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An Assessment of Multiple Drivers Determining Woody Species Composition and Structure: A Case Study from the Kalahari, Botswana

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Abstract: Savannas are extremely important socio-economic landscapes, with pastoralist societies relying on these ecosystems to sustain their livelihoods and economy. Globally, there is an increase of woody vegetation in these ecosystems, degrading the potential of these multi-functional landscapes to sustain societies and wildlife. Several mechanisms have been invoked to explain the processes responsible for woody vegetation composition; however, these are often investigated separately at scales not best suited to land-managers, thereby impeding the evaluation of their relative importance. We ran six transects at 15 sites along the Kalahari transect, collecting data on species identity, diversity, and abundance. We used Poisson and Tobit regression models to investigate the relationship among woody vegetation, precipitation, grazing, borehole density, and fire. We identified 44 species across 78 transects, with the highest species richness and abundance occurring at Kuke (middle of the rainfall gradient). Precipitation was the most important environmental variable across all species and various morphological groups, while increased borehole density and livestock resulted in lower bipinnate species abundance, contradicting the consensus that these managed features increase the presence of such species. Rotating cattle between boreholes subsequently reduces the impact of trampling and grazing on the soil and maintains and/or reduces woody vegetation abundance.

Keywords: conservation; fire; grazing; savanna; woody vegetation

1. Introduction

Unprecedented changes in climate, urbanization, and economic development are increasing the pressures that societies are enforcing on ecosystems [1]. Developing sustainable ecosystem services is subsequently a priority for conservation management, with savanna ecosystems a landscape of primary concern. Savannas are mixed plant communities comprised of grasses and woody vegetation that cover approximately a quarter of the Earth's land surface, including roughly half of the African continent [2]. Savannas are an extremely important socio-economic landscape in Africa, with over 80% of savanna land used to raise livestock [3], underpinning the economic stability of many countries [4,5]. The dynamic nature of savannas means they are susceptible to changes, particularly shifts in plant community composition associated with an increase in woody vegetation [6,7]. A particularly concerning aspect of this increased density of woody vegetation is the reduction of grasses and herbs by encroaching woody

species. These negative impacts are occurring at an increasingly frequent rate worldwide [8–10], which is a major threat to the ecosystem stewardship of these economically important landscapes.

The transition of savanna ecosystems to open shrubland across Botswana, and in particular the western part of the Kalahari, presents a considerable threat to the conservation of the economically important ranching industry. In order to develop adaptive management strategies, the underlying environmental drivers of woody vegetation species need to be better understood. By understanding the environmental drivers responsible for the diversity and abundance of woody vegetation, we can develop predictive models to identify 'high-risk' areas, and provide managers, farmers, and governments with decision support across savanna landscapes. Previous research addressing the ecological processes responsible for the observed vegetation patterns have often found conflicting results regarding the importance and significance of these environmental drivers [11–15], thus limiting the use of this knowledge as the basis for decision-making at a landscape scale. These differences will be discussed below in the context of savanna ecosystems.

1.1. Precipitation

Rainfall affects water availability, and this factor has been described as the most important determinant describing woody vegetation communities, particularly as it limits the amount of primary productivity within an area [16–20]. For example, in a continental study of African savannas, Sankaran et al. [16] identified that woody cover increased linearly with mean annual precipitation (MAP) above 150 mm until maximum woody cover was reached at 650 mm. Similarly, in a pot experiment studying the growth of *Acacia* (new *Senegalia* and *Vachellia* classifications) species, Kraaij and Ward [19] found that rainfall frequency was the most important factor affecting both germination and survival of seedlings. Joubert et al. [21] also found that at least two successive seasons of favorable rainfall was required for seed recruitment in *Senegalia mellifera*. While precipitation intensities [22], season lengths [23], and interactions with other factors (e.g., grazing [24]) all influence woody vegetation cover, the consensus is that MAP is the primary factor contributing to woody vegetation cover [10,16–20].

