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REGULAR PAPER

Patterns of plant species richness of temperate and tropical grassland in South Africa

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Background and aims – The grasslands of southern Africa are threatened by habitat transformation and invasive alien species. However, the resultant plant species loss per unit area cannot be quantified, as the true richness of grassland have not been determined accurately and current estimates of richness are generally based on once-off site visits. The aim of this study was to quantify and compare the species richness of selected transformed and untransformed grasslands of tropical and temperate regions in South Africa. The study sites were located in four grassland vegetation units: KwaZulu-Natal Coastal Belt and Maputaland Woody Grassland (tropical), and Paulpietersburg Moist Grassland and Rand Highveld Grassland (temperate).

Methods – Thirty-two plots of 10 × 10 m were sampled at the four sites, namely eight in each of the vegetation units. At each site four plots were sampled in untransformed grassland and four in adjacent transformed grassland. Thorough floristic sampling of each plot was undertaken three times during the peak growing seasons.

Key results – Plant species richness was higher for untransformed grassland than transformed grassland, and is higher than what was previously estimated. Species richness is not severely affected by alien cover and richness, as species losses are made up by better adapted native and alien species entering the transformed habitat. Rare species and habitat specialists are displaced. The type of transformation has a pronounced effect on species richness.

Conclusion – Plant species richness of grassland is higher than previous estimates. Increasing alien cover and richness reduces the species richness of certain grassland growth forms and replaces species of conservation importance such as endemics.

Key words – Alpha diversity, invasive aliens, plantations, species richness, temperate grassland, tropical grassland.

INTRODUCTION

Grasslands are so called based on the structural facet of this vegetation type. Grasslands are dominated by species of the Poaceae, are mostly one-layered in structure with few trees and shrubs, and are climatically controlled (Mucina & Rutherford 2006). Grasslands occur in both temperate and tropical regions of the world. In southern Africa, Mucina & Rutherford (2006) consider grasslands to be either sub-tropical or temperate. The differentiation between these two grassland types is based on the factors responsible for the maintenance thereof. Tropical grasslands are often regarded as secondary (e.g. fire maintained) or edaphic (e.g. shallow water table) (Matthews et al. 1999). Temperate grasslands are thought to be naturally maintained by subzero temperatures and dry winters, in combination with fire, which prevent colonisation of grasslands by the tropically-derived tree flora of southern Africa (Bredenkamp et al. 2002).

South African grasslands are characterised by plant species with special modified underground organs which enable them to escape fire (e.g. geoxylic suffrutices; White 1977) or become dormant in winter (e.g. geophytes; Tainton & Mentis 1984) when growing conditions become unfavourable. Such adaptations are thought to be major mechanisms whereby grassland plants survive severely cold, dry winters and subsequent fires in temperate southern African grasslands (Bredenkamp et al. 2002). Grassland species, especially perennial forbs, are usually quick in responding to the effects of fire and such plants are characterised by profuse flowering and mass seed production (Retief & Van Wyk 2002).

Grasslands of southern Africa have always been considered to be diverse (Matthews et al. 1993). Before the revised account on the vegetation of southern Africa was published (Mucina & Rutherford 2006), it was difficult to make informative comparisons regarding the plant species richness of South African grasslands. The benchmark for grassland richness, according to Mucina & Rutherford (2006), is 9–39 species in 100 m^2 of grassland with a single structure (i.e. treeless grassland) and 19–49 species in 100 m^2 of multi-structural grassland (i.e. groundlayer, shrub layer and tree layer). However, a study by Siebert et al. (2002) had previously revealed that single-layered grasslands have a species richness of 25–51 species per 100 m^2 and multi-layered grassland 45–66 species per 100 m^2. These findings were probably regarded as inflated and left out of the estimation, as the study was conducted in a Centre of Endemism and could not be regarded as the norm for southern Africa for extrapolation purposes. The hypothesis, that the plant species richness of southern African grasslands is higher than was previously thought, therefore still stands. The purpose of this study was therefore to determine the species richness patterns of grasslands in South Africa and to quantify native species losses as a result of habitat transformation.

