



# The role of low temperatures, water availability and fire for the grassland biome border in South Africa

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## ABSTRACT

Understanding the controls of biome distributions is crucial for assessing terrestrial ecosystem functioning and its response to climate change. We analysed to what extent differences in climate factors (minimum temperatures, water availability, and growing season temperatures (degree days above 5 °C (GDD5)) might explain the poorly understood borders between grasslands, savannas and shrublands in eastern South Africa. The results were used to improve bioclimatic limits in the dynamic global vegetation model (DGVM) LPJ-GUESS. The vegetation model was also used to explore the role of fire in the biome borders. Results show no clear differences between the adjacent biomes in water availability. Treeless grasslands primarily occur in areas with minimum temperatures and GDD5 values below that of savannas. The standard fire module in LPJ-GUESS is not able to reproduce observed burned area patterns in the study region, but simulations with prescribed fire return intervals show that a combination of low temperatures and fire can explain the treeless state of the grassland biome. These results confirm earlier hypotheses that a combination of low winter temperatures, causing frost damage to trees, and low growing season temperatures that impede tree sapling growth and recruitment, particularly under re-occurring fires, drive the grassland-savanna border. With these insights implemented, the LPJ-GUESS simulation results substantially improved grass distribution in the grassland biome, but challenges remain concerning the grassland-shrubland boundary, tree-grass competition and prognostic fire modelling.

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## 1. Introduction

Biome shifts have significant implications for biodiversity and ecosystem services (Moncrieff et al., 2015) emphasising the need to better understand the factors that define their limits for modelling and predictive purposes (Potts et al., 2015; Stevens et al., 2017). Dynamic global vegetation models (DGVMs) are employed to predict vegetation patterns on both regional and global scales based on multiple factors such as climatic tolerance and fire disturbance (Prentice et al., 2007; Scheiter et al., 2013; McLauchlan et al., 2020; Huntley et al., 2021; Argles et al., 2022). However, some bioclimatic limits and assumptions used in DGVMs have not been re-evaluated since their initial inclusion (Lüdeke et al., 1994; Smith et al., 2001; Bondeau et al., 2007; Schaphoff et al., 2018). And despite the availability of new process-based understanding of ecosystems and improved climate datasets, these resources have not been fully utilised.

DGVMs play a crucial role in studying biome boundaries by incorporating existing knowledge and assumptions about vegetation tolerance to climate conditions, here onwards referred to as “bioclimatic limits”. These limits determine suitable areas for plant functional types (PFTs) (Prentice et al., 1992; Smith et al., 2001). DGVMs leverage the existing understanding of plant behaviour by simulating climate’s direct influence on biome boundaries. They also simulate disturbance regimes and competition among PFTs (Friend et al., 2013), exploring the non-climatic factors affecting biome limits. However, DGVMs limitations are apparent when applied regionally, as they were primarily designed for continental and global scales (e.g., Sorokina et al., 2012; Moncrieff et al., 2015). Nevertheless, research conducted by Bond et al. (2003, 2005) and Moncrieff et al. (2015) have demonstrated the effectiveness of DGVMs in simulating the dynamics between woody and grassy vegetation. Utilising the latest climate data offers an opportunity to further test and synthesise experimental findings and observations into a mechanistic modelling framework, such as a DGVM.

The South African grassland biome, surrounded by shrub-dominated nama-karoo and woody-grass mixed savanna biomes, is a unique case study. Extensive research has focused on understanding

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factors governing the biome boundaries, especially with the savanna biome. Despite similar climates, tropical trees grow in savanna but not in grassland (Wakeling et al., 2012). Temperate trees, normally sensitive to fire, grow in the grassland biome only in extremely rare instances: either in fire-protected topographic refugia (eg, surrounded by rocks) or in already forested areas with low fire spread rate and limited fuel availability (Adie et al., 2017).

Evidence suggests that a combination of frost damage, fire damage, and slow growth due to low temperatures prevents trees from colonising the grasslands. Transplant experiments by Stevens et al. (2018) demonstrated the capability of savanna tree seedlings to survive in the grasslands, however, they were susceptible to frost damage, experiencing "top-kill" (ie. complete loss of above-ground biomass) but were able to resprout from below ground. Stevens et al. (2018) research further indicated that seedlings experienced slow growth due to grass competition and concluded that species distribution was dependent on the likelihood of escaping fire. Additionally, according to Higgins et al. (2007), fire plays a significant role in shaping the structure of savannas.

Russell and Tedder (2020) investigated the impact of frost on *Vachellia Sieberiana*, a common southern African savanna tree with potential encroachment into high-altitude grasslands. They found that temperatures below  $-6^{\circ}\text{C}$  limit tree establishment (graduation of a sapling into an adult tree) but not recruitment (graduation of a seedling to a sapling) or seed germination. Some saplings are susceptible to a "frost-trap" (repeated top-kill by frost which prevents trees from growing bigger) and other disturbances hindering productive maturity. Similarly, Wakeling et al. (2012) indicated slow tree growth in upland grasslands due to low temperatures, impeding maturity under frequent fire regimes. These findings align with observations by Low and Rebelo (1996), Bond et al. (2003), and Smit et al. (2016) that frosts and repeated high fires maintain grass dominance, prevent tree establishment or lead to tree loss.

Extensive studies have explored the dynamics of the grassland and nama-karoo boundary (Low and Rebelo, 1996). The transition of the two biomes occurs over a rainfall gradient, receiving between 380 mm of rain at the nama-karoo end and 450 mm at the grassland end (Zucchini and Nenadić, 2006). The boundary is said to be partly determined by the amount of rainfall and plant-available soil moisture (du Toit et al., 2015; Masubelele et al., 2015). Higher rainfall promotes grass dominance and thus fire spread (Bond et al., 2003). In contrast, shrubs are more sensitive to fires compared to grasses and increased fire frequency will reduce their competitive strength and capacity to regenerate (van Wilgen, 2013). According to Masubelele et al. (2014) there is an increase in grass and a decrease in dwarf shrubs across this boundary. This is in agreement with research by du Toit (2015), indicating that fires in the boundary result in grasses encroaching into the nama-karoo while removing dwarf shrubs. The research by du Toit et al. (2015) indicated that enough fire (no exact magnitude mentioned) will lead to shifts from dwarf-shrub to grass-dominated vegetation in the nama-karoo. Similar to the savanna boundary, the factors affecting the boundary warrant further investigation with spatial analysis or mechanistic models.