1.2. Grazing

The influence of grazing pressure as a driver for increased woody vegetation cover is a long established theory. Walter's [25] two-layered hypothesis proposes that in savannas, grasses dominate the top-most soil layers, while tree roots dominate lower layers. When grazing removes the grass cover, tree roots begin to dominate the upper layers and prevent the grasses from reestablishing. Studies have proven inconclusive for the two-layer hypothesis, finding evidence both in support [26–28] and in opposition [29–31]; however, while this theory is still accepted, the current consensus is that this hypothesis is too simplistic to represent the complex dynamic savanna processes [17].

1.3. Trampling

Another explanation for the increased abundance of woody vegetation is the effect of trampling. Trampling from the high frequency and density of pastoral farming causes significant declines in cyanobacterial soil crust [32,33]. Savannas are characterized by low soil nutrient content [34–36], although many areas have biological soil crusts that increase soil surface stability, thereby reducing nutrient loss by erosion and atmospheric nitrogen fixation [33]. Studies have found that the soil crust is greatly influenced by this pastoral trampling within 2 to 8 km of boreholes [37], and that *Acacia* (new *Senegalia* and *Vachellia* classifications) species are often found in higher abundances within areas closer to boreholes, due to their low palatability and the positive species-specific association between canopy and soil crust development [38]. Boreholes are narrow shafts drilled into the ground in order to extract water and are the primary source of water for livestock farmers in southern Africa. Furthermore, cattle rarely stray more than 13–18 km from these water sources in Africa [39], meaning areas closer to boreholes may have increased woody vegetation cover.

1.4. Fire

Fire is a factor that restricts woody vegetation diversity and abundance, preventing the formation of canopies [40–42] as well as removing seedlings and subsequently preventing the establishment of new trees [43]. Furthermore, for certain species fire can also kill the larger trees [44,45]. Seymour and Huyser [45] found that infrequent fires were enough to kill established *Vachellia erioloba* trees, which are an important keystone species in the region, meaning an increase in fire frequency could have implications on biodiversity. In unmanaged areas, the build-up of large quantities of grass biomass in the understory results in high-intensity fires that are capable of destroying juvenile trees [46]. For example, Sankaran et al. [11] studied the effect of fire return intervals on the percentage of woody cover in African savannas and found that a shorter return interval reduced established woody cover, which kept the community in a juvenile state by 'top-killing' seedlings. In managed landscapes, fires are not as frequent or intense enough to have a discernible impact on mature trees [40], and a common feature of savannas is the reduction of fires due to mitigation strategies [47]. However, Joubert et al. [48] note that fire is crucial to disrupt transition from grassy savanna to thicket, and that managers who prevent fires at this stage are likely to experience bush thickening in the future.

1.5. Research Gap and Questions

Variation in species characteristics is fundamental to understanding biogeographic patterns [49]. One reason for the possible lack of conclusive evidence explaining the main drivers of different woody vegetation patterns in previous research is the variation in how vegetation has been measured (e.g., single species, multiple species, richness, percent woody cover), as well as the differences in spatial scales of the previous studies (ranging from garden experiments to coarse continental extents). Assessing diversity as total species richness does not always adequately characterize the way in which species differ from each other, and it is these differences in traits, which often indicate that species respond in different ways to changes in the environment [50,51]. Alternatively, studying only one species in isolation could lead to species-specific results that are not generalizable to the larger system or to other species. Several mechanisms (outlined above) have been invoked to explain the processes responsible for woody vegetation composition; however, these are often investigated separately at scales not best suited to land-managers, thereby impeding the evaluation of their relative importance.

Subsequently, this study focuses on the vegetation composition of the Botswana Kalahari, with the aim to investigate the relative influence of the environmental drivers of woody vegetation at a regional scale. By classifying species into morphological groups based on shared physiological traits, the drivers of woody vegetation richness and abundance can be interpreted more meaningfully at a regional scale that is more appropriate for landscape management decisions. This study will explore three main questions: (1) what is the woody vegetation composition of the Kalahari in western Botswana? (2) What are the environmental drivers of woody species richness? and (3) what are the environmental drivers of woody species abundance?

