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ABSTRACT

Little attention has been placed on the biodiversity of natural savannas, which are declining worldwide. On the island of Trinidad, West Indies, many studies have been conducted on the flora in the Aripo Savannas Scientific Reserve, but none on the arachnid fauna it contains. This study aims to document and compare the biodiversity of the spiders found in the three main habitat types in the reserve: savanna, palm marsh and marsh forest. Three localities of each habitat were sampled for 15 hours each, utilising sweep-netting and visual search methods to collect spiders from a wide spectrum of microhabitats. The spider fauna was separated into three functional groups: plant wanderers, ground wanderers and web-builders. A total of 585 individuals belonging to 69 species distributed among 21 families were found on the reserve. Data were analysed using Analysis of Variance (ANOVA), species abundance models and multi-dimensional scaling plots. Habitat type was found to have no significant influence on species richness, diversity, evenness or dominance. All habitat types were dominated by web-builders; a smaller proportion of plant and ground wanderers were found as could be expected since most species in these groups are cryptic. However, the savanna possessed the most distinct spider species assemblage.

Key words: Araneae, marsh forest, palm marsh, savanna, biodiversity, species composition.

INTRODUCTION

Many studies state that tropical habitats possess high species richness and abundance, for example Robinson *et al.* (1974) and Wilson (1998) emphasize that rainforests have greater richness and abundance than other tropical habitats such as grasslands or savannas. Grassland habitats are not considered high in biodiversity and have largely been lost in parts of the world such as North America where approximately only 4% of this habitat remains (Richardson and Hanks 2009). The amount of natural savanna in Trinidad has decreased over the decades with the Piarco and O'Meara Savannas converted into an international airport and industrial estate respectively (Richardson 1963). The remaining savannas include the Aripo Savannas Scientific Reserve which experiences numerous threats from human activities including mining, logging, squatting (Lum Young 2006) and fires (Comeau 1990).

There is a consensus that information is lacking on the biodiversity of arthropods globally (Floren and Deeleman-Reinhold 2005). The Aripo Savannas are the best documented of all the savannas in Trinidad in terms of vegetation (Beard 1946; Richardson 1963), with many endemic species (Richardson 1963). However, very little has been focused on the fauna found in these savannas. Natural reserves provide the opportunity to study the biodiversity of habitats in their primary state. Knowledge of species distribution is also vital if they are to be conserved (Cardoso 2009). Since invertebrates are a major component of terrestrial ecosystems, they should be an important concern in terms of continued conservation

efforts (Haddad *et al.* 2009).

This study focuses on spiders, which make excellent subjects for studying biodiversity since they are abundant, diverse, easily collected and functionally significant in ecosystems as prey while acting as predators themselves (Cardoso *et al.* 2008; Oxborough *et al.* 2005; Sharma *et al.* 2010; Stratton *et al.* 1979; Wise 1993). Their interaction with the biotic and abiotic components of their environment reflects changes in the ecology of the habitat they occupy (Haddad *et al.* 2009; Uetz 1991; Hsieh *et al.* 2003; Hsieh and Linsenmair 2011). Spiders also depend on vegetation structure for protection from predators and the elements, maintenance of the microclimate and as structures for web attachment (Wise 1993).

This study aims to fill an important information gap by documenting the biodiversity and community structure of spiders in one of the most unique protected areas in this country and by examining species diversity and composition of the spider fauna of the major habitats found in the Aripo Savannas.

METHODOLOGY

Study site

The Aripo Savannas Scientific Reserve is located within the Long Stretch Forest Reserve in the east-central section of the Northern Plain (Richardson 1963) (10°35'30" N, 61°12'0" W) and is comprised of approximately 1800 hectares. The area experiences an average maximum monthly temperature of 32°C in May and an average minimum of around 20°C in May, with the diurnal variation

in temperature around 10°C and an annual rainfall of 250–280 cm (Richardson 1963). In this study I sampled three habitat types found in the Aripo Savannas (according to Beard 1946): savanna, palm marsh and marsh forest (Fig. 1). Sampling was carried out in Cumuto, Wallerfield and Valencia. Sites of savanna, marsh forest and palm marsh acting as representatives of these habitat types were sampled in each of these localities and selected based on accessibility and safety issues.

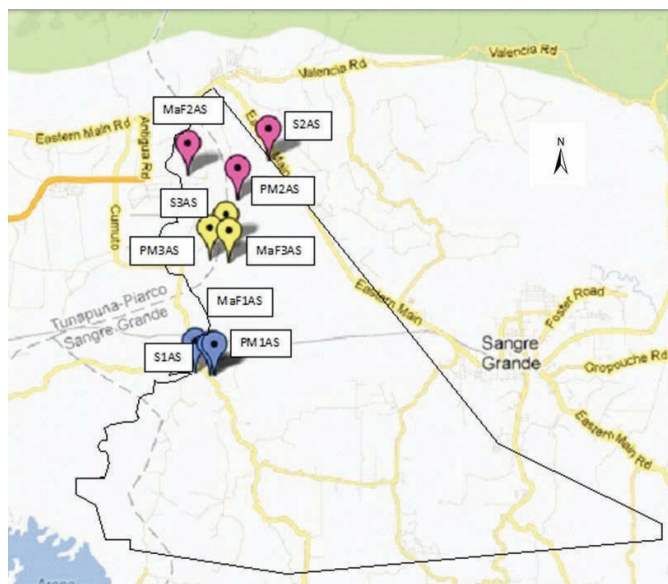


Fig. 1. Map showing sites sampled in the Aripo Savannas for the period March 2006 to May 2009. Site abbreviations as in Table 2.

