

Effects of aspect and altitude on scorpion diversity along an environmental gradient in the Soutpansberg, South Africa



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ABSTRACT

Landforms with steep environmental gradients provide natural laboratories for studying regional dynamics of diversity. The Soutpansberg range in South Africa presents contrasting habitats and climatic conditions on its northern and southern slopes. Scorpions are well adapted to arid environments, with greatest diversity in temperate deserts, but few studies have investigated the effects of aspect and altitude on scorpion diversity. We surveyed scorpion diversity along an altitudinal transect across the Soutpansberg by actively searching for scorpions during the night and day. Patterns of scorpion diversity along the transect were compared to those of ants and woody plants. Unlike these taxa, scorpions exhibited a significant difference in species richness between slopes; higher on the arid northern slope, and greater at lower than higher altitudes. Endemic taxa were restricted to mid-to higher altitudes of the northern slope. Species turnover decreased at higher altitudes and assemblage structure was influenced by slope, altitude and rock cover. The Soutpansberg appears to be a hotspot of scorpion richness and mimics patterns of diversity in southern Africa. The richness and endemism of the scorpion fauna of the arid northern slopes and foothills of the Soutpansberg emphasizes the need to prioritize the conservation of these areas.

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1. Introduction

Habitat heterogeneity plays an important role in generating biological diversity (Nevo, 1995) but assessing its influence may depend on the scale of investigation and the focal taxon considered (Barton et al., 2010). Natural laboratories with strong abiotic and biotic contrasts, such as mountain ranges, provide unique opportunities to study the factors responsible for generating biological diversity at regional and global scales (Raz et al., 2009). Although isolation and area usually exert disproportionately greater effects on biotic assemblages in mountains, differences in altitude and aspect may also generate rapid turnover across short distances (Longino and Colwell, 2011). In general, species richness decreases with altitude (Rahbek, 1995) but there are exceptions, including low altitude plateaus (McCain, 2009; Longino and Colwell, 2011) and mid-altitude peaks (Sanders et al., 2003; McCain, 2004; Bishop et al., 2014).

The dispersal ability and longevity of a focal taxon may also confound the interpretation of patterns of diversity across a landscape (Ozinga et al., 2005). As living fossils, with relatively limited vagility and long lifespans among invertebrates, scorpions offer a model system for studying the pattern and process of biological diversification (Prendini, 2001b; Bryson et al., 2013a, 2013b) and the effect of spatiotemporal change on diversity.

Scorpions reach their greatest diversity in temperate deserts. Hotspots of scorpion species richness at continental or regional scales are associated with areas of climatic, topographic, and geological complexity (Prendini, 2005). At local scales, scorpion assemblages are structured by temperature, precipitation, substrate (soil hardness and texture; amount of stone or litter cover) and vegetation physiognomy (Prendini, 2001b, 2005; Druce et al., 2007). Different substrates exert different selection pressures on scorpions, resulting in the evolution of ecomorphotypes varying from range-restricted stenotopic substrate specialists to more widespread eurytopic substrate generalists (Prendini, 2001b).

Scorpions can respond to aspect at scales of less than 100 m and are more diverse on slopes facing the equator (Raz et al., 2009) because of their ability conserve water (Hadley, 1970) and survive

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high temperatures (Cloudsley-Thompson, 1962). Few studies have investigated the effects of aspect and altitude on scorpion diversity, however. The only such study conducted in Africa found a decrease in scorpion species richness with increasing altitude on the Brandberg Massif, Namibia, and associated the high scorpion diversity of the Massif with its heterogeneous climate, topography and geology (Prendini and Bird, 2008).

The Soutpansberg range, a homoclinal ridge in the Limpopo Province of South Africa (Fig. 1), presents an environmental gradient with contrasting habitats, from arid savanna on its gentle northern slopes to evergreen forest on its steeper southern slopes. Its high plant diversity (over 2000 plant genera) results from desert, savanna, temperate (grassland/forest), and tropical botanical elements that overlap across its slopes (Van Wyk and Smith, 2001; Hahn, 2006). The fauna of the Soutpansberg, though far less studied than its flora, is similarly diverse. The Soutpansberg is a hotspot of scorpion richness in southern Africa, with 23 species,

including two endemics, recorded on the mountain range or immediate vicinity (Prendini, 2001a, 2005, 2006).