This study examines several factors that have been previously formulated and empirically tested with other methods. By critically evaluating these factors with a different approach and new data, we aim to explore their applicability and relevance. 1. The assumption that tropical trees cannot withstand freezing temperatures, a concept implemented in many DGVMs (Lüdeke et al. 1994; Smith et al., 2001; Bondeau et al., 2007; Schaphoff et al., 2018) and supported by recent research (Wakeling et al., 2012; Stevens et al., 2018; Russell and Tedder, 2020). In some DGVMs this assumption is applied by restricting tropical tree occurrence to regions with an average monthly temperature of the coldest month above  $15.5^{\circ}\text{C}$ , which excludes areas with daily frost events (Prentice et al., 1992; Sitch et al., 2003; Smith et al., 2014) as such monthly temperatures globally correlate with

occasional short frost periods; 2. The idea that water availability is a critical factor in defining the grassland biome existence, implying that increased soil water availability leads to increased grass competition (du Toit et al., 2015); 3. The notion that low growing season temperatures impede tree growth and maturity under regular fire in upland grasslands (Wakeling et al., 2012). We investigate if accumulated heat (quantified by cumulative growing degree days above a  $5^{\circ}$  base, GDD5) controls woody vegetation's ability to surpass local disturbance regimes; 4. The role of fire as the primary disturbance agent in mesic C4 grasses, significantly influencing tree distribution in open grassland systems (Bond et al., 2003; Bond, 2016; Pausas and Ribeiro, 2017; Botha et al., 2020). In this study, we assess the importance of these factors by investigating various climate factors such as minimum temperatures, water availability, and growing season temperatures (specifically, degree days above  $5^{\circ}\text{C}$  or GDD5) in how they play a role in maintaining the predominantly grass-dominated grassland biome without trees. To do this, we use the latest, high-resolution climate data available. Additionally, to assess the impact of fire, we employ the LPJ-GUESS DGVM (Smith et al., 2014) to analyse the threshold of fire frequency required to eliminate trees within the grassland ecosystem by prescribing it. Finally, we adjust LPJ-GUESS for our study region based on our climate analysis findings. By doing so, we aim to determine if incorporating new insights into ecosystem processes and utilising improved climate datasets can enhance the accuracy of model simulations.

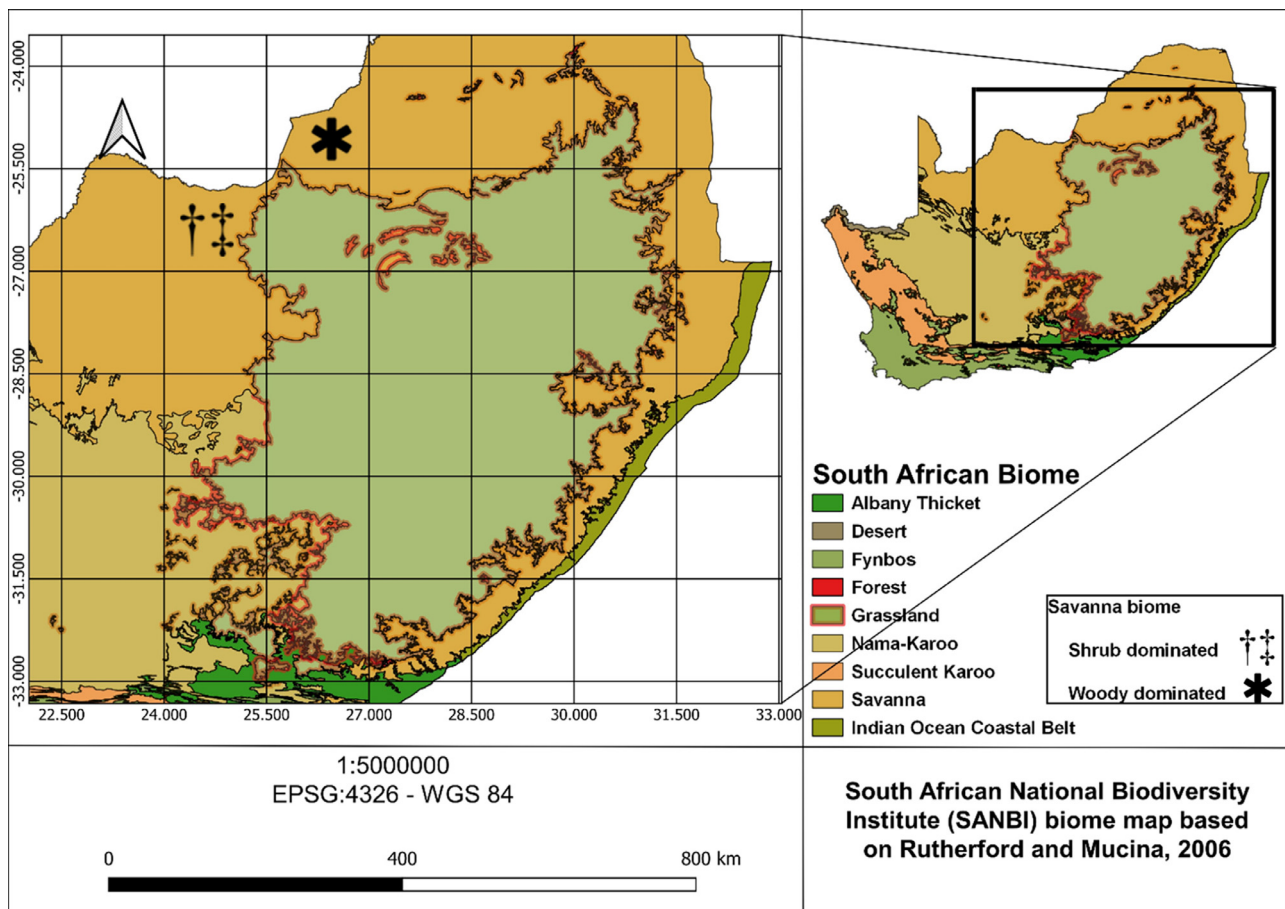
## 2. Materials and methods

### 2.1. Study region and biomes

South Africa is known for its varied terrain, ranging from forests and grasslands to deserts (Guo et al., 2017). In this study we use the biome classification developed by the South African National Biodiversity Institute (SANBI) developed and recorded in Rutherford et al. (2006). This classification comprises 7 biomes (Fig. 1): grassland, savanna, nama-karoo, albania thicket, fynbos, succulent-karoo, Indian Ocean coastal belt (IOCB) and the desert (Rutherford et al., 2006; Knowles et al., 2015; Schoeman and Monadjem, 2018). These biomes range from arid, in the west, to humid subtropical in the north and east, while much of the central part of Southern Africa is classified as semi-arid and the southwest as Mediterranean (Cooper et al., 2004; Daron, 2015). South Africa receives winter rainfall in the southwestern part and summer rainfall in other parts of the country (Rutherford et al., 2006). In this study we focus on the grassland biome and its boundaries with savanna, and nama-karoo (located between latitudes  $-24^{\circ}$  and  $-33^{\circ}$  and between longitudes  $22^{\circ}$  and  $33^{\circ}$ ) since they are ecologically interlinked (Palmer and Anslie, 1918).

#### 2.1.1. Savanna biome

The savanna biome covers approximately 46% of southern Africa, making it the largest biome in the region occupying over one-third of South Africa's total area (Low and Rebelo, 1996). The savanna is described as a biome distinguished through its continuous grass vegetation layers and distinct trees and/or shrubs layers (Bond and Midgley, 2012; Tokozwayo et al., 2021). The ratio of grasses to trees varies considerably among savanna vegetation types (Chidumayo, 2001). In tree-dominated savanna areas vegetation height varies from 1 to 20 m, while in shrub-dominated areas it ranges from 3 to 7 m. The savanna trees consist of evergreen and deciduous species (Masia et al., 2018). Rainfall varies from 235 to 1 000 mm per year. Near-annual fires occur in the biome due to summer rains, which allow for high fuel loads. Nearly all species are adapted to survive fires, with less than 10% of plants killed by fire (Low and Rebelo, 1996). The grass layer is dominated by C4 grasses and where rainfall has a stronger winter component or is too cold, C3 grasses dominate (Low and Rebelo, 1996; Rutherford et al., 2006).



**Fig. 1.** The South African National Biodiversity Institute (SANBI) biome map shows all nine biome systems based on Rutherford et al., 2006. This study focuses only on the Grassland/Savanna and Grassland>Nama-Karoo boundaries. †† marks the western savanna where the woody vegetation is dominated by shrubs and \* marks the eastern savanna region where woody vegetation is dominated by trees (Rutherford et al., 2006; Kurzweg, 2011).

