGlinn et al., 2021). The analysis of the residuals enabled a search for explanatory variables when the effect of the depression surface area was removed.

We first applied simple linear models between (i) the indicators of botanical composition, species richness and density (y variables) and (ii) the depression features, landscape metrics and connectivity metrics (x variables). In addition to simple linear models, we performed stepwise linear regressions to identify the strongest determinants of botanical composition and species richness pattern. Data were standardized prior to their integration into multiple regressions to allow a comparison between the regression coefficients. To avoid/detect multicollinearity, we computed the Variance Inflation Factors (VIF; Fox and Monette, 1992) for each model. It is commonly assumed that a VIF over three indicates correlations between the regression coefficients and variables have to be removed from the models.

3. Results

3.1. Botanical composition within depressions

We recorded 24 species, belonging to 11 families (Table 1). The two most represented families were the Fabaceae and the Combretaceae represented by five species each, followed by the Malvaceae with three species. Four species were present in more than half of the inventoried depressions: *Balanites aegyptiaca* (L.) Delile (frequency of 96.8%), *Boscia senegalensis* Lam. (71.4%), *Sclerocarya birrea* (A.Rich.) Hochst. (60.3%) and *Vachellia tortilis* (Forssk.) Galasso & Banfi (57.1). The nine rarest species, encountered in less than 10% of the depressions were all "depression-specific".

Table 1
List of the inventoried species sorted by their current frequencies, Fr2021. "Fr2015" gives species frequencies in the data set of Dendoncker and Vincke, 2020 and "Fr_F" frequencies in the FLOTROP historical surveys (Taugourdeau et al., 2019). "Dep-specific" indicates whether the species was only encountered in depressions in the field work of Dendoncker and Vincke (2020). "Mean R" gives the mean annual rainfall under which the species optimally grows.

Species	Code	Family	Dep-specific	Fr2021 (%)	Fr2015 (%)	FRF (%)	Mean R (mm)
Balanites aegyptiaca (L.) Delile	BAA	Zygophyllaceae	No	96.8	79.1	65.8	400
Boscia senegalensis Lam. J.St.-Hil.	BOS	Capparaceae	No	71.4	81.4	66.5	600
Sclerocarya birrea (A.Rich.) Hochst.	SCB	Anacardiaceae	No	60.3	46.5	78.1	800
Vachellia tortilis (Forssk.) Galasso & Banfi	VAT	Fabaceae	No	57.1	37.2	5.8	450
Grewia bicolor Juss.	GRB	Malvaceae	No	36.5	46.5	24.5	800
Feretia apodanthera Delile	FEA	Rubiaceae	Yes	34.9	9.3	2.2	900
Vachellia seyal (Delile) P.J.H.Hurter	VAS	Fabaceae	Yes	31.7	25.6	14.4	900
Senegalia senegal (L.) Britton	SES	Fabaceae	No	30.2	11.6	27	400
Ziziphus mauritiana Lam.	ZIM	Rhamnaceae	Yes	30.2	11.9	4.3	800
Adansonia digitata L.	ADD	Malvaceae	No	27.0	4.6	4.3	700
Calotropis procera (Aiton) W.T.Aiton	CAP	Apocynaceae	No	20.6	44.2	25.5	275
Combretum glutinosum Perr. ex DC.	COG	Combretaceae	No	15.9	11.6	38.5	775
Terminalia leiocarpa (DC.) Baill.	TEL	Combretaceae	Yes	14.3	4.6	1.4	775
Guiera senegalensis J.F.Gmel.	GUS	Combretaceae	No	14.3	16.3	55.4	700
Combretum aculeatum Vent.	COA	Combretaceae	Yes	12.7	2.3	21.9	575
Stereospermum kunthianum Cham.	STK	Bignoniaceae	Yes	9.5	2.3	0.4	1000
Combretum micranthum G.Don	CMI	Combretaceae	Yes	7.9	0	0	350
Vachellia nilotica (L.) P.J.H.Hurter & Mabb.	VAN	Fabaceae	Yes	6.3	6.7	0	700
Dalbergia melanoxylon Guill. & Perr.	DAM	Fabaceae	Yes	6.3	2.3	2.5	900
Loeseneriella africana (Willd.) R.Wilczek	LOA	Celastraceae	Yes	4.8	0	0	1100
Mitragyna inermis (Willd.) Kuntze	MII	Rubiaceae	Yes	4.8	0	1.1	1000
Adenium obesum (Forssk.) Roem. & Schult.	ADO	Apocynaceae	Yes	1.6	2.3	3.2	600
Gymnosporia senegalensis (Lam.) Loes.	GYS	Celastraceae	Yes	1.6	0	0.4	1100
Sterculia setigera Delile	STS	Malvaceae	Yes	1.6	0	8.6	1000