We present the first quantitative survey of the scorpion diversity of the Soutpansberg along an altitudinal transect from its arid northern slopes to its mesic southern slopes. Diversity patterns of ants and woody vegetation along this transect have been the subject of continued, long-term study (Munyai and Foord, 2012). We assess patterns of scorpion diversity and assembly along this transect, quantify the effect of altitude and aspect, and identify environmental correlates of scorpion distribution. As scorpions are adapted to arid environments, we predict higher scorpion species diversity on the arid northern slopes of the Soutpansberg than on its mesic southern slopes. We also predict greater turnover on the northern slope, due to its steeper environmental gradient and greater species diversity. We compare the patterns of diversity observed in scorpions, with those observed in ants and woody vegetation along the transect.

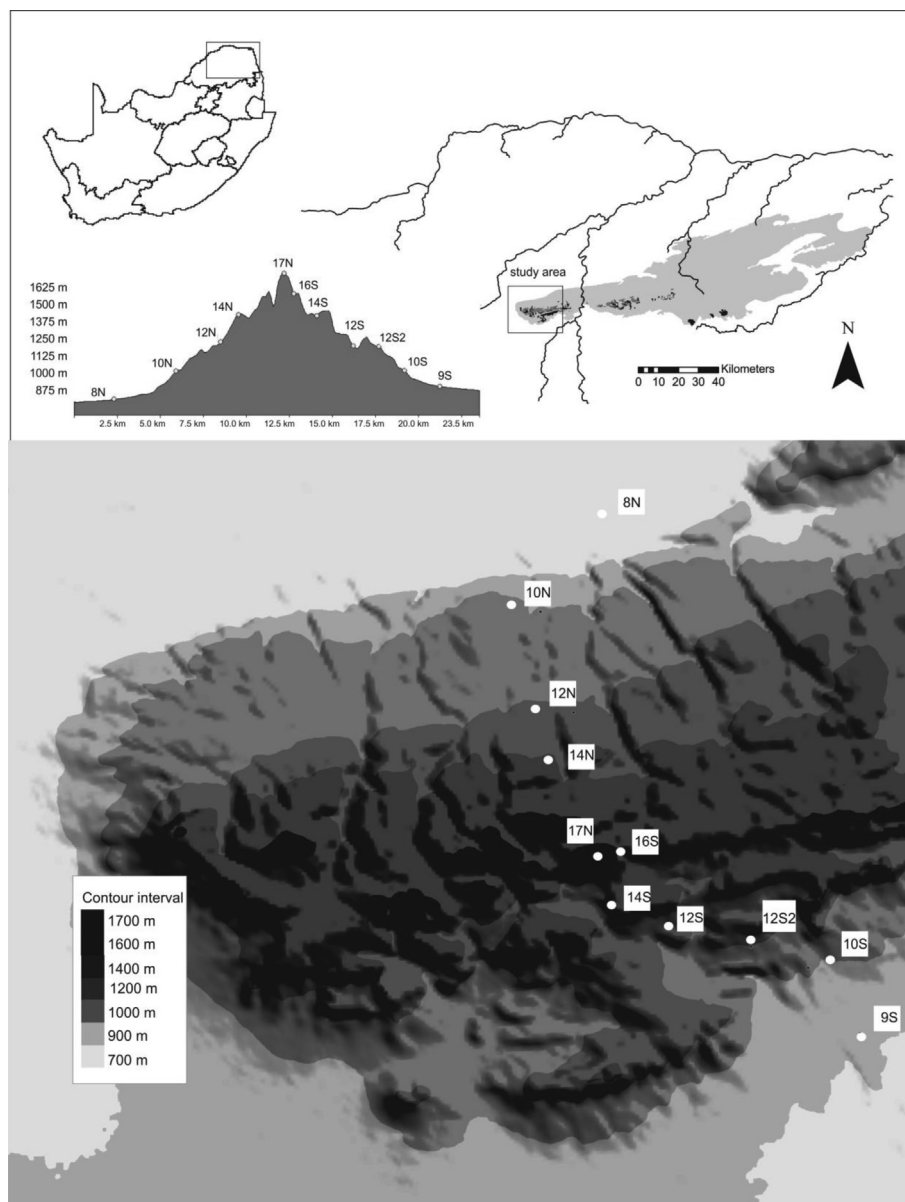


Fig. 1. Study area for survey of scorpion diversity in the western Soutpansberg, Limpopo Province, South Africa, showing location of eleven sampling sites along altitudinal transect from northern (N) to southern (S) slopes of the mountain range.

2. Methods

2.1. Study area

The Soutpansberg range extends in a northeast to southwest orientation from Pafuri to Vivo (Fig. 1). The mountain range was formed from an archaic group of basalt or sedimentary rocks and lava between 1800 and 1900 Ma. Extreme folds along the eastern–western seams form parallel ridges and valleys (Hahn, 2006). The geology of the Soutpansberg is dominated by erosion-resistant quartzite and sandstone. Soils derived from the quartzite and sandstone are generally shallow, skeletal and well drained, with low nutrient content and acidic characteristics, those derived from the basalt and diabase dykes on the southern aspect in particular are finely textured, clayey, well weathered and generally deep (Mostert et al., 2008).

The Soutpansberg borders the Limpopo Valley to the north, an arid region, receiving about 350–400 mm of rainfall annually. The southern slope of the mountain range is more mesic, with an average annual rainfall of about 700–800 mm, twice that of the northern slope. The climate of the Soutpansberg can be divided into warm, wet and cool, dry seasons. Temperature is strongly associated with seasonal conditions and topography, but minimum winter temperatures seldom drop below freezing (Mostert et al., 2008).

