

RESEARCH ARTICLE

Navigating uncertainty: Managing herbivore communities enhances Savanna ecosystem resilience under climate change

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Handling Editor: Izak Smit**Abstract**

1. Savannas are characterized by water scarcity and degradation, making them highly vulnerable to increased uncertainties in water availability resulting from climate change. This poses a significant threat to ecosystem services and rural livelihoods that depend on them. In addition, the lack of consensus among climate models on precipitation change makes it difficult for land managers to plan for the future. Therefore, Savanna rangeland management needs to develop strategies that can sustain Savanna resilience and avoid tipping points under an uncertain future climate.
2. Our study aims to analyse the impacts of climate change and rangeland management on degradation in Savanna ecosystems of southern Africa, providing insights for the management of semi-arid Savannas under uncertain conditions worldwide. To achieve this, we simulated the effects of projected changes in temperature and precipitation, as predicted by 10 global climate models, on water resources and vegetation (cover, functional diversity, tipping points (transition from grass-dominated to shrub-dominated vegetation)). We simulated three different rangeland management options (herbivore communities dominated by grazers, by browser and by mixed feeders), each with low and high animal densities, using the ecohydrological model EcoHyD.
3. Our results identified intensive grazing as the primary contributor to the increased risk of degradation in response to changing climatic conditions across all climate change scenarios. This degradation encompassed a reduction in available water for plant growth within the context of predicted climate change. It also entails a decline in the overall vegetation cover, the loss of functionally important plant species and the inefficient utilization of available water resources, leading to earlier tipping points.
4. *Synthesis and applications.* Our findings underscore that, in the face of climate uncertainty, farmers' most effective strategy for securing their livelihoods and ecosystem stability is to integrate browsers and apply management of mixed herbivore communities. This management approach not only significantly delays or averts tipping points but also maintained greater plant functional diversity,

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fostering a more robust and resilient ecosystem that acts as a vital buffer against adverse climatic conditions.

KEYWORDS

climate change, ecohydrological modelling, management strategies, resilience, Savanna ecosystems, tipping points, wildlife

1 | INTRODUCTION

The impacts of climate change on semi-arid Savannas worldwide are a significant concern, resulting in a decline in ecosystem functioning and services and affecting the livelihoods of local communities (Hoegh-Guldberg et al., 2019; Osborne et al., 2018). Savannas, woodland-grassland ecosystems that are subject to highly variable rainfall and low water availability (Scholes & Archer, 1997), are expected to face higher uncertainty of water availability due to climate change, which will have consequences for agriculture, health, ecosystems, biodiversity and energy generation (Kusangaya et al., 2014). Climate change has already caused changes in temperature and precipitation in Savannas, reducing soil water availability, altering soil conditions, vegetation cover and composition, soil moisture, groundwater recharge and the entire ecosystem (Mujere & Mazvimavi, 2012; Scheiter et al., 2019; Venter et al., 2018). Most climate change scenarios predict that these changes will only worsen and become more pronounced in the future. Impacts on a regional scale include a decline in vegetation productivity, decreasing habitat sizes and the mortality of various plant species (Lawal et al., 2019). The phenomenon driving these alterations is frequently referred to as 'desertification' (D'Odorico & Bhattachan, 2012). Desertification refers to the gradual degradation of land in arid, semi-arid and dry sub-humid areas, often leading to sudden tipping of the ecosystem to an undesirable, degraded state that is hardly reversible. Tipping points, characterized by catastrophic and irreversible shifts from grass-dominated to shrub-dominated states, are a global phenomenon in Savannas. These shifts are already occurring under current climatic conditions, with an expectation for a more frequent occurrence in the future (Stevens et al., 2017). These tipping points can be triggered by various factors, including non-linear responses to precipitation (Hirota et al., 2011), fire intensity and timing (Staver et al., 2009), CO₂-fertilization (Gillson, 2015) and grazing (Koch et al., 2023). Critical transitions like these can cause severe soil erosion, loss of biodiversity and reduced soil fertility (Buisson et al., 2019; Gillson & Ekblom, 2009). While global efforts have focused on reducing carbon emissions to mitigate the impacts of changing climate, there has been less focus on regional climate change adaptation to prevent such transitions.

Adaptation through changes in land management is an essential and realistic pathway to prepare humans and ecosystems for the impacts of climate change. However, the extent of change required can vary based on the specific system and location, necessitating either incremental adjustments or more transformative step changes

in management strategies. For instance, rangeland managers could consider measures such as preventing shrub encroachment, actively maintaining biodiversity, optimizing grazing practices and fostering resilient vegetation cover (Higgins et al., 2007; Tommasino et al., 2023; Wangai et al., 2016). These approaches should be evaluated within the context of their economic viability and potential benefits for sustaining ecosystem health and services. Vegetation conservation is a crucial aspect of management aimed at preserving important grass and tree species, preventing shrub encroachment and identifying critical tipping points (Irob et al., 2022; Kapuka et al., 2022; Lohmann et al., 2012). That is, maintaining a dense grass cover can protect the soil from hot and dry conditions, reducing soil water losses and increasing plant water availability (Castellanos et al., 2022; Irob et al., 2022). Moreover, the significance of maintaining plant functional diversity for ecosystem functioning has gained increasing recognition in recent years (Hagan et al., 2023; Osborne et al., 2018). Here, specific plant functional traits have been identified as crucial indicators of ecosystem functioning in the face of unpredictable disturbances (Osborne et al., 2018; St. James & Mallik, 2021).

In addition, conserving wildlife is just as crucial as preserving vegetation for the overall protection of biodiversity and the sustainable management of natural resources (Lunney & Hutchings, 2012). Wild herbivore communities offer two significant advantages for biodiversity conservation and natural resource management. First, they can alleviate pressure on certain vegetation types, particularly grasses, as they exhibit diverse feeding behaviours, but also by foraging and shifting their diets in response to changes in vegetation patterns and availability. This approach has been found to be effective, as studies by Asner et al. (2009), Irob et al. (2022) and Scogings and Sankaran (2019) have demonstrated. Second, mixed wild herbivore communities play a crucial role in shaping the structure and function of Savanna ecosystems, potentially enhancing their resilience to the impacts of climate change (Augustine et al., 2011; Knecht et al., 2008; Scogings & Sankaran, 2019). While vegetation and wildlife show promise for addressing conservation challenges, our understanding of their potential is limited by factors such as the complex and interconnected relationships, behaviours and dynamics among different species of wildlife, uncertainties surrounding climate change and a dearth of regional climate studies.

