Do arthropod assemblages fit the grassland and savanna biomes of South Africa?

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The long-standing tradition of classifying South Africa's biogeographical area into biomes is commonly linked to vegetation structure and climate. Because arthropod communities are often governed by both these factors, it can be expected that arthropod communities would fit the biomes. To test this hypothesis, we considered how well arthropod species assemblages fit South Africa's grassy biomes. Arthropod assemblages were sampled from six localities across the grassland and savanna biomes by means of suction sampling, to determine whether the two biomes have distinctive arthropod assemblages. Arthropod samples of these biomes clustered separately in multidimensional scaling analyses. Within biomes, arthropod assemblages were more distinctive for savanna localities than grassland. Arthropod samples of the two biomes clustered together when trophic groups were considered separately, suggesting some similarity in functional assemblages. Dissimilarity was greatest between biomes for phytophagous and predacious trophic groups, with most pronounced differentiation between biomes at sub-escarpment localities. Our results indicate that different arthropod assemblages do fit the grassy biomes to some extent, but the pattern is not as clear as it is for plant species.

Significance:

- Provides the first comparison of arthropod composition between grassland and savanna biomes of South Africa.
- Explores whether these two biomes show distinct arthropod assemblages.
- Documents the characteristics of arthropod assemblages.
- Confirms that plant assemblages of biomes are more distinguishable than arthropod assemblages.

Introduction

South Africa's rich biodiversity is largely the result of a wide range of climatic conditions and topographic variation, which give rise to relatively distinctive biomes, each with characteristic plant and animal species.[1,2] Vegetation categorisation in South Africa is nested within these biome concepts.[2] Insects are particularly relevant in biome comparisons as a large proportion of insects may be host-specific phytophagous species,[3] which is likely to make them vegetation-specific because of the intricate relationships. European studies have shown that local plant species composition is the most effective predictor of arthropod assemblage composition, even more so than vegetation structure and environmental conditions.[4] Furthermore, arthropod groups have been shown to be associated with particular plant assemblages in grassland, with certain insect orders responding positively to the increase in specific plant functional groups.[5]

Being ectotherms, arthropods are sensitive to their abiotic environments. The vegetation layer provides a biotic environment that buffers arthropods against changes in the abiotic environment. Several studies have shown that factors such as vegetation height, density and percentage cover, as well as the associated microclimate, have significant effects on species composition of grasshoppers[6-8] and dung beetles[9].

Despite the proven direct and indirect relationships between plant and insect composition, little research has been conducted on specific structures of insect communities in southern African biomes.[10-12] A study of four biomes in South Africa revealed that overall, differences between insect assemblages of different biomes are not as convincing as those between plant assemblages.[11] This is to be expected, considering the better dispersal ability of most insects because of their mobility and the frequent dispersal events characteristic of winged species. The transition from one biome to another therefore appears smoother for insect assemblages than it is for plant assemblages.[11]

In a previous study of maize-producing regions in South Africa, we collected data to compare insect and plant diversity of field margin habitats in two grassy biomes.[13] In the current study, we used the earlier non-crop dataset of untransformed areas to assess the compositional similarities and differences between the assemblages of arthropods and plants from grassland and savanna biomes. This contribution provides a first comparison of the arthropod composition of localities in these biomes, to establish whether they have distinctive arthropod assemblages.

Savannas are multi-structured and therefore have great structural complexity and niche diversification to house a wide variety of arthropod species.[14] As a result, the presence of a tree and shrub layer allows for more arthropod species and higher abundances per unit area compared with habitats that have simpler structures, such as grassland.[15,16] Savanna provides a wider variety of conditions and resources to be exploited, allowing a greater degree of species coexistence.[17,18] Considering the plant species, life forms and structure of savanna, we wanted to test whether the composition of arthropod assemblages varied between the grassland and savanna biomes – especially considering that biomes are defined by dominant vegetation and climatic variables. We tested whether arthropod assemblages in the grassland and savanna biomes follow the same biogeographical patterns as plant assemblages, and whether these biomes can be differentiated by arthropod species composition.

