Spider Assemblages in Costa Rican Cloud Forests: Effects of Forest Level and Forest Age

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Abstract

We investigated spider assemblages in trees at three cloud forest sites and in trees isolated in pasture habitat in Monteverde, Costa Rica. Spiders were collected from two forest types (primary and secondary) within each forest site, and at two different levels (canopy and understory) within forest types and the pasture. They were identified to family or genus level and assigned to morphospecies. Araneidae and Linyphiidae were the most commonly collected families at all locations. Although spider abundance and morphospecies richness did not differ between forest types, perhaps due to their close proximity, these parameters were generally lower in the forest canopy than in the understory. Relative abundances of nearly all common spider families also differed between canopy and understory levels within forests, suggesting that distinct sub-assemblages exist. However, spider abundance and morphospecies richness did not differ between canopy and understory in pasture trees. Spiders were generally more abundant and more diverse in the pasture than the forest, possibly due to its lower elevation or its greater habitat complexity in the form of vascular epiphytes.

Resumen

Se investigaron las comunidades de arañas en tres sitios de bosque nuboso y en árboles de potrero en Monteverde, Costa Rica. Las arañas fueron recogidas de dos tipos de bosque (primario y secundario) en cada sitio, y a dos niveles (copa de árboles y sotobosque) en cada tipo de bosque y en árboles del potrero. Fueron identificadas al nivel de familia o genero y clasificadas como morfoespecies. Las familias Araneidae y Linyphiidae eran las más comúnes. La abundancia y can-
tidad de morfoespecies no variaban entre los dos tipos del bosque, tal vez porque los dos tipos de bosque estuvieron próximos. Además, la abundancia y cantidad de morfoespecies eran menos en la copa de árboles que en el sotobosque. La abundancia proporcional de casi todas las familias comúnes también era diferente entre los dos niveles, el cual puede indicar que existen comunidades distintas. No se encontraron diferencias en la abundancia y cantidad de morfoespecies entre los dos niveles de árboles en el potrero. De todas maneras, las arañas eran más abundantes y más diversas en el potrero que en el bosque, posiblemente porque el potrero tiene menos altura y tiene una estructura mas compleja en la forma de epífitas vasculares.

Keywords: canopy, cloud forest, Costa Rica, disturbance, diversity, Monteverde, spiders.

Introduction

Organisms inhabiting tropical forests are influenced by a variety of abiotic factors that vary in time and space (e.g., Allee, 1926). Several of these factors (e.g., light availability, wind speed, relative humidity) change predictably from canopy to ground, resulting in a vertical gradient of conditions (e.g., Parker, 1995; Richards, 1996). This gradient potentially influences the distributions of many forest-dwelling species and species assemblages, including mammals (e.g., Emmons, 1995), lizards (Reagan, 1995), insects (e.g., Papageorgis, 1975; Nadkarni & Longino, 1990; Yanoviak, 1999; Basset et al., 2001), and spiders (e.g., Turnbull, 1973; Valderrama, 2000).

Anthropogenic factors also influence species distributions in forests. Forest conversion for agriculture and timber production has had large scale, well-publicized effects on biodiversity, climate, and geomorphology (e.g., Wilson, 1988; UNDP et al., 2000; Lawton et al., 2001). The secondary vegetative growth that follows such disturbance generally supports different arthropod assemblages from relatively undisturbed forests (e.g., Lawton et al., 1998; Floren & Linsenmair, 1999; Wagner, 2000).

Although montane forests are among the most threatened tropical habitats (UNDP et al., 2000), very little research has specifically addressed the ecological effects of disturbance in these systems (but see Pounds et al., 1999; Nadkarni & Wheelwright, 2000). Moreover, little or no baseline data exist for many montane taxa which may be good indicators of ecosystem disturbance and global change (but see Lawton et al., 1998). In this paper, we report on the patterns of distribution of one major component of the invertebrate fauna – the spiders – within a montane landscape of Costa Rica. Our specific objective was to determine if the abundance, morphospecies richness, and taxonomic composition of spiders differ among forest types (primary vs. secondary), sites (study plots within forest types), levels within forests (canopy vs. understory), and habitats (forest vs. pasture).

