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Stratification of the spider fauna in a Tanzanian forest

Line L. Sørensen

ABSTR4CT

The vertical distribution of arthropods in the vegetation of tropical forests in Africa has rarely been examined. In the present study, the stratification of true spiders (Araneae) was investigated in a montane forest in Tanzania. Spiders were chosen because they are generally not host specific. Their distribution relies mainly on the structure of the habitat and on prey availability (only a few species are prey specific). Sampling was carried out in a 1 ha plot in a mature and relativelb- homogeneous forest at the end of the rainy season. Three strata were recognized and sampled: the forest floor (the forest litter and vegetation below 50 cm), the understorey (vegetation between 50 crn and 3 m) and the canopy (vegetation taller than 3 m). The spider assemblage of the forest floor nas most diverse (Simpson's index), although the canopy and the understorey were more species rich. Spider composition of the understorey was more similar to that of the canopy than to that of the forest floor. Of the 175 species collected in total, 27 species were confined to the canopy (15%), whereas 32 species (18%) were restricted to the forest floor. Even given that different sampling methods do not sample all taxa with equal efficiency, specialization of spiders fron certain families within a particular strata was evident. This was even true for species that are regarded as being relatively mobile, like linyphiids. The present study indicates that the canopy should be included if a reasonably complete inventory of spiders is to be obtained.

IYTRODUCTION

Tropical rainforests are reputed to support most of the world's biodiversity (Wilson, 1988a) One possible reason for this high diversity may be the richness of vertically distributed microhabitats in these forests, although it is disputed ivhich strata may be the most important in this regard. Based on Panamanian beetle data, Erwin (1982) assumed that as many as 66% of the beetles were confined to the forest canopy, 20% of which were host-specific species. Stork (1988), by comparison, estimated that no more than 20% of the beetle species within his plot on Borneo were unique to the canopy. Similarly, Brühl *et al.* (1998) in their study on Borneo found that ***25%*** of the ants were unique to the canopy, and Mammond (1990) found oniy 10% of beetles to be unique to the canopy in Sulawesi. This lack of consensus, which precludes a precise estimate of global arthropod species richness (1–80 million species), indicates the need for studies of the distribution of taxa in stratiFred forests and of differences among forest types. The resulting understanding of stratification will be irnportant for management and conservation of the arthropod diversity of tropical forests.

Only a few tropical forest surveys have assessed the relative importance of the canopy and ground strata for the distribution of species within a particular area. These studies have focussed on four groups of invertebrates:

* highly mobile communities of insects (e.g. Sutton & Hudson, 1960; Sutton, 1983; Sutton *et al*, 1983a; Toda, 1992; DeVries *et al.*, 1997; Intachat & Holloway, 2000) sampled by various kinds 0f trap, attractive or nonattractive, and targeting specific taxa: baited traps have been used for beetles, butterflies and *Drosaphria* (e g Deiries et *al*, 1997) and unbaited traps, such as light traps and sticky traps (e g Sutton, 1983, Sutton *et al*, 1983a; Intachat & Holloway, 2000), for these and other taxa
* herbivorous insects in the upper canopy layer (e g Basset *et al*, 1992)

- all arthropods (e g Stork 1988, Hammond, 1990, Hammond *ei a l*, 1997) sampled using techniques such as flight-interception traps, litter samples, pitfall traps and qeilou pan traps (Hammond, 19901, Malaise traps (Wammond, 1990, Hammond *et a l*, 1997) and canopy fogging (Stork, 1988, Hammond, 1990)
- ground-living and canopy-duelling arthropods (e g arthropods associated M ith ground and arboreal 'soil' in the canopy) (Longino & Nadkarni, 1990, hadkarni Bi Longino, 1990, Paoietti *et a l*, 1991, Bruhl *e r a l*, 1998, Rodgers & Kitching 1998, baiter ez *a i*, 1998)

Despite differences in sampling methodology and analytical approaches, the studies above show that faunal stratification occurs in tropical forests and that there is a gradual turnover of faunal composition from the ground to the canopy Further, some studies reported a strong shift in faunal composition (e.g. Bruhl *et si.*, 1998). There is, however, no consensus as to the relative importance of the canopy for arthropods. There is a weak tendency for the canopy, broadly defined, to be richer in arthropod species, whereas the abundance of individuais is generally higher at ground level. Exceptions are the studies of butterflies by DeVries *er al.* (1997) and by Intachat and Hollowa); (2000), of macro- and microarthropods by Longino and Nadkarni (1990) and of ants by Bruhl *eral.* (1998).

The present study focusses on spiders, a cosmopolitan group, locally common and diverse. The group is not host specific, their distribution depending rather on the physical structure of the environment and on the availability of prey (Greenstone, 1982; Cetz, 1991; Halaj *et a l*, 2000).