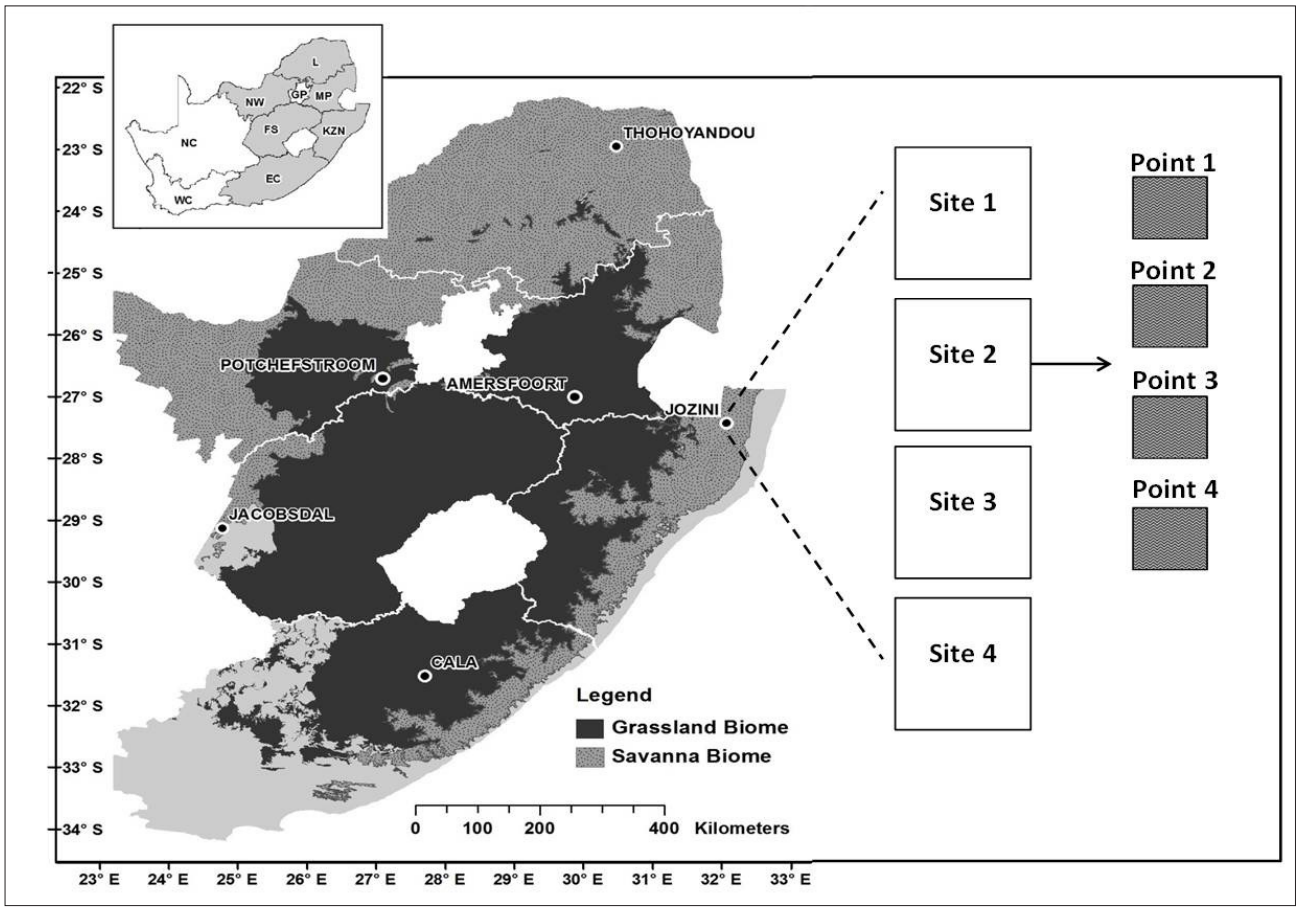

Figure 1: Localities across the six major maize-producing provinces of South Africa within grassland and savanna biomes. EC, Eastern Cape; FS, Free State; KZN, KwaZulu-Natal; L, Limpopo; MP, Mpumalanga; NW, North-West. Three localities were situated in the grassland biome (Amersfoort, Cala and Potchefstroom) and three in the savanna biome (Jacobsdal, Jozini and Thohoyandou). Within each locality, four sites were chosen as indicated. Each site contained four sampling points situated in a crop field margin habitat.

Methods

Experimental design

Our study investigated plants and plant-dwelling arthropods, sampled at six localities spread throughout South Africa in the core regions of the grassland and savanna biomes. The study covered the sub-escarpment (Cala and Jozini), escarpment (Amersfoort and Thohoyandou) and interior plateau (Potchefstroom and Jacobsdal) areas of each biome (Figure 1). To minimise possible spatial autocorrelation of data, the two localities representing similar elevations were chosen to represent different biomes (for instance, the sub-escarpment locality Cala represented grassland and the sub-escarpment locality Jozini represented savanna).

Arthropod data were generated within a total sampled area of 2400 m^2 (96 plots of 5 m x 5 m), and plant data were generated from a total sampled area of 38 400 m^2 (96 plots of 20 m x 20 m). At each locality, four sites were sampled 5 km apart, in a spatial layout designed to cover assemblage variation across several spatial scales.[13] To avoid pseudo-replication, two sites were sampled on hillslopes and two in the valleys of each locality. At each site we sampled two pairs of points 100 m apart at both ends of a 1-km transect, with one site upslope and the other downslope. This translated to 4 points per site, 16 per locality and 48 points for each of the biomes (Table 1). The data were collected during late morning and were scheduled to coincide with the season of maximum biological activity (January and February). Plants and insects that occur seasonally were therefore under-represented at some sites.

Table 1: Layout of sampling design indicating the number of sample repeats (*n*) in brackets for the respective areas

	Biome	Topographic region	Locality
Levels	Grassland (48)	Sub-escarpment (16)	Cala (16)
		Escarpment (16)	Amersfoort (16)
		Plateau (16)	Potchefstroom (16)
	Savanna (48)	Sub-escarpment (16)	Jozini (16)
		Escarpment (16)	Thohoyandou (16)
		Plateau (16)	Jacobsdal (16)

Arthropod sampling

Suction sampling of arthropods using an adapted D-Vac method[13] was conducted in 5 m x 5 m sampling points. The D-Vac provides a relatively fast method for sampling large areas of vegetation, although its effectiveness may be altered by weather conditions and vegetation characteristics. It was most effective in dry, upright grassy habitats. A further limitation was that certain species may selectively be extracted and others under-sampled during suction-sampling in dense vegetation.[19] However, compared with passive sampling methods, the D-Vac method is not as dependent on insect activity, is less prone to sampling error and

may represent one of the best techniques for sampling a wide range of arthropod taxa on vegetation.[20]

Seven swaths per plot were made, following a zigzag pattern with the D-Vac nozzle for each swath. Each swath was made through the vegetation from one side of the plot to the other. Where tall grass (>1 m), shrubs and trees were present within sampling points, arthropod individuals were sampled by moving the D-Vac over the branches and large leaves as well as the trunk or stem, up to a height of 2 m. Vegetation beneath dense shrubs and trees was also sampled where accessible. Soil-dwelling arthropods that were present on the lower parts of plants during the survey were also collected. We did not attempt to use the D-Vac to collect from the soil surface.