MATERIALS AND METHODS

Study area

Study sites were selected so as to represent both the tropical grasslands of the Indian Ocean Coastal Belt Biome and the temperate grasslands of the Grassland Biome (fig. 1). Vegetation units sampled from the former include the 'Maputaland Wooded Grassland' (MWG) and 'Kwa-Zulu-Natal Coastal Belt' (KCB) (Mucina & Rutherford 2006). In the case of the former, the name used by Mucina & Rutherford (2006) is incorrect, and from here onward the correct name as given in Matthews et al. (1999) will be used, namely 'Maputaland Woody Grassland'. Vegetation units of the Mesic Highveld Grassland Bioregion of the Grassland Biome were sampled, namely the 'Rand Highveld Grassland' (RHG) and 'Paulpietersburg Moist Grassland' (PMG) (Mucina & Rutherford 2006). For comparative purposes, the vegetation units were chosen to represent extreme climatic conditions from hot and humid to cold and dry (table 1).

Sampling, data collection and analysis

Eight plots were sampled in each of the four study sites in different vegetation units. Care was taken to place four plots 1 km apart in grassland areas in close proximity to what is

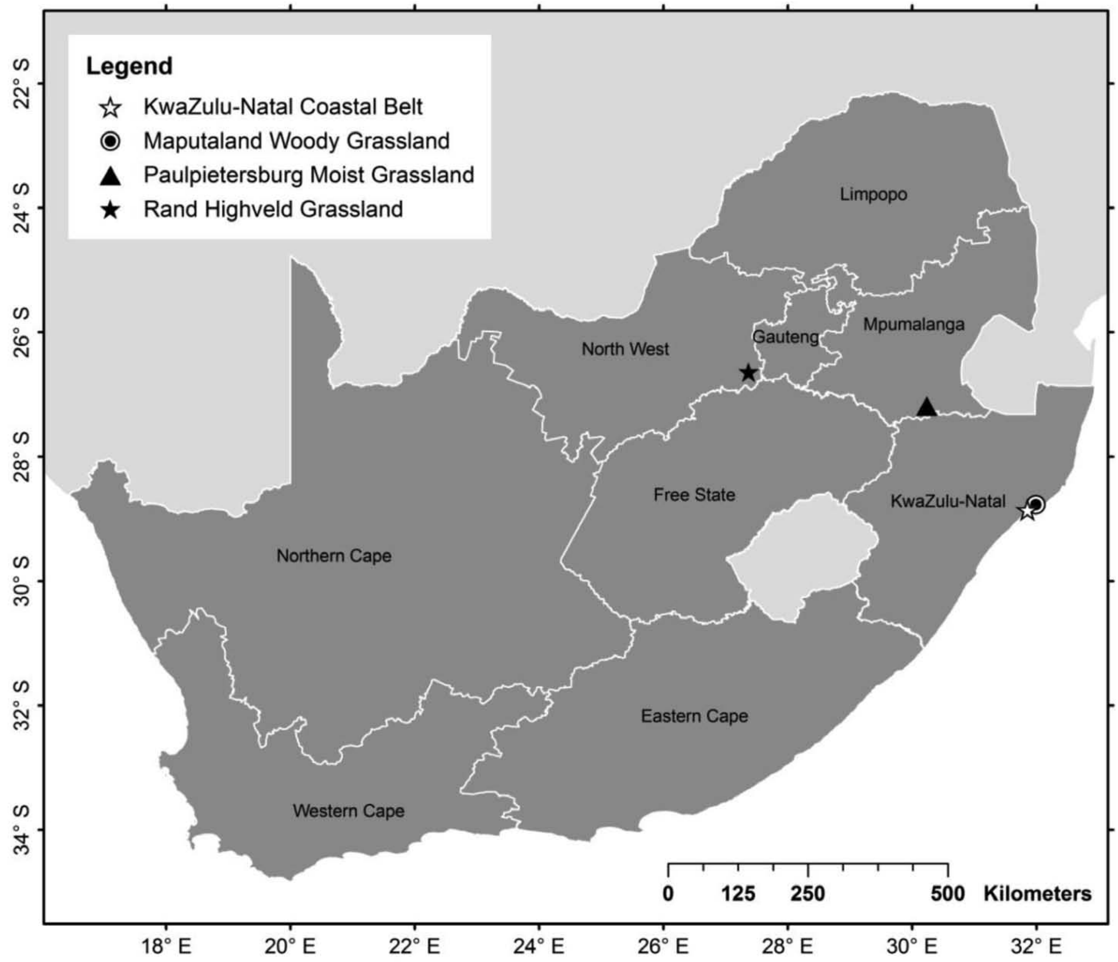

Figure 1 – Localities of the four study sites in South Africa and the associated vegetation units.