The objectives of the present study were to determine how the richness and the composition of the spider fauna change vertically between the forest floor and the canopy within 1 ha of montane forest in Tanzania. The study aimed to answer the following questions:

1. Are spider assemblages different among different microhabitats and strata surveyed?
2. Does sprder abundance differ among strata:
3. Is spider species richness in the canopy different from that in the lower strata of the forest (ground lebel and understorey);

METHODS

Study area

Spiders were collected in a montane forest of the Uzungwa Scarp Forest Reserve, Uzungwa Mountains, Tanzania (campsite 08"'22'05'' S, 35"' 58' 42" E) during a 2-week period in May 1997 at the end of the rainy season. Sampiing was performed on the forest floor, in the understorey and in the canopy layer within a 1 ha plot on a ridge (1800 to 1900m abose sea level) next to the campsite. The Uzungwa Mountains are part of the Eastern Arc Mountains, which are known for their high degree of floral and faunal endemism (Lovett Bi Wasser, 1993; Fjeldså, 1999; see these sources for full biological descriptions of the Uzungwa Mountains). The forest is primary and mature mixed forest, in uhich the common trees are *Allanblackia* spp., *Albzzia gummifera* (Gmelin) Smith, *Parinara exceisa* Sabine, *Agaurza salzcifolia* (Lam.) Hook and *Aphloza theifomis* (Vahl) Benett. In the sampling area, the forest was undisturbed by humans and was homogeneous. The understorey was fairly open with some *Tabernaemontana* sp., and the canopy did not exceed 30 m in height. Mosses and lichens were common on stems and branches in the canopy. The structure of the forest appeared rather similar to a mature European beech forest, with emergent crees of rather similar size and very few smaller trees (these srnalier trees were avoided in the canopy sampling). The rainfail is approximately 2000 rnm per year.

sampling methods

Spiders were collected by a team of 10 people within an 11-day period. Two collectors mainly sampled from the canopy while the others collected from the lower strata of the forest. The team Mas a mix of experienced and less-experienced collectors (three professional arachnologists, six students and one parataxonomist). The forest was divided into three strata: the *forest poor* (including ground, litter, low shrubs and herbs below 0.5 m); a higher herb, bush and shrub layer from 0.5m to 3 m *(understorey);* and an upper, closed *canopy* srratum (nnciuding all foliage above 3 rn, which was in practice almost exclusively above 15 mj.

It was not feasible to access the canopy using cranes or other technical devices. The canopy was, therefore, sampled using insecticidal knockdown sampling (canopy fogging) using a PulsFog^{TM} K-10 Standard Thermal fogger (PulsFog, Germany) releasing a solution of 0.8% natural pyrethrum diluted in water. Sampling took place early in the morning or late in the afternoon, when there was no wind. The sampling targeted vegetation higher than that which could be reached by hand, beating or sweep net. There were few smali trees and the sampling was, therefore, Eocussed on the closed canopy (and the tree trunks). It was not possible EO ensure that the uppermost canopy was well sampled, because both rising fog and falting arthropods may hase become trapped by the lower portion of the canopy. On 4 consecutive days, four areas of canopy were sampled within the 1ha plot. Each sample consisted of 90 subsamples of $1m^2$. The insecticide was applied from the ground and each application (2 litres) took 30 minutes. h 2-hour drop-time was allowed after the applrcation of the insecticide.

Various semiquantitative and quantitative sampling methods (Coddington *et ai.,* 1991, 1994) were used to sample the lower strata: forest floor and understorey. The forest floor was sampled by searching for spiders living in 'crqptic' habitats (litter, logs and mosses) and manual coîlecting where spiders were collected from the ground and vegetation up to knee-leve! ('ground'). Because the herb layer was relatively thin in the study area it was given less attention than other habitats. It was sampled mainly by sweep netting ('sweeping'). Samples obtained by sweeping were included as part of the foresc floor sample in the analyses of differences across strata.

The understorey stratum (shrub layer) was sampled by beating the vegetation and collecting the spiders from a tray ('beating') and by manual collection of spiders from shrubs and trunks from knee-Iev-el to as high as one can reach ('aerial' *sensu* Coddington *et al.,* 1996). Each sample of the methods – cryptic, ground, sweeping, beating and aerial – wastimed, with only actise sampling time being measured. One hour of active sampling represented one sample. Overall sampling totalled *200* hours, approximately one third during the day and two thirds at night. In order to avoid bias by collector, the eight collectors sampling forest floor and understorey applied al! methods both at night and during the day. Summary statistics of the inventory by method are given in Table 9.1

Coilected materiaî was stored in *709'0* alcohol and the spiders were subseqrently sorted to morphospecies (distinctive, recognizable morphological units, hereafter 'species'jbecause knowîedge oithe spider fauna remains incomplete. Juvenile spiders (representing ~60% ofthe specimens) here excluded because they could not be identified to species level

Statistical methods

Species-accumulation curves *(200* random resamplings of ail samples for each method and for each straturn) nere generared using the software Estimates 5.0.1 (Colwell, 1997b; Longino, *2000).* To compare species diversity among strata, Simpson's indices (Magurran, 1988) were also calculated.

Complementarity values between pairs of strata were calculated as the number of species unique to each stratum divided by the combined number of species of the two strata (Colwell & Coddington, 1994). Analyses were performed among all three combinations of strata: canopy, understorey and forest floor.

To investigate further the differences in spider assemblages among strata, a chi-square test (adopting the nul! hypothesis of no difference in overall distribution of individuals within families among strata) was performed on the number of individuals within the 13 most abundant families. This included the families Thomisidae and Salticidae, often abundant families in lowland tropical fores: (Russell-Smith & Stork, 1994, 1995; Silva, 1996), which were only the 12th and 13th most abundant families here These 13 families represented 94% of the total specimens collected.

The number of spider species for each stratum and for the total plot was estimated with the Chao 1 estimator using the software Estimates 5.0.1(Colwell, 1997b). Chao 1 (Chao, 1981) *MPS* selected rather than other *es*timators because it can be used to estimate species richness based on the number of observed species, number of singletons (species represented only by one specimen) and doubletons (species represented by two specimens) in a single sample and is, therefore, widely applicable The Chao 1 estimates gave intermediate species-richness esrimaies when compared with the other estimators included in the programme Estimates (results not showr?).

