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Biodiversity and Feeding Guilds of Spiders (Araneae) at the NamibRand Nature Reserve (Namibia) and the Influence of Vegetation and Vegetation Structure

Biodiversität und Nahrungsgilden von Spinnen (Araneae) im NamibRand Nature Reserve (Namibia) und der Einfluss von Vegetation und Vegetationsstruktur

Björn Kristian Klatt & Marian Ewald Siegert

Summary: Overall, 351 spiders from 25 families were collected on plots of twelve different vegetation areas at the NamibRand Nature Reserve (Namibia) between July and September 2007. The plots of eight vegetation areas, inhabited by the members of 23 families, were used to assess the influence of vegetation and vegetation structure on the appearance of the spider families on the plots, as well as spider density and spider diversity. The spiders could be divided into two different feeding guilds based on their hunting behaviour: active hunters and netdwellers. We found that the diversity and abundance of the active hunters was higher. Vegetation was classified into three biomes (Nama-Karoo, Desert, Transition-Karoo) and vegetation structure on each plot was analysed using plant species richness, vegetation cover and number of vegetation layers. The appearance on the plots varied between the families. Only the members of six families were found on five to eight plots; the members of the remaining families occurred only on three or fewer plots. Spider density was similar between Nama-Karoo and Transition-Karoo and noticeably less in Desert. Also the spider density varied between the plots of the Nama-Karoo but was similar between the plots of the Transition-Karoo. The α-diversity was highest on Transition-Karoo and considerably lower on Nama-Karoo and Desert. Concerning vegetation structure, family richness was highest at plots with high plant species richness and three vegetation layers. Nama-Karoo and Transition-Karoo displayed high similarity (β-diversity, Sørensen-Index), which was lower between the latter and the Desert biome.

Keywords: Spiders, Namibia, diversity, vegetation, feeding guilds

Zusammenfassung: Im Zeitraum von Juli bis September 2007 wurden im NamibRand Nature Reserve (Namibia) insgesamt 351 Spinnen (Araneae) aus 25 Familien auf Plots von zwölf verschiedenen Vegetationsarealen gefangen. Die Spinnen konnten zwei verschiedenen Nahrungsgilden, den aktiven Jägern und Netzjägern zugeordnet werden, wobei die Netzjäger eine höhere Abundanz und Diversität zeigten. Die Plots von acht Vegetationsarealen, auf denen Vertreter von 23 Familien vorkamen, wurden verwendet, um den Einfluss von Vegetation und Vegetationsstruktur auf Vorkommen der Spinnenfamilien, Spinnendichte und Diversität zu untersuchen. Die Vegetationsareale wurden in drei verschiedene Biome (Nama-Karoo, Wüste, Transition-Karoo) klassifiziert und die Vegetationsstruktur durch die Artenzahl der Pflanzen, Vegetationsbedeckung und Anzahl der Vegetationsschichten beschrieben. Das Vorkommen auf den Plots variierte zwischen den Familien. Nur Vertreter von sechs Familien wurden auf fünf bis acht und Vertreter der übrigen Familien auf drei und weniger Plots gefangen. Nama-Karoo und Transition-Karoo zeigten eine ähnliche Spinnendichte, während diese im Biom Wüste deutlich geringer war. Zudem variierte die Spinnendichte zwischen den einzelnen Vegetationsarealen des Nama-Karoo und war zwischen den Vegetationsarealen des Transition-Karoo ähnlich. Die α-Diversität war im Transition-Karoo am höchsten und deutlich niedriger in den Biomen Nama-Karoo und Wüste. Unter Betrachtung der Vegetationsstruktur auf den einzelnen Vegetationsarealen zeigten Flächen mit hoher Pflanzenartenzahl und dem Vorhandensein von drei Vegetationsschichten die höchste Anzahl an Spinnenfamilien. Nama-Karoo und Transition-Karoo zeigten eine hohe Ähnlichkeit in der Zusammensetzung der Spinnenfamilien (β-Diversität, Sörensen-Index), während die Ähnlichkeit von beiden mit dem Biom Wüste deutlich niedriger war.

