Urban Ecosystems (2025) 28:104
https://doi.org/10.1007/s11252-025-01718-2

Standing vegetation and seed bank patterns paint a bleak picture for urban grassland restoration

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Accepted: 26 March 2025 / Published online: 5 April 2025

Abstract
Urbanisation and urban sprawl are major drivers of global habitat transformation and biodiversity loss. Natural vegetation in urban areas is confined to remnant patches and, as a result, the conservation of these patches of vegetation is becoming increasingly important for biodiversity conservation. Globally grasslands experience high rates of transformation and are threatened by expanding urban areas, causing fragmentation, and facilitating the spread of invasive species. This study explores how above- and belowground vegetation communities within remnant grassland patches vary as a function of patch connectivity and patch size in the City of Tshwane, Gauteng, South Africa. We sampled twelve sites from eleven nature reserves within Tshwane to investigate the relationships between urbanisation and vegetation characteristics. Tshwane's grassland patches have high levels of invasion, with alien species making up a considerable portion of both standing (13% richness and a third of cover) and seed bank vegetation (31% richness and 26% abundance). Furthermore, we found low similarity between standing vegetation and the seed bank (mean ± SD = 0.25 ± 0.06). Neither road density nor reserve size were related to the total cover or richness of vascular plants, nor the cover or richness of alien species. Similarly, neither variable predicted above-belowground similarity. This suggests that the connectivity of remnant grassland patches does not have any significant effect on vegetation characteristics in this disturbed urban environment. Our results indicate that restoration relying only on natural revegetation from the seed bank is unlikely to be effective and we suggest that active restoration interventions, such as reseeding and invasive species control, may be needed to restore these grasslands and improve their long-term conservation value.

Keywords Alien species · Remnant vegetation · Seedbank · Urban ecosystems · Vegetation patches

Introduction

Urbanisation and urban sprawl are major drivers of habitat transformation globally (Goudie 2013; Ellis 2015). Ecological impacts associated with urbanisation include habitat fragmentation and isolation (Scolozzi and Geneletti 2012), heat island effects (Rao et al. 2014), increased soil and air pollution (Madrid et al. 2002; Rao et al. 2014), soil compaction (Madrid et al. 2002; Jeffery and Gardi 2010) and the increased dispersal and establishment of alien invasive species (Williams et al. 2015a, b; Skultety and Matthews 2017; Borden and Flory 2021). Urbanisation leads to biodiversity change, filtering species by their adaptability to urban environments (Duncan et al. 2011; McDonnell and Hahs 2015), and altering natural environments into anthropogenic ecosystems (Santangelo et al. 2022). Although disturbed, such anthropogenic ecosystems typically still contain native (and even endangered) species, potentially harbouring a high indigenous species richness (McKinney 2002; Thompson and McCarthy 2008; Shwartz et al. 2014; Natale et al. 2015). Such species are, however, often confined to remnant natural patches within urban systems (Kowarik and von der Lippe 2018), and, as a result, these remnant patches of native vegetation are increasingly important for urban

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biodiversity conservation (Dyderski et al. 2017; Kowarik and von derLippe 2018).

Grasslands are globally associated with high rates of human expansion and urbanisation (Ellis et al. 2010; Cadman et al. 2013; Carbutt et al. 2017), and house a disproportionate number of people compared to other biomes (White et al. 2000). As a result, grasslands are becoming ever more fragmented (Cadman et al. 2013), with human infrastructure, including roads and buildings, driving grassland fragmentation and the formation of isolated patches (White et al. 2000). Such fragmentation of grasslands is a key concern for conservation in urban grassland landscapes (Hejkal et al. 2017), as fragmentation, and the associated increase in isolation, acts as a powerful filter for species and gene flow (Soons et al. 2005; Williams et al. 2006; Plue and Cousins 2013).

Disturbance effects in urban environments are visible in both the standing vegetation and the seed bank (Overdyck and Clarkson 2012; Alue et al. 2022; Hou et al. 2023), and the relationship between the two (i.e., above- and belowground vegetation) can provide important information on restoration potential (Hopfensperger 2007). In general, undisturbed grasslands have a high similarity between the standing vegetation and the seed bank compared, e.g., to wetlands and forests (Hopfensperger 2007). However, this similarity may be reduced in disturbed, urban grasslands, where the seed bank is typically representative of only a small portion of the standing vegetation (Fischer et al. 2013a; Sershen et al. 2019), often lacking rare or threatened species (Sershen et al. 2019) and being relatively rich in ruderals (Fischer et al. 2013a). In such disturbed urban systems, the establishment of species with a persistent seed bank – typically annuals (Thompson and Grime 1979; Thompson and Jones 1999) – is favoured, as seed that remain ungerminated in the soil allows the species to persist despite frequent disturbances (Milton 2004). Furthermore, seed bank persistence also enhances the ability of alien species to naturalise and invade (Gioria et al. 2020, 2021), as it buffers against the risk of reproductive failure (Venable and Brown 1988) and increases the ability of a species to respond to temporal environmental variation (Donohue et al. 2005, 2010). The proportion of annual, ruderal and invasive species, with persistent seed banks, is therefore expected to be high in disturbed urban environments, leading to low similarity between the above- and belowground components.

Historically, urban grassland restoration has received minimal attention and aspects of this process are still poorly understood in many regions (Klaus 2013). The intensity of restoration interventions in urban grasslands vary greatly, with most degraded grasslands having very little to no active restoration, resulting in species richness remaining low (Klaus 2013; Fischer et al. 2013b; Mollashahi et al. 2024). Although literature on urban grassland restoration in South Africa is lacking, passive recovery techniques for non-urban grasslands have also been unsuccessful (Zaloumis and Bond 2016). However, in other similar non-urban grassland systems, active restoration with intensive reseeding approaches and appropriate fire management have promoted forb abundance and competitive C4 grass restoration (Török et al. 2021). The lack of recovery of grasslands under passive restoration techniques, highlights seed and dispersal limitations as key factors within urban grassland restoration and emphasize the dependence on local and landscape constraints in grassland restoration (Carbutt and Kirkman 2022; Suding 2011; Török et al. 2021; Zaloumis and Bond 2016).