2. Materials and Methods

2.1. Study Area

We conducted our research in western Botswana between 2009 and 2011 (Figure 1). We created a 950 km transect following the observed rainfall gradient along the western part of the Kalahari. This transect ran from Shakawe in the northwest of the country to Bokspits in the southwest of the country. Rainfall along the transect decreases from the north to south, ranging from a MAP of 550 mm to 350 mm [52]. Along this transect, we identified 15 regions (Figure 1) where we conducted multiple vegetation surveys. We selected regions on their accessibility and a minimum distance of 75 km to the previous region.

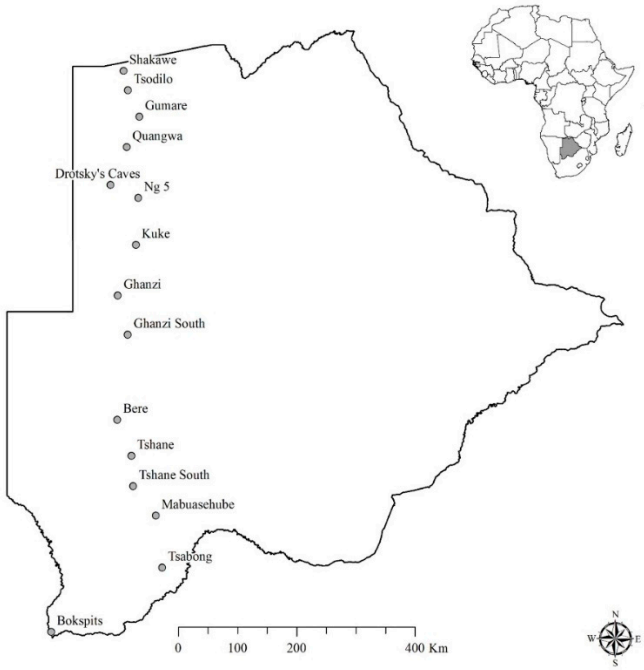

Figure 1. Location of the 15 regions along the Kalahari Transect where fieldwork was undertaken.

2.2. Data Collection

Vegetation was surveyed using the line interception transect (LIT) method. Within each region, we fixed six 100 m transects radially from a center point. For the dry season, the direction of the first transect was determined by a random number (between 0 and 360), and the further two transects were offset by 120 degrees. Transects of the wet season were spaced exactly between dry season transects, resulting in an offset of 60 degrees from the very first transect laid. Transects were placed 200 m from the center point to avoid over-sampling a small area. See Krebs [53] for a further description of the LIT methodology. We recorded all woody vegetation that was taller than 25 cm following the nomenclature provided by Palgrave [54], whereby average height, distance covered over the transect line, and distance and direction of the stem(s) were documented. Species richness and abundance were recorded at all transects, and species identity were recorded at all sites, with the exception of the wet season transects at Sites 1, 3, 4, and 5 due to uncertain species identification resulting from missing leaves. The results of the vegetation survey meant we had data from 78 transects for use in the statistical analysis.

Species were categorized into five morphological groups based on the classification guidelines outlined by Meyer et al. [55]. Morphological group I consisted of species characterized by bipinnate leaf structures and growth form ranging from multi-stemmed shrub like appearance to single-stemmed trees. Morphological group II included broad leaf species forming dense canopy structures where the majority of the growth form is either multi-stemmed (generally less than five stems) or single-stemmed. Morphological group III contained multi-stemmed broad leaf shrubs with closed canopies, seldom exceeding 2 m in height. In contrast, morphological group IV contained shrub species characterized by open canopies. Morphological Group V included relatively short shrub species (<1.5 m) with small, open canopies (<0.5 m in diameter). We also obtained data on precipitation, fire frequency, cattle density, and borehole locations that represent the possible drivers of diversity and abundance of woody vegetation (Table 1).

Table 1. Description of the environmental drivers used to explore the diversity and abundance of woody vegetation in western Botswana.

