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Transactions of the Royal Society of South Africa

ISSN: 0035-919X (Print) 2154-0098 (Online) Journal homepage: www.tandfonline.com/journals/ttrs20

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To cite this article: Kundai R. Dube, Gerald Chikowore, Kim Canavan, Grant D. Martin & Iain D. Paterson (27 May 2026): Landscape-scale patterns, temporal shifts, and impacts of invasive alien plant species in a montane grassland of Eastern Zimbabwe, Transactions of the Royal Society of South Africa, DOI: 10.1080/0035919X.2026.2672397

To link to this article: https://doi.org/10.1080/0035919X.2026.2672397

Published online: 27 May 2026.

Transactions of the Royal Society of South Africa, 2026
https://doi.org/10.1080/0035919X.2026.2672397

Landscape-scale patterns, temporal shifts, and impacts of invasive alien plant species in a montane grassland of Eastern Zimbabwe

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ABSTRACTThe Manica Highlands, which border Zimbabwe and Mozambique, support several endemic species of flora and fauna. Montane grasslands in this high-elevation region support the largest breeding pairs of an intra-African and endangered bird, the Blue Swallow, *Hirundo atrocaerulea*. However, these grasslands are increasingly fragmented, primarily due to the invasion by woody invasive alien plants (IAPs). Using a combination of satellite imagery (1984–2023), systematic field plots, and community level vegetation surveys, the study assessed the composition, rates of spread, and impacts of IAPs in Nyanga National Park (NNP), a protected area in the Manica Highlands of Zimbabwe. Results show that Australian *Acacia* species dominate the woody invasive flora, with *A. dealbata* (Silver wattle) and *A. decurrens* (Green wattle) now far more abundant than *A. mearnsii* (Black wattle). Satellite analysis revealed that woody IAPs have expanded by approximately 181% between 1984 and 2023, and vegetation surveys demonstrated that invasion is associated with altered community structure and reduced native grassland species richness. These findings indicate ongoing transformation of montane grasslands and emphasise the urgency of implementing more effective, sustainable control measures. In light of the successful classical biological control against *Acacia* spp. elsewhere in the region, such agents warrant careful evaluation as a complementary component of future invasive plant management in NNP.

Keywords: **biological Invasions; biodiversity; biological control; conservation; sustainability**

1. INTRODUCTION

Tropical montane habitats support high biodiversity and are hotspots of endemism, with grasslands as a key feature of these landscapes (Lele et al . 2020). Unlike forests, which have traditionally attracted significant conservation focus, montane ecosystems, particularly grasslands, have received comparatively little attention and are often perceived as underutilised landscapes targeted for afforestation or conversion to other land uses (Joshi, Sankaran, and Ratnam 2018; Parr et al . 2014). As a result, many have been transformed into commercial plantations, despite their vital ecological role as an essential source of water that sustains both biodiversity and downstream human communities (Boakes et al . 2009; Das, Ratnam, and Jathanna 2023). This land-use transformation, coupled with limited conservation prioritisation, has rendered montane grasslands increasingly susceptible to ecological degradation and proliferation of invasive alien plant species (IAPs). These IAPs threaten the structural integrity and functional resilience of these ecosystems. Notwithstanding their ecological importance, montane grasslands remain poorly studied, and the spatiotemporal dynamics and ecological consequences of plant invasions within these systems are still inadequately characterised, thereby constraining informed management and restoration interventions (Canavan et al . 2021).

The proliferation of IAPs within montane grassland ecosystems poses a significant threat to native biodiversity, ecosystem functioning, and land productivity (Chikowore, Martin, and Chidawanyika 2021). These plants frequently outcompete indigenous herbaceous vegetation, alter fire regimes, and disrupt essential ecosystem services such as forage provision, water infiltration, and nutrient cycling (Ehrenfeld 2010; Le Maitre et al . 2011; Yapi et al. 2018). In sub-Saharan Africa, invasion by species such as *Lantana camara* L. (Verbenaceae) and *Acacia mearnsii* De Wild. (Fabaceae) has been linked to declines in grassland-dependent species and in essential ecosystem services critical to local communities (Boy and Witt 2013; van Wilgen 2018; Witt, Beale, and van Wilgen 2018; Yapi et al. 2018).

Effective management of IAPs requires an integrated understanding of their population dynamics, spatial distribution, ecological consequences, and socioeconomic implications. In

Published online 27 May 2026

addition, monitoring IAPs is crucial for understanding and predicting future trends in environmental management, as it enables researchers and practitioners to anticipate potential challenges and shifts in dynamics (van Wilgen 2018). Hence, systematic monitoring of their spread and impacts is critical for detecting incipient invasions, evaluating ecological impacts, and informing timely management interventions (Oswalt et al . 2021). Additionally, determining the species composition and structural characteristics of woody IAPs is crucial for selecting suitable control strategies and prioritising restoration efforts (Finley, Dovciak, and Dean 2023). Species-specific information also supports policy development for invasive plant management in ecologically sensitive and socio-economically important landscapes, including montane grasslands (Clark and Martin 2024).

Recent advances in remote sensing technologies, including multispectral and hyperspectral imaging, light detection and ranging (LiDAR), and synthetic aperture radar (SAR), have significantly improved the capacity to detect, map, and monitor IAPs across various spatial and temporal scales (Arasumani et al . 2018, 2021). These tools support large-scale, repeatable, and cost-effective assessments of IAPs infestations, particularly when integrated with machine learning algorithms and cloud-based platforms such as Google Earth Engine (Große-Stoltenberg et al . 2023). Combining remote sensing data with ground-based surveys further enhances accuracy, supporting early detection and informing adaptive management responses that minimise the ecological and economic impacts of invasive IAPs.

Nyanga National Park (NNP) in Zimbabwe, which hosts an Afromontane ecosystem with montane grasslands and wetlands, is increasingly threatened by the spread of IAPs, particularly woody plants (Clark et al . 2021; Dube et al . 2025; Mahoyi et al . 2020; Maroyi 2015; Mujaju, Mudada, and Chikwenhere 2021). However, the spatiotemporal dynamics and composition of these invasions are poorly documented. Moreover, the impacts of these IAPs on native grasslands remain incompletely quantified. The study therefore aims to determine the composition and abundance of woody IAPs in NNP, Zimbabwe, to evaluate their spread into grasslands over time, and to assess their impact on the assembly of native grassland vegetation communities. Given the long-standing history of mechanical removal of woody IAPs in the park, the findings will inform the development of site-specific management interventions o enhance restoration and conservation efforts.

2. MATERIALS AND METHODS

2.1. Study site

The study was conducted in NNP (17°30′–18°30′S, 32°30′–33°00′E), a protected area in the Eastern Highlands of Zimbabwe, spanning approximately 470 km² (Figure 1). The park features an undulating landscape with elevations ranging from 1 800 to 2 200 meters above sea level. It also encompasses Mount Nyangani, Zimbabwe's highest point, rising to 2 593 meters above sea level. The climate is temperate, with annual rainfall ranging from 800–1 200 mm, concentrated in the summer months (November – April) and cool, dry winters (May–August) (Muvengwi et al . 2018). The region's soil is predominantly nutrient poor, derived from granite and sandstone, supporting fire-adapted grassland ecosystems (Soper 2000). The park comprises montane grasslands on the western side, tropical forests in the east, and patches of tropical forest in the south-east in the Mutarazi and Honde area (Dube et al . 2025). Mosaics of indigenous msasa woodlands are also found in the western area, mainly comprising *Julbernardia globiflora* (Benth.) Troupin (Fabaceae) and dwarf *Brachystegia spiciformis* Benth. (Fabaceae).

