



Composition and diversity of the spider fauna in the canopy of a montane forest in Tanzania

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Abstract. Spiders were sampled using insecticide knockdown in an African montane forest in the Uzungwa Mountains of Tanzania. The results are used to discuss the faunal composition at the site and in comparison to other sites, and the implications of the results for estimating spider diversity in Africa are discussed. A total of 5233 adults comprising 149 species were collected from 11 samples covering a total of 906 m² of projected area. Three species contributed 45% of the sample. Previous insecticide knockdown studies of tropical lowland forest canopies have shown a dominance of Theridiidae, Salticidae and Araneidae. In the present study Linyphiidae dominated in abundance and were the second most diverse in terms of species richness. Other abundant families were Oonopidae and Pholcidae, while Theridiidae, Salticidae and Araneidae were rich in species. This supports a previous study, which indicated that the importance of linyphiids increases with altitude. Species richness was predicted using a number of estimators, which produced relatively similar results. Using the abundance-based estimator, Chao 1, the predicted richness for the total area sampled is 183 ± 15 species. This indicates that at least 20% of the area's spider community remains unsampled. A high ratio of undescribed species (approximately 80%) and a relatively high species turnover compared to a site 20 km away within the same forest complex suggests that the number of spiders in Africa could well be much higher than the current, published estimate of 20000 species.

Introduction

The increased destruction of natural habitats by humans has intensified the need for collecting biodiversity data for support to conservation and management decisions. This is particularly the case for threatened and inaccessible faunas such as those of rainforest canopies. However, research on the biodiversity patterns of tropical rainforest canopies is still in its infancy (Lowman and Wittman 1996; Basset 2001).

Spiders appear to be good subjects for studying biodiversity patterns (Platnick 1999). They are often an abundant component of the canopy fauna (Basset 2001). For example, Majer et al. (1994) established that spiders were the third most species-rich group in their study of eastern and western Australian eucalypt forest, and Gagné (1979) observed, for both rainforest and savannah, that spiders were among the four most abundant groups of arthropods. However, their apparent abundance relative to other groups of arthropods differs between studies. Basset (1991) recorded the highest proportion of spiders in the canopy arthropod fauna (25% of the total number of individuals), Majer and Recher (1988) found 17%,

while Adis et al. (1984) found at most 12% spiders at one of their localities. Most other studies found that spiders make up less than 10% of the arthropod fauna.

A number of methods for sampling spiders in the canopy (e.g., insecticide or chemical knockdown, hand collecting, branchlet shaking, and various traps) are reported in the literature, but each has distinct biases (e.g., Majer et al. 1996; Basset et al. 1997). Insecticide knockdown ('fogging') is the preferred technique for collecting the large number of specimens necessary for the study of biodiversity patterns and estimation of arthropod densities and species diversity (Basset et al. 1997). This method overcomes the inaccessibility of the forest canopy by bringing part of its fauna to the researcher. The first investigation of a forest canopy fauna using chemical knockdown was performed in Canada in 1961 (Martin 1966), but it took more than a decade before the method became widely accepted. Only a handful of studies sampling canopies by means of insecticides have specifically focused on spider communities (Liao et al. 1993; Höfer et al. 1994; Russell-Smith and Stork 1994, 1995; Silva 1996), although several other general studies of canopy arthropods have included spiders (Martin 1966; Southwood et al. 1982; Basset 1990, 1991; Guilbert et al. 1994, 1995; Majer et al. 1994; Ozanne 1996, 1999; Watanabe 1997). The majority of these studies have focused on lowland tropical rainforest.

In this paper, the results of a canopy study focusing on spiders in a Tanzanian montane forest are presented. The observed and estimated species richness are evaluated, and the composition of the spider community is discussed. The diversity and richness of spiders revealed in this study are then compared to other studies treating tropical canopy spiders, and the importance of spiders for canopy faunas and the influences of altitude and habitat type on canopy spider composition are assessed.