The savanna biome is further divided into bioregions, the two major ones being Central bushveld in the north of South African savanna and Eastern Kalahari bushveld in the west of the savanna (Rutherford et al., 2006). The central bushveld is dominated by broad leaved deciduous tree species (Acacia trees) with a small layer dominated by grass species (Kurzweg, 2011), while the Eastern Kalahari bushveld is characterised by a prominent shrub layer predominantly composed of drought-tolerant shrubs, complemented by sporadic occurrences of small drought-resistant trees such as camelthorn and shepherd's tree (Rutherford et al., 2006).

### 2.1.2. Nama karoo biome

The nama-karoo Biome lies on the central plateau of the western half of the country (Mucina et al., 2006a). The nama-karoo gives way to arid grassland along its eastern border (du Toit et al., 2015). The transition between the nama-karoo and grassland has been recorded to fluctuate for many years depending on drought and rainy conditions (Mucina et al., 2006b; du Toit et al., 2015). The biome receives summer rainfall which varies between 100 and 520 mm per year. The vegetation consists of perennial grasses, annual grasses and perennial dwarf shrubs (Low and Rebelo, 1996; du Toit et al., 2015). Deciduous C4 grasses dominate due to heat and summer rains. Fires are rare due to insufficient fuel load (Low and Rebelo, 1996).

### 2.1.3. Grassland biome

The grassland Biome is located on the high central plateau of South Africa, and the inland eastern parts of the country. The rainfall varies from 400 to 2500 mm per year (Rutherford et al., 2006). C4

grasses dominate throughout the biome, except at the highest altitudes where C3 grasses are more prominent. Trees are absent, except in a few localised habitats, consisting of temperate trees. Grass plants tolerate fire, by using various strategies to immediately produce new stems (Bond et al., 2003). The grassland biome is where majority of maize cropping takes place and many grassland types have been converted to this crop (Rutherford et al., 2006).

## 2.2. Data sources

### 2.2.1. Meteorological data

Climate data from the ERA5-Land dataset were used both for investigating climatic limits and driving the LPJ-GUESS simulations. ERA5-Land is a reanalysis dataset. ERA5-Land has been produced by replaying the land component of the ECMWF ERA5 climate reanalysis Muñoz (2019). The data availability spans from January 1950 to the current date. The data is provided on a daily time scale and on a  $0.1 \times 0.1^\circ$  grid.

For investigating the bioclimatic limits we examined climate over a 20-year period from 1986 to 2005 (corresponding to the period immediately preceding the definition of the South African Biodiversity Institution (SANBI) biomes (Rutherford et al., 2006) (Fig. 1). Over this period we calculated (i) the coldest daily mean temperature (dtmin), (ii) the coldest monthly mean temperature (mtmin) and (iii) the 20-year mean of the coldest monthly mean temperature (mtmin\_mean20).

We further calculated water deficit which in this study is defined as the difference between annual precipitation and potential

evapotranspiration. The input parameters which were processed and used by LPJ-GUESS for this study were: 2 m dewpoint temperature, 2 m temperature, surface net solar radiation, surface solar radiation downwards, 10 m u-component of wind, 10 m v-component of wind and total precipitation. The data was processed using the Climate Data Operators (CDO) platform (Schulzweida, 2019).

### 2.2.2. Soil data

LPJ-GUESS requires soil texture (clay, silt, and sand fractions) for determining soil hydrological properties. For this study these were taken from the Harmonized World Soil Database v 1.2 (Fischer et al., 2008), a 30 arc-second raster database with over 15 000 different soil mapping units that combine existing regional and national updates of soil information worldwide (SOTER, ESD, Soil Map of China, WISE) with the information contained within the 1:5 000 000 scale FAO-UNESCO Soil Map of the World (FAO, 1971–1981). The data was cropped to the study region using one of the climate data NetCDF files. The data was then aggregated and resampled to a  $0.1 \times 0.1^\circ$  resolution to match the climate data.

### 2.3. Climate and disturbance factor analysis

We compared histograms of relevant climate variables from the ERA5-Land climate data (Section 2.2.1) for each biome to test for all the climate factors (minimum temperatures, water availability, and growing season temperatures (degree days above  $5^\circ\text{C}$  (GDD5)). If the histograms had extensive overlap, the factors were not supported since the biomes would exist in similar climate spaces. If the histograms showed little or no overlap, the factors were thus supported by data. LPJ-GUESS was then used to explore the impacts of new climate limits.

## 2.4. The LPJ-GUESS model and set-up

### 2.4.1. Model description

The Lund-Potsdam-Jena (LPJ) model has been developed as a process-based DGVM which can efficiently represent the land-atmosphere interaction and potentially be applied for broader global problems (Sitch et al., 2003). The Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) framework was originally developed to add a more detailed representation of vegetation dynamics through a 'forest-gap model' to the LPJ DGVM (Smith et al., 2001; Smith et al., 2014). Thus LPJ-GUESS is an individual (or cohort) based model which combines biogeography and biogeochemistry typical of a DGVM with a comparatively more detailed individual and patch-based PFT representation of vegetation structure, demography, growth, mortality, reproduction, carbon allocation and resource competition (Smith, 2001). The model now includes an interactive nitrogen cycle (Smith et al., 2014), which can limit photosynthesis and so is important to constrain future potential  $\text{CO}_2$  fertilisation effects (Hickler et al., 2015).

In the framework, productivity is simulated as the emergent outcome of growth and competition for light, space and soil resources among woody plant individuals and a herbaceous understory in a number of a replicate patches (typically 15–50) representing 'random samples' of each simulated locality or grid cell (Smith, 2001).

In this study, we used the standard version of the cohort based LPJ-GUESS model using 20 replicate patches at a spatial resolution of  $0.1 \times 0.1^\circ$ . Climate forcing data from the ERA5-Land dataset (details above) were used. The standard global plant functional types (PFTs) analysed in our model were: temperate broadleaf summergreen (TeBS), shade-intolerant broadleaf summergreen (IBS), temperate broadleaf evergreen (TeBE), tropical broadleaf evergreen (TrBE), tropical shade-intolerant broadleaf evergreen (TrIBE), tropical broadleaf raingreen (TrBR), C3 grasses (C3G), C4 grasses (C4G). In addition, we

tested the inclusion of shrub PFTs from a global PFT parameterisation Allen et al. (2020) which are not included in the current standard: temperate evergreen shrubs (TeESh), temperate raingreen shrubs (TeRSh), temperate summergreen shrubs (TeSSh), tropical evergreen shrubs (TrESh) and tropical raingreen shrubs (TrRSh). The model output includes LAI ( $\text{m}^2 \text{m}^{-2}$ ) and burnt area fraction among other outputs. The model was run on a daily time step. All simulations were initialised with a 500-year spinup to allow vegetation, soil carbon and nitrogen pools to build up from "bare ground" to a "steady state" and then the full transient period (1901–2018) was simulated.