Five major vegetation types occur in the western Soutpansberg (Mostert et al., 2008). Two of these represent arid or semi-arid habitats: *Adansonia digitata*-*Acacia nigrescens*, Soutpansberg Arid Northern Bushveld, confined to the rain shadow of the northern ridges; *Diplorhynchus condylocarpon*-*Burkea africana* Soutpansberg Leached Sandveld. Three represent mesic habitats: *Catha edulis*-*Flueggia virosa* Soutpansberg Moist Mountain Thickets, associated with high clay content and relatively moist conditions; *Searsia rigida* var. *rigida*-*Searsia magalismsontanum* subsp. *coddii* Soutpansberg Mistbelt Vegetation; *Xymalos monospora*-*Searsia chir- endensis* Soutpansberg Forest Vegetation.

The study area comprised a 16.3 km transect across the western part of the Soutpansberg (Fig. 1). The transect extended from north to south across the highest point of the mountain range, 1747 m, about 800–900 m higher than the surrounding plains, and included all five of the abovementioned vegetation types. Eleven sampling sites were located at 200 m intervals of altitude along the transect. Two sites were established at 1200 m on the southern aspect to represent the two habitats of mist belt forest in sheltered valleys and exposed thicket found at this altitude along the mountain range.

2.2. Environmental variables

Environmental variables were determined by randomly locating ten 1 m² quadrats at each sampling site. The horizontal distribution of vegetation was measured by recording the cover of vegetation, leaf litter, rock and bare ground. The vertical distribution of vegetation was measured with height profiles. Vegetation height was estimated at each corner of the quadrat, by recording the number of times vegetation touched a 1.5 m rod at 25 cm height intervals (0–25, 26–50, 51–75, 76–100, 101–125, 126–150 + cm), and calculating the average for each quadrat (Munyai and Foord, 2012).

Two Thermocron iButtons (Semiconductor Corporation, Dallas/Maxim, TX, U.S.A.) per sampling site recorded temperature, at hourly intervals, to calculate the mean and range of monthly temperatures. Soil samples were analyzed for sand, clay and silt content (%).

2.3. Scorpion sampling

Scorpions were collected at each sampling site by actively searching potential scorpion microhabitats during the day and at

night with ultraviolet light detection, the method of choice for collecting the greatest diversity and abundance of scorpions in a range of habitats (Sissom et al., 1990).