Schlüsselwörter: Spinnen, Namibia, Diversität, Vegetation, Nahrungsgilden

1. Introduction

Spiders are cosmopolites that inhabit in large numbers a wide and diverse range of terrestrial habitats. A number of publications reported a dependence of spiders on vegetation and vegetation structure in natural and anthropogenic-affected habitats. The biodiversity and abundance of spiders is positively correlated with an increasing complexity of trees (Gunnarsson 1988, 1990, 1992, 1996; Sundberg & Gunnarsson 1994; Halaj et al. 1998, 2000). Spider diversity is influenced, not only by the plant itself, but by the structural complexity of the local environment. Spiders show a higher diversity at organic farms than at conventional farms, due to the variety of natural plants between the crops that assures a heterogeneous habitat (Balfour & Rypstra 1998; Feber et al. 1998; Schmidt et al. 2005). Increasing acgricultural activities lower the diversity of spiders due to reduced habitat complexity (Downie et al. 1999; Grill et al. 2005). Depending on the particular species, further spider species richness is influenced by landscape heterogeneity (Claugh et al. 2005; Schmidt et al. 2008).

Although much is known about the influence of vegetation and habitat on spiders at different scales in moderate climate areas, there are still only few studies and little information about spider diversity and the influences in arid environments, especially in the dry regions of Namibia. Most studies that deal with Namibian spiders are based on taxonomical questions of undescribed species in southern Africa (e. g. Platnick & Griffin 1993; Lotz 1994a; Van den Berg & Dippenaar-Schoeman 1994) or the ecology of several spider taxa (e. g. Henschel 1994). An estimated 80 % of the spiders in Namibia are still unknown (Alderweireldt & Jocqué 1993). Griffin & Dippenaar-Schoeman (1991) provided a species list of Namibian spiders and Griffin (1998) described the distribution of spiders in Namibia. The higher abundance of spiders in the humid regions of Namibia is a result of a large number of trees and bushes and, therefore, high habitat complex-ity. Russel-Smith (2002) compared spider diversity and composition of two nature conservations in Tanzania and Namibia and found more species and families in Tanzania as well as differences in family composition.

The vegetation of parts of Southern Africa was classified into different biomes by Rutherford & Westfall (1986). Biomes are spacious ecosystems that diverge by dominant plant life-forms and climate character. Irish (1994) classified the vegetation of Namibia into four different biomes (Savanna, Nama-Karoo, Succulent Karoo, Desert). Further he showed that the dominance of plant life-forms is, beside climate characters, also influenced by edaphic factors, especially deep sand.

The aim of the present study is to give an overview of spiders and their biodiversity and the influence of vegetation and vegetation structure at the NamibRand Nature Reserve. Therefore, a species list was provided, and the vegetation and its structure was analysed and classified in different biomes. Further the biodiversity of spider families and feeding guilds were analysed by species richness and compared to the biomes and to different characteristics of the vegetation and vegetation structure.

2. Material and methods

2.1. Investigation area

Fieldwork was conducted on selected vegetation areas of the NamibRand Nature Reserve, a private nature conservation in Namibia. It is located between 15 ° and 16 ° eastern longitude and 24 ° and 25 ° southern latitude at the eastern border of the Namib Desert (Fig. 1). It was founded in 1991 out of 13 over utilised livestock farms. With an area of about 1722 km^2, it is one of the largest private nature conservations in southern Africa. Geologically the reserve is dominated by granite of different ages that shows all phases of alteration (Hart 2003) and the red sand of the Namib Desert. The climate is very arid with a mean precipitation of 81.3 mm per annum. The winters are dry and cool with a mean temperature of 12.5 °C, usually lacking precipitation. Summers are hot with a mean temperature of 34.2 °C and over 70 % of the entire precipitation occuring between January and March (Rathbun & Rathbun 2006). The main wind direction is west to northwest. Enframed by the Nubib mountains in the east and the Namib Desert in the west, the NamibRand Nature Reserve is almost enclosed from the surrounding landscape.

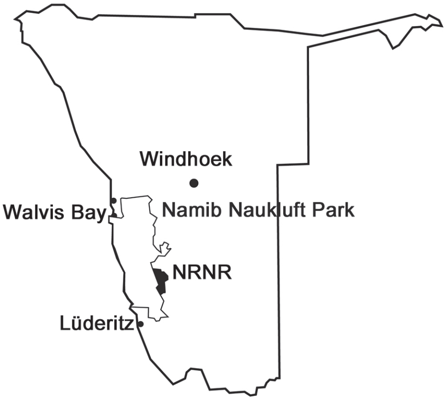

Fig. 1: Location of the NamibRand Nature Reserve (NRNR) in Namibia.
Abb. 1: Position des NamibRand Nature Reserve (NRNR) in Namibia.

