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Additive partitioning of spider diversity in a fragmented tropical dry forest (Valle del Cauca, Colombia)

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Abstract. Understanding the variation of diversity patterns requires analysis at multiple spatial scales. In this study we estimated the diversity components (alpha, beta and gamma) of the spider community at El Vínculo Natural Regional Park, using the additive partitioning of diversity (species richness, Shannon's diversity index and Simpson's index) for the first time on this taxon in Colombia. We collected the specimens following a nested sampling design that consisted of two spatial scales. At the local scale, we quantified additive diversity components in 238 sampling units, and at the regional scale in five vegetation types. Total observed regional diversity (γ) was partitioned into its additive components: within sampling units (α_1), among sampling units (β_1) and among vegetation types (β_2). We used the same approach to compare common and infrequent spider species and to compare sampling methods. A total of 1565 adult spiders and 72 identifiable juveniles, including 193 morphospecies from 36 families, was sampled during the study. In all cases (entire community, infrequent species, common species and four different sampling methods) we found that a significant percentage, relative to that of randomization tests, of the diversity measurements used was attributed to beta diversity among vegetation types. The relative contributions of alpha and beta diversity to total observed regional diversity depended on the diversity measurement used. The contribution of beta diversity with respect to alpha diversity was low using Simpson's index (less than 20%), whereas with species richness and Shannon's index the contribution was high (up to 90% and up to 66%, respectively). Our results suggest that beta diversity is the main component of diversity in the natural park. We concluded that the maintenance of a large variety of vegetation types can be an important tool for the conservation of spider richness at the natural park.

Keywords: Diversity components, spatial scale, sampling methods, El Vínculo Natural Regional Park

Traditional measurements of diversity have focused on the search for parameters to characterize it as an emergent property of biotic communities (Moreno 2001). However, since communities are not isolated in a neutral environment, the separation of alpha, beta and gamma components of diversity has been useful for measuring and monitoring the effects of human activities on biotic communities and understanding the changes of diversity related to landscape structure (Moreno 2001; Veech et al. 2002; Gering et al. 2003; Halfter & Moreno 2005).

Tropical dry forest (Bs-T) is one of the most endangered ecosystems in the Neotropics (Janzen 1988). Due to the fertility of its soils it has been the focus for the development of human populations, and it has suffered an intense transformation for the benefit of agriculture and livestock (Álvarez et al. 1998). In Colombia, the tropical dry forest is considered among the three ecosystems most degraded, fragmented and least known, with only 1.5% of its original area remaining. In the case of Valle del Cauca province, Arcila (2007) suggests that the fragmentation of the dry forest has been dramatic, because nearly the entire forest has been replaced with crops and pastures, leaving remnant fragments surrounded by a highly intervened matrix and therefore causing major changes in its physical environment and associated biota. The El Vínculo Natural Regional Park (NRP), is part of the few remaining remnants of Bs-T located in the valley of Cauca river and is the largest fragment in Valle del Cauca province, with an area of about 70 ha (Parra & Adarve 2001; Arcila 2007).

In areas with a high level of habitat loss, such as the Colombian tropical dry forest, conservation strategies focusing on the effective protection of the remaining habitats must take into account how biological diversity is organized across different spatial scales (Gering et al. 2003; Ribeiro et al. 2008). The additive partitioning of diversity is a promising approach that can address this problem. The additive model analytically demonstrated by Lande (1996) considered alpha diversity as the average of within-sample diversities, regardless of whether the diversities are measured by species richness, Simpson's index or Shannon's index. Likewise, beta diversity is an average of diversities among samples within a habitat (Veech et al. 2002). This implies that beta diversity can be measured and defined relative to alpha diversity, allowing direct comparison of its contributions to gamma diversity (Veech et al. 2002; Gering et al. 2003; Crist & Veech 2006). The additivity allows analysis of the proportion of total diversity found in a hierarchy of different scales (Ribeiro et al. 2008). Thus, gamma diversity in a given scale is equal to the alpha diversity at the next scale; for this reason total diversity can be conveniently expressed as $\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3 + \ldots\ldots + \beta n$, where *n* is the number of scales in the study (Veech et al. 2002).

