

Spiders as potential indicators of elephant-induced habitat changes in endemic sand forest, Maputaland, South Africa

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Abstract

Elephant impacts on spider assemblages, and the potential use of spiders as indicators of habitat changes was assessed in central Maputaland, South Africa. Three habitats, namely undisturbed sand forest, elephant disturbed sand forest and mixed woodland, were sampled. To ensure a thorough representation of all spider guilds, spiders were collected by tree beating, sweep netting, active searching, leaf litter sifting and pitfall traps. In total, 2808 individual spiders, representing 36 families, 144 determined genera and 251 species were collected. Spider abundance was highest in the undisturbed sand forest ($n = 1129$, $S = 179$), followed by elephant disturbed sand forest ($n = 1006$, $S = 165$) and mixed woodland ($n = 673$, $S = 171$). Assemblages of the two sand forests were more similar than to the mixed woodland assemblage. Active hunting species were indicators of the more open vegetation of elephant disturbed sand forest (six active hunters, no web-builders) and mixed woodland (ten active hunters, one web-builder), whereas web-builders are indicators of the dense, complex vegetation structure of undisturbed sand forest (six web-builders, three active hunters). Elephant-induced changes to the vegetation structure in this high diversity, high endemism region result in changes in the composition of spider assemblages, and may need to be mitigated by management intervention.

Keywords: Araneae, assemblage, guild, impact, woodland

Résumé

L'impact des éléphants sur les assemblages d'araignées, et l'utilisation éventuelle des araignées comme indicateurs de changements des habitats, ont été évalués dans le centre du Maputaland, en Afrique du Sud. Trois habitats ont été échantillonnés, à savoir la forêt sableuse intacte, la forêt sableuse perturbée par des éléphants et la forêt mixte. Pour garantir une représentation complète de toutes les guildes d'araignées, on a récolté des araignées en frappant sur les arbres, en agitant des filets, en pratiquant une recherche active, en tamisant la litière de feuilles, et avec des pièges. Au total, on a récolté 2 808 araignées; représentant 36 familles, 144 genres déterminés et 251 espèces. L'abondance d'araignées était la plus grande dans la forêt sableuse non perturbée ($n = 1129$, $S = 179$), suivie par la forêt sableuse perturbée par les éléphants ($n = 1006$, $S = 165$), puis par la forêt mixte ($n = 673$, $S = 171$). Les assemblages des deux forêts sableuses étaient plus semblables entre eux qu'avec celui de la forêt mixte. Les espèces d'araignées qui chassent activement étaient des indicateurs de la végétation plus ouverte de la forêt perturbée par les éléphants (six chasseurs actifs, aucun constructeur de toile) et de la forêt mixte (dix chasseurs actifs, un constructeur de toile), alors que les constructeurs de toile étaient des indicateurs de la structure dense et complexe de la végétation de la forêt sableuse intacte (six constructeurs de toile, trois chasseurs actifs). Les éléphants induisaient des changements dans la structure de la végétation de cette région à la diversité élevée et d'un fort endémisme, ce qui entraînait des modifications de la

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composition des assemblages d'araignées. Cela pourrait devoir être atténué par une intervention de la gestion.

Introduction

The Maputaland Centre of Endemism (MCE) is a region including the southern parts of Mozambique and northern parts of the KwaZulu-Natal Province, South Africa. According to Van Wyk (1994), the MCE lies at the northern-most part of the Tongaland-Pondoland Regional Mosaic and represents the southern-most geographical range of the tropics in Africa. Therefore, the MCE represents a regional biotic and abiotic transition zone that most likely contributes towards the associated high levels of endemism, biodiversity, and complex spatial patterns in local species distributions of plants (Van Wyk, 1996; Matthews, Van Wyk & Van Rooyen, 1999; Matthews *et al.*, 2001; Van Wyk & Smith, 2001), amphibians (Poynton, 1961; Poynton & Boycott, 1996), birds (Van Rensburg *et al.*, 2000; Van Eeden *et al.*, 2006), reptiles (Branch, 1995), dung beetles (Van Rensburg *et al.*, 1999; Botes, Mcgeoch & Van Rensburg, 2006) and mammals (Belton, Dalerum & Van Rensburg, 2008).

Sand forest is a dry forest type that is restricted in its distribution to the MCE (Van Wyk, 1996; Matthews *et al.*, 1999, 2001). Sand forest is primarily found on the sandy soils of north-south aligned ancient dunes that formed as a consequence of global sea level recessions, resulting in the deposition of deep-water marine and littoral sediments (Botha & Porat, 2007; Porat & Botha, 2008). These soils have a thin, organically enriched A-horizon, sandy subsoil, and are well-drained, being dry for much of the year, and these are key factors contributing to the unique plant community structure and high levels of plant endemism (Matthews *et al.*, 2001). High levels of dung beetle and bird assemblage heterogeneity have been shown both within and between sand forest and mixed woodland habitat types (Van Rensburg *et al.*, 1999, 2000; Van Eeden *et al.*, 2006). Of these, the sand forest habitat is considered to be the most biologically diverse habitat type within the MCE and harbours the highest proportion of endemic species (see Van Wyk, 1996; Van Rensburg *et al.*, 2000). Van Rensburg *et al.* (1999, 2000) indicated that these high heterogeneity levels were most likely due to different vegetation structure, which have pronounced effects on the species richness and species composition of dung beetles and birds.

Currently, the largest proportion of sand forest under formal protection in South Africa can be found in the Tembe Elephant Park (Fig. 1). Outside protected areas human impacts (deforestation for fuel wood and for agriculture) are threatening sand forest patches (Davis, Heywood & Hamilton, 1994; Cole & Landres, 1996). Inside Tembe, and also in the Maputo Elephant Reserve in southern Mozambique, high elephant (*Loxodonta africana* Blumenbach) densities and sand forest utilization are putting increasing pressure on this habitat and its associated endemic species (Ntumi *et al.*, 2005; Matthews, 2007), to such an extent that the structure might be changing to a more open mixed woodland structure (Van Rensburg *et al.*, 1999, 2000). This situation is compounded by the low recovery potential of sand forest following disturbances such as fire and intensive elephant foraging (Matthews, 2007). Consequently, the number of individuals of certain taxa (both plants and animals) may become too low to support viable populations, viz. elephant impacts on sand forest structure shifted dung beetle assemblages to a fauna more typical of savanna woodlands (Botes *et al.*, 2006).

With limited information about the impacts of dense elephant populations on invertebrate taxa (Cumming *et al.*, 1997; Van Rensburg *et al.*, 1999), the aim of the present study is to assess whether elephant-induced changes to vegetation structure result in changes in the assemblage structure of an important group of invertebrate predators, namely spiders. If so, then indicator species need to be identified that can be used to track habitat and assemblage changes, and evaluate the quality of the habitat. If these goals are realized, then spiders could be used widely in the Afrotropical Region as indicators of elephant-induced habitat disturbance.