Table 1 – Climate details for the vegetation units in which the four study sites were located.

	Mean annual precipitation (mm)	Mean annual temperature (°C)	Mean frost days (< 0°C)	Mean annual soil moisture stress (%)
Maputaland Wooded Grassland	964	21.0	0	68
KwaZulu-Natal Coastal Belt	989	19.6	0	65
Paulpietersburg Moist Grassland	902	16.8	11	69
Rand Highveld Grassland	654	15.8	28	76

regarded as the most transformed areas within each of the study sites. Such transformed areas have undergone a land-use change which has changed the structure of the vegetation beyond the definition of South African grassland as described by Mucina & Rutherford (2006). A second set of four plots were then sampled within these transformed areas of each of the study sites. Each sample plot in grassland was therefore associated with a neighbouring plot in transformed grassland, not more than 150–200 m apart. In the case of MWG, transformed areas were defined as grassland invaded by alien invasive trees (e.g. *Melia azederach*) and shrubs (e.g. *Lantana camara*) for the past ± 25 years, and transformed grassland of KCB were *Eucalyptus grandis* plantations abandoned for ± 15 years. The transformed grasslands of the drier interior were defined as river banks invaded by *Acacia mearnsii* for ± 15 years in the case of PMG, and maize (*Zea mays*) fields cultivated for ± 20 years represented transformation in RHG. All plots were sampled on three occasions, namely in October, December and February, during the peak growing season. The surveys were repeated to ensure that minimal plant species were overlooked.

Plot size was fixed at 10 × 10 m (Eckhardt et al. 1996) for comparative purposes. At each sample point, the 100 m^2 plot was subdivided into 25 quadrants of 4 m^2 each for recording the species richness. Data from the 25 quadrants was then lumped to compile a complete floristic inventory for each plot. Species richness, the most direct measure of alpha diversity, was determined for each plot. However, species richness is an incomplete surrogate for alpha diversity as measures of species diversity are based on relative abundance and richness (Wilsey et al. 2005). Therefore, the number of individuals per species was counted in each quadrant (abundance) and lumped together per plot to calculate the Shannon-Wiener Diversity Index:

$$H = -\sum (p_i \ln p_i)$$

Low species abundance does not suggest low cover. As alien species invasions of native grassland takes place from the edge where the cover of such species is highest (Cilliers et al. 2008), it was important to record species cover. This was calculated per species as: C_{sp} = abundance × mean crown diameter at widest point.

Species were distinguished as native or either naturalised and/or invasive aliens. Plant species names follow Germishuizen et al. (2006) and naturalised and invasive categories are according to Bromilow (2001) and Henderson (2001). Voucher specimens are housed at the University of Zululand Herbarium (ZULU), Pretoria National Herbarium (PRE), KwaZulu-Natal Herbarium (NH) and AP Goossens Herbarium (PUC).

RESULTS AND DISCUSSION

The untransformed grasslands sampled for this study, of both tropical and temperate grasslands, had a mean plant species richness of 61 ± 6 species per 100 m^2. This is more than the previously regarded 26 (up to 48) plant species per 100 m^2 based on mean data provided by O'Connor & Bredenkamp (1997), 45 (up to 51) species per 100 m^2 for single-layered grassland (Mucina & Rutherford 2006) and even within the range of 55 to 95 species per 1000 m^2 recorded by Cowling et al. (1989) for grassland. However, the above authors based their estimates on grassland richness excluding alien num-

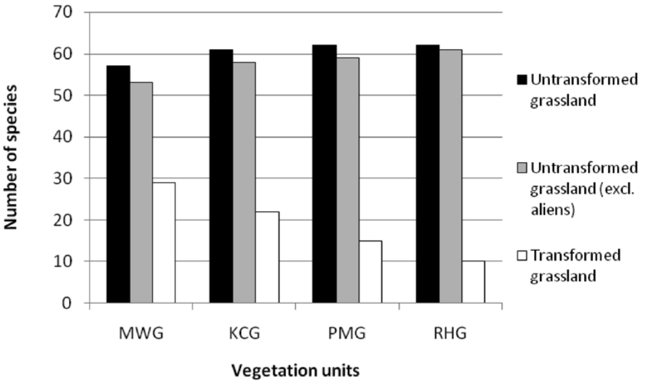

Figure 2 – Mean plant species richness per unit area (100 m^2) of untransformed and transformed grassland in each of the vegetation units. Tropical grassland: MWG, Maputaland Wooded Grassland; KCG, KwaZulu-Natal Coastal Belt; Temperate grassland: PMG, Paulpietersburg Moist Grassland; RHG, Rand Highveld Grassland.