Ten 1 ha quadrats were sampled per site. These were randomly located within a 1 km-stretch along the contour of each altitudinal zone, taking care not to cross more than 100 m in altitude. Each quadrat was sampled once only, sampling without replacement over time.

In order to cover the transect within a reasonable time, sampling effort per site was limited to 30 min in the day and 30 min at night. Each site was sampled on ten occasions, during the dry season (September) and wet season (January) over five years (2008–2012), to avoid missing species with seasonal activity, resulting in 10 h of search effort per site.

All specimens were collected, preserved in ethanol and deposited at the American Museum of Natural History, New York. Scorpions were identified to species and classified into ecomorphotypes according to the criteria of (Prendini, 2001b).

2.4. Data analysis

The ten quadrats per site were pooled for subsequent analysis. Estimates of scorpion species richness were calculated for each of the eleven sampling sites using the Chao 1, bootstrap and jackknife1 estimates. Rarefied richness was also calculated for each site. Multiple linear regression was used to identify environmental variables explaining significant amounts of variation in species richness among the 11 sites, using a forward selection process with the function 'step' in the R package 'stats' (R Development Core Team, 2013). Scorpion species assemblages were identified, using Ward's minimum variance clustering analysis with the Steinhaus (S17) dissimilarity coefficient (Legendre and Legendre, 1998), as groups with the highest mean silhouette widths. A silhouette width is a comparison of the average distance between an object and all other objects in the cluster to which it belongs, with the distance to the nearest cluster (Legendre and Legendre, 1998). Constrained ordination of species abundances was conducted with Canonical Correspondence Analysis (CCA). Environmental variables that explained a significant amount of the variation in diversity were identified with the CCA-based forward selection using vegan's ordistep (Oksanen et al., 2014). This procedure selects the most parsimonious combination of variables that explains assemblage structure. CCA assumes that species are measured over their entire ecological range and that their response is unimodal to ecological constraints. Co-linearity between predictive variables was assessed with the variance inflation factor (VIF), and co-variables with VIF greater than ten, removed. Factor analysis based on the Spearman correlation matrix was used to identify the factors (altitude vs aspect) that explain differences in species richness of scorpions and other taxa (ants, woody vegetation) among sites along the transect. The Mann–Whitney *U* test was used to test for differences in species richness between the slopes, significant at *P* = 0.05 if richness was higher among the sites on one slope than the other. Statistical analyses were performed in R.

3. Results

A total of 530 scorpions from 19 species, 8 genera and 3 families were collected over the period of 5 years in an area less than 16 km² in extent (Table 1). *Uroplectes triangulifer* (Thorell, 1876) was the most abundant species, comprising 21% of the material collected. Four species were represented by a singleton, and two by doubletons. Ward's minimum variance clustering recovered seven species assemblages as this partition had the highest mean silhouette width (Fig. 2a). Five of these (groups 1–5) were on the northern

Table 1

Scorpion species and ecomorphotypes collected at eleven sites along an altitudinal transect across the Soutpansberg range, Limpopo Province, South Africa. Ecomorphotype classification after [Prendini \(2001b\)](#).

