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The Impact of Nassella Neesiana on Plant Diversity, Richness, and Topsoil in Harrismith, the Eastern Free State, South Africa

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THE IMPACT OF *NASSELLA NEESIANA* ON PLANT DIVERSITY, RICHNESS, AND TOPSOIL IN HARRISMITH, THE EASTERN FREE STATE, SOUTH AFRICA

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ABSTRUCT

Nassella neesiana is a South American tussock-forming grass that has become invasive in several regions outside its native range. Despite its documented ecological impacts elsewhere, its distribution and ecological effects in South Africa remain poorly understood, and it is currently not included on the national Alien and Invasive Species List. We investigated the distribution, habitat, plant community effects, soil properties and density-dependent impacts of *N. neesiana* in Harrismith, Free State, where populations were recently confirmed. Seven subpopulations along a tributary of the Wilge River which rises from the Platberg Eco Reserve were studied using 14 paired invaded and uninvaded plots. Plant community composition, diversity, soil properties and *N. neesiana* abundance were assessed. *Nassella neesiana* occurred predominantly in disturbed, seasonally wet habitats, with subpopulations ranging from 32 to >17,000 m² and local cover reaching 90%. Binary comparisons revealed no significant differences in species richness, Shannon diversity, Simpson diversity, evenness or soil properties between invaded and uninvaded plots. However, species richness declined with increasing *N. neesiana* abundance, indicating a density-dependent association. Multivariate analyses also suggested differences in plant community and soil characteristics between invasion categories. Field observations indicated that

established tussocks can persist following fire. The inconspicuous nature of the species within resident vegetation, together with its occurrence in disturbed urban and riparian habitats, may contribute to under-detection. These findings support increased surveillance of *N. neesiana* in South Africa, particularly along disturbed riparian and transport corridors, and provides a basis for future assessment of its invasion risk and management status.

Keywords: Biodiversity; Invasive alien plants; Soil nutrients; Urban invasions

INTRODUCTION

Nassella neesiana (Trin. & Rupr.) Barkworth (Poaceae), commonly known as Chilean needle grass, is an alien tussock-forming grass species native to South America, including Argentina, Bolivia, Brazil, Chile, Ecuador, Paraguay, Peru, and Uruguay (Barkworth and Torres, 2001). Its ecology in southern Africa remains poorly documented. In contrast, its congeners *N. tenuissima* (Trin.) Barkworth and *N. trichotoma* (Nees) Hack. & Arechav have become high-profile invaders in southern Africa (Henderson, 2018). While *N. tenuissima* and *N. trichotoma* are regulated as Category 1b invasive species under South Africa's National Environmental Management: Biodiversity Act (NEM:BA, 10/2004 updated 2023) (South African Government, 2023), *N. neesiana* is currently not included on the national Alien and Invasive Species List, despite being naturalised in South Africa and recognised as a serious invader elsewhere. This difference in regulatory status is important because the absence of *N. neesiana* from the current regulatory list should not be interpreted as evidence of low invasion risk. Rather, it highlights a significant knowledge gap concerning its current distribution, ecological impacts and potential future trajectory in South Africa.

Globally, *N. neesiana* has naturalised widely, including in Australia, New Zealand, and parts of Europe, where it is considered a highly invasive species with serious impacts on pasture productivity and biodiversity (Faithfull, 2012; Howell and Sawyer, 2006). In these regions, the species forms dense tussocks, reduces native species richness, and alters ecosystem processes, including nutrient cycling and fire regimes (Bourdôt and Hurrell, 1989; Faithfull, 2012; Kriticos et al., 2010).

Despite its demonstrated impacts elsewhere, the distribution, abundance, and ecological impacts of *N. neesiana* in South Africa remain poorly understood. Herbarium and database records are sparse, with most collections dating back several decades and only a few recent observations extending its known range. Available records indicate that the species is often associated with disturbed or modified habitats, including urban and peri-urban environments. This concentration of recent observations in modified environments is important because such habitats may provide opportunities for establishment while simultaneously making early invasion difficult to detect against a background of disturbance.

This pattern suggests that *N. neesiana* may represent a cryptic invader, a class of invasive species that remain undetected or overlooked for extended periods due to not being recognised as

alien or being morphologically indistinguishable from other alien congeners (Morais and Reichard, 2018; Novak, 2011). Cryptic invasions are often associated with prolonged lag phases, during which populations persist at low densities before undergoing rapid expansion (Crooks and Soulé, 1999; Robeck et al., 2024). The recent confirmation of *N. neesiana* from Harrismith therefore provides an opportunity to examine whether an apparently localised population occurring in a disturbed urban–grassland interface is already associated with measurable ecological effects.

Urban and peri-urban environments are increasingly recognised as important entry points and reservoirs for invasive species (Aronson et al., 2014; Gaertner et al., 2017). These environments are characterised by high levels of disturbance, frequent propagule introduction, and heterogeneous habitats, all of which favour ruderal and non-native species (Aronson et al., 2014; Gaertner et al., 2017), potentially masking impacts on diversity (McKinney, 2006). Such systems may act as sources of propagules for invasions into surrounding natural ecosystems (Potgieter et al., 2019). However, the ecological impacts of invasive species in urban systems can differ from those in less disturbed environments, often reflecting interactions with habitat modification and disturbance, which may reduce or obscure their direct effects on biodiversity (Didham et al., 2005; McKinney, 2006; Shochat et al., 2006). Invasion impacts are also context-dependent and density-dependent, with many species exerting minimal detectable effects at low abundance but causing substantial ecological change once certain thresholds are exceeded (Bradley et al., 2019; Yokomizo et al., 2009). Consequently, studies that rely solely on binary comparisons of invaded versus uninvaded sites may underestimate early-stage impacts.

Given the lack of ecological data on *N. neesiana* in South Africa and its potential to be a cryptic invader, there is a need for detailed field-based studies to assess its distribution and ecological effects, particularly in urban and peri-urban environments where it may be establishing unnoticed. Such information is critical for informing management strategies and preventing further spread into more intact grassland ecosystems.

This study was carried out in the town of Harrismith (Free State, South Africa) where *N. neesiana* had recently been recorded. The objectives were to: (1) characterise its distribution and habitat; (2) compare plant community composition, and diversity in invaded vs uninvaded patches; (3) examine soil properties; and (4) test for density-dependent invasion effects. We used both traditional binary (invaded/uninvaded) comparisons and also analyses relating native diversity to

N. neesiana abundance. This is the first field study of *N. neesiana* impacts in South Africa, and informs whether urgent management is needed to prevent future spread.

MATERIALS AND METHODS

Study area

This study was carried out in Harrismith, a small town in the Thabo Mofutsanyane District, Free State province of South Africa (28°16′S, 29°10′E). The presence of *N. neesiana* in this area was discovered accidentally in 2020 by S. Soreng and S. Sylvester (Sylvester et al., 2021), and the discovery extended its distributional range significantly. The survey sites were situated along a perennial stream which rises in the Botanical Gardens / Platberg Eco Reserve at the western base of Platberg ("Flat-topped Mountain" in Afrikaans) and runs on the north-eastern edge of Harrismith (Fig. 1). It is a tributary of the Wilge River, which enters on the north-eastern edge of the town. The Wilge in turn is an important tributary of the Vaal River, which is one of South Africa's most important water resources (Tempelhoff et al., 2007). Harrismith was a major British military base during the Second Anglo-Boer War fought between 1899 and 1902 (Visser, 2012), and it is most likely that *N. neesiana* was introduced into the area during this time in hay (Henderson, 2018; Wells, 1978). If this is the case, it means this species has been present in the Harrismith vicinity since the British took control of Harrismith from the Boers in 1901 – a period of more than 120 years.