Field collection and lab analysis

Each habitat was sampled at three localities (Table 1) and sampling effort was standardised across all sites (Sewlal 2013). Data were collected using two methods; sweep-netting and visual search, which ensured thorough and rapid collection of a majority of species. Sweep-netting involved the use of a canvas insect net to sweep the understorey vegetation. After approximately 15 to 20 sweeps, the contents of the net were checked and large pieces of vegetation like leaves and twigs were shaken before removal to dislodge any spiders. Specimens were transferred to a vial of 70% alcohol within the net. Visual search involved the collector walking around and collecting the spiders seen by hand. This method included specimens found on the surface of stems, logs, plants and leaf litter, but excluded under stones and logs as it was primarily designed to look at orb-weavers (Sewlal 2013). Five sampling sessions at each locality, each consisting of a 2 h visual search and 1h of sweep-netting, were undertaken, as preliminary surveys indicated that this was sufficient in order to collect a majority of the species at each site (Sewlal 2013). A stopwatch was used to time each sampling session and it

Table 1. GPS co-ordinates of the sites of marsh forest, palm marsh and savanna habitats sampled in the Aripo Savannas Scientific Reserve for the period March 2006 to May 2009.

Habitat Type	Site 1	Site 2	Site 3
Marsh Forest	10.583608, -61.203461	10.630241, -61.209812	10.609931, -61.200006
Palm Marsh	10.584262, -61.207967	10.624589, -61.197925	10.610627, -61.204362
Savanna	10.583587, -61.203418	10.633615, -61.190758	10.613791, -61.2008

was paused during data recording. Sampling at each site was completed within a period of two weeks to reduce the possibility of species richness inflation due to transient species. Preliminary sampling carried out during both wet and dry seasons did not yield differences in species biodiversity (Sewlal 2013), therefore data from different seasons were combined. Night-time sampling was not carried out due to safety concerns. This was addressed by using sweep-netting which will dislodge nocturnal species resting in the vegetation.

Data analysis

Biodiversity

The completeness of sampling at each site was determined through the use of species accumulation curves of the observed species richness (S) (Fig. 2). The Shannon (H'), Simpson (D) and Berger-Parker (d) indices which determine species diversity, species evenness and dominance respectively, were also calculated. It should be noted that based on the recommendation of Downie *et al.* (1995) and Magurran (2004) in this study the Simpson index was calculated using $D = 1/y$, where $y = \sum(n_i(n_i - 1) / N(N-1))$ in its reciprocal form, in order to produce a measure directly related to diversity. All the data were first checked for normality using the Anderson Darling Normality Test in Minitab 14 and transformed if not normally distributed, after which a series of one-factor ANOVA tests were carried out for S , H' , D and d to determine if these biodiversity parameters were significantly different among the habitats sampled.

Species composition

Rank abundance curves were plotted to better illustrate the relationship between species richness and evenness (Magurran 2004). Each graph was fitted to four well-known species abundance models: log series, truncated log normal, geometric series and broken stick using calculations given in Magurran (1988, 2004) to determine the