The lack of science-based regional adaptation plans is reflected in the focus of climate change studies. Most studies are based on global vegetation models (Boone et al., 2018; Scheiter & Higgins, 2009) and/or on projections by a single global climate model (GCM) (e.g. Mujere & Mazvimavi, 2012). While a global approach

is essential for addressing global problems, we also recognize the importance of local solutions that are tailored to the needs of specific regions. Unfortunately, there is a significant lack of studies that downscale climate change projections to the regional level, limiting our understanding of how climate change may impact local ecosystems (Tadross et al., 2017). Regionally, climate projections are influenced by uncertainty in the representation of land use change, land-atmosphere interactions and the modelling of precipitation and temperature patterns (Schulze, 2011). These uncertainties make it difficult to make precise predictions about the impacts of climate change on southern Africa, which is already subject to huge climate variability (Mujere & Mazvimavi, 2012; Schulze, 2011; Tadross et al., 2017). Due to factors such as the typology and number of models used, the time period and emission scenario considered and the availability of data, there is an immense lack of consensus among studies on the likely impacts of climate change on water resources (Kusangaya et al., 2014). As a result of these factors, addressing the uncertainty in climate projections and their effects on water resources demands a multidisciplinary approach. This approach involves integrating hydrological and vegetation models with locally gathered data and expertise. Nevertheless, water resources planning and management decisions in Savannas are often based on simulated information using hydrological models only and are therefore likewise subject to uncertainty (Althoff et al., 2019; Kotir et al., 2016). Furthermore, it is important to note that, to our knowledge, no study has coupled a small-scale hydrological model with vegetation dynamics to examine feedbacks on the entire system, let alone under different rangeland management options.

Our study aimed to assess the animal density and climate change conditions under which grazing induces degradation in the Savanna ecosystems of Southern Africa. We addressed how rangeland managers could adjust their management to best deal with the uncertainties arising from uncertain future climate conditions. We used an ecohydrological model for drylands (EcoHyD) to test various climate change projections. Specifically, we focused on a Namibian rangeland and assessed the projected temperature and precipitation regimes of 10 GCMs under two climate change scenarios across different rangeland types, including grazer-dominated, mixed and browser-dominated ecosystems in low and high intensity. Our study, focusing on the uncertainties in different regional climate change model projections, aimed at answering the following two questions: (i) How uncertain are vegetation cover, functional vegetation composition and water resources under uncertain climate projections, and does this uncertainty differ under different rangeland management scenarios? (ii) Can adapting the number and types of herbivores promote ecosystem resilience in terms of stability, resistance and recovery to foster a more stable Savanna ecosystem, avoiding critical tipping points?

Our findings can be used to develop effective regional adaptation strategies that account for the complex interactions between climate change, rangeland management and ecosystem health. Such practices can protect the region's natural resources, support local livelihoods and be applied to similar semi-arid Savanna systems worldwide.

2 | MATERIALS AND METHODS

We modelled the temporal dynamics of soil water and plant growth using the ecohydrological model EcoHyD, depending on abiotic environmental conditions as present in a typical semi-arid Savanna in Namibia. For this purpose, we used data from a specific Savanna and corresponding climate data to test their influence under different rangeland management strategies, as described in detail below. We thank the Ministry of Environment, Tourism and Forestry, Namibia and the Namibian National Commission on Research, Science and Technology for research permission (certificate number RCIV00032018 with authorization numbers: 20190602, 20190808).

2.1 | Study site

Etosha Heights is a private wildlife reserve in Namibia's semi-arid Savanna, located at S19.1554°E15.1705°. The reserve was established in 2002 by merging eight livestock farms and replacing domestic stock with indigenous wildlife. It covers an area of 492 km², situated on the southern boundary of the Etosha National Park. The area is characterized by highly variable precipitation, mainly occurring in the summer months and a mean annual precipitation (MAP) of 298.67 ± 30.20 mm, with a mean annual temperature (MAT) of 26°C. The topography is relatively flat, with a mean elevation of 1995 m. The soil is loamy sand. The wildlife reserve is quite heterogeneous in soil conditions, leading to diverse dominance in plant species, but many parts are dominated by *Colophospermum mopane* and acacia species. Dominant herbivores are springbok (mixed feeder), oryx (grazer, but also browse), giraffe (browser) and plains zebra (grazer), with a grazer-to-browser ratio ranging between 1.2:1 and 0.9:1. More information can be found in Irob et al. (2022) and Hauptfleisch (2022). Regular game counts are infrequent; however, stocking densities vary from 10 to 50 ha/LSU based on field conditions, recent drought occurrences and fence management practices.

2.2 | Climate input data

In this study, we utilized the results of 10 GCMs from the Inter-Sectoral Impact Model Intercomparison Project Research (ISIMIP) that have been bias-corrected for the study site (S19.25°E15.25°) within Etosha Heights (Lange, 2021) using the ISIMIP3BASD v2.5 bias adjustment and statistical downscaling method (Lange, 2021). Here we used daily temperature and precipitation model outputs from the Coupled Model Intercomparison Project Phase 6 (CMIP6). The detailed methodology for these models can be found in the ISIMIP3b group I, II and III simulation protocols, which are based on historical and projected climate change as well as observed and fixed socio-economic forcing. To enhance the precision of our analysis, we adjusted the precipitation resolution from daily to hourly values, as described by Tietjen et al. (2010), and generated hourly temperatures based on a daily temperature cycle using the chillR

package according to Luedeling (2022). We used historical data from the period from 1970 to 2014 as the build-up phase to allow for vegetation stabilization before modelling the future time series from 2015 to 2099. We selected one historical time series of weather data that was closest to our station data and used it for all models.

