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The value of urban and peri-urban conservation efforts within a global biodiversity hotspot

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Background: Systematic conservation planning (SCP) is a key tool in conservation prioritisation. It has recently been applied within the eThekwini Municipal Area (EMA), South Africa, a rapidly developing metro located within a biodiversity hotspot. Most vegetation types within this region are threatened, yet have received limited scientific attention.

Objectives: To assess forb biodiversity of coastal and near-coastal grasslands and contextualise potential drivers of species variation to the EMA context.

Method: We quantified forb species richness, frequency and species composition, determined the variation of these amongst plots and sites, and assessed which variables were responsible for this variation.

Results: Site forb species richness ranged from 33 to 84 species per site, with the most frequent species differing across the seven sites. Beta diversity was higher across than within sites. Distance to the closest traditional medicine market and site perimeter-to-area ratio were the greatest drivers of species richness, whilst altitude, aspect, mean temperature and rainfall seasonality were the main contributors to species composition patterns.

Conclusion: SCP can use key environmental and climatic categories to improve selection of grasslands to maximise both species richness and variation in species composition. A more fine-scale systematic conservation plan will, in turn, provide a more robust basis for development decisions. The outcomes illustrate the importance of urban and peri-urban conservation efforts, including fine-scale conservation planning, in contributing to regional, national conservation targets.

Introduction

Conservation planning and sustainable environmental management have limited resources for implementation owing to competition with other socio-economic imperatives (Heywood & Iriondo 2003; Shankaran 2009; Schneider et al. 2011). Prioritisation of areas for conservation, through systematic conservation planning (SCP), has become a key tool in conservation resource allocation (Heywood & Iriondo 2003; Margules & Pressey, 2000; Pressey, Cowling & Rouget 2003). These algorithm-based planning tools use available data on habitats, species and ecosystem services to select priority sites based on important criteria (Margules & Pressey 2000). However, SCP outputs are only as good as the input data (Heywood & Iriondo 2003; Margules & Pressey 2000; Smith, Goodman & Matthews 2006), and conservation plans are often based on limited data, which requires conservation planners to define different environmental features by using environmental breaks or changes (termed mesofilters; Crous, Samways & Pryke 2013). These 'surrogate' habitats are then assumed to be representative of a set of species known to occur within them (Crous et al. 2013; Smith et al. 2006). Incorrect selection of surrogates may result in inaccurate SCP that does not sufficiently represent reality, leading to potentially wasted resource expenditure on marginal areas (Crous et al. 2013) and inappropriate protection for the species that need it most (Coppolillo et al., 2004).

The eThekwini Municipal Area (EMA), which includes the metropolitan city of Durban, is located on the central-southern coastal region of KwaZulu-Natal (KZN) Province and includes 99 728 ha of the original extent of the KwaZulu-Natal Coastal Belt Biome (KZNCB; Mclean, Ground & Boon 2014; Rutherford *et al*. 2006). This municipality is a hub of development, and the remaining grassland vegetation within the municipality currently represents less than 25% of its historical extent (eThekwini Municipality SDF 2013; Mclean *et al*. 2014; O'Conner 2005; Scott-Shaw & Styles 2012; Uys, Bond & Everson 2004). The EMA has distinct variations in climatic conditions, with subtropical to temperate conditions at higher elevations (high rainfall seasonality, high temperature seasonality, lower mean temperatures) and subtropical to tropical conditions at lower elevations approaching sea level (lower rainfall seasonality, lower temperature seasonality, higher mean temperatures) owing to climatic regulation from the warm Mozambique ocean current (Rutherford *et al*. 2006). This variation has created a heterogeneous region that supports tropical, sub-tropical and temperate mist-belt species (Eeley, Lawes & Piper 1999; Rutherford *et al*. 2006).

The grassland ecosystems of KZN have, until recently, had fairly limited scientific attention (O'Conner 2005; Scott-Shaw & Styles 2012; Uys *et al.* 2004; Zaloumis & Bond 2011), which imposes the risk of poor selection and representation of critical biodiversity areas (Crous *et al.*, 2013). Graminoides make up the majority of the biomass of a grassland system and have historically been the main focus of scientific studies (Zaloumis & Bond 2011). Conversely, the non-graminoid herbaceous component (commonly termed forbs, which include geophytes) contributes most to overall grassland species richness (Uys *et al*. 2004; Zaloumis & Bond 2011).

The scale of transformation in the EMA is likely to have affected ecosystem integrity and associated functioning. Fragmentation will have led to the disruption of natural spatial disturbance patterns, particularly fire and grazing, critical for the maintenance of the successional state of grasslands (Boakye *et al*. 2013; Snyman 2006; Uys *et al*. 2004). Management (including block burning, grazing regulation, alien plant clearing) is currently the primary method for ensuring simulation of natural disturbance. It is in these managed grasslands where one would expect to find higher species richness and a more representative species composition (comparative to unmanaged grassland; Uys *et al*. 2004; Van Wilgen *et al.* 2014). The discrepancy between species assemblages within and outside managed areas adds an additional anthropogenic-derived level of heterogeneity to an already complex ecosystem (Uys *et al*. 2004).