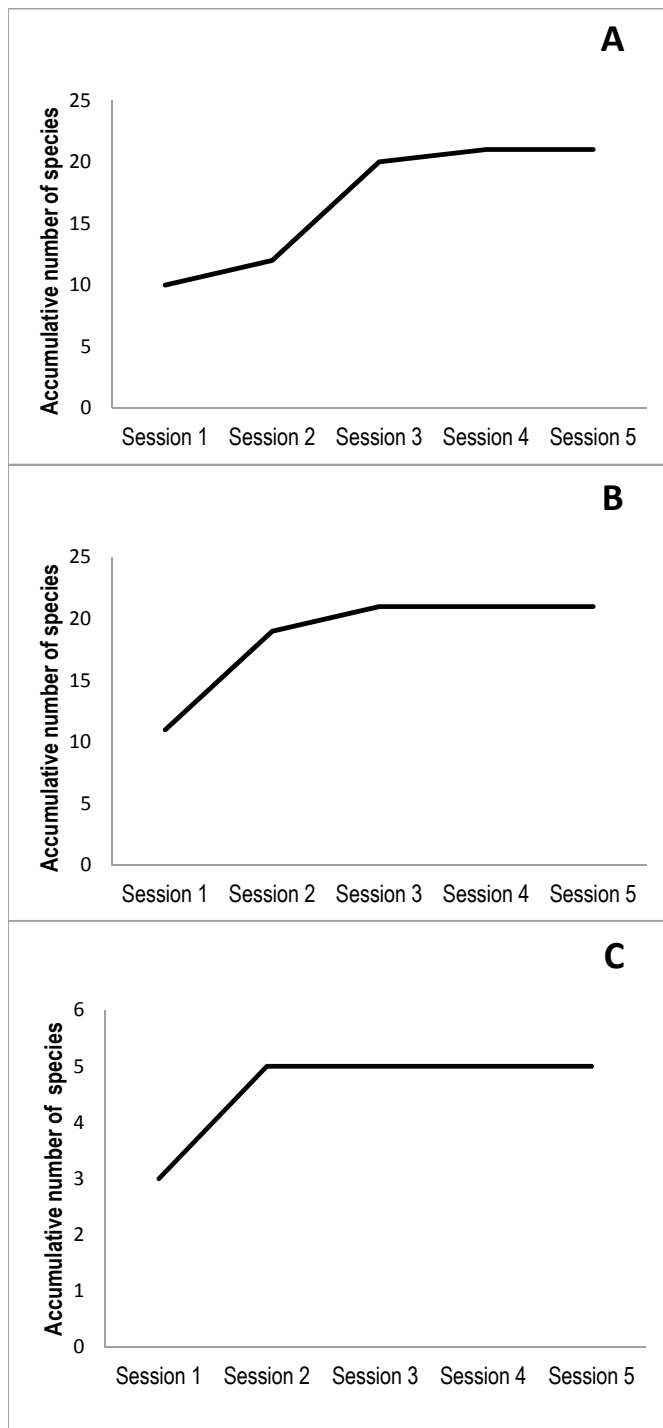


Fig. 2. Representative species accumulation curves for (A) marsh forest (site MaF1), (B) palm marsh (site PM2) and (C) savanna (site S3).

ecological conditions of the spider community found in these habitats. The curve was determined to fit the model if the test statistic was lower than the critical value. The test statistic and critical value for the log series, geometric series and truncated log normal curves were denoted by D and $D_{0.05}$ respectively, while for the broken stick model it was denoted by χ^2 and $\chi^2_{0.05}$. Community structure was

determined by conducting cluster analysis (Barlow *et al.* 2007; Gardner *et al.* 2007) using Primer 5 software (Clarke and Warwick 2001). The data were first transformed using presence/absence and Bray-Curtis similarity to produce a similarity matrix which was then used to generate a cluster dendrogram. The default options were selected for this calculation including the group average linkage cluster mode.

Functional groups

According to Whitmore *et al.* (2002), functional groups contain species that “potentially compete for jointly limited resources”. Separating spiders into functional groups provides valuable insight into their composition as each group has its own microhabitat, vegetation preferences and responds differently to changes in habitat (Haddad *et al.* 2009; Hsieh *et al.* 2003). In this study the spider families were arranged into three functional groups: ground wanderers, plant wanderers and web-builders, based on their predatory methods and habitat preferences (Whitmore *et al.* 2002).

RESULTS

Sampling yielded a total of 585 individuals belonging to 69 species and 21 families (Table 2) which were divided among savanna (254 individuals; 22 species), marsh forest (204 individuals; 43 species) and palm marsh (127 individuals; 37 species) (Table 3). However, there was no significant difference between the abundance of individuals found in each habitat type according to a one-way ANOVA ($F_{2,215} = 0.35$; $P = 0.704$). One-way ANOVA tests also showed that habitat did not influence species richness ($F_{2,8} = 1.16$; $P = 0.38$), species diversity ($F_{2,8} = 3.08$; $P = 0.12$), species evenness ($F_{2,8} = 3.11$; $P = 0.12$) or dominance ($F_{2,8} = 4.1$; $P = 0.076$).

The rank abundance curves (Fig. 3) for the savanna ($D = 0.087$; $D_{0.05} = 14.067$) and palm marsh ($D = 0.047$; $D_{0.05} = 14.067$) habitats were found to fit the log series model indicating that species arrived at the habitat in random intervals (Magurran 2004). However, marsh forest ($\chi^2_4 = 5.96$; $\chi^2_{0.05} = 14.067$) fitted the broken stick model as they generated a test statistic lower than the critical value. The latter model indicates that the species are uniformly distributed among the habitat, most likely due to a relatively even sharing of an important ecological factor between species (Murphy 2004), or that the species present possess equal competitive ability for niche space (Magurran 2004).

Species composition

Some families dominated specific habitat types, for instance, Miturgidae, Deinopidae, Theridiosomatidae and Prodomidae were only found in marsh forest, Sparassidae only in palm marsh and Anapidae, Nephilidae and Gna-

phosidae were only found in savanna (Fig. 4). Overall, a limited number of families were found in the savanna habitat.

A cluster dendrogram (Fig. 5) of the data shows that the marsh forest and palm marsh habitats at each site were most similar to each other, with the savanna habitat forming a distinct group. It must be noted that the borders of these habitats were not sampled, thus eliminating the influence of edge effects on the results.

Functional groups

Web-builders dominated all habitat types in terms of abundance and species richness (Fig. 6a and b). In terms of species richness, the number of web-builders and ground wanderers increases slightly from savanna to palm marsh and then to marsh forest, while the number of plant wanderers decreases. In terms of abundance, palm marsh contained the most plant wanderers followed by marsh forest then savanna. ANOVA tests showed that species richness and abundance were not significantly different among the different habitats for each functional group: web-builders (S: $F_{2,8}=1.76$; $P=0.25$), (N: $F_{2,8}=0.73$; $P=0.52$); ground wanderers (S: $F_{2,8}=0.78$; $P=0.501$), (N: $F_{2,8}=0.73$; $P=0.52$); or plant wanderers (S: $F_{2,8}=0.19$; $P=0.84$), (N: $F_{2,8}=0.08$; $P=0.92$).