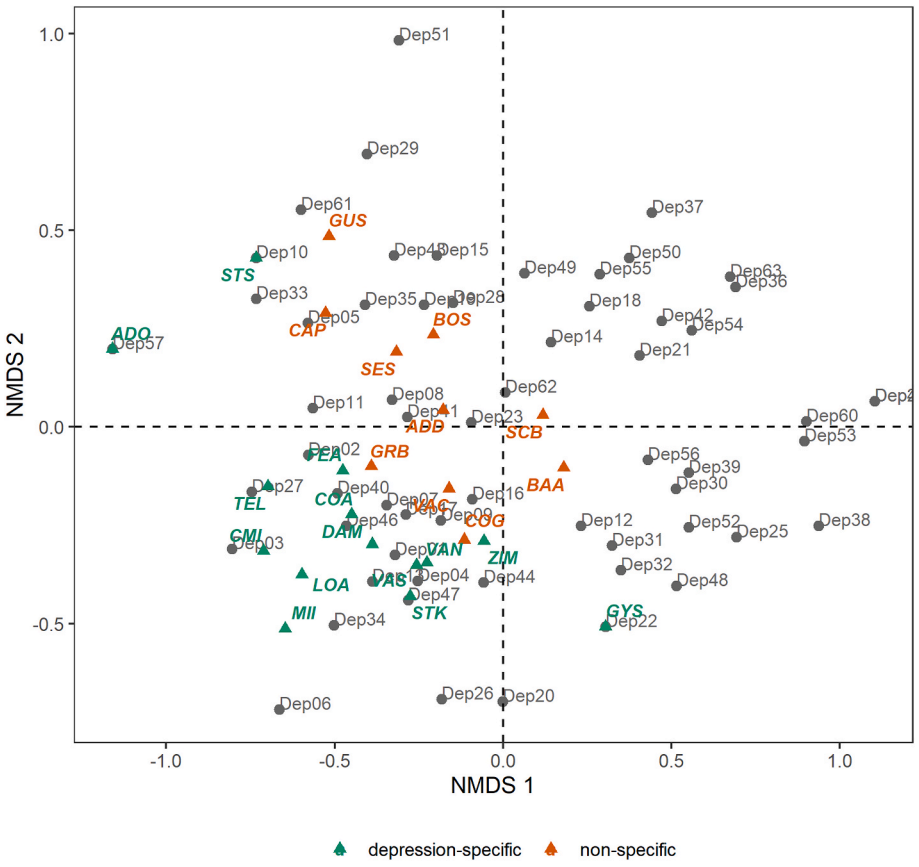

Fig. 3. Non-metric multidimensional scaling (NMDS) representation of the Bray Curtis botanical dissimilarities between botanical surveys. Dark gray circles correspond to the different inventoried depressions. Triangles represent the species with their three-letter code (see Table 1 for the corresponding botanical names): in green, "depression-specific" species; in orange, other species. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The NMDS shows a wide dispersion of the different surveys based on their Bray Curtis dissimilarities (Fig. 3). The majority of the species are on the left side of the NMDS. Depressions on the left side are the ones hosting a larger number of species, as shown by the strong linear relationship between species richness and the first axis of the NMDS (Fig. 5b, $R^2 = 0.75$). On the right side, the surveys present a lower species richness and are characterized by *Balanites aegyptiaca* (BAA) and *Sclerocarya birrea* (SCB).