Spiders were selected because they are diverse and abundant, easily collected, functionally significant in ecosystems as predators and food for other predators, and interact with their abiotic and biotic environment in a manner that reflects ecological change (Churchill, 1997). Also, they are diverse in their microhabitat selection on vegetation and on the ground, occupying several guilds within a habitat, and are a dominant predator group on invertebrates in ecosystems (Dippenaar-Schoeman & Jocqué, 1997). As Maputaland is the area with the highest known regional arachnid biodiversity in South Africa (Haddad, Dippenaar-Schoeman & Wesolowska, 2006), spiders were considered an ideal candidate for this study.

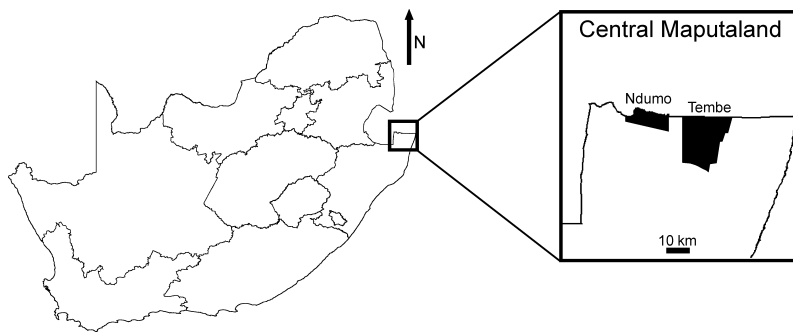


Fig 1 Location of central Maputaland within South Africa. Enlarged map indicates the location of the Tembe Elephant Park and Ndumo Game Reserve

Materials and methods

Study area and period

To determine the spider communities in sand forest habitats under different levels of utilization, and in mixed woodland habitats, this study was conducted during two weeks in March and April 2003 in central Maputaland, on the southern Mozambique Coastal Plain of northern KwaZulu-Natal, South Africa (Fig. 1). This time period was ideally suited for sampling, as spider populations in northern KwaZulu-Natal peak during this period (e.g. Van der Merwe, Dippenaar-Schoeman & Scholtz, 1996). Sand forest and mixed woodland are two of Maputaland's dominant habitat types (Matthews *et al.*, 2001), and thus most likely to be impacted on by elephants.

Spiders were collected in elephant disturbed sand forest habitats (ESF) inside Tembe Elephant Park (27°01'S, 32°24'E), and mixed woodland (MW) and undisturbed sand forest (USF) habitats adjacent to the western boundary of Tembe. Sand forest is characterized by tree species such as *Dialium schlechteri* Harms and *Erythrophleum lasianthum* Corbishley (Caesalpinioideae) (Moll, 1977; Van Wyk, 1996) and has a poorly developed understory. The surrounding, more open, MW is characterized by woody savanna species such as *Acacia burkei* Benth, *Albizia versicolor* Welw. ex Oliver and *A. adianthifolia* (Schumacher) W.F. Wight (Mimosoideae). It has a well developed grass understory represented by *Aristida*, *Pogonarthria* and *Perotis* species (Moll, 1977, 1980).

Sampling methods and identification

Although spiders were collected during a two-week period only, the use of rapid and intensive biodiversity assessments often results in the majority of the spider species present in an area being captured, as indicated by

cumulative diversity estimators (e.g. Jiménez-Valverde & Lobo, 2007; Cardoso *et al.*, 2008). For each of the three habitat types, five replicated habitat patches were chosen with a distance of approximately 1 km between them (to maintain independence between these sampling points). Patch sizes (in hectares) for the three habitats sampled were determined using IDRISI GIS (Clark Labs, <http://www.clarklabs.org/products/index.cfm>) by Wayne Matthews (KZN Wildlife) and are as follows: ESF (62, 52.4, 29.9, 17.2 and 15.8 ha), MW (218.8, 181.3, 105.3, 66.5 and 24.3 ha), and USF (26.6, 19.2, 15.1, 13.8 and 8.4 ha). The larger patch size of MW can be attributed to the relatively continuous structure of this habitat, while sand forest patches are more isolated and easier to delineate (Matthews *et al.*, 2001). Within each of the fifteen habitat patches various techniques were applied to collect spiders according to the availability of different vegetation layers, for example, sand forests lack a grass stratum. Although different methods were used across the habitat types, we believe that they provide comparable samples of the same guilds (functional groups) of spiders, as there is no grass layer in the sand forest and little leaf litter in the MW. The key comparison of USF versus ESF included all of the same techniques. Each of the sampling techniques described below was conducted once per site.

The following sampling methods were used: Pit traps ($n = 75$): five nonbaited pitfall traps (8.5 cm depth \times 10 cm diameter) filled with 70% ethyl alcohol were randomly placed in each of the fifteen habitat patches and checked every third day over the 14-day period ($n = 1050$ trap nights); tree beating ($n = 300$ tree samples): 20 randomly selected trees per patch received 20 beats per sample; active searching ($n = 75$ samples): five grids of 2×2 m² were searched for 15 min in each habitat patch; sweep netting ($n = 50$ sweep net samples): ten sweep net samples consisting of 20 sweeps each were taken in the mixed woodlands only; leaf litter ($n = 50$ samples): five leaf litter samples in a

2 × 2 m² grid were sifted on a white sheet and the spiders collected with a pooter, in the sand forest habitats only.

Specimens collected were identified up to species level, where possible, by the third author. Voucher specimens are housed at the National Collection of Arachnida (NCA), ARC-Plant Protection Research Institute, Pretoria, South Africa. Due to the large number of immatures collected and the unresolved taxonomy of many families (e.g. Linyphiidae and Theridiidae), some specimens could only be identified to genus or family level, and are referred to as morphospecies, where necessary.

Guilds

Functional groups (guilds) provide additional insight on habitat functioning and utilization by spiders and contribute to our knowledge of ecosystem functioning. This is because spiders have diverse lifestyles and have developed diverse methods of capturing prey (Foelix, 1996). Spiders are broadly grouped as web-builders and active hunters. The active hunters can be further divided into plant wanderers (PW) and ground wanderers (GW). The web-building spiders can be subdivided into different guilds based on the web types they construct: funnel-web builders (FWB), gum-foot-web builders (GWB), orb-web builders (OWB), modified orb-web builders (MOWB), retreat-web builders (RWB), sheet-web builders (SWB) and space-web builders (SPWB).

Statistical analysis

After identification, the data were compiled into a spreadsheet (Microsoft Excel) for analyses. The number of individuals of each species trapped over the course of the study period was summed for each sampling technique and each site. Total spider abundance and species richness per site was compared between habitats using ANOVA with a Tukey–Kramer post-test in GraphPad InStat 3.0 (GraphPad Software Inc., San Diego, CA, USA). In the post-test comparisons, a *q*-value above 3.773 indicates significant differences between the two compared habitats. A linear regression of species richness versus patch size was performed for each habitat separately, and since differences were not significant in any of the habitats this aspect was not considered further. Shannon–Wiener Index of Diversity was calculated for each site and compared between habitats using ANOVA.

Data were imported into Primer for community analyses (Clarke & Warwick, 2001), and habitat was included as a

factor. A species–accumulation curve was generated to assess the completeness of sampling. Within Primer, a presence–absence matrix of all species across all sites at all habitats was created. A Bray–Curtis similarity matrix was generated using the presence–absence transformation. Thereafter, we performed three analyses on the resulting matrix.