From a conservation perspective, the surrounding urban landscape matrix is often important for the vegetation that survives in remnant habitat patches (Ewers and Didham 2006; Williams et al. 2006; Szabó et al. 2012). Habitat patches typically follow the predictions of island biogeography, where patch size and connectivity are positively related to species richness (Lindgren and Cousins 2017). For example, higher densities of roads around habitat patches can lead to a decrease in the connectivity of grassland habitats, increasing the isolation and possibility of localised native extinctions in these patches (Soons et al. 2005; Williams et al. 2006), but at the same time facilitating the dispersal of alien species (Lemke et al. 2021). Furthermore, patch size is also important for conservation (Williams et al. 2005a; Bierwagen 2007), following predictions of island biogeography, that larger patches support larger populations and have lower edge effects (Lindgren and Cousins 2017). Native species within grasslands are often sensitive to patch size and connectivity (Wimberly et al. 2018), as most seeds do not distribute very far from the parent plant (Kiviniemi and Eriksson 1999) and rarely succeed in dispersing through unsuitable urban habitats around remnant patches, such as roads and built-up areas (Williams et al. 2006, 2009). In theory, therefore, species richness within an urban landscape should be highest in habitat patches surrounded by larger areas of natural vegetation, with higher connectivity to other suitable patches (Lindgren and Cousins 2017; Dembicz et al. 2021), and patches with less surrounding natural vegetation would be expected to have smaller population sizes and greater edge effects, resulting in higher extinction rates and a decrease in species richness (Mendenhall et al. 2014; Lindgren and Cousins 2017). However, more isolated urban grasslands are more likely to be invaded by non-native species, especially when surrounded by high road densities, as a result of decreased distances that invasive propagules have to travel (Lemke et al. 2021).

This study explores how above- and belowground vegetation in remnant urban grasslands varies as a function of patch connectivity and patch area. Specifically, we quantify how surrounding road density and the size of the remnant vegetation patch are related to 1) above-ground vegetation (cover and species richness), 2) belowground vegetation (seed abundance and species richness), and 3) above–belowground similarity of vegetation composition.

Materials and methods

Study area and sampling plots

Gauteng Province is South Africa's smallest, but most densely populated and most urbanised, province. This area is within a summer rainfall region, receiving 500–800 mm rainfall per annum, the majority of which falls between November and February. Average maximum temperatures range between 28 °C in summer and 22 °C in winter, with mean minimum temperatures of 16 °C and 5 °C in summer and winter, respectively (with occasional frost during the colder months; South African Weather Services, unpublished 2021).

Eleven nature reserves were selected within one of the metropolitan municipalities of the Gauteng Province, the City of Tshwane Municipality (Fig. 1). These reserves represent remnant patches of historically larger grassland expanses. For the majority of the reserves, one sampling plot of 18 m × 18 m was placed in the approximate centre of the reserve. However, because Rietvlei Nature Reserve is considerably larger than the other reserves, two plots were sampled here, one in the centre of the reserve and the other close to the boundary of the reserve, bringing the total to twelve sampling plots. All sampling plots were at least 1 km apart. The sampling plots fall into three grassland bioregions, i.e., Mesic Highveld Grassland, Dry Highveld Grassland and Central Bushveld (Fig. 1; Mucina et al. 2014), with all but three reserves in the Central Bushveld bioregion. The grasslands of this region are rich in grass, forb and woody species (Mucina and Rutherford 2006). Each reserve also has varying recreational activities (e.g., Groenkloof Nature reserve has mountain biking and hiking whereas Skuilkrans Kopje only has hiking) and management practices, ranging from active alien invasive control in Rietvlei Nature reserve and Voortrekker Monument, to little or no alien invasive management at Kruin Park and Skuilkrans Kopje.

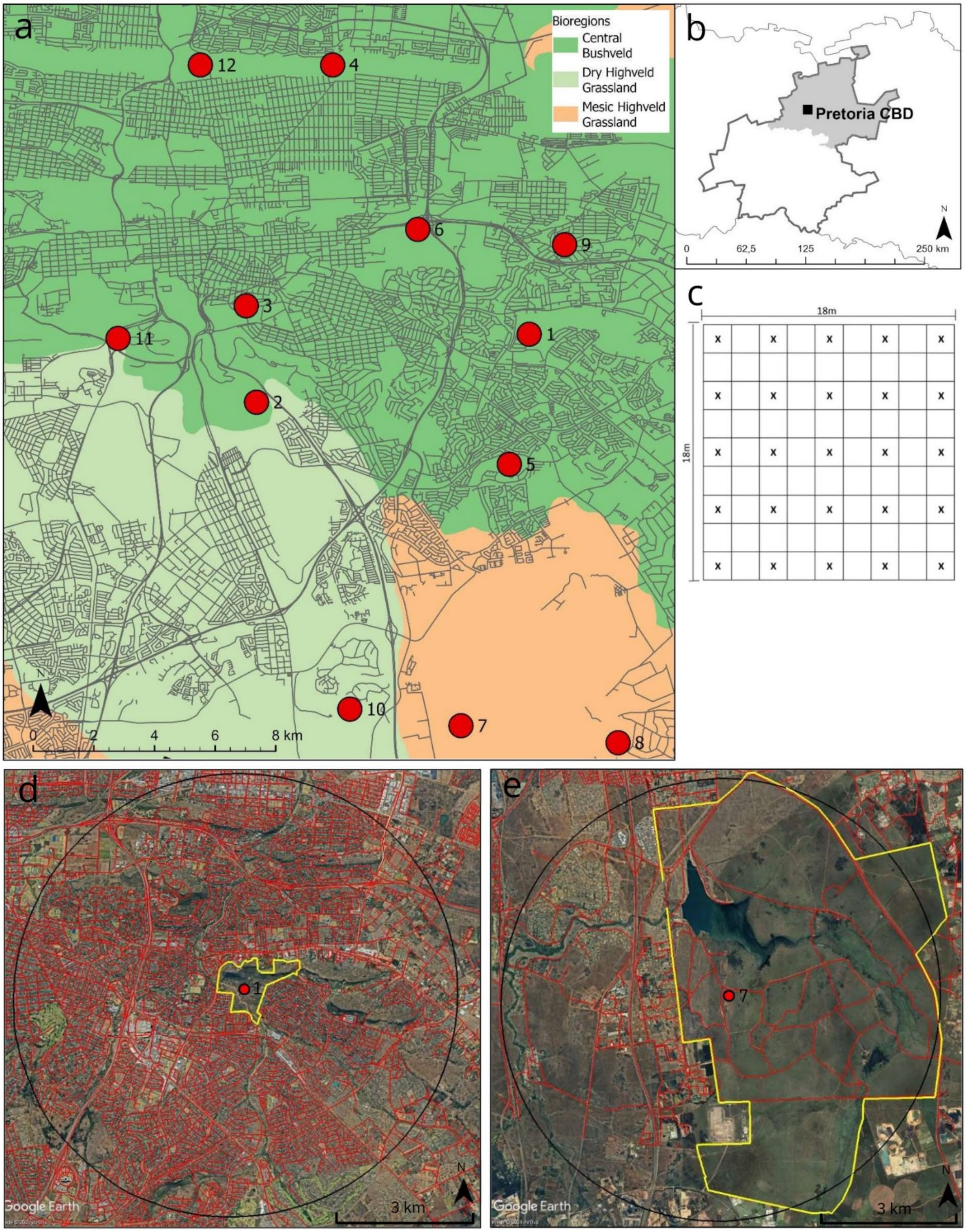
Within each sampling plot, 25 sub-plots of 2 m × 2 m were sampled. These were separated by 2 m (Fig. 1). Road density (defined as the total length of road within a 5 km radial buffer zone from the centre point of each sampling plot (following Williams et al. 2006) and the size of the surrounding protected area were calculated for each sampling plot, using ArcGIS Pro (2021 version 2.9.0). These calculated protected areas mostly coincide with the borders of the reserve, however, in the case of Magalies Biosphere Reserve, the official reserve borders included substantial built-up areas. Here we took the size of the surrounding conserved area not as the official reserve size, but as the size of the uninterrupted natural vegetation immediately surrounding our sample plot, i.e., viewing it from an ecological connectivity perspective, rather than an administrative perspective.