Both NMDS axes are explained by the depression area ($R^2 = 0.12$ and 0.11, Table 2). The largest depressions are generally in the bottom-left quadrant. The first NMDS axis is also negatively correlated to the number of strata ($R^2 = 0.22$) and weakly to the relief ($R^2 = 0.08$). This means that the depressions on the left side of the NMDS usually present more than one vegetation stratum and are more frequently located in plains.

The bottom-left quadrant also mostly gathers species that are "depression-specific". Indeed, the mean coordinates of these species on the second NMDS axis are significantly different from the mean coordinates of the non-specific species (p-value <0.05, Fig. 4a). The first axis shows the same trend event, though not significant (p-value = 0.056, Fig. 4b).

The depression-specific species had the lowest frequencies in the botanical surveys of 2021 and in the Flotrop database (p-values <0.05, Fig. 4d and e). On the other hand, the species with the highest frequencies in depressions and located on the right side of the NMDS (Fig. 4c), such as *Balanites, Boscia, Sclerocarya* and *Vachellia tortilis* are not depression-specific and can be found in all topographic positions (hilltops, slopes, depressions; Dendoncker and Vincke, 2020).

The rare "depression-specific" species had, on average, a different biogeographic range from the others. Indeed, the mean annual rainfall requirement of the "depression-specific" species (750 mm/year) is significantly different from the mean of the non-specific species (550 mm/year; p-value <0.05; Fig. 4f). The mean annual rainfall requirement of the depression-specific species is more likely to be met within the Sudanian zone (600–1100 mm/year).

3.2. Explaining species richness and botanical composition

The species richness of the inventoried depressions ranged from one to 14 species, with an average of 6.1 (±3.0 standard deviation) species. Simple linear regressions revealed three explanatory factors for the species richness in the inventoried depressions (Fig. 5). The first was the logarithm of the depression area (Fig. 5a, $R^2 = 0.32$): the larger the depression was the more species were present. However, while the largest depressions always displayed high species richness, there was substantial variability between the smallest depressions, with some of them hosting a number of species equivalent to the largest depressions. Of the 28 small depressions inventoried (<1 ha), 11 had more than 6 species; of the 25 average depressions, 15 had at least 6 species and the 8 largest depressions (>3 ha) had at least 8 species. The second factor was the number of strata, albeit weaker, with greater richness in depressions with two or three strata (Fig. 5c, $R^2 = 0.17$). The third factor was the location of the depressions on dunes or in plains, though with a weak R^2 of 0.05, with a higher species richness in the depressions located in plains. The two landscape metrics and the four connectivity metrics did not significantly influence species richness (p-values of linear models >0.05). The regressions on the residuals of the model between specific richness and area revealed no supplementary explanatory variables.

The stepwise regression ($R^2 = 0.45$) also yielded three significant explanatory factors (with VIF under 3), enabling their classification from strongest to weakest: depression area (coefficient of 0.6, p-value <0.001), the presence of a temporary pond (coefficient of −0.59, p-

Table 2
Cross-referenced table of the R^2 of linear models between (i) species richness, botanical composition, density in columns and (ii) the depression features, landscape metrics and connectivity metrics in rows. "ns" indicates that the model is not significant at the alpha level of 5%. In columns: the species richness (SR); the number of "depression-specific" species (SR dep); rarefied richness; the coordinates of the depressions on the two axes of the NMDS (NMDS1 and NMDS2); and the density (D). In brackets, the signs "+" and "-" indicate whether the slope of the regression is positive or negative.