Understanding the primary drivers of species heterogeneity within a grassland ecosystem is critical in ensuring the development of both adequate and accurate conservation targets, and associated conservation site selection (Crous *et al*. 2013; Pressey *et al*. 2003; Uys, Hamer & Slotow 2009). Scale is an important factor when investigating the mechanisms explaining species or ecosystem heterogeneity, as various factors have differing levels of influence at different scales (Gonzalez-Megias, Gomez & Sanchez-Pinero 2007; Huston, 1999). What may affect a particular site or area may not be as significant at a regional scale; similarly, a locally dominant species may be rare regionally, or a species recorded throughout a region may be sporadic in its local distribution (Gonzalez-Megias *et al*. 2007; Honnay & Hermy 2004; Hanski, 1994). These distributional differences may be caused by site-specific anthropogenic disturbances, or might be explained by environmental heterogeneity. Knowing the drivers of plant species abundance (including rarity) will significantly improve SCP output accuracy (Crous *et al*. 2013).

The coastal and near-coastal grasslands of the EMA are predominantly included in the Durban Metropole Grassland vegetation type (KZN2), Northern Coastal Grassland (KZN16), Ngongoni Veld (SVs4), or KZN Sandstone Sourveld (SVs5; Rutherford *et al*. 2006). These grasslands are nationally recognised as either vulnerable (SVs4), endangered (SVs5, KZN16) or critically endangered (KZN2), respectively (Rutherford *et al*. 2006). The percentage of these grassland types that are formally conserved, ranges between 1% and 4% (Rutherford *et al*. 2006), and the total remaining area of coastal and coastal-hinterland grassland within the EMA is 13 534 ha, which is only 12% of the pre-1850 distribution (Mclean *et al*. 2014). These grassland ecosystems are, therefore, under significant threat and require urgent scientific attention to optimise their conservation planning and management within the EMA spatial development plan (Rutherford *et al*. 2006; Uys *et al*. 2009).

The present study therefore attempts to improve the understanding of coastal and near-coastal grasslands within the central region of KZN, with a particular focus on key anthropogenic and environmental factors influencing species richness, species composition, species frequency, and species turnover (or beta diversity). For this purpose, we sampled sites situated in or near to the urban/peri-urban matrix of the EMA region of KZN, which contained primary coastal and near-coastal grassland. The main objectives of the study were: (1) to quantify the species richness and identify the level of variation in forb species composition at plot, site and regional scales of central KZN coastal grasslands; (2) to determine which disturbance, or biogeographic or environmental factors, may be responsible for any observed variation in forb species richness and composition; and (3) to understand the spatial distribution and frequency of occurrence of species at different spatial scales.

Methods

Study sites and sampling

After initial site inspections, seven sites (four formal municipal reserves, two formal provincial nature reserves, and one municipal managed site) were sampled within the coastal region of KZN (Table 1 and Figure 1). Six of the seven sites were located within the eThekwini Municipality (EM) while Vernon Crookes, considered a characteristic site for primary central KZN grassland in good condition, is located approximately 60 km south of the EM's southern boundary, within a peri-urban setting, similar to that of outlying areas of the EM (Figure 1; Rutherford *et al*. 2006).

A total of 36 plots were sampled across the seven sites (Table 1). At each site, a number of 10 m x 10 m plots were set out using tape measures and marker pegs. Species accumulation curves were used to determine required sampling effort (Willott 2001). Sampling was undertaken between October and March to ensure that seasonal forbs would be conspicuous. The positioning of plots within each site was done in a manner which covered as many grassland

TABLE 1: Description of the managing agent, altitude, surrounding land uses, geology, location, condition, management period, size, number of plots, species richness, plot richness range and mean plot richness, of the sampled sites.

Site	Managing agent	Mean altitude (m.a.s.l.)	Surrounding land uses	Underlying geology	GPS location (degrees)	Perceived condition (degraded 1–5 pristine)†	Management period‡	Open space (ha)	Number of 10 x 10 m sample plots	Forb species richness	Plot forb richness range	Mean plot richness (95% CI)
Giba Gorge environmental precinct (Giba East)	eThekwini Municipality	574	High-income residential, national freeway	Natal Group Sandstone	-29.80012972 30.76674694	4	Short	323	6	54	13–28	19.0 (±6.40)
New Germany	eThekwini Municipality	347	Middle-income residential	Natal Group Sandstone	-29.80022389 30.88358028	4	Long	106.6	6	67	20–28	24.0 (±3.70)
Sherwood	eThekwini Municipality	143	Middle – low-income residential, national freeway	Natal Group Sandstone	-29.83347111 30.95011417	2	None	17.0	4	50	22–28	25.0 (±5.51)
Silverglen	eThekwini Municipality	157	Lower middle-income residential	Natal Group Sandstone	-29.91694361 30.86667833	4	Long	458	7	65	22–29	24.6 (±2.44)
Stainbank	eKZN Wildlife	113	Middle-income residential	Natal Group Sandstone	-29.90026583 30.93337778	3	Long	211	5	55	17–25	21.0 (±4.39)
Treasure Beach	eThekwini Municipality	87	Middle-income residential	Berea Formation	-29.93355306 30.98346111	3	Short	17.8	4	33	14–19	16.8 (±3.53)
Vernon Crookes	eKZN Wildlife	425	Dense rural residential	Natal Group Sandstone	-30.26670556 30.60019972	5	Long	2189	4	84	30–52	36.5 (±16.56)