The completeness of sampling by method and by stratum was calculated by dividing the species-richness estimate (Chao 1) by the observed number of species (performance in Table 9.1). As the species-accumuiation curves and curves of the species-richness estimator did not tend to an asymptote, species richness was estimated based on *200* resamplings of 500 adult specimens for comparison among sampling methods

Table 9 1 *Summary of variables (i-standurd deviation) detailed by sampling methods and strata surveyed*

	Heating	Cryptic	Ground	Aerial	Sweeping	Forest floor	Understorey	Canopy (fogging)	Total
Sainplrs	49	45	41	48	17	103	97	325	525
Species	92	62	**66**	72	*4b*	96	114	95	I75
Species in 500 individuals	55 8 ± 5 7	59 1 ± 1 3	60 9 **t** 2 **6**	53 0 **i** 7 4	39 7 ± 1 3	63 44 **f** 4 1	57 9 **t** 5 6	62 5 ± 3 6	78 1 i 6 7
Adult spiders	1783	558	642	1141	584	1784	2924	1608	6316
Singletons	27	22	**19**	25	**13**	27	**36**	26	40
Doubletons	**16**	11	7	10	7	14	16	19	20
Unique	14	11	5	6	1	32	21	27	–
Simpson index	8 13	9 53	18 83	6 60	4 62	14 66	7 97	9 21	14 40
Chao **1**	1 1 4 8 1 1 1 5	84 ± 12.4	918.162	1 0 3 3 1 1 6 9	5 4 1 1 8 8	122.0 ± 13.2	154.5 ± 18.0	112.8 ± 9.1	215 ± 16 7
Per**for**inance	7 8 1 f 5 4	6 8 4 f 9 8	7 6 8 1 6 8	7 1 2 1 7 5	72.7 ± 7.8	7 4 6 1 7 2	7 4 6 f 6 4	806.49	81 1 f i 3
Chao I for 500 individuals	91 9 **f** 20 2	83 0 ± 13 *9*	87 5 ± 17 **6**	81 **6 1** 19 **1**	52 9 **f** 9 5	89 0 ± **I6** 7	95 2 ± 21 5	**98** 5 ± ***19*** I	118 2 **f** 19 4

Chao 1, estiinated nuniber of species **using** the Chao 1 estimator *(**see** text)*, singletons, single representatives of **a cpecies,** doublctons, **two** representatives of a **species,** unique, specie5 unique to sampling method or stratum, performance, Chao I divided by the observed number of species

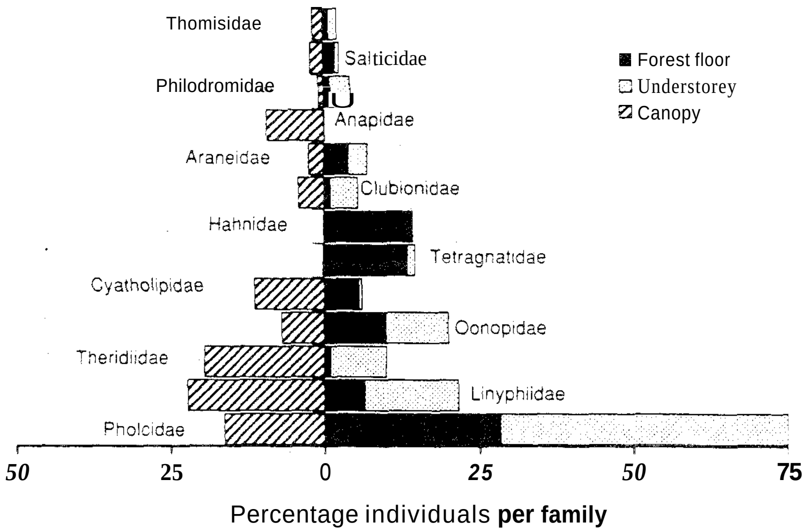

Fig 9 1 The relative abundance of rhe most abundant families of spiders in the three defined strata canopj, understorev and forest floor

and strata The number of species for 500 specimens and estimated richness are given in Table 9 1

RESULTS

In total, the three strata sampled included 6316 adult specimens representing 175species in 33 families Forty (22%) ofthe species collected were represented bv only one specimen (singletons) and ~80% were species new to science Overall, 1784 adult spiders were collected on the forest floor, representing 96 species in 28 families Thirty-one of these species were collected only on the forest floor and I E (11%) of them were singletons In the understore), 2924 adult spiders of 114 species representing 29 families were collected, including 23 species unique to this stratum (21%) Fourteen (13%) of these Mere singletons In the canopy, 1608 adults belonging t~ 95 species (including 24 families) were collected Of these, 27 (29%) species were coilected only in the canopq, including 15(16%) singletons (Table 9 i summarises the data by method and strata) The data at famil) level for the three strata within the plot are summarised in Table 9 2

Dissimilarities between strata

The spider communities on Fhe forest floor and in she canopy were the most different (complementarity 79.2) whereas the fauna in he understorey and in the canopy shared more species (complementarity 53.8).The fauna of the forest floor shared more species with the understorey (complementarity 58.1)than with the canopy.

The distribution of individuals in the 13 most abundant families also showed considerable differences among the three strata (Table 9.2, Fig. 9.1), as demonstrated by a chi-square test (chi-square$_{3,24}$ = 5557, $p < 0.0001$). The same pattern was reflected at species level (Fig. 9.2). Pholcidae were common in all strata, most noticeably in the understorey. The pholcid species collected from the forest floor were different from those found in the higher strata. The family Linyphiidae was very common in the canopy, along with the family hnapidae, which is normally considered to be associated with the litter and low vegetation (Dippenaar-Schoeman & Jocqüe, 1997). The families Tetragnarhidae and Hahnidae were sampled almost exclusively on the forest floor, whereas the family Cyathoiipidae was most common on the high vegetation (Fig. 9.1). One species that might be referred to the family Qonopidae was found primarily in the canopy. and although other species of Oonopidae were found on the ground, very few individuais were collected in the understorey. This family is normally considered to consist of ground dwellers (Dippenaar-Schoeman & Jocqué, 1997).

