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Strategies for habitat use among species of hunting spiders (Araneomorphae, Dionycha) in natural and artificial biotopes from southeastern Brazil

Estratégias para uso do habitat entre espécies de aranhas caçadoras (Araneomorphae, Dionycha) em biótopos do sudeste do Brasil

ISABELA M. P. RINALDI [1]
LUIZ CARLOS FORTI [2]

Distribution, abundance, and species interaction are influenced by a complex combination of biotic and abiotic factors. According to Hutchinson (SCHOENER, 1971), the way in which food is obtained by coexisting species is a result of competition rather than predator avoidance. Therefore, investigation of the strategies of spider species for obtaining food permits some degree of quantification of the amplitude of niche. After LEVINS (1968), measurements of the distribution of species might be used for achieve this quantification. Competitive interactions among species as well as resources partitioning of organisms of the same trophic level seems to be worth considering as factors in the community characterization. In dionychan spiders, the interactions between species must be restricted to competition, since mutualisme among them is unknown and perhaps very uncommon or even absent. According to CODDINGTON and LEVI (1991), araneophagy is a sinapomorphy of

[1] Departamento de Zoologia, Instituto de Biociências and [2] Departamento de Defesa Fitossanitária, Faculdade de Ciências Agronômicas — Universidade Estadual Paulista (UNESP), 18618-000 Botucatu, São Paulo, Brazil.

Mimetidae, Palpimanidae, and in some specialized taxa of Archaeoidea.

Competition between congeneric species of spiders has received the attention of a number of authors (KESSLER-GESCHIERE, 1971; SCHAEFER, 1975; ENDERS, 1976; SPILLER, 1986), while resources partitioning (UETZ, 1975; GERTSCH & RIECHERT, 1976) and patterns of interactions at community level (POST III & RIECHERT, 1977) have been scarcely studied.

A community matrix (WANDERMEER, 1970) for assemblages of spiders of sites under different conditions was used to analyze strategies of species coexistence. Therefore, this study is similar to that done by POST III and RIECHERT (1977), in which the species of spiders at sites with distinct vegetation physiognomies were focused.

The effect of each species in all others (and *vice-versa*) is estimated in accordance with whether the probability of each species meeting others in the community is greater than might be expected from the size of the population.

Coexistence of a large number of potencial predators depends on numerous factors including the availability of resources in the habitat. On other hand, it seems fair to presume that the configuration of vegetation distribution is correlated with the distribution of resources for each habitat. Therefore, a combination of overlapping informations from a community matrix containing co-variation data for pairs of more proeminent spiders is given.

This paper is the first attempt to identify strategies of coexistence in neotropical spider assemblages. Structure of fauna and distribution of abundance of 247 hunting species of spiders of the Dionycha clade (sensu CODDINGTON & LEVI, 1991) from six different communities are analyzed.

MATERIAL AND METHODS

STUDY AREAS — The study was done in Botucatu, in the southern-central region of the State of São Paulo, Brazil. The habitats chosen are: 1. *mesophytic semideciduous forest* in the phytogeographical province of the Atlantic Forest, one fragment on a farm known as the "Fazenda Edgardia" (22°48' 56"S, 48°23' 44"W), the other

fragment in the "Parque Municipal de Botucatu" (22°55' 38"S, 48°27' 33"S); 2. *gallery forest* (22° 52' 52"S, 48°29' 53"W); 3. *cerradão*, a form of savannah on poor dry soils (22°44' 14", 48°18'24"W); 4. *pastureland*, composed of *Brachiaria decumbens* and a very few native tree species; 5. *sugar-cane fields*, at ages varying from 5 to 16 months.

COLLECTING AND SAMPLING TECHNIQUES — A transect of 50 x 5 m was used, with collecting areas alternating every 125 m^2, and placed at a distance of at least 50 m from the edge of the habitat. Monthly collections were made over a two-year period, from July 1986 to August 1988, a total of 24 collections for each ecosystem. Various collecting methods were used: a modified beating tray (or "entomological tray"), pitfall traps, litter sieves and a Berlese-Tullgren funnel. For each habitat 120 traps were used, filled with 70% alcohol and left in the field for 5 days, and 120 litter samples were taken. Animals were selected with a stereoscopic microscope and transferred to 70% or 90% alcohol. All specimens are now in the Araneae collection in the Department of Zoology, Instituto de Biociências, UNESP, Botucatu SP.

ANALYSIS OF FAUNA. Data for relative abundance of spiders were used to calculate the proportional representation of each species in each of the 24 sampling units. The aij elements of the community matrix were estimated; also the community interaction coefficient (CIC), the community effect (CE), and the species effect (SE), in accordance with LEVINS (1968) and POST III & RIECHERT (1977). In a community matrix the aij element is the probability of an individual of species j meeting with an individual of a different species i (P_{ij}) in relation to the probability of meeting an individual of its own species (P_{jj}) where:

$$P_{jj} = 1/N^2 \, n_{jk}^2$$

is the probability of intraspecific meeting

$$Pjj = \frac{1}{N^2} \sum_{K=1}^{N} n_{jk}^2$$

$$P_{ij} = 1/N^2 \; n_{ik} \; n_{jk}$$

is the probability of interspecific meeting and

$$Pij = \frac{1}{N^2} \sum_{K=1}^{N} n_{ik} n_{jk}$$

aij = Pij/Pjj is the community interaction coefficient (CIC).

$$aij = \frac{Pij}{Pjj}$$

If one row of the community matrix is added up for a particular species,

$$CE = \sum_{J=1} a_{ij}$$

then one can determine the effect of all other species on that one species. If the columns of the community matrix are added up,

$$SE = \sum_{J=1} a_{ji},$$

then one can determine the effect of any given species on the rest of the community.

According to this model, a species which exerts a strong species effect will encounter another species more frequently than the size of its population would appear to warrant. A generalist species probably displays a strong species effect, *i.e.*, it exerts considerable influence on the community. Thus spiders with a strong species effect may be considered effective competitors, while those with a weak species effect and a strong community effect avoid competition by niche partition. The various combinations of species and community effects allow to map out seven strategies for spiders, used here in accordance with POST III & RECHERT (1977), on the basis of the interval of confidence [non-interactive (NINT), marginal (MAR), opportunist (OP), generalist (GEN), superspecialist (SUP), specialist (SP), and semispecialist (SEMI)].

