

RESEARCH ARTICLE

Savanna resilience to droughts increases with the proportion of browsing wild herbivores and plant functional diversity

Katja Irob¹  | Niels Blaum² | Alex Weiss-Aparicio¹ | Morgan Hauptfleisch³ | Robert Hering²  | Kenneth Uiseb⁴ | Britta Tietjen^{1,5} 

¹Freie Universität Berlin, Theoretical Ecology, Institute of Biology, Berlin, Germany

²Plant Ecology and Nature Conservation, University of Potsdam, Potsdam, Germany

³Biodiversity Research Centre, Namibia University of Science and Technology, Windhoek, Namibia

⁴Ministry of Environment, Forestry and Tourism, Windhoek, Namibia

⁵Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

Correspondence

Katja Irob

Email: irob.k@fu-berlin.de

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Abstract

1. Maintaining the resilience and functionality of savannas is key to sustaining the ecosystem services they provide. This maintenance is largely dependent on the resilience of savannas to stressors, such as prolonged droughts. The resilience to drought is largely determined by the interaction of herbivores and the functional composition of vegetation. So far, our understanding and ability to predict the response of savannas to drought under different types of rangeland use and as a function of vegetation composition are still limited.
2. In this study, we used the ecohydrological, spatially-explicit savanna model EcoHyD to determine if the resilience of a savanna rangeland towards prolonged droughts can be enhanced by the choice of rangeland use type (grazer-dominated, mixed-feeders or browser-dominated) and animal density. We evaluated the ability of a Namibian savanna system to withstand droughts and recover from droughts based on its perennial grass cover and the overall species composition.
3. Generally, we determined a low resilience under high grazer densities. Most importantly, we found that functional diversification of herbivores and plants acted as resilience insurance against droughts, leading to greater resistance and recovery of perennial grasses. In particular, a higher proportion of herbivores allowed for higher resilience, probably also due to a short-term switch to more drought-resistant or unpalatable species.
4. In this case, herbivore diversification was of high self-regulatory value by re-establishing trophic complexity, reducing the need for additional management interventions.
5. *Synthesis and applications:* Savanna systems will be more resistant to drought if (i) a dense perennial grass cover is maintained, protecting the topsoil from heat-induced water losses and erosion, encompassing functionally important species that are particularly well adapted to water stress and that are palatable, if (ii) the grazing pressure is adjusted to the productivity of the system, and (iii) the herbivore community includes browsers.

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KEYWORDS

browsing herbivores, drought resilience, ecohydrological modelling, ecosystem transition, grazing, land degradation, savanna vegetation, sustainable rangeland management

1 | INTRODUCTION

Extreme climatic events, such as droughts pose major challenges to the resilience of savanna systems and consequently the provision of important ecosystem services (Biggs et al., 2012; Zolli & Healy, 2012). Especially the combination of droughts with unsustainable rangeland management can decrease the resilience of savannas substantially by eliminating crucial self-regulatory mechanisms.

Since Holling (1973) introduced the concept of ecological resilience, numerous definitions have been proposed. Originally, resilience was defined as the recovery speed of the system after a disturbance (Pimm, 1984). This definition has gradually been replaced by a broader concept that recognises multiple stable states and the system's ability to withstand change while maintaining important ecosystem functioning (Gunderson, 2000). A recent definition of ecological resilience encompasses resistance to stress, recovery after stress, and persistence of the overall state (Weise et al., 2020). In this sense, we define resilience here as the degree of disturbance that an ecological system can accommodate without transitioning to a qualitatively different state (Gunderson & Holling, 2002), by either resisting change and/or recovering after the stress.

Savannas are woodland-grassland ecosystems that are subject to highly variable rainfall and low water availability with several qualitatively different ecological states (Sala et al., 2017). Savannas exhibit several self-regulatory mechanisms through which they generate or maintain important ecosystem functions. For example, wildfires are of highly self-regulatory value because they alter the composition and structure of vegetation and reduce fuel loads, minimising the potential for subsequent fires until sufficient fuel reaccumulates (Parks et al., 2015). Since greater species diversity increases the resilience to environmental change (Pettoirelli et al., 2019), it also contributes to self-regulation of a system by preventing the transition to a different ecological state and, thus, limits the need for additional land management. However, extreme events can stress a savanna to such an extent that the ability to self-regulate declines and the system transitions to a new state, often from grass- to-woody-dominated.

Applying the resilience concept to savannas, this means that self-regulatory, stabilising mechanisms increase the degree of disturbance that savannas can accommodate and prevent transitions among the multiple stable vegetation states. The latter include grass-dominated vegetation, a mixture of trees and grasses, or wood-dominated vegetation or potentially also bare soil (Jeltsch et al., 2000).

The ability of savanna vegetation to withstand extreme events such as droughts (periods of prolonged absence of precipitation or below-average precipitation amounts; Dai, 2013) is enhanced by two main mechanisms. First, drought-resistant species could increase and functionally compensate for decreased occurrence and

health of less resistant species (Gonzalez & Loreau, 2009; Hoover et al., 2014). Second, during short-term droughts, plants may physiologically respond by reducing growth and redistributing available water and nutrients towards below-ground resources (Connell & Ghedini, 2015).