Above- and belowground sampling and seed germination

Within each sub-plot all aboveground vascular plant species were identified, and their canopy cover visually estimated during the growing season (November 2022 to January 2023). Most taxa (88%) were identified to species level. However, 7% of the species were only identifiable to genus level, 2% to family level and 3% were unidentifiable at the family level and were consequently given morpho-species codes. To quantify belowground species composition, the seedling emergence approach was used (following Weerasinghe et al. 2008; Sershen et al. 2019). A soil core of 10 cm depth and 5 cm diameter was taken from the centre of each sub-plot. Core samples were transferred into individual pots and germinated separately, resulting in a total of 300 pots. Germination took place at the University of Pretoria, where the pots were kept outdoors in a partly enclosed space, but under a transparent roof, therefore subjecting them to a similar temperature regime as the reserves but preventing splash out during rainfall events. Germination took place for six months (13 January to 10 July 2023). Pots were watered every two to four days with 100–200 ml rainwater, depending on the weather. The location of the pots was randomized every third to fifth day. Once a species was identifiable it was recorded and removed from the pot to avoid overcrowding. The majority of the seedlings were identified up to species level (74% of species), 22% of seedlings were identified up to genus level and 4% to family level.

Data analyses

Sørenson's index of similarity (Sørensen 1948), was used to compare the similarity between above- and belowground species composition (following e.g., Hopfensperger 2007). Seed bank species that could only be identified up to genus level were assumed to be the same species as the most abundant aboveground species within that genus



(unless it was clearly a different species). For example: if a germinated *Eragrostis* sp. was only identifiable up to genus level and *E. lehmanniana* was the most abundant *Eragrostis* species aboveground for that grassland plot, the germinated seedling was assumed to be *E. lehmanniana*. This assumption was necessary for 685 out of 2670 seedlings (26%). Species richness was calculated across all 25 sub-plots, resulting in one above- and one belowground

◂**Fig. 1** **a**) Bioregions of Gauteng with the twelve sampling plots within the City of Tshwane, **b**) the location of Pretoria Central Business District (CBD) and the City of Tshwane Municipality (shaded) within Gauteng, South Africa and **c**) the sampling plot design, with X indicating the sub-plots that were sampled. The sizes of the reserves surrounding the sampling plots (yellow outlines in d and e), density of roads (red lines), and the surrounding land use differed between reserves. For example, Faerie Glen Nature Reserve (**d**), is a small reserve, within a densely urbanised matrix of many roads and buildings. Rietvlei Nature Reserve (**e**), in contrast, is a relatively large reserve, with a low road network density and surrounded mostly by farmland. Reserve numbers: 1. Faerie Glen, 2. Groenkloof, 3. Kruin Park, 4. Magalies, 5. Moreleta Kloof, 6. Moot Grassland, 7. Rietvlei A, 8. Rietvlei B, 9. Skuilkrans Kopje, 10. Smuts Koppie, 11. Voortrekker Monument, 12. Wonderboom

richness value per plot. Similarly, the total number of species (both above- and belowground) were used per plot (i.e., aggregating data across sub-plots) for calculating Sørensen similarity.

To test the effects of reserve area and road density on above- and belowground vegetation characteristics, we used generalised linear models (GLZs). For models of vegetation cover and above-belowground similarity a binomial distribution was used, and for models of species richness and abundance Poisson distribution. We modelled both total vegetation cover, richness and abundance, as well as the non-native species vegetation cover, richness and abundance. To control for false positives, we adjusted the alpha threshold using Bonferroni correction. All statistical analyses were performed in the R programming environment (R Core Team 2023).

Results

In total, across all eleven reserves and twelve sampling plots, 233 species were recorded in the standing vegetation, and 88 species (2669 individual seedlings) germinated from the seed bank (Appendix 1, Table 4). Out of the 233 standing vegetation species 34 were grass species and out of the 88 germinated species, 22 were grass species. Aboveground species richness varied between reserves, ranging from 33 to 56 species (mean $\pm$ SD $= 44.5 \pm 7.3$; Table 1), while belowground richness was 12–37 species (26.4 ± 7.4; Table 1). In the seed bank 31% of species were alien, but only 13% species in the standing vegetation were alien (Table 1). Mean standing vegetation cover was not significantly different between the sampling plots ($p = 0.44$), and, in general, was 90–100% cover, with most of the plots having 100% cover and one outlier plot, at a very rocky site, having only 58% cover (Table 1). Alien vegetation cover, however, varied much more considerably, ranging from 1 to 67%. On average, alien vegetation cover comprised 32% of total vegetation cover (Table 1). The most widespread alien species in the standing and seed bank vegetation was *Erigeron bonariensis* (Table 2). The similarity between the standing vegetation and the seed bank was low in all sampling plots (0.25 ± 0.06; with all of the sites < 0.35, Table 1), as well as for the data set overall, i.e., the City of Tshwane as a whole (Sørenson Similarity Index $= 0.31$).

