

Species composition and community structure of peruvian rainforest spiders: A case study from a seasonally inundated forest along the Samiria river

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Species composition and community structure of peruvian rainforest spiders: A case study from a seasonally inundated forest along the Samiria river. - Field work was carried out along the Samiria river, in the Pacaya-Samiria National Reserve, northeastern Peru (Loreto), at the end of the rainy season, May-June 1990. More than a thousand morphospecies belonging to at least 39 families of spiders were collected from various canopy and understory microhabitats by using a combination of fogging and conventional sampling techniques. Over half of the species belong to only three families: Salticidae (19%), Theridiidae (16%), and Araneidae (18%). Diversity and abundance for the former two families were higher in the canopy, while for the last one they were higher in the understory. The highest number of species (151) was found in one of the most heterogeneous canopy microhabitats. A few species accounted for 1-3 % of the adult spiders, the great majority did not reach 0.5 % of the total number of adults collected (5,895 indiv.). The two most complex categories of microhabitats from the canopy and the understory strata appeared to be moderately distinct, 59% of species were present in only one or the other. However, single sets of microhabitats from both strata exhibited a narrow spider species overlap, on average, 89% of complementarity.

Key-words: canopy-understory-spiders-Neotropics-fogging-biodiversity

INTRODUCTION

Trees provide a suite of useful microhabitats for the study of animal communities. Individuals in the arboreal community are all more or less trophically interlinked, and they are unified in their dependence on the tree. Trees are also structurally complex, providing potentially great niche diversification for their inhabitants. These attributes help account for the extraordinary species richness of arboreal communities (MORAN & SOUTHWOOD 1982; FARREL & ERWIN 1988; BASSET & ARTHINGTON 1992).

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In the last 15 years, it has been shown that tropical tree canopies are extremely rich in insects and other arthropod species (ERWIN 1983, ADIS *et al.* 1984; STORK 1991); recent studies are also providing new information about species richness, abundance and community structure of tropical spiders (BASSET 1991; GUILBERT *et al.* 1995; HÖFER *et al.* 1994; RUSSELL-SMITH & STORK 1994, 1995). It appears from them that microhabitat qualities are playing an important role in the distribution of the canopy spider species.

Physical qualities of particular microhabitats allow spiders to finely partition available space into specific, more narrowly defined niches. This in turn has an important effect on the species richness and abundance of spiders and although most species exhibit very narrow, patchy distributions, spiders as a whole comprise one of the most conspicuous and diverse groups of terrestrial invertebrates (BARNES 1953; DUFFEY 1978, 1993; HÖFER 1990; CODDINGTON & LEVI 1991; MASON 1992; NENTWIG 1993).

Based on semi-quantitative data, this paper attempts to provide comparative information on microhabitat differences in species richness, species composition, and community organization of the spiders from the canopy and understory of an Amazonian forest as well as to contribute towards a better understanding of spider species diversity.

MATERIALS AND METHODS

STUDY SITE. Samiria river is a blackwater river located in the Pacaya-Samiria National Reserve, northeastern Peru ($74^{\circ}21'-75^{\circ}28'W/04^{\circ}39'-05^{\circ}07'S$), 80-100 m elevation. Despite vast floodings during the rainy season, November to April, the forests along the Samiria river are highly diverse, and are characterized by buttressed trees up to 45-55 m high, forming an almost closed canopy with numerous epiphytes and vines. A detailed description of the study area is being prepared (Erwin, pers. comm.).

SAMPLING TECHNIQUES. During four weeks between May and June 1990, various microhabitats from the canopy (above 10 m high) and the understory (0-10 m high) strata were chosen along the Samiria river according to their distinctive architecture. These microhabitats fell into six main categories: 1) dry leaves hanging in the undercanopy, 2) vines mixed with dry leaves of trees, 3) vines, 4) palms, 5) epiphytes, and 6) one or more huge trees and associated vines plus epiphytes, e.g., more "complex" habitats (Table 1).