Vegetation sampling

After the arthropod sampling was completed, a fixed-width (2-metre) line transect approach was followed[21] to record plant species. The plot was adapted to include ten parallel transects (2 m wide and 20 m long). This ensured that the vegetation sampling would overlap and extend beyond the arthropod sampling area. At 1-metre intervals, one plant species was recorded for every major growth form – that is grass, forb, shrub and tree. Four species were therefore recorded at each interval, if all growth forms were represented. The number of individuals per species across the ten transects (100 points) was summed to determine the species abundances for each sample point.

Table 2: Number (*n*) of plant and arthropod species, and percentage of individuals per family, order or trophic group, and for each biome

		Grassland Biome		Savanna Biome		Total	
		Species (*n*)	**Individuals %**	**Species (*n*)**	**Individuals %**	**Species (*n*)**	**Individuals %**
Plant families	Poaceae	62	52.1	73	35.5	109	42.6
	Fabaceae	28	4.7	73	13.2	94	9.6
	Asteraceae	46	17.3	32	6.9	73	11.3
	Acanthaceae	7	1.4	25	7.3	30	4.8
	Rubiaceae	4	3.9	22	1.8	26	2.7
	Apocynaceae	9	0.3	16	1.5	25	1.1
	Euphorbiaceae	4	0.2	23	2.8	25	1.7
	Cyperaceae	17	3.4	7	0.9	24	1.9
	Malvaceae	6	0.6	20	1.9	22	1.4
	Lamiaceae	4	0.2	16	0.9	20	0.6
	Other families (83)	84	15.9	227	27.1	302	22.3
	All plants (93)	272	–	534	–	751	–
Arthropod orders	Hemiptera	198	25.9	194	32.3	340	26.7
	Diptera	126	8.9	128	18.7	233	10.1
	Hymenoptera	128	14.9	120	16.1	225	15.1
	Araneae	97	9.5	87	8.5	165	9.3
	Coleoptera	80	2.7	86	5.5	147	3.1
	Orthoptera	52	1.4	94	7.5	127	2.1
	Lepidoptera	37	0.6	62	3.5	89	0.9
	Acari	25	23.4	15	3.8	32	21.3
	Thysanoptera	15	4.2	15	1.3	22	3.8
	Mantodea	5	0.06	13	0.7	18	0.1
	Other orders (13)	23	8.4	23	2.2	38	7.4
	All arthropods (23)	786	–	837	–	1436	–
Arthropod trophic groups	Herbivores	339	43.1	430	51.4	667	46.4
	Predators	179	22.8	158	18.9	297	20.7
	Parasitoids	115	14.6	104	12.4	204	14.2
	Pollinators	49	6.2	75	9.0	112	7.8
	Other groups (5)	148	18.8	131	15.7	252	17.5

Statistical analysis

The non-parametric species estimators of observed species counts (Sobs), Chao2 and Jacknife1[22,23] were calculated using PRIMER 7[24] to determine how closely the sample resembled the extrapolated species richness. Non-metric multidimensional scaling (NMDS) analyses (samples clustered based on Bray–Curtis dissimilarity) in PRIMER 7 were used to visualise differences between sampling points in ordination space, in terms of plant and arthropod assemblages. For 2-dimensional ordinations, the stress value increases with decreasing dimensionality and increasing quantity of data. The general rule is as follows: stress ≤0.05 gives an excellent representation, with no prospect of misinterpretation of the data, and stress ≤0.1 represents a good ordination with no real risk of misinterpretation. Stress ≤0.2 may still give a potentially useful ordination, but cross-checks with other techniques are recommended.[25]

Significance of NMDS clusters were tested by permutational MANOVA (PERMANOVA), analysis of similarities (ANOSIM) and similarity percentage (SIMPER) analyses, using PRIMER 7. PERMANOVA is a multivariate analysis of variance technique suitable for abundance data and where significance is based on permutation of the dissimilarity matrix.[26] First, PERMANOVA was conducted using a Bray–Curtis dissimilarity matrix to determine the main and interactive effects of biome and topographic region on species composition (permutations=999; type III sums of squares). Then ANOSIM was used as a post hoc test for pairwise comparisons between localities within the grassland and savanna biomes, to assess compositional dissimilarity. ANOSIM is a non-parametric test that uses rank dissimilarities based on the Bray–Curtis coefficient of similarity. Significant separation of two distinct clusters in ordinal space is calculated using an *R*-statistic, which ranges from 1 (meaning clusters are totally different) to 0 (meaning clusters are indistinguishable).[27] Next, SIMPER was applied to the data set to assess which taxa were primarily responsible for observed differences in species composition between the biomes. A square root transformation of species data was performed for NMDS, PERMANOVA, ANOSIM and SIMPER analyses to reduce the influence of common species.[26]

As a final measure, canonical correspondence analysis (CCA) with forward selection was applied to the data, using CANOCO 4.5[28], as a cross-check to depict how different localities compared in terms of arthropod and plant species composition. The same analysis enabled us to assess the relative importance of selected environmental variables in determining plant and arthropod assemblages of grouped sampling points. Five biotic and abiotic environmental factors were considered for a biplot with species data. These included latitude and longitude (decimal degrees), altitude (m.a.s.l.), tree cover (%) and grass cover (%). Species data for CCA analyses were square-root transformed, and environmental data were normalised.

Results

The survey recorded 1436 arthropod morpho-species (35 193 individuals) from 23 orders (Table 2). The four largest trophic groups of arthropods were distinguished further for comparative analyses, namely herbivores (667 morpho-species), predators (297), parasitoids (204) and pollinators (112) (Table 2). Other groups not included in the analyses were decomposers, parasites, visitors, frugivores and omnivores. For plants, 740 species (10 856 individuals) from 93 families were recorded in the field margin habitats (Table 2).