Spiders are an appropriate focal group for studies of vertical distribution patterns and effects of disturbance. They are ecologically important as abundant mid-level predators in forest food webs (Turnbull, 1973; Wise, 1993; Halaj et al., 2000), are generally easy to locate and collect (Kaston, 1978), and are sensitive to variation in a variety of habitat characteristics (Turnbull, 1973; Wise, 1993). Some of these characteristics include forest canopy structure (Halaj et al., 1998, 2000), prey size and availability (Enders, 1974; Greenstone, 1984; Halaj et al., 1998), and local environmental conditions such as light, wind, and humidity (e.g., Enders, 1977; Biere & Uetz, 1981).

The structure of spider assemblages and factors influencing spider diversity are relatively poorly studied in tropical regions (but see Coddington & Levi, 1991; Flórez, 1999). Even less is known of the spiders of tropical montane regions (e.g., Hanson, 2000) and spiders of tropical forest canopies (Russell-Smith & Stork, 1994; Basset, 2001). Ecological information for most groups can be found only as comments in taxonomic surveys (e.g., Zuñiga, 1980; Nentwig, 1993). Exceptions include studies by Buskirk and Buskirk (1976) in montane forests of Costa Rica, Basset et al. (1992) in lowland forest canopies of Cameroon, and Valderrama (2000) in Colombian cloud forest.

In this investigation, we predicted that more spiders and more spider morphospecies would be found in primary forest due to its greater structural complexity relative to secondary forest (measured in terms of precipitation storage capacity; Clark et al., 2000). Montane forest canopies are subject to continuous disturbance in the form of wind, rain, and desiccation (Parker, 1995; Clark et al., 2000). Thus, we predicted that the calmer conditions in the understory would promote greater spider abundance and morphospecies richness than the more turbulent canopy. Finally, we predicted that spider assemblages of remnant forest trees in a pasture would be similar between canopy and understory because, unlike primary and secondary forest stands, environmental conditions appear to be relatively homogeneous from ground to tree crowns in this setting. We did not make predictions regarding variation in spider taxonomic composition among ecological factors.

Materials and methods

This study was conducted in the Monteverde region of Costa Rica (Cordillera de Tilarán, 10°20′N, 84°45′W; Fig. 1) between 15 September and 15 December 2000, which corresponds to late wet season and early transition season (Clark et al., 2000). Precipitation is mainly in the form of wind-blown mist and clouds, and mean monthly temperatures range from 14–20°C (see Nadkarni & Wheelwright (2000) for details about the region).
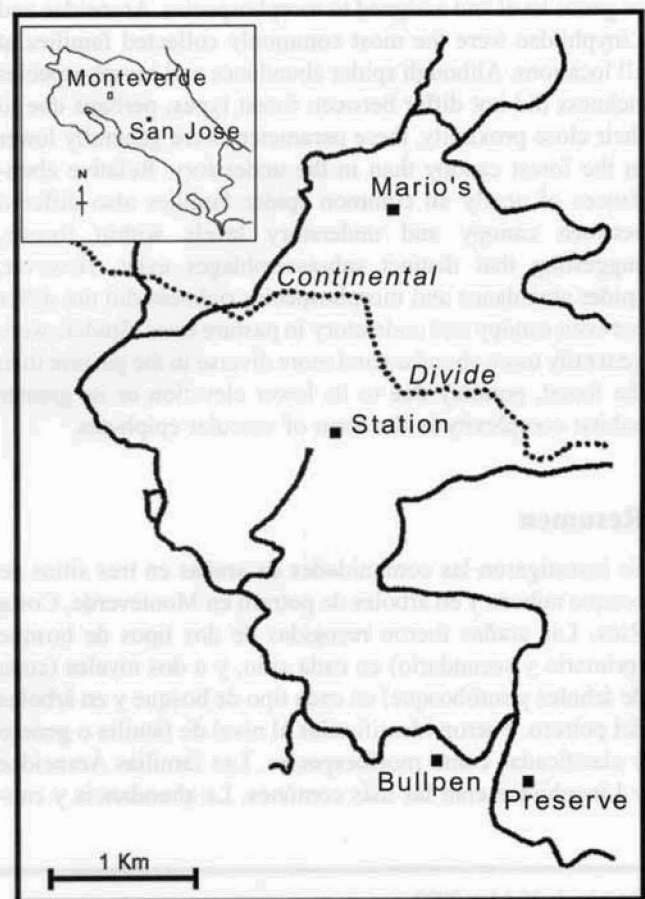