Despite their fundamental roles in natural ecosystems and their potential use in identifying conservation priority areas, arthropods have been largely ignored in conservation studies (Kremen et al. 1993; Cardoso et al. 2008). Some authors (Coddington et al. 1991; Kremen et al. 1993; Toti et al. 2000; Cardoso et al. 2008), argue that it is necessary to understand the diversity patterns in communities of terrestrial arthropods, because they can provide complementary information to that obtained with the traditional groups (vertebrates and vascular plants), due to their high species richness and abundance.

Spiders, which include about 41,000 described species (Platnick 2009), comprise a significant portion of the terrestrial arthropod diversity (Toti et al. 2000), being the top predators of invertebrate food webs in these environments (Foelix 1996). Spiders are abundant and ubiquitous, employ a remarkable diversity of predation strategies, occupy a wide array of spatial and temporal niches, exhibit taxon- and guild-specific responses to environmental changes and have close relationships with the structure of vegetation (Marc et al. 1999; Toti et al. 2000).

The features listed above, make the spiders a very important group for conservation studies. However, like any megadiverse taxon, the disadvantages associated with the sampling of spiders, such as the number of sampling methods, collectors and sampling units, the spatiotemporal scale associated with the sampling, taxonomic identification and details associated with data analysis, make the design of the sampling protocol a very important subject (Coddington et al. 1991; Cardoso et al. 2008). The objective of the present study is to estimate the components of spider diversity (alpha, beta and gamma) in a fragmented tropical dry forest using the additive partitioning of diversity. We collected spider species following a nested sampling design that consisted of two hierarchical scales (sampling units and vegetation types). We evaluated the relative contributions of diversity components to total observed regional diversity. In addition, we used the additive partitioning approach in a comparison of common and infrequent spider species and in a contrast between different sampling methods.

METHODS

Study area and sampling design.—The study was carried out in El Vínculo Natural Regional Park (3°50′23″N, 76°18′07″W), Buga municipality, Valle del Cauca province, southwest Colombia (Fig. 1). The park covers an area of about 70 ha in process of regeneration at different stages. The area belongs to the Instituto para la Investigación y la Preservación del Patrimonio Cultural y Natural del Valle del Cauca, INCIVA. The altitude is between 950–1150 m above sea level, the average annual temperature is 25° C and the average annual precipitation is 1400 mm. According to Holdridge's life zone classification system, the natural park belongs to the tropical dry forest (Bs-T) life zone.

We used a hierarchical sampling design that consisted of two nested spatial scales. The highest level (broadest spatial scale), was represented by five vegetation types based on the plant communities classification by Parra & Adarve (2001). In each vegetation type we collected spiders by means of five sampling methods, grouped into 238 sampling units (finest spatial scale). The vegetation types are as follows:

a) Secondary forest (SF): This forest type covers about 20 ha in the natural park and was probably dedicated to coffee cultivation about 40 yr ago. It is located on hills with moderate slopes. The most common tree species are *Eugenia biflora*, *Myrtus* sp., *Zanthoxylum verrucosa*, *Guazuma ulmifolia* and *Cytharexylum kunthianum*; the understory has an average height of 6 m. The shrub layer has tree saplings of the same species listed above and other species such as *Croton gossypiifolius*, *Euphorbia* sp., *Sapindus saponaria*, and *Amiris pinnata*.

b) Riparian forest (RF): This forest type covers an area of about 15 ha. Formerly it was used for coffee and cacao cultivation, as well as for provision of wood. The most common tree species are *Trichillia pallida*, *Licaria* sp., *Guapira* sp., *Myrtus* sp., *Croton gossypiifolius*, *Acalipha macrostachya*, *Pithecellobium lanceolatum* and *Senna spectabilis*, with average heights of 15 m. The shrub layer contains tree saplings of the same species as listed above.