DISCUSSION

This study shows that the Aripo Savannas contain substantial biodiversity in terms of spiders, containing 21 families out of the 52 (40%) confirmed to be present in Trinidad and Tobago (Sewlal 2012). However, one-way ANOVA tests confirm that there was no significant difference in the biodiversity components among the different habitat types. This lack of difference could be due to the relatively close proximity of these habitats to each other (Fig. 1) thus facilitating easy movement of species between them, especially with respect to the marsh forest and palm marsh habitats. Sensitivity to sample size was disadvantageous to the Shannon index (Magurran 2004) because it works on the assumption that all species are represented in the sample because individuals are randomly sampled from an infinitely large community. Therefore its sensitivity to relative species abundance and richness makes the interpretation of the results tricky when it comes to comparing sites (Magurran 2004).

The savanna habitat was shown to possess a unique species assemblage (Fig. 5). This study also showed that some families were found only in one habitat type (Fig. 4) however, further sampling of different habitats not included in this study may show them to be present in multiple habitats.

There were also no significant differences in species

richness and abundance among the habitats even when the data were organized into functional groups. Web-builders were found to dominate all habitat types in terms of species richness and abundance (Fig. 6a and b). The lack of ground wanderers could be due to the sampling methods used which did not include pitfall trapping which specifically targets members of this group. However, the placement of pitfall traps was not feasible in the sites of palm marsh sampled as the ground was very marshy and waterlogged and flooded in some instances which would cause the traps to fill with water rendering them useless. However, the low abundance and species richness of plant wanderers (Fig. 6a and b) could not be attributed to the collecting methods used, since sweep-netting would have collected members of this guild by dislodging them from the vegetation. Web-builder dominance of savanna habitat has also been observed in tropical savannas in other parts of the world like the Nylsvley Nature Reserve in South Africa (Dippenaar-Schoeman *et al.* 1989).

All functional groups in the Aripo Savannas follow the trend of an increase in species richness along with an increase in structural complexity (Fig. 6b). Many studies state habitat complexity as a major influencing factor of spider abundance and species richness (Hatley and MacMahon 1980; Halaj *et al.* 1998; Stratton *et al.* 1979), exhibiting a greater influence than prey abundance (Wise 1993). It is expected to be a major factor for web site selection for web-building spiders as habitat complexity provides more sites for web attachment (Riechert and Gillespie 1986; Uetz 1991). Habitat complexity also provides the spider with protection from strong winds or flying debris that could potentially damage the web (Enders 1974, 1976, 1977; Hodge 1988) and from thermal extremes allowing it to stay on its web for extended periods of time (Riechert and Gillespie 1986). Increased vegetation complexity means an increase in microhabitats (Greenstone 1984; Robinson 1981; Uetz 1991). Cardoso *et al.* (2007) showed that greater canopy cover resulted in a relatively constant microclimate as it acts as a buffer for the organisms in the understorey from rain, light intensity, wind and temperatures (Geiger *et al.* 2009), (Perfecto and Vandermeer 1996; Perfecto *et al.* 1996). This is supported by the community structure of marsh forest, the most structurally complex habitat, which was shown to contain species that evenly share an ecological factor or are equally capable of competing for niche space (Magurran 2004) (Fig. 3). Savanna and palm marsh had less structural diversity so that species were not evenly distributed but rather populated the area in random intervals. This absence of microhabitats and lack of protection from the elements and predators could also explain the greatly reduced presence of ground wanderers in the savanna habitat compared to the two other habitats.

Table 2. The spider fauna recorded from sites in savanna, palm marsh and marsh forest habitats in the Aripo Savannas Scientific Reserve sampled for the period March 2006 to May 2009.