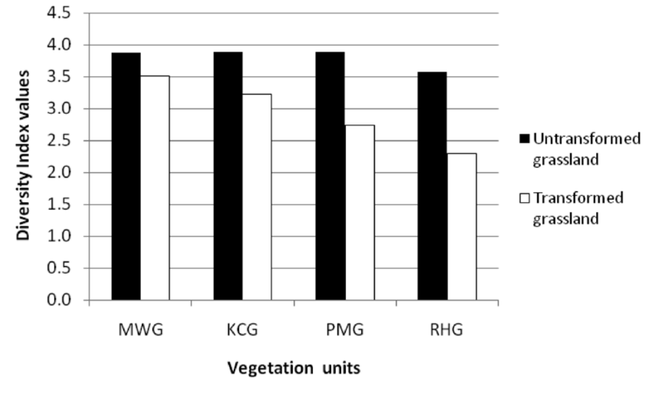

Figure 3 – Mean Shannon-Wiener Diversity Index values of untransformed and transformed grassland in each of the vegetation units. Tropical grassland: MWG, Maputaland Wooded Grassland; KCG, KwaZulu-Natal Coastal Belt; Temperate grassland: PMG, Paulpietersburg Moist Grassland; RHG, Rand Highveld Grassland.

Table 2 – Ten largest plant families of the combined study sites and the number of species per family for untransformed and transformed grassland.

Family	Number of species per family		
	Combined	Untransformed	Transformed
Asteraceae	88	69	37
Poaceae	73	56	36
Fabaceae	59	50	29
Apocynaceae	24	22	5
Cyperaceae	19	19	7
Convolvulaceae	13	9	5
Lamiaceae	11	10	4
Acanthaceae	11	10	3
Rubiaceae	10	7	4
Hyacinthaceae	9	9	2
Total	317	261	132

bers and with specific focus on temperate grasslands. When only vegetation units from the Mesic Highveld Grassland Bioregion are considered (excluding the tropical grasslands) and only native species are included in calculations, the plant species richness is 60 ± 6 species per 100 m^2. This result is substantially more than what was previously regarded as the norm for 100 m^2. These results also compare favourably with the findings of Siebert et al. (2002) that suggested the possibility of temperate grasslands to generally carry more than fifty species per 100 m^2. I speculate that the low estimates of grassland plant species richness is because the phytosociological studies that generated the species data for richness calculations are based on single site visits and are 'snapshots' of the flora which excludes dormant or non-flowering species. Phytosociological data from South Africa generally provide biased estimates of floristic data due to once off visits to sample plots. The multiple surveys of sample plots for this study provided opportunities to record species during the peak of their specific growing seasons which allowed for a more comprehensive floristic inventory.

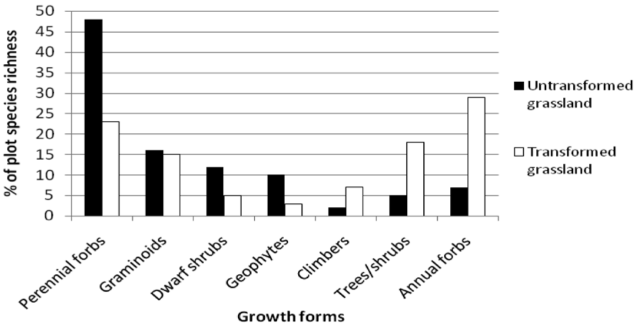

Figure 4 – Contribution that each growth form makes toward the mean species richness per plot for either untransformed or transformed grassland.