Grass species differ in their sensitivity to disturbance. Some can resist a higher degree of stress, i.e., they persist or recover quickly under drought and/or grazing, but recovery might still be slow, even after conditions have improved (Ludwig et al., 2001). The loss of these resistant species could open up colonisable space for shrubs to dominate the system. This shrub dominance likely shifts the ecosystem towards a degraded state marked by a decline of important ecosystem services (Dougill et al., 2010; Holling, 1996). The so-called shrub encroachment in response to heavy grazing is commonly accompanied by changes in taxonomic composition, an increase in unpalatable, trampling resistant and/or annual grasses (Milton et al., 1994; Tabares et al., 2020). A diminished grass layer increases the risk of soil erosion (Archer et al., 2017) and leads to altered productivity, nutrient cycling and water balance (Sankaran et al., 2004; Scholes & Archer, 1997). That is, a change in herbivory, fire or climatic conditions can lead to a savanna with a different dominant vegetation type and hence altered plant functional diversity, leading to implications for ecosystem functioning. Transitions in savannas are in most cases only measurable over years or decades (Oliver et al., 2015) and are therefore difficult to observe in short-term field experiments. It is therefore crucial to unravel the complex interactions between climate and rangeland use in savanna systems to maintain the resilience of the system and thus meet the future challenges of savanna management. For this disentanglement, models are ideal as they enable the understanding of future developments by reproducing key processes and elements of the system.

Climate change is expected to affect the resilience of the savanna by exacerbating the intensity and frequency of climatic extremes such as droughts (Dai, 2013; Tadross et al., 2017). Drought alone can cause a change in vegetation, but combined with unsustainable grazing management, the probability of transitioning to a new and possibly undesirable state increases. In particular, the combined impact of different types of rangeland use and droughts of different duration has been largely neglected (Smith et al., 2013; Wigley-Coetsee & Staver, 2020). Some efforts have been made for grazing systems (e.g. Ruppert et al., 2015; von Keyserlingk et al., 2021), but neither empirical nor modelling studies have analysed alternative rangeland use types, such as mixed-feeding or browser-dominated regimes, and their possible mitigation or exacerbation of the effects of droughts. Since recent studies already pointed out that reducing grazer densities and using wildlife increases habitat use and benefits ecosystem resilience (Brodie et al., 2013; Wells et al., 2022), we expect that reducing the number of grazing animals by using mixed herbivore

communities with more browsers will lead to a more balanced system and thus increase the resilience of savannas to droughts.

In this study, we used an ecohydrological savanna model to assess the resilience of savanna vegetation under three different types of rangeland use (grazer-dominated, mixed, and browser-dominated) at two animal densities exposed to drought periods of varying lengths (4 and 8 years).

We specifically addressed the following questions: (i) Is perennial grass cover resilient to extended droughts and does resilience vary with rangeland use type, rangeland use intensity, and drought length? (ii) What role does functional diversity play in post-drought resilience and does this role vary with rangeland use type, intensity, and drought length? (iii) What are the consequences for important self-regulation mechanisms within the ecosystem and (iv) hence the implications for land management?

2 | MATERIALS AND METHODS

2.1 | Study site

Etosha Heights is a private wildlife reserve in Namibia's arid savanna (S19.1554°E15.1705°E), established in 2002 by merging eight livestock farms and replacing the domestic stock with indigenous wildlife. The reserve covers an area of 492 km² bordering the southern boundary of Etosha National Park. It is within Namibia's arid savanna where precipitation is highly variable and occurs mainly in summer (October to April). The mean annual precipitation (MAP) is 298.67 ± 30.20 mm (retrieved from a local weather station from 2018 to 2021) and the mean annual temperature is 26°C. Topography (mean elevation: 1995 m, rather flat), soil (loamy sand), climate and vegetation characteristics are described in Irob et al. (2022) in detail. Much of the study area is already encroached by *Colophospermum mopane* and acacia species, but there are also mixed habitats and open plains. The corresponding parameters can be found in Appendix S2. Dominant herbivores are springbok, oryx, giraffe and plains zebra. The grazer-to-browser ratio has ranged between 1.2:1 and 0.9:1 (Hauptfleisch, 2022). Game counts are not conducted regularly, but stocking rates range between 10 and 50 ha/LSU depending on field condition and recent droughts, but also on fence management.

2.2 | Model description

We used the ecohydrological, spatially explicit dryland model EcoHyD (Guo et al., 2016; Irob et al., 2022; Lohmann et al., 2012; Tietjen et al., 2009, 2010). In this study, we extended the existing herbivory algorithm to allow for a more dynamic range of herbivory types (S1.2). We simulated a total area of 2.25 ha consisting of 900 grid cells, with a resolution of 5 × 5 m per cell. In the past, the model has been successfully applied and validated in different dryland ecosystems (Lohmann et al., 2012; Tietjen et al., 2010).

The model comprises two dynamically linked process-based submodels: a vegetation submodel and a hydrological submodel. A comprehensive model description and model parameters can be found in the Appendices (S1 and S2). The life cycle of different plant functional types (sub-PFTs) belonging to one of three major plant functional types (shrubs, perennial grasses and annual grasses) are simulated in the vegetation submodel. The main processes determining vegetation dynamics are growth, mortality, competition for water and space, seed dispersal, seedling establishment, and herbivory. Fires have not been considered in this study as they are usually suppressed at our study site. Plant dynamics are directly related to soil water dynamics, as growth is coupled with transpiration. Plant death is caused by water scarcity or senescence.

The hydrological submodel simulates the daily dynamics of surface water and soil moisture in two soil layers. These dynamics are determined by precipitation, lateral water redistribution of surface water, infiltration, vertical fluxes and water losses through evaporation and transpiration. Water losses to the atmosphere are related to the proportion of plant roots in the two soil layers and vegetation cover. Vegetation cover reduces evaporation but increases the transpiration of plant water. Although perennial grasses and shrubs have access to water in both layers, the root distribution of annual grasses allows them to access water only in the upper soil layer (Case et al., 2020).