2.3 | Climate change scenarios

The IPCC's Sixth Assessment Report (AR6) has introduced a new set of climate scenarios, the 'Shared Socioeconomic Pathways' (SSPs), that provide better representation of different socio-economic developments and greenhouse gas pathways. Based on our current climate trajectory, we are focusing on two main pathways: SSP3, a pathway of regional rivalry with rising nationalism and inequality; and SSP5, a fossil-fuelled development pathway with a focus on global economic growth and reliance on fossil fuels (IPCC, 2022). Within this pathway, the SSP370 scenario involves filling a gap in the CMIP5 forcing pathways with a medium to high radiative forcing trajectory by the end of the century that represents a common forcing level in unmitigated SSP370 baselines. The SSP585 scenario within the SSP5 pathway involves a high radiative forcing trajectory by the end of the century, which represents the high end of a plausible future.

2.4 | Climate model description

We described the 10 GCMs by analysing MAP, MAT and minimum and maximum values of both precipitation and temperature. In addition, we identified both meteorological droughts (precipitation below half of average annual rain, length of growing season) and ecological droughts (soil moisture below threshold, Figure A.1.6).

The climate models in all figures were ordered by the MAP of the SSP585 scenario from low to high.

2.5 | Precipitation and temperature projected by 10 GCMs

The 10 climate models differ in their assumptions, climate forcings and historical measurements. An overview of key climatic variables from the 10 GCMs and the two climate change scenarios is given in Table 1. The two climate scenarios differ in their projections of future greenhouse gas emissions, energy consumption and socio-economic development pathways. SSP370 envisions a more moderate emissions trajectory and sustainable development focus, while SSP585 depicts a high-emissions pathway with limited sustainability measures. In the SSP585 scenario, the CanESM5 model projects the strongest precipitation decrease, with 203 ± 104 mm on average (compared to today 298 ± 30 mm), and the IPSL-CM6A-LR model projects the highest MAP, with 331 ± 123 mm. CanESM5 is also the model projecting the strongest temperature increase to $27.6 \pm 1.2^\circ\text{C}$. In the SSP370 scenario, CanESM5 projects a similarly strong and highest decrease in precipitation (219 ± 119 mm) with a temperature increase to $26.5 \pm 1^\circ\text{C}$. On the contrary, IPSL-CM6A-LR SSP370 projects a precipitation increase to 339 ± 140 mm alongside a temperature increase to $25.1 \pm 0.9^\circ\text{C}$ (Figure A.1.5).

2.6 | Meteorological droughts

For each climate model and change scenario, we analysed the total number of years in which MAP fell below 150 mm during the last 30 years of the climate data, that is, between 2070 and 2099. Our findings indicate that the CNRM-ESM2-1 and CanESM5 models

TABLE 1 Mean values of key climatic variables for years 2070–2099: Mean annual precipitation (MAP), mean annual temperature (MAT), number of meteorological drought years (MAP <150 mm) and mean duration of growing season (GrowSeas) based on 10 different global climate models and two climate change scenarios (SSP370, SSP585). The models are ranked in descending order by MAP under the SSP585 scenario, ranging from the lowest to the highest.

SSP370					SSP585			
Model	MAP (mm)	MAT ($^\circ\text{C}$)	Drought (years)	GrowSeas (days)	MAP (mm)	MAT ($^\circ\text{C}$)	Drought (years)	GrowSeas (days)
CanESM5	220 ± 119	27 ± 1	8	181 ± 103	203 ± 105	28 ± 1	9	202 ± 96
CNRM-ESM2-1	269 ± 138	26 ± 1	9	207 ± 90	215 ± 113	27 ± 1	12	253 ± 66
CNRM-CM6-1	252 ± 85	26 ± 1	5	199 ± 92	230 ± 112	28 ± 1	7	218 ± 99
GFDL-ESM4	242 ± 108	25 ± 1	5	198 ± 77	244 ± 101	25 ± 1	5	212 ± 95
EC-Earth3	255 ± 97	25 ± 1	4	206 ± 85	252 ± 109	26 ± 2	6	206 ± 89
MPI-ESM1-2-HR	278 ± 108	24 ± 1	2	204 ± 107	264 ± 116	25 ± 1	5	225 ± 76
UKESM1-0-LL	298 ± 116	26 ± 1	3	216 ± 74	286 ± 126	28 ± 1	5	206 ± 84
MIROC6	306 ± 153	24 ± 1	7	181 ± 90	289 ± 106	25 ± 1	2	185 ± 89
MRI-ESM2-0	291 ± 106	25 ± 1	4	208 ± 88	294 ± 109	26 ± 1	2	232 ± 71
IPSL-CM6A-LR	339 ± 140	25 ± 1	2	185 ± 109	332 ± 124	26 ± 1	1	161 ± 101

projected the highest number of drought years under the SSP585 scenario, with a total of 12 and 9 years, respectively. This represents approximately one third of the analysed 30 years. Conversely, the IPSL-CM6A-LR and MIROC6 models projected only one and two dry years, respectively, due to their projection of increased precipitation. Additionally, we observed that the SSP585 scenario projected more droughts when compared to SSP370. Most models projected over 15% of drought years in the 30-year period studied.

2.7 | Growing season duration

We defined the growing season as the period between the first and last days with rain above 5 mm based on Tietjen et al. (2010) and NDVI data. We determined the length of the growing season for every year and calculated the mean value for the years 2070–2099 for every climate model and climate change scenario.

2.8 | Model description

We employed the EcoHyD model, an ecohydrological and spatially explicit model for dryland systems (Irob, Blaum, Weiss-Aparicio, et al., 2023; Irob et al., 2022; Lohmann et al., 2012; Tietjen et al., 2010), to simulate an area of 2.25 ha, which consists of 900 grid cells with a resolution of $5 \times 5 \text{ m}^2$ per cell. This model has been previously used and validated in different dryland ecosystems (Irob, Blaum, Weiss-Aparicio, et al., 2023; Appendix A5; Lohmann et al., 2012; Tietjen et al., 2010).

The EcoHyD model is a spatially explicit, process-based model that simulates the dynamics of vegetation and hydrology in dryland ecosystems. It consists of two submodels: a vegetation submodel and a hydrological submodel. The vegetation submodel simulates the life cycle of different plant functional types (PFTs), including shrubs, perennial grasses and annual grasses. It takes into account processes such as growth, mortality, competition for water and space (as a proxy for resources such as light or nutrients), seed dispersal, seedling establishment and herbivory. Since fires are usually suppressed at our study site, we did not include them in the model. The hydrological submodel simulates the daily dynamics of surface water and soil moisture in two soil layers. It is based on precipitation, lateral water redistribution, infiltration, vertical fluxes and water losses through evaporation and transpiration. The model also considers the impact of vegetation cover on evaporation and transpiration and the root distribution of annual grasses, which allows them to access water only in the upper soil layer. More details on the model's structure and parameters can be found in the Appendices (A1 and A2).