Methods

Study site

Field work took place at the end of the rainy season (17–27 May 1997) in an undisturbed primary montane forest at 1800–1900 m altitude southeast of Masisiwe village, above Kihanga stream, Uzungwa Scarp Forest Reserve, Iringa District, Tanzania (08°22'05.7' S, 35°58'41.6' E). The annual rainfall exceeds 1200 mm per year (Lovett and Wasser 1993). The forest is mature and homogeneous with an open understorey consisting of a few *Tabernaemontana* spp. Dominant trees of the canopy were: *Parinari excelsa* Sabine, *Aphloia theiformis* (Vahl) Bennett, *Agauria salicifolia* (Lam.) Hook., *Allanblackia* spp., and *Albizia gummifera* (Gmelin) Smith (Lovett (1992) gives general botanical details). There was very little low vegetation. Slopes did not exceed 30° and the canopy had at most two strata and did not exceed 30 m in height. It was lower on ridge tops. Sampling areas were randomly collected within an area of 25 ha around the junction of two ridges.

Canopy sampling

Arthropods were collected by means of knockdown sampling with insecticide using a K-10 Standard Thermal fogger (PulsFog, Germany) from the ground so that the mist drifted up through the canopy (McKamey 1999; Sørensen 2003). Canopy sampling was conducted either before sunrise or at sunset to minimise fog scatter, since wind speeds are low at these times. Sampling never took place after rain or during windy or misty conditions. The understorey was avoided and when low vegetation occurred in the plot, it was bent and tied to the ground or was shaken to remove spiders, in order to exclude arthropods from the lower vegetation layer from the samples. The sampling was thus limited to the canopy (almost exclusively vegetation above 15 m). Eleven samples of separate subsets of the canopy were collected within a period of 2 weeks. Each sample comprised approximately 90 m² and was completely covered by triangular funnel-like nets of 1 m². These are here treated as subsamples. The lowered centre was suspended 1 m above ground level between lines set at a distance of 70 cm. On slopes, the nets were set in terraces. All subsamples were mapped and each was assigned a unique code.

The fogger operated for approximately 30 min on each occasion and used 2 l of a 0.8% solution of natural, refined pyrethrum dissolved in water, with butoxide as the synergist. A 2 h drop-time was chosen in order to maximise the number of arthropods sampled and to reduce the number of animals escaping due to recovery from the toxic effect of the insecticide (Erwin 1989). The specimens were concentrated in the bottom of the nets by shaking and brushing and then preserved in 70% alcohol.

One caveat is that canopy fogging does not capture all invertebrates present. Collected invertebrates can become caught in canopy leaves, and spiders can stay attached to their silk. Shaking the trees after applying the insecticide could therefore potentially increase the number of spiders in the sampling nets, but was not feasible due to the size of the trees.

Material collected

All adult spiders were identified to family level, and, within family, to morpho-species (hereafter considered as 'species'). All morphospecies were confirmed by one other arachnologist (R. Baptista). Approximately 70% of the collected specimens were juveniles. These have been excluded from the analysis, because their identification is extremely difficult. Within each sex, genitalic characteristics were used to distinguish species. Males and females were generally matched using colour patterns and other morphological features, although relative abundance and co-occurrence were also considered. All species were assigned unique codes. Voucher specimens of the adult spiders (and other arthropods in the samples) were deposited at the Zoological Museum, University of Copenhagen. Duplicates of the spiders were deposited at the Department of Entomology, Smithsonian Institution, Washington, DC, USA and a set will, in agreement with the Zoological Department of the

University of Dar es Salaam, be sent to a museum in Tanzania once appropriate storage facilities are in place.

Data analysis

Species richness was estimated using the programme EstimateS[®] (Colwell 1997). A number of species richness estimators was used – Chao 1, Chao 2, ICE, ACE, jackknife 1, jackknife 2, bootstrap, MMeans, and MMRuns. Colwell and Coddington (1994), Colwell (1997) and Chazdon et al. (1998) give the formulas for and discuss in details these estimators. Furthermore, species richness based on a lognormal distribution was estimated using the procedure presented by Krebs (1989) and Magurran (1988). A one-way ANOVA with Dunn's multiple comparison test was then used to determine whether the estimates were clustered into groups, and estimates representative of any groups and any overlap were chosen for discussion.

