where they are both known to exist (C. R. E. Dallison and FSP colleagues, pers. observ.).

There was a higher abundance of sub-oscines at Corcovado, perhaps because of its geographical proximity to South America, where birds of this sub-order are better represented. The reasons for the higher proportion and abundance of oscines at La Selva and Monteverde compared to the other sites are not clear. The high abundance of columbiforms at Corcovado may indicate a greater amount of available resources (seeds, fruits) there on which these birds feed.

The high relative abundance of nectar-feeders at Monteverde is probably related to the greater abundance of hummingbird-pollinated flowering plants in this forest. Also, the high abundance of insectivores feeding on foliage at Monteverde be due to high epiphytic densities at this site (Appendix 1), which provide abundant habitats for insects. Relative abundance of aerially foraging insectivores was highest at Palo Verde, where the more open forest and neighboring marsh may provide a more favorable habitat for flying insects and a greater ease of capture for insectivores. Tropical lowland forests had the highest relative abundance of frugivores, probably because consistently high rainfall throughout the year may result in high fruit densities at these sites. Finally, the higher diversity of food resources in lowland rainforests may account for the high relative abundance of omnivores found at La Selva and Corcovado.

Though the limited sampling (24 point counts on one day at each site) probably does not provide a representative picture of the actual bird compostion, we did find that bird communities are larger and more diverse in tropical lowland rainforests and that this is correlated with greater structural complexity of the forest at those sites. Moreover, certain taxonomic groups and foraging guilds appear to be restricted to particular forest types, depending on the type of habitat and resources they provide. Thus, the structural complexity of the habitats, coupled with the resources they provide, largely accounts for the differences in bird diversity and abundance among these tropical habitats.

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Appendix 1: Characterization of the forests studied († from Hartshorn 1983, * from Barnhorst et al. 1995)

Site	Forest type†	Mean Annual Rainfall (m)†	Mean Tree Density (No./100m^2)*	Mean Tree Height (m)*	Mean % Epiphyte*	Elevation (m)†
Palo Verde	Tropical dry forest	1-1.5	16	12.0	0	100-200
Monteverde	Montane cloud forest	2-3	24	15.5	50	1500-1800
Corcovado	Lowland rain forest	3-6	37	21.1	10	100
La Selva	Lowland rain forest	3-4	26	19.0	25	70

Comparison of spider abundance and diversity in four Costa Rican forests

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Abstract. Greater structural complexity in primary forests may generate greater biological diversity. We predicted that diversity, abundance, and total biomass of spider feeding groups would be greatest in the wet and more structurally complex lowland forests at Corcovado and La Selva, intermediate in the dry lowland forest at Palo Verde, and lowest in the montane cloud forest of Monteverde, because these groups exploit different aspects of forest structure. We found the highest diversity of spiders at Corcovado and La Selva, and highest abundance and biomass at Corcovado. There was no relationship, however, between the abundance of spider groups and habitat structure. This suggests that other factors (such as prey diversity and abundance) may be more important determinants of spider diversity and abundance.

Key Words: spider community structure, structural complexity

INTRODUCTION

Forest structural complexity has been proposed as a determinant of arthropod diversity. Forests consisting of multiple strata and more heterogeneous vegetation may possess more niches available to arthropods. Increases in niches may be correlated with higher numbers of refuges (woody debris, leaf litter, rocks), herbaceous plant coverage and woody plants. This pattern of increased diversity with increased forest structural complexity has been shown in coleopterans (Dums et al. 1997). The positive effect of forest complexity on spider diversity may be a result of increased abundance of hiding places and lairs and/or of increased food variety and availability (primarily insects).

We hypothesized that structural complexity in primary forests would enhance spider diversity. We predicted that spider diversity would be greatest in the wet and more structurally complex lowland forests (Corcovado and La Selva), intermediate in the less structurally complex, highly seasonal dry lowland forest (Palo Verde), and lowest in the cool, wet windy highland forests (Monteverde).

Insect biomass is greater in wet lowland forests than wet highland forests (Hartshorn 1983). Therefore, we predicted spider biomass would be greater in lowland wet forest (Corcovado, La Selva) than in the highland wet forest (Monteverde) due to higher food availability. We also predicted spider biomass would be relatively high in the lowland dry forest of Palo Verde, due to the high availability of insect prey emerging from the marsh which was located ca. 300 m from the transects.