c) Shrubs (S): This vegetation type covers an area of about 15 ha and exhibits a strong exposure to sunlight and a high water deficit. The vegetation is dominated by *Panicum* sp., which can reach heights of 2 m. In addition, it has other plants between 1.2 and 2 m tall, such as *Acacia farnesiana* and *Bidens pilosa*. This area is periodically cut down by the staff of INCIVA.

d) Grasslands (G): This vegetation type corresponds to the area bordering the southern edge of the park that belongs to the farm "La Campiña", an area mainly devoted to livestock breeding, The area has some individuals of *Acacia farnesiana* that are pruned regularly. Floristically, these grasslands are composed of both native and introduced grass species and a few scattered shrubs.

e) Highly disturbed area (HA): This vegetation type consists of about one hectare in the southwestern extremity of the natural park. INCIVA constantly intervenes in this area, which is also open to the public. The most common tree species are *Guazuma ulmifolia*, *Senna spectabilis*, *Achatocarpus nigricans* and *Bambusa guadua*. This area is the closest to Panamericana highway, which borders the park on the west (Fig. 1).

Sampling methods.—Spiders were collected between August and December 2008 in three field trips carried out by a single collector (first author). Both day (07:00–17:00 h) and night (20:00–02:00 h) samples were collected. Specimens were collected with pitfall traps, Berlese funnel litter extraction and semi-quantitative methods. Sampling followed a balanced design as closely as possible, with the same effort applied to sampling schedule, sampling methods and vegetation types (Table 1). However, Berlese funnel litter extraction was not used in the shrubs and grasslands, where there was no defined litter layer, and beating was not used in shrubs due to the absence of a defined understory layer.

An hour of effective fieldwork was used as a sampling unit; this time included the logistics of handling samples in the collection sites and excluded interruptions. The main objective of this sampling design was to obtain a representative sample of each vegetation type to allow an objective comparison of spider assemblage composition and a better understanding of spider diversity organization across different spatial scales.

Pitfall traps (PT)*:* Traps consisted of plastic cups of 8 cm diameter and 10 cm depth filled with preservative (70% water, 29% ethanol and 1% detergent) and covered with a circular plastic plate placed about 10 cm above the ground. Thirty-two pitfall traps were laid along random transects in each vegetation type. Traps were left in the field for five days. A