The microhabitats in the canopy and the understory were sampled by using a fogging technique (ERWIN 1990). Each fogging consisted of sufficient biodegradable resmythrin insecticide to fog the entire selected microhabitat. One to six 2-m² plastic sheets were placed under the selected microhabitats, and all the arthropods which fell onto them during the 2 hr period after fogging were collected. The canopy fogging (at least 20 hours of collection) took place at dawn, while the fogging of the understory microhabitats (at least 78 hours) took place at different hours of the day depending on wind conditions.

Spiders from the understory were also collected by a time-based search of at least 84 hours of looking up and down (CODDINGTON *et al.* 1991), and by beating lower tree branches (at least 1 hour), and sweeping herbaceous vegetation (2 hours).

DATA ANALYSIS. The criterion used to determine species richness was the number of species present in each sample (SOUTHWOOD *et al.* 1982). The degree of complementarity (distinctness), "the proportion of all species in two sites that occurs in only one or the other of them," was measured by the formula suggested by COLWELL & CODDINGTON (1994:112): $C_{jk} = U_{jk}/S_{jk}$ [# species unique to either site)/(species richness for both sites combined)], where $U_{jk} = S_j + S_k - 2V_{jk}$, and $S_{jk} = S_j + S_k - V_{jk}$; S = # species in sites j and k , and V_{jk} = # species shared by sites j and k .

According to this formula, the fauna of two sites will be completely distinct when $C = 100\%$. Species density was summarized by a 3-point abundance scale: rare= 1-4; common= 5-15; dominant= over 15 individuals. All spiders were counted but only the adults were sorted to morphospecies. Juveniles and voucher specimens were deposited in the Natural History Museum of Lima, Peru.

Patterns of spider community organization were analyzed by assigning each family to one of four functional groups which were defined by differences in prey-capture strategies (RIECHERT & HARP 1987; UETZ 1992). Orb weavers and sheet-line weavers rely on vibratory cues through silk webs to detect their prey; ambush predators do not use capture webs and remain stationary for long periods of time waiting for prey; while cursorial hunters move more or less constantly searching for prey. It must be pointed out that this is just a way to facilitate future comparisons, because within any guild there is a great deal of variation in prey-capture strategies, and a much greater amount of work is required to do a more precise and meaningful partitioning of functional groups.

RESULTS

Microhabitat differences of abundance and species richness. In terms of abundance, about half the total number of spiders collected by fogging were recorded from the "complex" microhabitats (42%) alone, followed by dry leaves (24%). When only the adults (38% of the total) were considered, the spiders were about equally distributed across four samples, with the "complex" microhabitats as the most abundant (23%), followed by dry leaves (19%), vines (17%), and epiphytes (16%) (Tables 1-2).

Species richness varied markedly across microhabitats. However, comparisons of single samples showed the richest habitats were those with mixed vegetation (20%), vines (20%), dry leaves (18%), and epiphytes (16%) (Table 1).

Community organization. The most abundant functional groups were the cursorial hunters (30%) and the sheet-line weavers (29%). The orb weavers (22%) and the ambush spiders (19%) were also important components of this community (Table 2).

TABLE I

Microhabitats, abundance and number of spider species from the Samiria forest. Ca= canopy. Un= understory. Each of the microhabitats represent a single sample.