2.2. Experimental design

In 2007, twelve vegetation areas were selected at the northern part of the reserve (Fig. 2) with a minimal distance of 500 m from each other. Due to substrate and height conditions only on eight of the twelve vegetation areas (regular areas, F1-F8), all sampling methods could be used. On each of the eight vegetation areas, a plot consisting of an area of 500 m x 20 m (= 10,000 m^2 = 1 ha) was defined and marked by GPS coordinates. The data from the remaining four vegetation areas (special areas, S1-S4) were excluded from statistical analysis and only used to complete the species list (appendix).

2.3. Spider sampling

To asses overall spider diversity, three different sampling methods were used between July and September 2007: active searching by day and night, pitfall traps and a light trap. Every plot was examined once a month. To avoid mistakes, weather parameters (temperature, humidity, wind speed) were checked daily (Davis Instruments Vantage Pro 2); all methods were used under similar conditions. Pitfall traps consisted of plastic cups with a height of 12 cm and a diameter of 13 cm. Each trap was buried in the ground with the rim parallel to the soil line to avoid any restriction to the specimen in falling into the cups, particularly by the prominent rim of the cup. The cups were filled up to a third of its volume with water (Uetz & Unzicker 1976; Ubick et al. 2005). To catch specimens with active searching (Filmer 1991; Ubick et al. 2005) jars, tweezers and a self made aspirator to avoid bites and potential poisoning were used. The light trap consisted of a

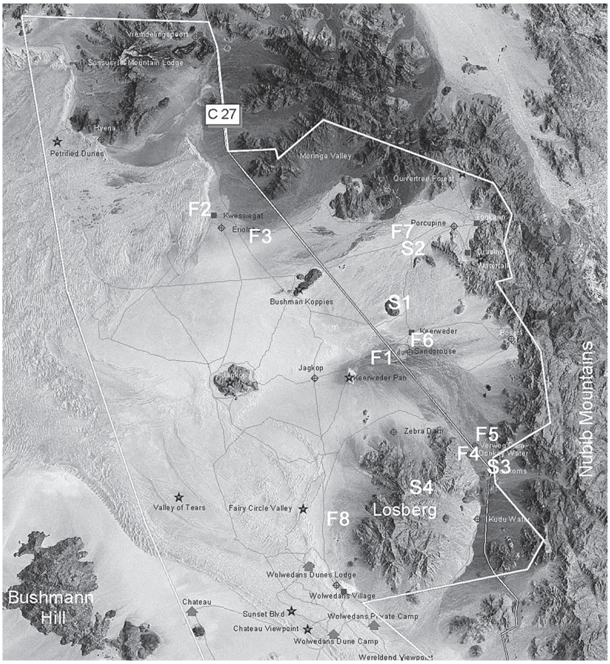

Fig. 2: Vegetation areas at the northern part of the NamibRand Nature Reserve. Regular areas (F1-F8) and special areas (S1-S4). Used and modified with permission of the NamibRand Nature Reserve.

Abb. 2: Vegetationsareale im nördlichen Teil des NamibRand Nature Reserve. Reguläre Flächen (F1-F8) und Sonderflächen (S1-S4). Verwendet und verändert mit Erlaubnis des NamibRand Nature Reserve.

wooden tripod that placed a light bulb above a quadrate bowl with an edge length of 40 cm that was filled up to a third of its volume with water. Electricity was supplied from a car battery that was connected with a voltage converter to generate alternate current and the correct voltage for the light bulb. Like the pitfall traps, the bowl was buried with the rim in line with the soil to avoid restrictions to the specimen from falling into the bowl by the prominent rim.

Pitfall traps were buried in 70 m distance from each other along the midline of every plot. For active searching vegetation, substrate and dead wood were scanned over entire plot within the next three hours and every observed spider was caught. Pitfall traps were checked after 24 hours on the plot and all caught specimen were preserved in jars filled with 70 % ethanol.

The light trap and active searching by night were only used in September with the higher night temperatures. The light trap was placed for 24 hours at a point at the center of the plots. Then active searching was conducted for three hours on the whole plot using a head light (Petzl Tikka plus). Specimen collected after that period were preserved in jars filled with 70 % ethanol.

All methods were used as carefully as possible to avoid disturbance of the sensitive desert ecosystem. The burrowed holes for the pitfall traps and all tracks made were reset after finishing the study.

Specimen were sorted and identified at family level during the field work in Namibia. Further identification occurred in Germany with special identification literature and the help of specialists. Nomenclature followed Dippenaar-Schoeman & Jocqué (1997) and Platnick (2009). After identification, all sampled specimen were sent back to Namibia and added to the collection of the National Museum of Namibia.