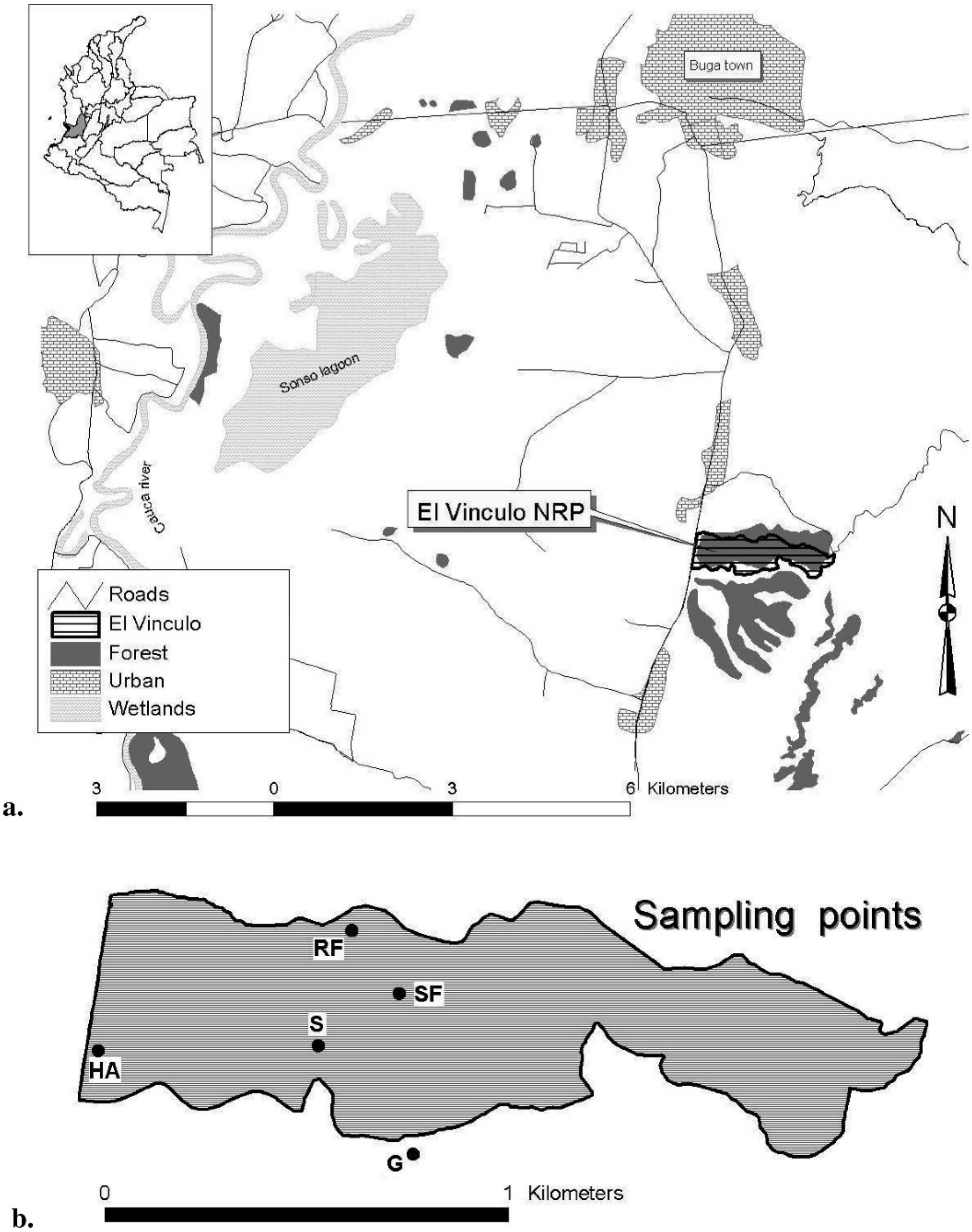

Figure 1.—Map of El Vínculo NRP, Colombia, showing the isolation of this forest fragment in a surrounding matrix composed mainly of sugar cane and cattle grasslands. a. Detailed map showing the location and relative distances of vegetation types. b. HA = Highly disturbed area; S = Shrubs; SF = Secondary forest; G = Grasslands; RF = Riparian forest.

group of four pooled traps (arranged in a square with an area of 1 m^2) separated by 5 m constituted one sampling unit.

Berlese funnel litter extraction (BF)*:* Samples of litter (5000 cm^3 each) were randomly collected in the vegetation types RF, SF, and HA for subsequent processing in Berlese funnels at the laboratory of Entomology at Universidad del Valle. Thirty samples were collected, each used as a sampling unit for the data analysis.

Semi-quantitative sampling: Three methods were included: a) Aerial hand collection, "looking up" according to Coddington et al. (1996), involved searching leaves, branches, tree trunks, and spaces in between, from knee height (50 cm) up to maximum overhead arm's reach (2 m). b) Ground hand collection, "looking down" according to Coddington et al. (1996), involved searching on hands and knees, exploring the leaf litter, logs, rocks, and plants that are below knee level (50 cm). The hand collection was performed with a dusting device for detecting inconspicuous webs. c) A beating event consisted of hitting a randomly chosen vegetation unit (shrub, tree or tree branch etc.) with a 1-m-long stick and catching the falling spiders on a tray (0.5 m^2) held horizontally below the vegetation until no more spiders fell down. In this study, 25 events constituted one sampling unit (Coddington et al. 1991).

