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Original research article

Determining the status of ecosystem degradation trends and their implications for ecological integrity in the southern African grassland biome

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A R T I C L E I N F O

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A B S T R A C T

The value of the southern African grassland biome as a biodiversity hotspot will be amplified by its potential to sequester carbon and contribute towards climate change mitigation. Despite this, several studies have reported alarming degradation and transformation of this biome, threatening its ecosystem functioning and services. Using a whole-biome assessment, we aimed: (1) to ascertain the dynamics in the vegetation cover over 34 years (1986–2020), assess the extent and trends of anthropogenic activities; (2) to assess the intensity of alien plant species (APS) invasions in different parts of the grassland biome; and from this (3) anticipate the conservation implications for this biome and identify and prioritise management needs for vulnerable parts of the biome (e.g., critical biodiversity and water sources). Our results showed that sparse vegetation (i.e., equivalent to indigenous grassland) lost 31.5 % of its cover between 1986 and 2020, while the "moderate vegetation cover" and "dense vegetation cover" (comparable to transformed grassland and associated with bush encroachment) increased by 16.8 % and 24.7 % respectively, indicating a substantial loss of biodiversity and ecosystem services. Overall, 39.2 % (365,629 km^2) of the grassland biome has been permanently modified, while 60.8 % of the basic ecosystems remain unchanged. We recorded eleven prominent land cover use classes dominated by agricultural activities accounting for 31.9 % (365,629 km^2) of which 27.4 % was cultivated area, and 4.5 % was forest plantation, and human settlement covered 4.2 %. Of the 1332 alien plant species recorded, 17.8 %-36.2 % were invasive. The hotspots for APS covered 19.7 % (374,002 km^2) of the biome, were concentrated in one province, and were highly dominated by herbs and woody species (46 % and 38 %, respectively). The abundance of APS increased by 13.64 % since the 1900s. Alien woody species increased from 2.2 % occupancy in 1980–4.0 % in 2020, covering 0.4 % (17,217 Km^2) of protected critical biodiversity areas and 9.6 % (102,123 Km^2) of important water source areas. Our study suggests that management efforts for woody alien invasions could usefully prioritise water source areas and sensitive biodiversity areas to achieve multiple objectives simultaneously, including carbon sequestration. We conclude that the functioning, biodiversity and services supplied by the southern African grassland biome is at risk that could be addressed by urgent context-specific management action, policy and selective habitat restoration/

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rehabilitation interventions. In particular, we recommend that the management efforts for woody alien invasions prioritise water sources and critical biodiversity areas.

1. Introduction

Grasslands are found in all continents except Antarctica and cover an area of 52.5 million km^2, comprising about 41 % of the earth's surface (Sala and Maestre, 2014). Grasslands store approximately 20 % of the world's soil organic carbon stocks with the potential to mitigate climate change (Naidoo et al., 2019; Bengtsson et al., 2019; Neary and Leonard, 2020; Bai et al., 2022). Carbon sequestration partly mitigates greenhouse gas emissions by capturing and facilitating the long-term storage of carbon dioxide from the atmosphere through biological or geological processes (Jones et al., 2005). Furthermore, grasslands contain high soil nutrients and, thus are preferred for agricultural crop production globally (Conant et al., 2001; SANBI, 2013; Mucina and Rutherford, 2006), which contributes to their degradation. Grasslands play a critical role in the hydrological cycle by reducing runoff that causes erosion (Mokotjomela et al., 2009; Carbutt, 2011), and by facilitating water infiltration for groundwater storage (Pelser et al., 2015; Milazzo et al., 2023 Bengtsson et al., 2019). Several studies also indicated that grasslands are more resilient to floods and erosion because of the herbaceous layer that reduces excess water flows (Milazzo et al., 2023; Strock et al., 2022).

Ecological integrity refers to a state of the habitat capable of supporting and maintaining ecological processes and a diverse and stable community of organisms integral to the structure, composition, function and connectivity of an ecosystem (Parrish et al., 2003; Faber-Langendoen et al., 2016; Brown and Williams, 2016; Wurtzebach and Schultz, 2016; Hill et al., 2022). Similarly, Martin and Proulx (2020) refer to ecological integrity as naturalness, and adopted an overarching definition by the Canadian National Parks Act S. C. 2000 c. 32 as: "a condition that is characteristic of its natural region and likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of change and supporting processes." Indeed, globally, ecological integrity has become an important measurable and quantitative index for the comprehensive monitoring of ecosystem conditions in conservation (Fraser et al., 2009; Faber-Langendoen et al., 2016), as well as monitoring of crop conditions in agriculture (Ji-Hua and Bing-Fang, 2008; Karmakar et al., 2023; Wu et al., 2023).

Different tools and approaches have been used to investigate the ecological integrity of the environment. For example, a biomonitoring system for grassland ecosystems using plants as primary producers and indicators of habitat change is an important approach for measuring ecological integrity (Del Vecchio et al., 2016; Vukeya et al., 2023a). In South Africa, ecological integrity was determined by estimating the proportion of natural habitat lost to infer the effect on the overall functionality of the ecosystem (Kleynhans et al., 2009; Mokotjomela and Nombewu, 2020). Logically, a large loss of natural habitat implies reduced functionality and integrity (Carter et al., 2019; Hill et al., 2022) because the dominant ecological characteristics suffer variations outside their natural ranges (Parrish et al., 2003). Complex modern methods involving the application of remote sensing and Geographical Information Systems (GIS) to monitor ecosystem changes over time have been effectively used to determine ecological integrity (Ramoelo et al., 2015; Madonsela et al., 2017; Hansen et al., 2021; Vukeya et al., 2023a, Pamla et al., 2024; Mokotjomela et al., 2024a). The use of multispectral remote sensing for acquiring visible, near-infra-red, and short-wave infra-red images in numerous broad wavelength bands makes it possible to predict trends in the change of a phenomenon of interest (Tuominen and Lipping, 2011; Cord et al., 2013; Cho et al., 2019). This approach also allows for mapping change in large spatial scales (Ramoelo et al., 2015; Madonsela et al., 2017).

Globally, habitat fragmentation contributes to a loss of 13–75 % of the diversity of plants, invertebrates, and birds and impairs critical ecosystem services such as seed dispersal, contributing to gene diversity (Haddad et al., 2015). For example, the increase of habitat fragmentation through human settlement development activities has been attributed globally to biodiversity loss and the shrinkage of natural habitats into smaller units not viable for supporting biodiversity (Matsika, 2008; Skowno et al., 2019, 2021; Carbutt and Kirkman, 2022; Vukeya et al., 2023a,b). In South Africa, Skowno et al. (2021) reported a 0.12 % loss of natural vegetation across the South African biomes per year between 1990 and 2018, thus reducing species diversity. Since continuous habitat fragmentation reduces the ecological resilience of natural habitats, urgent restoration and environmental rehabilitation are required for biodiversity conservation (Carbutt and Kirkman, 2022).

Plant invasions are also a substantial threat to the environment globally (Early et al., 2016; Turbelin et al., 2017; IPBES, 2023). The increasing occurrence of alien plant species in the natural habitat impairs native plant communities because of their rapid growth and reproduction, and aggressive competitive ability (Yapi et al., 2018; Van Wilgen et al., 2020; Zengeya and Wilson, 2023; Gioria et al., 2023). They can also over-exploit environmental resources to the detriment of native species (Yapi et al., 2018; Le Roux et al., 2020). The invasion by alien plant species with more abundant and attractive resources than native species may also disrupt critical plant-animal reproductive interactions essential for pollination and seed dispersal (Brooks et al., 2004; Mokotjomela et al., 2013; Holmes et al., 2020; Zengeya and Wilson, 2023). Several studies have demonstrated that flowers of alien plants received a higher number of pollinators than native species (Traveset and Richardson, 2006; Vila et al., 2009; Parra-Tabla et al., 2021), and seed dispersal services than native plant species, leading to reduced fitness of native species (Mokotjomela et al., 2013; Vanbergen et al., 2018; Bitani et al., 2022).