Firstly, we performed a nonmetric multi-dimensional scaling (MDS), which constructs a map of configuration of the samples based on the underlying similarity matrix and attempts to satisfy all of the rankings in similarities across sites (Clarke & Warwick, 2001). We plotted these results as an MDS plot, which provides a representation of the overall similarity among sites across many dimensions (Clarke & Warwick, 2001). We had high confidence in the resultant 2-D plot as the stress value was <0.05 (Clarke & Warwick, 2001).

Secondly, we performed Cluster analyses of the Bray–Curtis matrix using the CLUSTER procedure in Primer with the group average cluster mode. Contrasting the results of clustering and ordination allows effective interpretation of patterns (Clarke & Warwick, 2001). The information contained within nodes of the cluster dendrogram allows assessment of the percentage difference among associated samples on the MDS plot.

Thirdly, we performed an ANOSIM procedure to assess differences in assemblage structure among habitats. ANOSIM is analogous to an ANOVA, and is performed on the underlying Bray–Curtis similarity matrix (in this case with presence-absence transformations). The results are presented as a global *R* value (analogous to the *F* value from ANOVA), with pairwise *R* values between habitats (which are analogous to post-hoc contrasts) (Clarke & Warwick, 2001). A significant *R*-statistic of close to one indicates distinct differences between the assemblages/habitats compared.

Indicator spider species were identified for each habitat and represent those species assemblages that are characteristic of a particular habitat. Indicator values were obtained by combining a species' relative abundance with its relative frequency of occurrence in a particular habitat (Dufrene & Legendre, 1997). Thus a species' specificity (uniqueness to a particular habitat) and fidelity (frequency of being present in the particular habitat) is expressed as a percentage in comparison with other species in the sampled habitats (Dufrene & Legendre, 1997). A high indicator value illustrates a high affiliation of a species to a particular habitat, whereas a suitable benchmark is

approximately 70% (Van Rensburg *et al.*, 1999; Mcgeoch, Van Rensburg & Botes, 2002).

Results

Spider assemblages are difficult to sample completely, often due to the large number of rare species collected during surveys (generally low evenness), but we managed to accumulate a large proportion of the species present in our sampling (Fig. 2). However, further sampling would clearly be needed if all of the species present were to be sampled. In total, 2808 individual spiders representing 36 families, 144 identified genera and 251 species were collected (Table 1). Spider abundance was significantly different among habitats (ANOVA, $P = 0.011$). Total spider abundance and abundance per site was highest in the USF ($n = 1129$, mean \pm SD = 225.80 ± 54.08), followed by the ESF ($n = 1006$, 201.60 ± 38.77) and MW ($n = 673$, 134.60 ± 23.62). Total abundance was not significantly different between USF and ESF (Tukey–Kramer $q = 1.327$), but differed significantly between USF and MW ($q = 5.002$) and was almost significantly different between ESF and MW ($q = 3.675$).

Species richness was similar in the habitats sampled, being highest in the USF ($S = 179$), followed by the MW ($S = 171$) and ESF ($S = 165$). Differences in species richness (ANOVA, $P = 0.1995$) and Shannon–Wiener Index of Diversity (ANOVA, $P = 0.460$) were not significantly different when compared among habitats. The mean number of species per site was highest in the USF (mean \pm SD = 81.20 ± 14.77), followed by ESF (73.00 ± 6.44) and MW

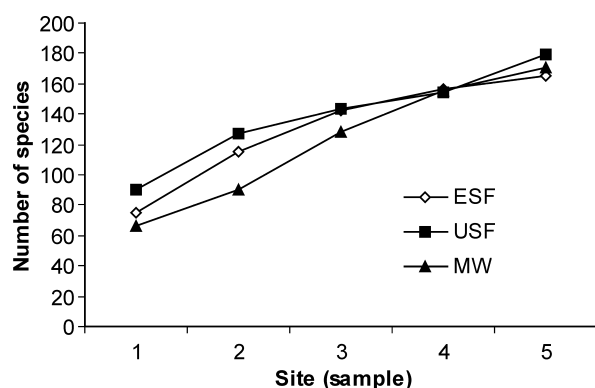


Fig 2 Species accumulation curves for spiders sampled in the Maputaland Centre of Endemism during 2003 in three habitat types (USF, undisturbed sand forest; ESF, elephant disturbed sand forest; MW, mixed woodland)

(68.00 ± 10.03). Despite the apparent similarity between habitats, the species comprising the communities of each habitat were often considerably different (Table 1). The number of individuals representing active hunters ($n = 2098$) far outweighed that of web-builders ($n = 710$). Species richness followed a similar pattern, with the active hunters contributing 165 species (65.7%) and the web-builders only 86 species (34.3%).

Comparison of the efficacy of different sampling methods indicated that beats, sweeps and leaf litter sifting were the most efficient in sampling high numbers and species of spiders compared to pitfall traps and active searching (Table 2). Differences in abundance and species richness collected by each sampling method were not significantly different among habitats, with the following exceptions: beats, which were significantly different among habitats in terms of abundance (ANOVA, $P = 0.0056$) and species richness ($P = 0.0043$), although abundance ($P < 0.01$) and species richness ($P < 0.01$) were only significantly higher in USF than in MW; active searching, where only abundance differed significantly among habitats (ANOVA, $P = 0.0046$), with significantly more spiders collected in USF and ESF than in MW ($P < 0.01$). Leaf litter sifting and sweep-netting did not differ significantly from each other in abundance or species richness, suggesting that the two methods capture comparable numbers and species richness, albeit the respective communities are different.

Regarding the most abundant families, the Thomisidae ($n = 426$) and Salticidae ($n = 403$) had a relatively higher abundance in the MW, the Theridiidae ($n = 366$) and Oxyopidae ($n = 199$) were most abundant in the USF, while Corinnidae ($n = 187$) were most common in the ESF (Fig. 3a). Regarding species richness of the dominant families, Theridiidae ($S = 40$) were most species rich in the USF, Thomisidae ($S = 40$) in the MW, and Salticidae ($S = 35$) in the ESF. Araneidae ($S = 26$) were similarly species rich in the three habitats, while Gnaphosidae ($S = 20$) were more species rich in the ESF and MW than in the USF (Fig. 3b).