Further examples of the stratification of species within families are given in Fig. 9.2. Species of Linyphiidae, such as *Mrcyntdir* spp. and *Callitrichia sellafionits* Scharff 1990 were collected primarily in the understorey and low vegetation whereas *Callirrtchin* sp. n. was

Table 9.2. *Numbers of adult spiders, species, singletons and pairs for each spider family collected in the 1 ha plot, detailed by forest strata (see methods)*

Family	Total data				Forest floor				Understorey				Canopy			
	Ind	Sp	1s	2s	Ind	Sp	1s	2s	Ind	Sp	1s	2s	Ind	Sp	1s	2s
Agelenidae	38	2	–	1	19	1	–	–	19	2	–	1	–	–	–	–
Amaurobiidae	4	1	–	–	–	–	–	–	2	1	–	1	2	1	–	1
Anapidae	152	3	1	–	2	2	2	–	2	2	2	–	148	2	–	–
Araneidae	201	12	3	–	71	3	1	–	91	10	4	–	39	10	3	2
Barychelidae	6	3	1	1	4	2	1	–	2	1	–	1	–	–	–	–
Clubionidae	217	6	1	–	19	2	1	–	131	5	1	–	67	6	1	1
Corinnidae	32	6	1	1	7	2	–	1	12	3	–	1	13	4	1	–
Ctenidae	45	3	–	–	42	3	–	–	3	1	–	–	–	–	–	–
Cyatholipidae	596	3	–	–	18	3	–	–	264	3	–	1	314	2	–	–
Dictynidae	19	1	–	–	1	1	1	–	10	1	–	–	8	1	–	–
Gnaphosidae	3	1	–	–	3	1	–	–	–	–	–	–	–	–	–	–
Hahnidae	257	4	–	–	252	4	–	1	4	2	–	2	1	1	1	
Heteropodidae	5	2	–	1	–	–	–	–	3	2	1	1	2	1		1
Linyphiidae	915	16	2	3	117	9	1	2	441	7	2	1	357	12	[illegible]	4
Liocranidae	32	6	3	–	29	5	2	1	3	2	1	1	–	–	–	–
Lycosidae	52	1	–	–	51	1	–	–	1	1	1	–	–	–	–	–
Mimetidae	47	6	1	1	6	5	4	1	38	5	1	–	3	3	3	–
Mysmenidae	3	2	1	1	2	1	–	1	–	–	–	–	1	1	1	–
Oonopidae	296	5	1	–	101	4	–	1	15	2	1	–	180	3	1	–
Palpimanidae	1	1	1	–	–	–	–	–	–	–	–	–	1	1	1	–
Philodromidae	128	2	–	–	20	2	–	–	95	2	–	1	13	1	–	–
Pholcidae	2134	7	2	–	506	5	1	–	1366	5	1	–	262	4	–	–
Salticidae	88	20	9	2	35	7	4	1	20	10	6	1	33	9	3	2
Scytodidae	14	1	–	–	–	–	–	–	3	1	–	–	11	1	–	–
Segestriidae	10	3	–	2	8	3	–	2	2	1	–	1	–	–	–	–
Selenopidae	15	1	–	–	1	1	1	–	6	1	–	–	8	1	–	–
Symphytognathidae	3	1	–	–	–	–	–	–	–	–	–	–	3	1	–	–
Tetragnathidae	279	6	–	1	239	6	1	–	37	5	2	–	3	2	1	1
Theridiidae	581	37	9	4	178	14	3	2	293	30	9	3	110	23	6	6
Thomisidae	83	8	3	1	16	4	2	–	40	5	2	–	27	4	1	
Theridiosomatidae	38	2	–	1	28	2	1	–	10	2	1	–	–	–	–	–
Uloboridae	14	1	–	–	2	1	–	1	10	1	–	–	2	1	–	1
Zodariidae	8	2	1	–	7	2	1	–	1	1	1	–	–			
Total	6316	175	40	20	1784	96	27	14	2924	114	36	16	1608	95	8	19

Ind, adult spiders; Sp, species; 1s, singletons; 2s, doubletons.

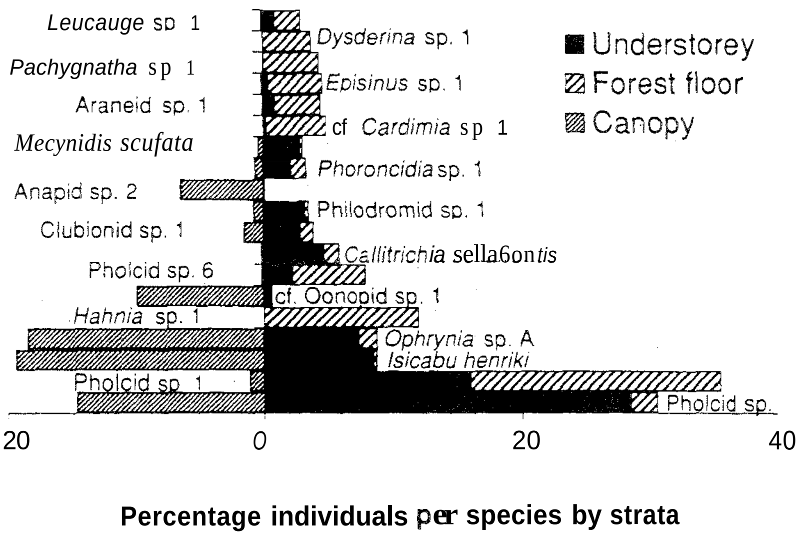

Fig. **9.2.** The relative abundance of the 19 most abundant of the 170 species of spiders in the three defined strata canopy, understorey and forest floor.