The southern African grassland biome (designated as the grassland biome hereafter) is recognised as a key biodiversity hot spot of botanical diversity - plant species richness and endemism (Carbutt et al., 2011; Skowno et al., 2019). Local human communities are heavily dependent on ecosystem services provided by grassland (Moffett, 2010; SANBI, 2013; Kemp et al., 2018; Reynolds et al., 2020; Nenungwi et al., 2024), partly due to the high levels of poverty (Kemp et al., 2018; Zhao et al., 2020). For example, medicinal plants in the grassland biome are intensively harvested and sold because of their easy access, availability and affordability (Seleteng-Kose et al., 2019; Kasilo et al., 2019; Nenungwi et al., 2024). Zhao et al. (2020) indicated that rural communities also rely on the grassland for livestock grazing. The grassland biome has been extensively studied (Neke and du Plessis, 2004; Bredenkamp et al., 2006; Matsika, 2008; Little et al., 2015; Yapi et al., 2018; Vukeya et al., 2023a, 2023b) although many studies focused on isolated and small patches rather than the entire biome, and this might lead to superficial generalisations and the decision-making for adaptive management against conservation threats. Furthermore, we are unaware of studies that have synthesised the existing literature to discern the

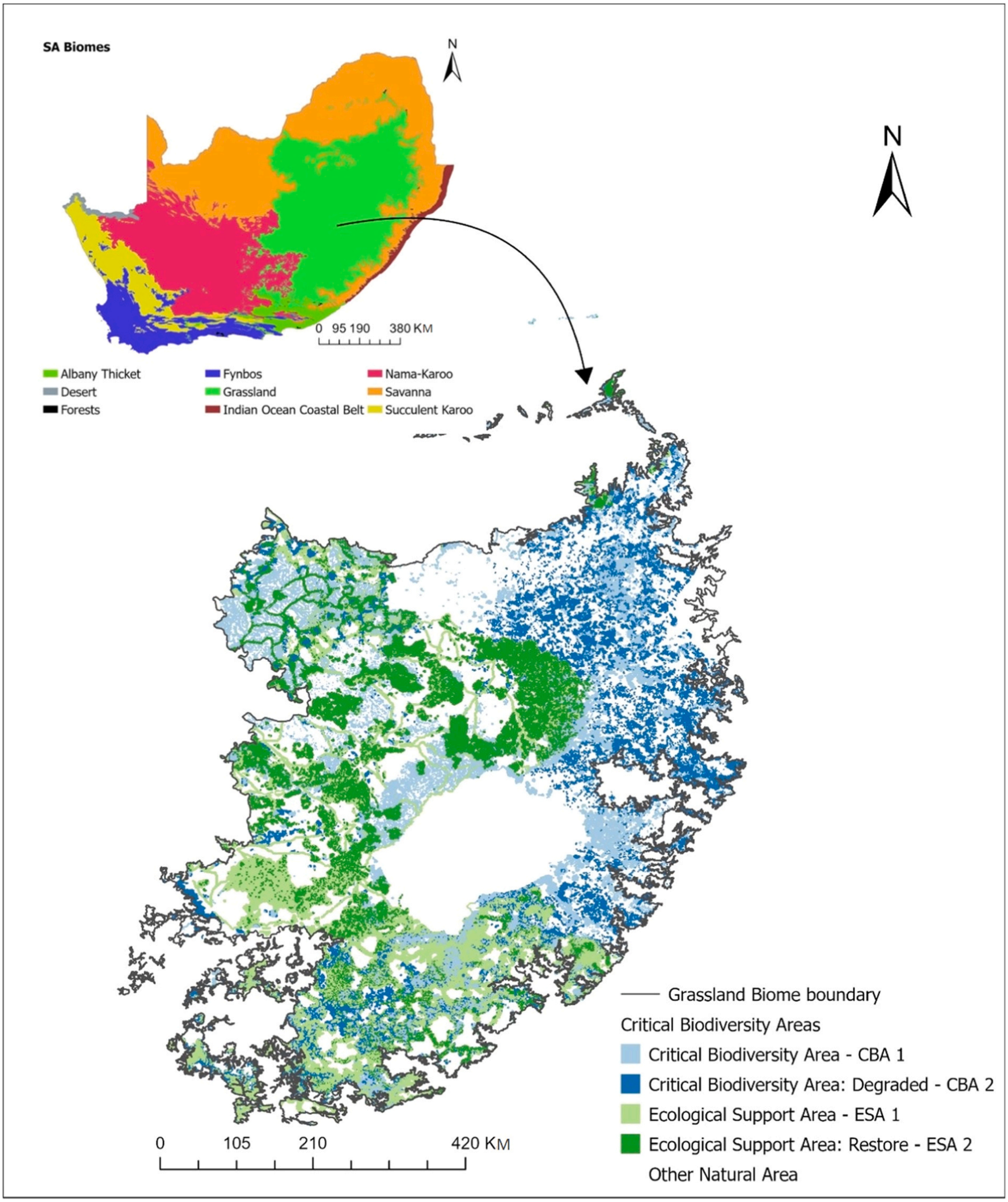

Fig. 1. The location of the study area: grassland biome (South Africa, Lesotho and Eswatini; Mucina and Rutherford, 2006). The Critical Biodiversity Area data for Lesotho and Eswatini were excluded due to a lack of data (https://www.sanbi.org/link/bgis-biodiversity-gis/).

conservation implications of grasslands in South Africa, apart from a study by Carbutt and Kirkman (2022), which assessed the overall restoration needs, focusing on biodiversity conservation goals. Although Matsika (2008) also evaluated the habitat transformation of the entire grassland biome, focusing on habitat fragmentation and biological invasion, the trends of observed changes were not assessed. Of particular concern is that studies have reported that habitat fragmentation creates multiple pressures in the grassland ecosystem (SANBI, 2013; Haddad et al., 2015; de Frutos et al., 2015; Reisch et al., 2017), and may reduce the ecological resilience against conservation threats such as biological invasions.

Habitat degradation through plant invasion is occurring worldwide and is characterised by the deterioration of the natural state of habitats, thus affecting their ecological integrity (Rai and Singh, 2020; Zengeya and Wilson, 2023; Mokotjomela et al., 2024b). Bezeng et al. (2020) modelled the spatial patterns of woody invasions and found that abundance increases from the drier western eastern in protected areas in South Africa. Mokotjomela et al. (2022) corroborated these findings while sampling alien plant species in the dumping sites, and Reynolds et al. (2020) demonstrated a similar pattern of their impacts on ecosystem services targeted by the people in rural areas. The grassland biome is the third heavily invaded biome after the fynbos and savanna biomes (Zengeya and Wilson, 2023). Moreover, less than 3 % of the grassland biome is formally protected (Carbutt and Martindale, 2014; Prinsloo et al., 2021; Skowno et al., 2019; Carbutt and Kirkman, 2022) yet contains critical water source areas that are highly susceptible to negative impacts of plant invasions (Mokotjomela et al., 2024b). Better knowledge of the current state of invasions is important for planning to reduce the density-dependent impacts on ecosystem service provision (Theuerkauf et al., 2017). Thus, it is necessary to investigate the large-scale spatial patterns and trends of invasions by alien plant species because such knowledge can help develop proactive management strategies and prioritise management resources (Yang et al., 2023; Mokotjomela et al., 2024c). Knowledge of patterns of change and their trends is important in informing planning and development response strategies (Fathizad et al., 2015; Muavhi, 2020; Khan et al., 2020; Venter et al., 2020; Selsam et al., 2024).