Elevation in the study site ranges from 1620–1725 m, with generally acidic loamy soils of the Eastern Free State Sandy Grassland (Mucina and Rutherford, 2006). Mean annual rainfall is ~800 mm, falling mainly between November to March; summers are warm (mean 22 °C), winters cold (mean 6 °C) with occasional frost (Brand et al., 2011; Merkel, 2020). Vegetation is C_4-dominated grassland with scattered shrubs and trees. Land use is semi-rural, with gumtree, pine, and wattle plantations and informal settlements near streams.

The native vegetation of the general area falls within the Eastern Free State Sandy Grasslands of the Grassland Biome (Mucina and Rutherford, 2006), still intact on most of the dryland slopes of Platberg. Native woody species of value (e.g. timber, firewood) may have been removed from the system in the mid-1800s already, given the original scarcity of natural wood on the Highveld. Two privately maintained recreation areas occur in the study site, viz. "Perdegat",

and the Harrismith Golf Course, with derelict recreation areas next to the two dams in the Platberg Eco Reserve.

A detailed population mapping exercise was done in March 2021 when most plants were in flower and easier to identify. This was achieved by visiting areas on the north-eastern side of Harrismith's urban area as well as systematically searching for subpopulations along the stream and other disturbed areas. These areas were prioritised because available records indicate that *N. neesiana* is associated with disturbed and seasonally wet habitats, while watercourses may also provide potential pathways for seed dispersal during flooding (Bourdôt et al., 2012; Fox et al., 2009). Any subpopulation noted was georeferenced using an ETrex 10 GPS machine (Fig. 1). The extent of the subpopulation was estimated by walking around it with the GPS in tracking mode and calculating the area in QGIS software. The invaded areas were described in terms of the general vegetation disturbance, and soil moisture condition (estimated from observation: dry, seasonal wetland, permanent wetland) (Table 1). Further surveys were done from mid-November to early December 2021 to see whether any subpopulations could have been missed in March. The subpopulations discovered during this survey were described but no further assessments were done, as with the seven sites determined in March.

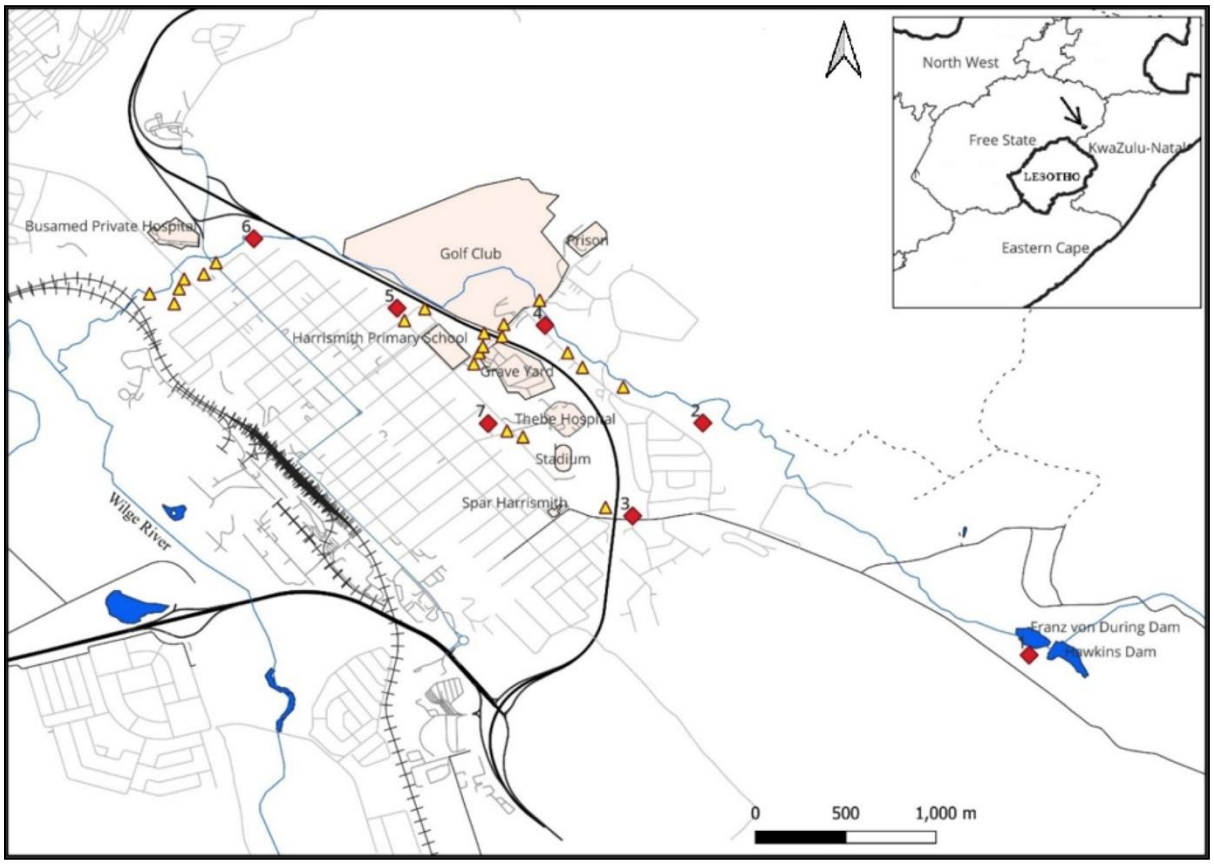

Fig. 1. Locations of subpopulation sites of *Nassella neesiana* along the Platberg Stream, Harrismith (Free State, South Africa). The red diamonds refer to studied subpopulations (the numbers against them refer to site numbers); yellow triangles refer to sites that were not studied but *N. neesiana* individuals were encountered. The location of Harrismith is indicated by an arrow on the inset map.

Table 1. Characteristics of the seven *Nassella neesiana* subpopulations sampled along the Platberg Stream, Harrismith, including site conditions, dominant grasses, and soil moisture classification (estimated from observation: dry, seasonal wetland).