A species accumulation curve (Gotelli and Colwell 2001) was calculated using the software programme EstimateS[®] using 200 randomisations and random number seed 13 (Colwell 1997). It was compared to a Coleman curve, which describes the theoretical or expected species–accumulation curve when data are randomly distributed among the samples (Coleman 1981; Coleman et al. 1982). I also plotted the accumulation curves for species richness estimates produced by Chao 1, for estimators representative of the groups determined by Dunn's multiple comparison test, and for singletons and doubletons (species represented by one and two specimens, respectively).

Results

The 11 samples of the present study produced a total of 5233 adult spiders, representing 28 families and 149 species. Thirty-five species (23%) were singletons while 18 (12%) were doubletons. Overall descriptive statistics and means (with SE) of the 11 samples are detailed in Table 1. The total number of adult spiders per sample was 476 ± 75 SE and the number of adult spiders m^{-2} was 5.78 ± 0.15 . The number of species $sample^{-1}$ was 58 ± 4 and the number of species m^{-2} was 4.03 ± 0.09 . Sample 5 was disturbed by rain after 1 h, and so the number of specimens (163) and species (41) in this sample were low. The inclusion of these data appears to cause the rather high observed variability in the overall analysis.

Two overlapping groups of species richness estimates were recognised using Dunn's multiple comparison test ($P < 0.05$) in an one-way ANOVA; one low group (MMeans, MMRuns, bootstrap, jackknife 1, ACE, ICE, lognormal), and one high group (ACE, ICE, lognormal, Chao 1, Chao 2, jackknife 2). MMeans and MMRuns were disregarded, as these produced estimates below the observed number of species when the number of samples was high. Of the remaining estimators, three – bootstrap (minimum estimate), lognormal (overlap), and jackknife 2 (maximum estimate) – were chosen based on the results of Dunn's multiple comparison test.

Table 1. Descriptive data and species richness estimates (lognormal, bootstrap, Chao 1 and jackknife 2) for spiders from canopy insecticide knockdown sampling in a montane forest in Tanzania, $n = 11$ samples.

	Total (for 11 samples)	Mean \pm SE (for each sample)
Number of subsamples (m ²)	906	82 \pm 2
Number of species	149	58 \pm 4
Number of adult specimens	5233	476 \pm 76
Number of singletons	35	25 \pm 1
% Singletons	23	42 \pm 3
Number of doubletons	18	10 \pm 1
% Doubletons	12	15 \pm 1
Estimated species richness		
Lognormal	186	95 \pm 10
Bootstrap	165	68 \pm 5
Chao 1	183 \pm 15	97 \pm 5
Jackknife 2	201	97 \pm 5

Chao 1 (Chao 1984) was also chosen, because it is an abundance-based estimator, which can be applied to single samples.

The bootstrap gave the lowest estimate (Table 1). The jackknife 2 estimate was in general higher than the others, although the lognormal species richness estimate gave very high values of estimated species richness in two samples; this was due to a large proportion of rare species among the observed species in these samples (Smith and van Belle 1984). The estimated total species richness using Chao 1 was 183 ± 15 SD for the complete sample, and was 97 ± 5 SE for the ~ 90 m² samples; similar estimates were given by the lognormal estimate.

The Coleman curve was indistinguishable from the real species–accumulation curve (Figure 1), indicating that the species in the sample are randomly distributed in the sampling universe (Colwell and Coddington 1994). The species–accumulation curve did not reach an asymptote (Figure 1), indicating that the sampling was incomplete. The ratio of observed to estimated (Chao 1) number of species was 80%, suggesting that at least 20% more species are to be expected in the area than were actually collected.

Data for individual families are presented in Table 2. Linyphiidae (20% of all adult specimens), Oonopidae and Pholcidae (both 17%) and Cyatholipidae (10%) were the most abundant families. Anapidae and Theridiidae both contributed up to 9%. On the other hand, Theridiidae (26%), Linyphiidae (13%), Salticidae (10%), Araneidae (9%), Thomisidae (7%) and Clubionidae (5%) were the most speciose families. Among the species-rich families (>10 species), singletons made up 14% of the species of Araneidae, 26% of the Salticidae, 28% of the Theridiidae, 37% of the Linyphiidae and 40% of the Thomisidae. The large number of rare species is indicated by the distribution function, which was a truncated lognormal distribution (\log_2 scale, $\chi^2_{(2,8)} = 14.0$, $P > 0.05$).