2.4. Vegetation analysis

The following characteristics of vegetation structure were identified on every plot: plant species richness, vegetation cover and number of vegetation layers. Plant species were identified during fieldwork at the reserve when possible. Specimen that could not be identified were taken to the National Herbarium of Namibia and identified. Nomenclature followed Palgrave (1996), Carruthers (1997) and van Oudtshoorn & van Wyk (1999). Vegetation cover was estimated from elevations near the plots and while walking through the plots. Vegetation layers were defined according to Raunkiaer (1934) using the clearly visible differences of the occurring life-forms. The first layer contained only grasses (here: hemicryptophytes following Irish 1994) and height ranges between 0 cm and 50 cm. The second layer was between 50 cm and 150 cm containing shrubs (chamaephytes). The third layer included plants higher than 150 cm, mostly phanerophytes. The relative percentage of every layer was estimated like the vegetation cover.

The vegetation areas were classified into three different biomes (Nama-Karoo, Desert, Transition-Karoo) due to vegetation and substrate structure following Rutherford & Westfall (1986) and Irish (1994; Tab. 1).

The combination of deep sand and water supplies caused the existence of Savanna-similar vegetation, the Transition Karoo also named as "False Savanna" or "Pseudo Fynbos" in a Nama-Karoo typical climatic area (Irish 1994). At the NamibRand Nature Reserve it could be found in and nearby temporary rivers, called "Riviere", that emerged from the surface-runoff of the surrounding mountains in summer and stored more available water than the surrounding areas. Because of the clearer differences compared to the Nama-Karoo, it was analysed as an adequate biome. The analysis of the biome Desert was based on only one vegetation area. Because of overgrown desert, only small stretches were available within the borders of the nothern part of the reserve.

2.5. Data analysis

Due to the high number of juveniles, analyses were based on family-level, which was the lowest taxa in which all specimen could be identified (Whitmore 2000; Sørensen 2004). The data of all sampling methods for every plot within a vegetation area were pooled and simple statistical anlyses were conducted, due to the low number of caught specimen. For each spider family the number of plots on which it appeared was given as a percentage of the entire number of plots. Besides spider density per m^2, α-diversity was analysed by comparing family richness to biomes and vegetation characteristics. β-diversity was analysed using the Sørensen-index (Legendre & Legendre 1998). Here it shows the similarity of spider family composition between the three biomes by comparing the number of shared and different families of two biomes at a time.

3. Results

Overall, 351 spiders belonging to 25 families were caught. Of these families, 23 (315

Tab. 1: Characterisation of the plots into biomes. Classification followed Rutherford & Westfall (1986) Irish (1994) using the dominance of lifeforms in combination with edaphic and climatic factors.

Tab. 1: Einordnung der Plots in Biome. Die Klassifizierung folgt Rutherford & Westfall (1986) Irish (1994) unter Verwendung der dominanten Lebensformen in Kombination mit edaphischen und klimatischen Faktoren.

plots	biomes	dominant lifeform(s)
F1, F3, F4, F6, F8	Nama-Karoo	hemicryptophytes
F2	Desert	chamaephytes, therophytes
F5, F6	Transition-Karoo	phanerophytes, chamaephytes

individuals) were sampled on the plots of the eight regular vegetation areas and used for further analysis. More than half of the specimen were juveniles (56.1 %) and could not, or not precisely be identified to genus or species level. All of the 315 specimen could be identified to family level, 250 (79.0 %) to genus level and 80 (25.0 %) to species level. Therefore all analyses were based on family-level. The appearance on the plots varied widely between the spider families (Fig. 3). Only members of the families Oxyopidae and Philodromidae occupied all eight plots. Members of Gnaphosidae (7), Salticidae (6) and Sparassidae (6) were also frequently found. Those of the Caponiidae, Filistatidae, Nemesiidae, Pisauridae, Selenopidae und Uloboridae appeared only on one plot, respectively. Based on the hunting behaviour, two different feeding guilds were found at the NamibRand Nature Reserve: active hunters and netdwellers. Altogether more families of the active hunters were caught. A total of 15 families (281 individuals, 89.2 %) belonged to the active hunters; whereas, eight Families (34 individuals, 10.8 %) could be allocated to the netdwellers (Fig. 3).