### 2.4.2. Fire models in LPJ-GUESS

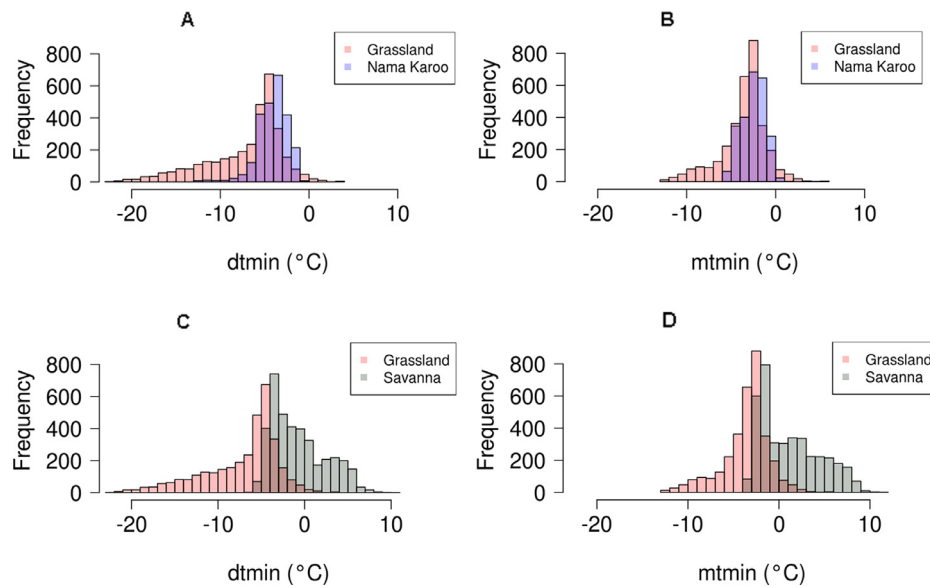
Fire was enabled through the SIMFIRE-BLAZE fire model (Knorr et al., 2016; Nieradzik et al., 2015) and SPITFIRE (SPread and InTensity of FIRE) (Thonicke et al., 2010). SPITFIRE calculates burnt area by explicitly simulating both the number of fires and fire size. Potential fire ignitions from humans and lightning are simulated and converted to actual ignitions based on fire weather. Fire size is calculated on rate of spread calculated from the Rothemel (1972) equations and a duration determined by fire weather. SIMFIRE-BLAZE calculates burnt area using an empirically-fitted function of population density, fire weather and fraction of absorbed photosynthetic radiation. Woody plant mortality in both models depends on both fire intensity and tree size (Rabin et al., 2017), so both can simulate the "fire-trap" where small trees are easily killed by fire but larger trees can survive fires depending on their size and the intensity of the fire. However, details of the implementation of mortality differ between the two. SPITFIRE resolves two mortality processes explicitly - cambial kill and crown scorch - and uses PFT specific parameters to represent both the characteristics of the fire (flame height, residence time) and the tree resistance (bark thickness, resistance to crown scorch, crown length). Thus fire-resistant PFTs (in this case tropical raingreen trees) have a better chance of surviving fires than other PFTs. SIMFIRE-BLAZE uses biome-specific mortality factors which uses an internal biome classification based on the vegetation in the gridcell. Neither model considers topkill as a distinct process, and LPJ-GUESS does not feature resprouting PFTs.

### 2.4.3. Regionalised vegetation configurations

We implemented the modified bioclimatic limits that emerged from the climate factor analysis in LPJ-GUESS, to develop an improved regional version. We also ran the model with and without temperate trees. In the model, the remaining tropical trees are then restricted to occur in areas with an average monthly temperature of the coldest month above  $15.5^\circ\text{C}$  (20-year average). In the global model version, this limit is implemented to exclude tropical trees from areas with occasional daily frost. It was developed before the existence of reasonable daily global weather data sets. The very strong distinction between tropical trees and temperate trees in the global model can create artefacts at the regional scale, where nature is less binary than in the model and intermediate tree types exist. To exclude such artefacts, we applied the new bioclimatic limits to all trees in the model and included a simulation without temperate trees, which are rare in the study region in any case (see above). The simulations were conducted using SIMFIRE-BLAZE because of its reasonable burnt area patterns.

### 2.4.4. Simulations with fixed fire return intervals

LPJ-GUESS-SPITFIRE was used to examine the fire disturbance by performing fixed fire experiments to see vegetation response to different fire return intervals (spatially constant). SPITFIRE was chosen over SIMFIRE-BLAZE because its PFT-specific approach aligns better with the goals of the study than SIMFIRE-BLAZE's biome-specific approach. Specifically, the PFT-specific approach allows fire resistance to vary between PFTs and enables a continuous response of mortality to changing vegetation (which may nonetheless exhibit



**Fig. 2.** Distribution of minimum temperature for the grassland/nama-karoo and grassland/savanna biomes for the period 1986–2005. The figure demonstrates overlaps of histograms to identify the minimum temperature limit between biomes.

threshold behaviour). In contrast, the biome-specific approach does not allow some PFTs to have greater fire resistance than others and produces discrete changes in the mortality processes as the vegetation changes, both of which are undesirable in this case.

### 2.5. Analysis software

The R statistical programming language version v4.2.2 was used for processing and for statistical analysis of the data. We used the DGVMTools R package to perform comparisons, analysis and plotting of the spatially explicit simulated and remotely sensed LAI and burnt area distribution across the study region. DGVMTools is a high-level framework for processing, analysing and visualising DGVM data output which easily interfaces with both the raster package and base R functionality. The ggplot2 package (Wickham, 2016) was used for additional plotting and analysis.

## 3. Results

### 3.1. Minimum temperature

The histograms indicate considerably lower temperatures within the grassland compared to the savanna and the nama-karoo (Fig. 2). The savanna biome reaches a low of  $-4^{\circ}\text{C}$  for mtmin and  $-6^{\circ}\text{C}$  for dtmin (Fig. 2C and D), while the grassland reaches dtmin as low as  $-22^{\circ}\text{C}$  (Fig. 2A and C). The results indicate a substantial overlap between the nama-karoo and grassland minimum temperatures, implying no support for minimum temperatures as a decisive factor controlling this boundary (Fig. 2A and B). In contrast, the boundary between the savanna and grassland biomes appears to be more distinct (Fig. 2C and D), suggesting that a minimum temperature limit may influence the establishment of tropical savanna trees and, consequently, the grassland-savanna boundary.

Simple spatial plotting reveals that a dtmin of  $-2^{\circ}\text{C}$ , an mtmin of  $4^{\circ}\text{C}$  and an mtmin\_mean20 of  $7.5^{\circ}\text{C}$  effectively defines the northern and eastern margins of the grassland biome (Fig. 3A, B and D). The 20-year mean coldest month temperature of  $15.5^{\circ}\text{C}$ , displayed in Fig. 3C, fails to define the grassland biome, with the biome limit being set at least 150 km too early along the warm-to-cool temperature gradient.

### 3.2. Water deficit

The histograms in Fig. 4 depict the distribution of water deficit of the grassland, nama-karoo and savanna biomes during the period 1986–2005. There is considerable separation in water deficit between the grassland and the other biomes (Fig. 4). The nama-karoo biome exclusively thrives at water deficits below  $-1200\text{ mm}$ , indicative of areas with comparatively low water availability. Thus, a potential boundary limit of  $-1200\text{ mm}$  for water deficit could be applied to the nama-karoo boundary. However, approximately half the grassland area also experiences a water deficit below  $-1200\text{ mm}$ , rendering a direct bioclimatic limit unsuitable. In comparing the grassland and savanna, it is evident that the savanna occurs at lower water deficit values, yet significant overlap exists (Fig. 4B). This implies that water deficit alone cannot be considered the primary factor governing the boundary between these two biomes.