	SR	SR dep	Rarefied richness	NMDS1	NMDS2	D
Depression features						
Logarithm of area	0.32 (+)	0.21 (+)	0.79 (+)	0.12 (−)	0.11 (−)	ns
Number of strata	0.17 (+)	ns	0.29 (+)	0.22 (−)	ns	0.17 (+)
Density	ns	ns	–	ns	ns	–
NMDS1	0.75 (−)	0.40 (−)	0.17 (−)	–	–	ns
NMDS2	0.06 (−)	0.30 (−)	ns	–	–	ns
Temporary pond (yes)	ns	ns	0.18 (+)	ns	ns	0.05
Relief (plains)	0.05	0.11	0.16 (+)	0.08	ns	ns
Landscape metrics						
Distance from the nearest borehole	ns	ns	ns	ns	ns	ns
Distance from the nearest camp	ns	ns	ns	ns	ns	0.12 (+)
Connectivity metrics						
Distance from the nearest depression	ns	ns	0.07 (+)	ns	ns	ns
Number of depressions within a 500 m radius	ns	ns	ns	ns	ns	ns
Mean area of the depressions within a 500 m radius	ns	ns	0.18 (+)	ns	ns	ns
Mean distance between all depressions within a 500m radius	ns	ns	ns	ns	ns	ns

value<0.05) and the number of strata (coefficient of 0.26, p-value <0.05). The discrepancy between the simple linear model and the stepwise regression regarding the explanatory variables of relief (in simple linear) and the temporary pond (in stepwise) was only apparent. Indeed, these two variables were correlated since temporary ponds only formed in depressions in the plains.

The linear regressions on the rarefied species richness showed a positive effect for the logarithm of the depression area ($R^2 = 0.79$, Table 2), the number of strata ($R^2 = 0.29$), the presence of a temporary pond ($R^2 = 0.18$), the relief ($R^2 = 0.16$) and the mean area of the depression within a 500 m radius ($R^2 = 0.18$). It also pointed to the distance from the nearest depression as an explanatory factor, albeit displaying a weak determination coefficient ($R^2 = 0.07$) and not ecologically explained. The stepwise regression ($R^2 = 0.87$, Table 3) revealed that the strongest determinant of rarefied richness was the area (estimated coefficient 0.75), followed by the presence of a temporary pond (coefficient of 0.26) and the number of strata (coefficient of 0.18). The distance from the nearest camp was also retained by the stepwise regression with a coefficient of 0.14.

The number of "depression-specific" species was positively correlated to the area of the depressions ($R^2 = 0.21$, Table 2). We found a similar phenomenon to that for species richness: the larger depressions always had high "depression-specific" richness, whereas the smaller ones could exhibit either low or high "depression-specific" richness (result not shown). The number of "depressions specific" species was also slightly explained by the location of the depressions on dunes or in plains ($R^2 = 0.11$) with higher "depression-specific" richness encountered in plains. The stepwise regression ($R^2 = 0.33$) indicated that the area of the depression was the most important factor (coefficient of 0.54, p-value <0.001) compared to relief (coefficient of 0.46, but not significant).

Botanical composition, expressed by the species coordinates on the first NMDS axis, was firstly influenced by the number of strata (p-value <0.001), secondly by the depressions area (p-value <0.01) and thirdly by the number of depressions within 500 m (p-value <0.01). The determination coefficient of the stepwise regression was 0.37. The stepwise regression for the second NMDS axis only revealed the distance from the nearest borehole as a significant explanatory factor, though with a weak determination coefficient of 0.05. An additional result was the strong relationship observed between the depressions coordinates on the first NMDS axis and the residuals of the model between specific richness and area (Fig. 5e, $R^2 = 0.63$). This indicated a link between species richness and botanical composition, which was not entirely explained by the depression area.

Finally, tree density was slightly linked to the number of vegetation strata in the depressions (Fig. 5d, $R^2 = 0.17$). Depressions presenting two or three strata had a higher density than depressions with one stratum. An increase in the distance from the nearest camp also led to higher densities ($R^2 = 0.12$). Finally, the presence of a temporary pond also weakly impacted density ($R^2 = 0.05$), with a higher density in depressions that turned into temporary ponds during the rainy season.