Also important to species abundance patterns in relation to

intraspecific interaction is co-variation. To measure the relative intensity of co-variation for pairs of species, we used Pearson's coefficient of correlation, following LUDWIG & REYNOLDS (1988). In this study only species with abundance equal or greater than three individuals were included.

INDEX OF PLANT DISPERSION. The index of associated vegetation dispersion was calculated in accordance with LUDWIG & REYNOLDS (1988). When the variance is equal to the mean (x), the dispersion index is equal to 1; when they are distinct, one can test the significance of deviations from ID = 1 and then use the chi square test: χ^2 = ID (n-1). Thus the results will be seen as: a. casual distribution ($s^2 = x$) [value of χ^2 between table values of 0.975 and 0.025 ($p > 0.05$)] b. regular distribution ($s^2 < x$) (value of $\chi^2 < 0.975$) and c. clumped distribution ($s^2 > x$) (value of $\chi^2 > 0.025$).

RESULTS

A total of 1,082 adult spiders belonging to 247 species in 12 families of Dionycha were investigated; most of them were found in vegetation up to 2 m tall. The largest percentage of species behaved as marginal members of the community; they were followed by generalist, specialist, semispecialist, opportunist, and finally non-interactive species (Fig. 1).

The average over all habitats (with the exception of the pastureland, where three species displayed different strategies) was 51.9% (s=3.16%) of rare species; the sugar-cane field, with 56.3% of marginal species, was of particular note. Among the ecologically more important species, the category of the generalist was the most frequent in all habitats; this was defined by a strong species effect and a community effect of little significance. The mesophytic forest of the Fazenda Edgardia differed from the other habitats in having a large number of semispecialist species; these, added to the specialists, exceeded the generalists in number. A tendency to exhibit specialist strategies was also observed among the spiders of the gallery forest and the sugar-cane field. The categories of opportunist and non-interactive species [that is, those present in areas which are unfavorable to other species, according to HORN & MCARTHUR

(1972)] occurred in smaller proportions. The behaviour of each dionychan spider species, as determined by the community and species effects in each habitat, is shown in the Table 1. Of species present in more than one ecosystem, it may be pointed out that:

a. 27 species were classified in the same categoria whichever habitat they occurred; 20 were marginals, two were specialists (*Cotinusa aff. dimidiata* and *Corinna* sp. 1), while five were generalists (*Trachelas* sp.1, *Beata cinereonitida*, *Consingis semicana*, *Neonella* sp.2, and *Hasariae* sp. 5).
b. 59 species changed their strategy; of these, the majority (44) behaved in one habitat as marginal (or rarely, as non-interactive) members, and in another as generalist (25 species), semispecialist (7 species), specialist (6 species) or opportunist (3 species) members.
c. If one excludes marginal species, since they denote rarity of occurrence in habitats which do not favour them, a predominance of generalist (30) over specialist (8) and semispecialist (7) species may be observed.
d. In behaving as specialists or semispecialists, the spiders display a lower relative abundance than they do as opportunists or generalists: *Aysha triunfo*, *Teudis procerus* and *Yepoella* sp.n. In some cases the abundance of species as specialists or semispecialists was lower than that observed when they were marginals: *Cotinusa* sp. 1 and *Evophrys?* sp. 3.
e. In general, low relative abundance was characteristic of specialists, while the abundance of generalists was proportionally high, independent of habitat. As examples of specialists, semispecialists and generalists we may take *Aysha aff. brevimana*, *Cotinusa aff. dimidiata* and *Continusa cf. albescens*. When abundance values for the generalists decreased, they were still greater than the values for the specialists; such was the case with *Beata cinereonitida* and *Consingis semicana*.
f. The following species are exceptions to the preceding generalizations: *Oxysoma aff cubana* group sp. 1, *Camillina claro*, *Atelurius segmentatus*, *Bucranium taurifrons*, *Phiale tristis*, and

Table 1. Strategy categories of hunting spider (Dionycha) in six habitats of Botucatu , São Paulo State, Brazil.[Strategy categories representing the relationships between values for the community effect, the species effect, and the interval of confidence for averages (standard deviation from the average number of species per sample)]. Categories: MAR = marginal (CE and SE: not significant), NINT = non interactive (CE and SE: significances negative), GEN = generalist (SE: significance positive), OP opportunist (CE and SE: significances positive), SEMI = semispecialist (SE: significance negative), SPE = specialist (CE = significance positive)

ANYPHAENIDAE	Gallery forest			Edgardia forest			Municipal Park forest			"Cerradão"			Sugar cane field		
	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.
Amaurobioidiinae sp.1													4.4	2.1	SEMI
Amaurobioidiinae sp.2													0.0	0.0	NINT
Amaurobioidiinae sp.3													2.7	0.9	MAR
Amaurobioidiinae sp.4	10.7	7.6	MAR												
Anyphaenidae gn.n.1 sp.n.1	10.5	5.9	MAR												
Anyphaenidae gn.n.1 sp.n.2										12.3	11.6	MAR			
Anyphaenidae gn.n.1 sp.n.3										16.9	13.5	OP			
Anyphaenidae gn.n.1 sp.n.4				9.1	3.6	MAR									
Anyphaenidae gn.n.2 sp.n.1										7.6	4.4	MAR			
Anyphaenidae gn.n.3 sp.n.1	14.3	6.0	MAR												
Aysha sp.										7.3	5.0	MAR			
Aysha aff. brevimana	5.1	2.0	SEMI				2.6	2.2	SPE						
Aysha borgmeyeri	13.2	4.9	MAR				11.0	4.7	MAR						
Aysha ericae							4.4	3.7	MAR						
Aysha fulviceps										17.9	10.5	SPE	1.4	0.3	SEMI
Aysha marinonii										14.1	6.0	SPE			
Aysha tortulia	14.3	6.2	MAR	9.1	8.0	MAR	6.4	8.0	MAR						
Aysha triunfo	16.7	59.8	OP	5.5	1.7	SEMI	4.0	14.8	GEN						
Aysha zenzesi							7.4	4.2	MAR						
Gn.n *aff. Temnida* sp.1	12.1	16.8	GEN												
Osoriella osoriana	9.0	5.9	MAR							2.8	8.8	GEN			
Oxysoma aff. grupo cubana sp.1										17.9	13.5	OP	8.7	9.3	MAR
Oxysoma aff. grupo cubana sp.2													3.3	2.3	MAR
Tasata sp.	7.3	2.7	MAR												
Teudis sp.										17.9	12.5	OP			
Teudis diversicolor							5.7	12.8	GEN						
Teudis longipes	12.2	9.9	MAR				7.1	9.6	MAR						
Teudis procerus	14.0	22.1	GEN	2.0	0.9	SEMI	9.2	12.8	GEN						
Teudis robustus	10.5	17.9	GEN	4.2	2.9	MAR	5.2	7.2	MAR						
Teudis rubromaculatus	13.0	9.1	MAR												
Teudis striolatus	5.6	3.8	MAR												
APHANTOCHILIDAE															
Bucranium taurifrons	12.5	16.3	GEN				12.0	8.0	GEN	8.8	5.6	MAR			