2.2.1 | Model inputs and scenarios

The model was parameterised to the environmental conditions of Etosha Heights Private Reserve, specifically topography and soil, climatic conditions and plant species characteristics.

Temperature, precipitation and drought

We approached the uncertainty of highly variable precipitation conditions by replicating simulation runs with stochastic precipitation time series generated by the NamRain precipitation generator (see Lohmann et al. (2012)). All 30 rainfall time series have the same MAP on average, but with a large variability of yearly sums ranging from 100 mm to 800 mm that are distributed differently over the 100 years (Figures S5.7 and S5.8). In addition to the control scenario without induced droughts, we simulated droughts with a single drought period after 60 years with a duration of 2 to 8 years. We determined extreme drought years at our study site as yearly precipitation sums of less than 100 mm (one-third of MAP). Droughts of 2 years are relatively common, 4 years are based on the extreme drought of 2012–2015 in Namibia and 6–8 years should reflect potential future droughts that fall outside historical norms (Cook et al., 2015).

Assemblage of plant sub-plant functional types

The model describes the fate of three major plant functional types (PFTs): woody vegetation (hereafter referred to as shrubs), perennial herbaceous vegetation (perennials) and annual herbaceous vegetation (annuals). The base subtype of each

meta-PFT (hereafter referred to as “base type”) had the same set of parameters as the original meta-PFT. We then derived additional subtypes (for shrubs and perennials) by defining individual life strategies that had trade-offs in two specific traits but were otherwise identical to the base type. Sub-PFTs were derived by defining individual life strategies based on the main species we found in Etosha Heights that we categorised into trade-offs in two particular characteristics, related to processes defence D, biomass production B, mortality M, palatability P, competitive strength for water C and resistance to drought R (Irob et al., 2022). For example, a sub-PFT could be very drought resistant and show a very low biomass production as a trade-off (Table 1). As annuals only dominate degraded systems (Archer et al., 2017; Case et al., 2020), we did not subdivide them further. In total, we selected five sub-PFTs for perennials and four for shrubs from our local species pool that exhibit potential relevant adaptation mechanisms to herbivory and/or drought. We tested the role of plant functional diversity (an assemblage of sub-PFTs) on modelled outcomes by comparing results for simulations with one meta-PFT each (low diversity, referred to as single) and with the results of simulations with several sub-PFTs of perennials and shrubs (high diversity, referred to as diversity).

Rangeland use scenarios

We analysed the effects of three types of rangeland use, namely rangeland use dominated by grazing, mixed feeding and browsing herbivores at two different intensities (animal density in hectare per livestock unit): 20 ha/LSU (high) and 40 ha/LSU (low). For rangelands dominated by grazing or browsing herbivores, we established a ratio of 80:20% between the diet preference of herbaceous vegetation and shrubs (and vice versa) with a flexibility of 15% to allow adaptive herbivory in response to changes in food availability. If there is not enough edible biomass of the preferred forage type available, the ratio is adjusted within the defined parameter range, and the animals can switch to a higher grazing/browse intake. This led to a minimum of 65% and a maximum of 95% herbaceous vegetation intake for the grazers. For mixed feeders, we set the ratio to 50:50%, again with a flexibility of 15%. This means that our communities do not represent specific animal species, but rather communities of different herbivore types that have on average the specified fodder demands described above. Depending on the density of the animal, the ratio of grazers to browsers then leads to an amount of biomass of a functional type of plant that can then be taken from the edible biomass. In addition, with this model setup, we do not account for the impact of large browsers, such as elephants.

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TABLE 1 Perennial grass and shrub plant life strategies in Etosha Heights. The two-letter code refers to the strategy name used in the text and figures and is adjacent to the two-letter code its description

Perennials	Example species	Shrubs	Example species
Bd	High biomass production—low forage defence	Bm	High biomass production—High mortality <i>Colophospermum mopane</i>
Cp	High competitive strength for water use efficiency—high palatability	Cb	High competitive strength for water use efficiency—Low biomass production <i>Acacia reficiens</i>
Pb	Low palatability—Low biomass production	Db	High forage defence—Low biomass production <i>Dichrostachys cinerea</i>
Pr	Low palatability—low resistance to drought	Rd	High resistance to drought—Low defence <i>Boscia albitrunca, Grewia olukondae</i>
Rp	High resistance to drought—high palatability		<i>Stipagrostis uniplumis</i>

2.3 | Data analysis

All simulated output was analysed and visualised using R (version 4.1.3, R Core Team, 2019). In the main part of this paper, we focus on the results of the 4- and 8-year long droughts. The complete set of results can be found in Appendix S5. In all statistical evaluations, climate repetitions were included as a random effect.

2.3.1 | Perennial grass cover

To analyse the effect of rangeland use, intensity and drought duration on post-drought perennial grass cover, we applied an aligned rank transform ANOVA (ART-ANOVA) using the ART_{OO}L R package (Wobbrock et al., 2011) and conducted post hoc pairwise tests using ART-C (Elkin et al., 2021). To investigate short-, medium-, and long-term plant cover recovery, we chose several points in time for this comparison: the year in which the drought ended (year 0), as well as 10 and 20 years afterwards. For the effect size statistic, we chose the partial *eta-squared*. The interpretations have been proposed by (Cohen, 1988) and consider an *eta squared* below 0.06 small, between 0.06 and 0.14 medium and above 0.14 as large.

2.3.2 | Resistance and recovery

We defined resistance as the amount the perennial grass cover can resist cover loss compared with the identical scenario without the induced drought (control). We determined the maximum cover loss in response to drought and compared it with undisturbed control cover at the same time.

$$\text{Max. cover loss} = \frac{\text{cover}_{\text{control}_i} - \text{cover}_i}{\text{cover}_{\text{control}_i}} \quad (1)$$

We applied generalised linear mixed models (GLMMs) with beta regression and a logit link using the GLMM_{ADAPTIVE} R-package (Pinheiro & Bates, 1995) to analyse the ability of grasses to resist cover loss.