Variable	Description	Source
Mean Annual Precipitation	We derived mean annual precipitation (MAP) from the isopleth vector data representing rainfall conditions across the Kalahari.	[56]
Fire Frequency	We derived fire frequency using the MODIS direct broadcast burned area product (MCD64A1) as described in Giglio et al. [57]. Fire frequency product and generation outlined in Appendix A.	[58]
Grazing	We identified density of cattle using the latest available Department of Wildlife and National Parks aerial counts of wildlife. This survey was conducted during the dry season of 2005.	[59]
Borehole Density	We counted the number of boreholes within an eight-kilometer (based on Dougill et al. [37]) radius.	[60]

2.3. Data Analysis

We performed regression analysis in order to explore the environmental drivers of woody species richness and species abundances. Environmental variables were checked for multicollinearity using variance inflation factor, then standardized using z-scores in order to compare their relative influence on the ecological indicators. We performed all regression analyses using R 3.3.0. [61]. We selected regression analyses based on a preliminary evaluation of the data and their error distribution. Histogram exploration identified a mixture of Poisson and censored Gaussian distributions. We subsequently used a combination of generalized linear models with Poisson error distributions and Tobit regression models to analyze our data. For data that had a Poisson distribution, a Generalized Linear Model procedure with a Poisson error distribution and a log link function was used:

$$\log(y) = \beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n \tag{1}$$

where y is the abundances, X_n is the nth predictor, and β_n is the Poisson regression coefficient.

A censored Gaussian distribution represents a dataset that has a normal error distribution, but has some limit, either from below or above. Ecological data is often collected with a large proportion of the observations just above zero, while data cannot extend below zero or above certain thresholds (e.g., percentage cover). Tobit regression overcomes this bias and has been shown to perform better than ordinary least squares (OLS) (e.g., [62]) and is widely used in criminology (e.g., [63]) and land use change research (e.g., [64]). Species richness of woody vegetation is censored at zero (i.e., there cannot be a species richness of −1), and so any parameter estimates obtained by conventional OLS would be biased. Developed by Tobin [65], the Tobit regression model fits a set of parameters to where the dependent variable is left-censored at zero:

$$y_i^* = x_i\beta + \varepsilon_i \tag{2a}$$

$$y_i = \begin{cases} 0 \text{ if } y_i^* \leq 0 \\ y_i^* \text{ if } y_i^* > 0 \end{cases} \tag{2b}$$

where the subscript i = 1, 2, 3 … n, indicates the observation, y_i^* is an unobservable variable, x_i is a vector of explanatory variables, β is a vector of unknown parameters, and ε_i is the error term. To estimate the censored regression models, we used the censReg [66] and MaxLik [67] packages. Final models were selected based on Akaike Information Criterion (AIC) using both forwards and backwards stepwise selection of models. We investigated third and fourth order interactions, but these did not improve the final models. Therefore, our final models only include main effects and second order interactions.

3. Results

3.1. Woody Vegetation Surveys

We identified 44 woody plant species across the 78 transects where taxonomic information was recorded. We recorded the highest diversity at Kuke (site 7), with 21 species found in all six transects in the region (Figure 2a), and 13 species found along transect four during the wet season. In general, both richness and abundance decreased as data collection moved southwards which follows the precipitation gradient, although Kuke is the notable exception. We recorded the lowest total abundances for all six transects at NG5 (Site 6) and Bokspits (Site 15) and the highest abundances at Quangwa (Site 4) and Kuke (Site 7) (Figure 2b). Supplementary Information provides the data which includes geographic location (WGS 1984), a list of species recorded, and their morphological classification. We recorded eight species in Morphological Group I (bipinnate leaf structure), fourteen species in Morphological Group II (tall dense canopies), fifteen species in Morphological Group III (small dense canopy species), five species in Morphological Group IV (tall open canopies), and two species in Morphological Group V (small open canopies). Due to the low number of species recorded in Morphological Group V, these were withheld from the statistical analysis to prevent any generalization or over-fitting of the models.