The sites within each of the habitat types clustered distinctly (Fig. 4), with the spider assemblage at any site being most similar to those at sites within the same habitat type. The spider assemblage within MW was distinct from those within the two sand forest habitats, which clustered closely (Fig. 4). The ANOSIM results indicated three distinct assemblages (Global $R = 0.834$, $P = 0.001$; pairwise: USF versus ESF: $R = 0.74$, $P = 0.008$; USF and ESF versus

Table 1 The total number of spider species obtained at Tembe Elephant Park and surrounding areas during a field survey during 2003

Family/Genus/Species	Guild	USF	ESF	MW	Total
Family: Araneidae					
<i>Arachnura</i> sp. imm.	OWB	0	0	1	1
<i>Araniella</i> sp. 1 imm.	OWB	4	1	0	5
<i>Araniella</i> sp. 2 imm.	OWB	1	0	1	2
<i>Araneus holzapfelae</i> Lessert, 1936	OWB	1	1	4	6
<i>A. nigroquadratus</i> Lawrence, 1937	OWB	0	0	1	1
<i>Araneus</i> sp. 3 imm.	OWB	1	0	1	2
<i>Caerostris sexcuspidata</i> (Fabricius, 1793)	OWB	0	0	1	1
<i>Cladomelea</i> sp. imm.	MOWB	0	1	2	3
<i>Cyphalonotus larvatus</i> (Simon, 1881)	OWB	7	1	10	18
<i>Cyrtophora citricola</i> (Forsskål, 1775)	OWB	0	1	1	2
<i>Gea infuscata</i> Tullgren, 1910	OWB	1	0	0	1
<i>Hypsosinga lithyphantoides</i> Caporiacco, 1947	OWB	2	0	0	2
<i>Hypsosinga</i> sp. 2 imm.	OWB	2	3	0	5
<i>Isoxya tabulata</i> (Thorell, 1859)	OWB	0	1	0	1
<i>Larinia natalensis</i> (Grasshoff, 1971)	OWB	0	0	2	2
<i>Nemoscolus elongatus</i> Lawrence, 1947	OWB	0	1	0	1
<i>Nemoscolus</i> sp. 2 imm.	OWB	1	2	1	4
<i>Nemoscolus</i> sp. 3 imm.	OWB	1	1	0	2
<i>Nemoscolus</i> sp. 4 imm.	OWB	2	1	1	4
<i>Nemoscolus</i> sp. 5	OWB	0	0	1	1
<i>Neoscona blondeli</i> (Simon, 1885)	OWB	0	2	5	7
<i>N. chiarinii</i> (Pavesi, 1883)	OWB	2	0	0	2
<i>N. quincasea</i> Roberts, 1983	OWB	0	0	1	1
<i>N. subfusca</i> (C.L. Koch, 1837)	OWB	1	1	3	5
<i>Pararaneus cyrtoscapus</i> (Pocock, 1898)	OWB	0	1	0	1
<i>Singa lawrencei</i> (Lessert, 1930)	OWB	2	1	4	7
Family: Barychelidae					
<i>Brachionopus</i> sp. ^a	GW	1	8	1	10
Family: Clubionidae					
<i>Clubiona pupillaris</i> Lawrence, 1938	PW	0	0	1	1
<i>C. umbilensis</i> Lessert, 1923	PW	2	11	6	19
Family: Corinnidae					
<i>Apochinomma formicaeforme</i> Pavesi, 1881	PW	0	2	0	2
<i>Cambalida coriacea</i> Simon, 1909	GW	14	22	1	37
<i>Castianeira</i> sp.	GW	0	0	1	1
<i>Cetonana</i> sp. ^a	PW	1	2	0	3
<i>Copa flavoplumosa</i> Simon, 1885	GW	11	18	3	32
Corinnidae sp. indet.	GW	16	45	0	61
<i>Hortipes aelurisiepae</i> Bosselaers & Jocqué, 2000	GW	3	0	0	3
<i>Merenius alberti</i> Lessert, 1923	GW	14	20	1	35
<i>Merenius</i> sp. 2	GW	1	1	0	2
<i>Orthobula radiata</i> Simon, 1897	GW	0	6	0	6
<i>Trachelas schenkeli</i> Lessert, 1923	PW	0	0	5	5
Family: Ctenidae					
<i>Ctenus gulosus</i> Des Arts, 1912	GW	69	80	7	156
Family: Cyatholipidae					
Cyatholipidae sp. indet.	SWB	2	0	0	2
Family: Cyrtaucheniidae					
<i>Ancylotrypa vryheidensis</i> Hewitt, 1915	GW	0	0	9	9

Table 1 (Continued)

Family/Genus/Species	Guild	USF	ESF	MW	Total
Family: Deinopidae					
<i>Deinopis cylindrica</i> Pocock, 1898	MOWB	1	2	0	3
<i>Menneus camelus</i> Pocock, 1902	MOWB	11	4	1	16
Family: Dictynidae					
<i>Dictyna</i> sp. 1	RWB	1	1	26	28
<i>Dictyna</i> sp. 2	RWB	0	1	1	2
<i>Dictyna</i> sp. 3	RWB	5	2	2	9
<i>Dictyna</i> sp. 4	RWB	1	0	9	10
Dictynidae sp. 1 indet.	RWB	8	3	10	21
Family: Gnaphosidae					
<i>Aphantaulax</i> sp. 1	GW	0	10	2	12
<i>Aphantaulax</i> sp. 2	GW	2	19	3	24
<i>Aphantaulax</i> sp. 3	GW	0	0	1	1
<i>Asemethes ceresicola</i> Tucker, 1923	GW	0	0	2	2
<i>A. numisma</i> Tucker, 1923	GW	0	0	3	3
<i>Asemethes</i> sp. 3	GW	0	0	1	1
<i>Asemethes</i> sp. 4	GW	0	0	1	1
<i>Camillina</i> sp. 1	GW	25	49	1	75
<i>Camillina</i> sp. 2	GW	0	3	0	3
<i>Camillina</i> sp. 3	GW	1	0	0	1
<i>Echeminae</i> sp. imm.	GW	4	5	2	11
<i>Echemus</i> sp. imm.	GW	0	2	0	2
<i>Haplodrassus</i> sp.	GW	0	2	0	2
<i>Megamyrmaekion transvaalensis</i> Tucker, 1923	GW	0	14	0	14
<i>Setaphis calviniensis</i> Tucker, 1923	GW	0	0	1	1
<i>Setaphis</i> sp. 2	GW	0	2	1	3
<i>Setaphis</i> sp. 3	GW	0	0	1	1
<i>Zelotes</i> sp. 1	GW	0	13	2	15
<i>Zelotes</i> sp. 2	GW	1	0	0	1
<i>Zelotinae</i> sp. imm.	GW	0	6	0	6
Family: Hahniidae					
<i>Hahnia lobata</i> Bosmans, 1981	SWB	9	14	0	23
Family: Hersiliidae					
<i>Hersilia sericea</i> Pocock, 1898	PW	0	1	0	1
Family: Linyphiidae					
Linyphiidae sp. 1 indet.	SWB	2	0	0	2
Linyphiidae sp. 2 indet.	SWB	2	4	7	13
Linyphiidae sp. 3 indet.	SWB	0	1	1	2
<i>Meioneta</i> sp. 1	SWB	40	24	2	66
Family: Lycosidae					
<i>Evipomma squamulatum</i> (Simon, 1898)	GW	1	0	0	1
<i>Hippasa australis</i> Lawrence, 1927	GW	1	0	1	2
Lycosidae sp. 1	GW	5	2	2	9
Lycosidae sp. 2	GW	5	16	7	28
Lycosidae sp. 3	GW	0	0	2	2
Lycosidae sp. 4	GW	0	0	1	1
<i>Pardosa</i> sp. 1	GW	0	1	3	4
<i>Pardosa</i> sp. 2	GW	1	2	3	6
<i>Trabea</i> sp. imm.	GW	2	2	3	7
<i>Zenonina mystacina</i> Simon, 1898	GW	1	0	4	5