We defined recovery as the time until perennial grass regained 80% of the control cover in the identical no-drought scenario after the respective drought event. To determine the impact of rangeland use type, drought duration and plant diversity on recovery rate, we applied GLMMs using the R package NLME (Pinheiro et al., 2021).

2.3.3 | Plant functional composition

We decided to focus on functional composition instead of biodiversity indices to identify functions and services of specific types and how they can increase rangeland resilience. To determine how the functional composition of perennial grasses and shrubs shifted directly after a drought, we looked at the composition in the year the drought ended. We evaluated the cover of each sub-PFT and

the cover relative to its control without drought. We conducted a structural equation modelling (SEM) approach using the package `PIECEWISESEM` (Lefcheck, 2016) and linear mixed regression models within the SEM. Direct effects assume that rangeland use and drought duration impact PFT cover and its cover relative to control directly. The indirect effect infers that intensity impacts cover by inducing changes in herbivory demand depending on the type of rangeland use. We encoded our questions into a conceptual path diagram (Figure S5.5):

$$\begin{aligned} \text{Log_cover} &\sim \text{rangeland use} + \text{intensity} + \text{drought length} \\ &+ \text{sub} - \text{PFT} + \text{random} = 1 | \text{climrep}, \end{aligned} \quad (2)$$

$$\text{Intensity} \sim \text{rangeland use} + \text{random } 1 | \text{climrep}, \quad (3)$$

$$\begin{aligned} \text{Cover_ratio}_{\text{control}} &\sim \text{rangeland use} + \text{intensity} + \text{drought length} \\ &+ \text{sub} - \text{PFT} + \text{random} = 1 | \text{climrep}. \end{aligned} \quad (4)$$

We tested several model combinations for the best fit using Akaike's information criterion (AIC) and selected the model with the lowest AIC. Global goodness of fit of the final piecewise SEM was assessed using the χ^2 distributed Fisher's C statistic and the log-likelihood-based χ^2 statistic. We used standardised coefficients to quantify marginal means for each path. We used ANOVA to identify the overall statistical significance of categorical predictors and to calculate marginal means for each level using the `EMMEANS` package (Lefcheck, 2016). Finally, we performed a pairwise post hoc test using the Tukey-Kramer method.

2.3.4 | Cover–NDVI comparison

We related the simulated dynamics of vegetation cover to NDVI time series from Landsat and Sentinel2 in two different habitats at our study site and compared the quantitative changes after a four-year drought. We chose an *Acacia reficiens* shrubland (representing shrub cover) and an open plain (representing grass cover), both at a spatial resolution of 30×30m. We compared the simulated drought scenario with high-density mixed animals to relate them to post-drought NDVI changes.

3 | RESULTS

3.1 | Resilience of perennial grasses to droughts

Grass cover was always highest in browsing scenarios, followed by mixed feeding and then grazing (Figure 1, Figure S5.1, Tables S6.2 and S6.4). Prolonged droughts, higher proportion of grazers and high intensity of rangeland use significantly decreased perennial grass cover. In the immediate response, the decrease in grass cover was more strongly controlled by the duration of the drought period. However, rangeland use (two-way interaction) and the intensity of this use (three-way interaction) altered this effect. Ten years after the drought, the impact of the duration of the drought on recovery