For the standing vegetation, neither road density nor reserve size were significant predictors of total species richness and cover, or alien species richness and cover. Similarly, neither of the predictors were significantly related to richness or abundance (both total and alien) in the seed bank. Lastly, road density and reserve size were also not related to above-belowground similarity (Table 3).

Discussion

Our results suggest that many of the urban grassland patches of the City of Tshwane are quite invaded. In our study, alien species were present, both above- and belowground, at all of the patches, and five of the patches had 20% or more alien cover. Although alien species presence is reasonably well-known for the aboveground component (Marais 2004; Nelufule et al. 2024), where the extent of the problem is readily visible, our results suggest that the belowground situation is also a cause for concern in terms of restoration. In this study, alien species comprised a maximum of two thirds of the aboveground cover and contributed up to 32% of the total aboveground species richness at some of the reserves. Although fewer species were recorded belowground, the contribution of alien species was high, comprising 31% of the total seed bank species and almost half of individual seedlings at some of the reserves, and more than 30% of individuals at six of the reserves. Furthermore, the three most abundant seed bank species were either weedy or alien species, and the most abundant of these, *Pseudognaphalium* sp., a weedy species of uncertain status (assumed to be indigenous in our analyses), was ubiquitous across all plots. This suggests that these systems will not restore passively, once aboveground alien species have been cleared.

Compared to typical global grassland values (Hopfensperger 2007), similarity between the standing vegetation and the seed bank was low. We found that the standing vegetation was poorly represented in the seed bank, with only 10% of species found in the standing vegetation present in the seed bank. This underrepresentation of standing vegetation species in the seed bank is common in temperate and subtropical grasslands globally (Everson et al. 2009; Scott et al. 2010; Sershen et al.

Table 1 Characteristics of the 12 sampling plots, namely surrounding reserve size, road density and vegetation statistics. All vegetation values are totals across all 25 sub-plots, except for standing vegetation cover, which is the mean (n = 25)

Sample plot	Reserve size (km^2)	Road density (km/km^2)	Number of above ground species	Above ground alien species (%)	Number of seed bank species	Seed bank alien species (%)	Standing vegetation cover (%; mean ± SD)	Standing alien vegetation cover (%)	Seed bank abundance	Alien seed bank abundance (%)	Sørenson similarity index
Skuilkrans Kopje	0.09	7.24	47	9	23	22	100 ± 0	3	148	10	0.26
Kruin Park	0.11	8.94	37	32	32	44	100 ± 0	31	483	31	0.34
Moot Grassland	0.35	10.38	45	22	20	40	100 ± 0	6	123	32	0.27
Moreleta Kloof	0.94	6.89	33	30	36	31	100 ± 0	29	357	44	0.31
Wonderboom	1.21	13.42	56	5	31	23	58 ± 6	20	183	12	0.16
Smuts Koppie	1.24	3.07	49	4	21	14	90 ± 0	1	152	10	0.20
Faerie Glen	1.27	8.48	50	28	23	48	93 ± 17	35	155	49	0.20
Voortrekker Monument	2.73	6.93	55	13	23	48	100 ± 0	8	162	31	0.30
Groenkloof	5.82	6.08	34	32	33	33	100 ± 0	67	343	34	0.27
Rietvlei A	44.82	2.47	45	9	36	31	100 ± 0	5	238	16	0.34
Rietvlei B	44.82	1.79	45	11	22	23	100 ± 0	1	137	16	0.24
Magalies	74.57	11.74	38	3	12	42	96 ± 13	4	188	3	0.16
Across all sites			233	13	88	31	94 ± 14	32	2669	26	0.31

Table 2 Cover (mean ± SD; %) of the widespread species in the standing vegetation, as well as the total number of seedlings of the widespread species present in the seed bank. Widespread species were defined as species found at eight or more of the sampling plots (n = 12), e.g., *Themeda triandra* was present at all plots in the standing vegetation. Values in brackets are the number of sub-plots that the species occurred in (total possible = 25). Blank cells indicate an absence of the species at the sample plot (* alien taxa, ^ grass species)

	Skuilkrans Kopje		Kruin Park		Moot Grassland		Moreleta Kloof		Wonderboom		Smuts Koppie		Faerie Glen		Voortrekker Monument		Groenkloof		Rietvlei A		Rietvlei B		Magalies	
Standing vegetation																								
Themeda triandra ^	5 ± 5	(18)	2 ± 3	(10)	31 ± 26	(23)	49 ± 27	(25)	1 ± 1	(4)	6 ± 6	(20)	19 ± 15	(20)	7 ± 5	(21)	14 ± 9	(24)	9 ± 12	(16)	9 ± 13	(14)	20 ± 14	(22)
Eragrostis lehmanniana ^	1 ± 2	(2)	1 ± 3	(3)	1 ± 3	(4)	14 ± 16	(17)	1 ± 2	(6)	1 ± 1	(2)	3 ± 7	(7)	1 ± 1	(2)	7 ± 6	(16)	5 ± 6	(12)	4 ± 10	(7)		
Eragrostis curvula ^			4 ± 4	(16)	13 ± 17	(14)	7 ± 10	(13)	4 ± 3	(18)			4 ± 6	(11)	1 ± 2	(3)	3 ± 4	(9)	12 ± 17	(16)	9 ± 15	(16)	1 ± 2	(1)
*Erigeron bonariensis**	1 ± 1	(7)	10 ± 13	(25)	2 ± 3	(12)	1 ± 1	(1)					2 ± 3	(14)	1 ± 1	(9)	6 ± 4	(23)	3 ± 8	(6)	1 ± 1	(5)		
Heteropogon contortus ^	1 ± 3	(3)	1 ± 1	(2)	2 ± 5	(7)			1 ± 1	(4)	1 ± 2	(9)	1 ± 3	(1)	14 ± 25	(14)	3 ± 4	(9)	4 ± 12	(10)				
Helichrysum luteoalbum	8 ± 10	(15)	4 ± 3	(20)	1 ± 3	(2)	4 ± 5	(13)					1 ± 1	(1)	1 ± 1	(2)			1 ± 2	(3)	18 ± 17	(21)		
Justicia anagalloides	1 ± 2	(2)			2 ± 6	(7)			1 ± 2	(13)	1 ± 2	(15)	2 ± 8	(7)					1 ± 1	(6)	2 ± 3	(12)	10 ± 5	(23)
Seed bank																								
Pseudognaphalium sp.	28	(14)	202	(24)	28	(19)	49	(20)	15	(10)	39	(17)	26	(17)	53	(20)	78	(14)	92	(24)	63	(20)	20	(10)
*Erigeron bonariensis**	2	(2)	1	(1)	8	(6)	7	(5)	3	(2)	11	(6)	5	(3)	12	(10)	2	(2)	6	(5)	10	(6)	1	(1)
Erigeron sp. (2 A)*	6	(5)	9	(6)	3	(3)	5	(5)	5	(4)			3	(2)	8	(5)	1	(1)	12	(7)	8	(5)	1	(1)
Oxalis sp.	11	(2)	39	(10)	26	(5)	1	(1)	3	(2)	4	(2)	3	(3)	12	(6)			12	(4)	5	(3)		
Dichondra repens	45	(4)	11	(2)	5	(4)			41	(6)	10	(1)	1	(1)	4	(2)			1	(1)	5	(2)		
Cyperus sp.	2	(1)	12	(7)	3	(2)	53	(14)			1	(1)					7	(3)	18	(3)	2	(2)		
Euphorbia inaequilatera			1	(1)			18	(7)	4	(3)	1	(1)	36	(13)	22	(11)	1	(1)	2	(2)				
Taraxacum sp.*	2	(2)	9	(5)			1	(1)	2	(2)					2	(2)	1	(1)	2	(2)			1	(1)