Given the concerns of the grassland biome, we aimed to assess the level of the ecological integrity of the grassland biome by (1) investigating the dynamics in the vegetation cover over 34 years (1986–2020) and assessing the extent and trends of anthropogenic activities, We hypothesised that grassland vegetation health has been deteriorating and undergoing woody encroachment because of anthropogenic land use practices and possibly biological invasions (2) assessing the intensity of the invasions by alien plant species in different parts of this grassland biome, and (3) anticipating the conservation implications for this biome and identify and prioritise management needs for differentially vulnerable parts of this biome (e.g., critical biodiversity and water sources). We need to understand the habitat changes of the grassland biome to mitigate the negative impacts of climate change and biological invasion and recommend policy interventions that are aligned with sustainable socio-economic and natural capital benefits set out in the Sustainable Development Goals (SDGs).

2. Method and materials

2.1. Study biome

The study area comprised the grassland biome (Fig. 1). The biome occupies approximately 360,589 km^2 of its area (Mucina and Rutherford, 2006) and is centrally located on the plateau of South Africa, and the inland areas of KwaZulu-Natal and the Eastern Cape Provinces and shares boundaries with the Savanna, Thicket, Nama Karoo, and Forest biomes (Mucina and Rutherford, 2006; Skowno et al., 2019). The biome makes up the greater portion of South Africa, Lesotho, and a portion of Eswatini (Fig. 1; Mucina and Rutherford, 2006; Skowno et al., 2019). In South Africa, the biome boundary covers an area in the interior of six provinces, Free State, KwaZulu-Natal, Eastern Cape, Gauteng, Mpumalanga and Northwest, with scattered patches in Limpopo and Northern Cape (Fig. 1; Skowno et al., 2019).

Based on the species composition, community structure and ecological functions that constitute their management requirements, the grassland biome is represented by five bioregions, namely: Dry Highveld Grassland, Mesic Highveld Grassland, High-Altitude Grassland, Sub-Escarpment Grassland and Coastal Grassland (Mucina and Rutherford, 2006; SANBI, 2013; Skowno et al., 2019) and 74 nationally recognised vegetation types under those bioregions (Dayaram et al., 2019). The biome is recognised as a biodiversity hotspot because it accounts for three centres of plant endemism: the Drakensberg Alpine Centre, Wolkberg Centre, and Midlands Putative Centre, and shares other centres of plant endemism with the Savanna Biome (Barberton, Sekhukhune and Southpansberg Centres; Mucina and Rutherford, 2006; Carbutt et al., 2011), with three World Heritage Sites (uKhahlamba Drakensberg; Cradle of Humankind and Vredefort Dome; Carbutt et al., 2011). The grassland biome is structurally dominated by herbaceous vegetation of tufted graminoids, mostly perennial grasses of the Poaceae family (Mucina and Rutherford, 2006; Carbutt et al., 2011), comprising approximately 4000 native species records (Cowling et al., 1989; Mucina and Rutherford, 2006). The C4 grasses predominate in most of the areas, and woody plants are rare or absent (Carbutt et al., 2011). Grasslands are fire-prone; hence, their structure and textural patterns require fire for maintenance and sustainability (Mucina and Rutherford, 2006).

The grassland biome lies in the summer rainfall region and usually receives more rain between November and March, with an average annual rainfall range from 400 to 2500 mm (Mucina and Rutherford, 2006; Carbutt et al., 2011). The grassland biome experiences a continental climate, characterised by hot summers of above 35°C and cold winters down to below 0°C with frequent snowfalls and severe frost (Mucina and Rutherford, 2006; Carbutt et al., 2011; Retief and Meyer, 2017) and fog that constantly occurs on the upper slopes of the Great Escarpment and seaward scarps (Mucina and Rutherford, 2006).

The topography is mainly flat to rolling with mountainous areas and escarpments (Mucina and Rutherford, 2006; Carbutt et al., 2011). The altitude varies from near sea level to 3482 m above sea level, with the Thabana Ntlenyana (i.e., in Lesotho) as the highest mountain in southern Africa (Mucina and Rutherford, 2006).

2.2. Spatial data collection and image processing of vegetation

We used spatial ecology technologies (Remote Sensing (RS) - Geographical Information System (GIS) – Spatial data, and shapefiles of the grassland biome to understand the extent of vegetation cover over 34 years (1986–2020), 1986 as a baseline due to data restriction. The approach was used because Hill et al. (2005) indicated that natural expression (i.e., growth, mortality and regeneration) can be measurable over 10 years or more for significant trend detection. The raster data were generated for the grassland biome as an area of interest to understand the extent of vegetation cover change over a longer period in 16/18-year intervals for significant trend detection. The pre-processed Satellite imagery—Landsat Collection 2 Level-2 imagery for Landsat 4–5 Thematic Mapper (TM), Landsat 7 Enhanced Thematic Mapper (ETM), and Landsat 8–9 Operational Land Imager (OLI)/Thermal Infra-red Sensor (TIRS) of the study area (path 171/row 80) was acquired for the years of interest period using the United States Geological Survey (USGS) – Earth Explorer (http://earthexplorer.usgs.gov). The USGS platform provides ready-to-use surface reflectance Landsat data processed by the EROS (Earth Resources Observation and Science) Science Processing Architecture (ESPA) on-demand interface and the Landsat Surface Reflectance Code (LaSRC) (https://www.usgs.gov). For comparison, extra care was taken to select images in the same season/-month–date range (January – April). We selected vegetation reflection data with a cloud cover of less than 10 %. The raster data were imported to ArcGIS Pro software (Esri, New York, USA). To scale the data to reflectance, the data were processed using Modelbuilder and iterators raster tools in ArcGIS Pro, and each raster imagery was multiplied by the scaling factor of 0.0000275 + -0.2 using the raster calculator.

The Landsat imagery set was used to classify the Normalised Difference Vegetation Index (NDVI) and determine the change in the vegetation cover distribution of the study area. The Landsat Level-2 imagery has already been processed for atmospheric and geometric corrections, and therefore, for the analysis, the digital number (DN) of bands was scaled up to the reflectance values. The NDVI remote sensing method displays the vegetation's healthiness and greenness (relative biomass). It measures the state of the plant health based on the plant reflection of light at specific frequencies. The band combination of channels that are used to obtain coverage of the vegetation indices' characteristics was selected. The NDVI is calculated as the ratio of the difference between the red and near-infra-red signal of the electrometric spectrum divided by the sum of both, which involves the spectral bands 4 and 5 (Landsat 8–9 OLI)/ TIRS) and bands 3 and 4 (Landsat 2–5 TM and Landsat 7 ETM). The scaled data were extracted for further analysis in the study biome. The NDVI value ranges between − 1.0 and + 1.0 and reflects the healthiness of plants (greens). An NDVI value of 0.6–1 represents dense vegetation cover, 0.4–0.6 represents moderate vegetation cover, 0.2–0.4 represents sparse vegetation cover, 0.1–0.2 shows the grass cover with bare space, and − 1–0.1 represents no vegetation (e.g., water cover) (Vukeya et al., 2023a).

2.3. Land use and cover change in the grassland biome

To assess the patterns in land use cover that can/possibly threaten the integrity of the grassland biome, the South Africa National Land Cover (NLC) dataset containing 72–73 land-use classes was downloaded from the Department of Forest, Fisheries and The Environment (DFFE) (https://egis.environment.gov.za/sa_national_land_cover_datasets) for the period of interest. The raster dataset has been generated from 20 m multi-seasonal Sentinel 2 satellite imagery (https://egis.environment.gov.za/sa_national_land_cover_datasets). According to DFFE (2023), the semi-automated spectral modelling procedures generated the basic land-cover components, i.e., water, tree, bush, grass and bare ground. The basic land-cover components form the 'building blocks' upon which the more detailed final land-cover/land-use data were derived and defined. These semi-automated land-cover mapping techniques offered a more efficient alternative to conventional classification techniques (i.e., analyst-assisted pixel-based classifiers), allowing for rapid production of standardised yet informative land-cover information and classification. This provided the standardised references from which landscape changes could be determined and quantified.