2.2. Invasive alien woody plant composition and abundance

To assess the composition and abundance of woody IAPs in NNP, a systematic sampling framework was developed using ArcGIS (version 10.9). The Park was divided into 1 km × 1 km grid cells, from which 19 grid cells were randomly selected from historically grassland areas. Within each selected 1 km² grid cell, a single 50 m × 50 m plot was randomly established for vegetation assessment. Plots falling in hazardous or inaccessible terrain (e.g., steep cliffs or the upper slopes of Mount Nyangani) were excluded on safety grounds and replaced by an alternative randomly located plot within the same grid cell to maintain randomisation while ensuring field-worker safety. Vegetation surveys were conducted during the main growing season, when most woody species had fully developed foliage, and many were flowering or fruiting, thereby maximising the reliability of field identification using morphological characteristics. Sampling focused on montane grasslands because these grasslands are the habitat of greatest conservation concern in NNP and are experiencing the most rapid encroachment by woody IAPs, therefore, adjacent forest and woodland types were not systematically sampled in this study. In each plot, all IAPs were identified to species level using field guides (Glen and van Wyk 2016; Henderson 2005), and the number of stems per species was recorded to quantify relative abundance. Particular attention was given to large adult stems (>3 m in height), as these canopy-forming trees significantly influence light availability, water use, fuel loads, and grassland replacement (Le Maitre et al . 2011; Richardson and Rejmánek, 2011).

For *Acacia* species, all stems >3 m rooted within the 50 m x 50 m plot boundaries were counted, and each stem was treated as an individual for subsequent analyses. *Acacia* individuals were identified to species level using vegetative and reproductive morphological traits (phyllodes/leaf form, inflorescence type, pod morphology, and bark characters) following Henderson (2005). Where necessary, uncertain specimens were examined with a hand lens and cross-checked against herbarium material and photographic plates and drawings in Henderson (2005) to minimise misidentification. To reduce observer fatigue and associated detection or identification errors, the number of plots surveyed per day was limited, counts were conducted during cooler morning hours, and a standardised *Acacia* identification protocol was followed.

2.3. Spatio-temporal dynamics of invasion

Spatio-temporal changes in woody vegetation encroachment into grassland areas within NNP were assessed using satellite imagery. Surface reflectance data from Landsat 5 TM (1984), Landsat 7 ETM + (2004), and Landsat 8 OLI/TIRS (2023) were accessed through the Google Earth Engine platform to ensure consistency across the study period. For each year, multiple images from the late wet to early dry season (April–July) were composited to minimise cloud

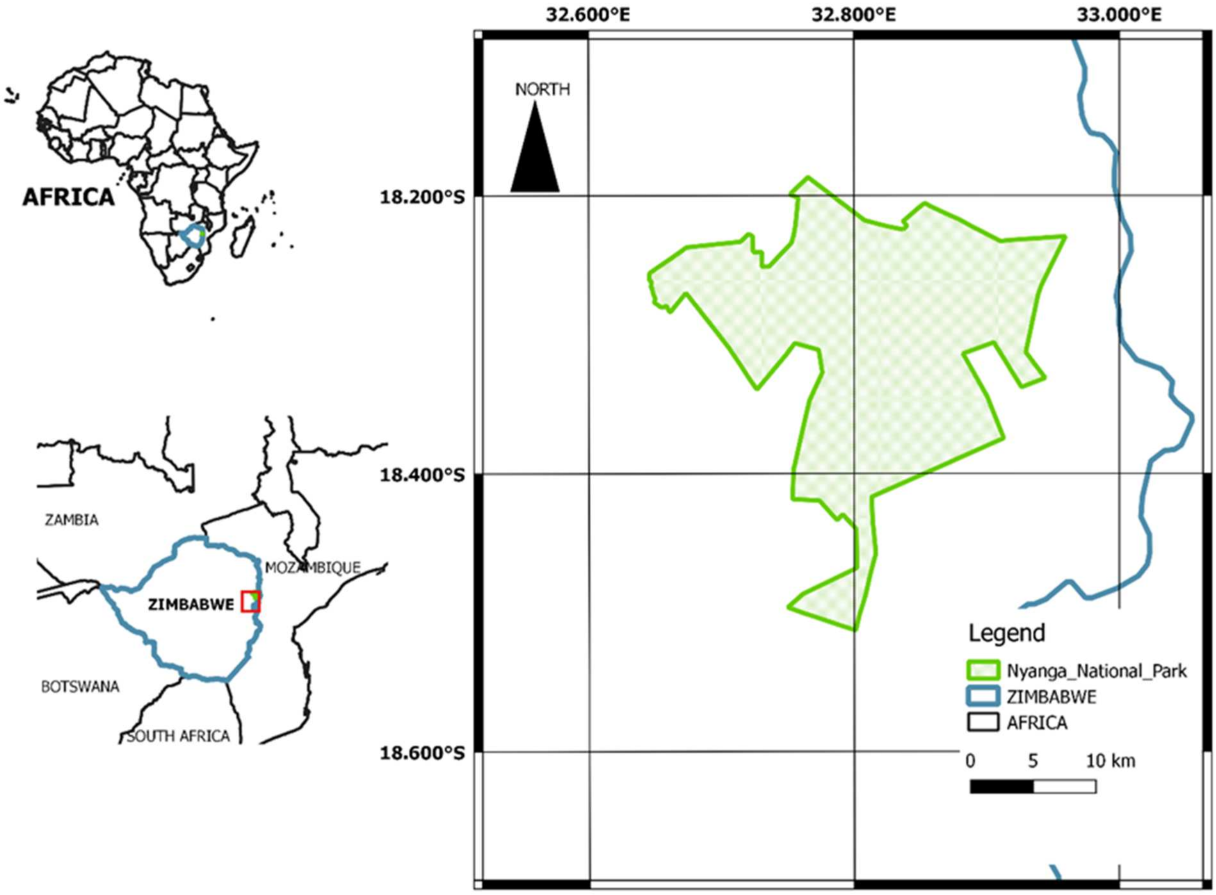

Figure 1. Map of the study area, Nyanga National Park, Zimbabwe.

contamination and capture peak vegetation greenness, thereby enhancing spectral separability between woody and herbaceous vegetation. All imagery was radiometrically standardised and resampled to a uniform spatial resolution of 30 m. Training data were derived from field vegetation surveys (described in section 2.2 above) and high-resolution imagery, from which 36 training polygons were digitised to represent invasive alien trees, native savanna trees, grasslands and water bodies, capturing within-class spectral variability while avoiding mixed pixels. Supervised classification was performed using a Maximum Likelihood Classifier implemented in the QGIS Semi-Automatic Classification plugin, utilising Landsat blue, green, red, near infrared, and short-wave infrared bands. Classification accuracy was evaluated using 114 independent GPS-referenced ground-truth points collected during field validation surveys, from which overall accuracy was derived. Post-classification outputs were converted to vector format and overlaid to quantify the spatial extent and temporal spread of woody invasive vegetation between assessment years.

2.4. Impacts of invasion on native grassland vegetation

To assess the impact of invasion on native grassland vegetation communities, a single field survey was conducted per site during the peak flowering and fruiting period between March and May 2023, when most herbaceous species could reliably be identified. Surveys were conducted at four sites (two invaded, two uninvaded), with dense monospecific *Acacia* stands deliberately paired with adjacent uninvaded montane grasslands for comparative analysis. A hierarchical sampling design was employed as follows: four sites were surveyed in total (two invaded wattle sites and two uninvaded grassland sites). At each site, three 50 m transects were established, separated by 50 m, yielding three transects per site. At 5 m intervals along each transect, a 1 m x 1 m quadrat was placed on the ground, giving 10 quadrats per transect. This yields a total sampling effort of 10 quadrats x 3 transects x 2 sites per treatment, resulting in 60 quadrats per treatment (invaded and uninvaded) and 120 quadrats overall. The percentage cover of different species of grasses and herbs within each quadrat was visually estimated (Peet, Wentworth, and White 1998). Plant specimens were collected on the first encounter and pressed for identification. Identification was done to species level, where possible, using reference specimens by experienced botanists at the National Herbarium in Harare, Zimbabwe.