Table 3 Generalised linear model outputs for standing vegetation, seed bank species and above-belowground similarity (based on the Sørensen similarity index), using road density and reserve size as predictor variables (n = 12). Significance level = 0.025 (based on the Bonferroni correction)

	Response	Road density		Reserve size		Model p	Deviance explained (%)
		Estimate	p	Estimate	p		
Standing vegetation	Total richness	0.01	0.74	– 0.01	0.43	0.69	5.0
	Alien richness	– 0.02	0.96	– 0.02	0.62	0.88	26.7
	Total cover	– 0.40	0.34	0.02	0.72	0.59	50.3
	Alien cover	0.03	0.90	– 0.03	0.49	0.76	18.7
Seed bank	Total richness	– 0.03	0.27	– 0.01	0.04	0.07	21.3
	Alien richness	0.09	0.63	0.01	0.93	0.89	27.2
	Total abundance	0.50	0.91	– 0.75	0.63	0.88	2.9
	Alien abundance	– 0.09	0.65	– 0.01	0.59	0.78	25.4
Above-belowground similarity		– 0.04	0.84	– 0.01	0.89	0.97	24.5

2019). In our study, the three most widespread standing vegetation species, *Themeda triandra*, *E. lehmanniana* and *E. curvula*, were all disproportionately low in abundance in the seed bank, being present aboveground at twelve, eleven and ten sampling plots, respectively, but only four, three and one plot belowground (Table 4). All three of these species exhibit long periods of seed dormancy (Roberts et al. 2021; Ziller 2022; Durnin et al. 2024), which could partly explain their frequent absence from the germinated component. In *T. triandra,* reliance on vegetative reproduction, rather than germination through seed (Snyman et al. 2013), probably contributes to its absence from the seed bank. Lastly, the poor representation of *T. triandra* in the seed bank is likely associated with human disturbances within South African grassland patches, as *T. triandra* exhibits high abundances in undisturbed, well-managed patches (Eckhardt et al. 1996; Sershen et al. 2019).

Addition to the absence of some aboveground species from the seed bank, some species were also found exclusively in the seed bank at many of the sample plots, contributing further to the low above-belowground similarity (Table 4). For example, *Pseudognaphalium* sp., was widespread in the seed bank – being present at all plots – but was absent from the standing vegetation entirely. The genus *Pseudognaphalium* is widespread in tropical and temperate grasslands (Nie et al. 2016; Blanco-Gavaldà et al. 2023) and consists mostly of weedy species with persistent seed banks (Kellerman 2004). Another persistent seed bank species found belowground at all plots, but absent from the aboveground component at a number of plots, is the alien *E. bonariensis*, whose seeds can survive up to three years under field conditions (Wu et al. 2007; Shrestha 2008). The lack of both *Pseudognaphalium* sp. and *E. bonariensis* in the standing vegetation may be attributed to the species' responses to specific disturbances (such as overgrazing, flooding and fire). *Pseudognaphalium* has higher abundances and dominance in overgrazed areas (Chen et al. 2024) and areas exposed to flooding events (Westbrooke et al. 2005), whereas *E. bonariensis* dominates in areas after fire as it prefers light for enhanced germination (Florentine et al. 2021; Khapugin et al. 2016). We therefore suggest that, in these highly transformed environments, the belowground presence of weedy and alien species, with seeds that remain viable in the soil for prolonged periods of time but do not germinate until after severe disturbances, is further contributing to the low similarity between the standing vegetation and seed bank, as shown in other studies (Gioria and Pyšek 2015; Gioria et al. 2021; Moravcová et al. 2022). If our sampling had targeted recently disturbed areas within the urban grasslands, we believe it likely that many more of the species in the seedbank would have been sampled aboveground too.

In urban grasslands, road-induced fragmentation and isolation typically lead to species population declines, local extinctions, the loss of genetic diversity and the loss of carbon stores (White et al. 2000; Hejkal et al. 2017). Isolated urban grassland patches can also experience substantial edge effects due to fragmentation, further contributing to species declines within these patches (Merola-Zwartjes 2004). As a result, a decrease in plant species richness in remnant patches along a gradient from rural to urbanised has generally been found, with a higher likelihood of localised extinctions in highly urbanised areas (Williams et al. 2005b). We, therefore, in this study expected to find higher numbers of species, both in the above- and belowground components, in plots within larger vegetation patches, as opposed to plots that form part of smaller, fragmented patches. In addition, we expected the contribution of alien species to increase as the surrounding road-density – and therefore propagule transport – increased. Contrary to these expectations, however, we did not find trends in any of the vegetation characteristics along such finer-scale gradients of urbanisation within this already disturbed urban environment. Nelufule et al. (2024) found similar results for a number of the same reserves. More specifically, at the larger spatial scale of the whole reserve, the number of documented alien species was not determined by reserve size (Nelufule et al. 2024). Our results complement this study, by showing similar trends at plot scale. We suggest that urbanisation in this region has potentially progressed beyond the point at which further increases in road density or reductions in surrounding grassland size affect vegetation indices, and that factors other than urbanisation are therefore now driving differences in vegetation between reserves.