Some groups of plants and arthropods (mobile, sensitive insects such as butterflies or grasshoppers and cryptic plants such as geophytes) might be under-represented in the samples because of the collection methods and specificity of season. It must be mentioned that a study targeting soil and flying arthropods could yield very different results. A selection of species accumulation curves (Figure 2) suggested that the saturation levels were not satisfactory for arthropods, and this should be kept in mind when interpreting the findings[22].

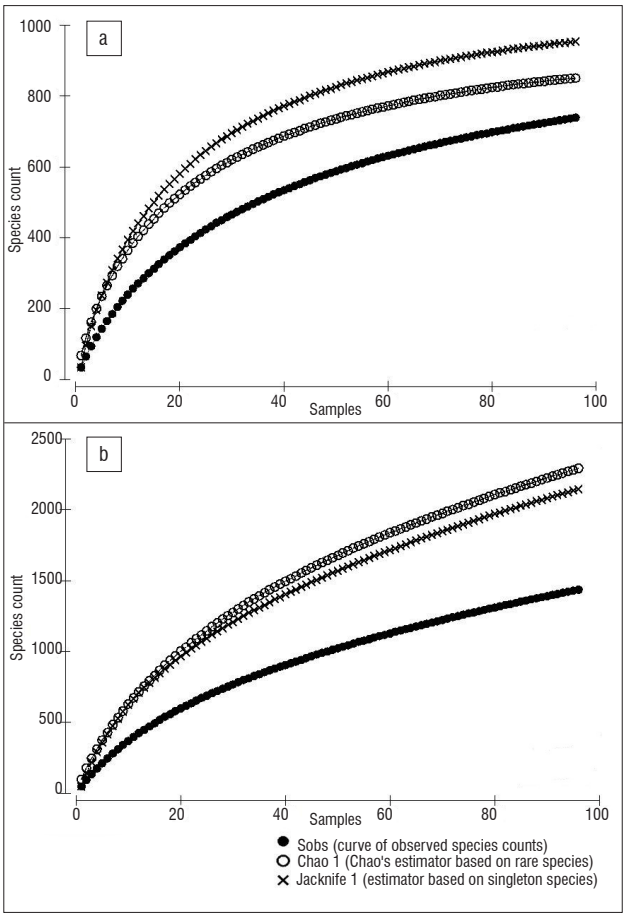

Figure 2: Species accumulation curves for (a) plants and (b) arthropods sampled in all grassland and savanna plots.

Plant assemblages across biomes

The NMDS analysis for plants revealed the tightest clustering and the lowest stress factor (0.14) compared with the results for arthropods (Figure 3). Clear distinctions in plant species composition were found between grassland and savanna sampling points, with a much tighter clustering for grassland samples (Figure 3a). Differences in plant species composition between biomes were confirmed by PERMANOVA results (pseudo-F=31.28; p=0.001) and Bray–Curtis similarity in ANOSIM ($p \leq 0.001$, R=0.68) (Table 3a).

A CCA biplot (Figure 4a) indicated that sampling points were strongly influenced by tree cover and altitude (Table 5, Axis 1). Clear distinctions were found between grassland and savanna sampling points in the CCA ordination, with increased tree cover being correlated with savanna plant assemblages. Forward selection results showed that all tested environmental factors contributed significantly (p=0.002) to variability of the ordination (Table 6). However, the effect of tree cover (a differentiating factor between grassland and savanna) was reduced with the inclusion of longitude, latitude and altitude variables (Table 6).

Plant assemblages across topographic regions

The NMDS results showed that sampling points for plants from each topographic region clustered together to some extent (Figure 3a). PERMANOVA confirmed the distinctions between topographic regions (pseudo-F=14.39; p=0.001). PERMANOVA also revealed a significant interaction between biome and topographic region (pseudo-F=14.83; p=0.001). Samples of savanna localities were more dispersed between sub-escarpment, plateau and escarpment grassland, in terms of plant species composition (Figure 3a and Figure 4). This was confirmed by ANOSIM analyses, which indicated higher R-values (greater distinctiveness) for comparisons between savanna localities than between grassland localities (Table 3a). Grassland sampling points revealed limited distinctiveness of plant species composition between topographic regions (Table 3a).