Fig. 1.   Location of the Monteverde region within Costa Rica (inset) and study sites within Monteverde (■). Solid lines indicate principal roads. Scale bar = approx. 1 km.

Forest sites

We sampled spiders from three montane forest sites: the Monteverde Cloud Forest Preserve (hereafter, 'MCFP'); private property adjacent to the Santa Elena Cloud Forest Reserve owned by Mario Solano (hereafter, 'Mario's'); and the Canadian Biological Station (hereafter, 'Station'). All three sites exist within a 5 km radius (Fig. 1). The MCFP and Station forests are located at 1500–1600 m elevation, and Mario's is at approximately 1700 m. This elevation range includes the lower montane wet forest (1450–1600 m) and lower montane rain forest (1550–1850 m) life zones (Haber, 2000).

Each site consists of relatively large tracts of primary forest surrounding 1–5 ha patches of secondary forest that have replaced abandoned pastures. Primary forest within the MCFP has been protected for >50 years and has received minimal direct anthropogenic disturbance during the past several centuries. Forests outside the MCFP have been variously disturbed, and our 'primary' forest designation at the Station and Mario's was based on stand composition and structure, as well as oral history from local residents. Primary forests at all sites range from ca. 150 to >400 years in age and are characterized by high tree species diversity. They have complex, multi-layered vegetation structure with canopies ca. 25 m above the ground. Secondary forest patches at all sites are 30–50 years old, are dominated by *Conostegia* spp. (Melastomataceae) trees, and have relatively flat canopies 15–17 m in height. Vegetation in the secondary forests is more sparse than in the primary forests, and is mainly confined to two strata: the understory (up to 3 m) and the tree crowns (15–20 m).

We collected spiders from the crowns and understory trunks of five trees in each forest type at each forest site (n = 60 samples; 5 trees × 2 levels × 2 forest types × 3 sites; Table 1). Within each site, study trees were ≤500 m apart and

were selected based on our ability to access their crowns using the single-rope technique (Perry, 1978). Understory spiders were collected from the trunks and attached vegetation of the trees up to a height of 2 m. Collections in the canopy focused on the trunk, accessible branches, and associated vascular epiphytes above the first major fork in each tree crown (above 10 m in all cases). Each canopy or understory trunk sample consisted of a 30 min intensive search of that portion of the tree, during which as many spiders as possible were collected by hand. Time spent moving between branches within tree crowns was not included in the 30 min collection period. Bark crevices and trunk cavities were searched with a flashlight. We used this technique because it is equally or more efficient than trapping or sweep netting for spider surveys (Turnbull, 1973; Flórez, 1999). Collections were conducted during morning or afternoon hours, with the majority taken between 08:00 and 12:00. We did not collect spiders during heavy rain.

Spiders were fixed in Oudeman's fluid (Borror et al., 1989: 131) at the time of collection to preserve coloration and prevent stiffening. After ≥24 hr in the fixative, individuals were identified to family and genus (when possible) with keys of Kaston (1978), Nentwig (1993), and Roth (1993), and assigned to morphospecies (Oliver & Beattie, 1996). All identifications and morphospecies assignments were done by the same person (GK) for consistency. Spiders were transferred to 70% ethanol for storage, and a complete reference collection was deposited at the MCFP research laboratory. Higher classifications used in this paper follow Nentwig (1993).