Species	S1	S2	S3	PM1	PM2	PM3	MaF1	MaF2	MaF3
Anapidae Sp. A	0	1	0	0	0	0	0	0	0
Araneidae <i>Acacesia hamata</i>	5	21	7	19	0	0	0	0	0
<i>Alpaida trispinosa</i>	1	0	0	0	0	0	0	0	0
<i>Argiope argentata</i>	3	1	6	3	0	3	0	0	3
<i>Cyclosa caroli</i>	0	0	0	0	0	0	2	2	0
<i>Cyclosa fililineata</i>	0	0	0	0	0	0	1	0	0
<i>Eriophora atrax</i>	0	0	0	2	1	1	1	1	1
<i>Eustala anastera</i>	0	0	0	0	1	0	3	0	0
<i>Eustala</i> sp. A	0	0	0	0	0	0	0	0	1
<i>Gea heptagon</i>	2	0	0	0	0	0	0	0	0
<i>Hypognatha scutata</i>	1	0	0	0	0	0	0	0	0
<i>Kaira cobimcha</i>	2	0	0	0	0	0	0	0	0
<i>Larinia</i> cf. <i>directa</i>	21	73	36	0	0	0	0	0	0
<i>Mangora melanocephala</i>	0	0	0	3	4	0	20	2	0
<i>Metazygia laticeps</i>	0	0	0	3	0	0	4	3	0
<i>Micrathena acuta</i>	0	0	0	0	0	0	8	0	0
<i>Micrathena evansi</i>	0	0	0	0	0	0	0	5	0
<i>Micrathena schrebersi</i>	0	0	0	2	0	0	0	0	0
<i>Micrathena triangularis</i>	0	0	0	1	0	0	12	0	2
<i>Micrathena triangularispinosa</i>	0	0	0	2	2	0	0	0	0
<i>Neoscona arenata</i>	0	0	0	0	0	0	0	0	1
<i>Ocrepeira maraca</i>	0	1	0	1	1	0	0	0	0
<i>Verrucosa</i> sp. A	0	0	0	1	0	0	5	0	0
<i>Verrucosa</i> sp. B	0	0	0	0	0	0	0	0	4
<i>Wagneriana jelskii</i>	0	0	0	0	2	0	5	0	1
Corinnidae Sp. A	0	0	0	0	2	0	1	3	0
Deinopidae Sp. A	0	0	0	0	0	0	5	0	0
Gnaphosidae Sp. A	1	0	0	0	0	0	0	0	0
Linyphiidae Sp. A	0	0	0	0	1	0	0	2	0
Lycosidae Sp. A	0	0	0	2	0	0	0	1	0

Species	S1	S2	S3	PM1	PM2	PM3	MaF1	MaF2	MaF3
Mimetidae									
Sp. A	4	0	0	0	0	0	0	0	0
Sp. B	0	0	0	0	0	0	0	4	0
<i>Ero</i> sp.	0	0	0	0	1	0	0	0	0
Miturgidae									
Sp. A	0	0	0	0	0	0	0	1	0
Nephilidae									
<i>Nephila clavipes</i>	2	0	0	4	2	4	6	4	3
Nesticidae									
Sp. A	1	0	0	0	0	0	0	0	0
Oxyopidae									
<i>Oxyopes salticus</i>	2	0	0	15	0	0	0	19	0
Sp. A	0	0	0	0	1	1	0	2	0
Pisauridae									
Sp. A	0	0	0	0	1	0	0	4	0
Prodomidae									
Sp. A	0	0	0	0	0	0	0	1	0
Salticidae									
Sp. A	4	0	0	0	0	0	0	0	0
Sp. B	3	0	0	0	0	0	1	0	0
Sp. C	11	0	0	0	0	0	0	0	0
Sp. D	1	0	0	0	0	0	0	0	0
<i>Maota</i> sp.	0	0	0	0	0	0	0	1	0
<i>Freya</i> sp.	0	0	0	0	0	0	0	1	0
<i>Scopocira</i> sp.	0	0	1	1	0	0	2	0	0
<i>Synesmosyna</i> sp.	0	0	0	0	1	0	0	0	0
<i>Hypaeus</i> cf. <i>flavipes</i>	0	0	0	0	1	0	0	0	0
<i>Freya</i> cf. <i>decorate</i>	0	0	0	0	0	0	0	3	0
<i>Chinoscopus maculipes</i>	0	0	0	0	0	0	0	0	1
<i>Euophryinae</i>	0	0	0	0	1	0	0	0	0
Sparassidae									
Sp. A	0	0	0	0	1	0	0	0	0
Theridiidae									
Sp. A	0	0	0	0	2	0	0	1	0
Sp. B	0	0	0	1	0	0	5	0	0
Sp. C	0	0	0	0	0	0	1	0	0
Sp. D	0	0	0	0	0	0	0	0	0
Sp. E	0	0	0	1	0	0	0	3	0
Theridiosomatidae									
Sp. A	0	0	0	0	0	0	3	0	0

Species	S1	S2	S3	PM1	PM2	PM3	MaF1	MaF2	MaF3
Sp. B	0	0	0	0	0	0	0	1	0
Tetragnathidae									
<i>Azilia vachoni</i>	0	0	0	4	0	0	4	1	0
<i>Leucauge argyra</i>	7	0	0	5	6	2	0	9	1
<i>Leucauge regnyi</i>	0	12	0	0	0	0	12	0	0
<i>Tetragnatha nitens</i>	0	0	0	0	0	2	0	0	0
<i>Tetragnatha pallenscens</i>	17	6	1	3	0	0	6	1	3
<i>Tetragnatha</i> (unidentified sp. A)	0	0	0	1	0	0	0	0	0
Thomisidae									
Sp. A	0	0	0	1	0	0	0	0	0
Sp. B	0	0	0	0	0	0	0	0	0
<i>Stephanopsis</i> sp.	0	0	0	0	1	0	0	0	0
Uloboridae									
Sp. A	0	0	0	0	2	1	0	1	0
Sp. B	0	0	0	0	4	0	0	0	0
TOTAL	88	115	51	75	38	14	107	76	21

Key to site abbreviations					
S1	Savanna site 1	PM1	Palm Marsh site 1	MaF1	Marsh Forest site 1
S2	Savanna site 2	PM2	Palm Marsh site 2	MaF2	Marsh Forest site 2
S3	Savanna site 3	PM3	Palm Marsh site 3	MaF3	Marsh Forest site 3

Table 3. Total abundance (N), observed species richness (S), Shannon index (H') (species diversity), Simpson index (D) (species evenness), Berger-Parker index (d) (dominance) across the samples for each site sampled for the period March 2006 to May 2009. Site abbreviations as in Table 2.