Table 1.*(continued)*

	Gallery forest			Edgardia forest			Municipal Park forest			"Cerradão"			Sugar cane field		
CLUBIONIDAE	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.
Cheiracanthium inclusum	20.0	8.9	SPE				6.5	3.9	MAR				1.5	0.8	MAR
Clubionoides brevipes	13.0	8.1	MAR							9.6	9.6	MAR			
CORINNIDAE															
Castianeira sp.1										7.1	5.2	MAR	1.0	2.0	MAR
Castianeira sp.2										6.4	4.0	MAR			
Castianeira sp.3															
Corinna sp.1							4.7	1.3	SPE	13.0	6.5	SPE			
Corinna sp.2	6.0	8.6	MAR												
Corinna aff. cribrosa															
Corinna aff. vertebrata													0.0	0.0	NINT
Gn.1 sp.n.1	8.3	4.4	MAR				4.9	3.2	MAR				0.4	0.1	MAR
Lausus sp.1										14.1	11.5	SPE			
Lausus sp.2							7.4	4.2	MAR						
Stethorhagus. sp.n.	5.8	3.8	MAR	5.5	3.8	MAR									
Trachelas sp.1	12.3	16.4	GEN	7.5	14.2	GEN	8.6	16.0	GEN						
Trachelopachys ignacio													2.7	6.9	GEN
GNAPHOSIDAE															
Apodrassodes mono	10.3	10.8	MAR	6.5	7.0	MAR	7.8	7.5	MAR						
Apopyllus isabelae	13.2	6.1	MAR	4.4	2.9	MAR				11.9	5.1	MAR			
Camillina sp.n.													2.7	0.7	MAR
Camillina claro							4.6	0.3	SPE	16.9	14.0	OP			
Camillina cordoba	0.0	1.0	NINT							7.8	5.6	MAR			
Camillina minuta													1.7	2.1	MAR
Camillia pilar							3.6	3.7	MAR	8.8	5.6	MAR			
Camillina pulcher															
Cesonia sp.1				9.1	4.6	MAR				5.1	1.9	SEMI			
Eilica maculipes										2.0	1.5	NINT			
Gn.n. sp.n.	1.7	2.3	NINT				7.0	1.9	SPE						
Zimiromus montenegro				4.5	3.6	MAR				6.1	4.2	MAR			
HETEROPODIDAE															
Olios sp.1	4.0	2.2	SEMI	4.3	0.9	SEMI	7.3	14.5	GEN						
Olios antiguensis													5.5	2.3	SPE.

Table 1.*(continued)*

HETEROPODIDAE	Gallery forest			Edgardia forest			Municipal Park forest			"Cerradão"			Sugar cane field		
	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.
Olios cf. caprinus	5.1	3.5	MAR												
Polybetes sp.1	12.2	9.1	MAR												
Polybetes sp.2										9.5	16.0	GEN			
Polybetes germaini	10.7	7.6	MAR												
LIOCRANIDAE															
Orthobula sp.1										8.4	3.7	MAR			
Orthobula sp.2							6.8	8.5	MAR						
PHILODROMIDAE															
Berlandiella robertae	12.2	32.4	GEN				10.6	11.9	GEN	10.3	9.1	MAR			
SALTICIDAE															
Agelista sp.										11.1	4.6	MAR			
Agelista andina	13.0	9.1	MAR												
Ailluticus nitens										9.6	6.2	MAR			
Amyceae gn.n										12.3	16.8	GEN			
Amycus sp. n.				4.2	4.0	MAR	9.0	14.8	GEN						
Aphirape sp. 1													3.3	2.3	MAR
Aphirape sp.2										6.6	4.5	MAR			
Aphirape misionensis	12.0	9.1	MAR												
Arachnomura hieroglyphica							10.2	14.4	GEN						
Arachnomura sp. n.										7.6	5.9	MAR			
Asaphobelis ? sp				2.3	0.7	SEMI				11.1	4.3	MAR			
Asaphopelis fasciventris	5.9	7.5	MAR	3.9	1.6	SEMI									
Asaphopelis physonychus	12.0	5.5	MAR												
Ashtabula sexguttata	10.4	14.0	MAR							9.6	4.1	MAR			
Atelurius segmentatus	19.0	10.0	SPE	9.3	4.3	MAR	11.9	3.9	SPE	17.9	13.5	OP			
Beata sp.1							9.6	4.8	MAR	10.7	19.9	GEN			
Beata sp.2										9.4	23.7	GEN			
Beata cinereonitida	7.1	16.9	GEN				10.2	13.4	GEN	9.3	21.1	GEN			
Breda sp.1				2.9	4.9	MAR	14.3	12.7	OP	6.4	4.7	MAR			
Breda sp.2				4.4	2.0	MAR	7.4	4.2	MAR						
Breda sp.3				10.4	4.4	SPE									
Chira lanei										8.5	24.3	GEN			