Bullpen pasture

In addition to the three forested sites, we collected spiders (as described above) from five *Ocotea tonduzii* (Lauraceae)

Table 1. Tree species used for spider collections in primary and secondary forests at the three research sites.

Tree	Station	Mario's	MCFP
Primary Forest			
1	*Pouteria reticulata*[1]	*Sapium rigidifolium*[9]	*Ficus tuerckheimii*[2]
2	*Pouteria reticulata*[1]	*Sapium rigidifolium*[9]	*Ficus tuerckheimii*[2]
3	*Quercus corrugata*[6]	*Sapium rigidifolium*[9]	*Ocotea tonduzii*[3]
4	*Pouteria reticulata*[1]	*Guarea tonduzii*[8]	*Ocotea tonduzii*[3]
5	*Gordonia brandegeei*[7]	*Ficus crassiuscula*[2]	*Ocotea tonduzii*[3]
Secondary Forest			
1	*Hampea appendiculata*[4]	*Conostegia rufescens*[5]	*Hampea appendiculata*[4]
2	*Persea americana*[3]	*Conostegia rufescens*[5]	*Hampea appendiculata*[4]
3	*Conostegia oerstediana*[5]	*Conostegia rufescens*[5]	*Conostegia oerstediana*[5]
4	*Conostegia oerstediana*[5]	*Conostegia rufescens*[5]	*Conostegia oerstediana*[5]
5	*Conostegia oerstediana*[5]	*Conostegia rufescens*[5]	*Conostegia oerstediana*[5]

[1] Sapotaceae; [2] Moraceae; [3] Lauraceae; [4] Malvaceae; [5] Melastomataceae; [6] Fagaceae; [7] Theaceae; [8] Meliaceae; [9] Euphorbiaceae.

trees in a private pasture known locally as the 'Bullpen' (1450 m elevation). The understory at this site is dominated by low grass subject to occasional cattle grazing. This pasture also contains numerous remnant primary forest trees with isolated crowns, giving it an arboretum-like appearance. Harvey and Haber (1999) provide more detailed descriptions of this habitat.

Analyses

We used the GLM procedure in SAS (1999) to compare mean spider abundance, morphospecies richness, and relative abundance of spider families among sites (MCFP, Mario's, Station), between forest types (primary, secondary) nested within sites, and between levels (canopy, understory) nested within forest types and sites. Because it was difficult to assign young individuals accurately to morphospecies, we repeated all morphospecies richness tests with juvenile spiders excluded. We restricted parametric analyses of relative abundance data to families representing >5% of the collection in order to meet test assumptions. Wilcoxon two-sample tests were used for relative abundance analyses involving less common families. Spider assemblage parameters were compared between canopy and understory in the Bullpen with t-tests. Normality was confirmed with Kolmogorov–Smirnov tests applied to ungrouped data (Sokal & Rohlf, 1995; SAS, 1999) and proportional abundance data were arcsine square-root transformed before analysis. All means reported include ±1 SE and were calculated from untransformed data. Bonferroni-adjusted alpha values were used to account for multiplicity when necessary.

Results

We collected 1163 spiders that represented 204 morphospecies and 19 families. These counts include juveniles; thus, the number of morphospecies is probably inflated. Excluding juveniles, we collected 298 individuals in 86 morphospecies. Twenty-four neonate spiders could not be identified to family due to their small size. Nine families comprised 93% of the total collection, and Araneidae (mostly *Cyclosa* spp. and *Eustala* spp.) and Linyphiidae together represented >50% overall (Fig. 2). Spiders that build aerial webs were the most conspicuous and most easily collected, and comprised 83% of the total collection (967 individuals, 150 morphospecies, and 10 families). Conversely, active hunters (e.g., salticids) and 'ambushers' (Nentwig, 1993) often escaped, and were thus underrepresented in our samples. A complete list of collected taxa is available from GK.