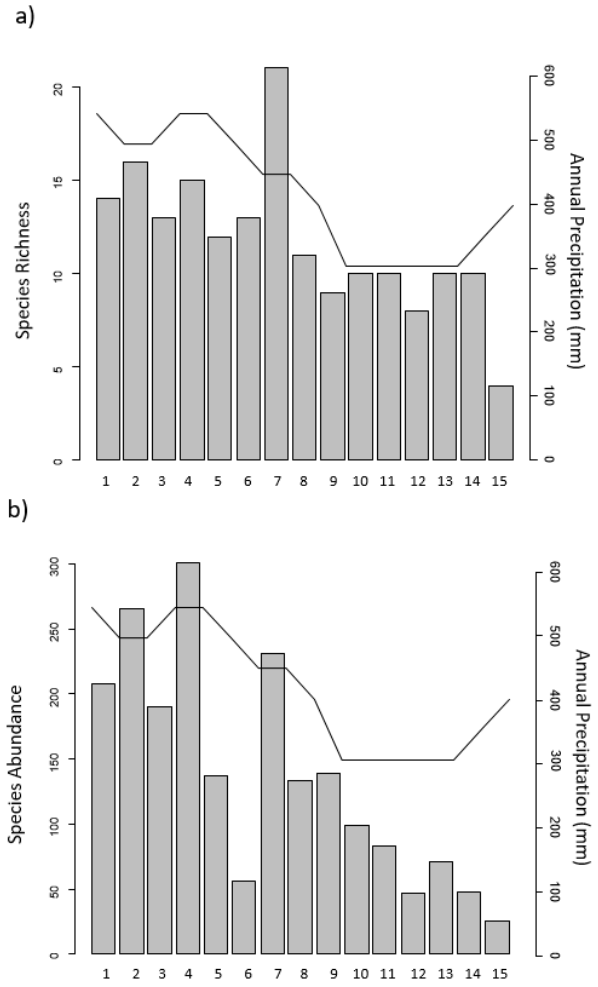

Figure 2. Total (**a**) woody vegetation species richness and (**b**) woody vegetation species abundance summed across the six transects at each of the 15 zones across the Kalahari Transect, plotted against annual precipitation (mm). Sites listed (1) Shakawe, (2) Tsodilo, (3) Gumare, (4) Quangwa, (5) Drotsky's Caves, (6) Ng 5, (7) Kuke, (8) Ghanzi, (9) Ghanzi South, (10) Bere, (11) Tshane, (12) Tshane South, (13) Mabuasehube, (14) Tsabong, and (15) Bokspits.

3.2. Regression Analysis

Our results indicated a number of important drivers of woody vegetation species richness and abundance (Table 2). Precipitation was the most important environmental variable when we considered all species together for both richness and abundance with borehole density and fire included in the final models. When species were deconstructed into morphological groups, we observed a variety of significant environmental drivers and interactions between these variables (** significant at $\alpha < 0.01$, * significant at $\alpha < 0.05$). The relative importance of each environmental driver often changed when we compared the regression models for richness and abundance of the same morphological group, indicating that the processes that determine diversity are different from those determining abundance. Boreholes were the most important driver for morphological groups II abundance and III richness, while livestock was the most important driver for morphological group IV abundance.

Table 2. Regression output for species richness (SR) and abundance (AB) for the four Morphological Groups (MG). ** significant at $\alpha < 0.01$, * significant at $\alpha < 0.05$. Tobit (T) and Poisson (P) regression analysis undertaken based on distribution of data.