Table 1.—Number of sampling units for the vegetation type, the sampling method and the time of day. RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs; B = Beating; AHC= Aerial hand collection; GHC = Ground hand collection; BF = Berlese funnel litter extraction; PT = Pitfall traps.

	Vegetation types										
	RF		SF		HA		G		S		
Method	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Total
B	6	6	6	6	6	6	6	6	0	0	48
AHC	6	6	6	6	6	6	6	6	6	6	60
GHC	6	6	6	6	6	6	6	6	6	6	60
BF	10		10		10		0		0		30
PT	8		8		8		8		8		40
Total	54		54		54		44		32		238

Processing samples.—We sorted spider specimens and identified them to family and then separated them into adults and juveniles. Each adult specimen was photographed and identified to species using existing identification keys wherever possible. Juvenile specimens were discarded from the data analysis because their identification to species level is difficult and ambiguous in many cases. However, because of careful observations in the field, juveniles of the following species were considered to be reliably identifiable and were included in the analyses: *Mimetus* sp. 1 (Mimetidae), *Thaumasia argenteonotata* Simon 1898 (Pisauridae), *Episinus* sp. 1 (Theridiidae), *Ypypuera* sp. 1 (Hersiliidae), *Micrathena horrida* Taczanowski 1873 (Araneidae), *Tibellus* sp. (Philodromidae), *Senoculus canaliculatus* F.O. Pickard-Cambridge 1902 (Senoculidae), *Dolichognatha* sp. (Tetragnathidae) and *Cybaeus* sp. (Cybaeidae).

The unidentified species were recorded as morphospecies, after a detailed analysis of male and female genitalia using the techniques of expansion of the male palpi and the clarification of the female epigynium placed in a 10% KOH solution. The vouchers are deposited in the arachnological collection of Museo de Entomología de la Universidad del Valle (MEUV), Cali, Colombia, and in the arachnological collection of Museo de Ciencias Naturales Federico Carlos Lehmann Valencia, Cali, Colombia (IMCN). In this study we use the term morphospecies for consistency with the previous investigations; however, as Krell (2004) says, the use of this term in the context of the analysis of diversity is inadequate.

Data analysis.—*General community patterns:* We estimated species richness for each vegetation type and sampling method as well as for the regional data set using the nonparametric estimators Chao 1, ACE, Chao 2, Jackknife 1, Jackknife 2 and ICE. We visualized differences of alpha diversity through the inspection of the 95% confidence intervals of both sample and individual-based rarefaction curves (Gotelli & Colwell 2001). Sample-based rarefaction curves were calculated using EstimateS© 8.0 (Colwell 2008), while individual-based curves were calculated using EcoSim© 7.0 (Gotelli & Entsminger 2008). The x-axis of both curves is scaled to represent the number of individuals (not the number of samples), as this process is necessary to evaluate patterns of richness at comparable levels of sampling effort when data sets are likely to differ systematically in the mean number of individuals per sample (Gotelli & Colwell 2001). In addition to assessing the performance of the sampling protocol, we calculate the completeness of the inventory for each data partition (by sampling method and vegetation type) and the natural park as a whole using the Chao 1 estimator, completeness being the ratio between observed and estimated richness (Sørensen et al. 2002; Scharff et al. 2003).

To examine the similarity of spider assemblages between vegetation types, we used hierarchical cluster analysis with the Jaccard index of similarity. Due to the differences in the sampling effort between vegetation types this index of similarity can be biased; however, this bias can be reduced if almost complete inventories are reached in each vegetation type (Chao et al. 2005). Moreover, we tested spatial autocorrelation in species composition data using the Mantel test to relate a matrix of similarity between vegetation types based on the Jaccard index of similarity to a matrix of geographic distance. This spatial analysis was carried out using XLStat© 9.0 (Addinsoft 2008).