The three most abundant species contributed 45% of the specimens: *Ophrynia* sp. A (Linyphiidae), Oonopid? sp. 1 (possibly Oonopidae), and Pholcid sp. 2 (Pholcidae), contributing approximately 15% each. In addition to a large number of

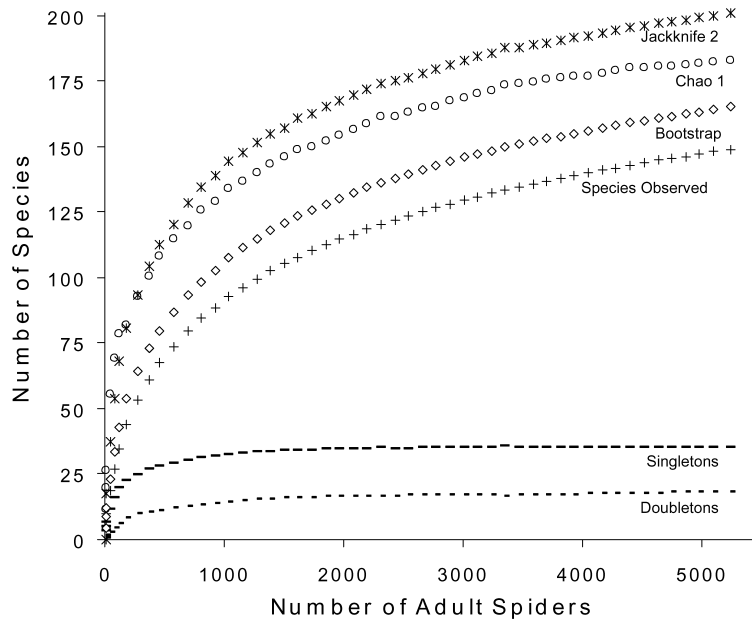


Figure 1. Species-accumulation curve and estimation curves Chao 1, jackknife 2, and bootstrap for the 11 canopy samples combined. The accumulation curves for singletons and doubletons are also presented.

apparently undescribed species (80%), at least one genus new to Africa was discovered, *Choriozopes* (L.L. Sørensen, unpublished data). It was only known from Asia until 1997, when it also was discovered in Madagascar (Emerit 1997).

The majority of previous canopy studies have investigated lowland tropical forests. Only a few have been conducted at higher altitudes (Appendix 1); only Russell-Smith and Stork (1994) compared spider communities from tropical forest canopies at different elevations (in Sulawesi). In Appendix 1 data collected on spiders in other studies of tropical and subtropical forest canopies are summarised for comparison with the present study. Specifically, data are presented on area sampled, type of sampling, numbers of species and specimens, numbers of specimens m^{-2} , and the proportion of spiders relative to all arthropods collected. The sampling methods used in previous studies include canopy fogging, selective fogging where single trees were sampled, restrictive sampling where parts of trees were sampled, and restricted canopy fogging (*sensu* Basset 1990).

Discussion

The present study is the first of its kind to have focused on the diversity of African spiders in montane forest canopies.

The overall species richness observed in the present study was 149 species, which was much lower than the observed richness in many tropical lowland forests

Table 2. Number of species of spiders, rare species (singletons and doubletons), and adult spiders (specimens) from the canopy of montane forest in Tanzania.

Family	Feeding guild	Number of specimens	Number of species	Number of singletons	Number of doubletons
Linyphiidae	SLW	1039	19	7	4
Oonopidae	AP	884	3	–	1
Pholcidae	SLW	872	4	–	–
Cyatholipidae	SLW	535	2	–	–
Anapidae	OW	452	2	–	–
Theridiidae	SLW	449	39	11	6
Clubionidae	CH	230	7	1	–
Araneidae	OW	170	14	2	1
Salticidae	CH	137	15	4	1
Thomisidae	AP	116	10	4	1
Scytodidae	SLW	60	1	–	–
Philodromidae	AP	53	3	1	–
Dictynidae	SLW	46	2	1	–
Amaurobiidae	SLW	45	1	–	–
Corinnidae	CH	36	5	1	–
Tetragnathidae	OW	23	5	1	2
Selenopidae	AP	17	1	–	–
Mimetidae	AP	16	4	–	–
Hahniidae	SLW	13	2	–	–
Heteropodidae	AP	10	2	–	–
Symphytognathidae	OW	10	1	–	–
Liocranidae	CH	5	1	–	–
Uloboridae	OW	5	1	–	–
Palpimanidae	CH	4	1	–	–
Agelenidae	SLW	2	1	–	1
Theridiosomatidae	OW	2	1	–	1
Ctenidae	AP	1	1	1	–
Mysmenidae	OW	1	1	1	–
Total		5233	149	35	18