Family	Species	Ecomorphotype	8N	10N	12N	14N	17N	16S	14S	12S	12S2	10S	9S	Totals	
Buthidae	<i>Hottentotta trilineatus</i> (Peters, 1861)	lapidicolous	2	85										87	
	<i>Parabuthus granulatus</i> (Ehrenberg, 1831)	semi-psammophilous	4											4	
	<i>Parabuthus kuanyamarum</i> (Monard, 1937)	psammophilous	2											2	
	<i>Parabuthus mossambicensis</i> (Peters, 1861)	psammophilous	6											6	
	<i>Parabuthus transvaalicus</i> (Purcell, 1899)	semi-psammophilous	10	16										26	
	<i>Pseudolychas ochraceus</i> (Hirst, 1911)	lapidicolous			3	3	3	1	8	6	3	4			31
	<i>Uroplectes carinatus</i> (Pocock, 1890)	lapidicolous			8	9						1			18
	<i>Uroplectes flavoviridis</i> (Peters, 1861)	lapidicolous		1											1
	<i>Uroplectes olivaceus</i> (Pocock, 1896)	lapidicolous											27	13	40
	<i>Uroplectes planimanus</i> (Karsch, 1879)	lithophilous		14					1						15
	<i>Uroplectes triangulifer</i> (Thorell, 1876)	lapidicolous				31	17	13	52						113
<i>Uroplectes vittatus</i> (Thorell, 1876)	corticulous		3		1			6	9	13	5	28		65	
Hormuridae	<i>Cheloctonus jonesii</i> (Pocock, 1892)	pelophilous								1	2	2		5	
	<i>Hadogenes soutpansbergensis</i> (Prendini, 2006)	lithophilous		1	3	3	4	4	2					17	
	<i>Opisthacanthus asper</i> (Peters, 1861)	corticulous	2											2	
Scorpionidae	<i>Opisthacanthus validus</i> (Thorell, 1876)	lithophilous				1								1	
	<i>Opisththalmus lawrencei</i> (Newlands, 1969)	semi-psammophilous		9	57	24						5		95	
	<i>Opisththalmus glabrifrons</i> (Peters, 1861)	pelophilous											1	1	
	<i>Opisththalmus wahlbergii</i> (Thorell, 1876)	psammophilous	1											1	
Totals		30	126	71	72	24	18	69	16	18	44	42	530		

slopes of the Soutpansberg and adjacent foothills, whereas only three (groups 5–7) were on the southern slopes. Ten species were restricted to the northern slopes and foothills ([Fig. 2a](#); [Table 1](#)). Eight species were restricted to particular sites along the transect ([Fig. 2a](#)), five to one site on the northern slope (the most diverse site with eight species collected). Six species occurred on both sides of the mountain range, but could be divided into higher altitude species and lower altitude species. One species was widely distributed along the transect, occurring at eight sites. The two Soutpansberg endemics were restricted to higher altitudes or to intermediate altitudes on the northern slopes ([Fig. 2a](#)). The distributions of several species at lower altitude were more restricted (i.e., occurred at fewer sites) than those at higher altitude.

Scorpion species richness was greater on the arid northern slope of the Soutpansberg than on the mesic southern slope. It was also the only taxon for which the asymmetry was significant ([Table 2](#)). Richness was also greater at lower than higher elevations, on both

slopes. Richness peaked in an area of arid savanna and deep sandy soils in the northern foothills of the Soutpansberg, and decreased southwards, with three smaller peaks ([Fig. 3](#)) in areas with rocky outcrops in a mosaic of savanna, thicket and grassland. The lowest species richness (two species) was recorded in the forest ([Fig. 3](#)). The decrease in richness and turnover with altitude were more pronounced on the northern slope ([Figs. 2b and 3b](#)).

Step-wise forward selection of the most parsimonious combination of environmental variables explained species richness with an $R^2 = 0.66$. Species richness was negatively correlated with bare soil (-0.15^{**}), vegetation cover (-0.11^{**}), and rock cover (-0.06^{**}), but positively correlated with aspect (0.76^{**}).

The CCA explained significant amounts of variation in species abundance ($\chi^2 = 2.4$, $F = 7.1$, $P < 0.001$). The most parsimonious combination of environmental variables, in decreasing order of importance, comprised the aspect, altitude and rock cover of sampling sites. These variables explained 63% of the variation in