Additive partitioning of diversity: Lande (1996) demonstrated that any metric can be partitioned into its components provided that it exhibits strict concavity, which means that the overall value of that metric for a pool set of communities equals or exceeds the average diversity within communities. Species richness, Simpson's index and Shannon's index are all strictly concave. The richness takes into account only the number of species, while the indices consider both the number of species and abundance. In this study, we evaluated the additive partitioning of the whole community and for each method using these three measures of diversity. The program PARTITION© 2.0 was used (Veech & Crist 2007) to additively decompose the total observed regional diversity (γ) into its average components within (α_2) and among (β_2) vegetation types. To investigate diversity patterns at the local scale of the hierarchical sampling design, we decomposed the average within-vegetation type (α_2) into the within- (α_1) and among-sampling unit (β_1) components, $\alpha_2 = \alpha_1 + \beta_1$. Therefore, the overall spider diversity in our study can be described by the following formula: $\gamma = \alpha_1 + \beta_1 + \beta_2$. The observed partitioning patterns were compared with a null distribution generated from a program of 10,000 individual-based randomizations (Crist et al. 2003). In addition, we applied separate analyses to compare common (abundance greater than 0.3% of the total identifiable specimens) and infrequent (abundance less than 0.12% of the total identifiable specimens) spider species and to analyze the effect of spatial scale on the diversity of these species. These cutoffs were defined considering the level of

Table 2.—Composition of the spider fauna sampled in five vegetation types at NRP El Vínculo. UJ = Unidentifiable juveniles; IJ = Identifiable juveniles.

Family	Total specimens	UJ	IJ	Adults	Morpho-species
Theridiidae	1474	1110	5	359	46
Araneidae	1125	939	1	185	28
Linyphiidae	362	141	0	221	14
Salticidae	349	234	0	115	22
Lycosidae	307	151	0	156	8
Tetragnathidae	235	197	10	28	4
Thomisidae	178	131	0	47	11
Uloboridae	160	101	0	59	5
Anyphaenidae	142	104	0	38	4
Ctenidae	129	114	0	15	6
Oxyopidae	102	76	0	26	5
Mimetidae	78	25	17	36	1
Sparassidae	68	41	0	27	2
Hersiliidae	62	0	15	47	1
Pholcidae	61	49	0	12	2
Ochyroceratidae	42	0	4	38	1
Miturgidae	36	14	0	22	2
Oonopidae	33	13	0	20	4
Theridiosomatidae	28	21	0	7	3
Dipluridae	25	9	0	16	1
Scytodidae	25	20	0	5	1
Hahniidae	24	0	0	24	1
Dictynidae	17	3	0	14	4
Corinnidae	14	1	0	13	4
Pisauridae	13	0	5	8	1
Senoculidae	13	0	10	3	1
Cybaeidae	10	0	4	6	1
Clubionidae	7	4	0	3	1
Mysmenidae	5	1	0	4	2
Deinopidae	3	0	0	3	1
Nephilidae	3	0	0	3	1
Theraphosidae	3	2	0	1	1
Gnaphosidae	2	0	0	2	1
Zodariidae	2	1	0	1	1
Philodromidae	1	0	1	0	1
Titanoecidae	1	0	0	1	1
Total	5139	3502	72	1565	193

rarity that quantifies the non-parametric, abundance-based estimators: number of species represented by only one or two individuals in the entire data set (Colwell & Coddignton 1994; Toti et al. 2000). Due to the different nature of the sampling methods used, we also analyzed the effect of spatial scale on spider diversity according to each sampling method.

RESULTS

General community patterns.—We captured 5139 spiders, of which 3502 (68.1%) were unidentified juveniles, 1565 (30.5%) were adults and 72 (1.4%) were identifiable juveniles (Table 2, Appendix 1). The most abundant and diverse families were Theridiidae and Araneidae, which contributed 50.57% of all captures and 74 of the 193 morphospecies collected (Table 2). Theridiidae was also the family with the largest number of identifiable specimens (364) and morphospecies (46). The second dominant group of families comprised the Linyphiidae, Salticidae, Lycosidae, Tetragnathidae, Thomisidae, Uloboridae, Anyphaenidae and Ctenidae, which collectively contributed 35.82% of all captures. This group includes 73 of the 193 morphospecies collected in the area (Table 2). All families were found in the five vegetation types. All other families contributed less than 2% of all captures each and contributed 46 morphospecies. Four families were represented only by singletons or doubletons (Table 2).