	Total SR	**Total AB**	**MG I SR**	**MG I AB**	**MG II SR**	**MG II AB**	**MG III SR**	**MG III AB**	**MG IV SR**	**MG IV AB**
Regression	T	T	T	P	T	P	T	P	P	P
AIC	319.72	597.98	218.54	398.95	223.60	588.33	226.76	450.45	126.61	488.37
Intercept	5.66 **	20.05 **	0.92 **	−1.81	1.18 **	−0.05	1.00	0.34	−40.69	−4.67
PPT	1.32 **	11.07 **	−0.40 **	1.71 **	3.51 **	2.36 **	0.92 **	−0.01	−27.03	−4.32
Boreholes	−0.57 **	−1.85 **	−0.31	4.06 **	−1.65 **	−3.24 **	−2.78 **	−2.51 **	51.60	−0.04
Livestock				−12.97	1.14 **	2.04 **	1.62 **	1.87 **	−132.0	−10.02
Fire		−3.16 **	−0.20	−9.96	−0.60 **	−0.61 **		0.39	−14.52	0.13
*PPT * Boreholes*	0.56 **			5.80 **				−2.83 **	56.83	
*PPT * Livestock*				−2.59 **	4.17 **	2.37 **	0.79	1.68 **	−109.8	−8.30
*PPT * Fire*				−0.46 **		0.28		0.29 **	−2.44	
*Boreholes * Livestock*				−5.05 **		1.86 **	1.31	2.82 **		
*Boreholes * Fire*			−0.76					1.19	−27.79	
*Livestock * Fire*				−18.08						
logSigma	0.57 **	2.28 **	−0.01		0.27 **		0.07			

Precipitation and borehole density were included in all final models for every morphological group, while livestock was not important when all species were considered together, but included for all morphological groups (both richness and abundance) with the exception of morphological group I richness. Similarly, fire frequency was included for most morphological groups, with the exception of morphological group III and total species richness. Several two-way interactions were returned across the different models, and these were often significant. Morphological groups I and III abundance had the most interactions among all variables, suggesting these species have a complex and dynamic relationship with the environment.

Precipitation was a significant variable in all final regression models for species richness and abundance for all but three morphological groups, and it was the most important variable for total species richness and abundance, and morphological group I richness (Table 2). Precipitation had a positive relationship with species richness for morphological groups II and III, and abundance for morphological group II. This relationship was expected since these groups are characterized by dense canopy broad leaf species resulting in higher Leaf Area Index (LAI) and hence higher water requirements [68]. A negative relationship for morphological group I (bipinnate species) richness and rainfall was identified. This could be due to the fact that in xeric environments such species outcompete the majority of broad-leaved vegetation due to their general morphological characteristics and ecological traits (such as long root traps [69]), meaning the diversity of these species increases in arid areas where other water-dependent species simply cannot survive.

Livestock density was not included in the final model as selected by AIC when all species were considered together, but it had a positive relationship with morphological groups II and III (Table 2). Small dense canopy species such as *Grewia spp*, *Rhus tenuivirus* and *Ziziphus mucronata* notably have relatively low palatability [70]. Thus, if these species were already established when grazing increased in the area, they would not be affected by livestock. It was also the most important variable in determining abundance of morphological group IV (tall open canopy), reporting a negative relationship. Borehole density also had the most influence in determining both abundance of morphological group II and richness of morphological group III, forming a negative relationship with both ecological indicators. Boreholes also had a negative relationship with all response variables with the exception of morphological group I abundance. However, the interaction between boreholes and livestock density was significant for morphological group I abundance, indicating a negative relationship. This interaction was also significant for morphological groups II and III (although positive). These findings contradict previous research, and indicate that broad leaf species thrive in locations where there are more cattle and boreholes, while bipinnate species decrease. Fire had a negative influence on both richness and abundance at a regional scale (Table 2). Fire was generally negatively correlated to the overall abundance of woody species, but had a positive relationship with abundance of morphological groups III and IV, albeit not significant.

4. Discussion

Following the global trend in the conversion of savanna landscapes to woodier landscapes [7,27], the aim of this research was to investigate the variables responsible for woody vegetation composition in the western Kalahari, in particular those that cause high diversity and abundance of these species. We identified a variety of environmental drivers that are responsible for high diversity and abundance of woody vegetation, most notably precipitation, borehole density, grazing, and fire.