Table 1 (Continued)

Family/Genus/Species	Guild	USF	ESF	MW	Total
Family: Mimetidae					
<i>Mimetus cornutus</i> Lawrence, 1947	PW	1	1	0	2
Family: Miturgidae					
<i>Cheiracanthium africanum</i> Lessert, 1921	PW	13	9	26	48
<i>C. vansoni</i> Lawrence, 1936	PW	3	0	2	5
<i>Cheiramiona paradisus</i> Lotz, 2002	PW	22	5	14	41
Family: Nemesiidae					
<i>Lepthercus</i> sp. ^a	GW	7	3	0	10
Family: Oecobiidae					
<i>Oecobius navus</i> Blackwall, 1859	PW	1	0	0	1
Family: Oonopidae					
<i>Dysderina speculifera</i> Simon, 1907	GW	0	1	0	1
<i>Gamasomorpha longisetosa</i> Lawrence, 1952	GW	12	7	1	20
<i>Oonops</i> sp. imm.	GW	5	1	0	6
<i>Orchestina</i> sp. imm.	GW	0	1	0	1
Family: Oxyopidae					
<i>Hamataliwa kulczynskii</i> (Lessert, 1915)	PW	9	7	0	16
<i>H. rostrifrons</i> (Lawrence, 1928)	PW	4	16	5	25
<i>Oxyopes jacksoni</i> Lessert, 1915	PW	0	2	11	13
<i>O. schenkeli</i> Lessert, 1927	PW	24	5	2	31
<i>O. vogelsangeri</i> Lessert, 1946	PW	35	20	1	56
<i>Oxyopes</i> sp. 4 imm.	PW	0	0	4	4
<i>Oxyopes</i> sp. 5 ^b	PW	1	1	1	3
<i>Oxyopes</i> sp. 6	PW	48	2	1	51
Family: Palpimanidae					
<i>Palpimanus potteri</i> Lawrence, 1937	GW	3	2	1	6
Family: Philodromidae					
<i>Gephyrota</i> sp. imm.	PW	0	0	1	1
<i>Philodromus brachycephalus</i> Lawrence, 1952	PW	29	21	10	60
<i>Suemus punctatus</i> Lawrence, 1938	GW	0	0	1	1
<i>Thanatus</i> sp. imm.	GW	3	0	0	3
<i>Tibellus minor</i> Lessert, 1919	PW	1	0	6	7
Family: Pholcidae					
<i>Leptopholcus</i> sp.	SPWB	21	0	1	22
Family: Pisauridae					
<i>Charminus</i> sp. imm.	PW	50	35	3	88
<i>Chiasmopes lineatus</i> (Pocock, 1898)	PW	1	4	0	5
<i>Cispius</i> sp. ^b	PW	42	14	2	58
<i>Thalassius margaritatus</i> Pocock, 1898	PW	0	0	1	1
Family: Prodidomidae					
<i>Prodidomus flavipes</i> Lawrence, 1952	GW	0	2	0	2
Family: Salticidae					
<i>Asemonea stella</i> Wanless, 1980	PW	1	1	0	2
<i>Evarcha dotata</i> (Peckham & Peckham, 1903)	PW	9	6	8	23
<i>Evarcha</i> sp. 2	PW	0	2	1	3
<i>Evarcha</i> sp. 3	PW	1	1	1	3
<i>Goleba puella</i> (Simon, 1885)	PW	0	1	0	1
<i>Heliophanus clarus</i> Peckham & Peckham, 1903	PW	1	4	0	5
<i>H. debilis</i> Simon, 1901	PW	0	1	0	1
<i>H. orchestra</i> Simon, 1885	PW	1	0	0	1

Table 1 (Continued)

Family/Genus/Species	Guild	USF	ESF	MW	Total
<i>Hispo inermis</i> (Caporiacco, 1947)	PW	5	5	0	10
<i>Holcolaetis zuluensis</i> Lawrence, 1937	PW	0	1	0	1
<i>Hyllus argyrotroxus</i> Simon, 1902	PW	1	0	5	6
<i>H. treleaveni</i> Peckham & Peckham, 1902	PW	0	0	2	2
<i>Hyllus</i> sp. 3 ^a	PW	1	0	0	1
<i>Icius</i> sp. ^a	GW	0	1	1	2
<i>Leptorchestes</i> sp. ^c	PW	1	4	0	5
<i>Mexcala elegans</i> Peckham & Peckham, 1903	GW	0	2	1	3
<i>Myrmarachne ichneumon</i> (Simon, 1885)	PW	1	0	1	2
<i>Myrmarachne</i> sp. 2 imm.	PW	1	0	0	1
<i>Natta horizontalis</i> Karsch, 1879	GW	0	10	0	10
<i>Pseudicius</i> sp. ^a	PW	0	1	2	3
<i>Rhene</i> sp. ^c	PW	5	1	0	6
<i>Stenaelurillus natalensis</i> Haddad & Wesolowska, 2006	GW	8	24	5	37
<i>Stenaelurillus</i> sp. 2	GW	0	19	1	20
<i>Stenaelurillus</i> sp. 3	GW	4	10	3	17
<i>Stenaelurillus</i> sp. 4	GW	0	3	4	7
<i>Thyene inflata</i> (Gerstaecker, 1873)	PW	9	9	18	36
<i>T. natali</i> Peckham & Peckham, 1903	PW	18	26	34	78
<i>T. semiargentea</i> (Simon, 1884)	PW	0	1	10	11
<i>Thyene</i> sp. 4	PW	4	4	3	11
<i>Thyenula ogdeni</i> Peckham & Peckham, 1903	GW	35	16	22	73
<i>Thyenula</i> sp. 2	GW	0	3	9	12
<i>Tusitala barbata</i> Peckham & Peckham, 1902	PW	2	1	1	4
<i>Viciria</i> sp. ^c	PW	0	2	2	4
Salticidae sp. 1	GW	0	1	0	1
Salticidae sp. 2	GW	0	1	0	1
Family: Scytodidae					
<i>Scytodes maritima</i> Lawrence, 1938	GW	0	0	2	2
Family: Segestriidae					
<i>Ariadna corticola</i> Lawrence, 1952	RWB	1	2	0	3
Family: Selenopidae					
<i>Anyphops decoratus</i> (Lawrence, 1940)	PW	1	1	0	2
Family: Sparassidae					
<i>Olios brachycephalus</i> Lawrence, 1938	PW	0	0	2	2
<i>O. chelififer</i> Lawrence, 1937	PW	9	9	7	25
<i>Olios</i> sp. 3 imm.	PW	0	1	0	1
<i>Palystes</i> sp. imm.	PW	0	2	0	2
Family: Theridiidae					
<i>Achaearanae</i> sp. 1	GWB	9	9	5	23
<i>Achaearanae</i> sp. 2	GWB	2	1	0	3
<i>Anelosimus</i> sp. 1	GWB	2	2	1	5
<i>Anelosimus</i> sp. 2	GWB	4	0	3	7
<i>Anelosimus</i> sp. 3	GWB	0	0	2	2
<i>Argyrodes</i> sp. 1	GWB	7	1	0	8
<i>Argyrodes</i> sp. 2	GWB	4	3	1	8
<i>Argyrodes</i> sp. 3	GWB	2	0	0	2
<i>Argyrodes</i> sp. 4	GWB	1	0	0	1
<i>Chorizopella</i> sp. 1	GWB	5	2	1	8
<i>Chorizopella</i> sp. 2 imm.	GWB	4	5	0	9