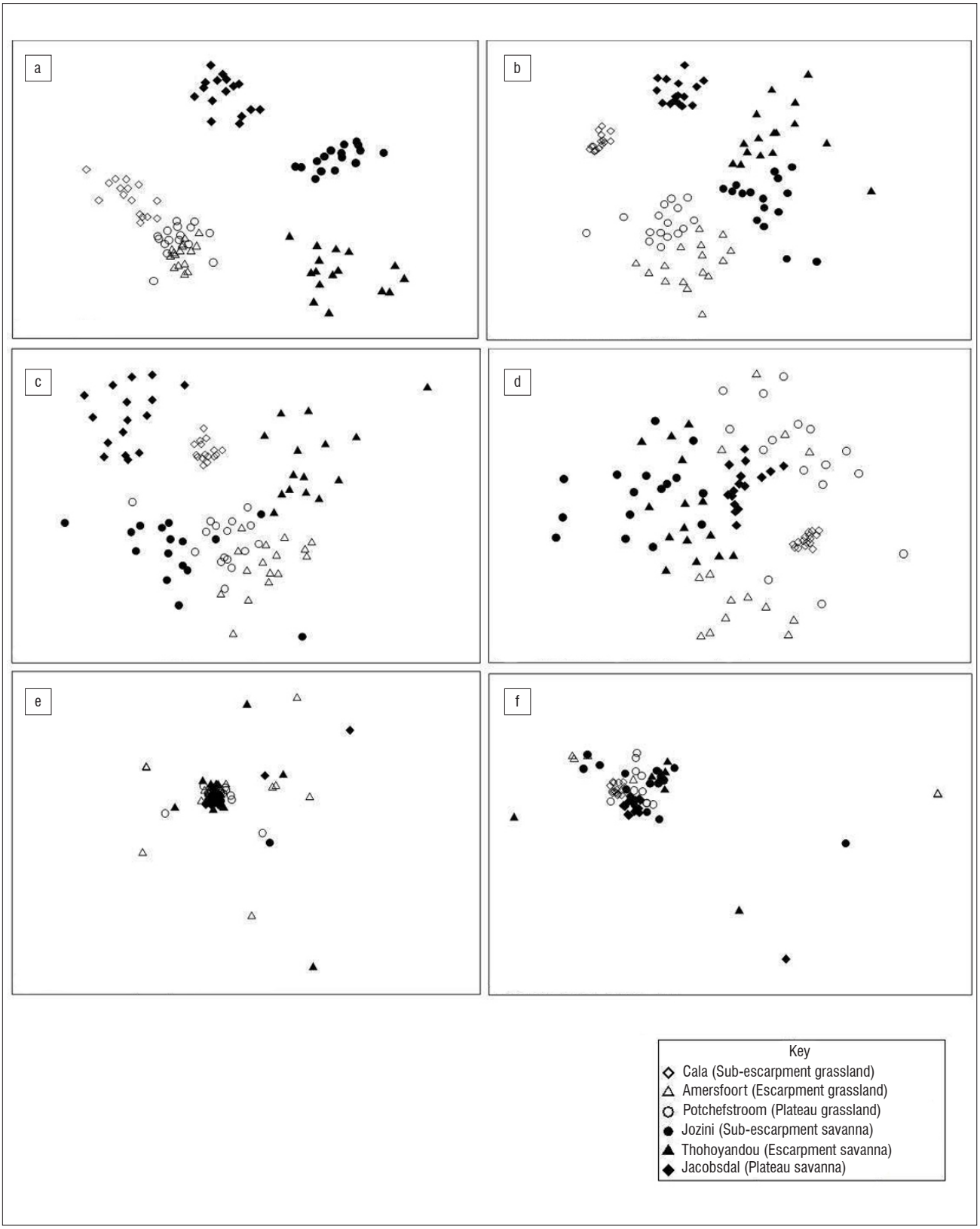

Figure 3: Non-metric multidimensional scaling (NMDS) analyses based on abundance data of plant and arthropod species recorded at maize field margin localities for (a) all plant species, 2D Stress: 0.14, (b) all arthropod species, 2D Stress: 0.23, (c) herbivorous arthropods, 2D Stress: 0.17, (d) predatory arthropods, 2D Stress: 0.16, (e) parasitoid arthropods, 2D Stress: 0.01, and (f) pollinators, 2D Stress: 0.01. Resemblance: S17 Bray–Curtis similarity; data transformation: square root.

Table 3: Results for ANOSIM and SIMPER analyses for biomes and topographic regions in terms of species composition

			ANOSIM *p*-value	ANOSIM *R*-value	SIMPER overall average dissimilarity
a) All plants	Between-biome comparison	Grassland x Savanna	0.0001*	0.68†	97.86
	Within-biome comparison (Grassland)	Escarpment x Plateau	0.0001*	0.52	77.75
		Escarpment x Sub-escarpment	0.0001*	0.94††	91.37
		Plateau x Sub-escarpment	0.0001*	0.81††	88.95
	Within-biome comparison (Savanna)	Escarpment x Plateau	0.0001*	0.99††	99.08
		Escarpment x Sub-escarpment	0.0001*	0.87††	94.25
		Plateau x Sub-escarpment	0.0001*	0.99††	97.23
b) All arthropods	Between-biome comparison	Grassland x Savanna	0.0001*	0.4	98.12
	Within-biome comparison (Grassland)	Escarpment x Plateau	0.0001*	0.5	92.62
		Escarpment x Sub-escarpment	0.0001*	0.98††	99.69
		Plateau x Sub-escarpment	0.0001*	1††	99.41
	Within-biome comparison (Savanna)	Escarpment x Plateau	0.0001*	0.9††	97.8
		Escarpment x Sub-escarpment	0.0001*	0.61†	96.07
		Plateau x Sub-escarpment	0.0001*	0.9††	98.15
c) Herbivores	Between-biome comparison	Grassland x Savanna	0.0001*	0.24	97.94
	Within-biome comparison (Grassland)	Escarpment x Plateau	0.0001*	0.39	90.33
		Escarpment x Sub-escarpment	0.0001*	0.94††	99.35
		Plateau x Sub-escarpment	0.0001*	0.97††	98.88
	Within-biome comparison (Savanna)	Escarpment x Plateau	0.0001*	0. 82††	99.56
		Escarpment x Sub-escarpment	0.0001*	0.57	98.34
		Plateau x Sub-escarpment	0.0001*	0.83††	99.45
d) Predators	Between-biome comparison	Grassland x Savanna	0.0001*	0.33	97.55
	Within-biome comparison (Grassland)	Escarpment x Plateau	0.0001*	0.28	96.13
		Escarpment x Sub-escarpment	0.0001*	0.49	99.47
		Plateau x Sub-escarpment	0.0001*	0.70††	98.98
	Within-biome comparison (Savanna)	Escarpment x Plateau	0.0001*	0.49	93.25
		Escarpment x Sub-escarpment	0.0001*	0.24	90.1
		Plateau x Sub-escarpment	0.0001*	0.63†	93.48
e) Parasitoids	Between-biome comparison	Grassland x Savanna	0.0001*	0.09	98.76
	Within-biome comparison (Grassland)	Escarpment x Plateau	0.0506	0.05	96.02
		Escarpment x Sub-escarpment	0.0001*	0.56†	99.99
		Plateau x Sub-escarpment	0.0001*	0.56†	99.98
	Within-biome comparison (Savanna)	Escarpment x Plateau	0.0001*	0.33	99.22
		Escarpment x Sub-escarpment	0.0025*	0.12	97.74
		Plateau x Sub-escarpment	0.0001*	0.35	99.76
f) Pollinators	Between-biome comparison	Grassland x Savanna	0.0001*	0.07	94.45
	Within-biome comparison (Grassland)	Escarpment x Plateau	0.0038*	0.11	92.38
		Escarpment x Sub-escarpment	0.0001*	0.53†	96.48
		Plateau x Sub-escarpment	0.0001*	0.44	99.09
	Within-biome comparison (Savanna)	Escarpment x Plateau	0.0001*	0.43	100
		Escarpment x Sub-escarpment	0.0074*	0.12	93.51
		Plateau x Sub-escarpment	0.0001*	0.35	99.54

** significant at $p<0.05$.*

†† large effect at $R\geq0.7$; † medium effect at $R\geq0.5$.