Although reserve size and isolation did not affect vegetation characteristics such as richness and cover, the urban grasslands of the City of Tshwane are not completely homogenised, and there are some clear differences in species composition between reserves. Each reserve, for example, had at least three species in the standing vegetation that were unique to that reserve (Table 4). The high representation of alien species in either the standing vegetation or seed bank at some of the reserves was also not caused by one specific alien species across the reserves, but rather by various different alien species and alien species combinations (Table 4). We propose that these differences are a result of a combination of dispersal limitations, as well as different environmental conditions (e.g., topography, geology and microclimate), land use histories and management practices between reserves. Long distance dispersal by wind is rare in grassland systems, with many grassland species displaying limited seed dispersal capacity (Tackenberg et al. 2003). For many species, therefore, seeds do not disperse much further than the immediate vicinity of the parent plant (Miller and Cummins 2003; Czarnecka 2004; Schleicher et al. 2011). Roads and buildings surrounding the grassland patches add an additional limitation, as they act as barriers, hindering dispersal and increasing isolation of grassland patches (Williams et al. 2005a; Kowarik and von der Lippe 2011; Niu et al. 2018), In addition to affecting native species, such dispersal limitations caused by fragmentation may also affect the spread of some of the alien species. For example, *Malvastrum coromandelianum*, which typically spreads via animals (Hill 1982), was limited to only one of the reserves, possibly due to the lack of animal dispersers between grassland patches.

Another contributor to the heterogeneity observed between these urban reserves, is the different recreation uses and management practices between the reserves. For example, the reserves are home to different species of larger mammals, e.g., a diversity of antelope and African buffalo (*Syncerus caffer*) at Rietvlei Nature Reserve, but a much lower density and much smaller antelope at Skuilkrans Kopje, which introduce different dispersal capabilities, as well as different types and intensities of disturbances. Furthermore, although all of the reserves are open to the public, the activities that are allowed differ. At Groenkloof Nature Reserve hiking and mountain biking take place, whereas at Rietvlei visitors are restricted to their vehicles. Annual visitor numbers also differ, with greater alien species richness found in reserves with greater visitor numbers (Nelufule et al. 2024). Lastly, differences in alien invasion between reserves could also be a consequence of different eradication strategies, with some reserves, such as Rietvlei Nature Reserve, actively employing aboveground alien species management such as controlled burning and invasive plant removal initiatives (1–5% aboveground alien cover), and others, such as Kruin Park (30% aboveground alien cover), having few to no alien control strategies in place.

The levels of alien invasion, specifically of the belowground vegetation component, paint a bleak picture in terms of the potential contribution of the soil seed bank to the future restoration of these patches. The number of seeds, persistent nature and high survival rate of the seed bank mean that alien species are likely to re-appear once they have been removed aboveground and control measures will, therefore, either need to be repeated or will have to affect the seedbank too. In addition, the long-range dispersal capability of several alien plant species, e.g., *E. bonariensis*, *Campuloclinium macrocephalum*, *Plantago lanceolata* and *Bidens pilosa* (Gitonga et al. 2015; Budumajji and Solomon Raju 2018; Iwanycki Ahlstrand et al. 2019; Bellache et al. 2022), means that isolated eradication efforts focused on individual reserves will probably be unsuccessful, as re-invasion from surrounding reserves is likely. We therefore suggest that eradication efforts should be ongoing, removing undesired aboveground species at a juvenile stage, before seed production and combining this with reseeding of desired species to replace the depleting alien seed bank. We further advocate that such restoration efforts should be well-coordinated between individual reserves, owners of other surrounding properties and the municipality as a whole, to prevent re-invasion of cleared patches.

Appendix 1

Table 4 Species identified above- and belowground at the 12 sampling plots. SV = species present in the standing vegetation, G = species present as a germinated seedling, SV + G = species was present in both the standing and germinated seed bank vegetation. * = alien taxa

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Abildgaardia ovata				SV				SV				
*Acacia mearnsii**		G										
Acalypha angustata	SV									SV	SV	
Acalypha caperonioides			SV									
Acalypha sp.		G	G	G			G		G	G		
Adromischus umbraticola					SV							SV
Afroaster serrulatus								SV				
Afrocathium mundianum		SV										
Afrosciadium magalismontanum			SV									
Albuca setosa	SV						SV					
Albuca virens											SV	
Aloe greatheadii	SV				SV		SV	SV				
Aloe maculata		SV				SV		SV				
*Alternanthera pungens**				SV								
Alysicarpus sp.			SV									
*Amaranthus hybridus**							G					
Anacampseros subnuda					SV + G							
Aristida adscensionis			G		G		G		G			
Aristida diffusa						SV		SV				
Aristida meridionalis												SV
Asparagus sp.				SV								
Asparagus suaveolens	SV				SV	SV	SV					
Asplenium aethiopicum											G	
Berkheya setifera				SV								
Bewsia biflora						SV						
*Bidens pilosa**		G		G				SV	SV			
Blepharis maderaspatensis							SV					

Table 4 (continued)

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Brachiaria serrata		SV +G	G	G	SV	SV	G	SV	G	SV +G	SV	SV
Brassicaceae sp.				SV								
Bulbine abyssinica	SV											
Bulbostylis burchelli										SV		
Bulbostylis sp.	G	G		G	G	G						G
*Campuloclinium macro-cephalum**		SV +G	SV +G	SV +G			G	SV +G	SV +G	G	SV	
Carex sp.	SV +G			G					G			
Celtis africana					SV							
Ceratotheca triloba					SV				SV			
Chamaecrista comosa												SV
Cheilanthes hirta					SV							
Cheilanthes viridis	SV	SV										
Chenopodium carinatum		G		G	G				G			
Chlorophytum cooperi	SV	SV			SV	SV						SV
Clematis brachiata								SV				
Cleome maculata					SV							
Cleome monophylla					SV				SV			SV
Coccinia adoensis									SV			
Commelina africana					SV							SV
Commelina benghalensis					SV							
Commelina erecta					SV							
Commelina sp.					G							G
Convolvulus sagittatus							SV					
Corchorus asplenifolius									SV			
*Cotula australis**			G				G					
Crassula lanceolata					SV							
Crassula setulosa												SV
Crassula sp.	G				G	G				SV		
Crassula swaziensis					SV							
Crystallopollen angusti-folium					SV							
Cucumis zeyheri											SV	
Cucurbitaceae sp.						SV						
Cyanodon dactylon									SV			