The dominant species (in terms of abundance) were *Ypypuera* sp. 1 (Hersiliidae), *Novafrontina uncata* F.O. Pickard-Cambridge 1902 (Linyphiidae), *Trochosa* sp. 1 (Lycosidae), *Mimetus* sp. 1 (Mimetidae), *Ochyrocera* sp. 1 (Ochyroceratidae), Salticidae sp. 5 (Salticidae), *Faiditus caudatus* Taczanowski 1874, *Episinus* sp. 1 (Theridiidae) and *Tidarren haemorrhoidale* Bertkau 1880 (Theridiidae), which accounted for 29.1% of all identifiable specimens collected in the natural park.

The non-parametric estimators used (Table 3) indicate variation in the estimated number of morphospecies between 41.68 (95% lower confidence limit of the Chao1 estimator at Shrubs) and 110.49 (95% upper confidence limit of the Chao1 estimator at secondary forest). More than 49% of the morphospecies were singletons or doubletons in each vegetation type (Table 3). The species accumulation curve does not reach the asymptote by the end of the sampling process (Fig. 2). However, curves representing the mean values of the non-parametric estimators approached the asymptote very closely. Based on estimated species richness our inventory was almost complete at the regional scale and in each vegetation type (Table 3). Both curves, based on samples and individuals (Fig. 3), indicate that there is no difference in the species richness of the five vegetation types.

Aerial hand collecting captured most species (Table 4). In general, all sampling methods presented high inventory completeness (more than 78% in all cases), despite the differences in sampling effort, and each method sampled unique species not found by the other methods (Table 4).

The cluster analysis used shows strong differences in community composition among vegetation types (Fig. 4). In general, there was a higher degree of similarity between areas without a defined canopy layer (grasslands and shrubs) than areas with a defined one. Due to the great number of rare species in each vegetation type and its possible influence in the similarity values (Table 3), we explored the effect of these species in the index value, removing all singleton species. In general the index values still indicate a large (although reduced) difference in species composition (Table 5). Furthermore, Mantel statistics supported the null hypothesis that no significant spatial autocorrelation was present between spider communities and the distance matrix for vegetation types ($r = -0.643$, $P = 0.092$).

Additive partitioning of diversity.—The additive partitioning showed in all cases that the highest beta component (β_2) in models was always greater than expected by chance (Table 6), whereas the β_1 component was always lower than expected, except for the Simpson's index of ground hand-collecting (Table 6). The contribution of the beta component to the regional diversity (γ) was in all cases more than 90% for the partitioning of species richness and more than 66% for that of the Shannon's index (Fig. 5). On the other hand, the contribution of the alpha component to the partitioning of Simpson's index was higher than 78% in all cases (Fig. 5). We

Table 3.—Summary data for the overall captures of this study. RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs.

	RF	SF	HA	G	S	Total
Morphospecies	69	71	79	51	42	193
Total specimens	1570	958	1417	785	409	5139
Identifiable specimens	382	402	510	207	136	1637
Sampling units	54	54	54	44	32	238
Identifiable specimens / sampling unit	7.07	7.44	9.44	4.70	4.25	6.88
Morphospecies / sampling unit	1.27	1.31	1.46	1.16	1.31	0.81
Singletons	9	26	21	17	6	40
Doubletons	26	13	20	8	23	36
Uniques	20	28	26	19	11	56
Duplicates	21	16	28	10	22	38
Estimates						
ACE	74.37	100.13	95.09	66.3	44.65	221.07
ICE	85.88	104.46	107.44	66.16	51.26	240.32
Chao 1 ± SD	70.56 ± 1.65	97 ± 13.49	90.03 ± 6.34	69.06 ± 11.65	42.78 ± 1.1	215.22 ± 9.24
Chao 2 ± SD	78.52 ± 5.6	95.5 ± 12.16	91.07 ± 6.3	69.05 ± 10.92	44.75 ± 2.42	234.26 ± 14.41
Jackknife 1 ± SD	88.55 ± 5.32	98.48 ± 5.9	104.41 ± 5.65	69.57 ± 4.72	52.66 ± 2.99	248.74 ± 8.32
Jackknife 2	88.06	110.33	103.12	78.38	43.01	266.75
Inventory completeness (%)	97.78	73.20	87.75	73.85	98.18	89.67