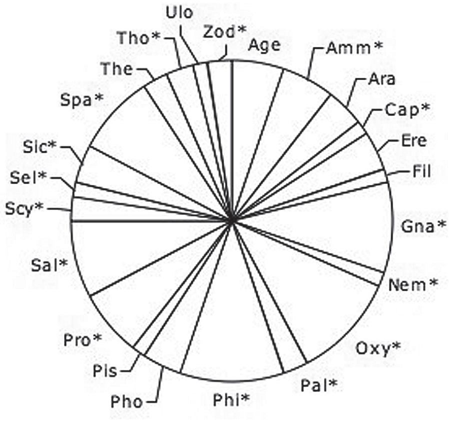

Fig. 3: Appearance of spider families and feeding guilds on the plots. Active hunters are signed with an asterisk.

Abb. 3: Vorkommen von Spinnenfamilien und Nahrungsgilden auf den Plots. Aktive Jäger sind mit einem Sternchen markiert.

Abbreviations/Abkürzungen: Age = Agelenidae; Amm = Ammoxenidae; Ara = Araneidae; Cap = Caponiidae; Ere = Eresidae; Fil = Filistatidae; Gna = Gnaphosidae; Nem = cf. Nemesiidae; Oxy = Oxyopidae; Pal = Palpimanidae; Phi = Philodromidae; Pho = Pholcidae; Pis = Pisauridae; Pro = Prodidomidae; Sal = Salticidae; Scy = Scytodidae; Sel = Selenopidae; Sic = Sicariidae; Spa = Sparassidae; The = Theridiidae; Tho = Thomisidae; Ulo = Uloboridae; Zod = Zodariidae.

Spider density per m^2 varied within biomes and plots (Tab. 2). Desert showed the lowest spider density; whereas, Nama-Karoo and Transition-Karoo showed higher and comparatively similar spider densities. Among the particular plots of the Nama-Karoo, there were great differences in spider density. F6 showed a very high density (8.3 x 10^{-3}) compared to the rest of the plots. Except for F3 (4.4 x 10^{-3}) and F6, the other plots showed lower spider density compared to the mean value. The two plots of the biome Transition Karoo (F5, F7) displayed similar spider density.

Transition-Karoo showed the highest average spider family richness, in contrast to Desert which showed the lowest spider family richness (Fig. 4). Average spider family richness was a little higher in Nama-Karoo when compared to Desert; however, it was much lower than in Transition-Karoo.

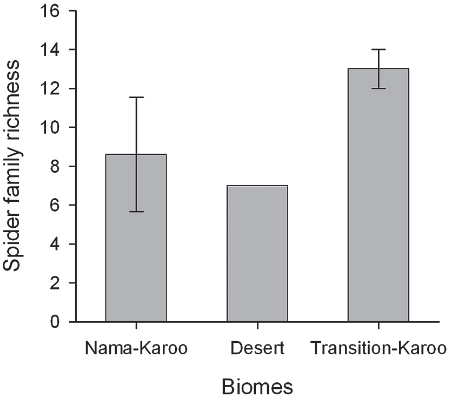

Fig. 4: Spider familiy richness on the three biomes.

Abb. 4: Anzahl der Spinnenfamilien auf den drei Biomen.

Tab. 2: Spider density (individuals per m^2) for plots and biomes.
Tab. 2: Spinnendichte (Individuen pro m^2) für Plots und Biome.

plot	individuals/m²	biomes	mean number of individuals/m² ± standard deviation
F1	2.9×10^{-3}	Nama-Karoo	$4.3 \times 10^{-3} \pm 2.1 \times 10^{-3}$
F3	4.4×10^{-3}		
F4	3.1×10^{-3}		
F6	8.3×10^{-3}		
F8	2.7×10^{-3}		
F2	2.4×10^{-3}	Desert	$2.4 \times 10^{-3} \pm 0$
F5	4.0×10^{-3}	Transition-Karoo	$3.9 \times 10^{-3} \pm 1.5 \times 10^{-4}$
F7	3.7×10^{-3}		