MICROHABITAT	JUVENILES		FEMALES		MALES		SPECIES	
	Ca	Un	Ca	Un	Ca	Un	Ca	Un
DRY LEAVES (DRL)								
Dry leaves clumped on vegetation at 1 m		36		10		13		19
Dry leaves scattered in undercanopy at 2 m		116		41		32		38
Dry leaves scattered in undercanopy at 2 m		28		12		8		15
Dry leaves scattered in undercanopy at 3 m		70		12		10		16
Dry leaves scattered in undercanopy at 3 m		82		21		22		32
Dry leaves in undercanopy at 3 m		175		42		41		51
Dry leaves in tree		113		44		56		44
Dry leaves in tree		159		88		52		66
Dry leaves in tree		36		15		10		19
Dry leaves in tree		82		16		26		28
Dry leaves hanging in undercanopy		920		141		143		137
DRY LEAVES AND VINES (DLV)								
Dry leaves of vine under dense canopy*		33		11		7		15
Dry leaves of vine under dense canopy		47		21		16		19
Dry leaves and vines at 5 m		24		27		22		32
VINES (VIN)								
Lethycidacea plus vines, nr. river (fog. 20 m up)	599		189		159		146	
Dead tree stump with leafy vines		168		52		56		55
Tree with vines		59		41		31		48
PALMS								
Scheelea palm surface, shady (PAL)		122		54		37		48
Scheelea palms (4) and understory leaves (PAU)		147		35		31		35
Scheelea palms with epiphytes at 4 m (PAE)		159		91		73		66
Dry hanging leaves of <i>Mauritia flexuosa</i> (MAU)**		62		50		53		41
MAU with vines at 5m (MAU)**		118		31		26		22
Dry hanging leaves of <i>Mauritia flexuosa</i> (MAU)**		146		33		26		42
EPIPHYTES (EPI)								
Ficus plus epiphytes (fog. 40 m up)	458		123		114		119	
Large bromeliads on side of tree at 2 m		279		33		10		25
Bromeliads in <i>Ficus</i> *		14		10		5		11
COMPLEX ARCHITECTURE (COM)								
Big tree with vines and epiphytes*** (FOG 1 TLE-May)		336		164		150		122
Big tree with vines and epiphytes (FOG 1 TLE-June)		120		30		42		42
3 huge trees with vines and epiphytes		777		195		210		146
Leguminosae with vines and epiphytes		429		120		96		126
Big tree with vines and epiphytes*** (FOG 2 TLE-May)		537		199		133		151
Big tree with vines and epiphytes (FOG 2 TLE-June)		361		56		79		89
Big tree with vines and epiphytes (FOG 3 TLE-June)		465		136		111		116
Tree nr. <i>Manguifera</i> , dense canopy*		11		3		4		7

* Rain drastically affected the time of collection (approx. 20 min.)

**Swamp forest outside the Samiria river (74°18'W/04°43'S)

*** The same tree was fogged a second time after three weeks, approx.

TABLE 2

Abundance of spider families collected by fogging canopy and understory microhabitats. DRL= dry leaves, DLV=dry leaves & vines, VIN= vines, EPI= epiphytes, COM= canopy mixed vegetation, PAL= *Scheelea palms*, PAU= palms & understory leaves, PAE=palms & epiphytes, MAU= *Mauritia* palms.

	DRL	DLV	VIN	EPI	COM	PAL	PAU	PAE	MAU	TOTAL (%)
ORB WEAVERS	137	13	84	65	252	1	8	7	37	604 (14.9)
Anapidae	1	0	1	12	-	-	-	-	-	14
Araneidae	85	9	67	35	181	1	4	4	16	402
Deinopidae	1	1	-	-	1	-	-	-	-	3
Mysmenidae	3	1	-	1	5	-	-	1	9	20
Tetragnathidae	4	1	3	2	7	-	1	1	-	19
Theridiosomatidae	33	-	6	12	47	-	2	1	8	109
Uloboridae	10	1	7	3	11	-	1	-	4	37
SHEET-LINE WEAVERS	269	39	127	108	498	47	18	50	58	1214 (30)
Dictynidae	1	-	-	-	6	-	-	-	-	7
Hahniidae	-	-	-	-	-	-	-	-	1	1
Linyphiidae	2	-	11	-	3	-	-	-	-	16
Ochyroceratidae	1	-	-	-	-	-	-	-	-	1
Pholcidae	21	18	16	9	61	11	3	7	21	167
Rhoicininae	-	-	1	2	9	-	-	-	-	12
Scytodidae	7	-	4	7	33	2	1	-	2	56
Theridiidae	237	21	95	90	386	34	14	43	34	954
AMBUSH PREDATORS (18.5)	170	18	100	44	333	14	5	29	38	751
Ctenidae	11	6	1	1	18	4	-	8	3	52
Hersiliidae	5	-	6	1	17	-	-	-	1	30
Heteropodidae	44	7	19	5	58	1	-	8	11	153
Mimetidae	7	-	5	9	20	-	-	2	7	50
Oxyopidae	2	-	1	1	26	-	-	-	1	31
Pisauridae	7	-	1	2	14	-	-	1	7	32
Selenopidae	-	-	-	-	4	-	-	-	-	4
Senoculidae	5	1	4	-	5	1	-	1	-	17
Thomisidae	88	4	62	25	171	8	5	9	8	380
Trechaleidae	1	-	1	-	-	-	-	-	-	2
CURSorial HUNTERS (36.6)	294	37	199	87	636	28	35	79	86	1481
Anypheidae	25	1	13	7	34	1	1	7	1	90
Aphantochilidae	3	-	13	-	13	-	1	1	2	33
Caponidae	4	2	-	1	10	1	-	1	1	20
Clubionidae	1	4	-	4	-	-	-	-	-	9
Corinnidae	41	3	17	7	74	5	1	4	21	173
Gnaphosidae	10	-	14	2	34	-	-	3	2	65
Liocranidae	5	-	6	1	12	1	-	-	3	28
Lycosidae	-	-	1	-	-	-	-	-	-	1
Miturgidae	5	-	1	4	9	-	-	-	-	19
Oonopidae	74	13	70	19	142	18	27	21	10	394
Palpimanidae	-	-	-	-	-	-	-	-	1	1
Salticidae	125	14	63	42	307	2	5	42	44	644
Tetrablemmidae	-	-	1	-	-	-	-	-	-	1
Undetermined	1	-	-	-	1	-	-	-	1	3
ABUNDANCE (%)	870 (21.5)	107 (2.6)	510 (12.3)	304 (7.5)	1719 (42.4)	90 (2.2)	66 (1.6)	165 (4.1)	219 (5.4)	4050