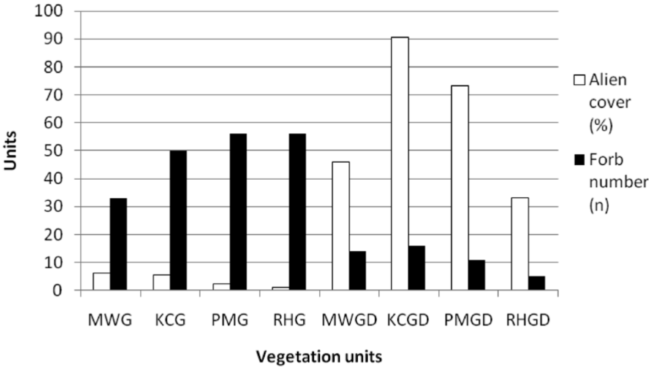

Figure 5 – Mean number of forb species and alien cover percentage per plot depicted separately for transformed and untransformed (acronyms ending with D) grassland of the different vegetation units.

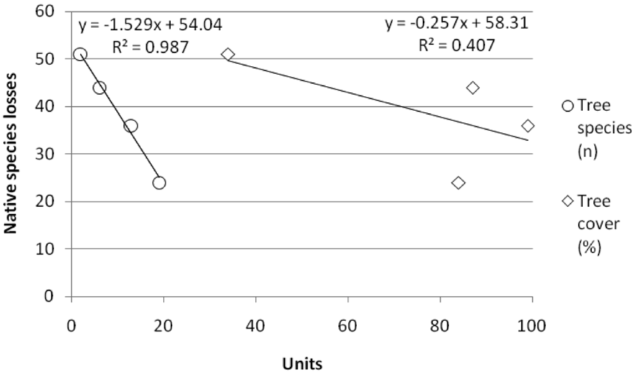

Figure 6 – Native species losses plotted against tree species richness and tree cover percentage for each of the four vegetation units. Native species losses = untransformed native species richness - transformed native species richness.

Transformed grasslands have lower species richness than untransformed grassland per unit area (fig. 2). The mean plant species richness for transformed grassland was 31 ± 8 with aliens included, and 19 ± 8 species per 100 m^2 without. When abundance is brought into the equation, the Shannon Wiener diversity index revealed a pattern of diversity corresponding with richness, with the index values of transformed sites being lower in all cases (fig. 3). Diversity indices also take the frequency (or abundance) of species into account, scoring lower for sites where species numbers are low and are dominated by a few species (with high abundance). Hence, when only transformed grassland is considered, then maize fields scored the lowest diversity value due to low species richness and dominance by a single species, whereas invaded grassland scored the highest. The latter usually consists of localised invasions, with patches of native species in-between, resulting in higher combined diversity. This suggests that the plot size of 100 m^2 is too large to evaluate the impact of alien invasions on native species richness in grassland as the patchiness of invasion is diluted by the numerous, interspersed non-invaded areas. Maize fields on the other hand, are exposed to added nitrogen and subsequent eutrophication, which has been shown to lead to losses in diversity and changes in plant species composition (Wedin & Tilman

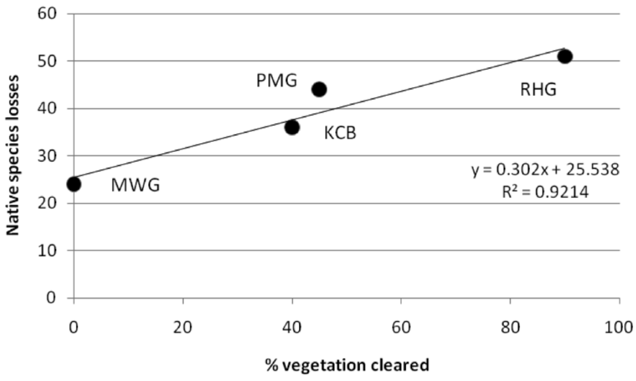

Figure 7 – Native species losses in transformed grassland plotted against a gradient of disturbance depicted here as the percentage of vegetation cleared at onset of disturbance. Onset vegetation loss was based on gross estimates obtained from the landowner.

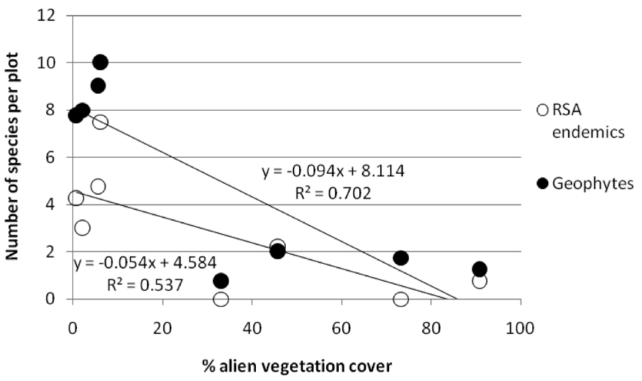

Figure 8 – Negative correlation between alien vegetation cover and the number of South African endemics and geophytes recorded from untransformed and transformed grassland in each of the vegetation units.