Finally, we predicted a positive relationship between the diversity of webless, non-burrowing spiders and the number of refuges in structurally complex environments. Similarly, we predicted a positive relationship between the number of web-weaving spiders and the number of potentially suitable web sites, as measured by the complexity of the shrub and herb layer, as another aspect of structurally complex environments.

METHODS

Six members of our 1999 Biology FSP gathered arachnid data during one morning of our stay at each of four sites: the OTS station at Parque Nacional Palo Verde, Monteverde Biological Station at Monteverde, Estación Sirena at Parque Nacional Corcovado, and the OTS station at La Selva.

At each site, data were collected along three randomly selected 2 x 25 m transects in

primary forest. All spiders were observed from the ground to 1.5 m in the vegetation without disturbing or lifting ground cover. The spiders were put into size classes (2.5 mm body length categories), and classified into families/feeding types (Table 1), using information from Jackman (1997). The substrate that each spider was found on was also recorded. Transect substrate was characterized by randomly selecting three 2 x 2 m quadrats within each transect. On each transect we measured the density of three classes of woody stems: less than 1 cm dbh, between 1 and 5 cm dbh, and > 5 cm dbh. A randomly selected 1 x 1 m quadrat from each transect was used to intensively sample for arachnids on the forest floor by removing all litter and debris.

The Shannon-Weiner Diversity Index was used to compare diversity and evenness between sites. A one-way ANOVA with a Tukey HSD test was used for pairwise comparisons. Body lengths of all spiders in each transect were summed, and the mean of the three transect sums was used as an index of spider biomass for each site.

RESULTS

The lowland tropical forests of La Selva and Corcovado had a greater diversity of spiders than the dry forest of Palo Verde and Monteverde's cloud forest (Table 2; Kruskal-Wallis, $X^2 = 8.44$, DF = 3, P = 0.04), as measured by the Shannon-Weiner Index. The cloud forest at Monteverde had a significantly lower evenness of spider families than Palo Verde, Corcovado, and La Selva (Table 2, Fig. 1; Kruskal-Wallis, $X^2 = 9.46$, DF = 3, P = 0.02). Total spider abundance was higher at Corcovado than at the other three sites (Table 2, Fig. 2; ANOVA, F = 9.93, DF = 3, P = 0.005). At all sites, tangle-web spiders (Theridiidae) were proportionally the most abundant family observed. At Palo Verde and Monteverde, web weaving spider families were the dominant functional group. In Corcovado and La Selva, web weaving spiders and non-web weaving spiders were more evenly represented (Fig. 1).

Forest structural complexity was measured by percent of substrate covered by woody debris, leaf litter and rock, as well as by the number of stems per transect. Neither percentage of refuge of substrate, nor the number stems differed significantly between sites (Table 2; Substrate refuge: Kruskal-Wallis, $X^2 = 4.95$, DF = 3, P = 0.13; Number of stems: Kruskal-Wallis, $X^2 = 1.132$, DF = 3, P = 0.77). Contrary to our predictions, the abundance of web-weaving spiders (Table 1) was not correlated with the number of stems within a transect ($r^2 = 0.09$, F = 1.04, P = 0.33). Similarly, the relative abundance of ground-dwelling, non-web-weaving spiders was not correlated with the percent refuges (ANOVA, F = 2.98, DF = 1, P = 0.15).

Table 1. Scientific and common names of spiders in our study, grouped by feeding type.

Feeding Strategy	Scientific Name	Common name
Web-Weavers	Araneidae	Orb Weavers
	Agelenidae	Funnelweb Weavers
	Linyphiidae	Cave Spiders or Dwarf Weaver
	Theridiidae	Tangleweb Weavers
	Thomisidae	Crab Spiders
NonWeb Weavers	Salticidae	Jumping Spiders
	Clubionidae, Gnaphosidae, Ctenidae	Ground Spiders
	Lycosidae	Wolf Spiders
	Pholcidae	Daddylongleg Spiders

Table 2. Characteristics of spider feeding groups and the understory habitat at four sites in Costa Rica. Values for abundance, diversity, evenness and mean sum body size (biomass) are means ± 1 SE for three 2 x 25 m transects. Values for number of stems and percent refuge are means ± 1 SE for nine 2 x 2 m subplots (three in each transect). Different letters in each row indicate significantly different values (Tukey HSD, P 0.05). There were no significant differences between sites in the number of stems or the percent refuge.