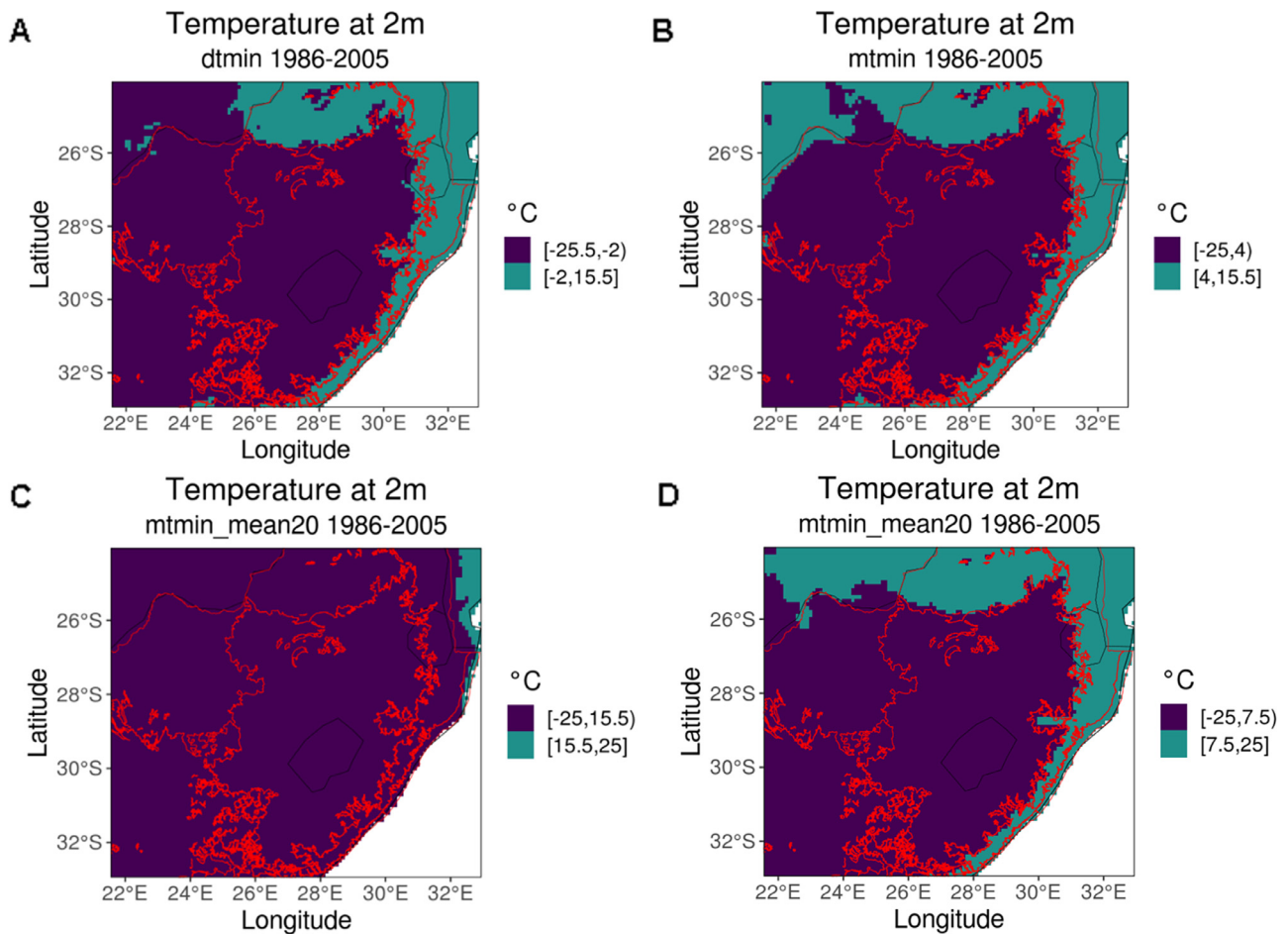
### 3.3. Growing degree days (GDD5)

The histograms depict the distribution of GDD5 ranges of the grassland, nama-karoo and savanna biomes during the period 1986–2005 (Fig. 5). The results indicate a notable degree of overlap, lacking a distinct definition of the nama-karoo and grassland boundary (Fig. 5A). However, reasonable separation is observed along the savanna and grassland boundary, with minimal savanna presence below a GDD5 of  $3800^{\circ}\text{C days}$  and, conversely, minimal grasslands occurring above  $4800^{\circ}\text{C days}$ . Consequently, a relatively narrow range of overlap exists between the biomes with a switch in dominance occurring sharply around  $4500^{\circ}\text{C days}$ .

Fig. 6 illustrates lower GDD5 experienced in the interior highlands of the region. The map highlights a clear boundary separation between the savanna and the grasslands at higher elevations in the east. However, no distinct separation is observed on the western side between the grassland and the nama-karoo, nor with parts of the savanna in the west.

### 3.4. Fire return interval required for grassland formation

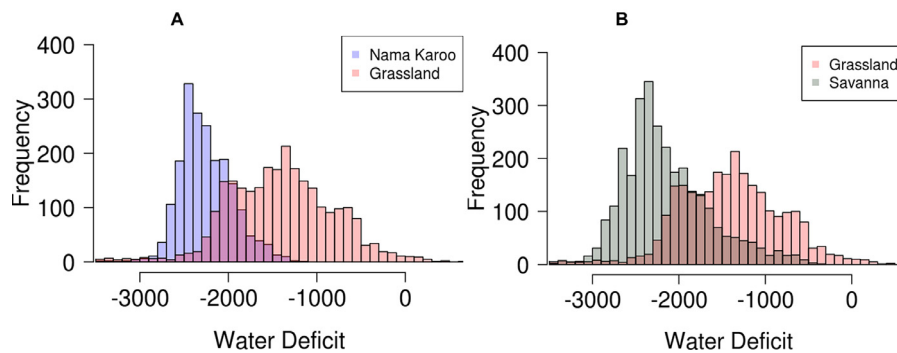
When applying successively higher fixed fire return intervals (FRI) in LPJ-GUESS-SPITFIRE (Fig. 7) we observe a gradual increase in woody biomass with increasing FRI, accompanied by a more



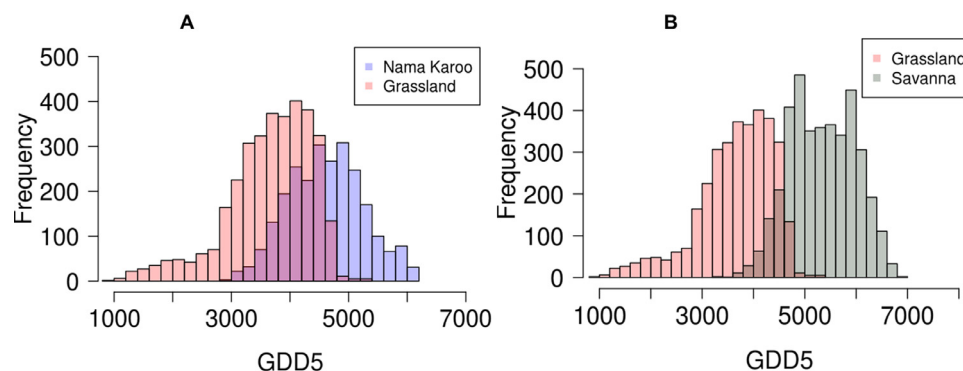
**Fig. 3.** Comparison of minimum temperature limits around the South African grassland. A) the coldest daily mean temperature (dtmin) limit of  $-2^{\circ}\text{C}$  B) the coldest monthly mean temperature (mtmin) limit of  $4^{\circ}\text{C}$  C) the 20-year mean of the coldest monthly mean temperature (mtmin\_mean20) of  $15.5^{\circ}\text{C}$  (often implemented in global vegetation models and DGVMs) D) the 20-year mean of the coldest monthly mean temperature (mtmin\_mean20) of  $7.5^{\circ}\text{C}$  (defines the north and eastern boundary of South African grassland). The spectral representation indicates the minimum temperature limit with dark violet and turquoise respectively indicating regions falling below and within the minimum temperature suitable for tropical tree growth.