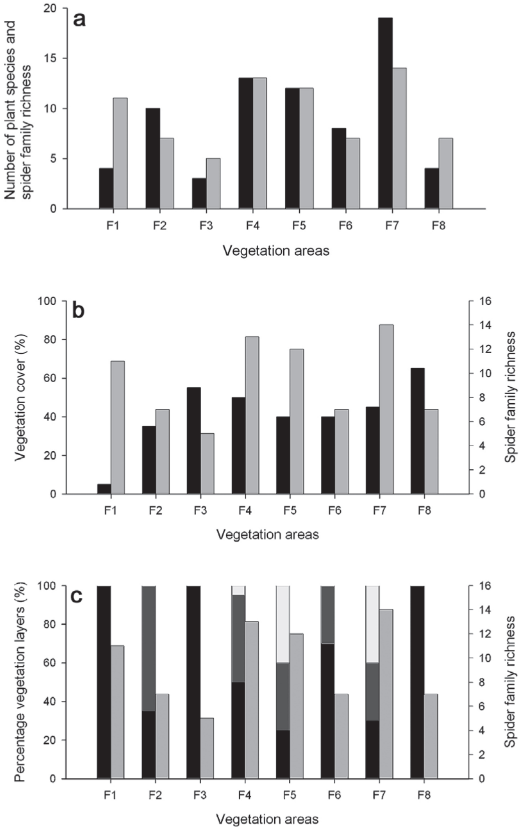

Fig. 5a-c: Spider family richness (gray columns) and vegetation structures (black columns and stacked columns, respectively) on the different plots. **a** Spider family richness and plant species richness. **b** Spider family richness and vegetation cover. **c** spider family richness and number and percentage of vegetation layers (lower stack = percentage vegetation layer 1, middle stack = percentage vegetation layer 2, upper stack = percentage vegetation layer 3.

Abb. 5a-c: Anzahl der Spinnenfamilien (graue Säulen) und Vegetationsstruktur (schwarze Säulen bzw. geschichtete Säulen) auf den verschiedenen Plots. **a** Anzahl der Spinnenfamilien und Artenreichtum der Pflanzen. **b** Anzahl der Spinnenfamilien und Vegetationsbedeckung. **c** Anzahl der Spinnenfamilien und Schichtaufbau der Vegetation (unterste Schicht = Anteil Vegetationsschicht 1, mittlere Schicht = Anteil Vegetationsschicht 2, obere Schicht = Anteil Vegetationsschicht 3).

Concerning the different characteristics of vegetation structure, spider family richness was highest on plots with high plant species richness, mid vegetation cover (40-50 %) and three layers of vegetation (Fig. 5a-c). Two of these three plots belonged to the biome Transition-Karoo (F5 and F7) and one to the biome Nama-Karoo (F4). Plots with high numbers of plant species were inhabited by a higher number of spider families than plots containing few plant species (Fig. 5a). In contrast, F2 had high plant species richness, but proportionally few spider families were found. Most of the plots showed a mid vegetation cover between 40 and 50 % (F3, F4, F5, F6, F7), but differ clearly in spider family richness (Fig. 5b).

The vegetation cover of plots F1 (5 %) and F8 (65 %) differed clearly from the other plots. Although the number of spider families of F8 was similar to F2 and F6, F8 showed a clearly higher vegetation cover. Except F1, all plots with only one vegetation layer were inhabited by a relatively low number of spider families (Fig. 5c). Apparently the occurrence of a second vegetation layer did not influence the number of spider families, because the values for these plots were not higher (F2 and F6 vs. F8), or only slightly higher (F6 and F8 vs. F3) than those of the plots with one vegetation layer, except F1. Spider family richness increased noticeably with the presence of a third vegetation layer, as on F4, F5 and F7. In contrast, F1 showed also a high spider family richness, although the vegetation characteristics appeared very low with few plant species, low vegetation cover and only one vegetation layer.

β-diversity was analysed by similarity using the Sørensen-index. Despite the differences of vegetation structure Nama-Karoo and Transition-Karoo displayed a similarity of 75,68 % (S = 0,76) in the composition of spider families (Tab. 3). Both biomes showed lower, but nearly equal similarity compared to the Desert biome with 53, 85 % (Nama-Karoo vs. Desert) and 56, 0 % (Transition-Karoo vs. Desert).

4. Discussion

Although most of the plots differ considerably in vegetation structure, the members of some families were found on all or on most of the plots. Families like the Oxyopidae or Salticidae are known as cosmopolitans that occur worldwide in a high number of different habitats (Platnick 2009). As habitat generalists, they are less dependent on the conditions of their environment (Wise 1993) and could therefore be found on all plots at the reserve, irrespective of the vegetation and vegetation structure. Others, like the genus *Carparachne* (family: Sparassidae) and some species of the genus *Sicarius* (family: Sicariidae) are endemic to Namibia (Griffin & Dippenaar-Schoeman 1991; Dippenaar-Schoeman & Jocqué 1997; Platnick 2009). They are habitat specialists that rely on special conditions in their environment (Wise 1993) and, therefore, were not found on all plots. Spider density was more constant between the plots of the Transtion-Karoo than between the plots of the Nama-Karoo. Hence, spider density displayed the differences of vegetation structure that varied considerably between the plots of the Nama-Karoo, but was very similar between the plots of the Transition-Karoo. On average spider density was similar between Nama-Karoo and Transition-Karoo. Some spider species are relatively mobile and could move between