In terms of abundance, families were not equitably distributed among the guilds (Tables 2-3). Salticidae (42%) were clearly dominant among cursorial spiders; while the most abundant orb weavers were Araneidae (65%). The great majority of sheet-line weavers were Theridiidae (79%), while among ambush predators the most abundant family was Thomisidae (39%).

When ranked according to the number of species (Table 3) cursorial spiders dominate all the microhabitats (36%), in part due to the high number of salticids. Orb weavers (28%), with Araneidae as the richest family, were also highly diverse. Sheet-line weavers ranked third (20%), with Theridiidae as the richest family. Among ambush predators (16%), Thomisidae was the most diverse family.

Species composition. A total of 5,895 adult spiders and 1,140 morphospecies, approx. 39 families, were recorded in this study (Table 3). A complete list is available on request. Over half of all adult spider species belong to only four families: Salticidae (220 species), Araneidae (207), Theridiidae (184) and Corinnidae (57).

The richest genera were *Eustala* (68 spp.), *Wagneriana* (25 spp.), *Micrathena* (14 spp.), and *Alpaida* (13 spp.) (Araneidae); *Dipoena* (46 spp.), and *Argyrodes* (28 spp.) (Theridiidae), *Encolpius* (17 spp.) (Salticidae); and *Tmarus* (11 spp.) (Thomisidae).

Despite the use of combined sampling techniques, some species, which accounted for 43% of the collection, were recorded from only one individual. Families like Hahniidae, Palpimanidae, and Tetrablemmidae were among the rarest taxa. Some other unidentified species with doubtful family placement were also very rare (Tables 2-3).

Species Dominance. Very few species, among them *Episinus erythrophthalmus* (2.5%), *Thwaitesia bracteata* (2.7%), and one unidentified oonopid (2.2 %), were collected in almost all microhabitats in high densities. Other species, like one unidentified Sparianthinae (1.8%), *Dipoena* nr. *nigra* (1.3%), *Tmarus* sp. (1.5%) and another oonopid (1.6%) were also abundant, either in the canopy and/or in the understory. Some other species such as aphantochilids, araneids, lycosids, theridiids, and thomisids, were commonly collected both in the canopy and the understory; however they accounted for less than 1 % of the total adult sample (Table 4). Species of *Ctenus*, *Corinna*, *Thaumasia*, and *Ancylometes*, were commonly found in the understory and, in terms of biomass, they were dominant in this stratum.

Complementarity. When all the microhabitats were pooled within their respective major categories and the categories compared, the proportion of species shared between pairs of samples (Table 5) was very low. The highest value (13 %) was found between dry leaves and complex microhabitats, which could be considered the most representative samples from the understory and canopy, respectively. These two microhabitats exhibited a moderate level of distinctness ($C = 59\%$), while most other sets showed a higher level of complementarity, on average 88%.