2.5. Data Analyses

To explore the community structure and diversity of woody IAPs in NNP, a Whittaker rank-abundance (dominance-diversity) curve was plotted. The curve visually depicts patterns in species richness, evenness, and dominance in the assemblage (Magurran 2003; Whittaker 1965). Species evenness is reflected in the steepness of the curve, with shallow slopes indicating more even distributions of relative abundance and steeper slopes indicating dominance by a few species (Magurran 2003). Species richness is the number of different species on the chart, that is, the number of species ranked. Species abundances were first sorted in descending order, assigned rank values, and then plotted against these ranks. For each invasive woody genus, we calculated mean stem density per 2 500 m² plot ± standard error (SE) across all plots to summarise abundance and associated uncertainty. This procedure was implemented in R using base sorting functions and visualised with the "*rankabundance*" and "*radfit*" functions from the *vegan* (version 2.6-6) and *BiodiversityR* (version 2.16-0) packages, respectively (Kindt and Coe 2005; Oksanen 2015). The dominant genus was further disaggregated into species to visualise species level dominance.

To assess the impact of Australian *Acacia* invasion on vegetation community assembly in montane grasslands, we analysed species composition data using the *vegan* package in R (Oksanen 2015). We first evaluated sampling adequacy and species richness patterns using rarefaction curves generated with "*rarecurve*" and "*specaccum*". Homogeneity of group variances in community dissimilarities between invaded and uninvaded grasslands was then tested using "*betadisper*" and "*permutest*" functions from the vegan package in R. Following this, community-level differences were assessed with PERMANOVA using the "*adonis2*" function based on Bray–Curtis dissimilarities, with habitat type as the main factor. Community composition was visualised using Principal Coordinates Analysis (PCoA), which is robust for abundance data with many zeros, as observed in sparsely vegetated invaded sites (Legendre and Legendre 2012). Indicator species analysis (multipatt, indicspecies) was then conducted to identify taxa characteristic of each habitat type, with species having significant indicator values ($p < 0.05$) considered indicative of either invaded or uninvaded communities (de Cáceres, Jansen, and Dell 2016).

3. RESULTS

3.1. Woody alien species composition

In NNP, *Acacia* spp. were the most common IAPs, with a mean density of 103.6 ± 30.8 stems per 2 500 m² plot and 1 762 stems in total across the 19 sampled plots, whereas *Pinus* spp. and *Eucalyptus* spp. showed intermediate densities of 31.5 ± 22.0 and 19.7 ± 13.2 stems per plot (totals 535 and 335 stems), respectively, and *Populus* spp. were the least common, with 5.8 ± 4.0 stems per plot and 99 individuals recorded in total (Figure 2). These values indicate a strongly right-skewed abundance distribution of *Acacia* spp. markedly dominant relative to the other three woody invasive genera. Furthermore, among the *Acacia* species, *A. dealbata* was most abundant (55.1% of all *Acacia* stems), followed by *A. decurrens* (24.7%) (Figure 3).

3.2. Changes in invasive woody species cover in grasslands

A progressive expansion in the cover of invasive alien woody plants in grasslands was noted between 1984 and 2023 in NNP (Figure 4). The area invaded expanded from 48 km^2 in 1984 to 117 km^2 by 2004, representing a 143.75% increase over the 20-year period. By 2023, the invaded area grew by a further 18 km^2, reaching a total of 135 km^2. This shows an additional 15.38% increase since 2004 and an overall increase of 181.25% relative to the 1984 baseline.

3.3. Impacts of invasion on grassland vegetation

The species accumulation curve for invaded sites reached an asymptote in less than 25 sampling sites (Figure 5). However, this was not the case for uninvaded grasslands, where new species continued to be recorded even after 75 sampling sites. Consistently, when directly comparing the number of different species present, the uninvaded grassland plots exhibited a significantly higher species richness (115) compared to the adjacent invaded areas that recorded only 11 species ($p < 0.001$; Figure 6).

Permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarities indicated a statistically significant difference in vegetation community composition between invaded and uninvaded habitats ($F = 12.765$, $df = 1, 178$, $p = 0.001$), with habitat type accounting for 10.2% of the total variation in community structure ($R^2 = 0.1015$). Principal Coordinates Analysis using the same Bray–Curtis distance matrix further illustrated this separation, with Axis 1 and Axis 2 explaining 20.3% and 13.3% of the variance in the multivariate community dissimilarity, respectively (Figure 7). In the ordination space, uninvaded plots exhibited greater spread, reflecting higher within-habitat variability, yet still formed a well-defined cluster within the 95% confidence ellipsoid. In contrast, invaded plots were more tightly grouped, indicating reduced community heterogeneity, and partially overlapped with uninvaded plots.

Indicator Species Analysis identified key species that are strongly associated with each habitat type (uninvaded and invaded), providing insight into the distinct vegetation compositions of these habitats. For the grassland habitat, 11 species were identified as significantly associated with this environment (Table 1). The species with the highest association was an unidentified *Eragrostis* sp. (Poaceae) (IndVal = 0.788, $p = 0.001$), followed by *Hyparrhenia cymbaria* L. Stapf (Poaceae) (IndVal = 0.699, $p = 0.003$). Other species, including *Oxalis* sp. (Oxalidaceae) and *Themeda triandra* Forssk (Poaceae), also exhibited significant associations. In the invaded habitat, six species were found to be significantly associated with this environment (Table 1). The most strongly associated species was a ruderal, *Bidens pilosa* L. (Asteraceae) (IndVal = 0.566, $p = 0.001$), which is also considered an invasive species in the region. Other species, such as *Cymbopogon nardus* L. Rendle (Poaceae), which is generally regarded as an invasive species, and *Eragrostis acraea* De Winter (Poaceae) showed moderate associations (IndVal range: 0.283–0.346, $p < 0.05$).

4. DISCUSSION

This study confirmed a significant increase in the presence of IAPs in NNP, most notably *Acacia* spp., *Eucalyptus* spp., and *Pinus* spp., which are known for their aggressive invasion patterns and potential to disrupt local biodiversity severely (Chikowore et al . 2023; Mujaju, Mudada, and Chikwenhere 2021; Sheppard et al . 2012). This finding is consistent with Matongo (2016), who reported an expansion in *Acacia* coverage between 1985 and 2010. However, our results indicate that despite an overall increase in *Acacia*, the rate of expansion has slowed over the past two decades. This is likely due to mechanical clearing efforts implemented in the park through small-scale timber operations over the past decades (Dube et al . 2025). More recently, in 2023, large-scale clearing operations in partnership with the Sustainable Afforestation