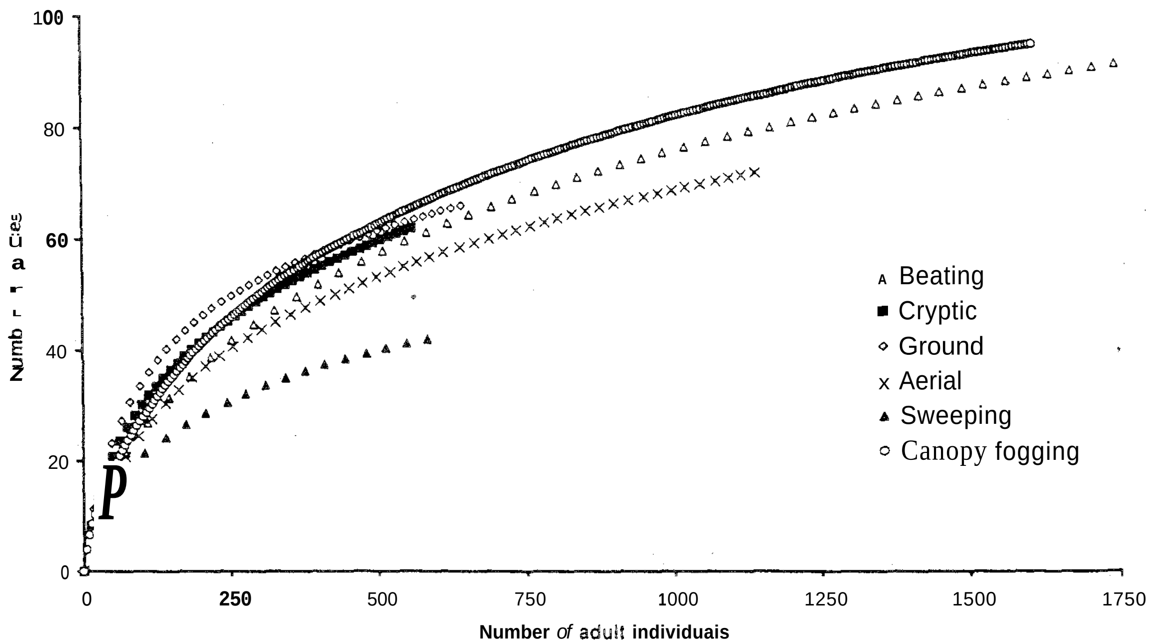

Fig **9.3.** Species-accumulation curves for spiders collected with differect sampling methods within differen: habitats

collected in the canopy Species of *Ophrynta* were observed mainly in the understore) and canopy. and *Ophrynta* sp **A** (8% of the tota! number of adults in the plot) was very common in both layers *Lepthqphavtes* spp were found only on the forest floor

Species richness

The species-accumulation curves for the different sampling methods (Fig 9 3) show that species saturation was not reached using any of the methods Sweeplng samples yielded the lowest number of species, and the shallow slope of the sweeping curve indicates a low within-sample diversity (Simpson'sindex 4.62). In contrast, ground sampling (in particular Simpson's index 18.83) showed a steep slope, indicating that the method detects many species in low numbers (high within-sample diversity). The canopy fogging seems to detect more species overall compared with beating and ground samples. Although the same microhabitats were surveyed by vegetation beating and by aerial manual collecting in the understorey, the observed species richness was lower using the latter method. Manual collecting of [he understorey may miss some of the cursoria! hunting spiders and rare spiders that are collected with beating. and sampling by beating is also likely to access more habitat volume than manual collecring of the different microhabitats. All methods contributed unique species within each stratum, resulting in an increase in species richness when samples were combined.

The results of the calculation of Simpson's indices for each stratum (Table 9.1) süpport the results of the species-accumulation curves (Fig. 9.4). Pn particular, the forest floor displays higher within-sample diversity (Simpson index 14.66) than both the understorey and the canopy, but the fact that its species-accumulation curve intersects with the curves for both other strata (Fig.9.4) indicates that its overail assemblage richness is lower. The aithin-sample diversity is higher for the canopy but close to that of the understorey; it is not clear whether their curves would intersect upon extrapolation

Overall, the rotal estimated species richness within the 1ha plot was 215 ± 17. The sample of the understorey seemed the richest in species whereas the canopy sample gave the lowest estimated richness. Comparable subsamples showed that the estimated richness of the canopy, in fact, was highest, bui that the understorel was *almost* as rich.