For time series analysis, the year of interest was imported into ArcGIS Pro as GeoTIFF images and regrouped the 72/3 classes into 10 classes (built-up, cultivated, grassland, shrubland, forest land, forest plantations, waterbodies, wetland, barren land, and mines & quarries) based on the objectives of the study. The imagery was masked with the area of interest – grassland biome shapefile. The scaled data were extracted for further analysis in the study area. The different proportions of land cover used (in hectares) were used to quantify the potential change in the study site. Lesotho and Swaziland were not included because of a lack of data.

Overall ecological integrity was determined by quantifying the extent of the spatial threats posed to the grassland biome by different land cover uses leading to habitat transformation (Jewitt et al., 2015; Fonteh et al., 2016; Carter et al., 2019; Nzuza et al., 2022). A modified generalised habitat integrity evaluation method adopted from Mokotjomela and Nombewu (2020) was used, in which a habitat with a minimum threshold of 60 % habitat intactness (category C: 60–79 %) was applied (Kleynhans et al., 2009), and used to infer the relative ecological integrity of the grassland biome. Below the minimum threshold categories shows that the basic ecosystem functions are extensive or destroyed i.e., category F (0–19 %), the habitat condition is extremely modified with almost complete loss of natural resources, and basic ecosystem functions have been destroyed, and the changes are irreversible; category E (20–39 %), seriously modified resulted on the natural habitat loss but basic ecosystem function is still extensive; category D (40–59 %) represents a habitat condition that is primarily modified but basic ecosystem function still occurs (Kleynhans et al., 2009). The above threshold categories indicate that ecosystem functions are still predominantly unchanged, i.e., category B (80–89 %) represents the habitat condition with few modifications, and the ecosystem functions are essentially unchanged; and category A (90–100 %) is natural and unmodified habitat (Kleynhans et al., 2009).

2.4. Alien plant species abundance trends in the grassland biome

2.4.1. Spatial data collection and statistical mapping

All floristic survey occurrence records of alien plant species were sourced from the Southern African Plant Invader Atlas (SAPIA) database and the Global Biodiversity Information Facility (GBIF) to assess the abundance of alien plant species in the grassland biome. These occurrence records were combined into one spreadsheet and classified based on the years of interest i.e., '1900, 1940, 1980, and 2020', and converted to text (tab delimited) (*.txt) and imported to ArcGIS Pro software. Several geoprocessing tasks were performed on the aggregated event points before performing a "Hot Spot Analysis (Getis-Ord GI*)". The even points were displayed based on the table's x,y values (longitude and latitude). The 'integrate' tool in ArcGIS Pro was used to coordinate locations of event points vertices among points in one or more feature classes that fall within a specified distance of one another and are assumed to represent the same location and were assigned a common coordinate value. In this study, 10 km was used to scale the assumption.

The 'Collect Events tool' in ArcGIS Pro was used to convert event data (i.e., event points) to weighted point data by combining the coincident points in a weighted point feature class –ICOUNT and holding the sum of all the event data at each unique location. The Hot Spot Analysis tool - Getis-Ord Gi* statistic (pronounced GI_Bin) was used to identify statistically significant spatial clusters of low to high values (i.e., hotspots) because the interval of each feature determined it within the context of neighbouring features. For example, positive spatial autocorrelation exists when values in a geographic unit are high and surrounded by other geographic units with similarly high values. Optimised hot spot analysis was used to validate the results from the Hot Spot Analysis tool.

Thereafter, the GiZScore was obtained from the Gi*statistic and was used in the IDW (Geostatistical Analyst) to visualise weighted points into density mapping areas with the index dividing polygons into categories (i.e., coldspot - low, no significance - moderate, and hotspot - high). The interpolation tools assessed the correlation between natural resource loss and alien plant species' occupancy in the grassland biome. For statistically significant z-scores, the larger the z-score is, the more intense the clustering of large values (hotspot) and vice versa for the small values (coldspot) (Huang et al., 2020). Different categories were used to quantify the potential of alien plant species abundance in the study biome.

Pyšek et al. (2012) reported that plant life forms may guide the prediction of the species' impact regardless of the habitat and geographical region, and thus we also classified the alien plant species into their life forms, namely bulbs, herbs, graminoids, succulents, and woody species for shrubs and trees following Mokotjomela et al. (2022). Woody alien species are known to be aggressive habitat transformers in South Africa (Mostert et al., 2017; Yapi et al., 2018; Henderson, 2020; O'Connor and van Wilgen, 2020), and thus all other life forms were evaluated against them.

To determine the potential impacts of alien species, we also classified the species using the South African National Environmental Management: Biodiversity Act 10 of 2004 (NEM: BA) - Alien and Invasive Species (AIS) Regulations of 2014 and updated in 2020 – categories: 1a, 1b, 2, and 3, and "Not listed species". South Africa has developed a robust invasion risk assessment criterion that screens the negative impacts of each alien species in the recipient environment, society and economy to determine the management prescripts (Zengeya et al., 2017; Kumschick et al., 2020; Wilson and Kumschick, 2024). Category 1a species are still restricted and targeted for eradication, and 1b is naturalised and widespread with an intensive negative impact on biodiversity but targeted for control (Supplementary Table S1; NEM: BA-AIS, 2020; Kumschick et al., 2020). Species in Category 2 & 3 require a permit for their use, but Category 3 species may be subjected to exemption (Table S1; NEMBA-AIS, 2020; Kumschick et al., 2020). The current study combined NEMBA-AIS Category 1a and 1b to infer the number of invasive species. Furthermore, the invasive status of each species was screened using the international criteria described by Blackburn et al. (2011) (introduced/casual, naturalised/established, and invasive). Species in the 'introduced/casual' stage are only present but not well established in the new environment. In contrast, species in the established stage can reproduce and maintain their population in the receptive environment (Blackburn et al., 2011) – they consider alien species in the 'invasive stage' spread significantly and cause adverse ecological impacts.

2.5. Developing management recommendations

Assessing occupancy of alien woody species in critical biodiversity areas and water source areas

2.5.1. Spatial data collection and statistical mapping

Because alien woody species have been reported as one of the main transformers of vegetation structure in South Africa (see, Mostert et al., 2017; Yapi et al., 2018; O'Connor and van Wilgen, 2020; Chikowore et al., 2021), we assessed the intensity of invasion by alien woody species in different parts of the grassland biome bearing critical biodiversity and water source areas. We identified the management needs and their prioritisation. Alien woody species distribution trends were mapped following the methods applied to mapping alien plant species abundance - the Hot Spot Analysis tool - Getis-Ord Gi* statistic. We overlaid wood alien species distribution to the protected areas and water source areas shapefiles. The critical biodiversity areas (protected areas), and water source areas (groundwater and surface water) shapefiles were downloaded from SANBI Biodiversity GIS (BGIS) (https://www.sanbi.org/link/bgis-biodiversity-gis/). The ground and surface water shapefiles were merged as they represent the water source areas.