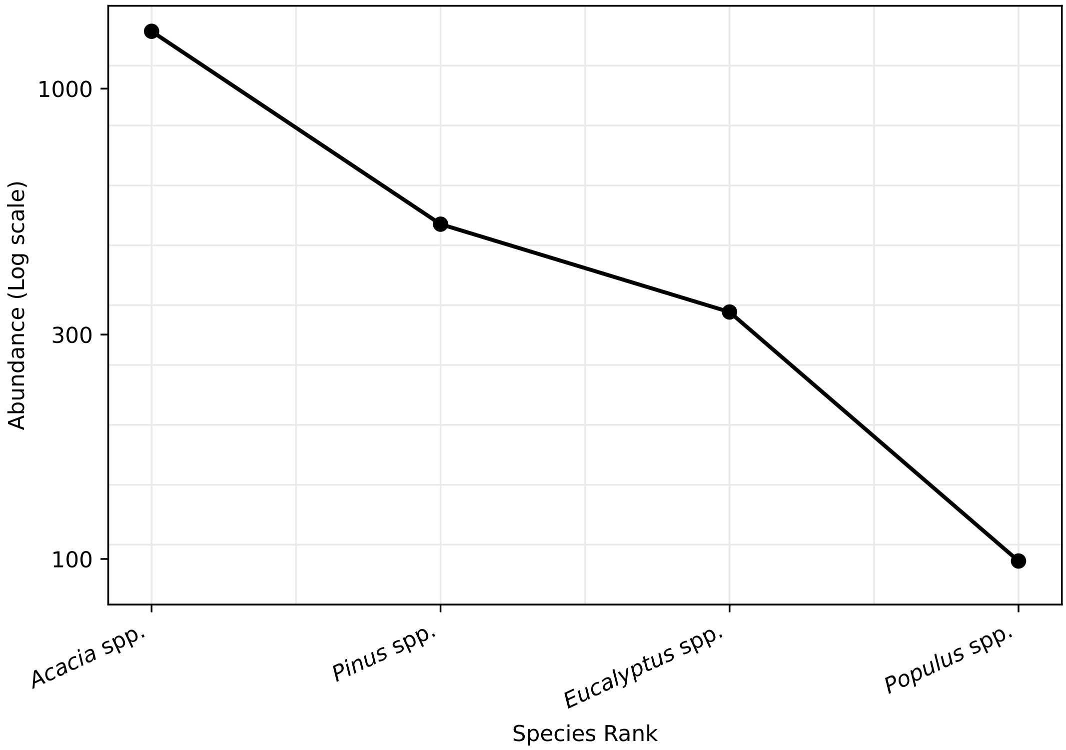

Figure 2. Whittaker rank-abundance curve for invasive alien woody plants in Nyanga National Park, Zimbabwe.

Association (SAA), a company that supplies fuelwood for tobacco curing to farmers, have been introduced in NNP (Dube et al . 2025), with approximately 2000 ha cleared (NNP internal records). Selected grassland areas within these cleared zones are being actively restored using native species sourced from within the park, indicating a shift from passive to active restoration management (NNP internal records). Additionally, any resprouted seedlings are monitored and uprooted by a dedicated follow-up team. However, there is evidence of newly invaded and re-

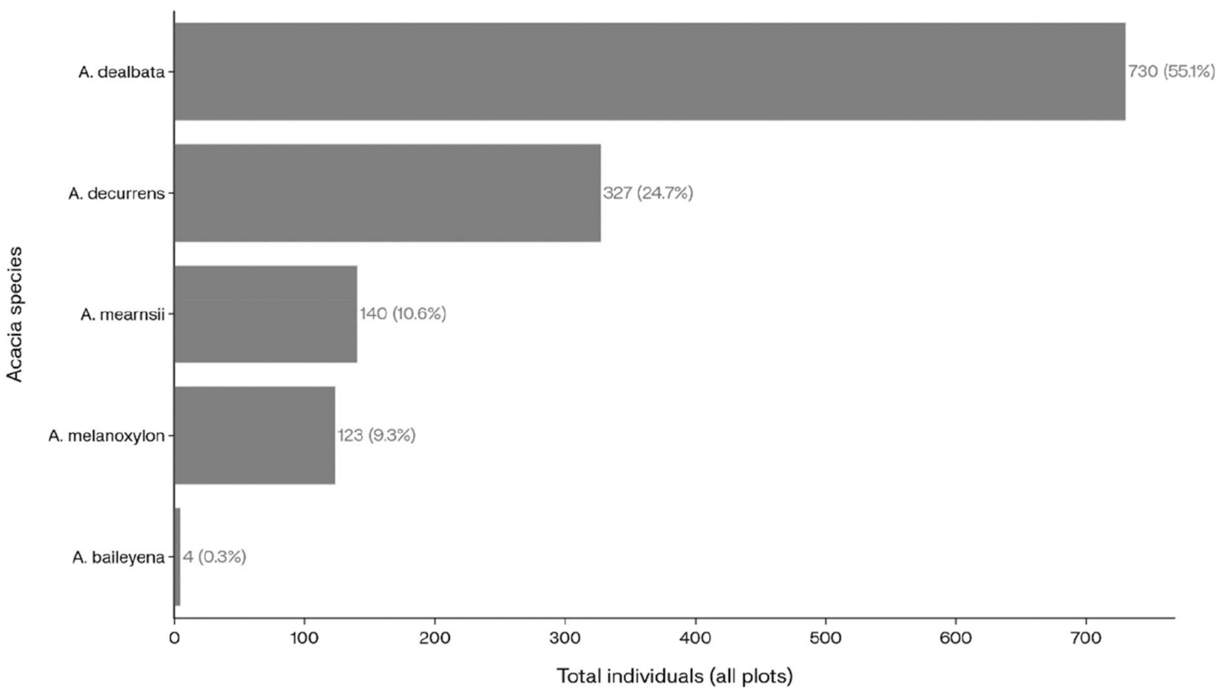

Figure 3. Total abundance of invasive *Acacia* species across 19 plots (2500 m² each) in Nyanga National Park.

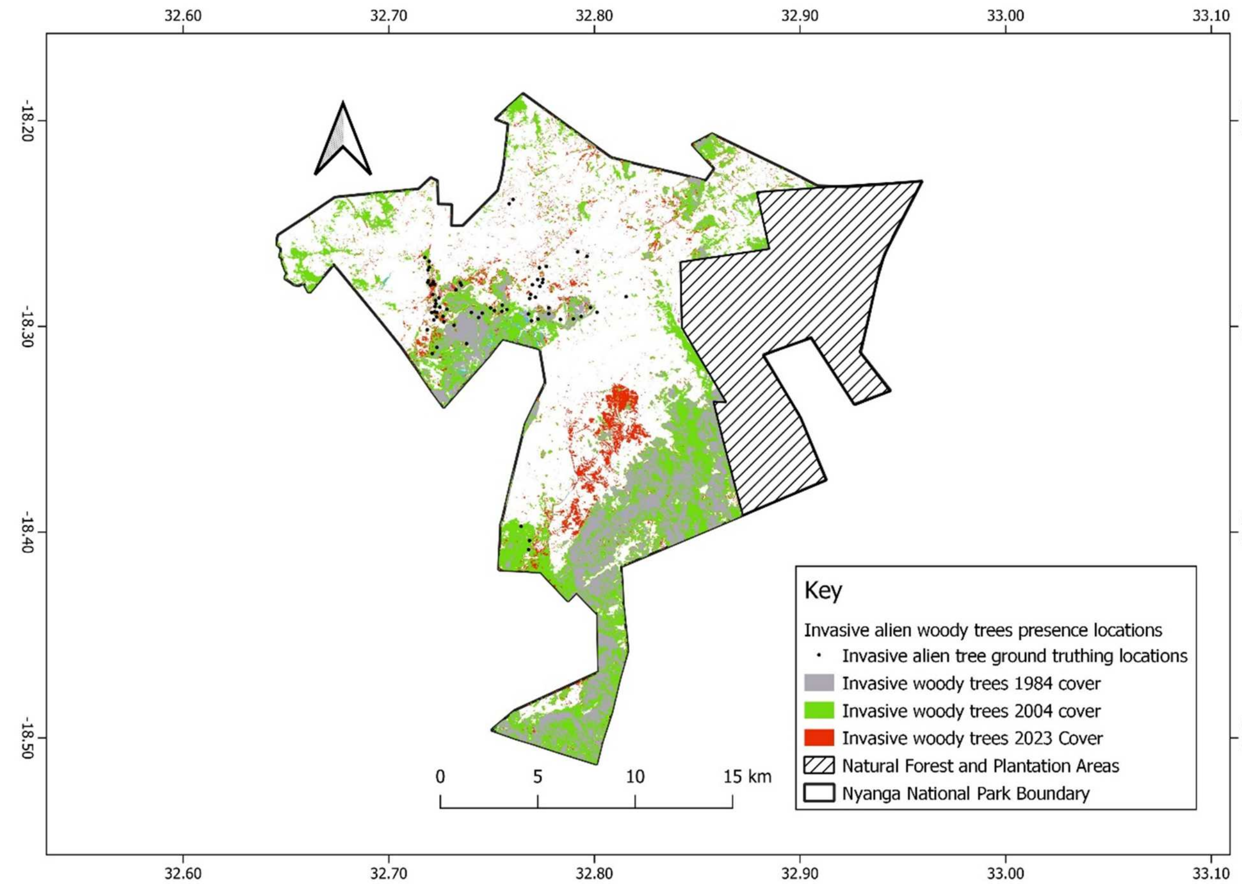

Figure 4. Changes in the cover of invasive alien trees in the grasslands of Nyanga National Park between 1984 and 2023. Green areas depict the expansion of woody cover in grassland areas by 2004, while red areas depict the expansion by 2023.

invaded areas, despite these efforts to restore native grassland vegetation. These interventions included felling and ringbarking of *Acacias*, which were reported to be effective only against large-boled trees (Muvengwi et al . 2018). The findings from this study, therefore, highlight the urgent need to develop a sustainable solution to the ongoing spread of woody IAPs in montane grasslands in the eastern highlands of Zimbabwe.