†, 1 – severely degraded, 2 – moderately degraded, 3 – intermediate, 4 – good, 5 – pristine. Perceived condition was obtained from the local and provincial systematic conservation plans, and was based on desktop assessments of condition indicators including basal coverage, erosion, and alien plant infestation.

‡, Long – > 10 years continuous management, Short > 5 years continuous management, None – no or sporadic management only.

patches as possible. Ten 1 m x 1 m subplots (quadrats) were then randomly sampled within the plot. Forb species presence-absence was recorded for each subplot. Species identifications were confirmed using local field guides (Jeppe 1975; Pooley 2005), local experts, and the KZN Herbarium. Photographic vouchers were taken for each unique species found at each site for offsite identification and record keeping.

Using ArcGIS v.10.1 (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute), sampling sites were digitised. Environmental, climatic and disturbance variables for each of the 36 plots were extracted. Altitude was extracted from EM's 2 m contour shapefile (Survey and Land Information Department, eThekwini Municipality). Aspect was extracted from the EM's 10 m digital elevation model raster dataset (Corporate GIS Department, eThekwini Municipality). Mean rainfall, mean temperature, rainfall seasonality, and temperature seasonality were extracted from the WorldClim (Hijmans *et al*. 2005) raster dataset. The size of the contiguous grassland patch in which a plot was located and the size of the total natural open spaces (total natural area, regardless of the relative composition of vegetation types) were digitised using EM's 2012 high-resolution aerial imagery (Survey and Land Information Department, eThekwini Municipality 2012) as reference. The areas of these shape files were then calculated in ArcGIS v. 10.1 using the 'calculate field' option in the shape file attribute table section. The reserve perimeter/area ratio was calculated initially by utilising the 'calculate field' option to determine the boundary perimeter of each reserve, and then by completing a ratio calculation with the area of each reserve. Distance to the nearest anthropogenic structure (e.g. house, factory, road) and distance to the closest major traditional medicinal market, in this case the Durban City Centre Victoria Market (-29.856689°S, 31.015287°E), was measured using the 'distance tool' in the ArcGIS v.10.1 and EM's 2012 high-resolution aerial imagery as a reference (Hartebeesthoek94 co-ordinate system).

Data analysis

Species frequency

The frequency of each species was calculated across all seven sites, based on their presence in the subplots. Species were ranked according to their frequencies within each site to understand the general trends of species distribution patterns within and across sites. In order to determine the most frequent species at a site scale, a one-way similarity percentages species contributions (SIMPER) analysis was performed in PRIMER v.6 (Clarke & Gorley 2006) to describe the most frequent species, as a percentage of the frequency of occurrence within each plot of a site. Species frequencies of occurrence were examined at local and regional scales to determine distribution patterns. 'Regional distribution' assesses the distribution of species across the different sites in the study (widespread = present in ≥6 sites; restricted = present in >1 and ≤4 sites; highly restricted = present in only 1 site). 'Local distribution' assesses the distribution of species within the sites by measuring the subplots in which they were present (widespread = present in ≥40 subplots; restricted = present in ≤10 subplots).

Beta diversity

Shared and unique species between combinations of plots and subplots were calculated using EstimateS (Colwell 2013). Beta diversity was assessed based on the framework proposed by Carvalho, Cardoso & Gomes (2012); where B_{cc} (value range 0–1) reflects overall beta diversity and comprises components of species turnover (β_{-3}, replacement of species between sites) and species richness differences (β_{rich}, difference in species

FIGURE 1: Map illustrating the location of the different sites sampled in relation to major roads and the eThekwini Municipality boundary.

richness between sites; Carvalho *et al*. 2012). A Kruskal-Wallis H-test was performed in SPSS (SPSS Inc., 2011) to determine if the mean of beta diversity measures within a site was significantly different from beta diversity across sites. The β_{rich} and β_{-3} values were standardised and compared in a Mann-Whitney test to determine which of these made a greater contribution to B_{cc} (Gutt & Piepenburg 2003).