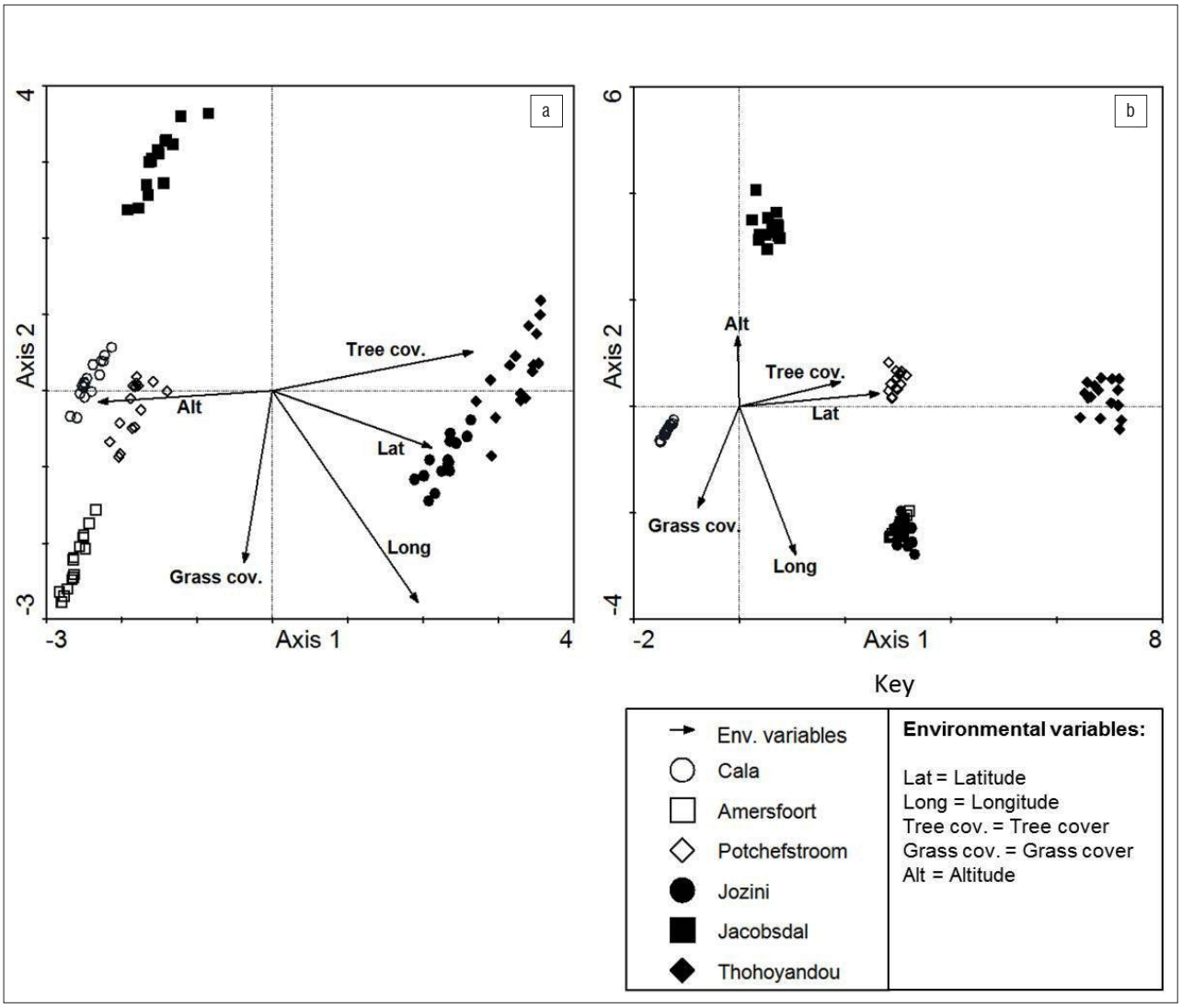

Figure 4: Canonical correspondence ordination of all sampled localities, showing correlations between environmental variables and sampling points for (a) plants and (b) arthropods. Each symbol represents the weighted average of one plot.

Contributing plant species

A total of 21 plant species each contributed more than 1% to the total variation between the biomes, according to SIMPER analysis. Among these, ten species collectively contributed 21% of the variation (Table 4). Six grasses (*Eragrostis curvula, Eragrostis plana, Heteropogon contortus, Hyparrhenia hirta, Sporobolus africanus* and *Themeda triandra*) and one forb (*Helichrysum rugulosum)* characterised the grassland points, whereas one forb (*Pentzia incana*) and two grasses (*Panicum maximum* and *Urochloa mosambicensis*) characterised the savanna points (Table 4).

Arthropod assemblages across biomes

In the NMDS analysis for all arthropod species, grassland sampling points were noted to cluster separately from savanna points (Figure 3b). The biomes, however, were more similar in arthropod species composition than plant species composition, as was evident from the PERMANOVA results (arthropods: pseudo-$F=9.712$; $p=0.001$; plants: pseudo-$F=31.278$, $p=0.001$). ANOSIM showed similar results, indicating less similarity among arthropods ($p \leq 0.001$; $R=0.4$) (Table 3b).