When single microhabitats were compared (Table 6), the complementarity was stronger than when the microhabitats were combined, 89 % on average, indicating a very narrow overlap in spider species composition across them. Even the two samples from the same tree exhibited a strong species distinctness, averaging 88%.

TABLE 3

Abundance and species richness of spider families from the Samiria river. Singletons refer to the number of species with only one individual. FOG=fogging, LUD=looking up & down (day/night), BEA=beating, SWE=sweeping.

	FOG		LUDd		LUDn		BEA		SWE		Singletons	
	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	Ind.	Spp.	No.	%
ORB WEAVERS												
Anapidae	14	1	8	1					4	1	0	
Araneidae	402	139	164	63	205	80	6	6	6	6	98	47.3
Deinopidae	2	1	2	1	3	2					0	
Mysmenidae	20	7	33	11	14	8			2	2	5	45.4
Symphytognathidae			6	2							1	50.0
Tetragnathidae	19	9	50	7	28	14			4	3	18	56.2
Theridiosomatidae	112	18	45	18	14	8					14	45.2
Uloboridae	36	20	31	7	30	14					19	63.3
SHEET-LINE W.												
Dictynidae	7	1									0	
Hahnidae	1	1									1	100
Linyphiidae	16	4	11	5					10	3	4	40.0
Ochyroceratidae	1	1									1	100
Pholcidae	167	25	38	9	15	3	4	2			8	28.6
Rhoicininae	12	1	1	1							0	
Scytodidae	56	6	3	2	19	3					1	16.7
Theridiidae	954	137	275	49	161	55	6	4	11	6	80	43.5
AMBUSH P.												
Ctenidae	52	9	20	9	66	16					13	50.0
Hersiliidae	30	8	2	1	3	3					2	22.0
Heteropodidae	153	13	4	4	9	6					9	50.0
Mimetidae	50	15	2	2	29	14					7	30.0
Oxyopidae	31	16	2	2	4	3					9	53.0
Pisauridae	32	7	24	14	63	15					18	64.3
Selenopidae	4	2			1	1					0	
Senoculidae	17	2			2	2					0	
Thomisidae	397	45	10	7	10	5	3	3	1	1	20	40.8
Trechaleidae	2	2	7	3	5	2					3	50.0
CURSorial H.												
Anyphaenidae	90	40	8	7	22	10			2	1	20	41.7
Aphantochilidae	33	2			2	1					1	50.0
Caponiidae	20	1					1	1			0	
Clubionidae	9	3			1	1					1	33.3
Corinnidae	173	49	8	6	5	5			2	2	30	52.6
Gnaphosidae	65	12									3	25.0
Liocranidae	28	9									3	33.3
Lycosidae	1	1	60	11	19	3			7	3	4	33.3
Miturgidae	19	7			2	1					3	42.9
Oonopidae	394	30	4	5	1	1	3	3			11	35.5
Palpimanidae	1	1									1	100
Salticidae	644	195	65	32	23	17	9	6	2	2	105	47.7
Tetrablemmidae	1	1									1	100
Undetermined	3	3		1	1	1	1	1			6	100

TABLE 4

Relative abundance of the most common spider species from Samiria.