Nestedness of the plots was assessed using a nestedness metric based on overlap and decreasing fill (NODF) run in ANINHADO (Guimarães & Guimarães 2006). In comparison with the nestedness temperature metric (which until recently had been the most popular nestedness metric used), the former metric is not sensitive to matrix shape and size, and therefore has a low probability for type I and type II error (Almeida-Neto *et al*. 2008). The maximum level of nestedness is obtained when a matrix has a complete overlap of presence across columns and rows, and decreasing totals between paired rows and columns. The value range of NODF is 0–100, where 100 is a completely nested system. Most observed matrices are known to have a degree of nestedness between 40 and 70 (Almeida-Neto *et al*. 2008). Observed nestedness values were then compared with expected nestedness values obtained from Er (the occurrence of a connection is attributed to a random cell in the matrix) and Ce (the varied placement of a connection in a cell based on the relationship between the number of ones, denoting the presence of a species, in a particular row and column in the observed matrix) models (Jędrzejewska-Szmek & Zych 2013).

Environmental variables

Univariate and multivariate analyses of environmental factor effects were performed in Primer v.6 (Clarke & Gorley 2006). Based on the presence and absence of species, a Bray-Curtis resemblance matrix (dataset standardised) was generated, and cluster and multi-dimensional scaling (MDS) analyses were performed in PRIMER. A principle component analysis (PCA) was performed on the continuous environmental variables, to identify the key variables contributing most to the variability in the species composition dataset (Ringner 2008). PC1 contributed 64.1% and PC2 24.0% to the observed variation. Variables that displayed eigenvalues (an indicator of significance of the corresponding component) >0.4 (the value at which a break was observed in the scree plot) were selected from PC1 and PC2 for further analysis (Johnstone 2001). The relationship between the distances between sites and site species composition similarity was investigated using the RELATE function within PRIMER (Clarke 1993). RELATE examines the correlation between the distance dataset and the species composition Bray-Curtis similarity index, and provides a coefficient and significance value as an output (Clarke & Gorley 2006).

The determination of significant difference between variability in species composition of each of the levels within each factor was tested using one-way PERMANOVA tests for each factor (Clarke 1993). Unfortunately, owing to limited degrees of freedom, multi-factor PERMANOVA could not be performed to determine the contribution of multiple variables and their interactions. A principal coordinate analysis (PCO) was employed to investigate patterns of correlations between environmental distances and species composition. BIOENV was used in PRIMER to determine the best combination of environmental variables that correlated with the Bray-Curtis species composition similarity matrix. BIOENV examines patterns within an environmental factor matrix and a species composition resemblance matrix, and explores all the possible combinations of factors to determine what combination of which factors best correlates with the species resemblance pattern, and gives a coefficient value related to this (Clarke 1993).

The Bayesian information criterion (BIC) was used to identify the combinations of environmental variables that best explain species richness variation, identifiable by comparatively low BIC values (Schwarz 1978). The variables within this model were then included in a regression (Schwarz 1978). A normality test (Shapiro-Wilk's test, Shapiro & Wilk 1965) was performed, after which a regression commonality analysis (RCA) was used to identify each variable's unique (the amount of variance accounted for by a single variable) and common variance (the amount of variance attributed to a set of variables). One key aspect of RCA is its ability to also identify specific suppressor variables (Ray-Mukherjee *et al*. 2014). Suppressor variables are variables that suppress irrelevant variance (variance not shared with the dependent variable) and improve the predictive capabilities of other key variables (Ray-Mukherjee *et al*. 2014).

Results

Species richness and frequency

A total of 192 native forb plant species was recorded across the seven sites. At a plot scale, forb species richness ranged from 14–52. Mean plot richness across all sites was 23.5 (± 2.4, 95% confidence interval (CI)). At a site scale, Vernon Crookes had the highest total forb species richness with 84 species, and Sherwood the lowest with 33 species (Table 1).

For the most part, plots within the same site clustered together in terms of forb community assemblages (Figure 2). The exceptions to this were in Giba East, where two plots clustered separately from the other four, in New Germany where two sets of three plots clustered separately, and in Stainbank where two plots clustered separately from the other three. Interestingly, four Giba East and three New Germany plots clustered together as a separate group, and the other two Giba East and three New Germany plots clustered together as a group with Vernon Crookes (Figure 2a and 2b). The Stainbank plots clustered either with Silverglen or Sherwood. The similarity amongst plots from different sites was relatively low (<35%), given the close proximity of sites. The three groupings which split plots within the same site were, in the case of Giba East, two sets of plots located above and below a scarp at two different elevations and, in the case of New Germany and Stainbank, two sets of