While the dominance of *Acacia* species has been well documented, making them the primary management priority, this study also recorded several other woody invasive alien trees within the national park. These include *Populus* spp., which occur in smaller but dense patches. The presence of these additional woody invaders highlights the need for continued monitoring and localised control to prevent secondary invasions following *Acacia* suppression. Notably, the study also confirms the occurrence of multiple Australian *Acacia* species within the national park and its surrounding areas. Unlike previous studies that reported only *A. mearnsii* in the area (Mahoyi et al . 2020; Jimu and Ngoroyemoto, 2011; Matongo, 2016; Muvengwi et al . 2018), this study found *A. dealbata* to be the most dominant species in the national park, followed by *A. decurrens*. This contrast with earlier work may reflect temporal shifts in dominance among congeners, possible taxonomic misidentification in past surveys, or a combination of both processes. Regardless of the underlying cause, the present study documents a significant change in the dominant *Acacia* spp., highlighting an important update for selecting appropriate management and biological control strategies (Impson, Kleinjan, and Hoffmann 2021). This finding also has implications for invasive species management, as different *Acacia* spp. may exhibit varying physiological traits and management responses (Richardson, Roux, and Marchante 2023). While all these species reproduce through seeds, root suckers, and stump sprouting, *A. dealbata* can create dense thickets and exhibits early seed production, starting between two and four years of age (Correia et al . 2014; Matukana 2021). In addition, biological control agents introduced in other areas are species-specific (Impson et al . 2011), hence their integration requires adequate taxonomic resolution. Therefore, it is important to identify the target weed correctly so the appropriate agent can be released.

This study finds that the invasion of grasslands by woody IAPs negatively impacts native vegetation assemblages, resulting in a significant reduction in species richness. These impacts have been reported in other regions, including the Maloti-Drakensberg in South Africa, where these species have similarly transformed grasslands into less diverse ecosystems dominated by alien flora (Hoogar, Malakannavar, and Sujatha 2019; Martin et al . 2025; Ricciardi 2013; Richardson, Roux, and Marchante 2023). Several mechanisms can be attributed to the loss of native vegetation species in invaded habitats, including alterations in soil physicochemical properties, changes in light availability and microclimatic conditions, and allelopathic effects (Chikowore, Martin, and Chidawanyika 2021; Mahlobo et al . 2025). For instance, invasive

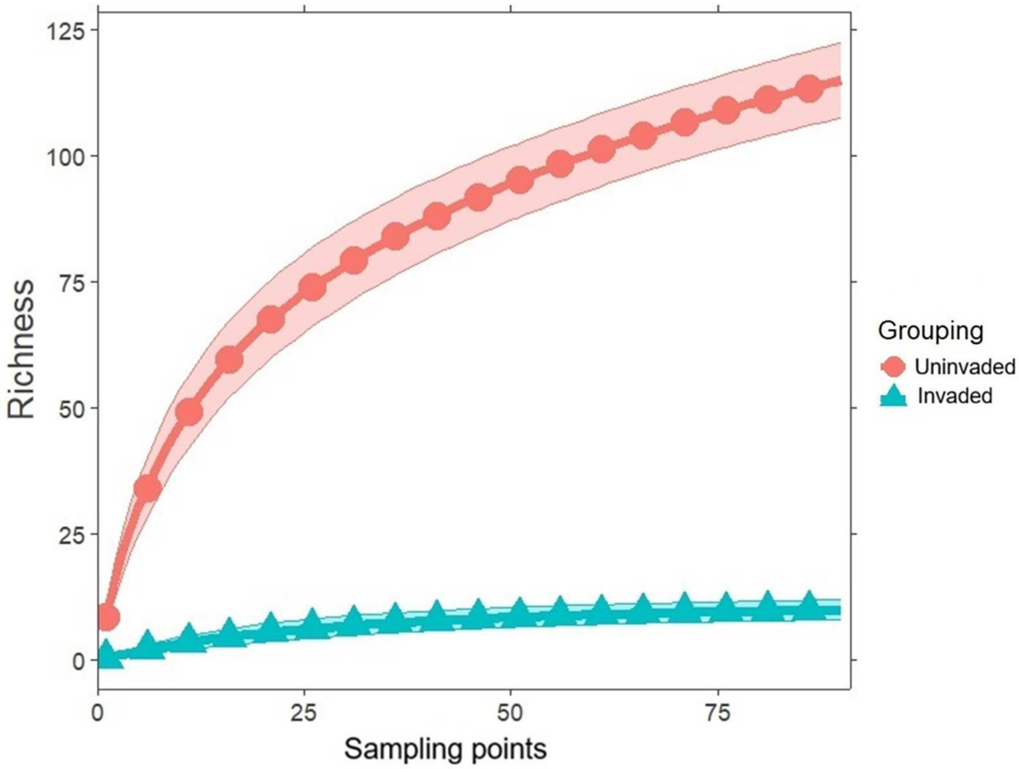

Figure 5. Species accumulation curves for the surveyed plots in invaded and uninvaded sites.

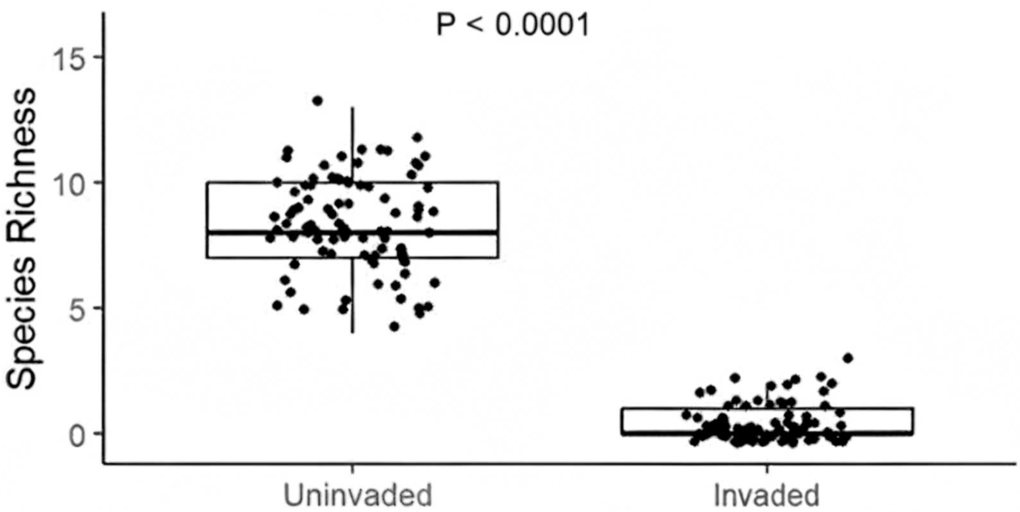

Figure 6. Species richness in uninvaded and adjacent invaded habitats.

woody trees from the Fabaceae family particularly alter the soil nitrogen composition of invaded habitats, favouring the proliferation of nitrophilous species in the understory (Aguilera et al . 2015; Chikowore, Martin, and Chidawanyika 2021).