2.9 | Assemblage of plant sub-PFTs

The model describes the fate of three major plant functional types (meta-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 default meta-PFT in Savannas. We then derived additional subtypes (for shrubs and perennials) by defining individual life strategies that have trade-offs in seven traits but are 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 (Table A.1.8). We categorized these into trade-offs in seven particular characteristics, related to processes: biomass production B, competitive strength for water C, defence D, establishment moisture need E, mortality M, palatability P and resistance to drought R (Irob et al., 2022). According to a vegetation survey carried out at our study site, species were assigned qualitative values for these traits that we translated into parameter values that resulted in a 10% cover increase or decrease according to a sensitivity analysis conducted (Appendix A4). For example, a sub-PFT could be very strong in competing for water resources with very little need for a lot of water to establish but exhibit a very low biomass production as a trade-off.

As annuals only dominate degraded systems (Case et al., 2020), we did not subdivide them further. In total, we parameterized each seven sub-PFTs for perennials and shrubs from our local species pool that exhibit potentially relevant adaptation mechanisms to herbivory, water use and/or climate. In previous studies, we successfully matched the occurrence of modelled functional types after different disturbances with empirical research (dominant grass types in response to herbivory intensity, Irob et al., 2022); PFT composition after drought (Irob, Blaum, Weiss-Aparicio, et al., 2023).

2.10 | Management scenarios

We investigated the impacts of three types of rangeland use defined by animal composition and density, which we refer to in our figures as land use and intensity. The herbivore communities in our model are defined by a specific biomass demand that they have to fulfil by feeding on PFTs. Accordingly, we defined three rangeland types based on their biomass demand: with mainly grazing herbivores, with mainly browsing herbivores or with mixed feeders. The animal density (in hectare per livestock unit [LSU]) of each type was set to high (15 ha/LSU) or low (40 ha/LSU). These chosen stocking rates correspond to the upper and lower bounds of stocking rates determined through game counts conducted at the actual study site (Hauptfleisch, 2022). Depending on the animal density, the ratio of the diet preference determines the amount of biomass of a functional plant type that can be taken from its edible biomass. Mega herbivores, such as elephants and giraffes, were not accounted for, as our primary focus is on herbivory impacts associated with different rangeland management practices not primarily intended for tourism. In grazing-dominated rangelands (by, for example zebras or oryx), the ratio of the diet preference can

be expected to be 80% herbaceous vegetation and 20% shrubs. Conversely, in browser-dominated rangelands, such as those inhabited by kudus, the ratio tends to be reversed (du Bothma & du Toit, 2016; Smithers, 2012). In rangelands dominated by mixed feeders, such as eland, the anticipated ratio is approximately 50:50 (du Bothma & du Toit, 2016). If the preferred forage type is not fully available, this ratio has a flexibility of 15% to enable meeting the feeding demand through adaptive herbivory. This allowed grazing herbivores to meet their feeding demand with 65%–95% herbaceous vegetation intake.

2.11 | Analysis

In the results and discussion section, we assess the outcomes by employing the principles of resilience and stability. In accordance with Irob, Blaum, Weiss-Aparicio, et al. (2023), resilience refers to the ecological system's capacity to endure disturbances without undergoing significant shifts in its state. This endurance is realized through either resistance to disturbances or the system's ability to recover from stressors. Ecological stability refers to a system's ability to remain resilient to disturbance while exhibiting limited variation in response (De Keersmaecker et al., 2014). For instance, a stable ecosystem can maintain its qualitative features or quickly recover after disturbance, with minimal variation in response across different climate projections or rangeland management strategies.

2.12 | Cover

To evaluate the effect of climate and rangeland management on vegetation cover, we calculated the mean cover and standard deviation for each vegetation type in response to MAP. To detect uncertainties resulting from management, we analysed the period from 2089 to 2099 for each climate and rangeland management scenario.

2.13 | Functional diversity

To assess the combined effect of climate and rangeland management on functional diversity, we calculated various functional diversity indices (functional richness, functional evenness, functional divergence, functional dispersion [FDis], Rao's Q and community weighted means; Table A1.5) based on the trait distribution and species abundance of the resulting communities. As most of the indices were highly correlated, we only present the distance-based multidimensional index of FDis. This index, calculated using the 'dbFD' function in the FD R-package (Laliberté & Legendre, 2010), considers the trait distribution and species abundance in the communities and measures the dissimilarity and evenness of trait distribution. It is weighted by the relative abundances of each species in the community. High values of FDis indicate a more diverse and evenly distributed set of traits, while low values indicate dominance

by a few similar traits. We then determined the average FDis at low and high rangeland use intensity scenarios in the last 10 years of simulation.

2.14 | Water use efficiency

To evaluate the ability of vegetation to utilize available water and the potential impact of rangeland management on this ability, we calculated water use efficiency (WUE). WUE was defined as the proportion of annual precipitation that plants can use for transpiration and growth. We quantified the mean WUE in low and high rangeland use intensity scenarios in the years 2089–2099.

2.15 | Tipping points

To investigate the impact of rangeland type and climate change on critical vegetation transitions, we determined the time point when a transition occurred from perennial grass dominance to shrub dominance. As all simulations began with perennial grasses as the dominant vegetation type, we defined the tipping point as the year when shrub cover turned equal to or higher than perennial grass cover. To assess the long-term implications of this tipping point and to confirm whether a true transition had occurred, that is shrub dominated or complete loss of grasses, we also analysed the total shrub cover at the end of the simulation and how it related to total cover.

3 | RESULTS

3.1 | Cover

Our analysis distinguishes between two main sources of uncertainty affecting rangeland management: those associated with climate model predictions and the underlying scenarios and those associated with animal type and density. For rangeland management with low animal densities, the cover of grass and shrub was relatively resilient over time (Figure A.1.7), with minimal variation between the three rangeland types at the end of the simulation. In terms of animal type and density, our simulations showed that the SSP370 scenario with low browser density had the highest perennial cover (across all GCMs: $58.1 \pm 4.8\%$), while the highest shrub cover was almost identical in both climate change scenarios with high grazer density (across all GCMs in SSP370: $41.6 \pm 4.6\%$ and SSP585: $42.6 \pm 4.6\%$). Furthermore, high grazing intensity resulted in a significant decrease in perennial grasses and near-complete loss, leading to more barren soil. Our results suggested that maintaining low grazing intensity and receiving higher precipitation are critical factors in achieving a high perennial grass coverage.