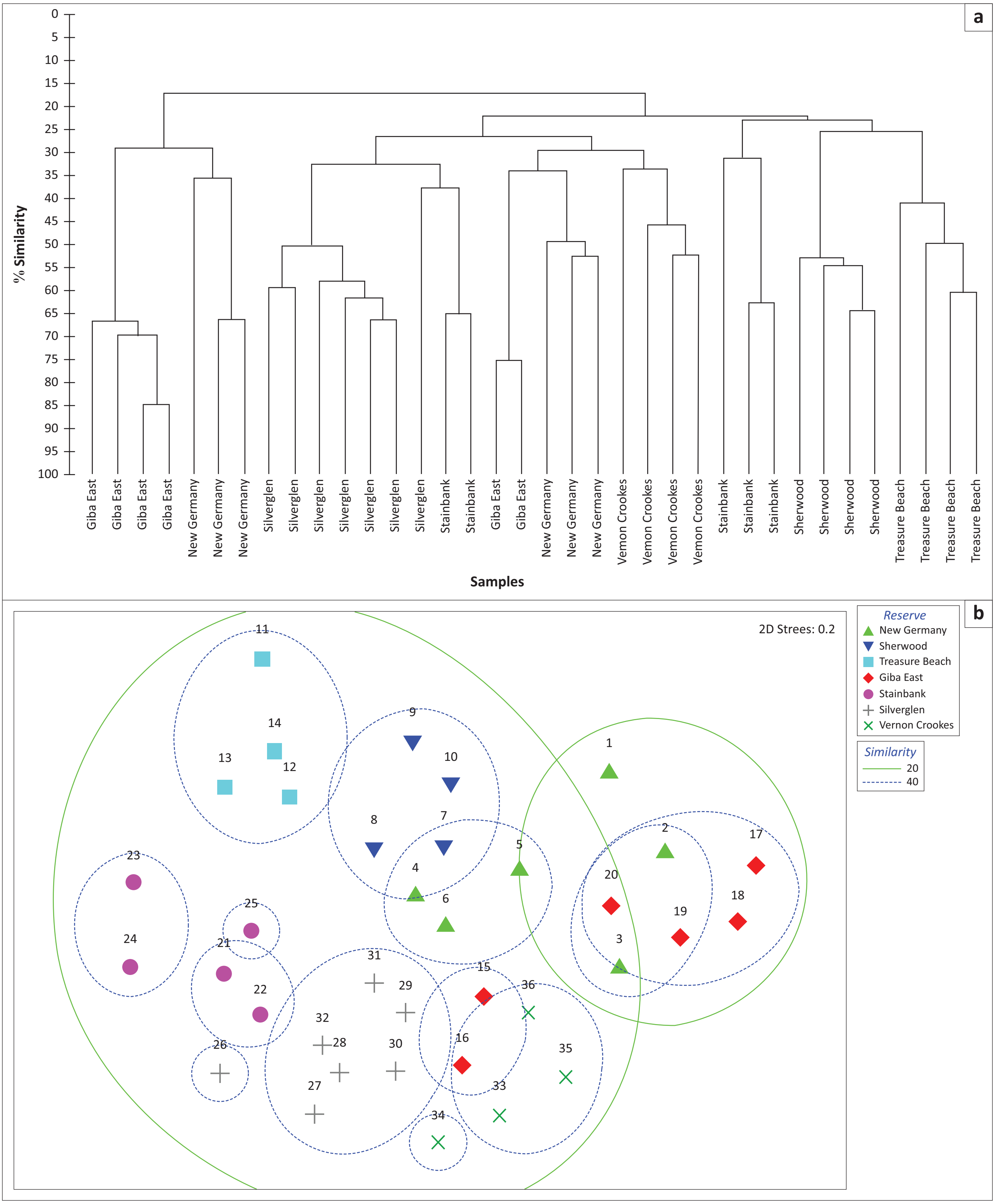

FIGURE 2: (a) Cluster dendogram and (b) MDS plot of the similarity of plots within sites illustrating that the majority of plots clustered with those within the same site.

plots located on different slope aspects. This observation reinforces the findings of the analysis of similarities (ANOSIM) and best subset of environmental variables with maximum correlation with community dissimilarities (BIOENV) analyses, which indicated aspect and elevation as important drivers in observed forb species composition variation.

Frequency data for plots within each site showed a consistent inverse proportional or hollow curve profile (Figure 3) which indicates that the majority of forb species present within a site have average to low frequencies of occurrence, with a limited number of very common species (McGill *et al*. 2007). The species recorded as common varied between sites. Frequency of occurrence of forb species within the local landscape varied amongst sites (Figure 3), with those which have been under protection for longer (Table 1) displaying a gentler slope with longer tails, suggesting a greater number of rare forb species (lower in frequency) and fewer high frequency species. The slopes for Giba East and Sherwood were comparatively steeper with shorter tails, indicating a comparative lack of rare forb species and dominance of a few, common species (although with only three shared species in the top ten most common species in each site).