The reduction in floral biodiversity and changes to the functional composition of plant communities from herbaceous grassland species to woody IAPs have knock-on effects on other organisms in the affected ecosystems. In NNP, for example, the grasslands are reported to support the largest breeding habitats of the vulnerable inter-African migratory bird, *H. atrocaerulea.* However, the transformation of these breeding grounds by woody tree invasion threatens their dwindling populations (Evans et al . 2015; Evans and Bouwman 2010). Other services derived from montane grasslands, including water provision, medicinal plants, and grazing, are also affected by the invasion of montane grasslands, further highlighting the need to implement effective management interventions (Kumar, Nisha Phukon, and Singh 2021; Martin et al . 2025; Ngorima and Shackleton 2019). In the NNP context, the progressive loss and fragmentation of open grassland reduce the availability of palatable forage and alter movement patterns of grazing ungulates,

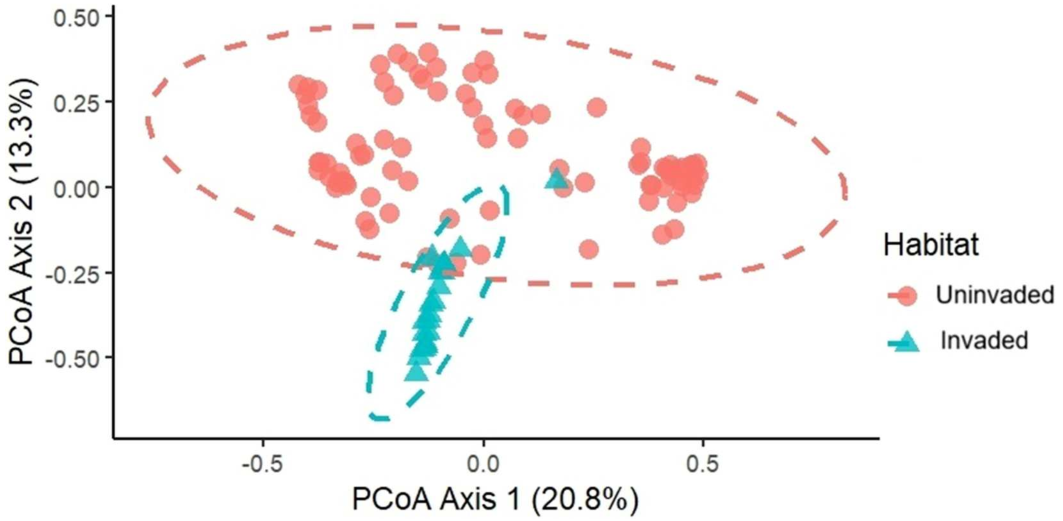

Figure 7. Principal Coordinates Analysis from uninvaded and adjacent invaded understory based on Bray-Curtis Dissimilarity.

Table 1. Indicator plant species associated with uninvaded montane grassland and Acacia dealbata–invaded grassland habitats in Nyanga National Park, eastern Zimbabwe, as identified by Indicator Values Analysis (IndVal). For each species, the IndVal represents the product of specificity and fidelity of occurrence within a given habitat type, and the associated *p*-value is based on permutation tests. Significance levels are coded as follows: *p < 0.05, **p < 0.01, ***p < 0.001; higher numbers of asterisks indicate stronger statistical evidence for the association.

Habitat	Species	IndVal	*p-value*	Significance
Uninvaded	*Eragrostis* sp.	0.788	*0.001*	***
Uninvaded	*Hyparrhenia cymbaria*	0.699	*0.003*	**
Uninvaded	*Hyparrhenia* sp.	0.606	*0.002*	**
Uninvaded	*Oxalis* sp.	0.568	*0.013*	*
Uninvaded	*Themeda triandra*	0.537	*0.011*	*
Uninvaded	Unknown (*Rosaceae*)	0.527	*0.012*	*
Uninvaded	*Sporobolus* sp.	0.506	*0.021*	*
Uninvaded	*Loudetia simplex*	0.471	*0.03*	*
Uninvaded	*Helichrysum nudifolium*	0.459	*0.036*	*
Uninvaded	Unknown	0.447	*0.046*	*
Uninvaded	*Satyrium* sp.	0.447	*0.048*	*
Invaded	*Bidens pilosa*	0.566	*0.001*	***
Invaded	*Carex* sp.	0.502	*0.002*	**
Invaded	Unknown (*Cyperaceae*)	0.447	*0.002*	**
Invaded	*Cymbopogon nardus*	0.346	*0.012*	*
Invaded	*Eragrostis acraea*	0.346	*0.013*	*
Invaded	Unknown (*Poaceae*)	0.283	*0.03*	*

potentially compromising their nutritional intake and long-term population viability. This shows the urgency of preventing further woody encroachment and restoring key grazing areas to maintain both herbivore populations and the ecosystem services they support.

Given the observed trends and the potential for continued invasion, conservation initiatives within the NNP must adopt a multifaceted approach. This includes enhancing stakeholder engagement, promoting awareness of the impacts of these IAPs, and fostering community-based approaches to manage and restore native grassland ecosystems. These approaches may include integrating classical biological control methods, drawing lessons from successful implementation in South Africa for the same species (Impson et al . 2021; Kotzé, Wannenburgh, and van Wilgen 2025; Richardson, Roux, and Marchante 2023; van Wilgen et al . 2025), which can provide an additional sustainable management option to address this problem. Implementing adaptive management strategies responsive to findings from ongoing research will be vital for mitigating the impacts of IAPs and ensuring the long-term conservation of NNP's unique biodiversity.

5. CONCLUSION

This study shows that woody IAPs have expanded their cover in NNP grasslands by 181.3% since 1984 and now form dense stands, significantly reducing native grassland species richness and altering community composition. A key and novel finding is that *A. dealbata* and *A. decurrens*, rather than the previously reported *A. mearnsii*, are now the dominant *Acacia* species, with several additional *Acacia* congeners present, correcting earlier taxonomic assumptions that underpin management planning. Given the extent and impacts of invasion and evidence that mechanical clearing alone has not prevented continued spread or reinvasion, classical biological control emerges as a viable and necessary complementary option for long-term suppression of these *Acacias* in NNP. This study connects updated taxonomy, measured invasion trajectories, and shows ecological impacts, establishing a clear foundation for incorporating species-specific biological control agents into current management plans. It also highlights the importance of prioritising high-diversity grassland habitats for conservation and restoration.

Acknowledgements

This work was supported by the Working for Water (WfW) program of the Department of Environment, Forestry and Fisheries: Natural Resource Management (DEFF: NRM) in South Africa, through the Centre for Biological Control (CBC) at Rhodes University. We would like to extend our gratitude to the Director-General of the Zimbabwe Parks and Wildlife Management Authority (Zimparks) for their institutional support, as well as to the management and staff of Nyanga

National Park for their assistance to Kundai R. Dube during fieldwork. We also thank the African Mountain Research Foundation (AMRF) for granting access to the Planet Labs satellite imagery used in this study.

Author contributions

CRediT: **Kundai R. Dube:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing; **Gerald Chikowore:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing; **Kim Canavan:** Methodology, Validation, Visualization, Writing – review & editing; **Grant D. Martin:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing; **Iain D. Paterson:** Conceptualization, Methodology, Supervision, Writing – review & editing

Disclosure statement

No potential conflict of interest was reported by the author(s).

FUNDING

This work was supported by Working for Water (WfW) program of the Department of Environment, Forestry and Fisheries: Natural Resource Management (DEFF: NRM), South Africa.