The CCA results for arthropods (Figure 4b) showed that sampling points were more strongly influenced by latitude (i.e. geographic position) than either plant cover or altitude (Axis 1, Table 5). Distinctions were not as clear between grassland and savanna sampling points for arthropods as they were for plants. Forward selection results confirmed the CCA ordination results, which suggests that longitude and latitude explained the most variation when all environmental factors were considered ($p=0.002$) (Table 6). This finding shows a notable division between samples taken from the eastern and western regions of South Africa.

Arthropod assemblages across topographic regions

For the complete arthropod dataset, sampling points from the same topographic region tended to cluster together (Figure 3b). This pattern was also evident in PERMANOVA results, which indicated significant differences between the regions (pseudo-$F=8.009$; $p=0.001$). PERMANOVA showed a smaller interactive effect between biome and topographic region for arthropods than for plants (arthropods: pseudo-$F=8.823$, $p=0.001$; plants: pseudo-$F=14.834$, $p=0.001$). Sampling points from sub-escarpment and escarpment localities in the eastern half of South Africa clustered more closely for savanna than for grassland. However, plateau and escarpment points in the eastern region of South Africa clustered together more strongly for grassland.

Contributing arthropod morpho-species

In the ordination of the total arthropod dataset, a total of ten arthropod morpho-species each contributed more than 1% to the total variation across the biomes, according to SIMPER analysis (Table 4).

Table 4: Results for SIMPER analyses indicating the top ten plant and arthropod species responsible for groupings of grassland and savanna plots in the NMDS graphs

	Species	Type	Ave. dis.	% Contr.	Cumul. %	Abund. Grassland	Abund. Savanna
Plants (overall average dissimilarity: 97.86)	*Themeda triandra*	Grass	3.684	3.764	3.764	8.27	1.6
	Panicum maximum	Grass	3.246	3.317	7.082	0	7.6
	Pentzia incana	Forb	2.355	2.406	9.488	0	4.88
	Helichrysum rugulosum	Forb	1.977	2.02	11.51	4.5	0
	Eragrostis curvula	Grass	1.753	1.791	13.3	3.25	1.27
	Eragrostis plana	Grass	1.741	1.779	15.08	3.94	0
	Sporobolus africanus	Grass	1.704	1.741	16.82	3.79	0.292
	Heteropogon contortus	Grass	1.45	1.482	18.3	2.83	0.979
	Hyparrhenia hirta	Grass	1.444	1.475	19.78	3.25	0
	Urochloa mosambicensis	Grass	1.438	1.47	21.25	0	3.21
Arthropods (overall average dissimilarity: 98.12)	Oribatulidae MS1	Detritivore	3.327	3.391	3.391	63	0.125
	Oribatulidae MS2	Detritivore	3.081	3.14	6.531	66.8	0
	Formicidae MS8	Predator	2.675	2.726	9.257	2.63	2.17
	Acrididae MS12	Herbivore	2.384	2.43	11.69	2.25	0.896
	Cicadellidae MS8	Herbivore	2.266	2.309	14	6.6	0.458
	Entomobryidae MS1	Detritivore	2.081	2.121	16.12	35	0.146
	Cicadellidae MS24	Herbivore	1.367	1.393	17.51	0	2.65
	Sciaridae MS10	Detritivore	1.233	1.257	18.77	0	4.79
	Cecidomyiidae MS1	Herbivore	1.227	1.251	20.02	17	1.02
	Formicidae MS9	Predator	1.17	1.192	21.21	14.8	0.313

Key to column headings: Ave. dis, average dissimilarity; % Contr., percentage contribution of each species to the average dissimilarity; Cumul. %, cumulative contribution percentage; Abund., mean abundance per plot.

Table 5: Correlations of ordination axes with selected environmental factors, eigenvalues and percentage variance explained for canonical correspondence analysis

Survey	Factor	Axis 1	Axis 2
Plants	Tree cover %	0.8975	0.1274
	Altitude	-0.7770	-0.0368
	Latitude	0.7133	0.1854
	Longitude	0.6511	-0.6904
	Grass cover %	-0.1252	-0.5610
	Eigenvalue	0.860	0.702
	% variance explained	29.8	24.3
Arthropods	Latitude	0.9866	0.0762
	Tree cover %	0.7128	0.1462
	Longitude	0.3969	-0.8754
	Grass cover %	-0.2880	-0.5962
	Altitude	-0.0126	0.4150
	Eigenvalue	0.824	0.717
	% variance explained	28.8	25.1

Collectively these species contributed 21% of all variation across biomes. Two mite (Oribatulidae), one springtail (Entomobryoidea), one gall gnat (Cecidomyiidae) and one ant (Formicidae) species characterised the grassland sampling points, whereas one leafhopper (Cicadellidae) and one fungus gnat (Sciaridae) species supported the distinctiveness of the savanna sampling points (Table 4).

Assemblages of arthropod trophic groups

The NMDS analyses for separate arthropod trophic groups showed a much more uniform distribution of sampling points than that of plants or the complete arthropod dataset (Figures 3c to f). However, PERMANOVA showed that differences in species composition between biomes were still significant for all arthropod trophic groups (herbivores: pseudo-F=9.013, p=0.001; predators: pseudo-F=12.317, p=0.001; parasitoids: pseudo-F=5.566, p=0.001; pollinators: pseudo-F=3.507, p=0.001). These results also show that the predators and herbivores displayed the most significant differences in species composition between biomes. The results were confirmed by the R-values of ANOSIM analyses (Table 3c to f).