	Corcovado	La Selva	Monteverde	Palo Verde
Abundance	124.0 ± 12.6 (a)	42.0 ± 12.3 (b)	61.7 ± 9.7 (b)	58.0 ± 11.1 (b)
Diversity (H)	1.57 ± 0.06 (a)	1.58 ± 0.09 (a)	0.92 ± 0.09 (b)	1.07 ± 0.14 (b)
Evenness (J)	0.81 ± 0.03 (a)	0.88 ± 0.01 (a)	0.53 ± 0.06 (b)	0.79 ± 0.04 (a)
Mean Sum Body Size (cm)	397.7 ± 50.9 (a)	152.5 ± 51.3 (b)	180.0 ± 26.5 (b)	200.0 ± 35.7 (b)
Number of Stems	39.4 ± 12.2	23.0 ± 13.9	43.0 ± 15.3	19.2 ± 7.7
Percent Refuge	80.6 ± 6.4	70.6 ± 7.8	93.8 ± 3.8	86.2 ± 7.6

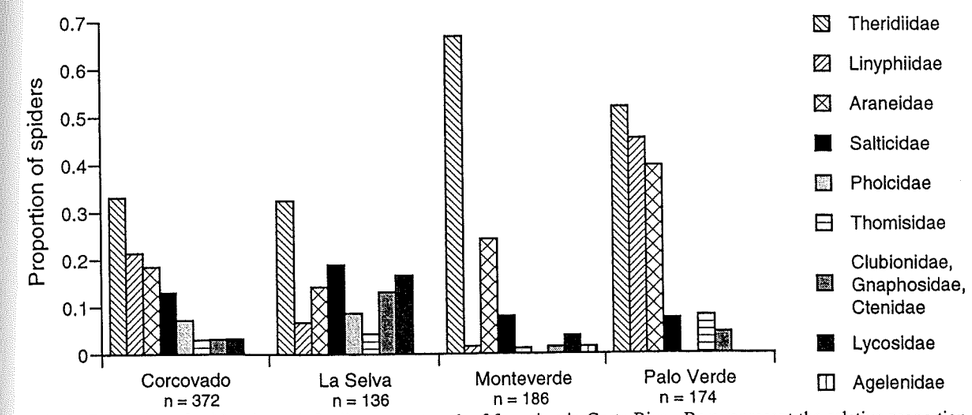

Fig.1. Proportion of spiders in each feeding type at each of four sites in Costa Rica. Bars represent the relative proportion of spiders of each feeding type to the total number of spiders in three 2 x 25 m transects. Hashed bars indicate web weaving groups; solid bars indicate non- web weaving groups.

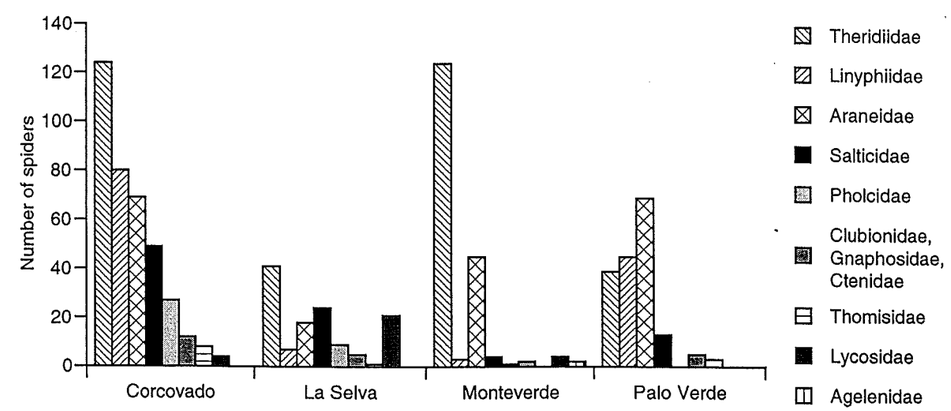

Fig. 2. Number of spiders of each feedingtype at four forest sites in Costa Rica. Bars represent the total number of spiders for three 2 x 25 m transects in primary forest. Hashed bars indicate web weaving groups; solid bars indicate non-web weaving groups.