Site	Altitude (m.a.s.l.)	Site description	Dominant grasses (uninvaded)	Soil moisture
1	1724.97	Former picnic site near weir in *Eucalyptus* plantation	*Cynodon aethiopicus*, *Digitaria sanguinalis*, *Sporobolus pyramidalis*	Seasonal wetland
2	1645.14	Disturbed dumpsite with soil movement	*Aristida adscensionis,* *Cynodon dactylon*, *Hyparrhenia hirta*	Seasonal wetland
3	1662.93	Riparian zone with litter disturbance	*Aristida junciformis*, *Cynodon aethiopicus*, *Sporobolus pyramidalis*	Wet (stream edge)
4	1632.34	Road verge between stream and N3 highway	*Cynodon aethiopicus*, *Eragrostius curvula*, *Setaria pumila*	Moist riparian
5	1620.91	Abandoned golf course wetland.	*Cynodon aethiopicus*, *Sporobolus pyramidalis*, *Themeda triandra,*	Seasonal wetland
6	1619.83	Disturbed area between houses and stream	*Cynodon dactylon*, *Brachiaria eruciformis*	Seasonal wetland
7	1624.27	Footpath-disturbed grassland	*Themeda triandra*, *Eragrostis curvula*	Seasonal wetland

Vegetation plots

Sites were sampled with two paired plots per invasion patch. This minimised the possibility of a few patches skewing the results. This gave four plot per site. Paired plots were chosen so that one plot of the pair had at least 5 % *N. neesiana* cover (invaded plot), with the other plot in a nearby area where *N. neesiana* had no cover at all (uninvaded plot). Both plots were placed so that

they had similar environmental conditions and site history (aspect, elevation, rockiness, etc.) (Hejda et al., 2009; Thomaz et al., 2012; Vanderhoeven et al., 2005). Plot pairs were 5–10 m apart. This cover limit and the need to have plot pairs within ten metres of each other excluded some subpopulations. One of the major criticisms of paired plot comparisons is that the differences between them may merely reflect pre-invasion conditions. Keeping both pairs within the same site and as close together as possible reduces this challenge (Maurel et al., 2010). To avoid ecotonal effects, recommendations from the Global Invader Impact Network (GIIN) were used (Barney et al., 2015). Using these recommendations, the minimum allowable distance of plots from the edge was determined to be 50 cm since *N. neesiana* has no stolons and its maximum height is 1 m. In all cases, plots were at least two metres from the edge. *Nassella neesiana* invasion in this area is not continuous but is patchy, with dense patches in some areas and other areas with very sparse or no cover, making it possible to find areas without *N. neesiana* within the general invaded area. A total of fourteen (14) paired 2 m x 2 m plots (total 28 plots) were sampled in the austral summer in March 2021. In each plot, all vascular plant species encountered were recorded, and the cover-abundance of each species visually estimated and written as a percentage cover of the whole plot. Plant species encountered were identified in the field; when this was not possible specimens were collected and identified using the Qwaqwa herbarium (QWA). Each species was assigned to one or more of the following categories – forbs, grasses, native species, endemic species, naturalised species, and naturalised invasive species. The status of each species was determined following The South African National Plant Checklist: 2025 (South African National Biodiversity Institute (SANBI), 2025) and SAPIA News Report 48 (Henderson, 2018) for naturalised invasive species. Other parameters measured per plot were bare ground (percentage of plot), slope (subjectively — gentle, moderate, steep), aspect, rock cover (percentage of plot), disturbance level (subjectively — low, medium, high). These parameters, except bare ground and litter, were assessed to ensure that the paired plots did not differ.

In each invaded plot, the number of *N. neesiana*, tufts were counted. A tuft was considered to be in the plot if part of its base was in the plot. The basal circumference of each tuft was measured to the nearest centimetre. To assess whether a fire event had occurred on grass tufts, all grass tufts were visually assessed for evidence of any charring at the base. The follow-up survey from mid-November to early December 2021 described any new subpopulations, however, did not assess their impacts as outlined here (Fig. 1).

Soil sampling

Soil sampling followed Vanderhoeven et al. (2005). For every plot surveyed a soil core (20 cm deep and 5 cm diameter) was collected from near the corners of each plot and at the centre. Wherever possible, sampling was done very close or under a *N. neesiana* tuft. The soil samples were then combined so that there was one cumulative soil sample for the invaded and uninvaded plots at each site. Any litter present was removed and discarded before soil sampling. Each composite soil sample was thoroughly mixed and a sub-sample weighing about 0.5 kg taken for soil testing. This gave a total of 14 soil samples (seven from the invaded plots and seven from uninvaded plots). The soil samples were collected in plastic zipper bags and kept in a fridge (4°C) until they were sent off for testing at the Soil, Water and Plant Diagnostics Laboratory, Elsenburg, Western Cape. Soil parameters tested at the lab were boron (B), calcium (Ca), carbon (C), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), nitrogen (N), pH, phosphorus (P), potassium (K), sodium (Na), total cations, zinc (Zn), and particle size (5 fraction). Boron was measured using the calcium chloride extraction method; carbon using the Walkley-Black method; soil particle size using the five-fraction hygrometer method; pH using the KCl extraction method; the ammonium EDTA method was used to measure Zn, Cu, Fe and Mn; and the citric acid analysis method was used to measure Mg, Na, P, Ca, and K. These soil variables were selected as they are considered to have the most influence on plant growth (Vanderhoeven et al., 2005). Soil testing was carried out following the handbook by the Non-Affiliated Soil Analysis Work Committee and Soil Science Society of South Africa (1990).

DATA ANALYSIS

All statistical analyses were performed in R-Statistical software version 4.0.5 (R Core Team, 2025).

Floristic composition and community structure

Differences in plant community composition between invaded and uninvaded plots were analysed using the mvabund package (Wang et al., 2012). A multivariate generalised linear model (manyglm) with a negative binomial error distribution was fitted using species abundances as the response variable. Plot status (invaded/uninvaded) and site were included as fixed effects. Statistical significance was assessed using likelihood ratio tests (LRT) with 999 pit-trap bootstrap

resamples. Univariate tests were conducted to identify species contributing to compositional differences, with p-values adjusted for multiple testing.

To further explore community structure, non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis dissimilarity was performed on Hellinger-transformed species data using the vegan package. Differences in community composition were tested using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations, including site as a blocking factor. To determine which environmental variables were strongly associated with species assemblages, the manyglm function was used to model the multispecies abundances as response variable and the environmental variables as fixed effects fitted with a negative binomial distribution. Variables such as rockiness, elevation, and distance from the nearest road/path were selected to ensure similar environmental conditions between paired plots, as differences in underlying site characteristics can strongly influence community composition and invasibility (Hejda et al., 2009; Tilman, 1997; Vanderhoeven et al., 2005).

Species richness (S), Shannon diversity (H), Simpson diversity (D), inverse Simpson (D1), and Pielou's evenness (J) were calculated for each plot using the vegan package (Oksanen et al., 2022). The effect of invasion (invaded vs uninvaded) on diversity metrics was assessed using linear mixed-effects models (LMMs), with plot status as a fixed effect and site and plot pair as nested random effects. Count-based variables (e.g., number of native, naturalised, and invasive species) were analysed using generalised linear mixed-effects models (GLMMs) with a negative binomial distribution to account for overdispersion.

To assess density-dependent effects, *N. neesiana* abundance (tuft density per plot) was incorporated as a continuous predictor variable. Relationships between invasion intensity and diversity metrics were analysed using linear mixed-effects models. Nonlinear responses were explored using generalised additive models (GAMs). Additionally, threshold responses were examined using segmented regression models to identify potential breakpoints in the relationship between invasion intensity and species richness.

Soil variables

Differences in soil physical and chemical properties between invaded and uninvaded plots were assessed using linear mixed-effects models with site as a random effect. P-values were adjusted for multiple comparisons using false discovery rate (FDR) correction. To evaluate multivariate soil patterns, principal component analysis (PCA) was conducted on scaled soil

variables. Differences between invaded and uninvaded plots in multivariate soil hyperspace were assessed visually and statistically.