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References

Aguilera, N., J. Becerra, C. Villaseñor-Parada, P. Lorenzo, L. González, and V. Hernández. 2015. "Effects and identification of chemical compounds released from the invasive*Acacia dealbata*Link." *Chemistry and Ecology* 31 (6): 479–493. doi:10.1080/02757540.2015.1050004.

Arasumani, M., M. Bunyan, and V. V. Robin. 2021. "Opportunities and challenges in using remote sensing for invasive tree species management, and in the identification of restoration sites in tropical montane grasslands." *Journal of Environmental Management* 280: 111759. doi:10.1016/j.jenvman.2020.111759.

Arasumani, M., D. Khan, A. Das, I. Lockwood, R. Stewart, R. A. Kiran, M. Muthukumar, M. Bunyan, and V. V. Robin. 2018. "Not seeing the grass for the trees: Timber plantations and agriculture shrink tropical montane grassland by two-thirds over four decades in the Palani Hills, a Western Ghats Sky Island." *PLoS One* 13 (1): e0190003. doi:10.1371/journal.pone.0190003.

Boakes, E. H., G. M. Mace, P. J. K. Mcgowan, and R. A. Fuller. 2009. "Extreme contagion in global habitat clearance." *Proceedings of the Royal Society B: Biological Sciences* 277 (1684): 1081–1085. doi:10.1098/rspb.2009.1771.

Boy, G., and A. Witt. 2013. *Invasive Alien Plants and their Management in Africa*. CABI. https://www.cabi.org/cabi-publications/invasive-alien-plants-and-their-management-in-africa/.

Canavan, K., S. Canavan, V. R. Clark, O. Gwate, D. M. Richardson, G. F. Sutton, and G. D. Martin. 2021. "The Alien Plants that Threaten South Africa's Mountain Ecosystems." *Land* 10 (2): 1–20. doi:10.3390/land10121393.

Chikowore, G., G. D. Martin, and F. Chidawanyika. 2021. "An assessment of the invasive alien tree, *Robinia pseudoacacia* canopy traits and its effect on grassland microclimates and subsequent arthropod assemblages." *Journal of Insect Conservation* 25 (3): 429–439. doi:10.1007/s10841-021-00311-0.

Chikowore, G., G. D. Martin, F. Chidawanyika, M. Hill, S. Neser, M. Day, T. Grice, G. Chikwenhere, E. Mangosho, and A. Sheppard. 2023. "Weed biological control in Zimbabwe: Challenges and future prospects." *South African Journal of Botany* 154: 336–345. doi:10.1016/j.sajb.2023.01.054.

Clark, V. R., K. Kunkel, T. O'connor, D. Jewitt, N. Sekhele, and K. Kirkman. 2021. "Montane rangelands in a changing world." *African Journal of Range & Forage Science* 38 (1): iii–vi. doi:10.2989/10220119.2021.1886434.

Clark, V. R., and G. Martin. 2024. "Risks and vulnerabilities to and from Africa's major mountain ranges (Africa-Introduction)." In *Safeguarding Mountain Social-Ecological Systems, Vol 2*, edited by S. Schneiderbauer, 65–72. Oxford: Elsevier.

Correia, M., S. Castro, V. Ferrero, J. A. Crisóstomo, and S. Rodríguez-Echeverría. 2014. "Reproductive biology and success of invasive Australian Acacias in Portugal." *Botanical Journal of the Linnean Society* 174 (4): 574–588. doi:10.1111/boj.12155.

Das, A. A., J. Ratnam, and D. Jathanna. 2023. "Patterns and consequences of invasion of tropical montane forests by *Cestrum aurantiacum* Lindl. In the Western Ghats." *Frontiers in Ecology and Evolution* 11. doi:10.3389/fevo.2023.1198085.

de Cáceres, M., F. Jansen, and N. Dell. 2016. "Indicspecies: Relationship between species and groups of sites." *R Package Version* 1 (6).

Dube, K. R., J. Zisadza, B. M. Mugaviri, and M. Tiki. 2025. "Invasive Alien Plant Species as a Revenue-Generating Resource for Conservation Efforts: The Case of Nyanga National Park, Zimbabwe." *Tropical Conservation Science* 18: 19400829251406155. doi:10.1177/19400829251406155.

Ehrenfeld, J. G. 2010. "Ecosystem consequences of biological invasions." *Annual Review of Ecology, Evolution, and Systematics* 41 (2010): 59–80. doi:10.1146/annurev-ecolsys-102209-144650.

Evans, S., E. Baker, N. Baker, and D. Cilliers. 2015. "Current distribution and population size of the Blue SwallowHirundo atrocaeruleain the southern Tanzanian highlands." *Ostrich* 87: 123–131. doi:10.2989/00306525.2015.1110843.

Evans, S. W., and H. Bouwman. 2010. "Habitat selection by blue swallows*Hirundo atrocaerulea* Sundevall, 1850 breeding in South Africa and its implications for conservation." *African Journal of Ecology* 48 (4): 871–879. doi:10.1111/j.1365-2028.2009.01183.x.

Finley, D., M. Dovciak, and J. Dean. 2023. "A data driven method for prioritizing invasive species to aid policy and management." *Biological Invasions* 25 (7): 2293–2307. doi:10.1007/s10530-023-03041-3.

Glen, H., and B. van Wyk. 2016. *Guide to Trees Introduced into Southern Africa*. Penguin Random House South Africa.

Große-Stoltenberg, A., I. Lizarazo, G. Brundu, V. Paiva Gonçalves, L. Prado Osco, C. Masemola, J. Müllerová, C. Werner, I. Kotze, and J. Oldeland. 2023. "Remote sensing of invasive Australian Acacia Species: State of the art and future perspectives." In *Wattles*, edited by D. M. Richardson, J. J. Le Roux, and E. Marchante, 474–495. Wallingford: CABI.

Henderson, L. 2005. *Distinguishing bi-pinnate Australian Acacia spp. In RSA. SAPIA News No. 8: Southern African Plant Invaders Atlas*. ARC-Plant Protection Research Institute, Weeds Division. www.agis.agric.za/wip.

Hoogar, R., S. Malakannavar, and H. T. Sujatha. 2019. "Impact of eucalyptus plantations on ground water and soil ecosystem in dry regions." *Journal of Pharmacognosy and Phytochemistry* 8 (4): 2929–2933.

Impson, F., C. Kleinjan, J. Hoffmann, and P. Mudavanhu. 2021. "A review of research and developments with insect agents used for biological control of Australian *Acacia* species (Caesalpinioideae) in South Africa." *African Entomology* 29: 693–712. doi:10.4001/003.029.0693.

Impson, F. A. C., C. A. Kleinjan, and J. H. Hoffmann. 2021. "Suppression of seed production as a long-term strategy in weed biological control: The combined impact of two biocontrol agents on *Acacia mearnsii* in South Africa." *Biological Control* 154: 104503. doi:10.1016/j.biocontrol.2020.104503.

Impson, F. A. C., C. A. Kleinjan, J. H. Hoffmann, J. A. Post, and A. R. Wood. 2011. "Biological Control of AustralianAcaciaSpecies andParaseriantheslophantha(Willd.) Nielsen (Mimosaceae) in South Africa." *African Entomology* 19 (2): 186–207. doi:10.4001/003.019.0210.

Jimu, L., and N. Ngoroyemoto. 2011. *Habitat Characteristics and Threat Factors of the Rare and Endangered Prunus Africana (Hook.F.).* Kalkman in Nyanga National Park, Zimbabwe.

Joshi, A. A., M. Sankaran, and J. Ratnam. 2018. "'Foresting' the grassland: Historical management legacies in forest-grassland mosaics in southern India, and lessons for the conservation of tropical grassy biomes." *Biological Conservation* 224: 144–152. doi:10.1016/j.biocon.2018.05.029.

Kindt, R., and R. Coe. 2005. *Tree Diversity Analysis: A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies*. World Agroforestry Centre.