2.6. Data analysis

2.6.1. Detecting vegetation cover trends in the grassland biome

To analyse the NDVI trends during the study period, different proportions of vegetation cover class in hectares were used to quantify the potential vegetation cover change in the study biome from 1986 to 2020. The NDVI values ranging between − 1.0 and

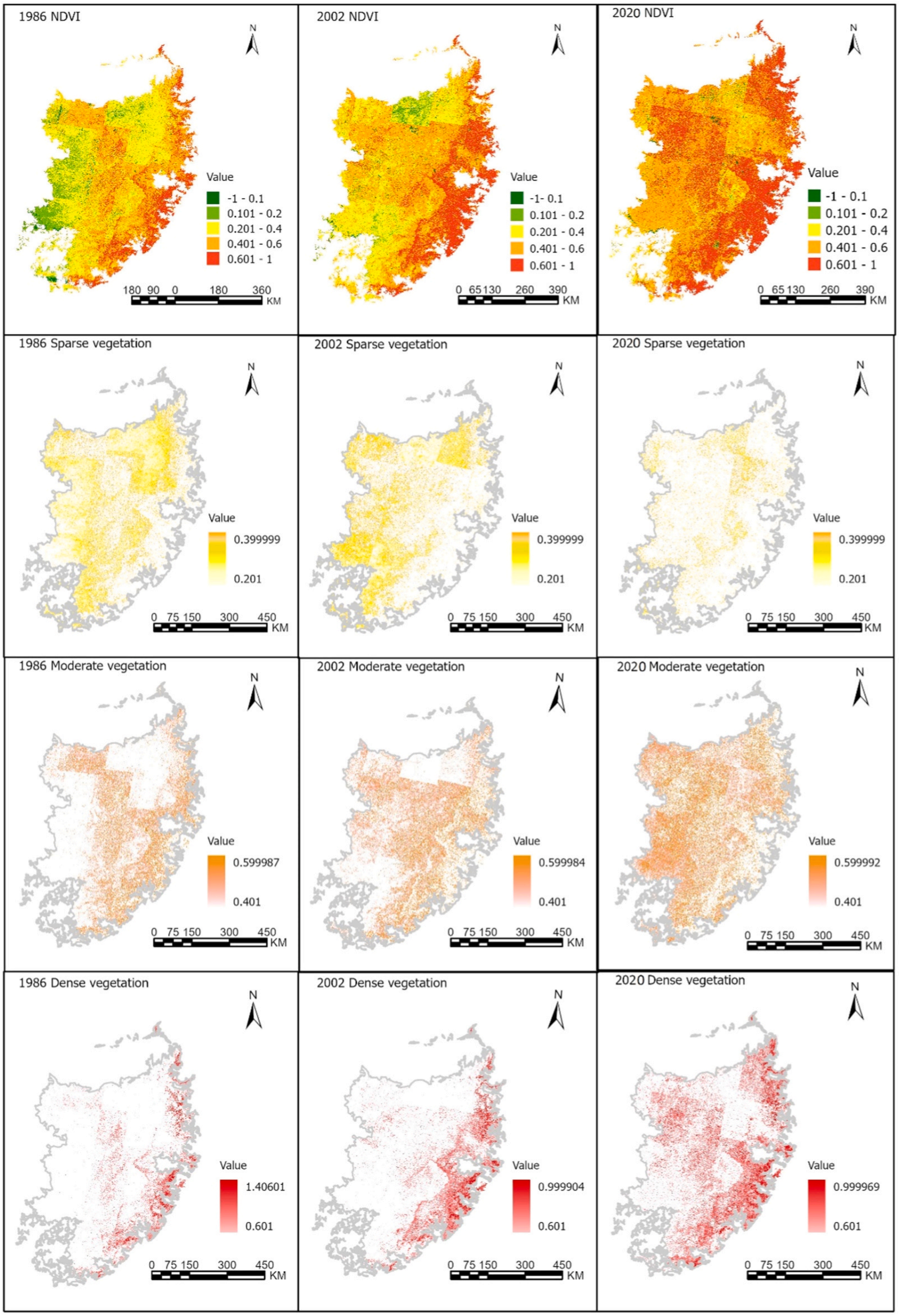

Fig. 2. NDVI images demonstrate the vegetation cover dynamics of the grassland biome from 1986 to 2020, in 16/18-year intervals (vegetation cover classification: 0.6–1 represent dense vegetation cover, 0.4–0.6 represent moderate vegetation cover, 0.2–0.4 represent sparse vegetation cover, 0.1–0.2 show the grass cover with bare space, and − 1–0.1 represent water cover).

+ 1.0 were mapped to reflect the health of vegetation: 0.6–1 for 'dense vegetation cover'; 0.4–0.6 for the 'moderate vegetation cover'; 0.2–0.4 for 'sparse vegetation cover'; 0.1–0.2 for the grass cover with bare space; and − 1–0.1 represented no vegetation (Vukeya et al., 2023a).

2.6.2. Detecting changes in the land use and cover disturbance in the grassland biome

Different proportions of land use practice trends in hectares were used to quantify the potential changes in the study biome. The percentages of natural vegetation transformed and degraded were estimated for each land cover use and were expressed as proportions of the total area of the biome. These measures were applied to assess the relative vegetation intactness of the grassland biome and used as proxies of ecological integrity. The changing trajectory of post-classification comparison was used to map the patterns and extents of land use cover in the study biome and determine the magnitude of changes between the years of interest, 1990 and 2020.

2.6.3. Mapping of alien plant species abundance trends and determining plant invasion risk in the grassland biome

We mapped alien plant species' occupancy using Kriging and reclassified them into abundance classes in planimetric and perspective views (i.e., low (-0.998– 0.215), moderate (0.216–4.014), and high (> 4.015). The occupied area (i.e., in hectares) was assessed to quantify the change using ArcGIS Pro software.

We compared other plant life forms with the woody alien species. The dataset was examined for over-dispersion or under-dispersion using the variance or deviance value of around 1 in the output to determine the best-fitting model during the data analysis. The GLM model fitted was rejected if the variance was significantly greater or less than 1. When the data were not over- or under-dispersed, the Omnibus Tests of Model Coefficients, followed by likelihood ratio chi-square with a high significance, were used to ensure that results could be interpreted confidently. Finally, the model with a comparatively lower variance was selected as the best-fitting model for the data.

A Generalised Linear Model (GLM) with Poisson and negative binomial error distributions in SPSS software (Version 29, IBM, New York, USA) was used to analyse the data as the best-fitting model to compare significant differences between the numbers of alien woody plants and other plant life forms (i.e., bulbs, succulents and graminoids). Comparing the model variance coefficients, a GLM with a negative binomial error distribution best fitted the data for the desired comparison. We specified the response variable as the counts/frequency generated from original records of individual plant species, and the plant life forms were predictor variables. Dunnett's post-hoc was used to compare the frequency means of other life forms to the woody life forms.

2.6.4. Quantifying the occupancy of alien woody species in critical biodiversity areas and water source areas

The alien woody invasion was mapped, and their abundance was quantified in hectares occupied following the classification developed for alien plant species abundance. Next, their occupancy was converted to percentages to infer vulnerability to the negative impacts on the critical biodiversity areas and important water source areas within the biome. High and increasing occupancy by woody invasions meant high vulnerability to the negative impacts through density-based mechanisms and vice-versa (Theuerkauf et al., 2017).