No clearly distinctive clustering could be observed for topographic regions for any of the arthropod trophic groups in the NMDS analyses. However, PERMANOVA indicated that there were significant differences in species composition between some topographic regions for all the trophic groups (herbivores: pseudo-F=8.127, p=0.001; predators: pseudo-F=8.207, p=0.001; parasitoids: pseudo-F=5.126, p=0.001; pollinators: pseudo-F=3.882, p=0.001).

Table 6: Marginal and conditional effects of automatic forward selection conducted for all plants and all arthropods

	Marginal effects			Conditional effects				
	Variable	**Var. N**	**Lambda1**	**Variable**	**Var. N**	**LambdaA**	***P***	***F***
Plants	Altitude	1	0.79	Altitude	1	0.79	0.002*	4.51
	Tree cover	2	0.77	Latitude	3	0.74	0.002*	4.42
	Latitude	3	0.77	Longitude	4	0.66	0.002*	4.06
	Longitude	4	0.76	Grass cover	5	0.39	0.002*	2.42
	Grass cover	5	0.49	Tree cover	2	0.31	0.002*	1.94
Arthropods	Latitude	1	0.82	Latitude	1	0.82	0.002*	2.71
	Longitude	2	0.73	Longitude	2	0.71	0.002*	2.37
	Tree cover	3	0.68	Altitude	4	0.63	0.002*	2.15
	Altitude	4	0.65	Tree cover	3	0.39	0.004*	1.32
	Grass cover	5	0.50	Grass cover	5	0.31	0.364	1.03

* significant p-values ($p<0.05$) as determined by Monte Carlo permutation tests (permutations=499)

These results show that the largest distinctions in species composition between topographic regions for the biomes were within the herbivore and predator groups (in both cases mainly between the plateau and sub-escarpment). For parasitoids and pollinators, there was almost complete species homogeneity between regions, as confirmed by ANOSIM ($R \leq 0.09$) (Table 3e and f). Across biomes, escarpment localities showed some clustering of points for herbivores (Figure 3c). Escarpment and plateau respectively showed clusters for predators across the two biomes (Figure 3d). Sub-escarpment localities had the most dissimilar arthropod composition between grassland (Cala) and savanna (Jozini) biomes, for herbivores and predators.

PERMANOVA also indicated significant interaction effects between biome and topographic region for all trophic groups (herbivores: pseudo-$F=9.463$, $p=0.001$; predators: pseudo-$F=7.462$, $p=0.001$; parasitoids: pseudo-$F=5.85$, $p=0.001$; pollinators: pseudo-$F=4.093$, $p=0.001$). This pattern was again more evident for herbivores and predators than for parasitoids and pollinators.

Discussion

Our results confirmed findings that between biomes, plant species assemblages were more distinguishable than arthropod assemblages.[11] The ordination of plant species had the tightest clustering and lowest stress value (0.14). The NMDS analysis for all arthropod morpho-species had a high stress value (0.23), which indicates that not too much reliance can be placed on the spacing of plots of the ordination without cross-checking the results through other statistical analyses.[25] However, the similar patterns in species composition between this ordination and other NMDS analyses (Figures 3c to f), which yielded low stress values, suggest that this plot is a reasonably good representation of the relationships between samples, and can be further interpreted.

Arthropod assemblages, based on all morpho-species, seem to cluster according to biomes at least to some extent, which is consistent with previous results[11]. The effect of tree cover (a differentiating factor between grassland and savanna) remained noteworthy even with the inclusion of longitude, latitude and altitude variables in the CCA forward selection (Table 6). Possible causes of the separate clusters of grassland and savanna arthropod assemblages can be ascribed to preferences for specific climatic conditions associated with the biomes.[29] However, the distinction between grassland and savanna arthropod species assemblages was far less marked than it was for plants. This distinction was even smaller for separate trophic groups.

The phytophagous and predacious arthropod groups showed the most distinctive groupings between the biomes, of all the trophic groups. This finding suggests that these groups are more specialised and adapted to the two biomes than are parasitoids, pollinators or other trophic groups.[14,29,30] High levels of similarity between the biomes with regard to insect species assemblages for parasitoids and pollinators can be ascribed to the extreme mobility of this group; many of these species are capable of flight[11]. In our study, the homogenisation effect for arthropods in these groups is probably related more to plant phylogenies of the biomes and host plant specificity.[3] These host plant taxa could be typical of either savanna or grassland, which could lead to homogenisation of the insect groups.

Our results seem to indicate that arthropod assemblages are better explained by their geographical position, particularly longitude and latitude, than by biome characteristics. This finding could be an effect of altitude (localities generally increase in altitude from north to south) and climate (localities become drier from east to west). In line with this reasoning, relatively distinct plant and arthropod assemblages occurred within each topographic region. The effect of altitude on species composition is well known.[31] Arthropod communities at different elevations often experience markedly different environmental conditions, particularly climatic. Several studies have demonstrated the dependence of species composition on altitude for several arthropod groups.[32-34]

Conclusion

When all arthropods are considered, the grassland and savanna biomes have distinct arthropod assemblages. However, the degree of dissimilarity among plant assemblages is greater between grassland and savanna biomes. When trophic levels were compared, the distinction between arthropod assemblages became even more obscured between biomes. Biomes were still distinguishable, albeit weakly, for phytophagous and predacious arthropod assemblages, but not for parasitoids and pollinators. The similarity in arthropod assemblages for different trophic levels can be ascribed to both biomes being characterised by a dominant grass layer and hence habitats. Arthropod species assemblages were better explained by their geographical position than by plant features associated with biome, such as tree and grass cover. It must be noted that our results are based on a limited range of environmental factors and species groups, and further research is required to confirm these patterns for arthropods under different conditions and spatial scales.

Authors' contributions

S.J.S. and J.v.d.B. were the project leaders, and were responsible for experimental and project design. All authors contributed towards data collection. M.B. and S.J.S. performed the statistical analyses and wrote the manuscript.

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