Tab. 3: β-diversity analysed as similarity using the Sørensen-index (S).
Tab. 3: β-Diversität, dargestellt als Ähnlichkeit anhand des Sørensen-Index (S).

similarity between	S	%
Nama-Karoo and Desert	0.54	53.85
Desert and Transition-Karoo	0.56	56.0
Nama-Karoo and Transition-Karoo	0.76	75.68

the two habitats. Movements between different habitat types are also known for farmland spiders in Europe (SUNDERLAND & SAMU 2000). The low spider density in the Desert biome was a result of remarkable differences in vegetation and edaphic structures as compared to Nama-Karoo and Transition-Karoo. Plants were offen separated from each other and the substrate as the whole plot consisted of deep and loose sand. In addition it showed an inclinitation from 5° up to 45° and was exposed in the north-eastern direction, so that the sun heated up this area more than the other areas without inclination. Spiders living in this biome need to be adapted to the extreme conditions. Some have special adaptations like the hairs on the tarsi of the Dancing White Lady (e. g. *Carparachne* spp.; FILMER 1991) that enable the spider to walk faster on the loose substrate by protecting the spider from subsidence. Others are in general adapted to arid environment like the family Gnaphosidae (GRIFFIN 1998).

Considerably more families and individuals of active hunters than netdwellers were found at the NamibRand Nature Reserve. According to HUHTA (1971) active hunters are more adapted to extreme climates and, therefore, are less dependent on the microclimate of their habitat than netdwellers. As a result of their mobility, active hunters are more flexible in the selection of habitat and shelter during extreme weather conditions. Due to the dependence on their webs, Netdwellers are less flexible in the selection of their habitat. Further they need vegetation structures that provide shelter with a constant and moderate microclimate and anchoring points for their webs (BRADLEY 1993; RIECHERT & GILLESPIE 1986), which were sparse at the NamibaRand Nature Reserve due to the strong aridity. Although personal observations at the NamibRand Nature Reserve corroborated previous studies, GRILL et al. (2005) displayed that netwdellers are not dependent on the vegetation, but use any available structure for anchoring their webs. In addition other variables like wind or further climate factors may be also important.

Spider family richness was highest on plots with high plant species richness and three vegetation layers. Plots with these characteristics could found in the Transition-Karoo and the biome Nama-Karoo. A high number of plant species and vegetation layers imply a high complexity of vegetation structure. This provides a great variety of ambushes and habitats, protection against enemies, e. g. birds (GUNNARSSON 1996), and the reduction of intra- and interspecific competition (BRADLEY 1993). In addition, a highly complex vegetation is inhabited by large number of potential prey animals (NENTWIG 1980; OXBROUGH et al. 2005) and provides a moderate and constant microclimate (GRILL et al. 2005). In contrast, spider family richness differed between the plots although vegetation cover was similar in most cases. This indicates that spider family richness was not-or only slightly-influenced by vegetation cover, although it was one of the mean characteristics of vegetation structure. A possible reason is, that due to the extreme climate changes between summer and winter and the frequent absence of precipitation (even in the summer months of the last few years) vegetation cover is very inconsistent at the NamibRand Nature Reserve (MENGE & ODENDAAL personal communication). The dominant plant life-forms are perennial, and as a result of this, the basic structure of the vegetation displayed by the dominant plant species and the number of vegetation layers was nearly consistent. Hence, it seemed to influence spider family richness more than vegetation cover, which changed with the availability of water. In contrast, the vegetation structure was considerably less complex on F1, but it was inhabited by a high number of spider families similar to the above mentioned plots with high vegetation complexity. This plot was also inhabited by a high number of termites which are a potential food source. Spiders may move from the surrounding area onto this plot for foraging. β-diversity was high between Nama-Karoo and Transition-Karoo. Similar species and family compositions are already known for crop fields and perennial vegetation constituted by surrounding natural habitats. Spiders hibernate in the perennial vegetation while the crop fields are uninhabitable in winter and become recolonised during spring (Schmidt & Tscharntke 2005). Transition-Karoo also showed a more constant vegetation during the change of seasons, as many trees and shrubs were foliated during the dry summer months, during which this study was conducted. Hence, the Nama-Karoo could be recolonised from the Transition-Karoo or at least spiders might switch between the two habitats, causing family composition to be similar. Further, β-diversity was lower but very similar between Nama-Karoo and Desert and Transition-Karoo and Desert. Here also climate, edaphic structure and inclination may be of importance.