pronounced rise in grass biomass, peaking at approximately 4–5 years. Subsequently, grass biomass decreases as woody vegetation is established. Biome comparisons indicate that savanna accumulates woody biomass more rapidly than grassland and nama-karoo, signifying both a high capacity for tree growth and resistance to moderate frequent fires. Additionally, the savanna maintains the highest level of grass biomass at high FRI, suggesting reasonable simulation of a mixed grass-woody system by LPJ-GUESS-SPITFIRE across

various FRIs. Grassland exhibits the highest grass biomass at frequent fires but experiences a decline to the lowest values at infrequent fires. Interestingly, these low grass biomass values are due to intense suppression by woody vegetation - in fact at high fire return intervals the grassland supports the highest woody biomass of all the biomes, indicating that trees could potentially thrive in the grasslands if they can overcome the disturbance regime. Nama-karoo simulations consistently portray the lowest woody biomass across FRIs compared to



**Fig. 4.** Distribution of water deficit for the grassland/nama-karoo and grassland/savanna biomes for the period 1986–2005. The figure demonstrates overlaps of histograms to identify water deficit limits between biomes.



**Fig. 5.** Distribution of Growing degree days above a 5 °C base (GDD5) for the grassland/nama-karoo and grassland/savanna biomes for the period 1986–2005. The figure demonstrates overlaps of histograms to identify the GDD5 limit between biomes.

grassland and savanna. However, nama-karoo maintains higher grass biomass at infrequent fire frequencies compared to grassland due to less competition from woody vegetation.

### 3.5. Bioclimatic limit implementation into LPJ-GUESS

Fig. 8 presents LPJ-GUESS standard results for the simulated Leaf Area Index (LAI) and the results with new developments informed by findings of this study. As the results above show a dtmin limit of  $-2^{\circ}\text{C}$  best distinguishes grassland from savanna vegetation, this limit was implemented here for all trees (“dtmin  $-2$ ”). In addition, results without temperate trees (“No Te trees”) and LPJ-GUESS with shrub PFTs included (“shrubs”) are shown. The standard LPJ-GUESS model simulates the presence of trees growing within the grassland, contrary to actual ecological conditions. Upon removing temperate trees, grasses dominate the grassland biome, but trees are also removed from adjacent savanna areas. Thus, the coldest month bioclimatic limit for tropical trees in the global standard version restricts tropical trees too much in the study in the region. The introduction of shrubs highlights the competition between trees and shrubs, with shrubs establishing to a degree in many places, but to a lesser extent in areas with stronger tree competition. Implementing the new dtmin limit for all trees removes trees from the grassland biome and still allows their existence in adjacent savanna areas. (Fig. 8, Grass “dtmin  $-2$ ”). This establishes a clear boundary in the northern and eastern sides of

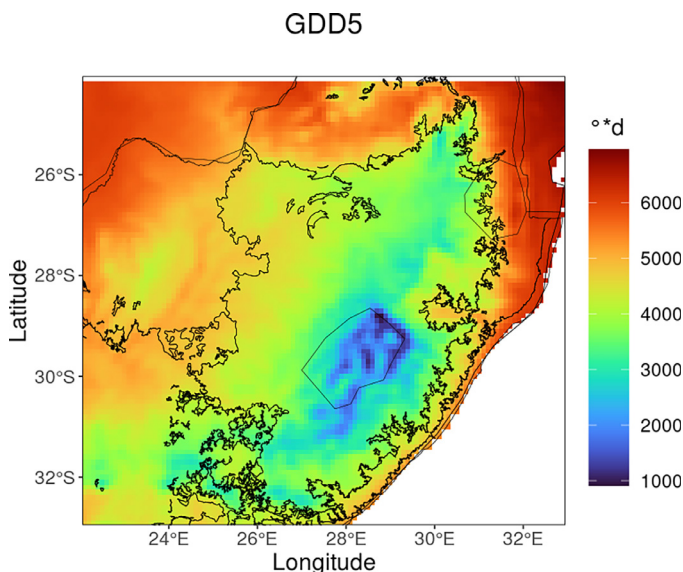
the grassland biome (Fig. 8, Tree “dtmin  $-2$ ”), but inadequately defines the western boundary with the savanna and nama-karoo. The “Regionalised” simulation reveals a comprehensively delineated grassland biome affirming the success of our grassland biome modelling attempts.

## 4. Discussion

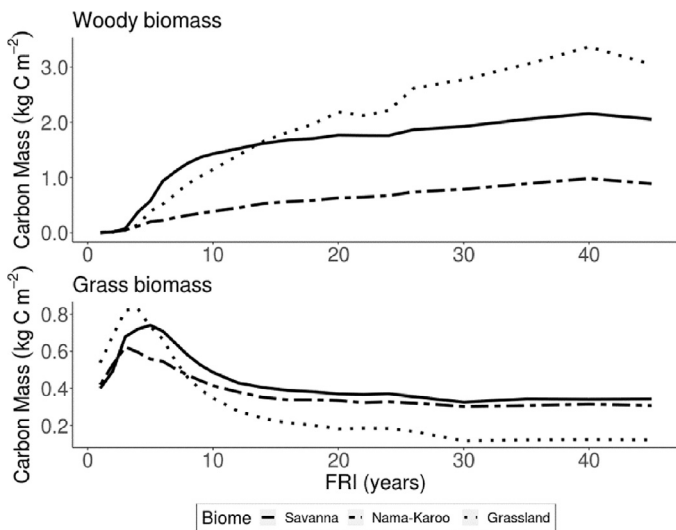
Our findings support the hypothesis proposed by multiple authors that low minimum temperatures, which cause frost damage to trees, and low growing season temperatures (here GDD5), which impede sapling growth, are critical limit determinants in maintaining the treeless state of the grassland biome in South Africa (Wakeling et al., 2012; Stevens et al., 2018; Russell and Tedder, 2020). The effects of growing season temperature most likely work in combination with fire (Huang et al., 2021; Zomer et al., 2022), which is also confirmed by the vegetation model simulations here with different fire return intervals, but modelling these complex interactions in a fully prognostic way is still challenging. The dtmin of  $-2^{\circ}\text{C}$ , mtmin of  $4^{\circ}\text{C}$  and mtmin\_mean20 of  $7.5^{\circ}\text{C}$  can be used as alternatives to define the South African north and eastern boundary of the grassland depending on the available data.

In contrast, grassland biome borders cannot be explained by thresholds in water availability. This is not to say that the respective processes of water availability are not important in defining the biomes, but rather that they cannot be directly quantified into a single limit. While past research emphasises the role of water availability in shaping the grassland and nama-karoo border (du Toit et al., 2015), the absence of an ecological rationale restricting shrub growth in grassland (without invoking disturbance) poses a challenge in establishing meaningful limits concerning water availability. Frequent fires likely keep shrubs out of the grassland since most shrubs are sensitive to fires and increased fire frequency does reduce their competitive strength and capacity to regenerate (van Wilgen, 2013). Herbivory could also impact the Karoo-grassland border. Acocks (1953), for example, observed heavy invasion of shrubs into heavily grazed grassland, but parameterising such interactions in a process-based model would require further research.