Table 1.*(continued)*

	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.
Chira micans				3.5	1.7	SEMI				9.5	25.9	GEN			
Chira simoni										8.9	10.6	MAR			
Chira spinosa				8.9	7.4	MAR	7.0	7.6	MAR	6.7	22.1	GEN	2.0	1.0	MAR
Chirotecia cf. semiornata							13.3	8.0	GEN						
Chirotecia soaresi	19.8	12.6	SPE												
Consingis semicana	12.7	42.5	GEN							6.4	13.2	GEN			
Coryphasia sp.1							9.1	4.8	MAR						
Coryphasia melloleitaoi ?	6.9	13.4	MAR				9.8	13.5	GEN	3.0	2.7	NINT			
Corythalia sp.1							9.1	4.8	MAR	9.2	15.8	GEN			
Corythalia sp.2										5.4	4.7	MAR			
Corythalia cf. spiralis										9.0	12.5	GEN			
Cotinusa sp.1	14.0	43.2	GEN	6.3	10.2	GEN	7.5	10.4	MAR	3.2	1.4	SEMI	2.0	0.8	MAR
Cotinusa sp.2	8.3	4.4	MAR	2.0	0.8	SEMI	7.7	12.5	GEN						
Cotinusa sp.3	15.5	16.1	OP	6.9	11.8	GEN	5.4	4.6	MAR	9.6	4.1	MAR	2.1	2.5	MAR
Cotinusa sp.4							10.9	3.9	MAR						
Cotinusa sp.5	10.7	7.6	MAR	4.5	3.6	MAR									
Cotinusa sp. n.	5.2	3.0	MAR												
Cotinusa cf. albescens	9.1	12.5	MAR	7.4	22.8	GEN	9.0	19.6	GEN						
Cotinusa aff. dimidiata	20.0	10.0	SPE	10.1	4.6	SPE									
Cotinusa aff. magna	5.9	2.1	SEMI												
Cylistella sp. n.	9.5	11.0	MAR	6.8	5.0	MAR									
Cyllodania sp. n.	14.3	6.2	MAR							7.9	25.0	GEN			
Deloripa semialba										7.1	4.2	MAR			
Dendryphanteae sp.													0.0	0.0	NINT
Dendryphantes sp.1	11.8	17.4	GEN							7.9	25.7	GEN			
Dendryphantes sp.2	4.6	2.2	SEMI										2.8	2.8	MAR
Dendryphantes sp.3										8.7	9.6	GEN			
Dendryphantes sexguttata	8.1	3.0	MAR							16.9	13.5	OP			
Descanso sobrius															
Dryphias aeneus															
Erica eugenia	12.5	13.8	SPE				8.7	6.4	MAR						
Evophrys? (gn.n)										6.6	4.3	MAR	3.0	8.1	GEN
Evophrys sp.1	7.3	3.7	MAR												
Evophrys sp. 2	20.5	11.3	SPE												

Table 1.*(continued)*

SALTICIDAE	Gallery forest			Edgardia forest			Municipal Park forest			"Cerradão"			Sugar cane field		
	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.
Evophrys ? sp.1										17.9	13.5	OP			
Evophrys ? sp.2										6.4	4.7	MAR			
Evophrys ? sp.3	4.6	2.2	SEMI	10.9	5.2	SPE				7.1	9.2	MAR			
Fissidentati sp.1	9.3	4.4	MAR							10.1	4.3	MAR			
Fissidentati sp.2	10.7	7.6	MAR												
Fissidentati sp.3	5.2	3.0	MAR												
Fissidentati sp.4	7.4	4.0	MAR												
Freya aff. regia										5.6	8.6	MAR	2.0	2.0	MAR
Freya strandi				9.3	2.1	MAR									
Frigga quintensis										10.9	5.1	MAR			
Gn. n. *aff. Phiale* sp.1	8.0	6.6	MAR							12.0	9.0	MAR			
Gn. n. *aff. Phiale* sp.2	17.6	16.6	OP							3.7	1.8	NINT			
Gn. n. *aff. Phiale* sp.n.3	20.0	10.0	SPE												
Hasarieae sp.1										8.4	3.3	MAR			
Hasarieae sp. 2	8.8	12.2	MAR	5.4	11.4	GEN									
Hasarieae sp.3	10.0	25.6	GEN												
Hasarieae sp.4	20.0	8.9	SPE												
Hasarieae sp.5	11.6	31.4	GEN	8.5	15.2	GEN									
Hasarieae sp.6				12.7	5.7	SPE									
Hasarieae sp.7										10.9	8.4	MAR			
Hasarieae sp.8										5.0	6.8	MAR			
Hurieae sp.1	13.0	9.1	MAR												
Hurieae sp.2				6.3	8.3	MAR									
Ilargus coccineus	4.9	2.1	SEMI												
Lapsias sp.										8.4	3.7	MAR			
Lyssomanes sp.										11.7	10.8	MAR			
Lyssomanes cf. leucomelas	9.6	12.2	MAR							16.9	13.5	OP			
Lyssomanes nigrofimbriatus							8.0	5.0	MAR						
Lyssomanes pauper										18.9	13.5	OP			
Lyssomanes tristis							4.4	3.7	MAR						
Maeota sp.n.										5.7	7.8	MAR	4.4	2.1	SPE
Myrmarachne sp.	13.6	23.7	GEN												
Myrmarachne brasiliensis	13.2	13.1	MAR												
Neonella sp.1				7.8	4.6	MAR									

Table 1.*(continued)*

SALTICIDAE	Gallery forest			Edgardia forest			Municipal Park forest			"Cerradão"			Sugar cane field		
	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.
Neonella sp.2	12.6	19.7	GEN	6.13	22.1	GEN									
Neonella sp.3							10.9	3.9	MAR						
Neonella sp.4							7.5	3.9	MAR						
Noegus bidens	12.7	19.9	GEN												
Pockhamia sp	12.2	5.5	MAR												
Phiale bipunctata				4.5	2.6	MAR									
Phiale tristis	10.7	7.6	MAR				11.8	6.5	GEN	12.0	24.0	GEN			
Psecas cf. chapoda													3.9	9.7	GEN
Psecas cf. zonatus													2.4	4.9	GEN
Rhyphelia variegata							13.3	8.5	GEN						
Saiteae sp.1													1.0	0.5	SEMI
Saiteae sp.2										7.8	5.6	MAR	2.1	0.7	MAR
Saiteae sp.3										11.0	16.5	GEN			
Saiteae sp.4										6.6	5.5	MAR			
Saiteae sp.5	5.2	3.0	MAR												
Saitis sp.1	13.0	8.1	MAR	4.5	3.6	MAR				8.3	9.2	MAR			
Saitis sp.2	16.1	14.1	SPE				12.8	7.7	GEN						
Saitis spinosus	0.3	0.1	NINT				9.7	16.4	GEN						
Salticidae sp.1	6.4	4.0	MAR	8.3	24.4	GEN									
Salticidae sp.2				2.1	1.4	SEMI									
Sarinda aff. marcosi										6.6	5.0	MAR			
Sarinda nigra										5.3	6.7	MAR			
Sassacus cf. arcuatus										9.5	11.2	MAR			
Scopocira sp.										4.7	7.7	MAR			
Scopocira cf. dentichelis										3.9	2.0	SEMI			
Semiopyla sp.n.										5.0	2.5	SEMI			
Semiopyla cataphracta															
Semiopyla viperina										8.4	12.2	MAR			
Semnolius chrysotricus							5.6	3.2	MAR	4.7	2.1	SEMI			
Semora (Semorina ?) sp.													1.6	1.8	MAR
Simaetheae sp.										6.6	4.4	MAR			
Sitticus sp.													1.2	0.7	MAR
Stenodeza sp.n.	8.8	3.0	MAR												
Synemosyna aurantiaca										9.8	14.7	GEN			