However, the different projections of the 10 GCM caused variation of 20%–25% in perennial grass cover within one rangeland type (Figure 1; Table A.1.4). In contrast, shrub cover was relatively stable

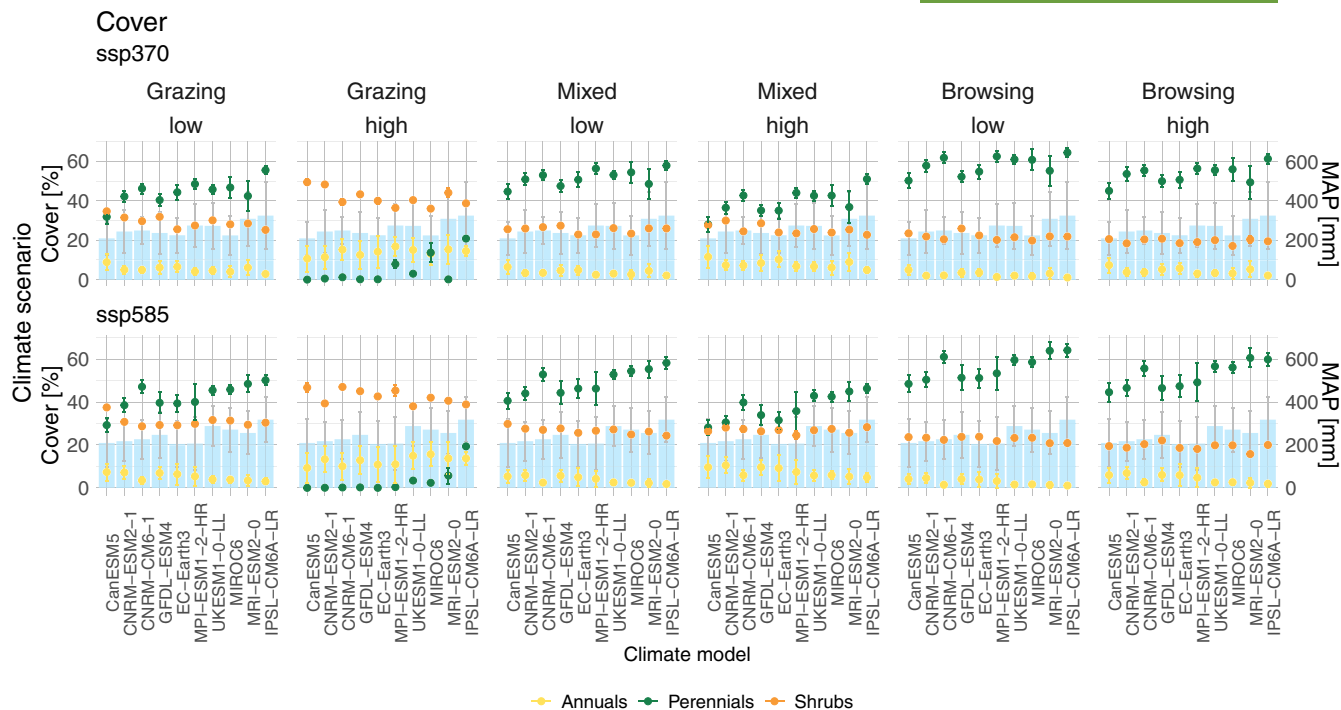


FIGURE 1 The relationship between precipitation and vegetation cover under different management. The blue bars represent the mean annual precipitation (MAP) \pm SD, while points depict the mean cover \pm SD of perennial (green), annual grasses (yellow) and shrubs (orange) averaged over the years 2089–2099. Changes shown across 10 different global climate models and two climate change scenarios under three rangeland types in two intensities.

in response to different climate projections with biggest variations in the high grazing scenario, with differences of up to 12%. The SSP585 scenario showed slightly lower grass cover and higher shrub cover than SSP370 but exhibited similar trends.

3.2 | Functional diversity

Our analysis of functional dispersion among different rangeland types and intensities revealed the importance of considering multiple sources of uncertainty, including climate scenarios and the respective model predictions and animal type/density factors. Our simulation showed that the resulting plant community was generally stable in response to different animal types, densities and climatic conditions, indicating a high resilience of the ecosystem. However, for a high density of grazing animals, we observed significant reductions in functional diversity and substantial uncertainties in response to climate projections (Figure 2; Table A.1.5). This highlights the vulnerability of high-intensity grazing systems and the importance of addressing these factors in rangeland management plans. In these cases, lower values of functional dispersion indicated that the system was dominated by species with few distinguishing characteristics. This trend was particularly evident in the SSP585 scenario, where functional diversity reduction was more pronounced. While the relationship between precipitation gradient and FDis was not clear in this analysis, we observed that IPSL-CM6A-LR—the climate

model with the highest MAP—was the only one that did not show a reduction in FDis under high grazing.

Despite the negative effects of high-intensity grazing, our analysis suggested that mixed herbivore and browsing scenarios were the most effective at maintaining species with a range of different traits, regardless of animal density.

3.3 | Water use efficiency

The analysis of WUE revealed that maintaining low animal densities resulted in similar WUE values across all rangeland types, averaging around 80% of precipitation that could be used by plants for growth (Figure 3). This low animal density helped to minimize uncertainty in the response to different climate scenarios, as the variation in WUE was lower compared to higher animal densities. Under high animal density, grazing scenarios had the lowest WUE values (65%), while browser-dominated scenarios had the highest (on average 79%), followed by mixed-feeder scenarios (on average 76%, Table A1.6). The differences between climate models or climate scenarios were not significant, but differences in animal densities were evident, with lower WUE at high intensity. For instance, high grazing intensity in the SSP585 scenario resulted in a sharp decline of WUE, with a reduction of $19.5 \pm 4\%$ compared to low grazing. However, the difference in WUE within the other rangeland types and intensities was less strong, ranging between 4% and 7%.