Among the four sites, Corcovado had a significantly greater spider biomass (Table 1, Fig. 3; Tukey HSD, $P < 0.05$). Because wet sites included both the sites with the greatest and lowest biomass, we did not perform a statistical comparison of biomass between wet and dry sites nor between high and low elevation sites. Both of the more climatically extreme sites, the cool, high elevation site, Monteverde, and the seasonally dry site, Palo Verde, had similar spider biomass totals (approximately half of that at Corcovado, Fig. 3).

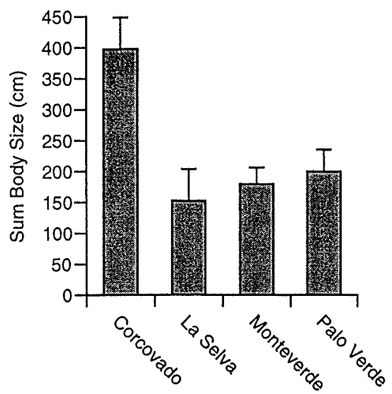

Fig. 3. Sum of body size (a proxy for biomass) of all spiders per transect at four sites in Costa Rica (means of three 2 x 25 m transects ± 1 SE). Sum body size is significantly higher at Corcovado than all other sites (Tukey HSD, $P < 0.05$).

DISCUSSION

As evaluated by our sampling methods, the wet lowland forests of Corcovado and La Selva had a significantly higher diversity of spider families than did the montane cloud forest of Monteverde or the lowland dry forest of Palo Verde (Table 2). For many taxonomic groups, wet lowland tropical forests are known to be the most species rich in Costa Rica (Hartshorn 1983), although the underlying mechanisms for this high diversity are still unclear. Though we hypothesized that increased forest structural complexity would create more niches and therefore support more species, our results suggest that structural complexity may not be the most important determinant of spider diversity. Of course, our measures of structural complexity may not have been adequate to characterize this parameter, so a more comprehensive survey of habitat complexity and its relation to spider abundance and diversity would be useful.

In Palo Verde and Monteverde, almost all spiders found were web weavers, but ground dwelling spiders were more evenly represented at Corcovado and La Selva (Fig. 1). Since we found no evidence for differences in habitat complexity between the sites, we believe that a more species-rich arthropod community in the lowland rainforests may allow more spider feeding types to coexist.

The high abundance and total biomass (as estimated by body size) of spiders found at Corcovado (Table 2, Fig. 3) may be explained by the high primary productivity observed in wet lowland forests (Whittaker 1975), since higher productivity should support more prey items for spiders. We expected to find similar spider abundance and biomass at La Selva and Corcovado, but the heavy rains the night before our La Selva survey could have contributed to the low spider abundance we observed there. A survey under dryer conditions could yield a more accurate comparison.

The abundance of webless, non-burrowing spiders did not increase with the availability of refuge sites, such as woody debris, rock, and leaf litter. This result is contrary to our prediction, since we assumed that such refuges would provide these spiders with more microhabitats to exploit. It is plausible that an increase in the number of refuge sites would impede our ability to observe spiders, although our intensive plots showed no trend of increasing spider density as refuge density increased. It may be that refuge is not a limiting factor in the abundance of webless non-burrowing spiders. The amount of suitable habitat for web building (e.g., stems) did not significantly affect the abundance of web weaving spiders. However, most of the web weaving spiders we found were small ($\leq$ 2.5 mm) Araneidae and Theridiidae, which can construct webs on many types of substrate, such as woody debris and rock.

Although limited to a few sites, these comparisons are consistent with our observations that forest structural complexity may not be an accurate predictor of spider abundance. Our results suggest that other factors, such as system productivity or prey diversity, may be more important in determining spider community compositions in the forests of Costa Rica. A comparison of the abundance and diversity of spider prey between the four sites could reveal a mechanism for differences in spider diversity.

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