The majority of forb species were categorised as either 'restricted in regional distribution' or 'restricted in local distribution' (39 species) or as 'very restricted in regional distribution and restricted in local distribution' (63 species). Only two species, *Tephrosia macropoda (E. Mey.) Harv. var. macropoda* (Fabaceae) and *Senecio glaberrimus DC.* (Asteraceae), were widespread at both the regional and local scale. Eight species were considered locally common but restricted in their regional distribution.

Beta diversity

The means of all three forb beta diversity index values were significantly higher amongst sites than within sites (Table 2). B_{-3} had a significantly larger mean rank and sum of ranks than B_{rich} (654 and 41 1821, compared with 607 and 382 609 respectively; Mann-Whitney U-test: $p < 0.05$), i.e., B_{-3} was a larger contributor to B_{cc}. This suggests that forb species turnover, or changes in forb species compositions across sites, is a more important factor in driving beta diversity amongst these grasslands than species richness differences across sites.

The NODF value of the nestedness of plots was 27.90, which indicates a medium-to-low level of plot nestedness. Observed nestedness was, however, not randomly distributed and the null model nestedness value of 19.36 was significantly lower than the expected nestedness ($p < 0.05$ for both the Er and Ce models). The observed nestedness of the pooled site species compositions can therefore be attributed to ecological processes. The NODF value of the nestedness of plots was 40.34, indicating a higher level of nestedness amongst the sites. This value was statistically significant for the Er model ($p < 0.05$), but not significant for the Ce model ($p = 0.34$), suggesting that the nestedness may be randomly derived (Jędrzejewska-Szmek & Zych 2013).

Drivers of species composition and species richness

Three principle components contributed 92.6% of the forb species' composition variability (PC1 = 57.0%, PC2 = 24.3%, PC3 = 11.3%). All environmental variables were included within these three components, and all had eigenvalues higher than 0.4 (threshold for consideration as an important contributor) in at least one principle component (Ringner 2008). Hence, all the continuous environmental variables were used for further analysis.

Forb species composition differed significantly with altitude, mean temperature, mean rainfall, temperature seasonality, rainfall seasonality, reserve size, contiguous grassland

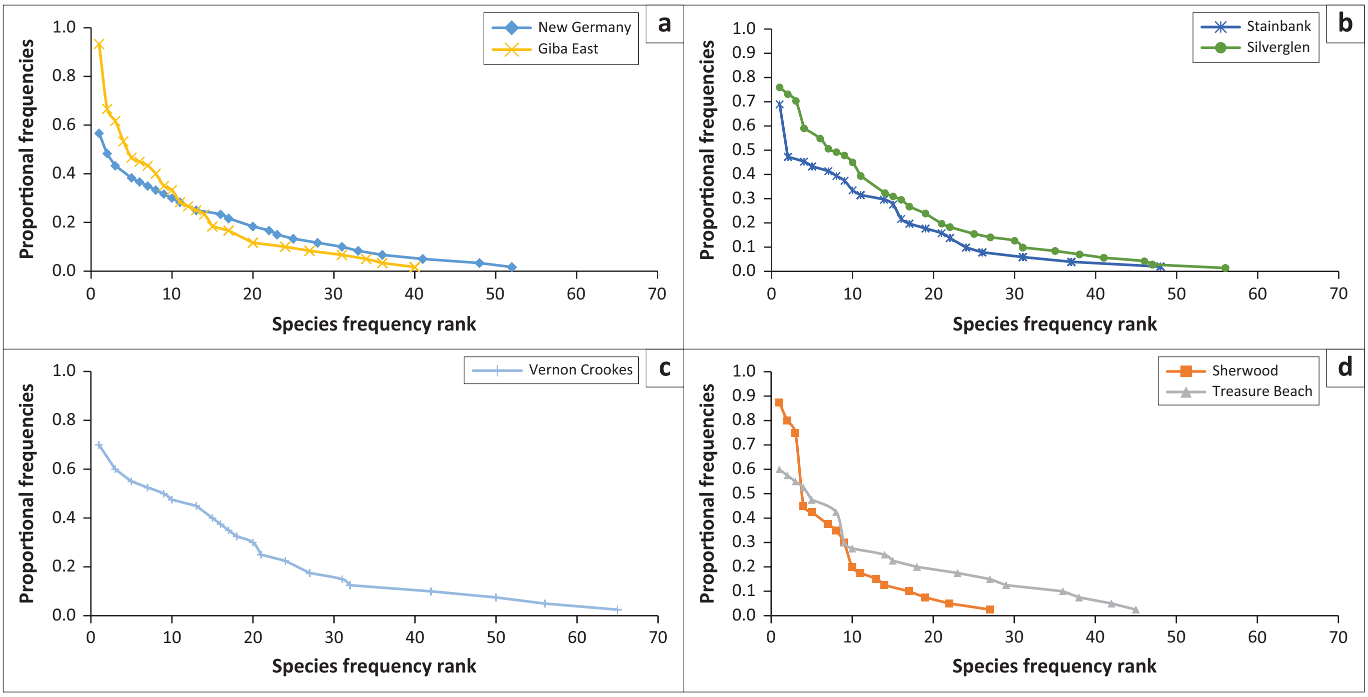

FIGURE 3: Proportional frequency rank curves illustrating the different profiles of ranked species proportional frequency for each of the sites sampled. The Vernon Crookes profile is considered the closest to a pristine state. Sherwood and Giba East have a higher proportion of common species with high frequencies. Axis ranges are consistent to allow ease of comparison.