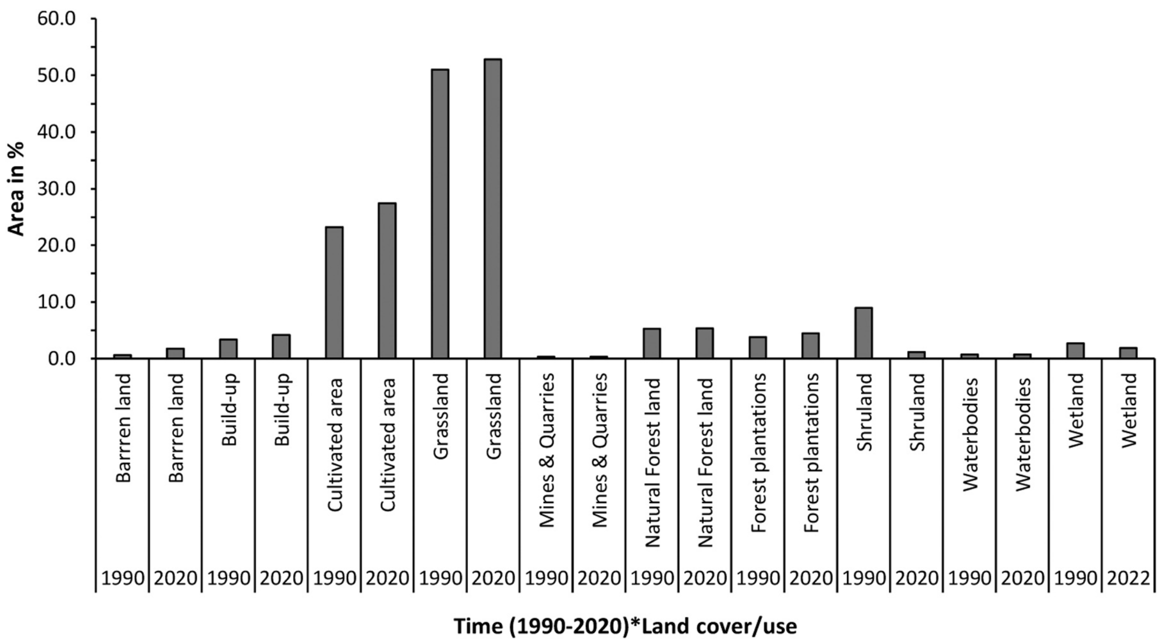

Fig. 3. Spatial coverage of various prominent land uses and cover (%) in the grassland biome between the years 1990 and 2020.

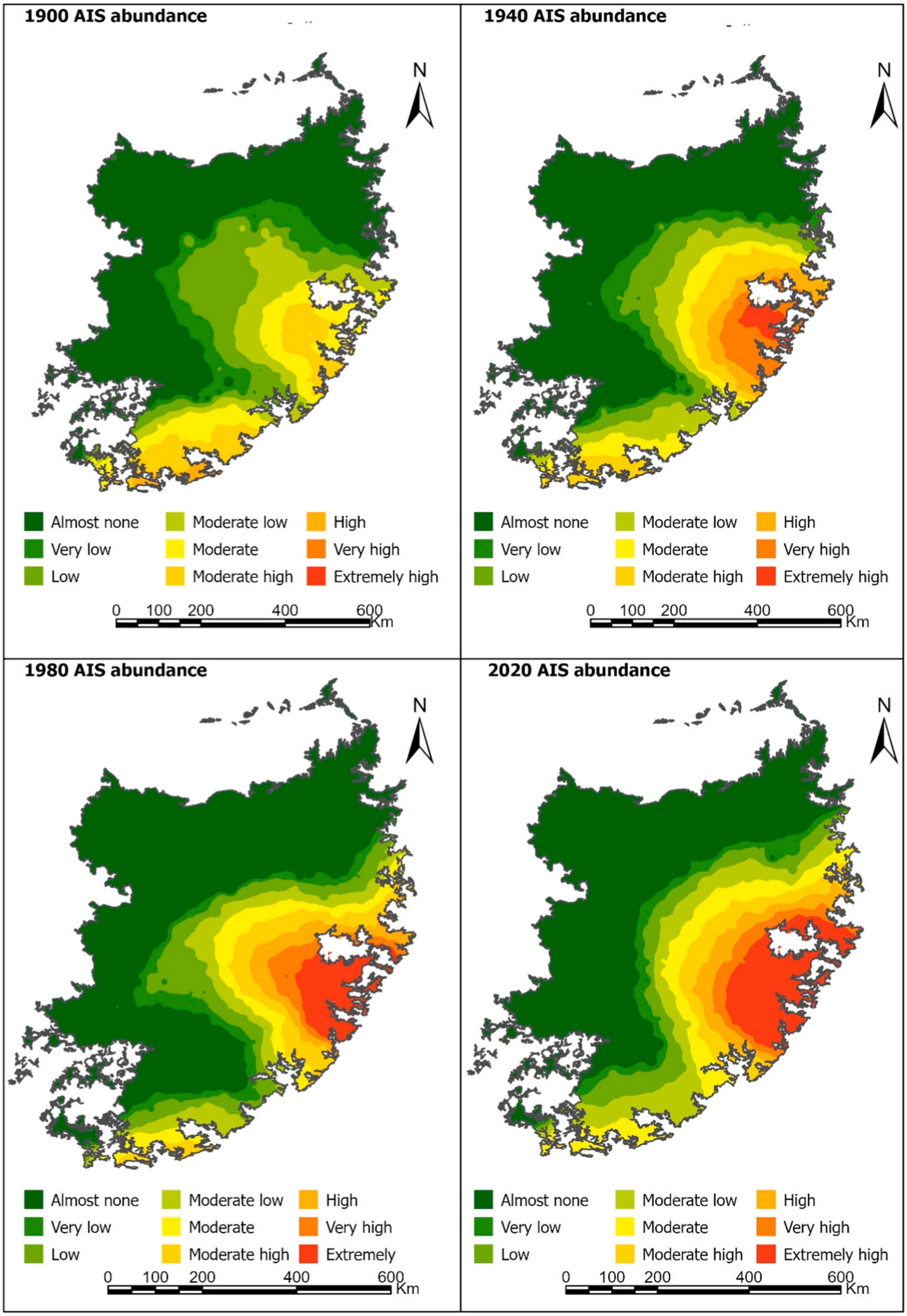

Fig. 4. Spatial coverage patterns of AIS distribution throughout the grassland biome with various colours showing species abundance: Coldspot – least abundant and low; no significance – moderate; and hotspot – high).

3. Results

3.1. Detecting vegetation cover change: spatial data collection of vegetation

Overall, the NDVI displayed a significant change in vegetation integrity over time (1986–2020) in the grassland biome (Fig. 2). In support of the study hypotheses, the vegetation cover changes were predominantly associated with bush encroachment by the "moderate vegetation cover" having expanded by 16.8 % (374,002 km^2), and the "dense vegetation" also having expanded by 24.7 % (374,002 km^2) over 34 years (Fig. 2). In contrast, the predominant grassland vegetation - 'sparse vegetation cover' (i.e., the reference cover change equivalent to grassland) had declined progressively by 31.5 % (374,002 km^2; Fig. 2).

3.2. Land use and cover in the grassland biome

Overall, the NLC 2020 database showed that the ecological integrity of the grassland biome has been moderately modified, with 60.8 % (N = 365,629 km^2) of vegetation remaining as semi-pristine grassland (Fig. 3), while 39.2 % has been permanently modified. We found eleven prominent land cover uses being dominated by agricultural activities, accounting for 31.9 % (N = 365,629 km^2) of which 27.4 % was cultivated area and 4.5 % was forest plantation, followed by human settlement (4.2 %; N = 365, 629 km^2; Fig. 3). Agricultural activities have increased by 5 % since 1990. Native shrubland had progressively lost about 7.84 % (N = 365,629 km^2) of its cover between 1990 and 2020 (Fig. 3).

3.3. Alien plant species abundance trends in the grassland biome

In total, we obtained 56,244 alien plant species records containing 1332 alien plant species, which were classified into 157 families. Overall, an abundance of woody alien species was clustered in the grassland biome's central north and southeastern parts (Gauteng, Kwa-Zulu Natal, and Eastern Cape Provinces). The APS hotspots covered 19.7 % (374,002 km^2) of the biome, being concentrated in the urban area of Kwa-Zulu Natal (Fig. 4). The abundance of alien plant species increased from 6.1 % to 13.6 % between the 1900s and 2020 (Fig. 4).