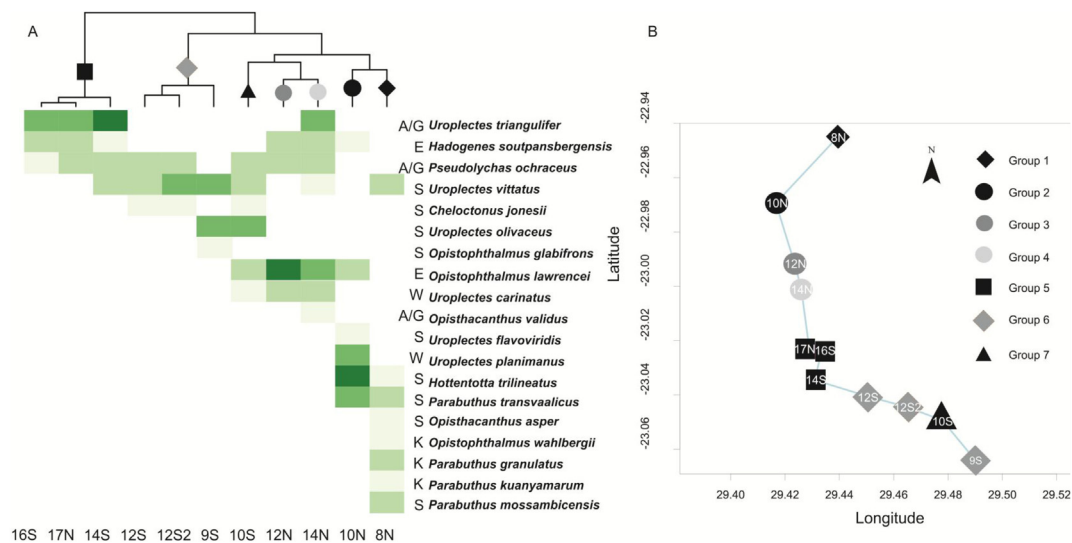


Fig. 2. Scorpion diversity at eleven sites along an altitudinal transect across the Soutpansberg range, Limpopo Province, South Africa. a) Heatmap of species distributions (intensity of shading represents relative abundance) along transect with scorpion species assemblages identified by Ward's cluster analysis (above). Abbreviations in front of species represent faunal elements from which species are derived: widespread (W); endemic (E); Kalahari (K); Afrotropical/grassland (A/G); Savanna (S). b) Scorpion species assemblages with highest silhouette width identified along transect by Ward's clustering.

Table 2
Ranking by increasing richness of sampling sites along an altitudinal transect across the Soutpansberg range, Limpopo Province, South Africa. Asterisk denotes a significant difference according to the inter-slope difference model. Dim1 and Dim2 explain the estimated variability in the Spearman correlation matrix by means of factor analysis.

	8N	10N	12N	14N	17N	16S	14S	12S	12S2	10S	9S	Dim1	Dim2
Ants	2	8	10	9	1	3	7	6	4	5	11	-0.94	-1.2
Scorpions*	11	8.5	6.5	10	3.5	3.5	6.5	3.5	3.5	8.5	1	0.96	0.29
Trees	3	5	1	4	8	2	9	7	NA	6	NA	-3.8	0.63

scorpion assemblages. Four groups were evident in the triplot of scorpion responses to environmental variables (Fig. 4), the first two occurring on the hot northern slopes of the mountain range, the third at cooler, high altitudes, and the fourth, at lower altitudes on the southern slopes. CCA3 explained much of the variation in scorpion assemblages in areas with extensive rock cover, whereas CCA1 explained differences between scorpion assemblages at lower altitudes of the northern slopes, and the rest of the study area. CCA2 explained differences between scorpion diversity associated with the high altitude sites around the summit of the mountain range, and the thickets and forests of its southern slopes.

When assessed in terms of ecomorphotypes (Fig. 4; Table 1), scorpion species were found to occupy predictable habitats along the transect. Stenotopic taxa were generally more restricted in distribution across the mountain range. Lithophilous species were restricted to areas with extensive rock cover; psammophilous and semi-psammophilous species to sandy areas (Fig. 2b); pelophilous species to areas with loamy, clayey soils on the southern slopes; and corticolous (arboreal) species to areas with an abundance of large trees at the lower altitudes. Eurytopic taxa, such as the lapidicolous species, were more widely distributed across a range of mid-to high altitudes (Fig. 2).