Our results generally agree with the observation that the rainfall gradient of the Kalahari is associated with an increase in woody vegetation [16–20]. Interestingly, the highest species richness was recorded at Kuke (Figure 1—Site 7), where the annual precipitation is 450 mm (in the middle of the rainfall gradient). The substantially higher species richness at Kuke can be explained by the site being located in an area buffering the Ghanzi farm-block to the south and the wildlife areas to the north. Both livestock and wildlife numbers are low here, and furthermore, fires have not occurred in this area due to both fire prevention strategies and the existence of the veterinary cordon fences acting as fire breaks. Therefore, our results indicate that while rainfall has a strong influence on woody vegetation, other factors also contribute significantly.

Our findings corroborate the positive association of bipinnate abundance (morphological group I) in areas close to boreholes [38], as well as an overall reduction in woody vegetation cover [71]. The negative relationship with small dense species is intuitive, as trampling loosens the soil and prevents these species from rooting. However, when grazing is high, the significant negative interaction between borehole density and grazing with bipinnate abundance contradicts the existing theories behind woody vegetation patterns. This relationship is a result of the fact that a higher number of boreholes and cattle represent more managed commercial ranches where cattle are routinely rotated between fields, and the regular use of multiple boreholes by the livestock negates the impact of trampling on the soil. This subsequently reduces the rate of bush encroachment by the unpalatable and thorny bipinnate species, and a positive relationship with other morphological groups is observed.

The negative relationship between fire frequency and woody vegetation corroborates observations from other dryland ecosystems [9,41] and supports a mechanistic understanding of the effect of fires in mixed tree-grass plant communities [40,72–74]. These findings support the observations at Kuke, that absence of fire does increase vegetation diversity and abundance (particularly for smaller species), and that the removal of fire from a landscape could increase bush thickening [49]. However, when fire was included in the models, it was seldom the most important variable (Table 2), with the exception of a positive interaction between livestock and fire when modelling morphological group I abundance

(albeit not significant). While diversity and abundance did decrease, the lesser impact compared to the other environmental variables suggests that frequent fires may not have such severe implications on the ecosystem's biodiversity as proposed [45]. However, the MODIS MCD64A1 product used in this study ([57]; Appendix A) does not account for fire intensity which could still negatively impact the landscape.

The deconstruction of species into morphological groups that are internally homogenous provided an opportunity for an improved understanding of the processes that underlie the patterns [50]. Despite this, in savanna ecosystems, research has focused on individual species (e.g., [21,24,45]) where findings are generally not always scalable to the wider ecosystem as species do exhibit idiosyncratic responses to the environment [75]. Subsequently, we feel that our analysis has related the importance of environmental drivers on the structure and physiological properties of the species, while it is not so specific that we cannot generalize processes to a scale that is useful for land managers.

It should also be noted that other factors may influence woody vegetation patterns. Topographic heterogeneity [76], atmospheric carbon [46], and harvesting [77] have all been found to influence woody vegetation communities. These factors were excluded due to the topographically homogenous landscape under study, and the fact that regional data on carbon and harvesting are difficult to obtain; however, future research should continue to explore the impact of these factors. We also investigated time since last fire as a variable in the regression analysis; however, fire frequency was found to have more influence on woody vegetation patterns and was subsequently the only fire variable retained in the final models to prevent any issues of multicollinearity. Similarly, we measured grazing as density of cattle recorded from aerial surveys, although grazing could be represented using intensity (e.g., quantification of herbaceous tissue removal or an assessment of high, medium, or low). However, available data on such features was not available to this study. Recently, the statistical effects of spatial autocorrelation have been noted [78] and methods to incorporate and explore this into regression models have become more common [79–81]. However, we made the decision not to incorporate spatial autocorrelation in our analysis so that discussion could focus specifically on the environmental factors across the transect.