Compared to woody life forms, all other life forms had significantly smaller numbers of species (Wald $\chi^2 = 452.5$; df = 5; $p < 0.001$; Table 1), except the herbaceous species, which were greater than the woody species but not significantly different (Wald $\chi^2 = 1.9$; df = 1; p = 0.167; Table 1). Dunnett's post-hoc test showed that the three other life forms (i.e., succulents, bulbs and graminoids) had non-significantly different numbers of species among themselves.

The "Not listed" species were the most dominant in the records (78 %; N = 1332). The alien plant species categorised as "invasive" described in NEMBA-AIS and Blackburn et al. (2011) accounted for 17.8 % - 36.2 % (N = 1332).

3.4. Developing management recommendations

Assessing occupancy of alien woody species in critical biodiversity areas and water source areas.

The woody alien species hotspot constituted 2.2 % (374,002 km^2) in 1980 and increased by 1.8 % in 2020 to cover 0.4 % (17,217 Km^2) of protected critical biodiversity areas, and 9.6 % (102,123 Km^2) of important water source areas in the biome. The occupancy of woody plant species hotspots expanded from 3.8 % to 9.6 % over the important water source areas between 1980 and 2020 (Fig. 5).

4. Discussion

Grasslands biomes are hotspots of biodiversity, providing ecosystem services and representing important carbon storage, thereby contributing to the mitigation of climate change impacts (Mucina and Rutherford, 2006; Carbutt et al., 2011; Carbutt and Kirkman, 2022). In support of our hypotheses, time-series assessments showed that the vegetation health of the biome has been deteriorating because of anthropogenic land use practices and possibly biological invasions. The observed loss of functionality requires urgent management attention for its sustainable conservation and reducing the negative impacts of climate change on human well-being.

Table 1
Generalised Linear Models (GLM) significant differences between the number of plant species within different life forms. Superscript "a" represents a parameter which was selected as a reference for multi-comparison among the plant life forms.

Parameter	ß	Std. Error	Hypothesis Test		
			Wald χ^2	df	Sig.
Model effect			452.527	5	< 0.001
Bulb	−4.852	0.5145	88.942	1	< 0.001
Ferns	−3.466	0.2778	155.603	1	< 0.001
Grass	−1.356	0.1492	82.516	1	< 0.001
Herb	0.177	0.1278	1.914	1	0.167
Succulent	−2.144	0.1771	146.583	1	< 0.001
Woody	0[a]	.	.	.	.

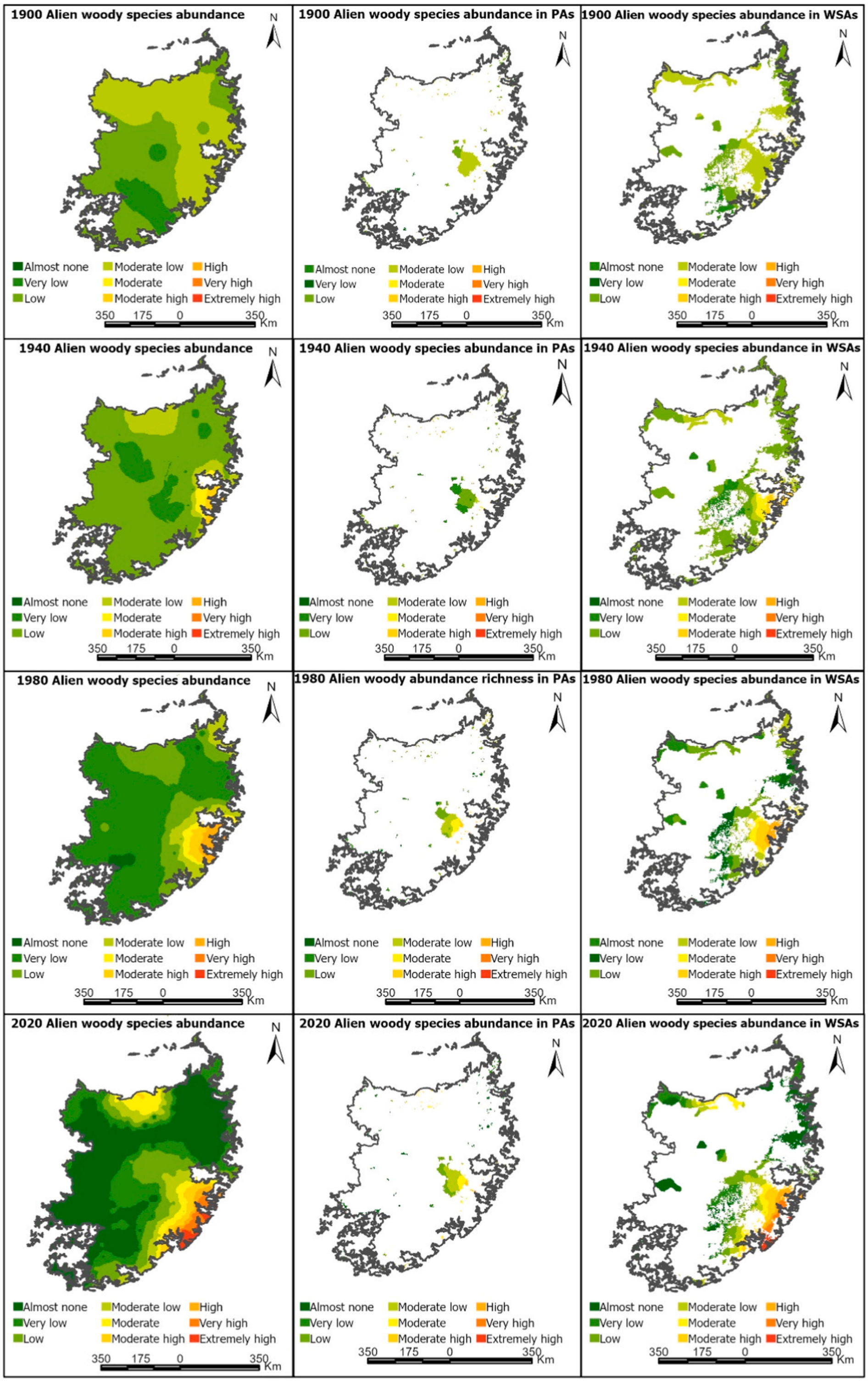

Fig. 5. Cumulative presence of woody alien species in the grassland biome with a specific focus on the location of protected critical biodiversity areas (PAs), and important water source areas (WSAs) from 1900 to 2020. Variation in colours showing species abundance (coldspot i.e., least abundant and low, no significance - moderate, and hotspot – high).

The NDVI assessment showed that moderate to dense vegetation cover expanded over the 34 years in the grassland biome as an outcome of land degradation and associated increasing woody plant invasions (Archer et al., 2017; Yapi et al., 2018; Trisos et al., 2020; Vukeya et al., 2023a; Mokotjomela et al., 2024b). Despite the small observed biome transformation, we propose that the synergistic interaction of environmental degradation and other biome stressors associated with global climate change might have a disproportionately large effect on degrading the biome through disruption of the functionality and ecosystem services (Malhi et al., 2020; Orr et al., 2020; Pascual et al., 2022). For example, the drastic disturbance in species interactions may reduce resource exchange, possibly compounding the risk of microsystems' collapse (Buma, 2015; White et al., 2024), and indirectly causing the extinction of other species in the maintenance of the biome (Mancin et al., 2023; Arrigo et al., 2020).