4. Discussion and conclusion

4.1. Depressions as biodiversity hotspots in the landscape

We mapped more than 8000 topographic depressions within an area of more than 700 km^2 (15 km-radius circle) and conducted botanical surveys of the woody vegetation in 61 of them, presenting a wide range of surface areas (between 0.1 ha and 5.3 ha). We recorded 24 woody species belonging to 11 families. This number was similar to that found by Dendoncker and Vincke (2020) in a nearby area (Widou Thiengoly and Tessékéré boreholes). The most frequent species were *Balanites aegyptiaca, Boscia senegalensis, Sclerocarya birrea* and *Vachellia tortilis*, which were found in more than half of the depressions inventoried. Of the 24 species, 13 were "depression-specific", meaning they were exclusively found in depressions and were absent from hilltops and slopes (Dendoncker and Vincke, 2020). In an area of the North Ferlo, Poupon (1980) found that *Balanites aegyptiaca* was not frequent in depressions, which contrasts somewhat with the large frequency of this species present in 96.8% of our surveys.

Species exclusively found in depressions in recent inventories (Dendoncker and Vincke, 2020, "depression-specific"), were less frequent in our surveys. They differ from other species by their biogeographic affinities. Indeed, according to Arbonnier (2019), the distribution area of these species mostly covers the Sahel-Sudanian zone (mean annual rainfall of 700 mm) and the Sudanian zone (mean annual rainfall of 1000 mm). On the other hand, species found in all topographic positions are species requiring annual rainfall between 200 and 500 m, which is typically encountered in the Sahelian zone *sensu stricto*. Topographic depressions offer higher water availability than slopes and hilltops (Cornet, 1976), which enables species with higher water requirements to survive in the Sahelian zone. Depressions can thus be considered as a specific habitat within a fragmented landscape.

The presence and the number of these "depression-specific" species in a depression explained a significant share of its total species richness