Table 1 (Continued)

Family/Genus/Species	Guild	USF	ESF	MW	Total
<i>Chorizopella</i> sp. 3 imm.	GWB	11	1	1	13
<i>Dipoena</i> sp. 1	GWB	3	0	2	5
<i>Dipoena</i> sp. 2	GWB	0	0	1	1
<i>Dipoena</i> sp. 3	GWB	1	1	0	2
<i>Dipoena</i> sp. 4	GWB	9	2	11	22
<i>Dipoenura</i> sp. 1	GWB	11	5	2	18
<i>Dipoenura</i> sp. 2	GWB	1	7	1	9
<i>Dipoenura</i> sp. 3 imm.	GWB	4	1	0	5
<i>Dipoenura</i> sp. 4	GWB	2	0	1	3
<i>Enoplognatha</i> sp.	GWB	22	0	0	22
<i>Episinus</i> sp. 1	GWB	3	0	1	4
<i>Episinus</i> sp. 2	GWB	0	1	4	5
<i>Episinus</i> sp. 3	GWB	5	0	1	6
<i>Euryopsis</i> sp. 1	GWB	1	3	1	5
<i>Euryopsis</i> sp. 2	GWB	6	2	1	9
<i>Latrodectus cinctus</i> (Blackwall, 1865)	GWB	0	0	1	1
<i>L. geometricus</i> (C.L. Koch, 1841)	GWB	1	0	8	9
<i>Phoroncidia</i> sp. 1	GWB	28	13	13	54
<i>Phoroncidia</i> sp. 2	GWB	8	0	0	8
<i>Phoroncidia</i> sp. 3	GWB	1	3	2	6
<i>Steatoda</i> sp.	GWB	1	0	0	1
<i>Theridion</i> sp. 1	GWB	7	4	5	16
<i>Theridion</i> sp. 2	GWB	14	6	8	28
<i>Theridion</i> sp. 3	GWB	6	7	2	15
<i>Theridion</i> sp. 4	GWB	1	1	0	2
<i>Theridion</i> sp. 5	GWB	7	0	0	7
<i>Theridion</i> sp. 6	GWB	1	0	2	3
<i>Theridion</i> sp. 7	GWB	1	0	0	1
<i>Tidarren</i> sp.	GWB	10	0	0	10
Family: Thomisidae					
<i>Cynathea bicolor</i> Simon, 1895	PW	0	0	1	1
<i>Diaea puncta</i> Karsch, 1884	PW	7	6	8	21
<i>Firmicus bragantinus</i> (Brito Capello, 1866)	PW	1	0	1	2
<i>Firmicus</i> sp. 2	PW	1	0	0	1
<i>Heriaeus crassispinus</i> Lawrence, 1942	PW	0	4	1	5
<i>H. fimbriatus</i> Lawrence, 1942	PW	3	0	0	3
<i>Monaeses austrinus</i> Simon, 1910	PW	0	0	16	16
<i>M. paradoxus</i> (Lucas, 1846)	PW	0	0	1	1
<i>M. pustulosus</i> Pavesi, 1895	PW	0	0	4	4
<i>Mystaria</i> sp.	PW	3	1	0	4
<i>Oxytate ribes</i> (Jézéquel, 1964)	PW	1	4	1	6
<i>Pactates compactus</i> Lawrence, 1947	PW	4	5	1	10
<i>Parabomis anabensis</i> Lawrence, 1928	PW	3	0	0	3
<i>Paramystaria variabilis</i> Lessert, 1919	PW	1	3	1	5
<i>Parasmodix quadrituberculata</i> Jézéquel, 1966	PW	0	0	1	1
<i>Pherecydes zebra</i> Lawrence, 1927	PW	0	1	0	1
<i>Pherecydes</i> sp. 2	PW	1	3	3	7
<i>Phrynarachne</i> sp.	PW	3	1	0	4
<i>Runcinia erythrina</i> Jézéquel, 1964	PW	0	0	4	4
<i>R. flavida</i> (Simon, 1881)	PW	0	0	22	22

Table 1 (Continued)

Family/Genus/Species	Guild	USF	ESF	MW	Total
<i>Simorcus cotti</i> Lessert, 1936	PW	1	2	18	21
<i>Stephanopsis</i> sp.	PW	1	10	0	11
<i>Stiphropus</i> sp.	PW	0	1	0	1
<i>Sylligma hirsutus</i> Simon, 1895	GW	0	0	1	1
<i>Sylligma</i> sp. 2	GW	0	1	0	1
<i>Synema decens</i> (Karsch, 1878)	PW	0	0	16	16
<i>S. langheldi</i> Dahl, 1907	PW	1	0	0	1
<i>S. vallotoni</i> Lessert, 1923	PW	0	0	2	2
<i>Tagulis granulatus</i> Simon, 1895	PW	12	2	0	14
<i>Thomisops bullatus</i> Simon, 1895	PW	1	0	19	20
<i>Thomisus blandus</i> Karsch, 1880	PW	0	0	5	5
<i>T. daradioides</i> Simon, 1890	PW	0	0	2	2
<i>T. granulatus</i> Karsch, 1880	PW	0	0	8	8
<i>T. kalaharinus</i> Lawrence, 1936	PW	0	0	1	1
<i>T. scrupus</i> (Simon, 1886)	PW	0	2	0	2
<i>T. spiculosus</i> Pocock, 1901	PW	0	0	4	4
<i>Tmarus comellinii</i> Garcia-Neto, 1989	PW	6	8	3	17
<i>T. hirsutus</i> Comellini, 1955	PW	43	47	10	100
<i>T. natalensis</i> Lessert, 1925	PW	43	21	12	76
<i>Trichopagis manicata</i> Simon, 1886	PW	0	0	2	2
Family: Trochanteriidae					
<i>Platyoides walteri</i> (Karsch, 1886)	PW	0	1	0	1
Family: Uloboridae					
<i>Miagrammopes constrictus</i> Purcell, 1904	MOWB	10	3	0	13
<i>Miagrammopes</i> sp. 2	MOWB	1	0	0	1
<i>Philoponella angolensis</i> (Lessert, 1933)	MOWB	6	0	0	6
<i>Uloborus plumipes</i> Lucas, 1846	OWB	2	1	0	3
<i>Zosis geniculata</i> (Olivier, 1789)	MOWB	10	2	0	12
Family: Zodariidae					
<i>Caesetius biprocessiger</i> (Lawrence, 1952)	GW	5	4	1	10
<i>Diores</i> sp.	GW	0	0	1	1
<i>Hermippus tenebrosus</i> Jocqué, 1986	GW	2	18	0	20
<i>Ranops</i> sp. ^a	GW	1	0	2	3
<i>Systemoplacis fagei</i> (Lawrence, 1936)	GW	5	0	0	5
<i>Thaumastochilus</i> sp. imm.	PW	1	0	0	1
Family: Zoropsidae					
<i>Griswoldia</i> sp. imm.	GW	0	1	0	1
Total		1129	1006	673	2808

^aA new species.