The number of individuals and number of morphospecies per sample were significantly correlated for both the total collection ($r = 0.88$, $P < 0.0001$) and with juveniles excluded ($r = 0.76$, $P < 0.0001$), which is often the case with survey data. Given the short duration of the field work, we expected no significant temporal variation in the number of
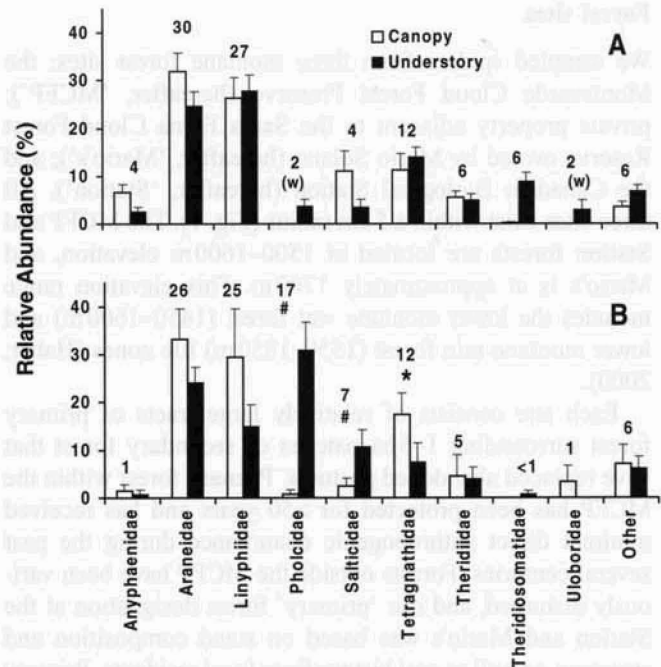

Fig. 2. Average (+SE) relative abundance of the nine most frequently collected spider families in cloud forest sites (A), and the Bullpen pasture (B). 'Other' includes Agelenidae, Amaurobiidae, Anapidae, Clubionidae, Corinnidae, Gnaphosidae, Lycosidae, Pisauridae, Tengellidae, Thomisidae, and unidentified individuals. n = 30 trees for each mean in A (sites and forest types pooled) and n = 5 trees for each mean in B. Numbers above columns indicate the total % abundance of each group (canopy + understory) within A or B. (w) = $P < 0.025$ based on Wilcoxon tests applied to families representing <5% of the collection in A. # = $P < 0.06$ and * = $P < 0.05$ based on t-tests in B. Nested ANOVA results for families representing >5% in A are given in Table 4. Significance designations appear errant in some cases because means and SE bars are from untransformed data.

spiders or morphospecies encountered. Linear regressions showed no relationship between Julian date and spider abundance or morphospecies richness ($r^2 < 0.02$, $F_{1,68} < 1.10$, $P > 0.29$).

Forest sites

The three forest sites used in this study were chosen *a priori* to serve as ecological replicates of typical cloud forest in the region. This assumption of replication was upheld for spider abundance, as indicated by the lack of statistical difference in this parameter among sites (Tables 2, 3). Likewise, family-level taxonomic composition was similar among the three forest sites (Sørensen coefficients > 0.785 and Morisita index > 0.941 for all site × site comparisons). In contrast, morphospecies richness was significantly lower on average at Mario's than at the Station ($F_{2,48} = 3.63$, $P = 0.034$; Table 2). Thus, we analyzed richness data separately for each forest site using the same nested model reduced by one level (Table

Table 2. Mean (SE) abundance and morphospecies richness of spiders per sample at three different forest sites and two forest types within each site.

	Station		Mario's		MCFP	
Abundance	17.1 (2.09)		13.1 (1.92)		15.3 (1.78)	
Richness	10.2 (1.12) a		7.3 (0.89) b		8.4 (0.70) ab	
	Primary	*Secondary*	*Primary*	*Secondary*	*Primary*	*Secondary*
Abundance	15.1 (3.42)	19.1 (2.42)	11.9 (3.24)	14.3 (2.20)	17.7 (2.66)	12.8 (2.24)
Richness	9.7 (1.97)	10.7 (1.17)	7.2 (1.66)	7.4 (0.79)	9.3 (1.14)	7.5 (0.79)

$n = 20$ for each site mean and $n = 10$ for each forest type mean. Abundance means do not differ among sites (see Table 3). Richness means followed by the same letter do not differ.