Species	Canopy	Understory	% Genus	% Family	% adults
ARANEIDAE					
<i>Eustala</i> (ARA140)	6	33	16.6	4.6	0.7
<i>Eustala</i> (ARA146)	32		13.6	3.8	0.5
APHANTOCHILIDAE					
<i>Bucranium</i> (APH1)	25	10	100	97	0.6
CAPONIIDAE					
<i>Nops</i> (CAPH)	9	12	100	100	0.4
CORINNIDAE					
<i>Castianeira</i> (COR33)		18	56.2	9.5	0.3
<i>Corinna</i> (COR4)	9	7	36.4	8.4	0.3
<i>Trachelas</i> (COR12)	6	22	62.2	14.7	0.5
CTENIDAE					
<i>Ctenus</i> (CTE12)		28	80	16.7	0.5
<i>Gephyroctenus</i> (CTE6)		25	62.5	14.9	0.4
HETEROPODIDAE					
Sparianthinae (HET2)	33	74	98	62.5	1.8
LYCOSIDAE 1	1	51		53.6	0.9
MIMETIDAE					
<i>Ero</i> (MIM10)	11	5	32.6	34.4	0.3
MYSMENIDAE					
<i>Mysmenopsis</i> (MYS2)	3	13	44.4	34.0	0.3
OONOPIDAE 10	82	45		31.6	2.2
OONOPIDAE 11	36	57		23.1	1.6
OONOPIDAE 6	39	16		13.7	0.9
OONOPIDAE 5	8	16		6.0	0.4
PISAURIDAE					
<i>Paradosenus</i> (PIS12)		19	100	13.6	0.3
<i>Thaumasia</i> (PIS14)	1	13	15.4	10.0	0.2
SALTICIDAE					
<i>Acragras</i> (SAL11)	2	19	62	2.8	0.4
TETRAGNATHIDAE					
<i>Azilia</i> (TET10)		26	92.8	27.1	0.4
THERIDIIDAE					
<i>Dipoena</i> (THD38)	29	15	10.7	3.3	0.7
<i>Dipoena</i> (THD57)	56	22	18.9	5.8	1.3
<i>Dipoena</i> (THD65)	29	26	13.3	4.1	0.9
<i>Argyrodes</i> (THD58)	4	16	17	1.5	0.3
<i>Episinus</i> (THD35)	53	94	79	38	2.5
<i>Thwaitesia</i> (THD2)	80	77	100	11.7	2.7
THERIDIOSOMATIDAE					
<i>Naatlo</i> (THS8)	20	9	44.6	18.0	0.5
<i>Ogulnius</i> (THS3)	11	12	68.8	19.9	0.5
THOMISIDAE					
<i>Tmarus</i> (THO1)	30	13	22.0	10.2	0.7
<i>Tmarus</i> (THO3)	29	13	21.5	10.0	0.7
<i>Tmarus</i> (THO13)	25	61	44.1	20.4	1.5
<i>Acentroscelus</i> (THO4)	41	5	55.4	10.9	0.8
<i>Acentroscelus</i> (THO23)	13	6	22.9	4.5	0.3
<i>Strophius</i> (THO24)	13	3	55.2	3.8	0.3

TABLE 5

Number of species shared between canopy and understory strata. The values of relative complementarity (%) are given only for the biggest samples. $S_{jk} = S_j + S_k - V_{jk}$, where V_{jk} = number of species shared by two microhabitats. C = complementarity.

Microhabitats	Orb weavers	Sheet-line weavers	Ambush predators	Cursorial hunters	Total	Species richness (S_{jk})	C (%)
DRL-COM	28	35	22	57	142	347	59
DRL-VIN	19	22	17	25	83	249	67
DRL-DLV	-	1	4	5	10	-	-
DRL-EPI	10	20	3	29	62	229	73
DRL-PAL	3	17	7	-	27	-	-
DRL-MAU	4	-	-	-	4	-	-
DLV-COM	1	4	3	5	13	-	-
DLV-VIN	-	1	-	3	4	-	-
DLV-EPI	-	3	2	4	9	-	-
DLV-PAL	-	2	3	-	5	-	-
VIN-COM	18	28	21	40	107	306	65
VIN-EPI	8	19	5	17	49	182	73
VIN-PAL	2	15	6	-	23	209	89
VIN-MAU	2	-	-	-	2	-	-
EPI-COM	15	31	9	26	81	291	72
EPI-MAU	1	-	-	-	1	-	-
PAU-COM	2	8	2	8	20	282	93
PAU-DRL	4	-	1	6	11	210	95
PAU-VIN	2	3	2	4	11	-	-
PAU-EPI	1	5	1	3	10	-	-
PAU-PAL	1	5	1	3	10	-	-
PAU-MAU	1	-	-	6	7	-	-
PAU-PAE	2	4	2	3	11	56	80
PAE-COM	3	8	12	10	33	286	88
PAE-DRL	3	5	8	13	29	213	86
PAE-DLV	-	1	-	2	3	-	-
PAE-VIN	1	6	10	10	27	-	-
PAE-EPI	1	7	4	7	19	-	-
PAE-PAL	-	1	7	5	13	-	-
DRL-LUDD	14	18	7	4	43	353	88
DRL-LUDN	26	14	13	3	56	326	83
COM-LUDD	15	26	10	8	59	418	86
COM-LUDN	2	19	15	16	52	411	87