Table 1 *(continued)*

	Gallery forest			Edgardia forest			Municipal Park forest			"Cerradão"			Sugar cane field		
SALTICIDAE	EC	EE	ESTR.	EC	EE	ESTR	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR.
Tacuna delecta	20.6	16.1	OP												
Tariona sp.1	2.8	5.3	MAR				8.3	29.4	GEN						
Tariona sp2										10.5	14.1	GEN			
Thiodina sp.	10.1	11.2	MAR												
Thiodina germaini										8.9	15.1	GEN	3.3	3.4	MAR
Thiodina melanogaster													5.5	2.3	SPE
Unidentati gn.n sp.n.1							8.0	3.4	MAR						
Unidentati gn.n sp.n.2	18.4	8.9	SPE												
Vinnius uncatus	8.8	15.5	GEN	6.4	17.0	GEN	7.1	16.2	GEN	4.7	2.1	SEMI			
Wedoquela punctata										5.1	1.9	SEMI			
Yepoella sp.n.	15.1	20.1	OP				6.6	2.4	SPE						
Zuniga magna	16.0	14.8	SPE												
SELENOPIDAE															
Selenops punctatus							1.4	0.4	NINT						
THOMISIDAE															
Acentroscelus albipes							8.2	8.2	MAR						
Cerarachne germaini	20.5	10.0	SPE				12.0	9.0	GEN						
Epicadus sp.	2.7	1.2	SEMI												
Misumenoides sp.1	10.7	7.9	MAR												
Misumenops argenteus	11.7	7.6	MAR												
Misumenops pallens										7.2	15.0	GEN			
Misumenops pallidus				7.9	7.6	MAR				3.9	1.1	SEMI			
Onoculus intermedius							6.1	5.5	MAR						
Stephanopoides? sp.										6.6	8.9	MAR			
Strophius nigricans	13.0	27.6	GEN	9.4	4.3	MAR	7.0	4.0	MAR	13.8	18.8	OP			
Sydymella longispina				0.0	0.0	NINT									
Sydymella multispinulosa				2.7	2.4	MAR									
Synstrophius blanci							8.0	5.0	MAR						
Titidiops ? sp.1	18.8	24.4	OP	V											
Titidius ? sp.1	11.3	18.4	GEN				7.0	4.0	MAR						
Tmarus sp.1	6.3	3.7	MAR	12.7	5.2	SPE	3.5	1.2	SPE						
Tmarus sp.2				14.0	8.0	SPE	2.2	3.6	MAR						
Tmarus sp.3	20.0	8.9	SPE	5.4	13.7	GEN	11.0	12.1	GEN						

Table 1.*(continued)*

THOMISIDAE	Gallery forest			Edgardia forest			Municipal Park forest			"Cerradão"			Sugar cane field		
	EC	EE	ESTR	EC	EE	EST	EC	EE	ESTR.	EC	EE	ESTR.	EC	EE	ESTR
Tmarus sp.4				3.6	0.6	SEMI									
Tmarus sp.5	7.3	2.9	MAR							11.0	15.8	GEN			
Tmarus sp.6										12.8	18.8	OP			
Tmarus sp.7													3.3	2.3	MAR
Tmarus sp.8				2.1	1.4	SEMI									
Tmarus sp.9										7.5	9.0	MAR			
Tmarus sp.10										5.0	2.5	SEMI			
Tmarus aff. albifrons	15.8	21.8	OP	4.1	7.1	MAR	6.7	21.1	GEN	5.0	2.4	SEMI			
Tmarus albolineatus	11.5	15.2	GEN												
Tmarus aff. alticola							8.0	7.5	MAR						
Tmarus cf. caeruleus				7.9	13.3	GEN				8.8	5.6	MAR			
Tmarus aff. caretta										17.9	13.5	OP			
Tmarus clavipes				5.4	2.8	MAR	5.1	3.2	MAR						
Tmarus estyliferus										7.1	4.2	MAR			
Tmarus aff. morosus				5.1	2.8	MAR									
Tmarus mutabilis	14.9	14.5	MAR				4.7	11.6	GEN						
Tmarus nigroviridis				6.6	8.2	MAR									
Tmarus parki										2.3	0.6	NINT			
Tmarus pleuronotatus							4.7	2.3	SPE						
Tmarus primitivus	13.2	5.9	MAR												
Tmarus pugnax							3.7	6.0	MAR						
Tmarus striolatus				5.6	1.6	SEMI	7.2	8.1	MAR						
Tobias gradiens				4.9	5.3	MAR									
ZORIDAE															
Zoridae gn.n sp.n				2.0	1.2	SEMI	5.1	3.2	MAR						

Exclusive species of the pastureland:

	CE	SE	STRATEGY
Castianeira sp.3	1.3	0.3	SPE
Camillina pulcher	0.0	0.0	MAR
Semiophyla cataphracta	0.3	1.3	GEN