^bA possible new species.

^cAn uncertain determination

imm., immature; USF, undisturbed sand forest; ESF, elephant disturbed sand forest; MW, mixed woodland. Guild abbreviations: PW, plant wanderers; GW, ground wanderers; FWB, funnel-web builders; GWB, gumfoot-web builders; OWB, orb-web builders; MOWB, modified orb-web builders; RWB, retreat-web builders; SWB, sheet-web builders; SPWB, space-web builders.

MW: both $R = 1.0$, $P = 0.008$). The range in similarity among sites within the USF was 48–58%, within the ESF was 43–53%, and within the MW was 41–49%. The range in similarity between sites within the two sand forest types

and the MW was 20–38%, while between the two sand forest types it was 38–51%.

The largest number of characteristic species, i.e. those with percentage indicator values $\geq 70\%$, were identified for

Table 2 Summary of sampling efficacy (range and mean \pm SD number of individuals and number of species for five sites in each habitat) for five methods used to collect spiders at Tembe Elephant Park and surrounding areas during a field survey during 2003

	USF		ESF		MW		Average
	Range	Mean \pm SD	Range	Mean \pm SD	Range	Mean \pm SD	Mean \pm SD
<i>Abundance</i>							
Active searching	22–36	26.6 \pm 6.5	23–41	33.8 \pm 7.3	5–31	12.0 \pm 10.8	24.1 \pm 12.2
Beats	82–191	126.4 \pm 43.6	50–116	81.8 \pm 24.1	29–82	46.6 \pm 20.9	84.9 \pm 44.5
Litter sifting	51–67	54.8 \pm 7.9	45–95	68.2 \pm 21.7	–	–	61.5 \pm 16.9
Pitfall traps	11–35	18.0 \pm 9.9	8–38	17.4 \pm 11.9	7–23	14.6 \pm 7.4	16.7 \pm 9.3
Sweeps	–	–	–	–	54–74	61.8 \pm 8.7	61.8 \pm 8.7
<i>Species richness</i>							
Active searching	11–17	14.6 \pm 2.3	11–20	16.2 \pm 3.3	5–21	9.6 \pm 6.7	13.5 \pm 5.1
Beats	37–60	50.6 \pm 9.0	29–47	40.0 \pm 7.1	23–41	29.2 \pm 8.0	39.9 \pm 11.7
Litter sifting	23–38	27.8 \pm 5.9	22–33	27.8 \pm 4.3	–	–	27.8 \pm 4.9
Pitfall traps	6–15	8.2 \pm 4.0	2–13	8.8 \pm 4.2	5–19	11.4 \pm 6.3	9.5 \pm 4.8
Sweeps	–	–	–	–	27–38	31.4 \pm 4.4	31.4 \pm 4.4

Habitat abbreviations: USF, undisturbed sand forest; ESF, elephant disturbed sand forest; MW, mixed woodland.

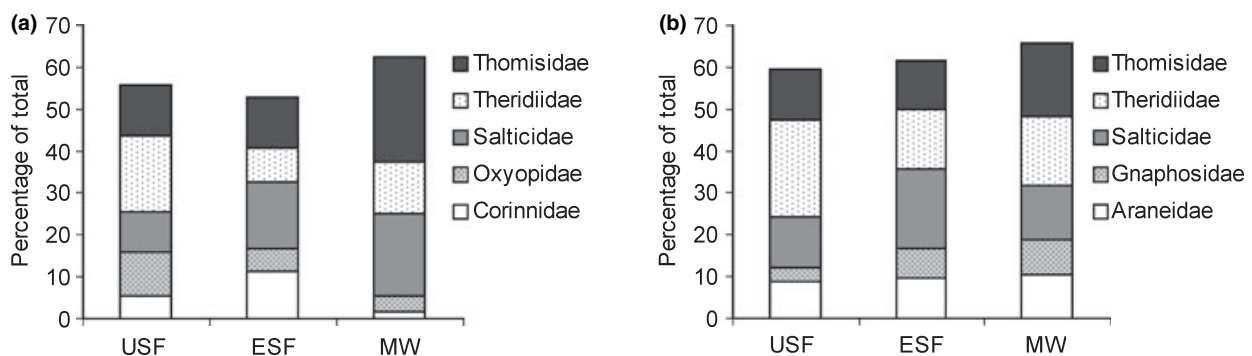


Fig 3 Percentage of total fauna of the five most abundant (a) and species rich (b) spider families collected in the Maputaland Centre of Endemism during 2003 (USF, undisturbed sand forest; ESF, elephant disturbed sand forest; MW, mixed woodland)

MW, followed by USF and ESF (Table 3). USF was dominated mainly by web-builders (67%), while 100% of the indicator species in ESF and 91% of the species in MW were either plant or ground wanderers (Tables 1 and 3). This result supports the notion that, as for the vegetation structure (see proposal of Van Rensburg *et al.*, 2000), general spider functional groups for those species characteristic of ESF and MW are more similar than those of ESF compared to USF.

Among the more abundant species, *Ctenus gulosus* Des Arts (Ctenidae), *Oxyopes vogelsangeri* Lessert (Oxyopidae), *Charminus* sp. (Pisauridae) and *Tmarus comellinii* Garcia-Neto (Thomisidae) are similarly abundant in ESF and USF and less common in MW, and are not negatively impacted by elephant disturbance (Table 1). *Camillina* sp. 1 (Gnaphosi-

dae), *Natta horizontalis* Karsch (Salticidae), *Brachionopus* sp. (Barychelidae) and several Corinnidae species apparently benefit from habitat degradation caused by elephants, and were clearly more abundant in ESF than USF and MW (Table 1). Several species seem to be distinctly negatively impacted by elephant foraging, including *Oxyopes schenkeli* Lessert and *Oxyopes* sp. 6, *Cispus* sp. (Pisauridae) and *Enoplognatha* sp. (Theridiidae), and were more abundant in USF (Table 1). Apparent MW specialists include *Dictyna* sp. 1 (Dictynidae), *Monaeses austrinus* Simon, *Runcinia flavida* Simon, *Synema decens* (Karsch) and *Thomisops bullatus* Simon (Thomisidae). No species were common in ESF and MW and scarce in USF, suggesting that elephant-induced impacts on sand forest spider assemblages do not lead to an immediate transition towards a MW assemblage structure.