To investigate relationships between plant community composition, invasion intensity, and soil variables, redundancy analysis (RDA) was conducted using Hellinger-transformed species data. Invasion intensity and soil principal components were included as explanatory variables, with site included as a conditioning variable to account for spatial structure. Statistical significance was assessed using permutation tests (999 permutations).

RESULTS

Distribution and population characteristics

A total of seven *N. neesiana* subpopulations were analysed in detail. These occurred predominantly in disturbed, seasonally wet environments along the Platberg Stream. Subpopulation sizes ranged from 32 m² to over 17,000 m², with a combined area exceeding 350,000 m². Tuft densities ranged from 2.75 to 21.5 tufts m^{-2} (mean = 6.07 tufts m^{-2}), with basal circumferences ranging from 2 cm to 96 cm (mean = 17.01 cm). Cover of *N. neesiana* ranged from 15% to 90% (mean = 51.07%).

Fire history and tuft structure.

Evidence of previous burning was observed on more than 80% of *N. neesiana* tufts that appeared to be more than one year old. These tufts commonly showed charring at the base, while the current-season culms appeared to represent post-fire regrowth. In contrast, several smaller flowering tufts, with basal circumferences of less than 4 cm, appeared to be current-season plants originating from seed. These smaller plants had no visible old culms or evidence of previous burning, despite fires having occurred during the preceding dry season. Larger and apparently older tufts frequently showed disintegration of the original tussock base, with new tillers developing around the margins. In some cases, decomposition of the original base made it difficult to determine whether apparently separate tillers represented a single ageing tuft or multiple individuals (S1).

Plant community composition

A total of 35 vascular plant species representing 12 families were recorded. Across all plots, 30 species were recorded in the uninvaded treatment compared with 25 species in the invaded treatment. However, plot-level species richness did not differ significantly between

invasion statuses ($p > 0.05$) (Fig. 2). Multivariate analysis using mvabund revealed no significant difference in overall community composition between invaded and uninvaded plots (LRT, $p > 0.05$). Similarly, PERMANOVA analysis indicated no significant effect of invasion status on community composition, while site explained a significant proportion of variation.

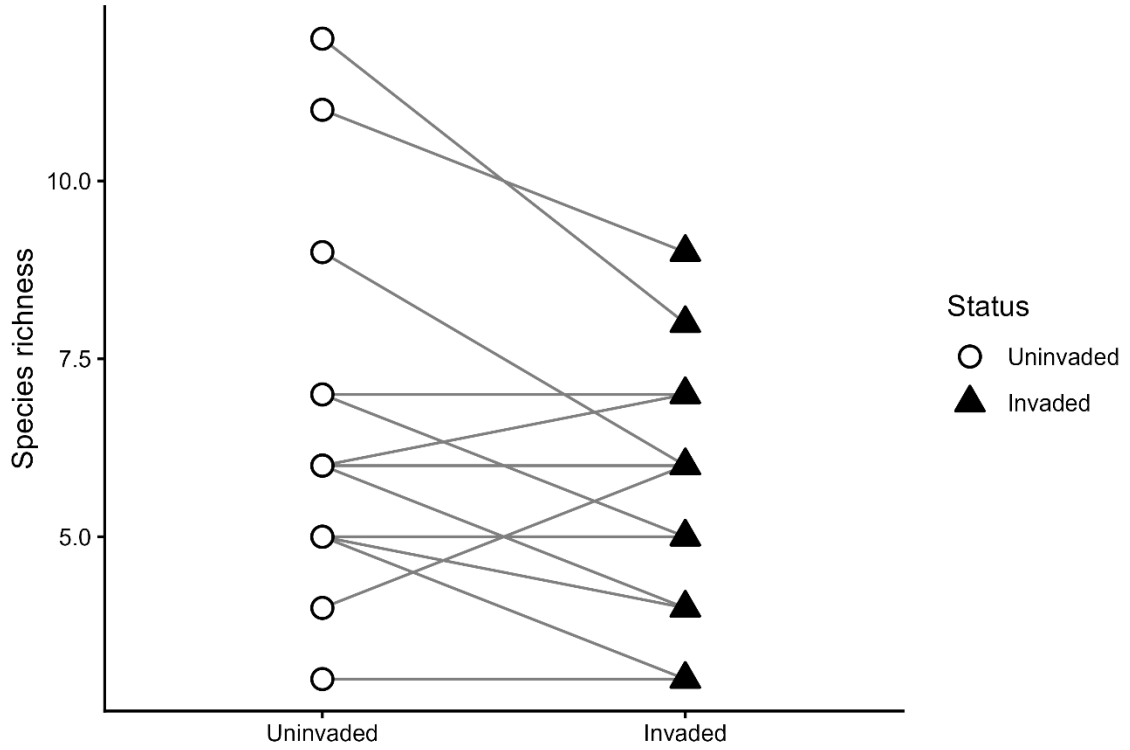

Fig. 2. Vascular plant species richness in Nassella neesiana-invaded and uninvaded plots across seven sites in the Harrismith area. Points represent individual plots, and lines connect paired invaded and uninvaded plots within sites. Species richness was not significantly different between invasion statuses based on a linear mixed-effects model ($p > 0.05$), although richness was generally higher in uninvaded plots.

However, NMDS ordination indicated substantial overlap between invaded and uninvaded plots, with partial separation along the primary ordination axes (Fig. 3), suggesting subtle shifts in species assemblages not captured by univariate analyses.