DISCUSSION

Spiders are adapted *to* a wide range ofhabitats and it is difficult to use comparably efficient collecting methods

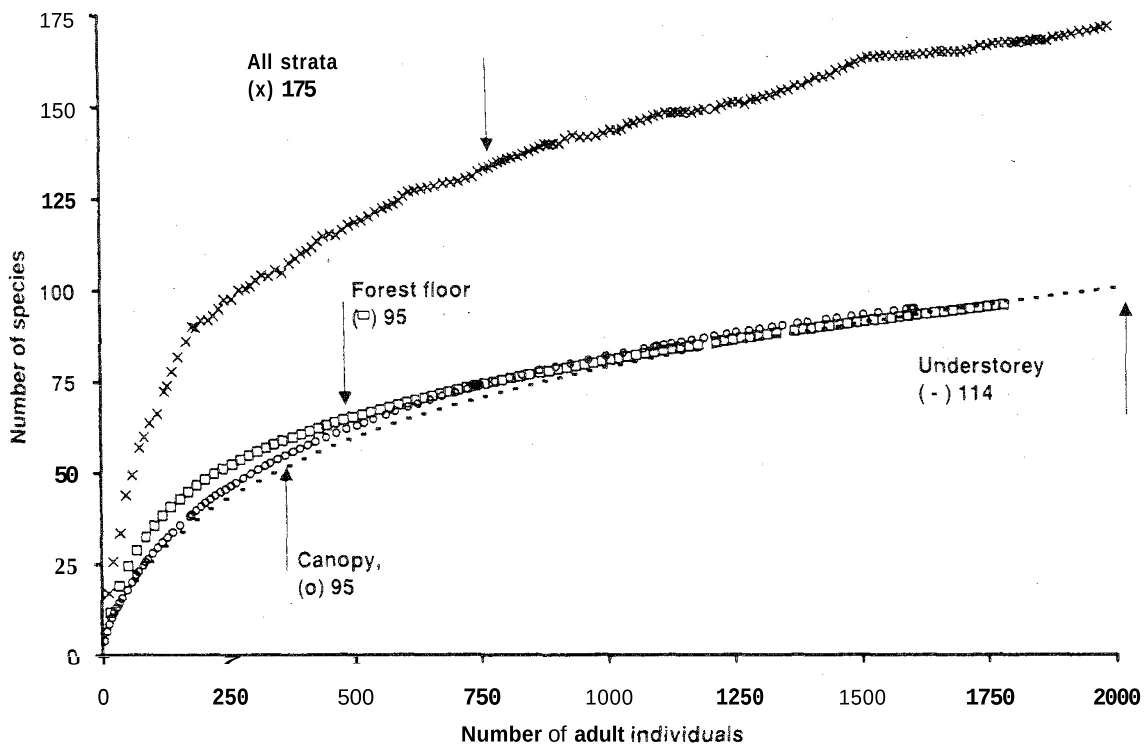

Fig. 9.4. Species-accumulation curve for spiders collected from the forest floor, understorey and canopy, and for all strata combined The total number of species obserbed is givcn for each area

to cover all the different microhabitats in which they live (Turnbull, 1973). Because the original purpose of the inventor). was in part to obtain data for the study of species richness and to assess the importance of the canopy, several methods were used, including manual collecting methods. Longino and Colwell (1997) have stressed the importance of using methods in 'strict inventories' that sample complementary sets ofspecies. In many tropical rainforests, arrhropod species richness is so high an3 many species are so rare (Novotny & Basset, *2000)* that it is nearly impossible to obtain sufficient complete data to do actual comparisons across different strata based on species lists or for species richness (Longino, 2000). This incomplete sampling is reflected in the accumulation curves (Figs 9.3 and 9.4) and emphasizes the difficulties of obtaining sufficient samples for reliable estimates of species richness.

A high number ofrare species (singletons and pairs) were observed in the Tanzanian samples when considering either sampling methods or the strata sampled (Table 9.2). Differences in patterns of diurnal activity were accounted for by sampling both at night and during the day. However, the apparent rarity of some species might be explained by seasonality. The present knowledge ofthe biology of the Tanzanian spider fauna is limited and it is, therefore, not possible to assess the extent to which phenology can be used to explain the occurrence of rare species. In the present samples, 80% of the species were undescribed taxa There is clearly a need for more studies on tropical invertebrates both from the forest floor and the canopy.

This is one of the first studies that focusses specifically on the vertical distribution o l spiders in tropical forests. This verticae distribution indicated complex assemblages with a strong stratification pattern across the defined strata (forest floor, understorey and canopy), even though the understorey ivas more intensely sampled than the other strata.

The canopy and understorey showed much similarity in species composition whereas the canopy shared fewer species with the forest floor. Since the understorey included low vegetation (above 50 cm) it was expected that this stratum would have shown the highest species diversity, with an influx of forest floor and canopy fauna. However, the understorey appears to have a distinctive fauna, with more species shared with the canopy than with the forest floor. The forest floor, Furthermore, iias a number of distinctive species confined to it.

A larger sample size would undoubtedly have yieided additional species in al! strata and also would have included species that were previously considered 'unique' in other strata. Nevertheless, the data still reflect a high degree of habitat specificity. The iinyphiids, of which few species were unique to single strata, are a good example. They showed a high degree of specialization, with the majority of individuals of most species collected in a single stratum, even though juvenile Iinyphiids are known to disperse by ballooning Millidge and Russell-Smith (1992) found that linyphiids collected in the canopy of Brunei and Sulawesi rainforests were clearly distinct species from those of the lower Strata.

The uniqueness ofthe canopy fauna (approximately 20% unique species) was close to the data reported by Stork (1988: 17%) and Bruhi *ei al.* (1998: 25%). Aithough considering the 19 most common species revealed no unique species to the canopy, distinct differences in species abundance were apparent (Fig.9.2). Many species appeared to have their highest populations in the canopy, suggesting that the canopy supports a distinctive fauna.