In general, the most common species found in the Samiria river have been also recorded from other Peruvian forests (Table 7), and most species shared by two or more microhabitats appear to be widespread in the Amazonian basin (Silva pers. obs.). However, the proportion of identified species is still low (less than 20 %).

DISCUSSION

In the Samiria river forest, most microhabitats were found to support a high diversity of spiders, despite any mismatching of males and females or unrecognized intraspecific variation.

TABLE 6

Degree of complementarity across canopy and understory microhabitats. Sjk = combined species richness; Vjk = number of species shared by two sets. COM=complex microhabitat, DLV=dry leaves & vines, DRL=dry leaves, EPI=epiphytes, MAU=*Mauritia* palm, PAE=*Scheelea* palm & epiphytes, PAL=*Scheelea* palms, VIN=vines.

Microhabitats	Species Richness	Vjk	Sjk	Complementarity (%)
DRL1 - COM1	137 vs 126	25	238	89
DRL1 - VIN1	137 vs 146	32	250	94
DRL1 - PAL1	137 vs 37	10	164	94
DRL1 - DRL2	137 vs 44	11	170	93
DRL1 - DRL3	137 vs 51	13	175	93
DRL1 - DRL4	137 vs 66	18	185	90
DRL1 - DLV1	137 vs 32	11	158	93
COM2 - DRL1	122 vs 137	28	231	88
COM2 (May-June)	122 vs 42	16	148	89
COM3 (May-June)	151 vs 87	27	211	87
COM3 - DRL1	151 vs 137	26	262	90
COM2 - COM3	122 vs 151	43	226	81
VIN1 - EPI1	146 vs 119	27	238	89
VIN2 - PAE1	55 vs 66	12	109	89
VIN2 - VIN3	55 vs 48	13	90	88
EPI1 - DRL1	119 vs 137	36	220	84
EPI1 - EPI2	119 vs 25	3	139	96
PAL2 - MAU1	39 vs 54	8	85	91
MAU1 - MAU2	54 vs 41	5	85	88

Although there were differences in sample size, canopy microhabitats showed, on average, a higher number of species and individuals than those in the understory. Nevertheless, the most complex microhabitats from the understory presented also a high species richness and density of spiders, sometimes as rich as those in the canopy.

It might appear that there is no strong division between canopy and understory in terms of species numbers and abundance when massive methods of collecting are employed. However, the species composition between these two strata is in fact drastically different.

It was rare to find dominant species in the fogging samples. Further, the most common spider species were distributed differently across various microhabitats. Typically, most species did not reach 0.5% of the total number of adult specimens for each fogging sample. Such results agree with other fogging studies from the understory and canopy of other tropical forests (HÖFER *et al.* 1994; RUSSEL-SMITH & STORK 1994; SILVA & CODDINGTON, in press). It has been shown that spider communities have few dominant species and that species richness and abundance vary not only according to forest type, altitude, or on a diurnal/nocturnal basis, but also with microhabitat qualities (i.e., fine differences in geomorphology, vegetation, microclimate, etc.).

Although the data at the present time show that most canopy microhabitats appear more distinct one from another than from any of the most heterogeneous

TABLE 7

Species richness and abundance of spiders from some Peruvian rainforests. Tambopata-Candamo National Reserve, some samples from fogging 1983-1984; Pakitza reserved zone, Manu National Park, conventional sampling, 1991; Samiria.