Table 3. ANOVA output for spider abundance and morphospecies richness.

Variable	Factor	df	SS[1]	F^2
Abundance	Site	2	160.30	1.58
	Type (site)	3	228.85	1.50
	Level (type*site)	6	1610.90	5.29**
	Error	48	2437.60	
Richness (all)				
1. Station	Type	1	5.00	0.28
	Level (type)	2	185.0	5.15*
	Error	16	287.2	
2. Mario's	Type	1	0.20	0.03
	Level (type)	2	180.0	11.61**
	Error	16	124.0	
3. MCFP	Type	1	16.20	1.67
	Level (type)	2	17.00	0.87
	Error	16	155.6	
Richness (adult)	Site	2	13.23	1.88
	Type (site)	3	32.10	3.04
	Level (type*site)	6	86.80	4.10**
	Error	48	169.2	

[1] SS = sum of squares; [2] * = $P < 0.025$, ** = $P < 0.005$, $\alpha = 0.017$ for richness tests.
'all' = all spiders included in the analysis, 'adult' = juveniles excluded. 'Type (site)' and similar notation indicate an analysis of differences between forest types nested within sites.

3). Morphospecies richness did not differ among sites when juveniles were excluded from the analysis (Table 3).

Based on analyses of relative abundance, only Theridiidae (mainly *Theridion* spp. and *Steatoda* spp.) differed among sites ($F_{2,48} = 10.14$, $P = 0.0002$), representing a smaller average percentage of the collection at Mario's (1.3 ± 0.76; $n = 20$) than at the Station (9.4 ± 1.97) or MCFP (5.0 ± 1.07). As described above, we subsequently analyzed the relative abundance of theridiids separately for each site (Table 4).

Spider abundance, morphospecies richness, and relative abundance patterns of commonly collected families were generally similar between primary and secondary forest types (Tables 2, 3). Theridiosomatidae was the only common family that differed in relative abundance between forest types (Table 4). Although statistically significant, this difference was not very large; theridiosomatids comprised 6.8% (± 2.39) of the collection from primary forest and 2.2% (± 1.06) from secondary forest. Among the less common families, anyphaenids were collected relatively more often in secondary forest (7.0% ± 1.90) vs. primary forest (2.4% ± 1.21; Wilcoxon $Z = 2.88$, $P = 0.004$), and uloborids were absent from secondary forest collections.

Forest level (canopy or understory) had the strongest effect on quantitative characteristics of spider assemblages. Spiders were generally less abundant and less morphospecies-rich in tree crowns than on the understory trunks and associated vegetation, especially within primary forests (Fig. 3). The only exception was a lack of difference

Table 4. ANOVA output for proportional abundance of common spider families.

Taxon	Factor	df	SS	F^1
Araneidae	Site	2	0.0389	1.24
	Type (site)	3	0.0392	0.84
	Level (type*site)	6	0.4653	4.96**
	Error	48	0.7509	
Linyphiidae	Site	2	0.0237	0.88
	Type (site)	3	0.0294	1.09
	Level (type*site)	6	0.0682	2.53*
	Error	48	0.2946	
Tetragnathidae	Site	2	0.0453	1.22
	Type (site)	3	0.0577	1.04
	Level (type*site)	6	0.4225	3.80**
	Error	48	0.8884	
Theridiidae—Station	Type	1	0.0590	5.88
	Level (type)	2	0.0162	0.81
	Error	16	0.1604	
Theridiidae—Mario's	Type	1	0.0005	0.12
	Level (type)	2	0.0135	1.73
	Error	16	0.0625	
Theridiidae—MCFP	Type	1	0.0063	0.81
	Level (type)	2	0.0114	0.74
	Error	16	0.1240	
Theridiosomatidae	Site	2	0.0266	2.96
	Type (site)	3	0.0791	5.86**
	Level (type*site)	6	0.3556	13.16**
	Error	48	0.2162	
Other	Site	2	0.0366	2.21
	Type (site)	3	0.0024	0.10
	Level (type*site)	6	0.1080	2.17
	Error	48	0.3974	

To meet model assumptions, only families representing 5% of the total collection from the three forest sites were included. See Fig. 2 legend for contents of 'Other'. $\alpha = 0.025$ for Theridiidae tests.