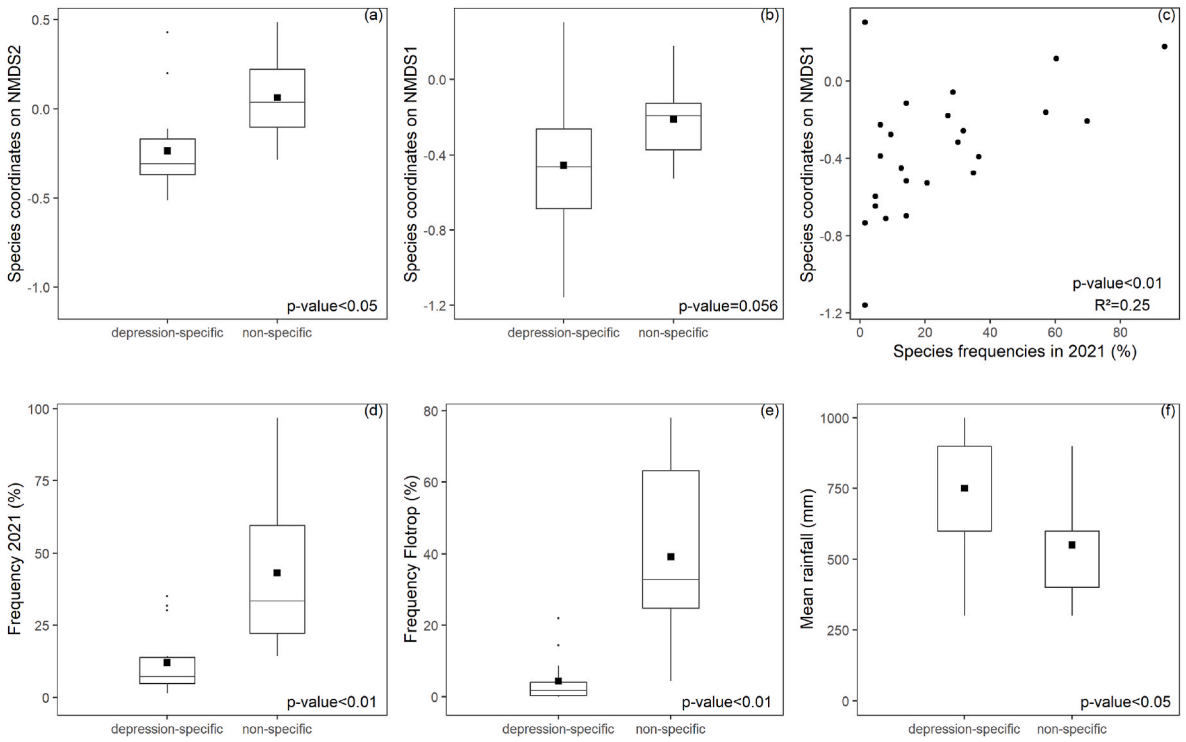

Fig. 4. Relationships between the species coordinates on the NMDS, species frequencies (in the dataset and the FLOTROP historical dataset) and the fact that the species were only found in a depression ("depression-specific" vs "non-specific"). P-values at the bottom right of the panels (a-b-d-e-f) come from Wilcoxon rank tests and the annotations in panel (c) give the adjusted R^2 for the linear regression and p-value for the coefficient "species frequencies in 2021".

($R^2 = 0.65$; linear regression between species richness and number of "depression-specific" species; result not shown). Indeed, the depressions with the highest species richness also hosted the largest number of "depression-specific" species. Studying species richness in depressions therefore mainly amounts to studying the number of "depression-specific" species. This differentiation of woody communities according to landforms and toposequences is encountered in other savanna ecosystems in Africa (Axelsson and Hanan, 2017; Coughenour and Ellis, 1993).

4.2. *Explaining species richness and botanical composition*

We tested the influence of five depression features, two landscape metrics and four connectivity metrics on the botanical composition, species richness and tree density of the 61 inventoried depressions.

Of the depression features and the landscape and connectivity metrics tested as explanatory variables for species richness, the strongest determinant was the depression area. Large depressions always had high species richness (and a large number of "depression-specific" species). An interesting observation was that some of the small depressions were also diversity hotspots, to the same degree as the large ones. However, we were not able to identify factors that might explain the species richness variability observed between the smallest depressions. Indeed, analyses of the residuals of the model between species richness and depression area did not reveal any significant drivers.

Other explanatory factors of species richness, albeit with a weaker effect, were the relief or the temporary pond (according to a simple regression versus a stepwise multiple regression) and the number of strata. It is important to note that there is a correlation firstly between relief and temporary pond and secondly between relief, depression area and the connectivity metrics. Indeed, temporary ponds only form in the depressions located in plains and the largest depressions are also located in plains. In addition, the frequency of depressions is higher in plains than on dunes. It is therefore difficult to disentangle the effect of these factors on species richness.

Finally, we found a non-significant effect of the distances from camps and boreholes on species richness, and a small positive effect of camp distance on density. These results are partially in line with the work of Dendoncker and Vincke (2020), who found no effect of borehole distances on woody vegetation density and species richness for plots located on hilltops and in depressions in the same study area. Other studies showed that the distance from boreholes had a negative effect (Vincke et al., 2010), or a positive effect, on the overall vegetation (Rasmussen et al., 2018).

To explain this variation in species richness between small depressions, we can make several assumptions. Our first hypothesis is a difference in soil water availability between depressions, a variable that we did not measure. Differences in soil water availability could lead to different species assembly (Méndez-Toribio et al., 2020). In this work, relief location and temporary pond formation could be seen as proxy indicators of water availability, as the soil in plains contains more clay and has a higher organic matter content compared to dune soil. However, a more precise assessment of soil water availability and associated variables (soil properties, rooting strategies, water fluxes, slope and depths of topographic depression, etc.) could be enlightening. To our knowledge, there have been no studies assessing water availability among depressions in drylands, as studies often focus on assessing this parameter along toposequences (Cornet, 1976, 1992; Veste et al., 2008).

A second hypothesis is that rare species could be old trees, remnants from the wet period of the 1950s–1960s and their presence could therefore not be explained by current environmental conditions. They could have survived the drought of the 1970–1980s in depressions as wetter refuge zones, but may be unable to regenerate under the current climatic conditions combined with grazing pressure. Indeed, no regeneration of species such as *Stereospermum kunthianum*, *Dalbergia melanoxylon*, *Vachellia nilotica, Mitragyna inermis* and *Sterculia setigera* was found in the same area in 2015 (Dendoncker and Vincke, 2020).