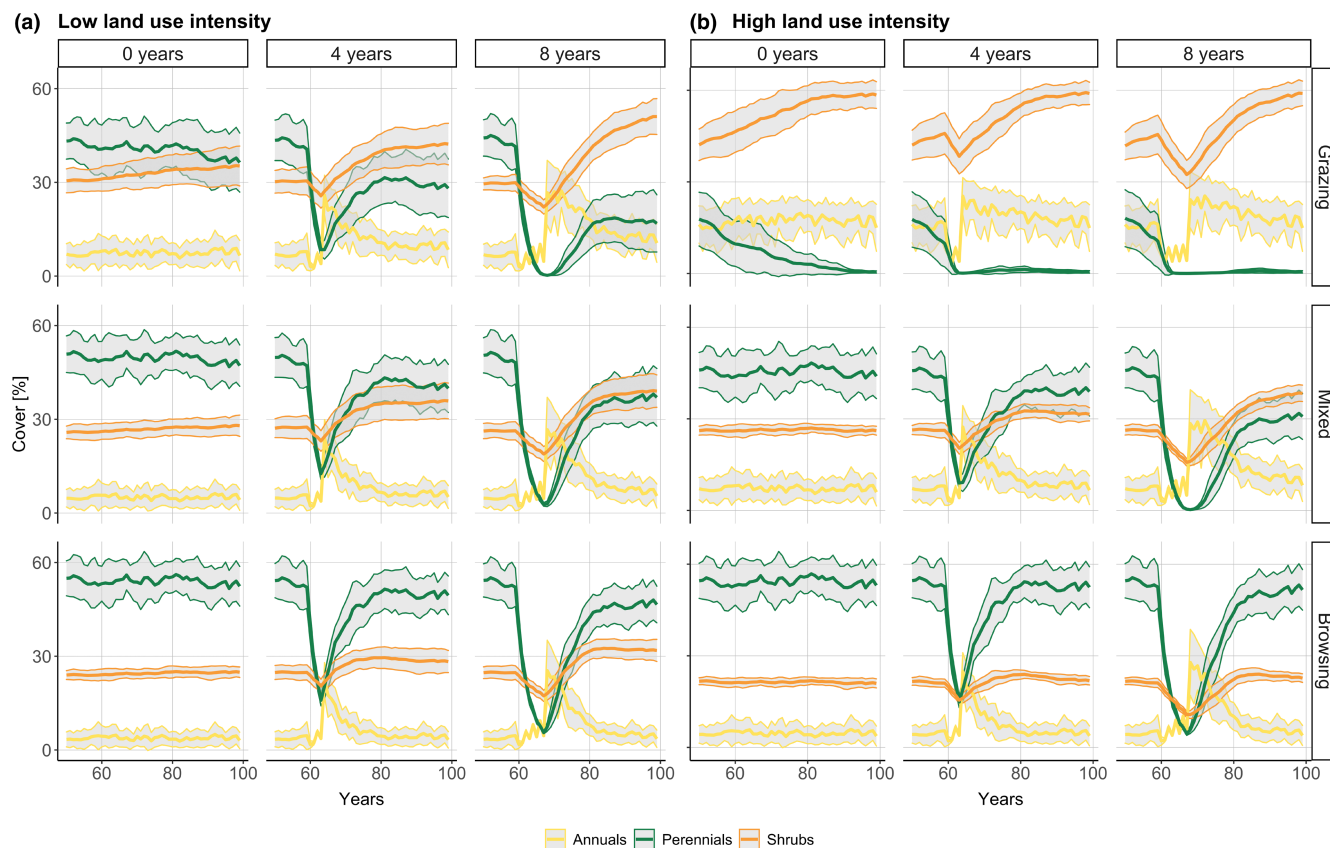


FIGURE 1 Change in vegetation cover over time and relating to rangeland scenario. Predicted mean cover \pm SD [%] of the three meta-PFTs (lines) under various drought period lengths for all rangeland use scenarios in two intensities (a,b). The numbers (0, 4, 8) at the top correspond to drought duration in years. All droughts began in the year 60. The graphs are shown from year 50 onwards. All simulations were repeated 30 times with varying climates.

decreased, making rangeland use the strongest determinant of recovery and current cover. Consequently, the combined impact with other factors also decreased. Again, intensity (two-way interaction) and duration of drought (three-way interaction) could enhance or decrease this effect (Tables S6.4 and S6.5). In long-term recovery, the impact of rangeland use and intensity increased, but the impact of drought length decreased.

3.2 | Effects of plant functional diversity on resistance and recovery

In the regimes dominated by grazers, there was no resistance with almost a total loss of perennial grass cover, apart from the regimes with low intensity and no or only a short drought duration (Figure 2a, Table S6.6). Vegetation cover losses were strongest during prolonged droughts in combination with high intensity of rangeland use. Independent of intensity, resistance was highest under browsing regimes. Plant diversity served as a buffer against losses during drought periods. Grazing, high intensity of rangeland use, prolonged droughts, and low plant diversity (single) prolonged the recovery time of perennial grasses (Tables S6.7 and S6.17, Figure 2b). Perennial grasses could not recover under high grazing intensity.

We also found faster and more frequent recovery events for diverse plant communities and with more browsers in our climate replicates. However, in a mixed system, there was no significant difference in recovery between communities with high or low plant functional diversity.

3.3 | Shifts in plant functional composition

In general, the shift of cover was positively influenced by mixed feeding and browsing (Figure S5.5, Table S6.8). Rangeland use intensity and drought duration had a negative effect on the extent of cover change (Tables S6.9 and S6.10, 83% explained variation, Table S6.8). Grazing led to the highest deviation in the cover of each sub-PFT and browsing to the lowest (Tables S6.11 and S6.12, 53% of the variation explained).

Under a low intensity of grazing, the resulting perennial grass community was dominated by the PFT with low palatability and low drought resistance (Pr) and the highly water-competitive and high drought-resistant PFTs, but very palatable (Cp, Rp, Table 1, Figure 3a). Water-efficient and low-palatable PFTs were more abundant than PFTs with high biomass production. The longer the drought lasted, the more dominant Pr and Cp were. As the number