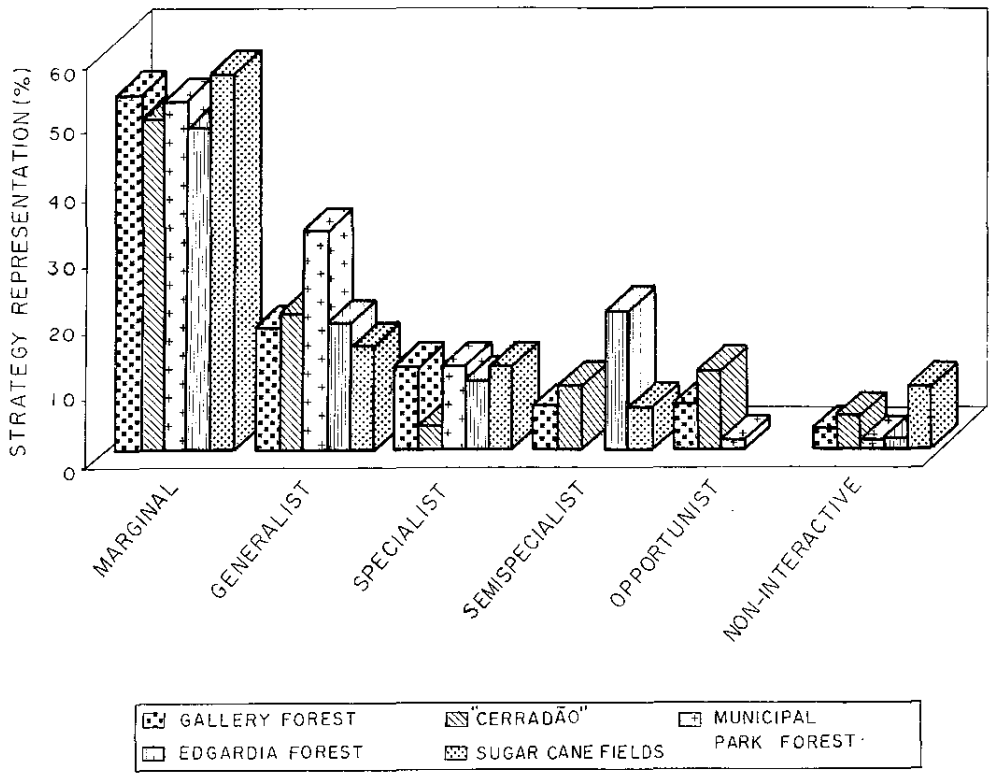
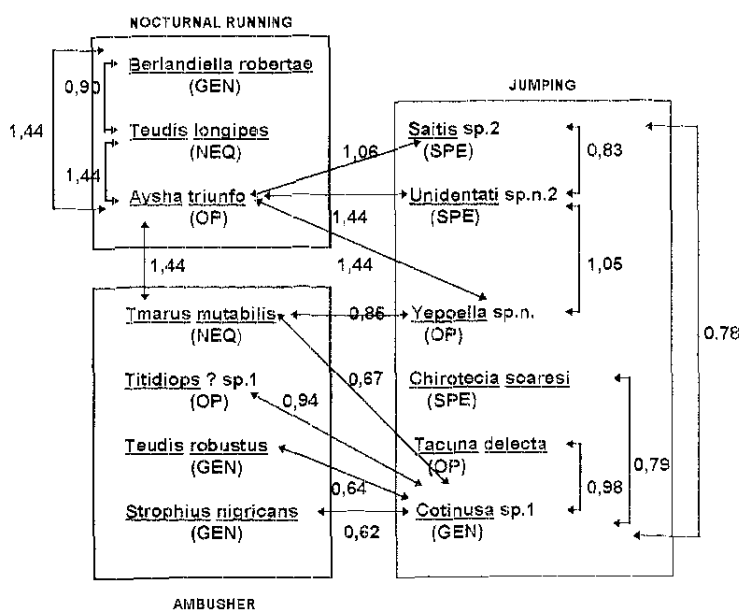


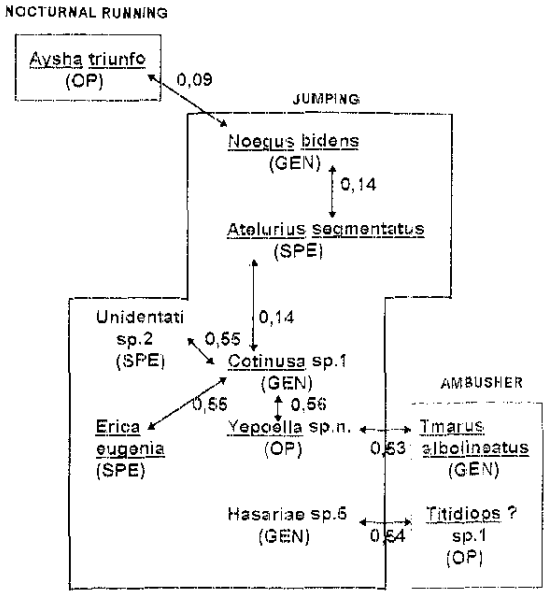
Fig. 1. Strategies for habitats use by 247 species of Dionycha spiders clade in various habiatats from southeastern Brazil (sampling from September 1986 to August 1988).

Habitats (ID)	Edgardia Farm Forest (9,75)	Gallery Forest (7,86)	"Cerradão" (2,97)	Municipal Park Forest (1,58)	Sugar cane fields (1,37)
	aggregate distribution			casual distribution	
GENERALISTS	7%	20,9%	41,9%	20,9%	3,1%
		70%		30%	
SPECIALISTS	25%	43,7%	6,2%	6,2%	18,7%
		75%			
SEMISPECIALISTS	38,5%	15,4%	38,5%		7,7%
		92%			
SPECIALISTS / GENERALISTS RATIO	9,07	2,8	1,06	0,29	2,9

Fig. 2. Frequency comparison between species of Dionycha spiders clade in various habiatats from southeastern Brazil (sampling from September 1986 to August 1988), which occupy a single habitat. (N = 72 spider species; ID = plant dispersion).



A. SPACE SHARING



B. NICHE PARTITION

Fig. 3. Inter and intraguild interactions among the most abundant hunting spider species (Dionycha cladei in a gallery forest. Rubião Junior district, Botucatu, State of São Paulo, Brazil. (Values for the CIC between pairs of species area shown by the arrows).