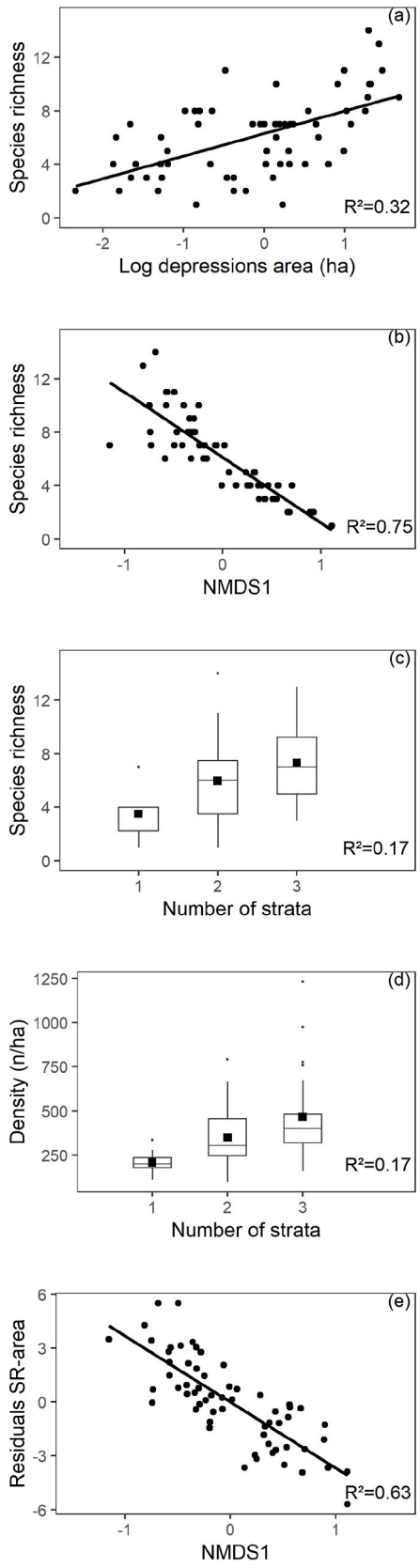

Fig. 5. (a-b-c) Relationships between species richness and: (a) the area of the depressions; (b) the first axis of the NMDS; (c) the number of vegetation strata. (d) Relationship between density and the number of strata. (e) Relationship between the residuals of the model number of species-area and the first axis of the NMDS. All models are significant (p-values <0.05).

Depressions can be seen as witnesses of the ecological memory of the landscape. A final hypothesis is that stochastic effects play a significant role in species distribution and assembly among depressions, as some authors suggest that stochastic effects are the main driver of community assemblage (Hubbell, 2005).

Overall, the studied indicators of species richness (number of species, number of "depression-specific" species and rarefied richness) were found to be more influenced by the depression features (area, presence of a temporary pond, relief location and number of strata) than by the landscape and connectivity metrics. This result highlights the need to better understand some of these depression features, such as water availability. The connectivity and landscape metrics seemed rather to influence the variation in botanical composition between depressions (expressed by the species axis coordinates on the NMDS), albeit to a lesser extent than depression features.

4.3. *Depressions as targets for management*

Topographic depressions play an important role in pastoral land-use systems: firstly as a water source for livestock during the rainy season and the beginning of the dry season with the creation of temporary ponds; secondly, as a fodder reserve given the higher density of woody vegetation; thirdly, as places to rest in the shade of tall trees, for livestock and herders. Depressions also play a role in greenhouse gas balances (N_2O, NH_4, CO_2) in pastoral ecosystems (Assouma et al., 2017). Finally, the high density of trees in depressions reinforces the effects of woody vegetation on ecosystem functioning, such as increased water infiltration, enhanced soil quality and fertility, changes in microclimate, and the positive influence on regeneration (Akpo et al., 2005; Barbier et al., 2014; Bargués Tobella et al., 2014; Diallo et al., 2017).