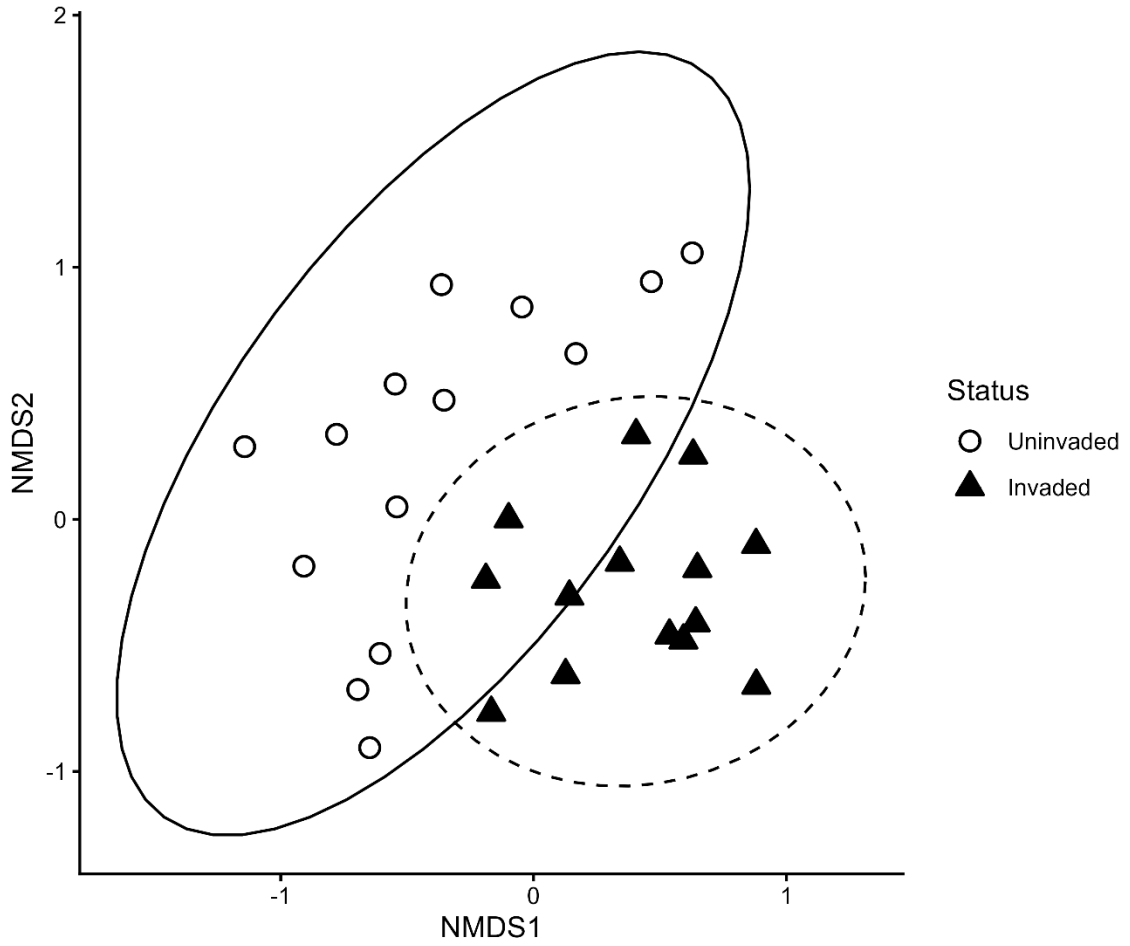

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of plant community composition based on Bray–Curtis dissimilarity of Hellinger-transformed species abundance data. Points represent individual plots, coloured by invasion status. Ellipses indicate 95% confidence intervals around group centroids. Substantial overlap between invaded and uninvaded plots indicates limited compositional differentiation, although partial separation suggests subtle shifts in community structure.

Diversity and functional group responses

None of the diversity indices (species richness, Shannon diversity, Simpson diversity, inverse Simpson, or evenness) differed significantly between invaded and uninvaded plots ($p > 0.05$ for all metrics). Similarly, there were no significant differences in the number of grass species, naturalised species, or invasive species between invaded and uninvaded plots. However, native species richness and total species richness were consistently higher in uninvaded plots. More alien naturalised and invasive species were recorded in invaded plots than in uninvaded plots (Table 2).

315 Table 2. Comparison of plant diversity metrics and functional group composition between
316 invaded and uninvaded plots. Values represent means per plot, with total species counts in
317 parentheses. Statistical significance assessed using mixed-effects models.

Parameter	Mean values per plot		χ^2 / F	d.f.	p-value
	Invaded	Uninvaded			
Native species	2.29 (12)	3.0 (17)	4.742	1	0.059
Forb species	2.5 (13)	3.5 (19)	2.315	1	0.128
Naturalised species	2.21 (13)	1.7 (13)	0.640	1	0.423
Naturalised invasive	1.14 (6)	1.29 (4)	0.117	1	0.731
Species richness (S)	5.64 (20)	6.57 (30)	3.158	1	0.076
Shannon-Weaver (H)	0.941	0.986	0.112	1	0.737
Simpson (D)	0.479	0.463	0.050	1	0.822
Inverse Simpson (D1)	2.18	2.33	0.063	1	0.801
Pielou's evenness (J)	0.544	0.514	0.162	1	0.687
			F		
Grass species	3.14 (12)	3.07 (11)	0.019	1	0.892

318

319 **Density-dependent effects of invasion**

320 When analysed as a continuous variable, *N. neesiana* abundance showed a negative relationship
321 with species richness, indicating a density-dependent effect (Fig. 4.). Although this relationship
322 was moderate, it suggests that ecological impacts increase with invasion intensity. Generalised
323 additive models indicated a potential nonlinear response, with declines in richness becoming more

pronounced at higher invasion densities. Segmented regression analysis further suggested the presence of a potential threshold, beyond which species richness declined more sharply.

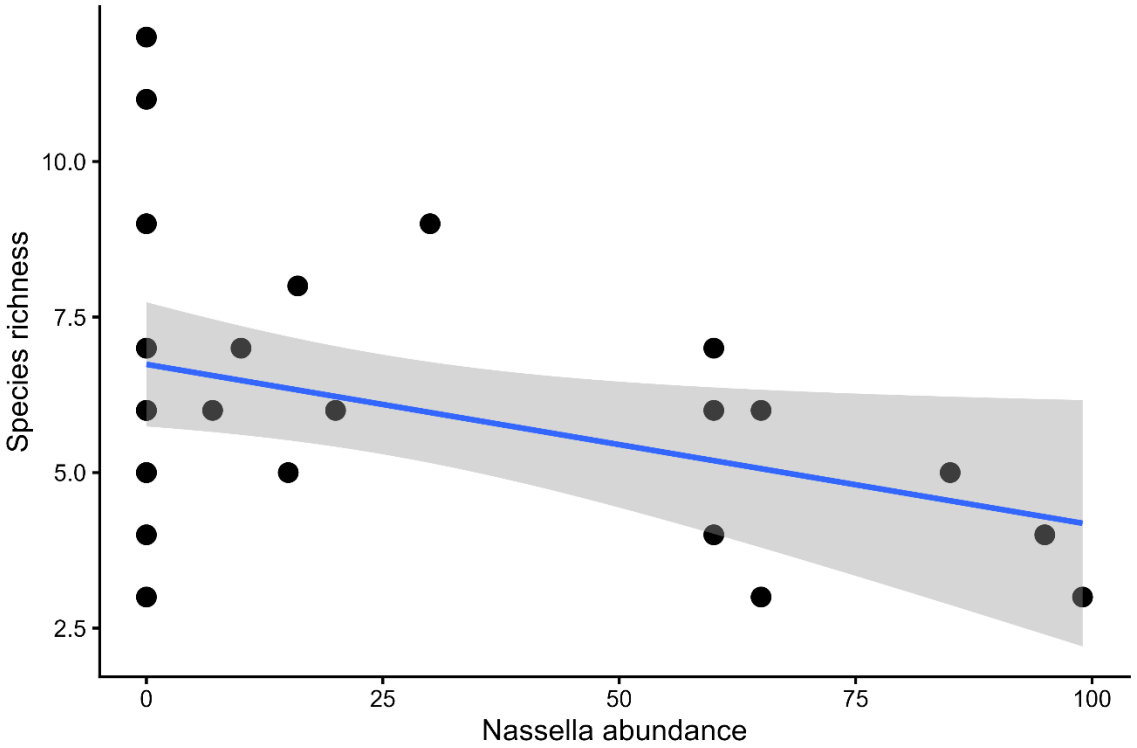

Fig. 4. Relationship between *Nassella neesiana* abundance (tuft density per plot) and species richness. The solid line represents the fitted linear model, with shaded areas indicating 95% confidence intervals. Species richness declined with increasing invasion intensity, indicating a density-dependent effect of invasion, despite the absence of significant differences under binary comparisons

Soil physical and chemical properties

No individual soil variables differed significantly between invaded and uninvaded plots after correcting for multiple comparisons ($p > 0.05$ for all variables). However, carbon, copper, medium sand, phosphorus, silt, and sulphur were higher in the uninvaded plots (Table 3). In contrast, principal component analysis (PCA) revealed emerging multivariate patterns. Invaded and uninvaded plots showed substantial overlap in ordination space but exhibited partial separation along principal component axes, indicating some shifts in soil properties (Fig. 5).