TABLE 2: Assessment of beta diversity across and within sites. Kruskal-Wallis H-test significance values for within site versus between site B_{cc} (overall beta diversity), B_{-3} (replacement of species between sites), and B_{rich} (difference in species richness between sites) value comparisons.

Index	Comparison	Mean (std error)	Range	*p*
B_{cc}	Between	0.874 (±0.0024)	0.594–1.000	<0.001
	Within	0.702 (±0.0164)	0.263–0.925	
B_{-3}	Between	0.349 (±0.0029)	0.133–0.500	<0.001
	Within	0.286 (±0.0082)	0.053–0.439	
B_{rich}	Between	0.175 (±0.0054)	0–0.650	0.010
	Within	0.130 (±0.0106)	0–0.395	

Note that the between site mean value was significantly higher than the within site mean value for all indices.

TABLE 3A: The effect of environmental and anthropogenic variables on species composition variation between plots. One-way PERMANOVA output F scores, and *P* values for environmental and anthropogenic factors.

Environmental factor	F score	*p*
Altitude (2)	3.6503	0.001
Aspect (1)	1.7724	0.001
Boundary length-area ratio	4.3322	0.001
Distance to city centre	4.0098	0.001
Grassland size	3.7211	0.001
Mean rainfall	2.2723	0.009
Mean temperature(8)	2.7696	0.001
Rainfall seasonality (11)	4.8588	0.001
Reserve size	5.2394	0.001
Temperature seasonality	3.346	0.001

TABLE 3B: The effect of environmental and anthropogenic variables on species composition variation between plots .The top 10 best combination of variables (numbers as per Table 3a) which correlate with the species composition resemblance matrix and which indicate the best relationship between environmental change and species composition variaition.

Combination	Correlation coefficient
2, 8, 11	0.500
8, 11	0.496
11	0.495
2, 11	0.494
1, 2, 8, 11	0.477
1, 2, 11	0.474
1, 8, 11	0.471
1, 11	0.467
2, 8	0.451
2	0.429

patch size, distance to settlement, distance to the traditional medicine market, and reserve perimeter to area ratio (Table 3a). Combinations of altitude, aspect, mean temperature and rainfall seasonality had the highest correlations with the species Bray-Curtis similarity matrix (Table 3b). No significant correlation was found between distances between sites and their similarities (rho 0.027, $p > 0.05$).

Grassland size, distance to traditional medicine market, perimeter to area ratio, temperature seasonality, and rainfall seasonality together explained 70.67% of variation in species richness (regression commonality analysis: $p < 0.0001$). In terms of the variables' unique contribution (UC), grassland size, distance to traditional medicine market, perimeter to area ratio, and rainfall seasonality contributed significantly to the variation in the model, whilst temperature seasonality contributed marginally (Table 4) to the regression model. Grassland size was, however, reflected as a suppressor variable, mainly because it had a high negative commonality coefficient (-0.1626), cancelling out its unique contribution (0.1730), and resulting in a negligent total contribution (0.0104) to the model. Removal of grassland size from the regression lowered the R^2 value, a further indication of a suppressor variable, as grassland size improved the predictive capabilities of other variables. Distance to traditional medicine market (total correlation (TC) 0.1967) and perimeter to area ratio (TC 0.0671) were the two variables with greatest total contribution to the variation in species richness model (Table 4).

Discussion

The EMA's coastal and near-coastal grasslands had a high number of forb species when compared with similar South African grassland studies. Between 30 and 44 forb taxa per plot were recorded within 1000 m^2 Whittaker plots in natural dolerite and sandstone grasslands of the Drakensberg, KZN (O'Conner 2005), and 8 – 30 graminoid and forb taxa per 16 m^2 plots in urban Bloemfontein, Karoo-Supergroup underlain grasslands (Dingaan & Dupreez 2013). Closer to the central KZN region, 118 taxa were recorded from 27 (100 m^2) mesic grassland plots within the rural midlands of KZN (840 metres above sea level (m.a.s.l.); Uys *et al*. 2004). Whilst the level of species richness we recorded is expected at a coastal and near-coastal region, it is high, given the location of our sites within an urban and peri-urban landscape (Dingaan & Dupreez 2013; Knight, Crowe & Siegfried 1982; *et al*. 2004). This finding, combined with the absence of disturbance as a factor influencing species composition, highlights the ongoing conservation value of these threatened grasslands within this global biodiversity hotspot (Maurer, Durka & Stocklin 2003; Steenkamp *et al*. 2004).