Families are listed by abundance. Foraging guilds: orb weavers (OW) (25 species; 663 specimens), sheet-line weavers (SLW) (71 species; 3061 specimens), ambush predators (AP) (21 species; 213 specimens), and cursorial hunters (CH) (32 species; 1296 specimens). The feedings guilds are, with few modifications, in accordance to Silva (1996) and Silva and Coddington (1996).

(Russell-Smith and Stork 1995; Silva 1996). However, using a Chao 1 estimate (183 species) to validate the observed richness (149 species) suggests that approximately 80% of the species were sampled, maybe less, given that this estimate does not include spider groups that are not readily collectable by the fogging method, e.g., species in retreats and cryptic species.

Despite the relatively low number of rare species (singletons and doubletons) the non-asymptotic species–accumulation curve indicates that more sampling would be needed for a full inventory. Nevertheless, only 23% of the species collected were singletons, compared to Silva and Coddington (1996) 56% and Russell-Smith and Stork (1995) 71%; Höfer et al. (1994) also collected as many as 51–76% of all species to be singletons (Appendix 1). Interestingly, the accumulation curve for the

Chao 1 estimator appears to be reaching an asymptote at rather smaller sample sizes than the curves for the bootstrap and jackknife 2 estimators. All curves suggest that the spider fauna remains undersampled and the sample size would have to be increased (Figure 1) to get a stable estimate. According to Chao (1984) the estimators used are lower-bound and, because they only estimate the fauna available to the method, many more species could be expected in the sampling area.

Family level comparisons with other tropical canopy spider communities

The families Theridiidae (sheet-line weaving spiders), Araneidae (orb weaving spiders), Salticidae and Clubionidae, both classified as cursorial hunters (Silva 1996), tend to dominate tropical canopy spider communities in terms of species richness (Majer and Recher 1988; Stork 1991; Basset and Arthington 1992; Guilbert et al. 1994; Höfer et al. 1994; Majer et al. 1994; Russell-Smith and Stork 1995; Silva 1996; Guilbert 1997), with Theridiidae often being the single most important family (Basset 1990, 1991; Stork 1991; Basset and Arthington 1992; Russell-Smith and Stork 1994). This was confirmed by the present data. Linyphiidae were the second most species-rich family, followed by Salticidae and Araneidae. No previous insecticide knockdown canopy studies have found a similarly high species richness of linyphiids in tropical forests.

The families Theridiidae, Araneidae, Salticidae and Clubionidae also tend to dominate in terms of specimen numbers (Majer and Recher 1988; Stork 1991; Basset and Arthington 1992; Guilbert et al. 1994; Höfer et al. 1994; Majer et al. 1994; Russell-Smith and Stork 1995; Silva 1996; Guilbert 1997). The Theridiidae are often the single most important family with respect to abundance (Basset 1990, 1991; Stork 1991; Basset and Arthington 1992; Russell-Smith and Stork 1994). However, in the present study this family contributed only 9% of the specimens, while the Linyphiidae contributed 20% of the specimens and were the most abundant family, followed by the Oonopidae and the Pholcidae. The only other tropical study, which observed a similarly high abundance of linyphiids (19%), was that of Russell-Smith and Stork (1994) in Sulawesi, but this high abundance was due to a few very abundant species.