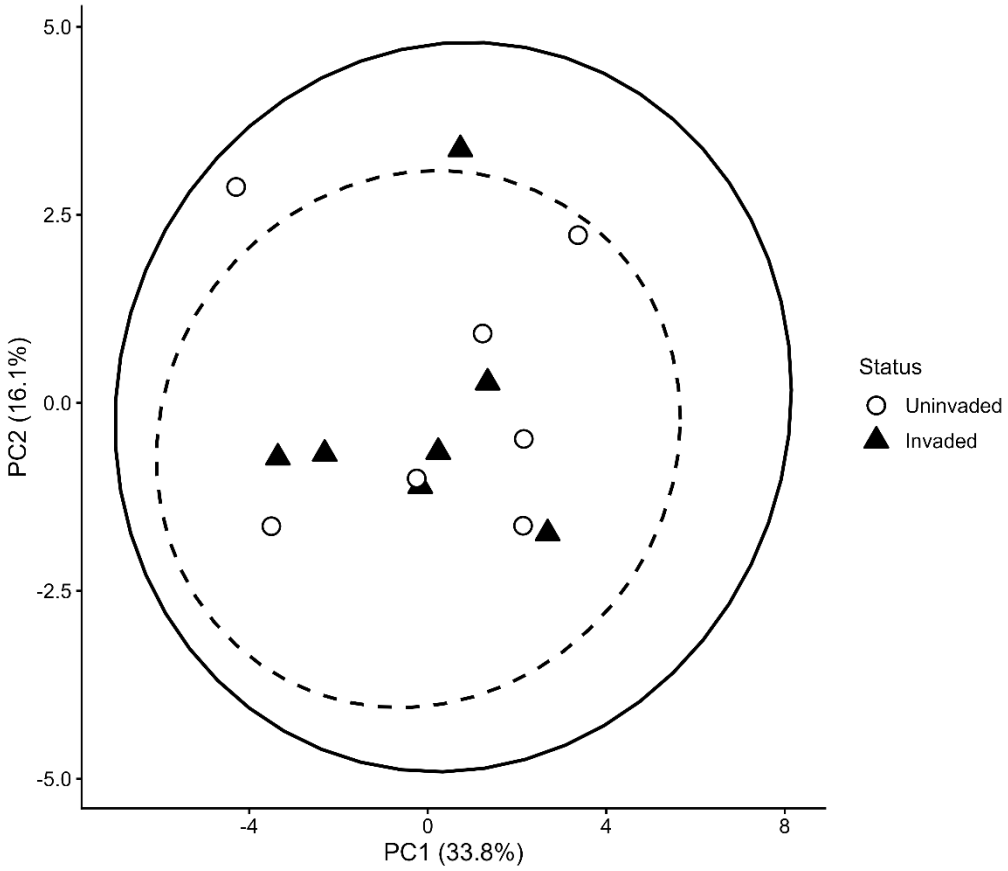

Fig. 5. Principal component analysis (PCA) of soil physical and chemical properties across *Nassella neesiana* invaded and uninvaded plots. Points represent composite soil samples from each site and invasion status. Ellipses represent 95% confidence intervals. Although univariate analyses detected no significant differences, partial separation along principal component axes indicates multivariate shifts in soil properties associated with invasion.

Table 3. Comparison of soil physical and chemical properties between *Nassella neesiana* invaded and uninvaded plots across seven sites. Values represent means across sites. No variables differed significantly after multiple comparison correction.

Soil parameter	Mean		F	d.f.	p-value
	Invaded	Uninvaded			
Boron (mg/ kg)	0.21	0.19	1.55	1	0.236
Calcium (cmol(+)/ kg)	8.63	8.21	0.10	1	0.76

Carbon	3.50	3.60	0.05	1	0.83
Clay (%)	13.43	13.14	0.01	1	0.92
Coarse sand (%)	10.71	9.43	0.15	1	0.71
Copper (mg/kg)	3.75	4.03	0.36	1	0.56
Fine sand (%)	49.00	46.86	0.15	1	0.71
Magnesium (cmol(+)/ kg)	3.77	3.74	0.00	1	0.97
Manganese (mg/ kg)	242.67	238.37	0.06	1	0.82
Medium sand (%)	6.00	7.14	0.17	1	0.69
Phosphorus (mg/kg)	144.29	147.00	0.00	1	0.96
pH	6.03	5.97	0.04	1	0.84
Potassium (mg/ kg)	499.00	435.57	3.21	1	0.10
Silt (%)	17.14	23.43	3.16	1	0.10
Sulphur	6.26	7.014	0.59	1	0.46
Sodium (mg/ kg)	39.29	101.29	1.28	1	0.28
Total cations (cmol(+)/ kg)	13.86	13.99	0.01	1	0.94
Zinc (mg/ kg)	14.32	13.91	0.01	1	0.94

Linking vegetation, soil, and invasion

Redundancy analysis (RDA) revealed that variation in plant community composition was weakly associated with invasion intensity and soil gradients (Fig. 6). While the overall model explained a modest proportion of variation, invasion intensity contributed more strongly than binary invasion status. Permutation tests indicated that invasion intensity and soil variables jointly influenced community composition, although these effects were relatively subtle.