	SAMIRIA		PAKITZA		TAMBOPATA	
	Ind. (%)	Spp. (%)	Ind. (%)	Spp. (%)	Ind. (%)	Spp. (%)
ORB WEAVERS	1311 (22.2)	318 (27.9)	1242 (47.5)	235 (47.3)	225 (15.8)	108 (16.0)
Anapidae	26	3	2	1	2	2
Araneidae	853	207	743	145	91	75
Deinopidae	7	2	7	2	-	-
Mysmenidae	47	11	36	9	38	14
Symphytognathidae	6	2	-	-	-	-
Tetragnathidae	100	32	132	35	1	1
Theridiosomatidae	163	31	137	19	93	12
Uloboridae	109	30	185	24	-	4
SHEET-LINE WEAVERS	1702 (28.9)	233 (20.4)	876 (33.5)	111 (22.3)	554 (38.8)	146 (21.7)
Dictynidae	7	2	1	1	5	1
Hahniidae	1	1	-	-	1	1
Linyphiidae	38	10	25	6	43	14
Ochyroceratidae	1	1	-	-	-	-
Pholcidae	221	28	84	12	12	5
Rhoicininae	13	1	-	-	-	-
Scytodidae	78	6	19	2	15	3
Theridiidae	1343	184	747	90	478	122
AMBUSH PREDATORS	1114 (18.9)	180 (15.8)	237 (9.1)	67 (13.5)	119 (8.3)	172 (25.6)
Ctenidae	181	26	45	16	1	1
Hersiliidae	37	9	14	2	4	1
Heteropodidae	174	18	13	5	11	4
Mimetidae	103	23	59	11	13	4
Oxyopidae	39	17	29	8	14	6
Philodromidae	-	-	1	1	3	1
Pisauridae	140	28	27	3	2	1
Selenopidae	5	2	2	1	2	119
Senoculidae	19	2	18	4	6	4
Thomisidae	432	49	22	12	63	31
Trechaleidae	14	6	7	4	-	-
CURSORIAL HUNTERS	1768 (30.0)	409 (35.9)	261 (10)	84 (16.9)	529 (37)	247 (36.7)
Anyphaenidae	126	48	29	13	115	39
Aphantochilidae	36	2	5	1	1	1
Caponiidae	21	1	1	1	-	-
Clubionidae	10	3	3	3	36	-
Corinnidae	196	57	26	13	44	27
Gnaphosidae	67	12	1	1	6	4
Liocranidae	28	9	-	-	9	3
Lycosidae	106	12	22	6	-	-
Miturgidae	21	6	8	3	2	1
Oonopidae	402	31	6	3	73	34
Palpimanidae	1	1	-	-	-	-
Salicidae	747	220	160	40	243	129
Tetrablemmidae	1	1	-	-	-	-
Undetermined	6	6	-	-	-	9
TOTAL	5,895	1,140	2,616	497	1,427	673

understory microhabitats, it is necessary to take into account the effect of under-sampling before making generalizations about degrees of faunal complementarity.

Undersampling is known to underestimate local species richness, ecological preferences, and geographical ranges, among other variables (COLWELL & CODDINGTON 1994). Such effects were obvious in the comparisons of single microhabitats and also when the spider fauna from the three Peruvian forests were compared (Table 7). It could appear that some taxa are absent or very poorly represented either in Tambopata or Pakitza; however, other data (Silva, pers. obs.) indicate that both localities are about as rich as the Samiria forest and, with exception of Tetrablemmidae, all other families are well represented in both sites.

While many spider species from the Samiria river appear to be recorded from other Amazonian forests, the taxonomic identity of most species is still uncertain and almost nothing is known about their true geographic distribution.

In general, the Neotropical spider fauna is still very poorly known. Many species collected in recent years are waiting for formal descriptions and many of the already known species present problems for accurate taxonomic identification. The latter were often described without the use of modern taxonomic criteria, were based on juvenile specimens lacking the structures necessary for accurate species identification, or were described from only one sex. All these factors contribute to an incomplete species inventory and, therefore, to a lack of accurate estimates of species diversity.

Finally, only further taxonomic work and phylogenetic analyses will provide the hypotheses needed to better assess distributional ranges and to clearly determine the historical factors responsible for the high species diversity found in the Samiria river. This information will make it possible to better establish the levels of distinctness among the microhabitats of the Samiria and other Peruvian rainforests, and, in turn, to provide a more rigorous scientific base from which to make conservation decisions regarding threatened areas in various tropical forests.

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