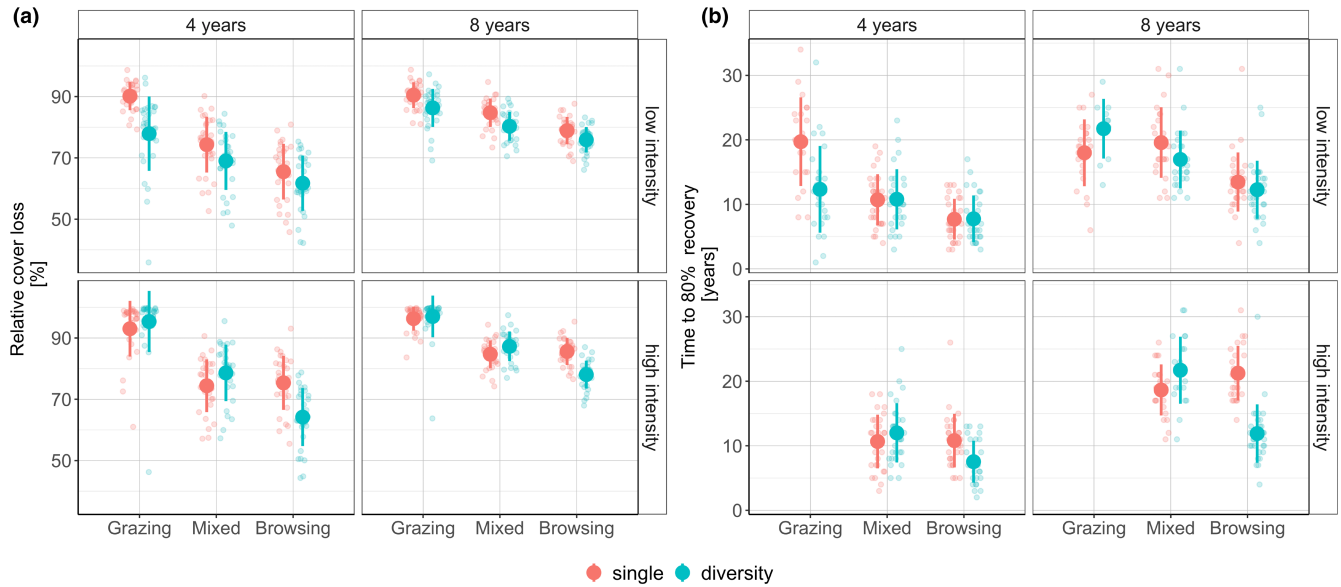


FIGURE 2 Resistance and recovery of perennial grasses in response to droughts. (a) Highest mean cover loss \pm SD [%] (large points + range) of perennial grasses during the 4- and 8-year long drought periods compared with the cover in the no-drought control scenario for all three rangeland use types (x-axis). (b) Mean time \pm SD [years] until 80% of the perennial grass cover in the control scenario was reached after the drought period ended (large point + range). Red indicates scenarios with a single FPT (single), and blue indicates scenarios with high plant functional diversity. Small points show each of the climate repetitions when 80% of the control cover was reached again (maximum of 30 repetitions per scenario).

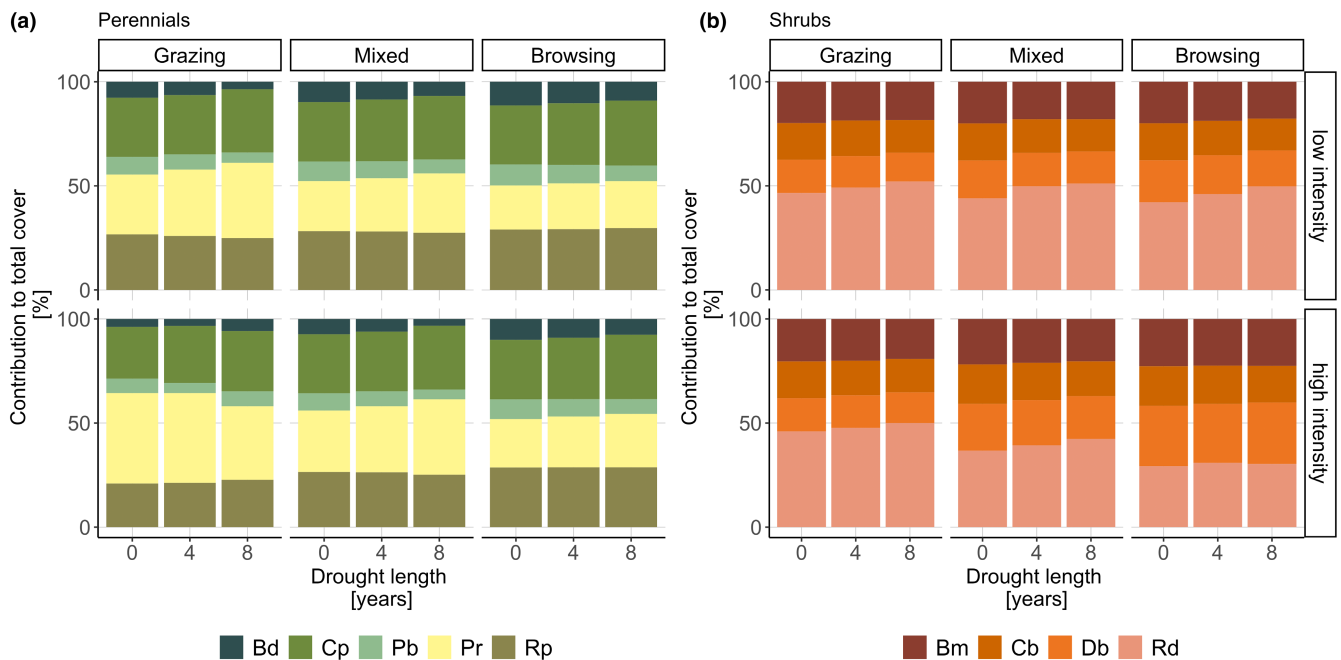


FIGURE 3 Mean relative cover shift of perennial (a) and shrub (b) sub-PFTs in all rangeland use scenarios and under different drought lengths (0, 4 and 8 years). Results represent mean vegetation cover of the first year post-drought repeated 30 times with varying climates.

of grazers in the mixed feeder and browser-dominated scenarios decreased, the less palatable and drought-resistant PFT (Pr) became slightly less abundant and its dominance was replaced by PFTs of high palatability with efficient water use (Cp, Rp, Table S6.13).

At low herbivore densities, the type of rangeland use affected the shrub composition only slightly (Figure 3b). Rangeland use type

and intensity, trait combination and duration of drought were the main drivers of each PFT cover (78% of the variation explained) and the respective change in cover compared with the control cover (59% of the variation explained, Table S6.14). The PFT with high drought resistance and low defence (Rd) was predominant in all scenarios except when there was heavy browsing (Table S6.16). The PFT with

high defence and low biomass production (Db) increased with higher browser proportion and intensity. The longer the drought lasted, the more dominant the drought-resistant and low-defended PFT (Rd).