Table 4 (continued)

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Cyanotis speciosa	SV				SV	SV				SV	SV	SV
Cycnium adonense												SV
Cymbopogon caesius	SV							SV				
Cyperaceae sp.		SV										
Cyperus cristatus												SV
Cyperus cyperoides						SV					SV	
Cyperus denudatus					SV					SV		
Cyperus eragrostis					SV							SV
Cyperus erectus	G				G	G			G	G		G
Cyperus esculentus									SV			
Cyperus marginatus					SV	SV						
Cyperus niveus	SV									SV		
Cyperus obtusiflorus				SV						SV		
Cyperus polystachyas										SV		
Cyperus rotundus									G		G	
Cyperus sp.	SV + G	SV + G	G	G	SV	G			G	G	G	
Cyperus sphaerocesphalus												SV
Dianthes mooiensis					SV							
Dichondra repens	SV + G	G		SV + G	G	G	G	G		G	G	
Dicoma anomala										G		
Dierama sp.								SV				
Digitaria diagonalis					G			SV				
Digitaria eriantha	G			G	SV		SV	SV		SV		SV
Digitaria longiflora				G								
Digitaria monodactyla						SV						
Digitaria sanguinalis			SV				G					
Digitaria sp.		G		G		G		G		G		
Digitaria ternata	SV						SV					
Digitaria tricholaenoides	SV		SV									
Diheteropogon amplectens					SV							
Diospyros lycioides				SV						SV		
Dipcadi viride			SV	SV		SV						
Dodonaea Angustifolia								G				
Dodonaea sp.								SV				

Table 4 (continued)

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Dodonaea viscosa								SV				
Dyschoriste setigera	SV											
Elephantorrhiza elephantina			SV			SV	SV		SV			
Eragrostis biflora						G						
Eragrostis capensis						SV					SV	
Eragrostis chloromelas			SV									
Eragrostis cilianensis	G	SV +G		G		SV	SV	SV +G	G	SV +G	SV	SV
Eragrostis curvula		SV	SV	SV	SV +G		SV	SV	SV	SV	SV	SV
Eragrostis lehmanniana	SV	SV	SV +G	SV +G	SV	SV	SV	SV	SV	SV	SV +G	
Eragrostis racemosa		G										
Eragrostis sp.		G	G	G						G	G	
*Erigeron bonariensis**	SV +G	SV +G	SV +G	SV +G	G	G	SV +G	SV +G	SV +G	SV +G	SV +G	G
Erigeron sp. *(2 A)**	G	G					G		G	G		
Erigeron sp. *(2B)**	G	G	G	G	G		G	G	G	G	G	G
Eriosema salignum										SV		
Eriospermum cooperi												SV
Eucomis autumnalis											SV	
Euphorbia clavarioides					SV							
Euphorbia inaequilatera		G		G	G	G	G	G	G	G		
Euphorbia schinzii												SV
Euphorbia tirucalli								SV				
Evolvulus alsinoides												SV
Fabacea sp.										SV		
Faboideae sp.				SV	SV	SV						SV
Faboideae sp. *(1 A)*						G						
Faboideae sp. *(1B)*	G		G									
Felicia muricata	SV	SV										
Fimbristylis dichotoma	G				SV +G	G		SV	G		G	SV +G
*Galinsorga parviflora**	G			G	G	G	G	G	G			
Gazania krebsiana											SV	
Gazania sp.								SV				
Gerbera pilloselloides								SV				
Gerbera viridifolia			SV							SV	SV	

Table 4 (continued)

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Gisekia africana					SV							
*Glandularia aristigera**		SV +G	SV				SV +G					
*Gomphocarpus fruticosus**		SV					SV					
Graderia scabra								SV				
Gymnosporia sp.							SV					
Helichrysum nudifolium				G								
*Heliotropium amplexicaule**		SV					SV		SV			
Hellichrysum luteoalbum	SV +G	SV	SV	SV +G			SV	SV		SV	SV	
Hellichrysum pallidium	SV	SV				SV		SV		SV	SV	
Hellichrysum setosum					SV							
Hellichrysum sp.	G	G			G		G	G		G	G	
Hermannia depressa	G		SV				SV		G		SV	
Heteropogon contortus	SV	SV	SV		SV	SV	SV	SV +G	SV +G	SV		
Hibiscus microcarpus			SV									
Hilliardiella aristata			SV	SV		SV		SV		SV	SV	
Hilliardiella elaeagnoides							SV			SV	SV	
Hilliardiella hisuta			SV			SV	SV					
Hyparrhenia hirta								SV				
Hypericum aethiopicum								SV		SV	SV	
*Hypochaeris albiflora**				SV								
*Hypochaeris glabra**										G		
*Hypochaeris radicata**				SV		G		G		G		
Hypoxis hemerocallidea			SV								SV	
Hypoxis rigidula			SV	SV						SV	SV	
Hypoxis sp.					G			SV				SV
Indigofera hilaris			SV									SV
Indigofera melanadenia					SV	SV						
Indigofera oxytropis					SV							SV
Indigofera sp.										G		
*Ipomoea obscura**						SV			SV			
Justicia anagalloides	SV		SV		SV	SV	SV			SV	SV	SV
Kalanchoe paniculata	SV											
Kalanchoe thyrsiflora					SV	SV						
Kohautia amatymbica			SV			SV	SV				SV	

Table 4 (continued)