Site	N	S	H'	$1/D$	d
S1AS	88	18	2.39	8.43	0.24
S2AS	115	7	1.11	2.24	0.64
S3AS	51	5	0.92	1.91	0.71
PM1AS	75	21	2.52	8.83	0.25
PM2AS	38	21	2.84	21.3	0.16
PM3AS	14	7	1.8	8.27	0.29
MaFAS	107	21	2.7	12.88	0.19
MaFAS	76	25	2.76	11.35	0.25
MaFAS	21	11	2.24	13.12	0.19

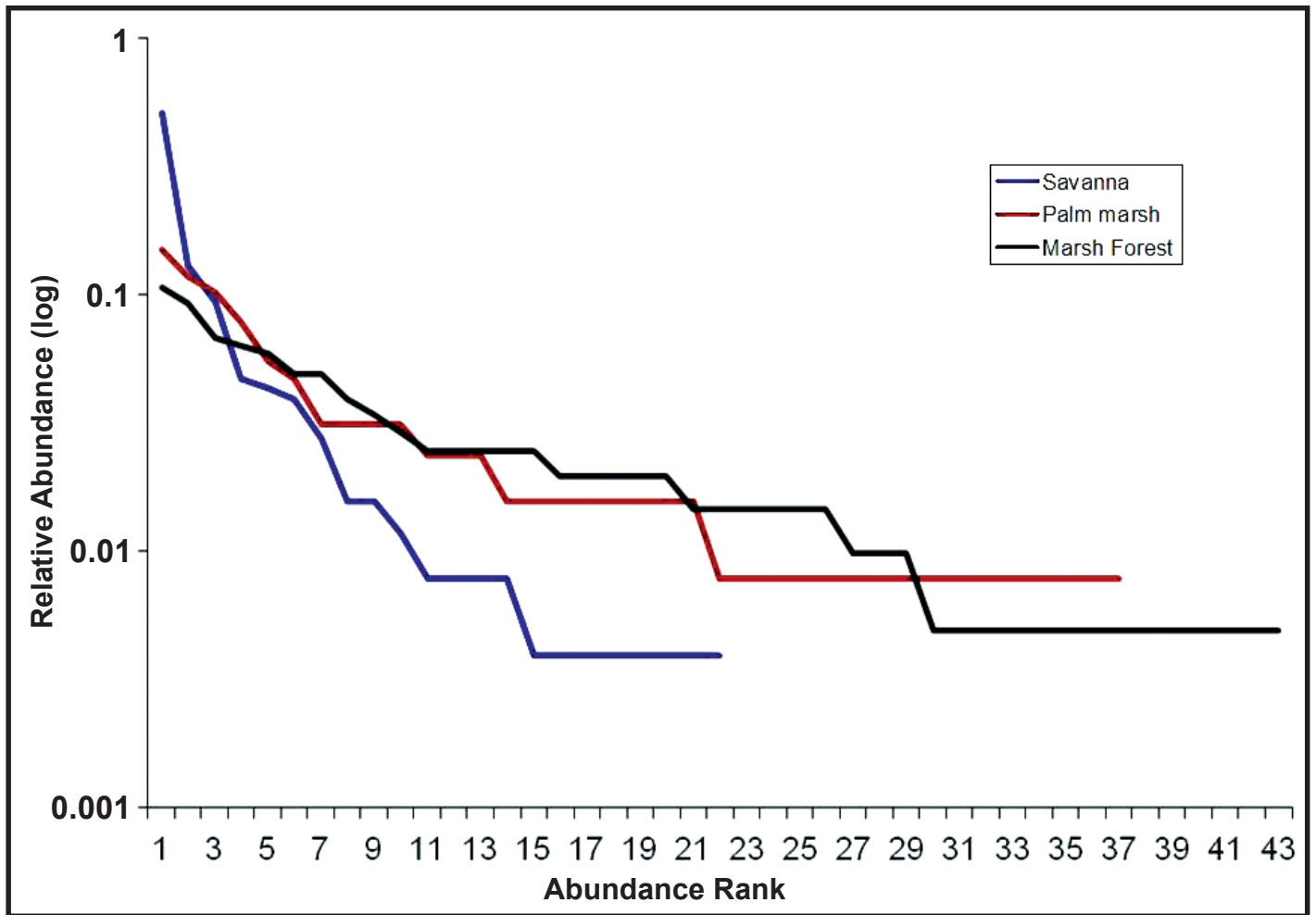


Fig. 3. Rank abundance curves of the spider families in savanna, marsh forest and palm marsh habitats sampled in the Aripo Savannas for the period March 2006 to May 2009.

Future studies in this area could include sub-dividing the largest functional group of web-builders into different types to see the effects of vegetation and habitat type.