3.4 | Cover–NDVI comparison

We found that the mean loss of grass cover and the loss of NDVI were identical (37%, [Figure S5.8](#)). The loss of shrub cover after the drought was 5%, while the loss of NDVI was 25%. Since NDVI loss directly translates into grass loss, the model seems to have done a good job. The loss of shrub cover was lower than the NDVI loss, which is probably because there was still non-green shrub biomass in the model, while in the real system the shrubs were no longer very green and, therefore, had a lower NDVI.

4 | DISCUSSION

We investigated the combined effects of rangeland use, drought and plant diversity on savanna resilience through modelling. Our findings provide insight into (i) the role of rangeland use type and intensity, drought duration and functional diversity for the resistance and recovery of perennial grasses cover, (ii) the change of vegetation composition in response to prolonged drought, as well as (iii) the importance of self-regulation in ecological processes and (iv) the implications for land management.

4.1 | Resilience of perennial grasses to droughts

The ability of the perennial grass layer to resist drought-induced loss of plant cover and subsequently recover from these droughts varied greatly depending on the rangeland use type. Changes in perennial cover and subsequent shrub encroachment can be very abrupt ([Lohmann et al., 2012](#); [Stuart-Haëntjens et al., 2018](#)), which we found already in single climate repetitions ([Figure S5.7](#)). The dominant presence of grazers significantly reduced the grasses' ability to recover from droughts and suppressed recovery at high intensity of use. That is, when prolonged droughts occur in a savanna system already prone to severe herbivore-induced losses of perennial grasses, the system crossed a threshold that no longer allowed perennial grasses to recover. At the same time, the system degraded even further as shrubs encroached and annuals increased, leading to more bare ground during the dry season. In contrast, the difference in grass cover loss between high and low rangeland use intensity by browsers was only marginal. However, in the scenario with a high number of browsers and grazers, we found a reduction in competition for water. This reduction was caused by browsing limiting shrub cover and allowing higher grass cover (compared with the scenario with a low number of browsing and grazing animals), demonstrating a higher resilience of the system. Our results support the findings of [Porensky et al. \(2013\)](#), who found that more intense grazing by

cattle had a greater effect on plant community dynamics than intense grazing by wild herbivores dominated by browsers. We found no differences in the recovery of low- or high-diversity vegetation communities in a mixed herbivore system, which suggests that the balanced effects of herbivory already mitigated some pressure on the vegetation.

The underlying processes determining the performance of perennial grasses are essential to better understand the causes of drought-induced shift of savanna vegetation from a grass-dominated state to a shrub-encroached state, it is necessary to closely look at the underlying processes determining the performance of perennial grasses. Savannas are frequently exposed to droughts, with low soil water content causing extreme stress to plants. Prolonged drought periods can lead to a strong reduction in net primary grass production ([Gao et al., 2019](#)) or even to the senescence of most above-ground parts ([De Boeck et al., 2011](#)). However, various adaptive physiological and reproductive mechanisms can still allow for a slow growth leading to some recovery ([Gao et al., 2019](#)). The speed of perennial grass recovery is highly variable: For example, while some studies found grasses to recover within weeks and a few years after the drought ([Wigley-Coetsee & Staver, 2020](#); [Wilcox et al., 2020](#)), others found this to occur only after several years or even decades ([Haddad et al., 2002](#); [Ruppert et al., 2015](#)). These contrasting findings show that the severity of a drought and its impact on grass recovery depend on many underlying processes and factors, such as competition for resources, impaired reproduction and ability to re-sprout ([Ruppert et al., 2015](#)), compositional shifts towards loss of dominant species ([Sankaran et al., 2004](#)) and post-drought rainfall ([Stuart-Haëntjens et al., 2018](#)). In our study, we focussed on a subset of these factors and found that when perennial grass cover decreased significantly or recovered too slowly, shrubs used their competitive advantage in the acquisition of water from deep soil layers and shrub seedlings established on the available space hence limiting the regrowth of grasses. These results are also in line with previous findings showing that grass removal increased sapling growth and woody plant cover ([LaMalfa et al., 2021](#)). Additionally, our model showed the stabilising effect of reduced herbivory pressure on grasses initiated by the introduction of browsing herbivores. Notably, the simulated changes in vegetation are consistent with the remote sensed NDVI changes after a 4-year drought at our study site.

4.2 | The role of plant functional diversity

Droughts in combination with rangeland use can affect the abundance and composition of savanna vegetation. In particular, drought exempts subordinate taxa from competitive exclusion facilitating their establishment ([Porensky et al., 2013](#)), which might partly compensate for loss-induced declines in ecosystem functioning.

In our study, the most dominant grass types always showed adaptations to resist one of the stressors, that is, grazing or drought. Low grazing intensity allows selective grazing with

strong benefits for less palatable species. When grazing pressure increases, feeding is no longer selective and, therefore, being superior in the acquisition of resource water becomes more important. The increase in drought-resistant or grazing-tolerant grass species in response to heavy grazing and low rainfall is well known. In response to stress, Fynn and O'Connor (2000) and Wigley-Coetsee & Staver (2020) found an increase in annual grasses as well as weakly tufted perennial grasses, such as *Urochloa mosambicensis* (corresponding to the traits of Rp and Cp in this study) and *Bothriochloa radicans* (equivalent to our other dominant type Pr, Table S7.1). Although these opposing strategies seem to contradict each other, they show that the importance of a particular adaptation in the recovery phase may be greater than its trade-off.

In stressful environments, short-lived plant species and species with higher persistence and faster recovery after disturbance become dominant (Connell & Ghedini, 2015; Wilcox et al., 2020), as seen by the increase in annuals in this study.