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Kruin Park grass A		SV										
Lannea edulis								SV				
*Lantana camara**		SV										
*Lantana rugosa**		SV	SV				SV	SV			SV	
Lasiosiphon kraussianus	SV											
Ledebouria ovatifolia	SV					SV					SV	
Ledebouria revoluta	SV			SV		SV	SV			SV	SV	
Ledebouria sp.						G	G					
Leonotis leonurus		SV		G					SV			
*Lepidium bonariense**	SV											
Lobelia anceps				SV								
Lophiocarpus tenuissimus						G						
Lopholaena coriifolia	SV											
Loudetia simplex					SV				SV			
*Malvastrum coromandelianum**							SV					
Melinis nerviglumis		SV			G	SV	SV			SV + G	SV + G	G
Melinis repens	SV			G	SV			SV	SV + G			SV
Magalies grass A					SV							SV
Nidourella hottentotica	SV	SV				SV		SV				
Nidourella porodocephalla			SV				SV				SV	
Nidourella sp.	G	G			G	G		G	G		G	
Ocimum obovatum						SV				SV		
*Oenothera rosea**				SV								
*Oenothera tetraptera**			SV + G	G						G		
Oldenlandia herbacea					G				SV + G	G		
Osteospermum muricatum			SV									
Oxalis corniculata			SV	SV			SV			SV		
Oxalis obliquifolia		SV				SV						
Oxalis sp.	G	G	G	G	G	G	G	G		G	G	
Parinari capensis	SV					SV		SV		SV		
Paspalum scrobiculatum				G						G		
Pavonia burchelli			SV				SV					
Pellaea calomelanos	SV				SV	SV		SV	SV			SV
Pentanisia angustifolia										SV	SV	

Table 4 (continued)

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Pentarrhinum insipidum							SV	SV				
Phyllanthus parvifolius	G				G	G			G	G		
Phyllanthus parvulus				G	G	G	SV	G		G	G	
Phyllanthus sp.					G				SV			
*Physalis angulata**								G			G	
*Physalis viscosa**		SV	SV	SV			SV		SV			
*Plantago lanceolata**		G	SV + G	SV + G			SV + G		G	G		
*Plantago virginica**										G		G
Poaceae sp.		G				G		G		G		
Pogonarthria squarrosa									SV			
Pollichia campestris	SV										SV	
*Polycarpea corombosa**												G
Polygala amatymbica				SV			SV					
Polygala hottentotta			SV			SV	SV	SV			SV	
Polygala uncinata												SV
*Portulaca carmeciliana**					G							
*Portulaca oleracea**					G			G				
*Primula malacoides**		G							G	G	G	
Pseudognaphalium sp.	G	G	G	G	G	G	G	G	G	G	G	G
Raphionacme hirsuta						SV						
Rhoicissus sp.									SV			
Rhoicissus tridentata	SV											
Rhynchosia caribaea											SV	
Rhynchosia monophylla					SV							SV
*Richardia brasiliensis**		G							SV			
Rotheca hirsuta											SV	
Rietvlei species E										SV		
Rietvlei species F			SV								SV	
Rubiaceae anthospermum			G						G		G	
Ruellia cordata						SV						
*Salvia tiliifolia**				SV + G			SV					
Sansevieria aethiopica	SV											
Scabiosa columbaria			SV			SV					SV	
*Schkuria pinnata**	SV	G	G	G	SV	SV	SV + G	SV + G	G			
Searsia lancea		G										

Table 4 (continued)

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Searsia leptodictya									SV			
Searsia pyroides				SV			SV					
Searsia sp.		SV		SV	SV		SV	SV				
Searsia zeyheri						SV		SV	SV			
Selaginella dregei												SV +G
*Selaginella selaginoides**												SV
Senecio coronatus	SV				SV			SV				
Senecio oxyriifolius	SV											
Senegalia caffra	SV											
Senegalia sp.				SV			SV	SV				
Setaria pumila		G	SV	G	SV	SV	SV			SV +G	SV	
Setaria sphacelata var. sphacelata		SV				SV						
*Sida abutifolia**		SV					SV					
Skuilkrans species A	SV											
*Solanum campylacanthium**	SV							SV	SV	SV	SV	
*Solanum elaeagnifolium**										SV		
Solanum sp.*		G						G	G		G	
*Solanum cerasiferum**				G								
Spermacoce sinensis									G			
Sphenostylis augustifolia								SV		SV	SV	
Sporobolus africanus				SV								
Sporobolus festivus						SV						
Stoebe capitata										SV		
Striga bilabiata			SV		SV						SV	
*Tagetes minuta**		SV +G	G		SV +G		SV +G	SV +G	SV +G			
Taraxacum sp.*	G	G		G	G			G	G	G		G
Tephrosia capensis			SV			SV	SV	SV		SV		SV
Tephrosia elongata	SV	SV			SV			SV		SV	SV	
Tephrosia sp.					SV							
Teucrium trifidum					SV							
Themeda triandra	SV +G	SV	SV	SV +G	SV	SV	SV	SV	SV +G	SV +G	SV	SV
Thesium sp.		SV	SV			SV			SV	SV		
Trachypogon spicatus	SV					SV		SV	G	SV +G	SV	

Table 4 (continued)

Species	Skuilkrans Kopje	Kruin Park	Moot Grassland	Moreleta Kloof	Wonderboom	Smuts Koppie	Faerie Glen	Voortrekker Monument	Groenkloof	Rietvlei A	Rietvlei B	Magalies
Tragus berteronianus					SV							
Tristachya leucothrix	SV	SV	G	G	G	SV	G	SV		G	G	
Triumfetta sonderi								SV	SV			
Tulbaghia acutiloba			SV									
Ursinia nana												SV
*Verbena bonariensis**											SV	
*Verbena brasiliensis**			SV							SV		
*Verbena incompta**		SV	SV	SV			SV		SV			
*Vigna vexillate**			SV									
Voortrekker Monument species A								SV				
Voortrekker Monument species B								SV				
Wahlenbergia undulata							SV			G	G	
Waltheria sp.					SV							
Xenostegia tridentata												SV
Xerophyta retinervis	SV				SV	SV						SV
*Zinnia peruviana**		SV			SV		SV		SV			
Ziziphus mucronata							SV					
Ziziphus zeyheriana										SV		

Acknowledgements We thank the City of Tshwane for permission to work in its nature reserves (permit 20220523_120724, issued by the Department of Nature Conservation), and Anika Oosthuizen and Tiaan Geldenhuys for assistance in the field and with the germination process. We also thank our editor and reviewers for their thoughtful and detailed comments that helped to refine this article.

Author contributions The study was conceptualized and designed by MM, PCLR and NSH. MM applied for permits, collected the data, performed data analysis, and wrote the initial draft. NSH and PCLR provided input on data analysis and revised drafts of the manuscript.

Funding Open access funding provided by University of Pretoria. This work was financially supported by the National Research Foundation (grant no. 120404). The opinions, findings and conclusions expressed here is that of the authors alone, and the NRF accepts no liability in this regard for research supported.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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