We used a combination of generalized linear models with Poisson error distributions and Tobit regression models to analyze our data. Biodiversity indicators such as species richness and abundance often exhibit distributions that are unsuitable for a number of statistical techniques. The literature surrounding the use of statistical analyses that do not account for lower limits to explore ecological questions is perhaps part of the reason we still have ambiguity surrounding the drivers of woody vegetation in savanna ecosystems. While our results corroborate the existence of well-established biodiversity-environment relationships (e.g., positive relationship with MAP), we also identified several novel biodiversity-environment relationships from the Tobit models (e.g., positive relationships with livestock). Subsequently, research should continue to explore more suitable statistical methodologies with which to analyze ecological data so that any management strategies implemented from findings are better informed.

5. Conclusions

Savannas are an extremely important socio-economic landscape in Africa. These landscapes are inherently multi-functional, balancing the needs of pastoral societies with conservation of these dynamic ecosystems. Global trends of savanna to shrubland conversion [6,7] will have important ecological and economic consequences. Here we investigated the impact of regional scale environmental drivers (a scale that is more relevant to governments and land managers across Africa and beyond) on woody vegetation diversity and abundance. Data on over 44 species was collected over a two-year period at fifteen sites along the Kalahari transect. At each site, six 100 m transects recorded diversity ranging from one species to thirteen species, and abundance ranging from two individuals to 62 individuals. A mixture of Poisson and Tobit regression models identified that rainfall was the most important environmental variable when all species were considered equally, corroborating previous research

conducted at continental [11,16] and garden [17,19] scales. Interestingly, bipinnate species abundance decreased with increasing boreholes and livestock. These results contradict the consensus that borehole density and grazing increase the presence of such species, and suggest that by rotating cattle between boreholes, the impact of trampling and grazing on the soil is reduced and savanna landscapes are maintained. The deconstruction of species into different morphological groups provided better insights into the differences in the ways woody vegetation responds to environmental factors, and this deconstruction could aid in reconciling the divergent hypotheses surrounding woody vegetation patterns in savanna ecosystems, as all variables had a significant relationship with richness and abundance across all morphological groups. The results of this research should support land managers, governments and researchers working in transitional savanna landscapes worldwide.

Supplementary Materials: The following are available online at http://www.mdpi.com/2073-445X/8/8/122/s1, Data.

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Appendix A Derived Burned Area Product

The MODIS MCD64A1 (LP DAAC 2010b) burned area product as described by Giglio et al. (2009) was used to determine the fire locations and fire frequency across Botswana from year 2001 to 2011. Fire frequency was calculated on a per pixel basis based on MODIS derived fire events, with frequency ranging from no fire to a maximum of eleven fires recorded for the northern part of the country along the northern border with Namibia. Due to fire frequency having more influence on vegetation than time since last fire, the estimated uncertainty in date of burn was not incorporated in the fire frequency product as this does not impact the output. Figure A1 shows that most areas that burned have a fire frequency between one fire and three fires for the observed time frame. Most of these areas are located in the northern and central parts of the region. Across all field sites, fire frequency ranged from 0–6, with a total of eight sites having been affected at least once during the time period. Return intervals for fire occurrences seem to be higher at the northern site locations (sites 1–6) while all central to southern sites (sites 7–15) with the exception the Bere and Tshane South (site 10 and 12) were unaffected by fire.

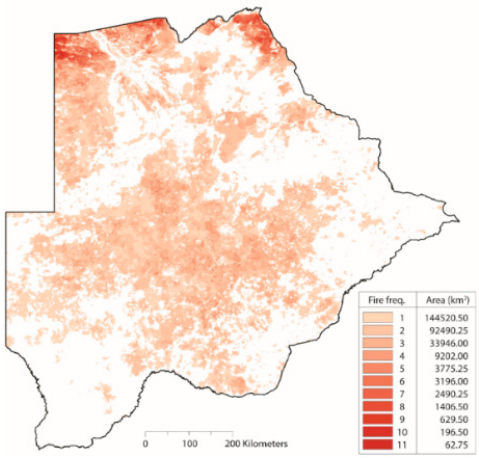

Figure A1. Fire frequency and burned area across Botswana from 2001 to 2011.

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