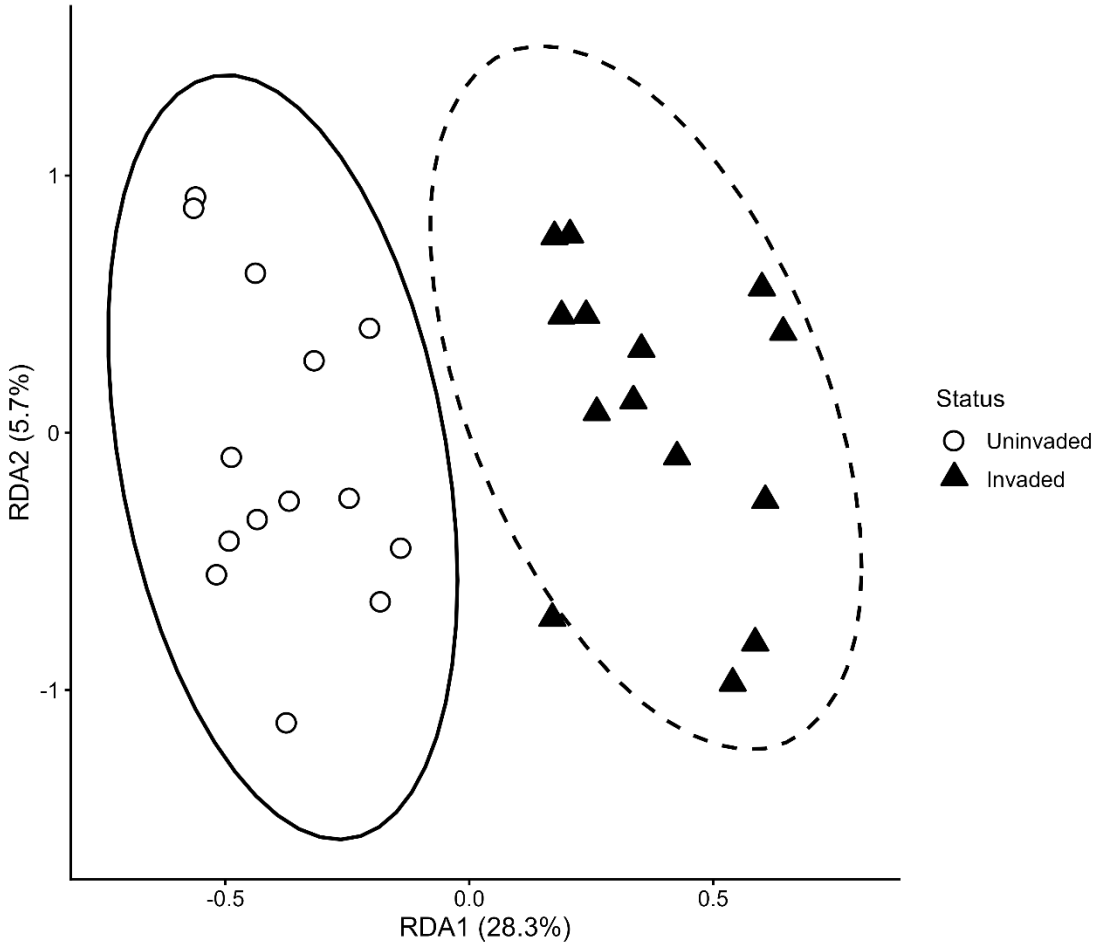

Fig. 6. Redundancy analysis (RDA) showing relationships between plant community composition, *Nassella neesiana* abundance, and soil gradients. Species are represented by vectors, and plots by points coloured by invasion status. Invasion intensity and soil variables explain a modest proportion of variation in species composition, indicating subtle but structured ecological effects.

DISCUSSION

This study provides the first ecological assessment of *Nassella neesiana* in South Africa and demonstrates that it currently exhibits characteristics consistent with a cryptic invasion. Despite evidence of long-term presence in the Harrismith area, the species has remained largely undetected until recently, likely due to its morphological similarity to native tufted grasses and its ability to integrate into existing vegetation without forming conspicuous monocultures.

Cryptic invasions are increasingly recognised as a major challenge in invasion ecology, as species may remain undetected for extended periods before entering phases of rapid expansion (Morais and Reichard, 2018). The apparent lag phase observed in *N. neesiana* is consistent with

patterns reported in other regions, where populations may persist at low densities for decades before expanding (Crooks, 2005). Despite its supposed introduction in the early 1900s, it had not been recorded in the study area until early 2020. No specimen could be found among the Harrismith plant collection housed in the Qwaqwa herbarium and the plant checklists of Harrismith stored in the herbarium, nor the online national database. This is despite its wide distribution along the stream to the north-eastern part of Harrismith town (Fig. 1). Some populations had densities of 4.64 tufts.m^{-2} with a basal circumference averaging 17.01 cm being recorded in this research suggesting that they have been growing in this area for many years.

Nassella neesiana was found to establish more readily along watercourses and seasonal wetlands that have experienced significant anthropogenic disturbance. This pattern is consistent with broader findings that *N. neesiana* invasions are strongly associated with habitat disturbance and reductions in native vegetation cover (Visser et al., 2017). Vegetation clearing and increased resource availability, particularly moisture, are known to facilitate invasion success in grassland systems (Catford et al., 2009).

The observations of post-fire resprouting and tuft expansion suggest that *N. neesiana* may possess traits that enhance persistence under disturbances such as fire. Alteration of fire regimes is a well-documented mechanism by which invasive grasses modify ecosystems (D'Antonio and Vitousek, 1992). The ability to remain green late into the season may further influence fire timing and intensity, potentially reinforcing invasion dynamics. Most larger tufts showed evidence of previous burning, with current-season culms apparently developing from surviving basal structures, whereas small flowering tufts without evidence of previous burning may represent recent recruitment from seed. The common occurrence of burnt old tufts suggests that fire does not necessarily prevent persistence of *N. neesiana* at the study sites. However, fire frequency, intensity and timing were not experimentally or quantitatively assessed, so these observations should be regarded as preliminary rather than evidence of fire-driven population expansion.

Together, these observations suggest a potentially important combination of vegetative persistence and seedling recruitment within the Harrismith populations. Larger tussocks appeared capable of surviving previous fires through post-fire basal regrowth, while the presence of small flowering plants without evidence of previous burning suggests ongoing recruitment from seed. Further demographic studies are required to determine the relative contribution of vegetative persistence and sexual reproduction to population expansion.

Furthermore, the ability of *N. neesiana* to persist and expand following fire may further enhance its invasiveness. Alien grasses are often able to resprout rapidly after fire and outcompete native species, which frequently rely on recruitment from seed (Tooth and Leishman, 2013). In addition, invasive grasses can increase fuel loads and alter fire regimes, reinforcing their dominance through positive feedbacks (Brooks et al., 2004). These dynamics have also been observed in *Nassella*-dominated systems, where invasion is associated with altered ecosystem structure and function (Humphries et al., 2022).

The urban areas sampled were heavily disturbed and full of weedy aliens such as *Bidens pilosa*, *Bromus catharticus*, *Physalis viscosa*, *Tagetes minuta* and *Verbena brasiliensis* which are ruderal species and well adapted to disturbance. The native species such as *Aristida junciformis*, *Cynodon dactylon*, *Eragrostis curvula*, *Paspalum scrobiculatum* and *Sporobolus pyramidalis* are common on disturbed areas and are considered invasives in other parts of the world (CABI, 2022). The weedy characteristics of both native and alien flora found in the studied areas enables them to coexist in a regularly re-disturbed context, with propagules very regularly added from illicit garden refuse dumping along the stream. *Nassella neesiana* was found to have little to no effect on plant species composition and other diversity measures in this area. This differs from the findings of research done in Australia on natural vegetation (Faithfull, 2012) where *N. neesiana* was found to reduce diversity of native species but facilitated alien species. It would therefore appear that the impact of *N. neesiana* on species richness and diversity in a disturbed urban setting may be less than in undisturbed habitats.

Although topsoil nutrient concentrations did not differ significantly between invaded and uninvaded plots, invaded plots had marginally higher average concentrations. This is consistent with the conclusions that invasive alien plants are often associated with heightened levels of topsoil nutrients (Dassonville et al., 2008; Ehrenfeld, 2003; Gibbons et al., 2017; Vanderhoeven et al., 2005). The actual mechanism by which *N. neesiana* achieves this is not known at this stage. The higher litter levels recorded in the invaded areas compared to the adjacent uninvaded areas suggests that replenishment of nutrients in the topsoil might be from the dead material. The disjunct nature of *N. neesiana* distribution in the grasslands can be accounted for by the fact that the seeds are predisposed to fall close to their parent plant and germinate there (Bourdôt and Hurrell, 1989). The few individuals that were found growing alone in the grasslands were possibly carried there by dispersal agents such as animals, and water.