The habitats found in the reserve display a range of structural complexity and in turn possess a range of microhabitats. Unfortunately these habitats face numerous threats due to human activities, in most instances illegal in nature, and is cause for better enforcement of laws that are in place to protect biodiversity and the maintenance of conservation efforts which will not only protect spiders, but the other species in the food webs in these habitats.

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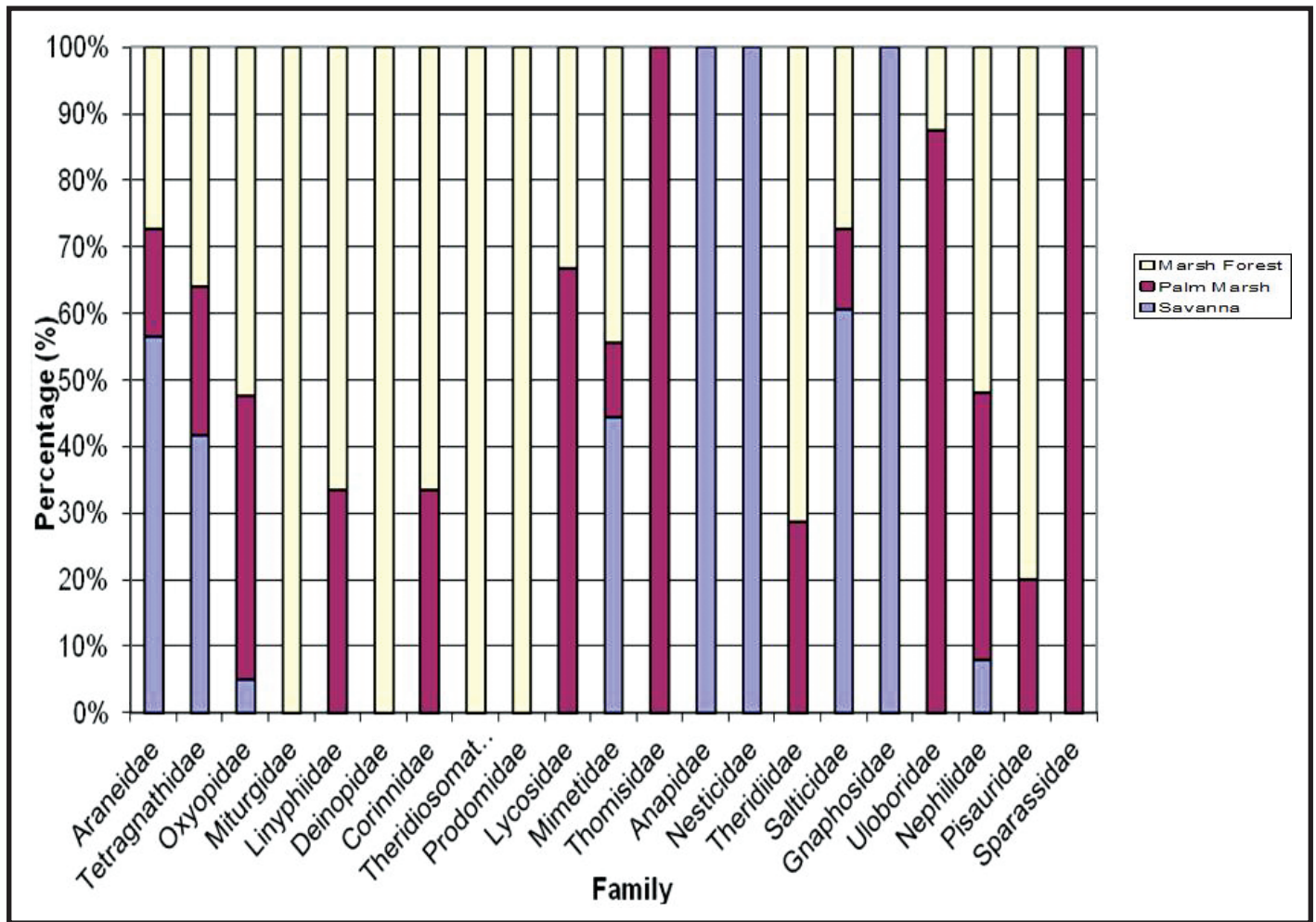


Fig. 4. 100% stacked column chart comparing the family composition in each habitat type, savanna, marsh forest and palm marsh habitats, sampled according to site for the period March 2006 to May 2009.