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Appendix

Tab. 4: Species list of the Araneae at the NamibRand Nature Reserve. Nomenclature follows Dippenaar-Schoeman & Jocqué (1997) and Platnick (2008).
Tab. 4: Artenliste der Araneae des NamibRand Nature Reserve. Nomenklatur folgt Dippenaar-Schoeman & Jocqué (1997) und Platnick (2008).

family	subfamily	genus and species
Agelenidae	Ageleninae	cf. *Agelena* sp. Walckenaer, 1805
		cf. *Olorunia* sp. Lehtinen, 1967
Ammoxenidae	–	*Ammoxenus coccineus* Simon, 1893
		Ammoxenus sp. nov. Simon, 1893
		Ammoxenus sp. Simon, 1893
Araneidae	cf. Araneinae	genus indet.
Caponiidae	Caponiinae	*Caponia* sp. Simon, 1887
cf. Nemesiidae	unidentified subfamily	
Eresidae	Eresinae	cf. *Gandanameno* sp. Lehtinen, 1967
Filistatidae	–	cf. *Kukulcania* sp. Lehtinen, 1967
Gnaphosidae	Gnaphosinae	*Amusia* sp. Tullgren, 1910
		cf. *Amusia* sp. Tullgren, 1910
		Asemesthes fodina Tucker, 1923
		*Asemesthes*cf.*flavipes* Purcell, 1908
		Asemesthes lineatus Purcell, 1908
		Asemesthes montanus Tucker, 1923
		Asemesthes sp. Simon, 1887
	unidentified subfamily	
	Echeminae	cf. *Megamyrmaekion* sp. Ruess, 1834
	cf. Micarinae	cf. *Micaria* sp. Westring, 1851
	cf. Zelotinae	genus indet.
Oecobiidae	cf. Uroecobiinae	cf. *Uroctea* sp. Dufour, 1820
Oxyopidae	–	*Oxyopes* sp. Latreille, 1804
		Peucetia viridis (Blackwall, 1858)
		Peucetia sp. Thorell, 1869
Palpimanidae	Cheiminae	*Diaphorocellus* cf. *albooculatus* Lawrence, 1927
	Palpimaninae	*Palpimanus* sp. Dufour, 1820
Philodromidae	–	cf. *Thanatus* sp. C.L.Koch, 1837
		cf. *Tibitanus* sp. Simon, 1907
Pholcidae	Smeringopinae	*Smeringopus atomarius* Simon, 1910
		Smeringopus cf. *pallidus* (Blackwall, 1858)
		Smeringopus sp. Simon, 1890
Pisauridae	Pisaura	cf. *Tetragonophthalma* sp. Karsch, 1878
Prodidomidae	Anagraphinae	cf. *Theuma* sp. Simon, 1893
	Prodidominae	*Prodidomus reticulatus* Lawrence, 1927
		Prodidomus cf. *lampei* Strand, 1915
Salticidae	Aelurillinae	genus indet.
	Heliophaninae	cf. *Icius insolidus* (Wesolowska, 1999)
	Mogrinae	cf. *Mogrus semicanus* Simon, 1910
	unidentified subfamily	
Scytodidae	–	*Scytodes* sp. Latreille, 1804
Selenopidae	–	*Anyphops* sp. Benoit, 1968
Sicariidae	Loxoscelinae	*Loxosceles* sp. Heinecken & Lowe, 1835
	Sicariinae	*Sicarius* sp. Walckenaer, 1847
Sparassidae	?	cf. *Palystella* sp. Lawrence, 1928
		Carparachne sp. Lawrence, 1962
		genus indet.
Theridiidae	?	*Latrodectus renivulvatus* Dahl, 1902
		Latrodectus sp. Walckenaer, 1805
	unidentified subfamily	
Thomisidae	Thomisinae	*Thomisus* cf. *zuluanus* Lawrence, 1942
		genus indet.
Trochanteriidae	–	*Platyoides* sp. O.P.-Cambridge, 1890
Uloboridae	Uloborinae	cf. *Uloborus plumipes* Lucas, 1846
Zodariidae	Cydrelinae	*Capheris crassimana* (Simon, 1887)
		cf. *Psammorygma* sp. Jocqué, 1991