Nassella neesiana integrates well into the resident vegetation making it difficult to spot from more than 10 m away even when flowering, unless the cover is sufficiently high for the drooping inflorescences to stand out. The plants are nearly impossible to identify reliably when they are not flowering. Healthy-looking individual *N. neesiana* plants were observed growing among other plant species, and the presence of other species did not appear to prevent their establishment or growth. These characteristics may contribute to the cryptic nature of *N. neesiana* in the field, particularly where populations occur at low density or outside the flowering period. The use of DNA-based species identification can therefore complement field-based detection by providing a reliable means of confirming suspected individuals, including plants that are difficult to identify morphologically ((Mapaura, Canavan, Richardson, Le Maitre, et al., 2025). Improved identification and confirmation of field records can, in turn, contribute to more accurate estimates of the species' distribution and facilitate early detection and monitoring of populations.

The invasions in Harrismith are a concern considering that Platberg, being an inselberg, is of conservation importance because inselbergs harbour many endemics and act as reservoirs and refugia for unique genetic material (Brand et al., 2011). Elsewhere in South Africa, *N. neesiana* is a well-integrated component of grassy mountain landscapes, such as in the Witteberg area (Eastern Cape Drakensberg), and the Boschberg (Somerset East, Eastern Cape) – so its eventual colonisation beyond Platberg Stream is not implausible (although it has not been noticed outside the current riparian zone as yet). In New Zealand, *N. neesiana* has been reported to have a lag phase spanning several decades and was still in its lag phase after more than 60 years after introduction (BourdôtT and Hurrell, 1989). The increasing number of recent observations of *N. neesiana* in South Africa raises the possibility that populations may be undergoing local expansion, although the available data are insufficient to determine whether the species has entered a geometric phase of population growth (Mapaura, Canavan, Richardson, Vidal Junior, et al., 2025). This uncertainty highlights the need for improved surveillance and systematic monitoring of established populations.

A possible starting point to survey for more invaded areas is scouting all known British posts during the Anglo-Boer war that would likely be points of introduction. Given that riparian areas are naturally ecologically dynamic zones of regular disturbance, favouring species such as *N. neesiana*, it may be that *N. neesiana* has successfully colonised much of the Wilge River system, from this Anglo-Boer War source population in Harrismith. While this study did not explore the

Platberg Stream-Wilge River confluence and below-stream, this is an important future study need. The occurrence of *N. neesiana* populations within the N3 road reserve raises the possibility that routine road-verge management activities, including mowing, seasonal grass baling and other road maintenance operations, could facilitate the secondary movement of seeds or plant material along the road corridor. Such activities could potentially contribute to the spread of *N. neesiana* between otherwise isolated populations and may provide a mechanism for dispersal to additional locations along the N3 and beyond. Targeted surveys of road reserves and other disturbed corridors could therefore provide an efficient means of detecting previously unrecorded populations.

The absence of significant differences in species richness, diversity, and community composition between invaded and uninvaded plots suggests that *N. neesiana* currently exerts limited detectable impact under binary comparisons. However, this finding should be interpreted cautiously. Urban and peri-urban ecosystems are inherently disturbed and often dominated by ruderal species adapted to frequent disturbance (McKinney, 2006). In such systems, the addition of another disturbance-tolerant species may not result in strong detectable shifts in diversity metrics (Didham et al., 2005). This may explain why the results differ from studies conducted in relatively intact grasslands in Australia, where *N. neesiana* has been shown to reduce native diversity. Although binary comparisons showed no significant effects, analyses incorporating invasion intensity revealed a negative relationship between *N. neesiana* abundance and species richness, indicating that impacts are likely density-dependent. Density-dependent invasion effects are well documented, with many invasive species exerting minimal impacts at low abundance but causing substantial ecological change once thresholds are exceeded (Bradley et al., 2019; Yokomizo et al., 2009).

The identification of a potential threshold response suggests that *N. neesiana* may currently be in a transitional phase, where impacts are beginning to emerge but have not yet reached levels detectable through traditional binary comparisons. Multivariate analyses (NMDS, PCA, RDA) revealed subtle shifts in both plant community composition and soil properties associated with invasion. Although these shifts were not statistically significant in univariate tests, their consistent direction suggests early-stage ecosystem modification.

Such patterns are characteristic of early invasion stages, where changes in ecosystem processes precede detectable changes in species richness or composition (Ehrenfeld, 2010). The slightly elevated nutrient levels observed in invaded plots are consistent with previous studies

showing that invasive plants can alter nutrient cycling through litter inputs and root processes (Dassonville et al., 2008; Vanderhoeven et al., 2005). The strong association of *N. neesiana* with disturbed, seasonally wet habitats suggests that disturbance and moisture availability are key drivers of its establishment and persistence. This aligns with broader invasion theory, which emphasises disturbance as a critical facilitator of invasion (Hobbs and Huenneke, 1992). The absence of *N. neesiana* in relatively undisturbed areas further supports the hypothesis that intact vegetation may resist invasion, at least during early stages.

The ecological effects examined here represent only one aspect of the potential impacts of *N. neesiana*. In addition to possible effects on plant community composition and diversity, invasive *Nassella* species are known to have consequences for livestock production, ecosystem services, and socio-economic wellbeing of affected communities (Anderson et al., 2010; Nkuna et al., 2018). Such impacts were beyond the scope of the present study and warrant consideration in future assessments of the species in South Africa.

The findings suggest that *N. neesiana* may currently be in an early or transitional invasion stage in Harrismith. The lack of strong impacts should not be interpreted as evidence of low risk, but rather as an indication that management interventions may still be effective. Early detection and rapid response are critical for managing invasive species during lag phases, before exponential spread occurs, as impacts of invasive species may be delayed or difficult to detect, highlighting the importance of early intervention (Coutts et al., 2018; Hyndman et al., 2015; Osunkoya et al., 2021; Simberloff et al., 2013).

CONCLUSIONS

Nassella neesiana is established in the Harrismith area and exhibits characteristics of a cryptic invader with a potentially long lag phase. While no significant differences in plant diversity or soil properties were detected under binary comparisons, analyses incorporating invasion intensity revealed emerging density-dependent impacts on species richness. Multivariate analyses further indicated subtle shifts in community composition and soil properties, suggesting early-stage ecosystem modification. The species appears to be strongly associated with disturbed, seasonally wet environments, where it can establish and persist without immediately displacing resident species.

These findings highlight the importance of moving beyond binary invasion assessments and incorporating invasion intensity and multivariate approaches to detect early ecological impacts. Given its demonstrated impacts in other regions and its apparent expansion in South Africa, *N. neesiana* should be considered a species of management concern. Proactive monitoring and management are recommended to prevent further spread and potential impacts on more intact grassland ecosystems.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Anthony Mapaura. The first draft of the manuscript was written by Anthony Mapaura and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.



S1. An older *Nassella neesiana* tussock showing evidence of previous burning and subsequent disintegration of the basal structure, with current tillers occurring around the margins. The yellow outline indicates the approximate extent of the former tussock base. The breakdown of the original base can make it difficult to determine whether peripheral tillers represent a single ageing individual or multiple plants.