A further major difference between the present study and previous studies of canopy spider composition (Basset 1990, 1991; Liao et al. 1993; Höfer et al. 1994; Russell-Smith and Stork 1994, 1995; Silva 1996) was that Oonopidae, Anapidae and Cyatholipidae were here found to be abundant in the canopy. The latter two families are normally considered exclusively present in the litter or the low vegetation at ground level (Platnick and Forster 1989; Dippenaar-Schoeman and Jocqué 1997). Furthermore, in a few studies, other families were found to exceed 10% of the total number of specimens in a site, for instance Philodromidae and Oonopidae (Guilbert et al. 1994; Guilbert 1997), and Pholcidae (Russell-Smith and Stork 1994). The present study found the latter two families similarly abundant. Juveniles were excluded from this study due to the extreme difficulties of identification to species level; however, a quantitative assessment of their identities at the family level suggested a similar frequency distribution as with adults.

Effects of elevation on tropical canopy spider composition

Even though only few studies have been conducted at higher altitude, some patterns do however emerge with regard to the composition of canopy spider communities at different altitudes. Most notably, Russell-Smith and Stork (1994) indicate that species richness and density of spiders increase with increasing elevation and as the climate gets more temperate. The present study likewise shows a higher density of spiders than that found by most studies in lowland tropical forest. This is somewhat surprising, because the canopy in the Uzungwas consists of only a single layer, and the leaf area sampled was therefore presumably smaller than that of more complex lowland forests; however, it might indicate that the epiphyte load is important. Nevertheless, the mean of 5.8 specimens m^{-2} collected in this study is considerably higher than that of most of the other studies listed in Appendix 1. The only studies which revealed higher densities of spiders than the current study were those which used restrictive sampling techniques (e.g., Basset 1991), and Russell-Smith and Stork's (1994) sampling site at an elevation of 1150 m in Sulawesi.

Overall, seven out of the nine commonest families (>100 specimens) of the present study were also abundant at high elevations in Sulawesi (Russell-Smith and Stork 1994). In Sulawesi, at the family level, Theridiidae, Araneidae and Salticidae were the most important groups at low elevations with regard to specimen numbers, while the importance of the families Clubionidae and Oonopidae increased at higher elevations and Linyphiidae were only abundant at high altitudes, comprising 15% of all spiders at these elevations (Russell-Smith and Stork 1994). A reasonable hypothesis may therefore be that the importance of Linyphiidae increases with elevation in tropical forest. Whether this is due to: (a) better climatic adaptations of linyphiids, (b) advantages to linyphiids caused by changes in prey by altitude, (c) structural changes of the habitat with altitude (discussed below), (d) a remnant distribution pattern from previous colder global periods, or a combination of several factors cannot be resolved without further study.

It is also noteworthy that the composition of the spider community of a subtropical New Caledonian evergreen forest (Guilbert et al. 1995) had some similarity to that of montane Sulawesi, in that Clubionidae (29%) and Linyphiidae (20%) were important families. However, a study of submontane subtropical rainforest of Australia showed a lower abundance of linyphiids (Basset 1990).

Other determinants of spider community composition

Comparison of spiders between studies is difficult because of possible seasonal variation and the largely unknown effect of vegetation type and structure on the community structure. However, as Samu and Lövei (1995) conclude, short and intensive trapping can be a useful tool for comparative purposes, as it excludes the effect of immigration and emigration and seasonal activity. This study, like most of the studies listed in Appendix 1, represents a temporally constrained 'snapshot' of the canopy fauna, and hence does not reflect seasonal variation of species. It only includes adult individuals and provides information on diurnal regimes only.

Further, seasonal variation in spider abundance, as a response to change in prey availability, has been shown through canopy knockdown sampling (Recher et al. 1998). These factors may therefore give a biased impression of the relative importance of the different spider families. Nevertheless, it is assumed that the relative spider abundances reflect the sampled faunas.

Whether the differences in spider community composition between elevations and sites (Appendix 1) can be attributed to differences in the composition of vegetation remains unclear until studies have been carried out to reveal general patterns. Spiders have not been shown to be host-specific (Guilbert et al. 1995; Russell-Smith and Stork 1995). However, habitat structure does influence their density and richness (Stratton et al. 1979; Stevenson and Dindal 1982; Greenstone 1984; Uetz 1991; Halaj et al. 1998, 2000; Ozanne et al. 2000; Stuntz 2001), and more complex habitats can be expected to be more diverse. Uetz (1991) suggests that vegetation structure can be determined by tree species alone, but occurrence of epiphytes (Stuntz 2001) and age of vegetation (Jennings and Collins 1987; Uetz 1991) may also explain some of the variation in spider communities. Ozanne et al. (2000) found that exposed trees affect the structure and microclimate, and hence the spider community; for example, some species of linyphiids were confined to the interior forest.