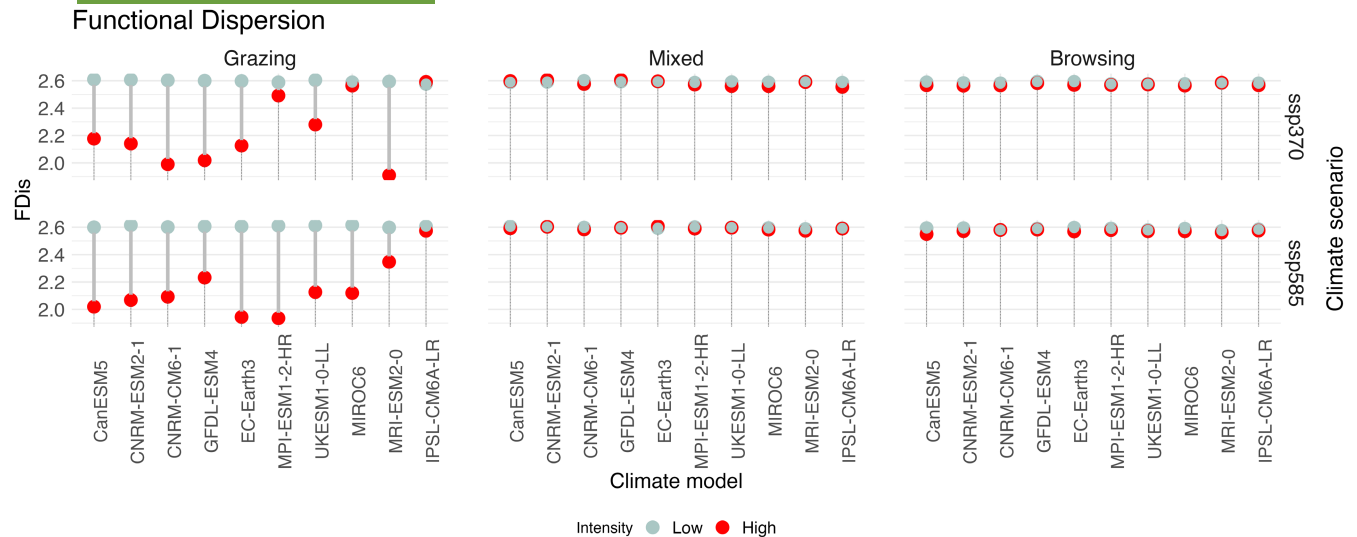


FIGURE 2 Functional dispersion (FDIs) in the last 10 years of simulation between low (grey) and high (red) land use intensity. All simulations were repeated for 10 climate models under two climate change scenarios for three rangeland types.

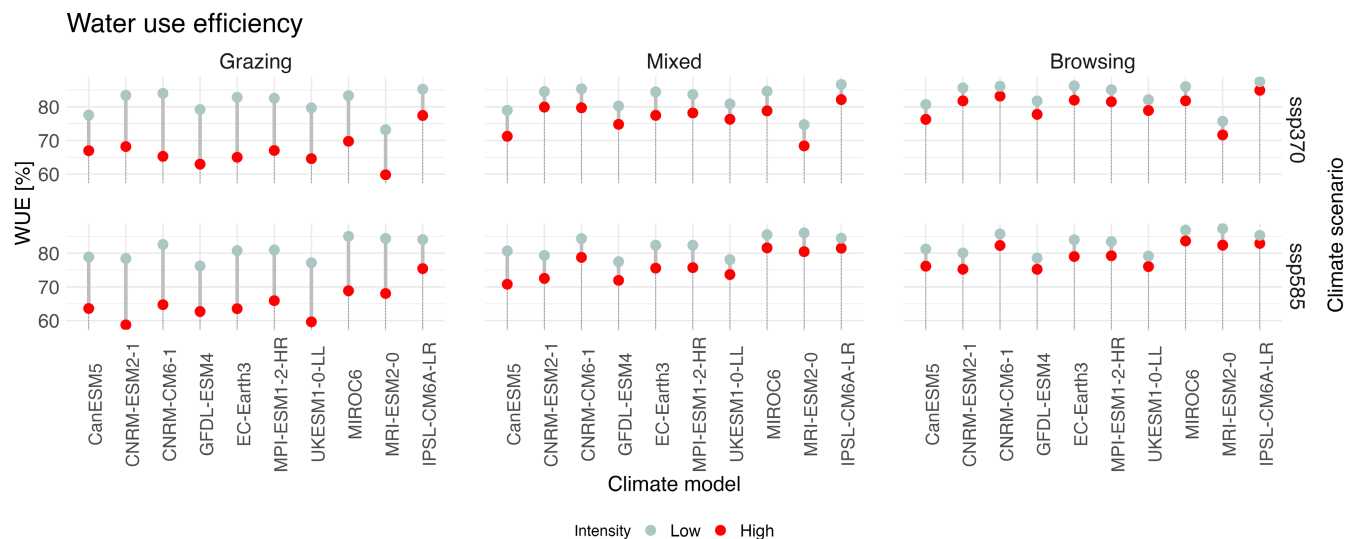


FIGURE 3 Comparison of water use efficiency (WUE) across three rangeland types with varying intensities (low = grey, high = red) using data from 10 climate models under two different climate change scenarios. The WUE values are calculated as the ratio of transpiration to annual rainfall and are shown for the final 10 years of the simulation.

3.4 | Tipping points

We found that grazing at high stocking rates was the primary driver of vegetation transitions, resulting in a shift towards a shrub-dominated state with reduced cover of perennial grasses (Figure 4; Table A.1.7). For grazing-dominated scenarios, tipping points, that is strong and normally hard-to-reverse shifts from grass-dominated to shrub-dominated Savannas, were observed in all models and climate change scenarios within the first 10 years of simulations, with the highest probability occurring in the most arid models, CanESM5 and CNRM-ESM2-1. While no tipping occurred in browsing-dominated scenarios, tipping points were also detected in the mixed scenario at high intensity. This indicates that the intensity of grass removal had a greater impact on vegetation shifts than climate change alone. The

timing of the tipping points showed a clear relationship with shrub abundance, with earlier tipping points resulting in higher shrub cover at the end of the simulation. The marginal difference in tipping point timing between climate change scenarios suggested that uncertainties related to animal type and density were more significant than those related to climate.