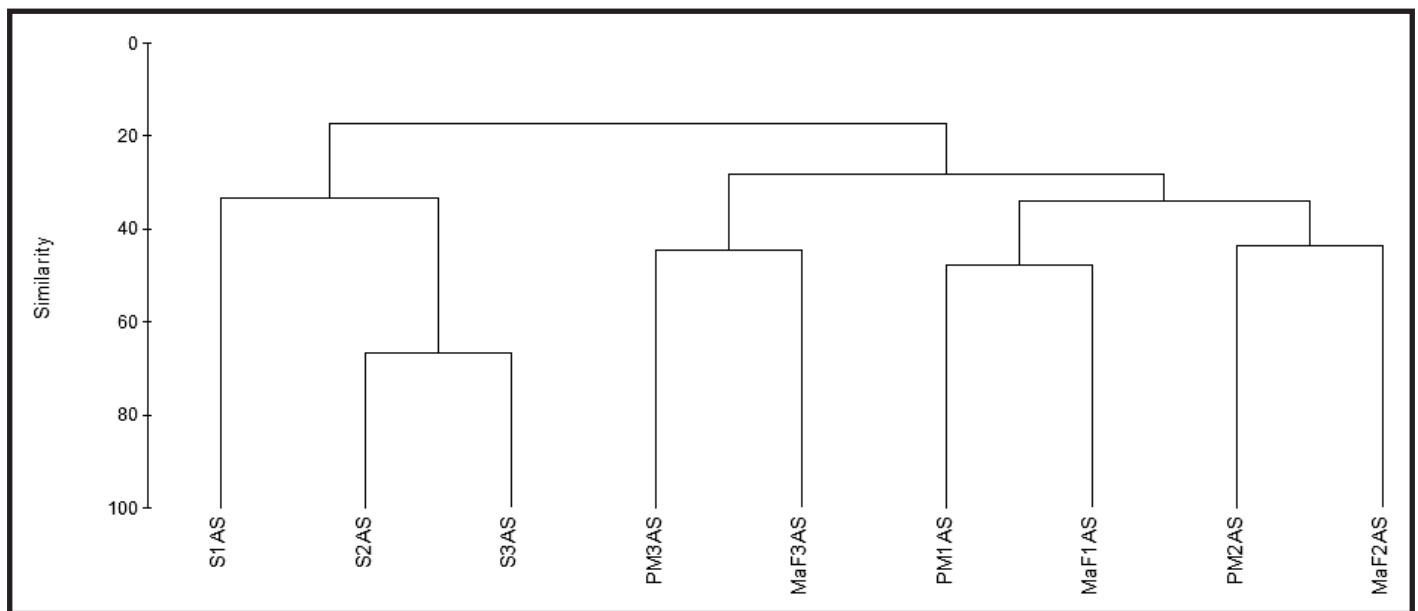


Fig. 5. Dendrogram of cluster analysis done on the savanna, marsh forest and palm marsh habitats sampled according to site for the period March 2006 to May 2009.

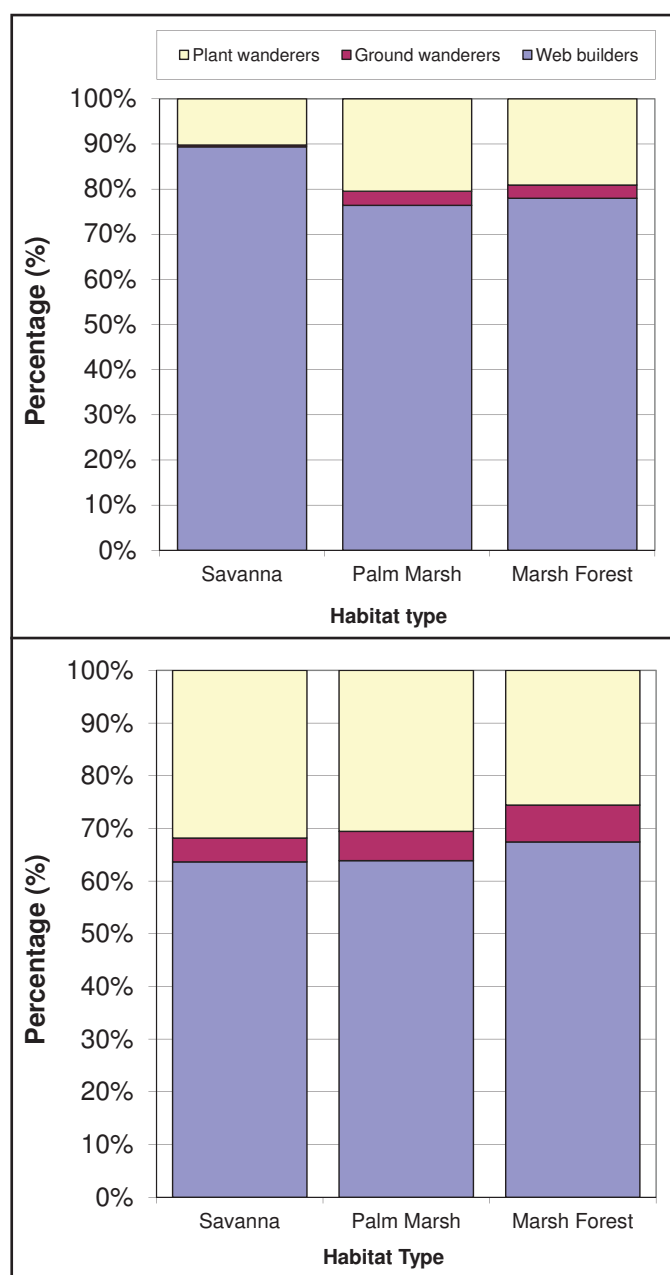


Fig. 6. 100% stacked column chart comparing the abundance (a) and species richness (b) of the functional groups in each habitat type, savanna, marsh forest and palm marsh habitats, sampled according to site for the period March 2006 to May 2009.

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