The observed shift in shrub composition resulted from the adaptation of certain shrub sub-PFTs towards severe disturbances. The duration of the drought had only a marginal effect on the shrub composition, as all shrub sub-PFTs benefited from sufficient access to water in deeper soil layers due to their deep rooting system (Joubert et al., 2017; Yang et al., 2021), as well as residual water in the upper soil layer due to low grass cover.

In general, a more diverse plant functional trait composition was more resilient to prolonged droughts and served as a buffer mechanism reducing plant cover losses (e.g. Smith et al., 2013; Wilcox et al., 2020) and supporting faster recovery. However, in some cases of the mixed feeder- and grazer-dominated scenarios, recovery times were prolonged since slow-growing types increased. The slightly slower recovery in the scenarios with more grazers was contrary to our expectations. Here, our approach of including only sub-PFTs with single trade-offs might be too simplified to capture the full picture. Nevertheless, when plant diversity accelerated recovery, we also observed an increase in drought-resilient and palatable species. Nevertheless, the slightly slower recovery in the scenarios with more grazers was still contrary to our expectations.

4.3 | Building savanna resilience through rangeland management

Many nature-based management measures (e.g. restoration, re-introduction, conservation) aim to restore an ecosystem to a previous state that was either 'healthier', had a higher degree of 'self-regulation' or an 'important species composition'. Although the management approaches are different, they commonly follow the same objectives: restoration of ecological processes and functions, species restoration and/or the reduction of management interventions (Lorimer et al., 2015; Naundrup & Svenning, 2015; Prior & Brady, 2017). However, to date, it is not clear which

ecological processes or functions allow for an appropriate level of self-regulation.

With our results, we could determine key factors that contribute to the self-regulation of an ecosystem by reestablishing trophic complexity.

First, we found that the maintenance of a dense perennial grass cover can protect the soil from hot and dry conditions, which decreases soil water losses. Limiting decreases the pressure on grasses by reducing competition for water and space, and thus the need for further management measures, such as fodder supplementation. However, here it is important not only to exclude grazers but also to implement some form of shrub control. As large-scale manual and chemical debushing is costly, and fires are often suppressed in rangelands, the use of browsing herbivores to suppress shrubs can serve as an alternative. Moreover, since wildlife cannot be forced to 'debush' small-scale parts of the rangeland, rangeland managers should focus on keeping plains open by systematically removing shrubs before they encroach.

Second, a higher level of functional diversity in the plant community leads to greater resistance and recovery of grasses in response to drought. Although some species were lost, few functionally important species could compensate for their loss and maintain a productive system. In addition, reducing grazing pressure also resulted in a more resilient plant community. Therefore, we conclude that the use of a mix of animal types with more wild browsing herbivores can maintain the perennial grass cover, conserve important functional types and balance the competition between grasses and shrubs, and is therefore of high self-regulatory value. However, in our study, we did not vary the timing of the herbivory impact, which is a critical component of rangeland management. Stimulating grasses by grazing in the growing season can increase growth and enhance productivity (Oba et al., 2000). As animals in game reserves no longer migrate and feeding pressure on plants is high throughout the year, managers must take care of plants and ensure recovery. Feeding pressure can be minimised by effective fence management (Hering et al., 2022), or be reduced by rotation of water points. Consequently, the diversification of animals and plants and good management of the timing and intensity of herbivory have tremendous potential to mitigate climate change and allow for sustainable utilisation of natural resources. For conservation and restoration efforts, we highlight the importance of plant species that are adapted to different environmental stressors and take on appropriate functions. Conserving fast-growing, water-efficient and palatable species can be essential to achieve conservation or restoration objectives in the long term.

We propose the following steps to increase the resilience of savannas:

1. Adjust the number of grazers to the system's productivity (Nott & Boys, 2022) and integrate browsers or mixed feeders. We propose that the coexistence of wildlife and livestock is possible in many rangeland types (e.g. conservancy, communal and commercial).

- Identify plant species that are functionally important for the maintenance of the target ecological processes in the study system (e.g. drought resistant, palatable/nutritional) and include measures to conserve these.
- Reduce animal stocking rates in anticipation of droughts, during drought conditions, and in the recovery phase afterwards, and manage the timing of high herbivore impact to stimulate plant growth.
- Consider vegetation dynamics and soil conditions when evaluating changes in animal composition.

Furthermore, in anticipation of droughts, we suggest that rangeland managers diversify their incomes, that is, tourism, meat production, environmental education and fodder production to buffer potential losses within one source of income.

In this context, ecological or socioecological models are a useful tool to identify key factors that increase the self-regulation of ecological processes under different management regimes. Moving forward, we advocate integrating local managers early into the development of models and scenarios, as their combined knowledge of ecology, drought resistance and resilience of savannas will provide crucial guidance for climate-resilient management plans.

AUTHOR CONTRIBUTIONS

Katja Irob, Britta Tietjen and Niels Blaum: Conceptualisation, Methodology, Writing, Review & Editing. Katja Irob: Visualisation, data curation and analysis. Alex Weiss Aparicio: Algorithm extension, Methodology. Morgan Hauptfleisch: Conceptualisation, Review & editing, Kenneth Uiseb: Methodology. Robert Hering: Data acquisition, Review & editing. Our study involves authors from different countries, including researchers from the country where the study was conducted. Authors from both countries were involved at an early stage to ensure that different perspectives were considered. The findings were discussed with local scientists and stakeholders to embed our research in Namibia's national context and research priorities and needs.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Model code, simulation data and scripts to reproduce the results and figures of this manuscript are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.4j0zpc8gn> (Irob, 2022).

ORCID

Katja Irob  <https://orcid.org/0000-0002-6507-7450>

Robert Hering  <https://orcid.org/0000-0001-6098-0387>

Britta Tietjen  <https://orcid.org/0000-0003-4767-6406>

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