Reproducing fire patterns in the region proved challenging for the tested global fire models, with both SIMFIRE-BLAZE and SPITFIRE producing inaccurate burnt area patterns (Fig. S.1). SPITFIRE with only lightning ignitions follows the distribution from SIMFIRE-BLAZE but when human ignitions are introduced an overestimation of fire is observed, highlighting the models’ limitations. However, the hypothetical fixed fire experiments highlighted an approximate FRI of 4 years as sufficient to remove trees in the grassland. Notably, this falls within the median range of fire return intervals (1.7 to 10 years) observed in the grassland and savanna systems of southern Africa, as shown by Archibald (2010). Other studies from Brooke et al. (2018)



**Fig. 6.** Spatial distribution of annual mean growing degree days above 5 °C (GDD5) for the period 1986 to 2005.



**Fig. 7.** Illustrates the representation of carbon mass for grass and woody vegetation (expressed in kg C m<sup>-2</sup>) averaged for each biome. The vertical axis (Y-axis) denotes standing biomass, while the horizontal axis (X-axis) represents the fire return interval (years).

and Smith et al. (2013) have shown that FRI of 2 to 3 years maintain an open grassland state. This is consistent with the observed FRIs at the margins of the grasslands (Fig. S.1) where we expect a quasi-natural fire regime because there are hardly any croplands in this area. The high grass biomass at frequent FRIs, and decline to the lowest values at infrequent fires in grassland, highlights the important role of fires in maintaining the biome (Ribeiro et al., 2019).

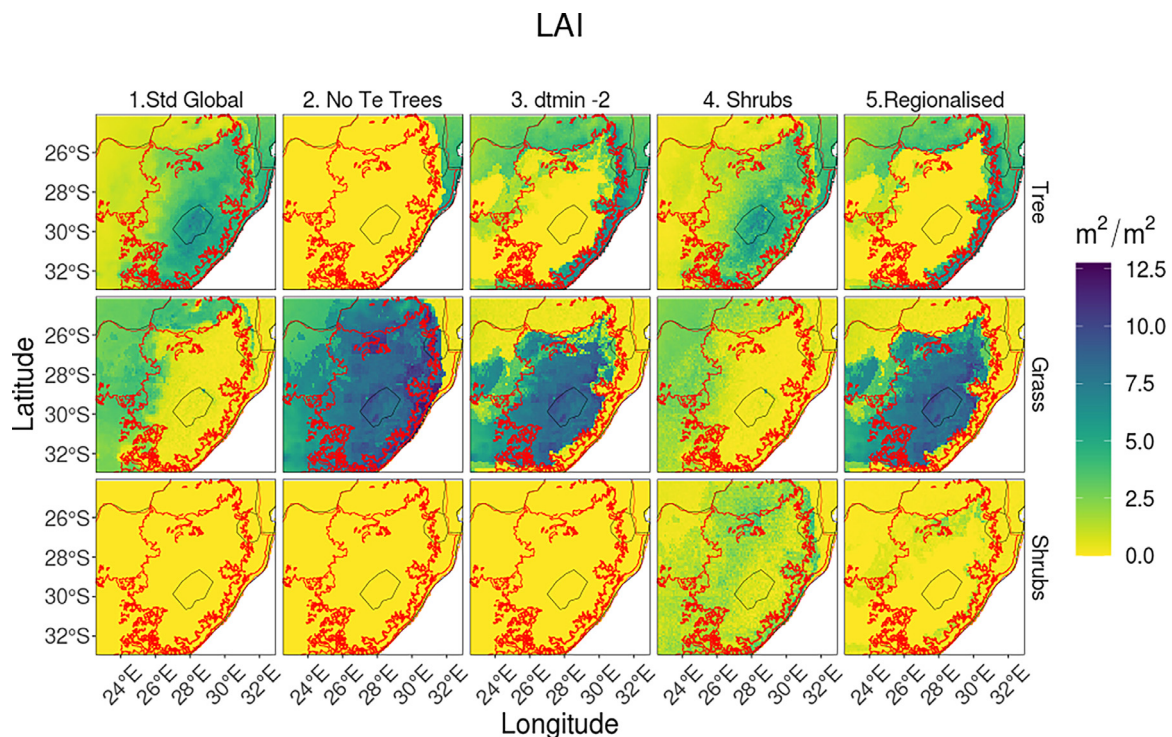
#### 4.1. Low-temperature limits

The well-established bioclimatic limit used in global vegetation models (15.5 °C long-term mean minimum monthly temperatures

which globally correspond with occasional frosts, Prentice et al., 1992) fails to reproduce the boundary between savanna and grassland. The dtmin, mtmin and the mtmin\_mean20 of 7.5 °C provide a better definition of the biome border between grasslands and savannas in the north and east of the biome extent (Fig. 3A and B). This confirms the crucial role that minimum temperature plays in determining the grassland and savanna biome border, supporting the hypothesis that tropical trees are comprehensively outcompeted at low temperatures due to frost damage (Stevens et al., 2018; Russell and Tedder, 2020) even though they can survive. Frost or freezing temperatures impede tropical tree growth by either killing the saplings at the germination stage or they become susceptible to a “frost trap” (Joshi et al., 2020). Contrary to the assumption in global models that use the long-term mean coldest month limit for the survival of tropical trees, with the biome limit being set at least 150 km too early along the warm-to-cool temperature gradient (Fig. 3C), the savanna trees in South Africa can still thrive in colder temperatures than often assumed. At the regional scale, this discrepancy represents a significant error, highlighting the importance of re-parameterising global models for regional studies. Furthermore, it suggests an opportunity for improving global models by re-evaluating previous assumptions regarding the distribution of tropical trees using modern climate data.

Regarding details of the limit, a dtmin of -2 °C can distinguish slightly better between savannas with trees and grasslands than an mtmin of 4 °C (Fig. 3A and B). The dtmin delineated the northern and eastern boundary remarkably well, attesting to both the effectiveness of the limit and the quality of the ERA5-Land temperature data. The mtmin of 4 °C and mtmin\_mean20 of 7.5 °C are also reasonable and could be used as alternatives depending on available data.

While the implementation of minimum temperature limit to tropical trees is a global standardised approach, our regional findings hold potential applicability for other regional studies that adopt similar mechanisms. However, it's essential to acknowledge the limitations of this approach, as it does not consider disturbances like herbivory and land use changes, which can significantly influence biome delineation.



**Fig. 8.** LPJ-GUESS LAI for trees, grass and shrubs for the standard global version, simulations with three regional changes applied individually (removal of temperate trees, application of dtmin limit of -2 °C to all trees and inclusion of shrubs) and the regionalised version with all three regional changes applied.



#### 4.2. The overlooked importance of shrubs

Despite the successful application of the minimum temperature limit on the northern and eastern boundaries of the grassland-savanna transition, it proves ineffective on the western edge, specifically at the boundary with both the nama-karoo and the western savanna. Notably, the savanna on the western limit of the grassland is characterised by shrub dominance rather than tree dominance (Kurzweg, 2011; Rutherford et al., 2006). We hypothesise that the failure of the minimum temperature is attributed to the woody component of these adjacent biomes being dominated by shrubs rather than trees (Rutherford et al., 2006). In contrast to true tropical trees found in the warmer savanna regions, these shrubs and small trees have evolved cold tolerance and other mechanisms to maintain competitiveness at low temperatures at the cost of shorter stature (Rutherford et al., 2006). Although their lower stature makes them more susceptible to top-kill from fire, the impact is mitigated by the comparatively low fire activity in these regions (Fig. S.1).