In this study, we also showed that depressions are biodiversity hotspots. This further highlights their importance in ecosystem functioning, particularly in a context of the decreasing trend in species richness and changes in species composition observed in the Sahel in recent decades (Dendoncker et al., 2020; Gonzalez, 2001; Gonzalez et al., 2012; Hänke et al., 2016; Wezel and Lykke, 2006). Yet, not all depressions contribute in the same way to this biodiversity role. We identified their area, the number of strata and their position in the relief as explanatory factors for species richness.

Nevertheless, our study has certain limitations and there are probably additional factors, not tested in this research, that influence species richness and botanical composition. In addition to the variation in water availability between depressions, which could be viewed through several indicators as discussed in section 4.2, functional traits related to dispersion could also provide some information about the ability of species to disperse throughout the landscape and/or their capacity to form persistent seed banks. Indeed, Sahel species display various dissemination modes, such as anemochory (e.g. *Calotropis procera, Combretum* sp., *Senegalia senegal*), zoochory (e.g. *Boscia senegalensis, Balanites aegyptiaca, Vachellia tortilis, Senegalia senegal*) and barochory (e.g. *Sclerocarya birrea*; Tybirk, 1991). Another limitation of our study was the mapping of depressions, which could benefit from improvement as it was carried out by hand. Indeed, the landscape and connectivity metrics were directly derived from this cartography. Finally, future research could also apply a network approach through an analysis of landscape connectivity, which could help in understanding how depressions are connected and how this diversity could travel through landscapes (Craven et al., 2016). This kind of approach can be used to evaluate landscape resilience (Messier et al., 2019).

Even so, our study offers the advantage of covering an area not much studied in the field of community ecology and which was greatly impacted by severe droughts in the 1970s–1980s. We also inventoried a large variety of depressions and tested multiple factors as drivers of species richness and botanical composition. In a dryland management context, strengthening landscape resilience should be a goal. Restoration work should take into account the ecological processes related to

Table 3
Results of the stepwise regressions for the three indicators of richness (species richness, "depression-specific" richness, rarefied richness) and the two indicators of botanical composition (depression coordinates on the two NMDS axes).

Y variables and R^2	X variables	Estimated coefficient	p-values
Species richness $R^2 = 0.47$	Intercept	0.125	ns
	Area	0.601	<0.001
	Temporary pond (yes)	0.589	<0.05
	Number of strata	0.260	<0.05
"Depression-specific" richness $R^2 = 0.34$	Intercept	−0.237	ns
	Area	0.544	<0.001
	Relief (plain)	0.459	0.080 (ns)
	Temporary pond (yes)	−0.441	ns
Rarefied species richness $R^2 = 0.87$	Intercept	−0.188	<0.05
	Area	0.750	<0.001
	Temporary pond (yes)	0.264	<0.05
	Number of strata	0.178	<0.01
	Distance from the nearest camp	0.138	<0.01
	Relief (plain)	0.183	ns
NMDS1 $R^2 = 0.37$	Intercept	−0.105	ns
	Number of strata	−0.427	<0.001
	Area	−0.335	<0.01
	Number of depressions within a 500 m radius	−0.307	<0.01
	Temporary pond (yes)	0.49	0.074 (ns)
NMDS2 $R^2 = 0.05$	Intercept	$-7.25*10^{-17}$	ns
	Distance from the nearest borehole	0.265	<0.05

topographic depressions as an essential feature in the system, given their higher water availability (Davies et al., 2016; Siyum, 2020). This would mean upscaling reforestation initiatives from local to landscape, by considering ecological processes related to fertility islands and functional connectivity (Ellison and Speranza, 2020).

CRediT authorship contribution statement

Morgane Dendoncker: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Visualization. **Caroline Vincke:** Conceptualization, Writing – review & editing, Supervision. **Samantha Bazan:** Methodology, Writing – review & editing. **Mady Parfait Noé Madingou:** Investigation. **Simon Taugourdeau:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Visualization, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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