Stork (1987a) found that taxonomic similarity of the 'host' trees, proximity between sites and similarity in epiphytes increased the similarity of arthropod communities in the canopies. The study of spider communities in Douglas fir canopies by Halaj et al. (2000) also showed that the density of most spider groups increased with structural complexity. Differences in dominance of families between studies could therefore be explained by variation with regard to the sampled habitat types.

Both linyphiids and theridiids are often found in structurally rich areas (Stratton et al. 1979), while araneids that catch flying prey prefer more open habitats (Nyffeler and Benz 1979; Halaj et al. 2000). In a montane cloud forest (as in the present study), the cover of epiphytes, mosses and lichens is high, providing suitable habitat for linyphiids, oonopids, and anapids. Furthermore, the high humidity of a montane forest should provide good canopy conditions for otherwise ground-dwelling spiders, e.g., cyatholipids and anapids, and for linyphiids. Anapids have been considered cryptic species confined to the litter layer, while cyatholipids mainly have been found in low vegetation (Dippenaar-Schoeman and Jocqué 1997). Although Salticidae and Thomisidae are commonly found in 'edge' habitats and open areas (Turnbull 1973; Dippenaar-Schoeman and Jocqué 1997) which include the foliage of the upper canopies, Halaj et al. (2000) showed that the number of both jumping spiders (e.g., salticids) and cursorial hunters (e.g., clubionids) also increases with complexity. Dominance of salticids and thomisids in other studies could, however, indicate that the extreme upper portions of the canopies have been better sampled in some of the previous canopy studies.

The presence of ants could also affect the abundance and composition of the spider fauna. Ants have been suggested to exclude spiders from the litter layer (Jocqué 1984). If the same occurs in the forest canopy, as discussed by Guilbert et al. (1995), it could explain some of the differences in spider community com-

position between study sites, especially in the tropics where ants often dominate the fauna (e.g., Stork 1991).

African spider species richness

The African spider fauna is still poorly investigated; about 6000 species are known and more than 20000 are estimated to exist (Alderweireldt and Jocqué 1994), although this is a disputed number. Platnick (1999), for example, has suggested a much lower number. The global species estimate for spiders is 76000–170000 species (Adis and Harvey 2000). In the present study only ~20% of all species were known to science, and it has been suggested that in some African localities as little as 10% of the fauna are known to science (Alderweireldt and Jocqué 1994).

The studies of Russell-Smith and Stork (1994, 1995) showed that the overlap in spider fauna between two sites collected 1100 km apart was 1.7%, while Colwell and Coddington (1994) found that less than 3% of spider species were shared between communities collected on a gradient in Bolivia about 100 km apart. The total number of linyphiids in the present Masisiwe forest site, including the lower layer of the forest, was 23 species (Sørensen et al. (2002), and this study). A comparison of the linyphiid fauna to another site, above Chita village (Scharff 1990) within the same forest complex approximately 20 km from Masisiwe, showed an overlap of only six species (26%), which were all found in the canopy (present study). Furthermore, Scharff (1992) found no overlap in true forest species of linyphiids between 300–500 and 1700–1800 m above sea level. Prior taxonomic work has in general focused on conspicuous and easily collected species, and the rich canopy fauna has been largely ignored (Alderweireldt and Jocqué 1994). The high proportion of undescribed species in this study, along with the low overlap with spider faunas at adjacent sites, may suggest that the African spider fauna is considerably richer than previously estimated.

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Appendix 1

Published information on species richness, abundance, density and proportion (relative to all arthropods) of spiders from subtropical and tropical forest canopies sampled by insecticide knockdown sampling. Key: m^2 – the total area sampled, N – number of specimens, $N m^{-2}$ – number of specimens m^{-2} , and %Total – number of spiders of total number of individuals.