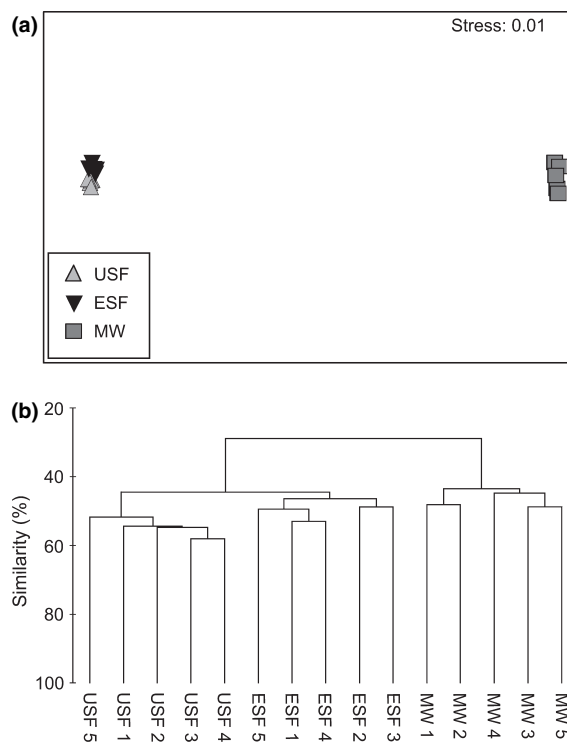


Fig 4 Differences in spider community structure among sites in different habitat types sampled in the Maputaland Centre of Endemism during 2003 based on Bray-Curtis Similarity Matrix with presence-absence transformation. (a) MDS plot with sites within the two sand forest habitats clustering separately to those within the mixed woodland habitat. (b) Cluster dendrogram with three distinct clusters according to habitat (USF, undisturbed sand forest; ESF, elephant disturbed sand forest; MW, mixed woodland)

Discussion

Spider assemblages exhibited a large degree of homogeneity within the habitats examined. Numerous studies explain vegetation influences on spider ecology (e.g. Robinson, 1981; Greenstone, 1984; Hurd & Fagan, 1992; Hsieh, Lin & Tso, 2003). Spider assemblages of USF and ESF showed the greatest similarity despite clear differences in the structural complexity of the vegetation. The five sites sampled within each were also more similar to each other than to the other sand forest habitat, suggesting distinctive assemblages occur in each, despite considerable species overlap. This could be because USF provides very dense and complex vegetation structures, whereas animals (especially elephants) foraging in the ESF inside Tembe open up this vegetation type (Van Rensburg *et al.*, 1999), affecting the resident spider assemblages. This is supported by the contrasting abundance of spider species comprising the assemblages of USF and ESF, which differed between the two habitats (Table 1), and also the lower abundance and species richness of foliage-dwelling spiders collected in ESF, albeit not significantly different (Table 2).

Functional groups give important insight in guild composition of spiders, and by having their own microhabitat preferences for specific vegetation, each responds differently to changes in habitat (Hsieh *et al.*, 2003). Complex vegetation provides more options for microhabitat selection and prey capture, especially amongst web-builders (Robinson, 1981; Greenstone, 1984). The USF habitats supply stable and complex architectural configurations ideal for web-

Table 3 Percentage indicator values (IndVal > 70%) of spider species for three different habitat comparisons in the Maputaland Centre of Endemism sampled during 2003, relative to their habitat fidelity and frequency

Undisturbed sand forest	% IndVal	Elephant disturbed sand forest	% IndVal	Mixed woodland	% IndVal
<i>Leptopholcus</i> sp. (SPWB)	95	<i>Orthobula radiata</i> (GW)	100	<i>Monaeses austrinus</i> (PW)	100
<i>Oxyopes</i> sp. 6 (PW)	94	<i>Megamyrmaekion transvaalensis</i> (GW)	80	<i>Runcinia flavida</i> (PW)	100
<i>Chorizopella</i> sp. 3 (GWB)	85	<i>Natta horizontalis</i> (GW)	80	<i>Thomisops bullatus</i> (PW)	95
<i>Philoponella angolensis</i> (MOWB)	80	<i>Zelotinae</i> sp. (GW)	80	<i>Dictyna</i> sp. 1 (RWB)	93
<i>Tidarren</i> sp. 1 (GWB)	80	<i>Corinnidae</i> sp. (GW)	74	<i>Simorcus zuluanus</i> (PW)	86
<i>Oxyopes schenkeli</i> (PW)	77	<i>Stephanopsis</i> sp. (PW)	73	<i>Oxyopes</i> sp. 4 (PW)	85
<i>Miagrammopes constrictus</i> (MOWB)	77			<i>Ancylotrypa vryheidensis</i> (GW)	80
<i>Cispius</i> sp. (PW)	74			<i>Synema decens</i> (PW)	80
<i>Argyrodes</i> sp. 1 (GWB)	70			<i>Thomisus blandus</i> (PW)	80
				<i>Thomisus granulatus</i> (PW)	80
				<i>Thyene semiargentea</i> (PW)	77

The functional group or guild of each species is given in parentheses. Guild abbreviations: PW, plant wanderers; GW, ground wanderers; GWB, gumfoot-web builders; MOWB, modified orb-web builders; RWB, retreat-web builders; SPWB, space-web builders.

builders, which is reflected in the high proportion of web-building indicator species in this habitat. Spider guilds in the ESF show different interacting patterns, and spiders might compete for microhabitats such as structural retreats that are less exposed to predators.

Leaf litter depth may influence the presence of prey species, temperature variation, moisture and structural retreats (Uetz, 1979), with web-builders being more sensitive to leaf litter depth than hunting spiders (Bultman & Uetz, 1982). The ESF, with its lower vegetative density, might affect web-builders by not providing as deep a leaf litter layer as in the USF. Spider densities and diversity may be higher near logs than in surrounding areas on the forest floor (Varady-Szabo & Buddle, 2006), so trampling (leaf litter compaction) and feeding by elephants (higher log densities) may further affect spider communities.

The changes in sand forest structure and composition translates into changes within the invertebrate community (Botes *et al.*, 2006; this study). Invertebrates comprise the vast majority of species in terrestrial ecosystems, and as such should be an important concern for conservation managers. Elephant impacts on vegetation certainly alter the structure of sand forest spider assemblages, but these impacts also raise the species richness of sand forest through the creation of new microhabitats. Ideally, elephant populations need to be maintained at levels that do not result in sand forest degradation, as the conservation of sand forest endemics should enjoy preference over raising general biodiversity.

We have identified indicator species that can be used to compliment those based purely on vegetative communities, to monitor shifts in community structure and indicate the quality/disturbance status of particular sand forest patches as a result of elephant impacts. However, further investigations are necessary to verify the application (i.e. robustness of the species to identify thresholds of concern) of the indicator species in monitoring changes in sand forest, on various temporal and spatial scales. As potential indicator species may often be lost from one area to the next (Sætersdal, Gjerde & Blom, 2005), the use of such assessments using spiders would require thorough baseline sampling to identify indicator species at a particular site. Using a holistic approach in elephant management (integrating data on invertebrates with reptiles, birds and small mammals) is necessary, as each species adapts differently to environmental pressures. Within Maputaland, the use of these indicator species should be further investigated to assess

whether similar responses are demonstrated to human disturbance, fire and drought, which represent other threats to sand forests (Matthews *et al.*, 2001).

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