[1] * = $P < 0.05$, ** = $P < 0.005$. 'Type (site)' and similar notation indicate an analysis of differences between forest types nested within sites.

in morphospecies richness between canopy and understory at MCFP (Table 3). Statistical independence was potentially compromised in this analysis because we used the same individual trees for observations at both levels. However, post hoc Wilcoxon tests also supported the conclusion that spider abundance and morphospecies richness are significantly lower in the canopy than in the understory ($Z > 2.41$, $P < 0.016$).

All of the common spider families except Theridiidae and the catch-all group 'Other' showed significant differences in relative abundance between canopy and understory (Table 4). Araneids were relatively more abundant in the canopy than in the understory, whereas linyphiids, tetragnathids and theridiosomatids comprised a smaller fraction of collections from the canopy than from the understory (Fig 2A; note that variances used in the nested ANOVA differ from the figure). Among families representing <5% of the forest collection, only Anyphaenidae (mainly *Anyphaena* spp. and *Teudis* spp.)

and Salticidae were statistically similar in relative abundance between canopy and understory (Fig. 2A).

We chose to ignore possible tree species effects at the start of this study. However, it appeared that more spiders occurred in the convoluted understory trunk portions of *Ficus tuerckheimii* than in association with other primary forest tree species that have structurally simpler trunks. Despite this apparent tree species effect, there was no difference in understory spider abundance among *F. tuerckheimii*, *Pouteria reticulata* and *Sapium rigidifolium* (Kruskal–Wallis $X^2 = 2.19$, df = 2, $P = 0.33$).

Bullpen pasture

Spider abundance and morphospecies richness (for all individuals and for juveniles excluded) did not differ between canopy and understory in *Ocotea tonduzii* trees of the Bullpen pasture ($t < 1.87$, df = 8, $P > 0.10$; Fig. 4). Wilcoxon
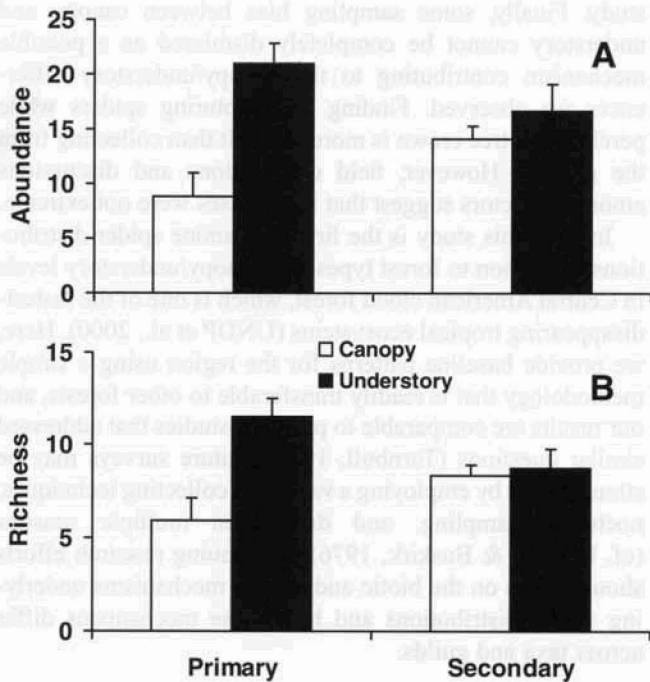
Fig. 3. Mean (+SE) spider abundance (A) and morphospecies richness (B) at canopy and understory heights within primary and secondary forest types. $n = 15$ trees for each mean. Data from the different forest sites were pooled for clarity.
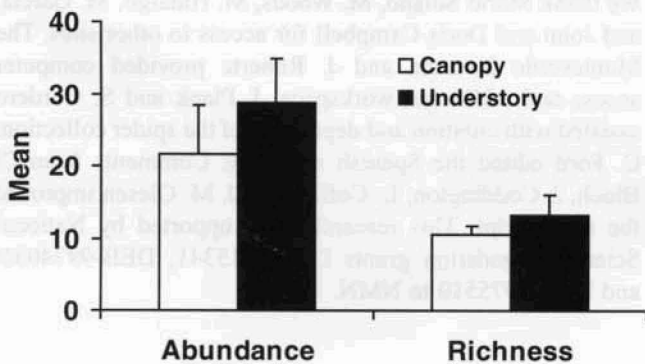