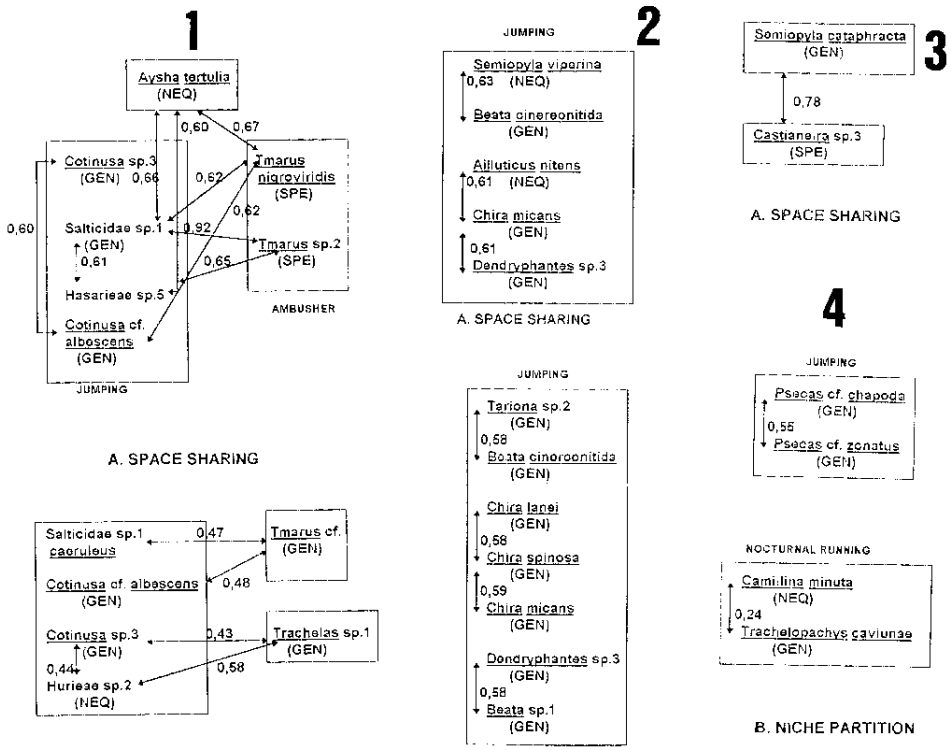


Fig. 4. Inter and intraguild interactions among the most abundant hunting spider species (Dionycha clade) in four habitats. 1. mesophytic forest (Edgardia Farm); 2. "Cerradão"; 3. pastureland ; 4. sugar-cane field. Botucatu, State of São Paulo, Brazil. (Values for the CIC between pairs of species area shown by the arrows).

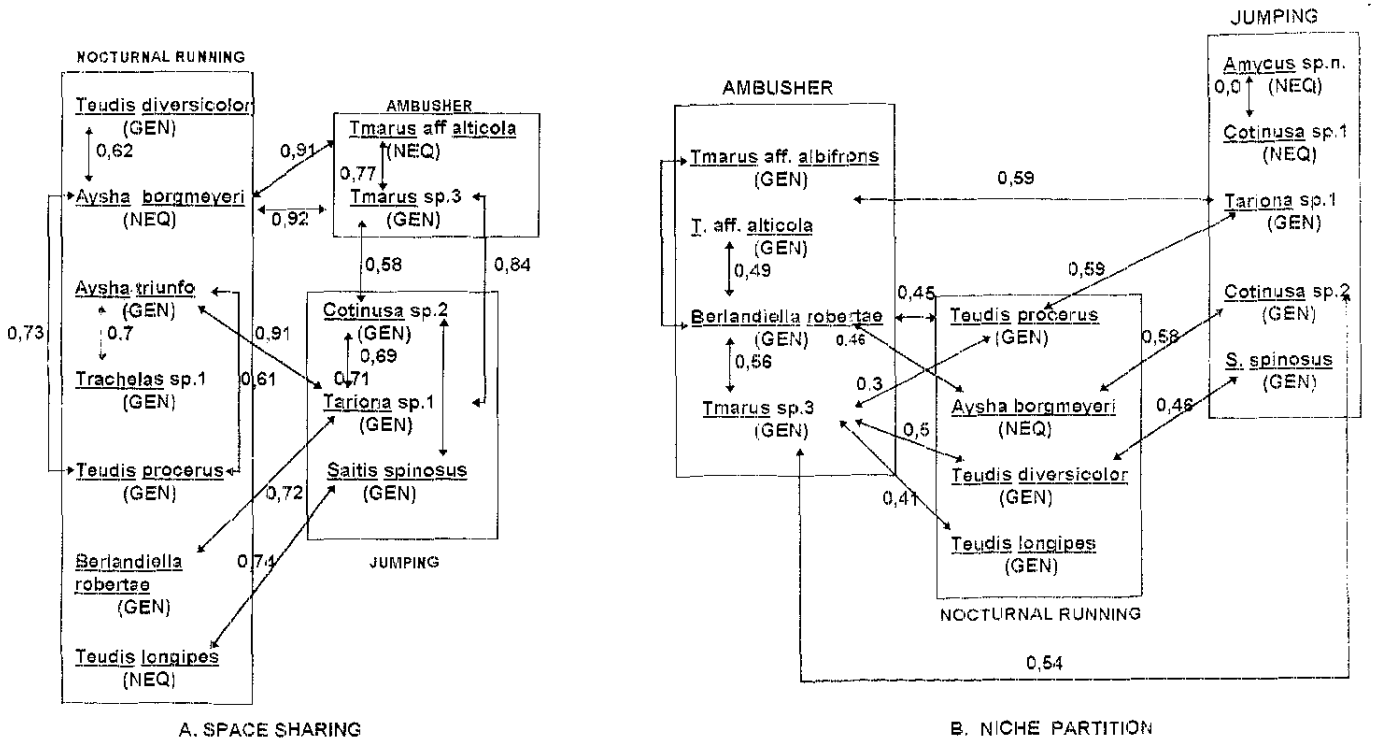


Fig. 5. Inter and intraguild interactions among the most abundant hunting spider species (Dionycha clade) in a mesophytic forest, the Municipal Park, Botucatu, State of São Paulo, Brazil. (Values for the CIC between pairs of species area shown by the arrows).

Saitis sp. 2.

Results of Pearson's correlation (r) indicate that, for the abundance of the most prominent species in each ecosystem, co-variance is positive or null; no negative correlation was found. The absolute value of the coefficient of correlation was equal to r=0.42 at a probability level of 5%. Values for the community interaction coefficient (CIC) varied from 0.0 to 1.44. Spatial partition of the niche is found when values for this coefficient are low, while high values indicate that the species are sharing the space. Inter and intraguild interactions of co-variant species of spider in each ecosystem are schematized (Figs. 3 to 5) for: A. space sharing and B. niche partition. The CIC values for pairs of species are given.