Biome functionality is at stake partly because of various land uses contributing to the local economy and upliftment of the livelihoods of people and driving major biodiversity loss and the associated ecosystem goods and services (Kang et al., 2018). A large portion of the grassland biome was subjected to agricultural activities (27 %), possibly due to high nutrient concentration (Conant et al., 2001; Mucina and Rutherford, 2006; SANBI, 2013). Because 80–90 % of carbon is stored in the soil (Liu et al., 2023), we argue that intensive cultivation has reduced the storage capacity of organic carbon (Bardgett et al., 2021), partly through crop exploitation. Cultivation involves permanently removing typical vegetation from the soil surface, thus exposing topsoil to erosion by wind and water flow (Le Roux, 2011; Mararakanye and Le Roux, 2011; Wantzen and Mol, 2013). Land cover by agricultural area has increased by 5 % since 1990, possibly because slow economic growth generates pressures on commercial farmers and small-scale subsistence farmers (i.e., food production goal set by the Gross Domestic Product (GDP)) and to overcome poverty in South Africa (Pfunzo, 2017; Meyer, 2019; Ransom et al., 2019; Okole et al., 2022). The observed loss of native shrubland might be partly attributed to increased agricultural activities putting pressure on the grassland ecosystem (Wantzen and Mol, 2013). Owing to habitat loss, Skowno et al. (2019) reported that the grassland biome has the second highest number of threatened ecosystem types (21 out of 52) after the Fynbos biome. In support of the observation, Red Data Stats (2023) reported that 275 plant taxa are threatened in the grassland biome, excluding Lesotho and Eswatini (http://redlist.sanbi.org/stats.php). The progress made for formally protected areas to conserved grassland is still minimal and needs attention, particularly against human-mediated activities. We suggest expanding protected areas, ideally connecting existing protected areas through corridors to maintain the species gene flow (Taylor and Atkinson, 2012; Das and Angadi, 2022).

We recorded 1332 alien plant species, which highlights the vulnerability of the remaining semi-pristine grassland biome primarily used as grazing land to the negative impact of invasive alien plant species (Richardson and van Wilgen, 2004; Matsika, 2008; Yapi et al., 2018; O'Connor and van Wilgen, 2020; IPBES, 2023). Consistent with reports of humans' recent use of alien species for various purposes (i.e., ornamental plants in home gardens) (Howard et al., 2019), the hotspot of alien plant abundance occurred in urbanised business areas and heavily fragmented KwaZulu-Natal Province human settlement areas. It is possible that habitat fragmentation partly from human settlement and agriculture could have reduced the ecological resilience of the natural areas, thereby making them susceptible to invasion by alien plant species (Pyšek, 1998; McLean et al., 2018; Mokotjomela et al., 2022 & 2023; Pamla et al., 2024). The observed increase in alien plant species abundance (13.6 %) between 1900 and 2020 in the grassland biome was expected because it concurs with the findings of previous studies showing that alien plant species have been expanding their range and possibly their negative impacts (van Wilgen et al., 2022; IPBES, 2023). We suggest that the economic value of some alien plant species, together with limited law enforcement, particularly in the horticultural industry (e.g., retail nurseries), could have contributed significantly to observed trends in alien plant invasion (Cronin et al., 2017; Seebens et al., 2018; van Kleunen et al., 2018; Mokotjomela et al., 2024b). In support, Scheba et al. (2017) and Cavannas et al. (2019) both indicated that the cultivation of bamboo species in South Africa has increased over decades because of their socio-economic values.

Our finding of many herbs and woody alien species in the grassland biome is possibly ascribed to agricultural food security innovation because Süle et al. (2023) reported that most woody and herbaceous species were introduced for use as ornamental plants and fodder. The poor management of ornamental plants and fodder varieties may have resulted in species release and overcoming invasion barriers from their initial introduction grounds (Richardson et al., 2000; Turbelin et al., 2022; Süle et al., 2023). This finding corroborates the trend from previous studies demonstrating that alien herbs and woody species dominate South Africa (Carbutt, 2011; O'Connor and van Wilgen, 2020; Mokotjomela et al., 2023 & 2024b). The dominance of alien herbs in the grassland biome could be explained by environmental chemistry filters, such as higher phosphorus and poor boron, that reduce anabolism and the need for catabolic nutrients that subsequently limit woody species from building up a surplus of photosynthates (Mills and Allen, 2018; Wilson et al., 2020). In support, other studies reported that alien woody species invasions are often observed in abandoned agricultural lands and homesteads having low-nutrient environmental filters modified by human-dominated land use (Richardson, 1998; Scorer et al., 2019). Our finding that alien woody species hotspots erupted in 1980 complements the report from IPBES (2023) that estimated that the numbers of alien and invasive species started increasing by about 70 % since 1970 (Brondizio et al., 2019). The expansion of alien woody species hotspots might be attributed to the increase in human-driven land use, particularly in the agricultural sector, which reported a growth of over 91,000 commercial farmers in 1970 in South Africa (Liebenberg, 2012; Greyling et al., 2015).

We observed low occupancy of woody alien species (0.4 %) in the protected areas, possibly due to limited anthropogenic activities that facilitate the spread of alien plant propagules (Lockwood et al., 2005), and partly the compliance with the legal obligation of National Environmental Management: Biodiversity Act 10 of 2004 (NEM: BA) section 64 that mandates landowners and organs of state to control alien species. Our findings support the reports demonstrating that effectively managing alien and invasive species in critical conservation areas can safeguard biodiversity and build resilience against various threats (Soares-Filho et al., 2010; Hoffmann, 2022; IPBES, 2023). The increased occurrence of alien plant species poses an uncertain future for protected areas by impeding the proper ecosystem function and structure and limiting the availability of essential natural resources (Goodman, 2003; Moodley et al., 2020). In support, Thomas (1980) found that two species of alien and invasive vines inhibit the recruitment of native forest species in the

Theodore Roosevelt Island Nature Reserve, Washington, United States of America.

Alien woody species abundance has expanded by 5 % in the critical water source of the grassland biome since 1980, suggesting limited remedial action has been taken (Kotzé et al., 2010; Le Maitre et al., 2016; 2020). The negative impacts of plant invasions in critical water source areas were previously reported (Brooks et al., 2004; Le Maitre et al., 2000 & 2004; Mokotjomela et al., 2024b). Le Maitre et al. (2020) estimated a loss of 1.44–2.44 billion m^3 per year of surface terrestrial water runoff in South Africa due to the invasion of alien woody species. Controlling and managing alien and invasive plant species is necessary for protecting water. For example, Scott (1999) found that clearing riparian scrub lightly invaded by pines increased streamflow by 797 mm/year in the riparian zones of South Africa. The degradation of critical water sources is of great concern because South Africa is a water-limited country (Trisos et al., 2020; IPBES, 2023; Viljoen and van der Walt, 2018), and water demand is rising with the current population growth (du Plessis, 2017).

5. Conclusions

The grassland biome has undergone significant transformation over the past 34 years, resulting in their decreased resilience to emerging conservation threats. The decline in vegetation cover, likely due to environmental degradation in synergy with other stressors, has facilitated plant invasions and impaired ecosystem functions and services. To mitigate these impacts, it is crucial to address unmanaged threats, such as the spread of alien plant invasions, particularly in critical biodiversity areas and essential water sources. Management efforts should prioritise clearing woody alien invasions in these areas. In addition, further studies are needed to understand the impacts of biological invasions and their interactive effects on the environment. Urgent, context-specific management actions, policies, and selective habitat restoration or rehabilitation interventions are required to preserve the functionality of the southern African grassland biome. These efforts should align with sustainable socio-economic and natural capital benefits outlined in the Sustainable Development Goals (SDGs).

Ethical Statement

Ethical approval is not applicable for this article

Declaration of Competing Interest

The authors declare no conflict of interest in the MS.

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Declarations

All authors have read, understood, and have complied as applicable with the statement on "Ethical responsibilities of Authors" as found in the Instructions for Authors

Authors' contributions

Loyd R Vukeya & Thabiso M Mokotjomela: Conceptualised the study; Loyd R. Vukeya: Analysed spatial data, drew maps, wrote MS; Neville Pillay read, edited the MS and provided important insight for improving the study.

Consent for publication

Not applicable

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03462.

Data availability

The data that has been used is confidential.

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