4. Discussion

The Soutpansberg is a hotspot of scorpion richness in southern Africa, based on surveys in the more mesic regions of southern Africa, which have not recorded more than eight species (Haddad

et al., 2006; Druce et al., 2007; Dippenaar-Schoeman and Prendini, 2009), and the arid hotspots where Prendini and Bird (2008) recorded a record number of 20 species. The scorpion diversity of the Soutpansberg may be partly due to the convergence of several scorpion faunas (Prendini, 2005). Most species inhabiting the mountain range are typical elements of the Bushveld. However, the fauna of the arid northern slopes contains elements from the Kalahari, whereas the more mesic higher altitudes and southern slopes contain elements from the Afromontane forest and grassland. At least one species reaches the southern limit of its distribution at the Soutpansberg, whereas three others reach their northern limits.

An important explanation for the scorpion species diversity of the Soutpansberg is the marked difference between the faunas of its slopes. As predicted, the greatest diversity occurred on the northern slope, which may be attributed to its greater aridity, caused by rain shadow and higher insolation, compared with the summit and southern slopes. 48% of the endemic plant species on the Soutpansberg are succulents (Hahn, 2006), highlighting the importance of aridity in the evolution of its endemic taxa. Among other taxa for which species richness has thus far been studied along the Soutpansberg transect, only scorpions exhibited a significant difference in species richness between slopes of different aspect (Table 2). The present study emphasizes the importance of aspect in determining scorpion diversity, as previously concluded by Raz et al. (2009), who demonstrated a significant difference in scorpion species richness between the mesic northern and arid southern slopes of Mount Carmel, Israel.

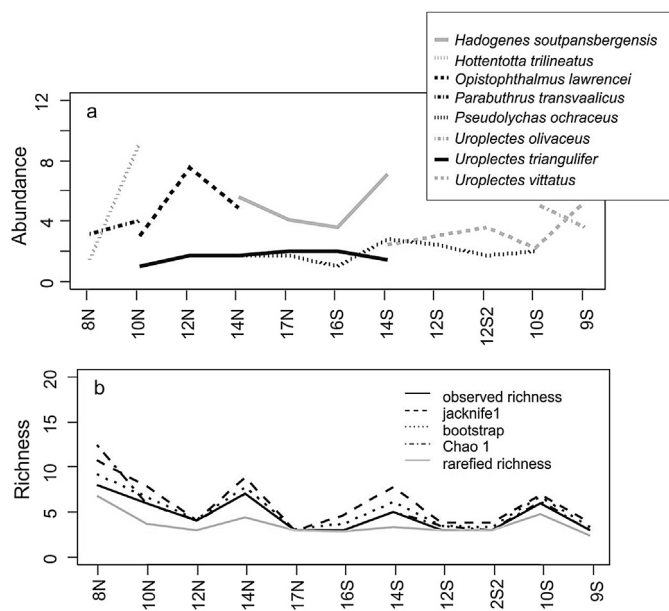


Fig. 3. Patterns of scorpion abundance, species richness and turnover at eleven sites along an altitudinal transect across the Soutpansberg range, Limpopo Province, South Africa. a) Observed abundance (square root transformed) of the eight most common species. b) Species richness, observed and estimated.