1996). This also makes the system vulnerable to invasions by alien species and inhibits natural succession.

Analysis of floristic data at family level suggested a loss of species from transformed grassland (table 2). This could be due to the profound effect that alien cover has on the richness of untransformed grasslands (Belcher & Scott 1989). Considering that each study site consisted of plots in untransformed and adjacent transformed grassland, comparisons could be made. Although grasslands, as the name indicates, is generally recognisable and distinguishable according to its grass assemblages (O'Connor et al. 2003, Siebert et al. 2004), the greatest variety lies with its associated forb species (Matthews et al. 1993, 1999). Forb species (excluding annual and grass species) are a good indicator of the health of the grassland ecosystem, as these species are specifically adapted to specific habitat types, and make up the bulk (> 45%) of the diversity in untransformed grasslands (fig. 4). 'Forbs' refer to perennial forbs, dwarf shrubs and geophytes. In contrast, annual forbs contribute the most to overall richness in transformed grassland (fig. 4). In the transformed grasslands sites there is the formation of new vegetation structures and the associated plant functional trait responses will be similar to what would be expected during normal grassland succession from grassland to forest (Kahmen & Poschlod 2004). This is already evident for the transformed grassland areas. When the alien cover was between 30 and 90%, the mean 'forb' richness was 5–15 species per 100 m^2 (fig. 5) compared to an alien cover of below 10% in untransformed grassland that is associated with a 'forb' richness of 30–55 species per 100 m^2 (fig. 5).

The shading effect of trees is known to decrease forb richness in grasslands of the northern hemisphere (Pykäla et al. 2005) and is known to aid the conversion of grassland communities to woodlands (Siemann & Rogers 2003). However, these trends were not conclusive for the study sites as is evident from regressions of native species losses against number of tree species and tree cover respectively (fig. 6). In both cases native species losses decrease as the cover and richness of tree species (mostly alien) increases. Invaded grassland therefore has the least losses of native species, despite its above average tree species richness and high alien cover. Obviously there is another factor at play, and in this case it is the hidden effect of comparing different disturbances (and processes) with one another. There could be many transformation effects, but it is probably the frequency whereby vegetation is cleared (e.g. annually for maize fields), the extent of vegetation clearance (fig. 7) and time since abandonment (Zhang & Dong 2010) that have a pronounced influence on variation of species richness and diversity. Native species losses in invaded grassland are a slower process as no initial clearing of vegetation takes place. However, invasion does lead to local shading and loss of species of which proof lies in the comparison of transformed and untransformed plot richness. The rate of species loss is slow and a result of habitat fragmentation. On the long run native species will be lost from the invaded habitat as fragmentation reduces colonization rates in species rich grasslands (Joshi et al. 2006). In all the transformed grasslands similar losses of key grassland species occurred, such as geophytes and South African endemics (fig. 8), suggesting that vegetation clearing and shading effects are equally severe in reducing the richness of species of conservation priority.

CONCLUSIONS

There is a definite pattern in the richness of untransformed and transformed grassland per unit area, irrespective of whether the grasslands of two different biomes were considered. In all cases the richness of untransformed grasslands was higher than that of transformed grasslands. Species richness of untransformed grasslands was also higher than previous estimates. Future studies will have to consider recording species richness for 1 m^2 to make data comparable with European studies.

The term 'pattern' refers to predictable variation in species richness. In this study this variation was quantifiable and measured against different levels of transformation. In all cases the density of alien species resulted in lower diversity for transformed grasslands. Cover percentage of alien species led to changes in the growth form composition and a decrease in the forb species richness of transformed grasslands. These findings were repeated across different transformations irrespective of the grassland type.

Although the results showed that species losses were not necessarily a result of increasing tree cover or tree richness, findings did, however, lead to a proposal that the type of transformation has a more immediate effect on species losses with the frequency and extent of clearing affecting the species pool much more severely. Transformations were of such an extent, that even the plant family composition of untransformed versus transformed grassland had changed.

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