4 | DISCUSSION

Through our modelling approach, we were able to comprehensively explore the interplay between Savanna vegetation response to different climate scenarios and management practices. Our findings pinpointed intensive grazing as the primary factor contributing

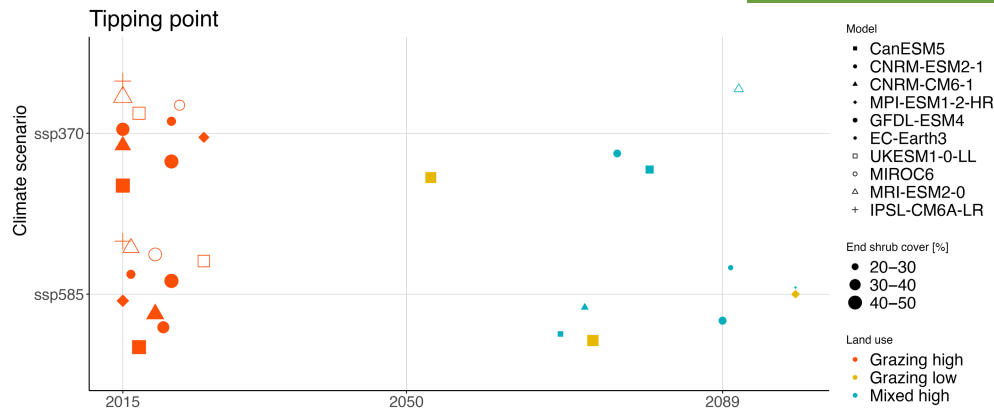


FIGURE 4 Time point (year) when a vegetation shift occurred from perennial grass to shrub dominance. Results are shown for two climate change scenarios (SSP370/SSP585) and 10 climate models. The figure only displays the cases where the vegetation shift occurred. The colour of the symbols represents the rangeland type (land use), their shape indicate the model and the symbol's size indicates the shrub cover in the last year of the simulation. The number of points for a given climate and land use scenario provides information about the uncertainty of a tipping point, which is highest for moderate numbers.

to the high probability of degradation in response to changing climatic conditions. Notably, the highest degree of uncertainty prevailed under moderate stocking rates of grazers, signifying the system's inclination to tip. This was marked by vegetation loss, shifts in composition, decreased WUE and accelerated tipping points. We demonstrated that only ecosystems with mixed and browsing herbivores exhibited greater stability across diverse climatic scenarios. This stability was attributed to the sustained higher grass cover and preserved functional diversity in these systems.

4.1 | Climate change-related uncertainty in vegetation in grazing systems

Vegetation changes are influenced by a variety of factors, including both climatic conditions and management practices. However, the effect of management practices is heavily dependent on prevailing climate conditions. While the response of grasses to water availability is well understood and predictable—grass cover increases with increasing MAP—the response of shrubs to climate change is more uncertain. This is because shrubs are not directly responsive to rainfall and are instead strongly influenced by competition with perennial grasses, as also seen in February et al. (2013). Grasses are stronger competitors for surface water due to their extensive root systems in the upper soil layer, which can limit the growth and abundance of shrubs (Case et al., 2020). The competition between shrubs and grasses helps maintain a balance between different plant species, ensuring the coexistence of diverse plant communities (Holdo & Nippert, 2023).

However, we found that the uncertainty in vegetation response was strongly correlated with grazing intensity. Overgrazing can lead to a reduction in grass biomass, which can result in more bare and unstable soil surfaces (Washington-Allen et al., 2010), with negative

consequences for plant diversity and ecosystem services such as soil conservation, water regulation and carbon sequestration (Maestre et al., 2022). Heavy grazing reduces grass cover, thereby increasing the amount of water available for shrubs, leading to a release from competition and the expansion of shrub cover. This pattern was confirmed in this study and has been observed in many overgrazed Savanna systems (Pfeiffer et al., 2019; Polley et al., 2017). The drastic reduction in grass cover in grazing systems in simulations with less precipitation may not be solely due to less rainfall. It could also result from other unpredictable water availability reductions, such as more frequent drought years, shorter growing seasons (Table 1) and less available water for plant growth (Figure A.1.6), with consequences for plant functional diversity.

The diversity of plant functional traits, as measured by FDis, is a measure of the diversity of plant functional traits within a community, and it is an important indicator of ecosystem health and resilience in rangeland management (St. James & Mallik, 2021). We found that high grazing intensity had a negative effect on functional dispersion, as also found in Chillo et al. (2017), indicating that here, one or a few similar traits dominated the system. Low functional diversity can be a warning sign of declining ecosystem health, as it is often associated with reduced grass cover, increased shrub encroachment (Ford et al., 2018; Irob, Blaum, Weiss-Aparicio, et al., 2023; Osborne et al., 2018) and low plant water availability (Castellanos et al., 2022; Irob et al., 2022). That is, the response of trait diversity to grazing pressure appeared to be considerably more uncertain when compared to the response to climate conditions.

While the response of vegetation to climate change-related uncertainty is complex and multifaceted, our findings suggested that understanding the interactions between climatic conditions, management practices and plant competition can help improve our ability to manage vegetation and promote ecosystem resilience in the face of changing environmental conditions.

4.2 | Navigating uncertainty: Best practices for vegetation and water management

4.2.1 | Best practices for risk adverse managers

If the management objective is to minimize degradation with a high level of certainty, we have identified specific principles to guide this endeavour. We found that effective management of grazing intensity and animal populations can mitigate the negative impacts of climate change on ecosystems. Specifically, we found that systems incorporating mixed herbivores and browsers, as well as those employing lower grazing intensities, exhibited greater stability in terms of perennial herbaceous plant cover and functional diversity. Despite fluctuations in grass and shrub abundance, the constancy of functional diversity implied the presence of diverse functional traits within the community, which in turn promoted the continued functioning and provision of services amid changing environmental conditions. These findings highlight the importance of managing grazing intensity and promoting functional diversity to increase the resilience of Savannas under climate change. The stable response to different climate projections suggests that diverse plant communities can adapt well to climatic variations (Carmona et al., 2012).