Fig. 4. Mean (+SE) spider abundance and morphospecies richness at canopy and understory heights in the Bullpen pasture. $n = 5$ trees for each mean.

tests gave the same result ($Z < 1.70$, $P > 0.09$). Likewise, most families had similar mean relative abundance between canopy and understory (Fig 2B). However, Pholcidae (*Modisimus* spp.) and Salticidae comprised a marginally larger percentage of the understory spider assemblage, and Tetragnathidae (*Leucauge* spp.) were better represented in the canopy (Fig. 2B).

Overall, characteristics of spider assemblages in the Bullpen were similar to those of the forested sites. Average morphospecies richness in the 10 Bullpen samples (11.9 ± 1.50) did not differ from the Station or MCFP (cf. Table 2),

and was greater than mean richness at Mario's (one-way ANOVA using GLM for unbalanced data: $F_{3,66} = 3.32$, $P = 0.025$). Excluding juvenile spiders from these morphospecies analyses did not change the outcome. Mean spider abundance was larger at the Bullpen (25.2 ± 4.48) than at the forest sites (pooled mean = 15.2 ± 1.12; $F_{1,68} = 9.43$, $P = 0.003$). Relative abundance patterns of common families were similar between the Bullpen and forest (Fig. 2). Two clear exceptions to the latter were the greater frequency of Pholcidae and lower relative abundance of Theridiosomatidae in the Bullpen (Fig. 2).

Discussion

Our results strongly support the prediction that spider abundance and morphospecies richness are greater in the forest understory than in the canopy. Relative abundance results, albeit at the family level, further suggest that the canopy and understory support different spider sub-assemblages. This general pattern has been observed in many different forests and on different continents (Turnbull, 1973; Basset et al., 2001). However, to our knowledge, only one such study has been conducted in a neotropical cloud forest (Valderrama, 2000), and none has examined spider assemblages in pasture trees.

Our prediction of greater spider abundance and morphospecies richness in the primary forests was not supported. Although it is possible that spider diversity is not strongly affected by forest type, this seems unlikely given the gross structural and microclimatic differences that exist between primary and secondary forests in general. In Monteverde, these differences are most pronounced in the forest midstory (ca. 5–15 m, see Methods), and it is probable that spider data from that level would have shown a significant forest type effect. Alternatively, the lack of observed difference between forest types may be a consequence of the unique distribution of forest types in Monteverde. Whereas most secondary forests in Central America are contiguous with highly disturbed habitats, secondary forests in Monteverde typically exist as islands of regeneration within tracts of primary forest. Thus, the vagility of spiders allows considerable faunal exchange between these forest types in Monteverde due to their proximity. Evidence supporting such a faunal exchange (e.g., using marked individuals) is needed, and could support arguments for forest conservation.

Differences that occurred among forest sites (e.g., in overall morphospecies richness and in relative abundance of Theridiidae) indicate that Mario's is not a perfect replicate of the other two forests. We attribute this difference primarily to geography. Mario's is located on the eastern (windward) slope of the Continental Divide, whereas the Station and MCFP (and the Bullpen) exist on the western (leeward) side. Furthermore, Mario's is ca. 100 m higher than the other sites. Although climate data were not available at the scale of individual study sites, it is reasonable to assume that Mario's is

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