The dispersion index for plants and the frequency of species exclusive to each ecosystem are given in Table 2.

DISCUSSION

As potential competitors the more prominent dionychan spider species (relative abundance >/3 individuals) in all ecosystems studied behaved as generalists (except for *Tmarus* sp. 2, which was the 11th most abundant of the 58 species from the Fazenda Edgardia and behaved as a specialist). A similar tendency was found by POST III & RIECHERT (1977) of spiders living in three different ecosystems in Tennessee.

Most of the species in all ecosystems were found in the shrub and tree layers, and those with significant co-variation always had some mechanism which suggests avoidance of competition. The mechanisms observed were: spatial niche partition (principally in cases where CIC values were very low), separation by habitat use strategies (revealed by analysis of interspecific encounters), the fact of belonging to different guilds, and - in cases where none of these mechanisms was found - differences in seasonal periodicity of occurrence. In a number of cases, spatial partition was accompanied by separation in the exploitation of resources and/or in the type of strategy adopted.

The generalists and specialists studied here were, characteristically and respectively, high and low in their relative abundance. According

to PIANKA (1974), generalist organisms are able to exploit more types of food, to occupy a greater variety of habitats, and to build up large populations. However, abundant species may be opportunists - that is, their broad limits of tolerance allow them to occupy relatively broad niches, but although they reproduce rapidly, selection does not favour them for competition. It may be observed that the literature usually associated with insect pests and their natural enemies draws conclusions about the more important predators on the basis of their abundance values. Therefore, studies dealing with predator assemblages may led to a more accurate analysis of community structure. Such interactions associated with the physiognomy of the vegetation of ecosystems may give an idea of the food resources (productivity) available for the spiders. Thus aggregate-type vegetation, together with a larger quantity of niches, may explain the supremacy of specialists and semispecialists in the mesophytic forest of the Fazenda Edgardia and the gallery forest. However, in the sugar-cane field the distribution of plants is casual, and the number of specialists cannot be associated with the physiognomy of the ecosystem. Agricultural ecosystems may determine extreme adaptations which favor the success of specialists. According to PIANKA (1974), more specialized individuals are more efficient than generalists under extreme circumstances of adaptation. The specialists hold on to certain resources, in spite of loss of potential resources and reduction in population size; according to PONTIN (1982) this avoids competition and increases efficiency in searching for and assimilating a particular type of food. The sugar-cane field had the largest percentage of marginal species (56.3%; it may be inferred that the spiders have not yet established themselves in the habitat, or that the environment has not allowed populations of these hunters to develop further.

The availability of resources certainly influences the strategies adopted by hunting spiders. In aggregate-type plant distribution areas the probability of interspecific encounters increases; with it comes an increase in competition. This may cause a larger number of species to become specialists. The proportion of specialists to generalists increased as the index of plant dispersion in the various ecosystems increased. The presence of generalists in ecosystems with aggregate-type vegetation was highest in the cerradão, which

had the lowest dispersion index of all.

LOCKLEY & RIECHERT (1986) put forward an argument for the value of the spider community as a whole for biological control of agricultural pests, rather than use of selected species. The idea presupposes that most spiders are polyphagous. However, discrimination between types of prey (ROBINSON & ROBINSON, 1976) and above of all a preference for a particular type of prey have been broadly demonstrated (CORRIGAN & BENNET, 1987; ALDERWEIRELDT, 1994; RICHMAN *et al.*, 1990). Furthermore it is known that interactions between predators (spiders or not) may be complementary, independent, or even negative for a certain type of prey (SPILLER, 1986; HURD & EISENBERG, 1990). This may indicate a need for studies to shed more light on the importance of "subgroups" of spiders for pest control, rather than that of the community as a whole. The possibility of habitat management with use of specialists in given situations needs further investigation, particularly for agricultural ecosystems.

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RESUMO

Foram estudadas 247 espécies de aranhas (Araneomorphae, Dionycha) dos estratos arbustivo e arbóreo de seis ecossistemas na região de Botucatu, São Paulo, Brasil, e sua coexistência foi analisada por meio de uma matriz de comunidade. Espécies relativamente abundantes são predominantemente generalistas, independente de seu ambiente; espécies representadas apenas por poucos indivíduos foram numerosas, e consideradas como membros marginais das comunidades. O coeficiente médio de interação comunitária foi estimado para cada espécie, assim como a co-variação para as espécies mais abundantes em cada ecossistema. Há evidência de que a distribuição agregada de plantas favorece as espécies mais especializadas.

PALAVRAS-CHAVE: Araneomorphae, Dionycha, ecologia.

SUMMARY

Two hundred and forty seven species of dionychan spiders from the shrub and tree layers of six habitats in the region of Botucatu, State of São Paulo, Brazil, were studied, and their strategies for coexistence were determined through construction of a community matrix. Spiders with relatively greater abundance behaved largely as generalists, independent of their environment; species represented by only a few individuals were numerous, and were considered to be marginal members of the communities. Estimates of the average community interaction coefficient for each species, and of covariation of the more abundant species in each ecosystem, indicate that the spiders avoid competition by spatial partioning, or by adopting differential strategies for habitat use, or because they belong to different guilds. In relation to the aggregate distribution of plants, species tend to specialization, and thus alter their strategy to follow the availability of resources in the environment. These results, together with accumulated knowledge of the ecology of spiders, lead to observations on the subgroup as agent of stabilization in insect populations.

KEY WORDS: Araneomorphae, Dionycha, ecology.

RÈSUMÈ

Un programme de prospection des araignées a été reàlisé dans la règion de Botucatu (São Paulo, Brésil). Les strates arbustifs et arboricoles de six écosystèmes ont ètè echantillonnés et 247 espèces d'àraignées (Araneomorphae, Dionycha) ont ètè recueillies. Leur coexistence a ètè analyseé par une matrice de communauté. Les espèces relativament abundantes sont dans la grande majorité des espèces généralistes, quelque que soit leur habitat. Beaucoup d'espèces avaient peu d'individus et peuvent être considérées comme espèces marginales. Le coèfficient moyen d'interaction de communauté a été estimé pour chaque espèce, aussi bien que la covariation pour les espèces les plus abondantes dans chaque ecosystème. Nousavons aperçu que la distribution agrégeé des plantas rend évident la présence des espèces les plus spécialiseés.

MOTS CLÉS: Araneomorphae, Dionycha, écologie.

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