This significance of shrubs as a biome-defining growth form is often overlooked in vegetation modelling with DGVMs that lack shrubs in their standard global PFT sets. Additionally, this crucial distinction is not addressed in the SANBI biome scheme, which features only one type of savanna and consequently fails to differentiate between the shrub-dominated savanna in the west and the tree-dominated savanna in the north and east. Our results suggest that including shrubs in global and regional models will likely improve simulated vegetation patterns in subtropical areas. Further studies are essential to explore potential avenues for improving the representation of shrubs in DGVMs. This could involve considering introducing a different PFT or refining how shrubs compete within the model framework. However, this work is also challenged by the fact that we lack clear mechanistic hypotheses for when shrubs prevail over grasses and vice versa. Even defining shrubs can be challenging. Gaillard et al. (2018) implemented shrubs as multi-stemmed small wood plants into the adaptive DGVM version two (aDGVM2), but their model does not accurately predict the border between Karoo shrublands and grasslands in South Africa either.

#### 4.3. Heat accumulation and the fire trap

The diagnostic effectiveness of the minimum temperature limit makes it suitable as a bioclimatic limit in DGVMs or similar models. However, these limits need to be reconciled with the findings from transplant experiments conducted by Stevens et al. (2018) on two common savanna trees. Their conclusion that low temperatures constrain sapling growth and hinder their escape from the fire trap is consistent with our result that growing season temperature sums (GDD5) also can distinguish well between savannas and grasslands (Figs. 5 and 6). Additionally, there appears to be a notable GDD5 distinction, although to a lesser extent, between grasslands and nama-karoo (Fig. 5), suggesting that low-temperature constraints on growth might also play a role in the survival of shrub saplings, possibly in combination with the impact of fire (Higgins et al., 2007). The low woody biomass of nama-karoo across FRIs compared to grassland and savanna indicates that the shrubby nature of nama-karoo is less competitive, especially under frequent FRIs.

#### 4.4. DGVM limitations and potential improvements

Initial model simulations inadequately represented the characteristics known for the grassland biome, with the main problem being an unrealistic dominance of trees in contrast to the actual treeless nature of grasslands. Solving this required two changes and is only partially satisfactory. Revisiting the cold temperature limit for tropical trees works well in the study region. However, without a well-performing fire model for the region, we took the step of excluding

temperate trees from our simulation to get a treeless grassland. From one perspective this is entirely reasonable: northern afro-temperate trees endemic to the region are fire sensitive (Esrikson et al., 2003; Giddey et al., 2022), although we do note that there is some fire tolerance as indicated by many species' ability to resprout (Adie et al., 2017). But regardless of adaptation, due to the high prevalence of fire such trees are present in only very small amounts in fire refugia and very specific topographical situations (Adie et al., 2017). Thus, from a practical perspective, simulation of ecosystem services and small-to-moderate biome shifts can safely ignore temperate trees in the region. But if a model is required to simulate processes in more detail, perhaps to look at ecological functioning or biome changes under larger climate perturbations (such as extreme past or future climate conditions), a more mechanistic solution would be required. Such a solution should include temperate tree PFTs which would be vulnerable to fire (although perhaps able to resprout) but resistant to frost, and a complementary simulation of fire occurrence and intensity to control their distribution. This research is beyond the scope of the present study but would be a major improvement in simulating the limits and dynamics of the grassland biome. Furthermore, the LPJ-GUESS model does not represent resprouting, which is a crucial survival mechanism for many woody plants in the study region. Representing resprouting would be desirable to improve the representation of woody population dynamics, fire effects and competition with grasses, but such a parameterisation will require a solid underpinning of process-based understanding to function effectively.

The inclusion of shrubs into our simulation resulted in interesting competitive dynamics with both trees and grasses. When shrubs are added to the standard version (i.e. with no changes to tree distributions), they establish over large areas of the study domain including the grasslands, nama-karoo and western shrub-dominated savanna (Fig. 8, third column). However, when trees are restricted through the other regionalisation changes, the shrub extent is very much reduced (Fig. 8, fifth column). This is because, in the absence of trees, grass abundance increases greatly which in turn increases fire occurrence (data not shown). Whilst this is the desired outcome in terms of simulating the grasslands, it is not a desirable outcome for simulating the nama-karoo where the shrubs are reduced to an unrealistically low amount. This result highlights the challenge of correctly simulating competition between trees, grasses and shrubs - particularly with the mediating influence of fire. Even independently of the issue of shrubs, our improvements to the limits of tropical trees resulted in a large and unrealistic decrease in grasses in the savannas, indicating that tree-grass competition - again likely mediated by fire - could also be improved. This issue might not be readily apparent when using DGVMs at global scope, but regional studies such as this one which focuses on the boundaries between distinct vegetation types can investigate such issues and thus inform model development, potentially improving models for use at regional and global scale. We acknowledge that improving a process-based DGVM, which is largely based on ecophysiological processes, based on a correlative analysis like here might not appear to be ideal. Correlations might not be as robust under climate change as the process-representations of photosynthesis, for example. However, most, if not all, DGVMs also include parameters that are fitted to observations, in particular bioclimatic limits. Minimum temperature limits, as defined here, are probably quite robust under climate change. The cold growing season effect on tree sapling growth might be to some extent alleviated under further increasing atmospheric CO<sub>2</sub> because of CO<sub>2</sub> fertilisation (Bond and Midgley, 2012), but this effect is, in principle, represented by LPJ-GUESS.

## 5. Conclusions

Our study supports the hypothesis that minimum temperature and growing season temperatures play a crucial role in maintaining

the treeless state of grassland. The establishment of a daily temperature limit which remarkably defined the northern and eastern boundary well, underscores the efficacy of this parameter and the reliability of ERA5-Land temperature data. Furthermore, our findings challenge the conventional reliance on the long-term mean coldest month limit for defining tropical tree extent, exposing a significant error and emphasises the need for the re-parameterisation of global models when applied to regional studies, coupled with the significance of using modern climate data. Our study sheds light on the often neglected crucial role of shrubs as a biome-defining growth form in models such as LPJ-GUESS and this highlights the potential for improvement by incorporating shrubs in global and regional simulations, particularly in subtropical regions. Our investigation into fire modelling identified notable challenges, with global models failing to accurately reproduce burnt area patterns. However, the use of idealised fixed fire return intervals experiments revealed the importance of fire in sustaining the grassland biome. This dual influence of temperature limits and fire dynamics emphasises the importance of simultaneously simulating frost and fire tolerance for vegetation, alongside refining fire simulations in DGVMs. Issues concerning competition between different plant growth forms (trees, shrubs and grasses) were also identified. These topics represent a promising area for future improvements, but our regionalised model improved the delineation of the grassland biome, affirming the success of our modelling attempts. In summary, our study not only confirms existing hypotheses but also highlights critical areas for improvement in global and regional ecological simulations, paving the way for a more nuanced understanding of the factors governing tropical and subtropical grassland ecosystems.

#### Declaration of competing interest

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

#### CRediT authorship contribution statement

**M.P. Thavhana:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **T. Hickler:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **M. Forrest:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Funding acquisition, Data curation, Conceptualization.

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#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.sajb.2024.07.017](https://doi.org/10.1016/j.sajb.2024.07.017).

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