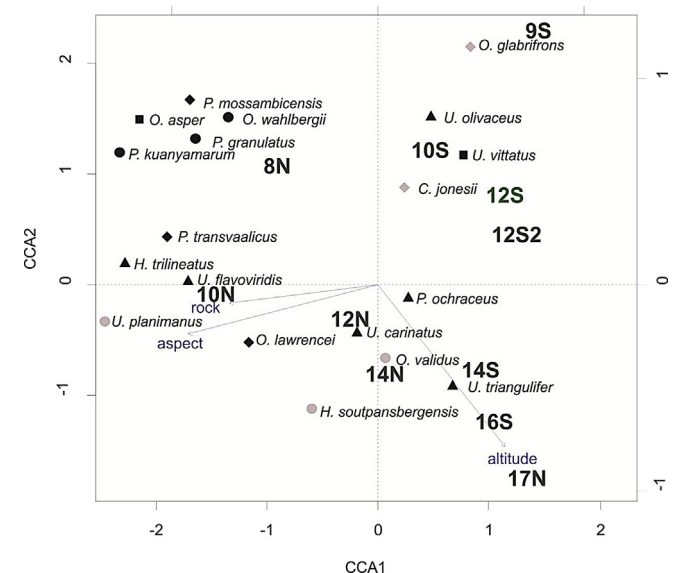


Fig. 4. Triplot of Canonical Correspondence Analysis with fitted scores for scorpion assemblages at eleven sites along an altitudinal transect across the Soutpansberg range, Limpopo Province, South Africa. Rock denotes proportion of rock cover. Symbols denote ecomorphotypes (after Prendini, 2001b) as follows: ■ (corticolous); ▲ (lapidicolous); ● (lithophilous); ◆ (pelophilous); ◆ (semi-psammophilous).

The higher richness on the northern slopes and foothills of the Soutpansberg may also be partly attributed to the presence of species widespread in the Limpopo Valley, on the northern side of the mountain range, but absent on the southern side (Prendini, 2001a, 2005, 2006). The Limpopo Valley serves as an east–west corridor for migration of arid-adapted species (Hahn, 2006).

In addition to the difference in scorpion species richness on slopes of different aspect in the Soutpansberg, richness decreased with altitude, as observed in the Brandberg, Namibia (Prendini and Bird (2008), but not the Andes of South America (Fernández Campón et al., 2014). The decrease in richness with altitude was more pronounced on the northern slope of the Soutpansberg, however. Richness peaked on the plains adjacent to the northern foothills of the mountain range and decreased southwards. The more pronounced decrease in richness with altitude on the arid northern slopes of the Soutpansberg, compared with its mesic southern slopes, may be explained by the steeper environmental gradient and greater diversity of species on this slope. Patterns of scorpion species richness on the arid northern slopes of the Soutpansberg resemble those on the Brandberg more closely than on its mesic southern slopes. This difference may be explained by the fact that the Soutpansberg is a homoclinal ridge, with markedly contrasting habitats and climatic conditions on its gentle northern and steep southern slopes, unlike the Brandberg, a roughly circular inselberg on the gravel plains of the central Namib Desert, all slopes of which are arid (Prendini, 2003).

Altitude exhibited a significant effect on the structure of scorpion assemblages on the Soutpansberg. Lower altitude sites comprised distinct, non-overlapping assemblages compared with higher altitude sites, which overlapped considerably in assemblage structure. This finding suggests that species turnover is greater at lower than at higher altitudes in the Soutpansberg, and contrasts with tropical mountains in which less turnover has been observed at lower than higher altitudes (Longino and Colwell, 2011).

Scorpion diversity, turnover and richness were strongly influenced by the presence of rocks in the Soutpansberg. Although rock cover was negatively associated with scorpion richness, probably because the richest site was sandy with no rock cover, it played a significant role in explaining differences in scorpion composition and structure. Rocky sites contained distinct scorpion assemblages and both endemic taxa were associated with rocky habitats. Druce et al. (2007) also reported highest scorpion diversity in rocky habitats.

The observed difference in species richness across the Soutpansberg range mimics the patterns of scorpion richness at a broader scale across southern Africa, where greater diversity occurs in arid areas (Prendini, 2001b). The significance of this local pattern in understanding continental patterns may have implications for other taxa. For example, ants are predicted to reach their highest richness in lower altitude mesic habitats and woody vegetation in mid-altitude mesic habitats.

The asymmetry in species richness of scorpions between aspects emphasizes the need for caution when using other taxa as surrogates of scorpion diversity. Beta diversity across the Soutpansberg contrasts with that of mountains at lower tropical latitudes where there is low turnover between sites at low altitudes and little overlap between sites at higher altitudes (Longino and Colwell, 2011). High levels of generic and species level endemism in the Soutpansberg (Foord and Dippenaar-Schoeman, 2005; Jocqué, 2008; Haddad, 2009; Edwards et al., 2013) justify its status as a critical biodiversity hotspot. However, the richness and endemism of the scorpion fauna of the arid northern slopes and foothills of the Soutpansberg places new emphasis on prioritizing the conservation of these areas, which were previously underrepresented in conservation assessments.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2014.10.006>.

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