Degradation can also be avoided by employing rangeland management that aims at protecting grass cover, which is essential for maintaining water-related aspects impacted by climate and grazing practices. Reduced grass cover can increase the amount of bare soil, radiative heating and evaporation, which negatively affects WUE (measured as the amount of precipitation that was used for plant transpiration), leading to less effective transfer of precipitation to soil moisture and resulting in landscapes with low WUE and heterogeneous vegetation patches (Abraha et al., 2016; Tian et al., 2011). These outcomes can lead to desertification (D'Odorico & Bhattachan, 2012), that is degraded ecosystems that may not recover from environmental changes or disturbances.

However, by maintaining adequate vegetation cover and leaf area index, water loss through evapotranspiration is minimized, leading to increased water availability for ecosystem services, other purposes and the restoration of degraded ecosystems (Irob, Blaum, Weiss-Aparicio, et al., 2023; Tommasino et al., 2023).

Rangeland management that maintains high grazing pressure, especially under arid conditions, bares a high risk of causing tipping points, leading to dramatic and permanent changes in ecosystem functioning. Research by Koch et al. (2023) highlights the risk of critical transitions to a state dominated by shrub encroachment when grazing is combined with other disturbances, such as drought. Importantly, this transition does not occur during the drought itself but as a consequence of drought-induced degradation, creating favourable conditions for subsequent shrub encroachment in the following years. It is important to note that the tipping points we described are a local-scale phenomenon and may not be applicable to larger landscapes or regions.

Even in mixed scenarios with both grazers and browsers present, high animal densities can still result in tipping points, albeit later than in scenarios with predominantly grazers.

4.2.2 | Best practices for risk taking managers

If rangeland managers are open to assuming a degree of risk through the use of moderate grazer stocking rates, we recommend implementing ongoing farm monitoring to enable prompt responses. This approach may enable the pursuit of a variety of activities.

However, to reduce risks, managers should consider reducing animal densities pro-actively and during recovery phases to minimize the potential for ecosystem destabilization. Managers should prioritize promoting a more diverse herbivore community to increase ecosystem resilience to changing conditions. Low animal densities and browser-dominated rangeland types can help prevent tipping points, whereas mixed rangeland types with high animal densities present uncertain risks for ecosystem stability. Due to the uncertain impact of climate change, managers should invest in further research and monitoring to improve their understanding of ecosystem dynamics and inform effective management strategies.

Our research demonstrated that diverse herbivores and browsing species are crucial for stabilizing ecosystems, as confirmed by similar semi-arid Savanna studies (Koch et al., 2023; Scogings & Gowda, 2019). Additionally, stabilizing effects can be achieved by combining browsing herbivores and prescribed fires (Staver et al., 2009). Finally, several management tools have been identified, such as diversifying herbivore composition and lowering densities, monitoring critical ecological variables (e.g. grass cover, functional vegetation composition and soil water), enhancing functional diversity and promoting self-regulation factors that can influence ecosystem transitions.

These findings highlight the pivotal role of politicians and policy-makers in fostering Savanna resilience to climate change. By crafting incentives that encourage landowners to adopt science-based, ecologically sound management practices, politicians can stimulate positive change. These incentives can yield both ecological and economic benefits, benefiting not only landowners but also conservation efforts. This collaborative approach aligns the interests of both land managers and conservationists, driving collective action towards safeguarding the Savanna ecosystem.

5 | CONCLUSION

Future climate change projections vary significantly, posing a challenge for developing effective rangeland management strategies to enhance Savanna resilience and mitigate uncertainties. Thus, proactive and adaptive management approaches are necessary to account for the complexity and unpredictability of climate change.

Our research revealed that mixed or browser-dominated herbivore communities can yield positive results associated with less uncertainties. We observed stable vegetation cover under various

climate projections, such as low rainfall and droughts, with high functional diversity and a high WUE, highlighting the adaptability of the Savanna plant community to different precipitation and temperature conditions. Our study confirmed that the degradation of rangeland ecosystems is not solely driven by climate change, but rather by the interaction of climate change with high grazing pressure. In conclusion, our research has demonstrated that local managers have the power to prevent or facilitate transitions using various management tools at their disposal, such as diversifying herbivores, promoting plant functional diversity and reducing grazer stocking rates. Through this study, we have demonstrated that commonly employed grazer stocking rates (e.g. 10–20 ha/LSU) can result in substantial degradation. We recommend the use of mixed herbivore communities with a higher proportion of browsers as a means of maintaining a healthy, productive and resilient ecosystem while mitigating the impacts of climate change-induced disturbances.

AUTHOR CONTRIBUTIONS

Katja Irob, Britta Tietjen and Niels Blaum: Conceptualization, Methodology, Writing, Review & Editing. Katja Irob: Visualization, data curation and analysis. The concept and 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 STATEMENT

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.ngf1vhj1t>) (Irob, Blaum, & Tietjen, 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Precipitation and temperature projections from the year 2015 until 2100 predicted by 10 global climate change models under two different climate change scenarios (ssp370/585). The blue bars show annual precipitation sums. The red dashed line depicts the moving average over a 4-year window. The straight black line is the current MAP (292 mm). The orange line depicts MAT.

Figure S2. Changes in available water for plant growth in upper (a) and lower (b) soil layer. Average number of days from 2050 to 2060 compared to the average number of days between 2089 to 2099 with moisture above viable threshold. The dashed line at zero depicts the mean number of days in the decade starting 2050. The numbers to the left and right depict by how much this number increased or decreased in 50 years. Output is shown for 10 different GCMs (rows) and 2 climate change scenarios (panels) under 3 land use scenarios (columns).

Figure S3. (a) Vegetation cover under different climate change predictions in the SSP370 scenario and three rangeland types at two intensities (a: low, b: high). The simulation starts with historical (partially modelled) data in the year 1970. The horizontal line in the year 2015 depicts the start of the modelled data by the respective GCM. Blue bars in the background denote annual precipitation sums. (b) Vegetation cover under different climate change predictions in the ssp585 scenario and three rangeland types at two intensities (a: low, b: high). The simulation starts with historical (partially modelled) data in the year 1970. The horizontal line in the year 2015 depicts the start of the modelled data by the respective GCM. Blue bars in the background denote annual precipitation sums.

Appendix S1. The supporting information provides a comprehensive model description, including detailed information on rules, processes, parameters, model calibration, and validation. Additionally, it includes supplementary figures and tables relevant to this study.

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