Study site	m^2	Species	N	$N m^{-2}$	%Total	Pesticide used	Reference and remarks
<i>Evergreen forest</i>							
Peru, lowland	34*(2–12)	844*	4068*	(5–30)*	?	Resmethrin	Silva (1996), Samiria River, 34 sites representing 2–12 m^2 ; dry leaves, epiphytes, vines and trees
Peru, lowland	?	555*	1427*	?	?	?	Silva (1996), Tambopata
Brazil, lowland	56	123*	245*	3.14*	?	1% Pyrethrum, 0.15% Baythroid	Höfer et al. (1994), Reserva Florestal Adolpho Ducke, one site resampled twice
Brazil, lowland	43.2	?	168	3.9	12.1	3% Pyrethrum	Adis et al. (1984), Varzea forest, inundated
Brazil, lowland	33.6	?	50	1.5	2.4	3% Pyrethrum	Adis et al. (1984), Igapo forest
Brazil, lowland	38.4	?	184	4.8	3.0	3% Pyrethrum	Adis et al. (1984), Terra Firma, dry land forest
Brazil, lowland	36	?	63	3.5	2.9	1% Pyrethrum, 0.15% Baythroid	Adis et al. (1997, 1998), <i>Goupia glabra</i> tree resampled. High number of ants
Sulawesi, lowland	120	20	113	0.9	0.8	2% Reslin (Bioresmethrin)	Russell-Smith and Stork (1994), Dumoga-Bone National Park (210 m a.s.l.)
Sulawesi, lowland	120	59	450	3.8	?	2% Reslin (Bioresmethrin)	Russell-Smith and Stork (1994), Dumoga-Bone National Park (300 m a.s.l.)
Sulawesi, lowland	120	69	648	5.4	3.1	2% Reslin (Bioresmethrin)	Russell-Smith and Stork (1994), Dumoga-Bone National Park (400 m a.s.l.)
Sulawesi, montane	30	50	438	14.6	6.2	2% Reslin (Bioresmethrin)	Russell-Smith and Stork (1994), Dumoga-Bone National Park, (1150 m a.s.l.)
Brunei, lowland	200	190	945	4.7	4.0	2% Reslin (Bioresmethrin)	Russell-Smith and Stork (1995), Stork (1987a, 1987b, 1988, 1991), Bukit Sulang, Laden Hills Forest Reserve
New Caledonia, lowland	640	18 fam.	1594	2.5	6.1	Cyfluthrin (Baythroid)	Guilbert et al. (1994), Guilbert (1997) (Appendix 13A), four seasons, evergreen forest
Australia, submontane	~72 [#]	72*	1408*	~19.5*	25.1	Carbon dioxide	Basset (1990, 1991), Mt Glorious State Forest, subtropical, 10 trees of <i>Argyrodendron actinophyllum</i>
Australia, lowland	~30	?	621	~20.3	6.2	Pyrethrins 2EL™	Kitching et al. (1993), Cape Tribulation, North Queensland, tropical forest
Australia, lowland	~45	?	1549	~34.4	6.7	Pyrethrins 2EL™	Kitching et al. (1993), Lamington National Park, Southeast Queensland, subtropical rainforest
Tanzania, montane	906	149	5233	5.8	?	0.8% Pyrethrum	Present study (1800–1900 m a.s.l.)
<i>Sclerophyllous forest</i>							
New Caledonia, lowland	640	11 fam.	4947	7.7	9	Cyfluthrin (Baythroid)	Guilbert et al. (1994), Mt Nondoué, Paita, four seasons
New Caledonia, lowland	640	18 fam.	6768	10.6	6.1	Cyfluthrin (Baythroid)	Guilbert et al. (1994), Guilbert (1997) (Appendix 13A), Pindai, four seasons
Dry evergreen forest	80	?	?	1.1–12.9	0.9–5.0	DDVP and MEP	Watanabe and Ruyssoongern (1989), Watanabe (1997), submontane, Nam Phrom, Chaiyaphoon, four seasons $\times 20 m^2$ each
Thailand, submontane	224	25	199	0.8	12–15	Fenvalerate	Liao et al. (1993), He Shan, Guangzhou, <i>Acacia mangium</i> , four plots sampled monthly April–October

*Including juvenile; # area according to Basset (1990).

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