Further studies are needed in order to clarify shether there is an exchange of species between the canopy and the ground or whether species occurring in high numbers in the canopy biit collected in low numbers at ground·level should be considered as transient at the lower levels. Because of their predatory nature, spiders cannot be classified as 'tourists' (hloran si Southwood, 1982) even though their biology indicates that they do have certain habitat preferences. Species from the canopy are more likely *to* occur as 'transient' in lower strata than vice versa.

Studies in temperate climates have shown that the composition of spider assemblages are determined by the structure of the habitat and its microclimate (Duffey, 1966; Scheidler, 1990; Haiaj *et a l*, 2000). Vertical stratification has previously been shown for spiders in temperate deciduous forests (e.g. Elliott, 1930; Gibson, 1947; Turnbull, 1960) and in pine forests (Docherty si Leather, 1997). Despite the fact that many temperate species overwinter in the ground and migrate in the spring to higher strata, stratification is stili apparent although :he phenomenon of species tending to extend their ranges into adjacent strata has been observed (Turnbull, 1960). Seasonal variation in the composirion of the spider assemblage in the temperate forests is high (Elliott, 1930; Gibson, 1947; Turnbull! 1960).

Turnbull (1960) found that the abundance of spiders is much higher in the ground stratum (forest floor) than in any of the other strata, and that h e held layer (understorey) uas richest in species. He attributed these observations mainly to the large open non-inhabitable spaces in the canopy. In lowland Cameroon, Basser *et al.* (1992) also reported that, when beating the vegetation, the understorey was richer in number of families of spiders than the upper canopy. though no significan: difference could be detected in number of individüals.

In the present study, the forest floor turned out to be the most diverse stratum though the canopy was more species rich. In the' canopy and understorey, many species occurred in low abundances, and a few species of pholcids and a single species of linyphiid dominated in terms of adult numbers (Ssrensen, 2000). This might indicate that the fauna is less dense at ground level, perhaps because of fewer available rnicrohabitats, However, this could also be explained by the choice of sampling methods. Canopy fogging. despite the method's apparent inability to access cryptic living species, might sample more broadly than manual coilecting methods, where the collector may be biased against less-abundant species. This could be the reason why more species are represenred in low numbers in rhe canopy compared with those collected manually from the ground and understorey.

Canopy fogging. as applied in the present study, will not allow the same degree ofresolution of animai distribution across microhabitats as the methods applied on the forest floor and in the understorey. Since the method was applied from the ground, the sampling probably focussed on the fauna of the lower parts of the canopy, which may be more comparable with the understorey with regard to microclimate. It is likely that the exposed upper canopy would reveal a fauna that differs from that of the lower canopy; for instance, it is likely that active hunters will be more abundant in the former location. The high species richness in the canopy migh: be explained by a high density and diversity of prey (Sutton & Hudson, 1980; Surton *et al.*, 1983a; Sutton, 1983, Sadkarni & Longino, 1990; DeVries *et ai.*, 1991). Spiders, then, differ from less-mobile organisms such as mites, which exhibit greater diversity at the forest floor

The srratificarion pattern of the spiders and other inkertebrate groups (Stork, 1988, Bruhl *ei al,* 1998) seems similar If correct, this implies that a relatively high proportron of the fauna is confined to the canopy The resuits of the present study indicate that for reasonably complete inbentories of the spider fama the rich canopy fauna must be included Neverrheless, a survey of the understorey in the present study encountered a high proportion of the species occurring in the canopy, albeit in lower numbers

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REFERENCES FOR CHAPTER 9

Basset, Y., Aberlenc, H.-P. & Delvare, G. (1992). Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecological Entomology,* **17**, 310-318.
Brühl, C. A., Gunsalam, G. & Linsenmair, K. E. (1998). Stratification of ants (Hymenoptera, Formicidae) in a primary rain forest in Sabah, Borneo. *Journal of Tropical Ecology,* **14**, 285-297.
Chao, A. (1984). Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics,* **11**, 265-270.
Coddington, J. A., Griswold, C. E., Dávila, D. S., Peñaranda, E. & Larcher, S. F. (1991). Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. In *The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*, ed. E. C. Dudley, pp. 44-60. Portland: Dioscorides Press.
Coddington, J. A., Young, L. H. & Coyle, F. A. (1996). Estimating spider species richness in a Southern Appalachian cove hardwood forest. *The Journal of Arachnology,* **24**, 111-124.
Colwell, R. K. (1997b). EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.
Colwell, R. K. & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London, Series B,* **345**, 101-118.
DeVries, P. J., Murray, D. & Lande, R. (1997). Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society,* **62**, 343-364.
Dippenaar-Schoeman, A. S. & Jocqué, R. (1997). *African Spiders. An Identification Manual. Plant Protection Research Institute Handbook No. 9*. Pretoria: ARC-Plant Protection Research Institute.
Docherty, M. & Leather, S. R. (1997). Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. *Forest Ecology and Management,* **95**, 197-207.
Duffey, E. (1966). Spider ecology and habitat structure. *Senckenbergiana Biologica,* **47**, 45-49.
Elliott, F. R. (1930). An ecological study of the spiders of the beech-maple forest. *The Ohio Journal of Science,* **30**, 1-22.
Erwin, T. L. (1982). Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin,* **36**, 74-75.
Fjeldså, J. (1999). The impact of human a forest disturbance on the endemic avifauna of the Udzungwa Mountains, Tanzania. *Bird Conservation International,* **9**, 47-62.
Gibson, W. W. (1947). An ecological study of the spiders of a river terrace forest in Western Tennessee. *The Ohio Journal of Science,* **47**, 38-44.
Greenstone, M. H. (1982). Determinants of web species diversity: vegetation structural diversity vs. prey availability. *Oecologia,* **62**, 299-304.
Halaj, J., Ross, D. W. & Moldenke, A. R. (2000). Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos,* **90**, 139-152.
Hammond, P. M. (1990). Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. In *Insects and the Rain Forests of South East Asia (Wallacea)*, eds W. J. Knight & J. D. Holloway, pp. 197-254. London: The Royal Entomological Society of London.
Hammond, P. M., Stork, N. E. & Brendell, M. J. D. (1997). Tree-crown beetles in context: a comparison of canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi. In *Canopy Arthropods*, eds N. E. Stork, J. Adis & R. K. Didham, pp. 184-223. London: Chapman & Hall.
Intachat, J. & Holloway, J. D. (2000). Is there stratification in diversity or preferred flight height of geometroid moths in Malaysian lowland tropical forest? *Biodiversity and Conservation,* **9**, 1417-1439.
Longino, J. T. (2000). What to do with data. In *Ants. Standard Methods for Measuring and Monitoring Biodiversity*, eds D. Agosti, J. D. Majer, L. E. Alonso & T. R. Schultz, pp. 186-203. Washington D.C.: Smithsonian Institution Press.
Longino, J. T. & Colwell, R. C. (1997). Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecological Applications,* **7**, 1263-1277.
Longino, J. T. & Nadkarni, N. M. (1990). A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. *Psyche,* **97**, 81-93.
Lovett, J. C. & Wasser, S. (eds) (1993). *Biogeography and Ecology of the Rainforest of Eastern Africa*. Cambridge: Cambridge University Press.