Kotzé, J. D. F., A. Wannenburgh, and B. W. van Wilgen. 2025. "Changes in the cover of selected invasive alien plant taxa between 2008 and 2023 in South Africa." *Biological Invasions* 27 (3): 98. doi:10.1007/s10530-025-03558-9.

Kumar, M., S. Nisha Phukon, and H. Singh. 2021. "Chapter 24—The role of communities in sustainable land and forest management." In *Forest Resources Resilience and Conflicts*, edited by P. Kumar Shit, H. R. Pourghasemi, P. P. Adhikary, G. S. Bhunia, and V. P. Sati, 305–318. Amsterdam: Elsevier.

Legendre, P., and L. Legendre. 2012. Numerical Ecology. 3rd English ed. Development in Environmental Modelling Vol. 24.

Lele, A., M. Arasumani, C. K. Vishnudas, V. Joshi, D. Jathanna, and V. V. Robin. 2020. "Elevation and landscape change drive the distribution of a montane, endemic grassland bird." *Ecology and Evolution* 10 (14): 7755–7767. doi:10.1002/ece3.6500.

Le Maitre, D. C., M. Gaertner, E. Marchante, E.-J. Ens, P. M. Holmes, A. Pauchard, P. J. O'Farrell, et al. 2011. "Impacts of invasive Australian acacias: Implications for management and restoration." *Diversity and Distributions* 17 (5): 1015–1029. doi:10.1111/j.1472-4642.2011.00816.x.

Magurran, A. E. 2003. *Measuring biological diversity.* Oxford, UK: John Wiley & Sons.

Mahlobo, T., C. Munyai, G. Martin, and N. Dube. 2025. "Response of grassland insect diversity and assemblages to the invasive *Gleditsia triacanthos* in South Africa." *Research Square*. doi:10.21203/rs.3.rs-7026506/v1.

Mahoyi, H., H. Ndaimani, T. Paradzayi, K. S. Mpakairi, and G. Eliah. 2020. "Predicting the invasion of a southern African savannah by the black wattle (*Acacia mearnsii*)." *Journal of Forestry Research* 31 (5): 1995–2003. doi:10.1007/s11676-019-00975-0.

Maroyi, A. 2015. Exotic Acacia Species in Zimbabwe: A Historical and Ecological Perspective. *Studies on Ethno-Medicine*. https://www.tandfonline.com/doi/abs/10.108009735070.2015.11905457.

Martin, G., K. Canavan, G. Chikowore, R. Bugan, W. de Lange, B. du Toit, G. Harding, et al. 2025. "Managing wilding pines in the Cape Floristic Region, South Africa: Progress and prospects." *South African Journal of Botany* 177: 377–391. doi:10.1016/j.sajb.2024.12.011.

Matongo, V. 2016. *Trends in Spatial Distribution of Alien Woody Species and Primary Production on Invaded Sites in Nyanga National Park, Zimbabwe*. Unpublished Master's thesis, University of Zimbabwe.

Matukana, V. 2021. *The Survival of Acacia decurrens, Acacia melanoxylon and Populus alba in Vaalwater, Waterberg Biosphere Reserve, Limpopo Province, South Africa*. https://univendspace.univen.ac.za/handle/11602/1706.

Mujaju, C., N. Mudada, and G. Chikwenhere. 2021. *Invasive Alien Species in Zimbabwe (Southern Africa)* (pp. 330–361). doi:10.1002/9781119607045.ch12.

Muvengwi, J., M. Mbiba, L. Jimu, A. Mureva, and B. Dodzo. 2018. "An assessment of the effectiveness of cut and ring barking as a method for control of invasive *Acacia mearnsii* in Nyanga National Park, Zimbabwe." *Forest Ecology and Management* 427: 1–6. doi:10.1016/j.foreco.2018.05.034.

Ngorima, A., and C. M. Shackleton. 2019. "Livelihood benefits and costs from an invasive alien tree (*Acacia dealbata*) to rural communities in the Eastern Cape, South Africa." *Journal of Environmental Management* 229: 158–165. doi:10.1016/j.jenvman.2018.05.077.

Oksanen, J. 2015. "Vegan: Community ecology package." *R Package Version* 2: 3.

Oswalt, S., C. Oswalt, A. Crall, R. Rabaglia, M. K. Schwartz, and B. K. Kerns. 2021. "Inventory and Monitoring of Invasive Species." In *Invasive Species in Forests and Rangelands of the United States: A Comprehensive Science Synthesis for the United States Forest Sector*, edited by T. M. Poland, T. Patel-Weynand, D. M. Finch, C. F. Miniat, D. C. Hayes, and V. M. Lopez, 231–242. Washington, DC: Springer International Publishing.

Parr, C. L., C. E. R. Lehmann, W. J. Bond, W. A. Hoffmann, and A. N. Andersen. 2014. "Tropical grassy biomes: Misunderstood, neglected, and under threat." *Trends in Ecology & Evolution* 29 (4): 205–213. doi:10.1016/j.tree.2014.02.004.

Peet, R. K., T. R. Wentworth, and P. S. White. 1998. "A flexible, multipurpose method for recording vegetation composition and structure." *Castanea* 63: 262–274.

Ricciardi, A. 2013. "Invasive Species." In *Ecological Systems: Selected Entries from the Encyclopedia of Sustainability Science and Technology*, edited by R. Leemans, 161–178. Oxford: Springer.

Richardson, D., J. J. L. Roux, and E. Marchante. 2023. "Wattles: Australian Acacia species around the world." In *Wattles: Australian Acacia Species Around the World*, edited by D. M. Richardson, J. J. Le Roux, and E. Marchante, 131–147. Wallingford, UK: CABI.

Richardson, D. M., and M. Rejmánek. 2011. "Trees and Shrubs as Invasive Alien Species: A Global Review." *Diversity and Distributions* 17 (5): 788–809. doi:10.1111/j.1472-4642.2011.00782.x.

Sheppard, A. W., M. D. Day, A. C. Grice, S. Neser, G. P. Chikwenhere, and P. Mangosho. 2012. *An Assessment of the status, Impact and Management of Weeds in Zimbabwe, with Particular Focus on Biological control, in the Context of Food Security and Sustainable Production from Smallholdings and Water Use in Lakes and Rivers*. Australian Centre for International Agricultural Research. Final Report.

Soper, R. 2000. "12The agricultural landscape of the Nyanga area of Zimbabwe." In *The Archaeology of Drylands*, edited by G. Barker and D. Gilbertson, 13–18. London: Routledge.

van Wilgen, B. W. 2018. "The management of invasive alien plants in South Africa: Strategy, progress and challenges." *Outlooks on Pest Management* 29 (1): 13–17. doi:10.1564/v29_feb_04.

van Wilgen, B. W., N. S. Cole, J. Baard, C. Cheney, K. Engelbrecht, L. Stafford, A. A. Turner, N. J. van Wilgen, and A. M. Wannenburgh. 2025. "Progress towards the control of invasive alien species in the Cape Floristic Region's protected areas." *Biological Invasions* 27 (1): 1–8. doi:10.1007/s10530-024-03459-3.

Whittaker, R. H. 1965. "Dominance and diversity in land plant communities: Numerical relations of species express the importance of competition in community function and evolution." *Science* 147 (3655): 250–260.

Witt, A., T. Beale, and B. W. van Wilgen. 2018. "An assessment of the distribution and potential ecological impacts of invasive alien plant species in eastern Africa." *Transactions of the Royal Society of South Africa* 73 (3): 217–236. doi:10.1080/0035919X.2018.1529003.

Yapi, T. S., P. J. O'farrell, L. E. Dziba, and K. J. Esler. 2018. "Alien tree invasion into a South African montane grassland ecosystem: impact of Acacia species on rangeland condition and livestock carrying capacity." *International Journal of Biodiversity Science, Ecosystem Services & Management* 14 (1): 105–116. doi:10.1080/21513732.2018.1450291.