The high beta diversity and nestedness observed, both within and across sites, is in accord with other KZN grasslands studies, which showed significant correlation between environmental and climatic mesofilter types and species composition and richness variation (Crous *et al*. 2013; Uys *et al*., 2004; Pausas & Austin, 2001). That plots within a site were more similar to plots in other sites, and that there was a biological basis to this pattern, is an important result which indicates that grassland patches within close proximity are not necessarily the same, and that stratified conservation planning, which incorporates quantified determinants of species variation, and uses the boundaries or thresholds of these determinants for defining subtypes, is needed to ensure adequate species variation selection (mesofilter determination; Crous *et al*. 2013; Laliberte et al., 2009 Gabriel et al., 2006; Coppolillo et al., 2004).

TABLE 4: An indication of the different contributions of key variables, selected by the Bayesian information criterion, to the variation in species richness across plots.

Variable	β†	UC‡	CC§	TC¶
Grassland size***	-4.136	0.1730	-0.1626	0.0104
Distance to medicinal market***	7.338	0.5445	-0.3478	0.1967
Boundary length-area ratio**	2.795	0.0790	-0.0119	0.0671
Temperature Seasonality*	-1.862	0.0351	-0.0261	0.0090
Rainfall seasonality***	-5.270	0.2809	-0.2497	0.0312

Significance codes: 0 < ***; 0.001 < **; 0.05 < *.

†, beta coefficient (β) – an indication of the importance of a particular variable.

‡, unique coefficient (UC) – how much variance is unique to an observed variable.

§, common coefficient (CC) – how much variance is common in groups of variables.

¶, total coefficient (TC) – sum of the unique and common effects, giving total variance.

The species frequency curves, however, suggest that these grassland systems are not entirely unaffected by urbanisation-associated impacts. The observed higher number of dominant species, and the relatively higher frequencies of those dominant species in Giba East and Sherwood (both subjected to sporadic management or periods of no management), may be an outcome of modified disturbance and patch size patterns resulting in the diminishing competitiveness of certain species, as well as the entire exclusion of other species from the grassland (as shown by the significant influence of disturbance and size factors on total species richness; O'Conner & Hurt, 2009). These patterns are consistent with observations made in other grassland disturbance response studies (Menge & Sutherland 1987; Pooley *et al*. 2005; Zaloumis & Bond 2011).

Reserve managers should therefore strive to create an environment where natural disturbance is maintained at historical levels, and anthropogenic disturbance is excluded as far as possible, to ensure maintenance and improvement of species diversity within these grasslands (Connell 1978; Roberts & Gilliam 1995; Tilman & Lehman 2001). The size of a contiguous grassland patch, its distance to the traditional medicine market, and the shape of the grassland patch, were the biggest drivers of species richness variation. Special management attention should therefore be given to (1) the maintenance and expansion of grassland patch size, and the reduction of perimeter-to-area ratios by controlling bush encroachment and restoring appropriate adjacent areas to grassland; and (2) managing public access to and activities within grassland sites (O'Conner 2005; O'Conner & Hurt 2009; Scott-Shaw & Morris 2014; Zaloumis & Bond 2011). Considering the limitations of plant seed dispersal, reintroduction of key species, based on local ecological requirements, would assist in species richness improvement (Soons & Heil 2002; Soons *et al*. 2005).

The outcomes of the present study highlight the often underappreciated importance of conservation efforts in urban and peri-urban landscapes. Considering that global biodiversity hotspots often have above average population densities, urban and peri-urban conservation, through protection of relatively small (when compared with traditional 'game reserves' such as Kruger National Park and Hluhluwe Imfolozi Park) high biodiversity areas cannot be ignored in the pursuit of global conservation goals (Miller & Hobbs 2002). Broad-scale systematic conservation plans cannot be solely relied on, and urban and peri-urban systematic conservation plans will need to be developed with a focus on finer-scale, local-level variances in ecosystem types (Knight *et al*. 2006). Urban and peri-urban systematic conservation plans should consider variables such as aspect, altitude, and climate as potential indicators of fine-scale variation in ecosystem types (Crous *et al*. 2013). These fine-scale variations will, in turn, provide a more robust basis for development decisions (Crous *et al*. 2013). Without these efforts, urban biodiversity hotspots are likely to suffer continued degradation and associated species losses (Malcolm *et al*. 2005).

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Competing interest

The authors declare that they have no financial or personal relationships which may have inappropriately influenced them in writing this article.

Authors' contributions

L.G. was the principal author, conceptualised key aspects of the paper, and undertook field work, data analysis, discussion formulation, and the write-up. R.S. undertook the discussion formulation, conceptual thinking around the paper focus, and participated in the transcript review. J.M. undertook data analysis and participated in the transcript review.

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