Magurran, A. E. (1988). *Ecological Diversity and its Measurement*. London: Chapman & Hall.
Millidge, A. F. & Russell-Smith, A. (1992). Linyphiidae from rain forests of Southeast Asia (Araneae). *Journal of Natural History,* **26**, 1367-1404.
Moran, V. C. & Southwood, T. R. E. (1982). The guild composition of arthropod communities in trees. *Journal of Animal Ecology,* **51**, 289-306.
Nadkarni, N. M. & Longino, J. T. (1990). Invertebrates in canopy and ground organic matter in a Neotropical montane forest, Costa Rica. *Biotropica,* **22**, 286-289.
Novotny, V. & Basset, Y. (2000). Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos,* **89**, 564-572.
Paoletti, M. G., Taylor, R. A. J., Stinner, B. R., Stinner, D. H. & Benzing, D. H. (1991). Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. *Journal of Tropical Ecology,* **7**, 373-383.
Rodgers, D. J. & Kitching, R. L. (1998). Vertical stratification of rainforest collembolan (Collembola: Insecta) assemblages: description of ecological patterns and hypotheses concerning their generation. *Ecography,* **21**, 392-400.
Russell-Smith, A. & Stork, N. E. (1994). Abundance and diversity of spiders from the canopy of tropical rainforests with particular reference to Sulawesi, Indonesia. *Journal of Tropical Ecology,* **10**, 545-558.
Russell-Smith, A. & Stork, N. E. (1995). Composition of spider communities in the canopies of rainforest trees in Borneo. *Journal of Tropical Ecology,* **11**, 223-235.
Scheidler, M. (1990). Influence of habitat structure and vegetation architecture on spiders. *Zoologische Anzeiger,* **225**, 333-340.
Silva, D. (1996). Species composition and community structure of Peruvian rainforest spiders: A case study from seasonally inundated forest along the Samiria river. Proceedings of the XIIIth International Congress of Arachnology, Geneva, 3-8. IX.1995. *Revue Suisse de Zoologie,* **vol. hors série**, 597-610.
Sørensen, L. L. (2000). *Biodiversity in Space - a Three-Dimensional Comparison of Spider Faunas in East African Forests*. Ph.D. dissertation. Copenhagen, Denmark: University of Copenhagen.
Stork, N. E. (1988). Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society,* **35**, 321-337.
Sutton, S. L. (1983). The spatial distribution of flying insects in tropical rain forests. In *Tropical Rain Forest: Ecology and Management*, eds S. L. Sutton, T. C. Whitmore & A. C. Chadwick, pp. 77-92. Oxford: Blackwell.
Sutton, S. L., Ash, C. P. & Grundy, A. (1983a). The vertical distribution of flying insects in the lowland rain forest of Panama, Papua New Guinea and Brunei. *Zoological Journal of the Linnean Society,* **78**, 287-297.
Sutton, S. L. & Hudson, P. J. (1980). The vertical distribution of small flying insects in the lowland rain forest of Zaire. *Zoological Journal of the Linnean Society,* **68**, 111-123.
Toda, M. J. (1992). Three-dimensional dispersion of drosophilid flies in a cool temperate forest in northern Japan. *Ecological Research,* **7**, 283-295.
Turnbull, A. L. (1960). The spider population of a stand of oak (*Quercus robur* L.) in Wytham Wood, Berks., England. *The Canadian Entomologist,* **92**, 110-124.
Turnbull, A. L. (1973). The ecology of the true spiders (Aranemorphae). *Annual Review of Entomology,* **18**, 305-348.
Uetz, G. W. (1991). Habitat structure and spider foraging. In *Habitat Structure. The Physical Arrangement of Objects in Space*, eds S. S. Bell, E. D. McCoy & H. R. Muhinsky, pp. 325-348. London: Chapman & Hall.
Walter, D. E., Seeman, O., Rodgers, D. & Kitching, R. L. (1998). Mites in the mist: how unique is a rainforest canopy-knockdown fauna? *Australian Journal of Ecology,* **23**, 501-508.
Wilson, E. O. (ed.) (1988a). *Biodiversity*. Washington, D.C.: National Academy Press.