do not employ the additive partitioning for Berlese funnel litter extraction due to its low capture rate (Table 4).

DISCUSSION

The additive partitioning of species richness and Shannon's index suggest that beta diversity was the principal component of regional diversity in all cases (total community, infrequent and common species). Likewise, our results suggest that this pattern remains constant in the samples obtained with different sampling methods.

Our finding that the broad-scale beta component of diversity was greater than expected supports the idea that vegetation types structure the composition of spiders in the El Vínculo NRP. This is supported by the cluster analysis, which identified strong differences in community composition between vegetation types. The contribution of each vegetation type to the regional diversity in terms of unique species highlights the importance of evaluating different elements in the natural park for the analysis of diversity patterns. In the case of spider fauna, if the sampling had been focused on the secondary forest, we might have reached an asymptote of accumulation curves (due to the reduction of the area covered by the sampling), but at the same time, we had extremely undervalued species richness for the whole park.

The richness of both common and infrequent species was enhanced (i.e., greater than expected) only at the highest level (β_2). These results contrast with those obtained by Gering et al. (2003) for beetle communities, who reported this trend only

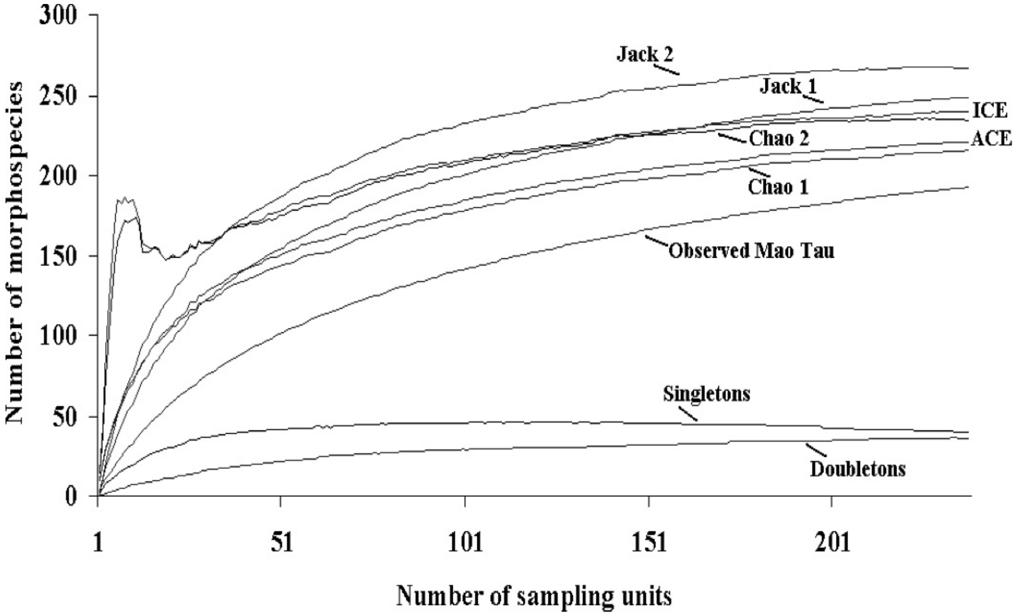

Figure 2.—Randomized accumulation curves for observed species richness, singletons, doubletons, uniques, duplicates and richness estimators for all data. Curves were generated from 100 randomizations.

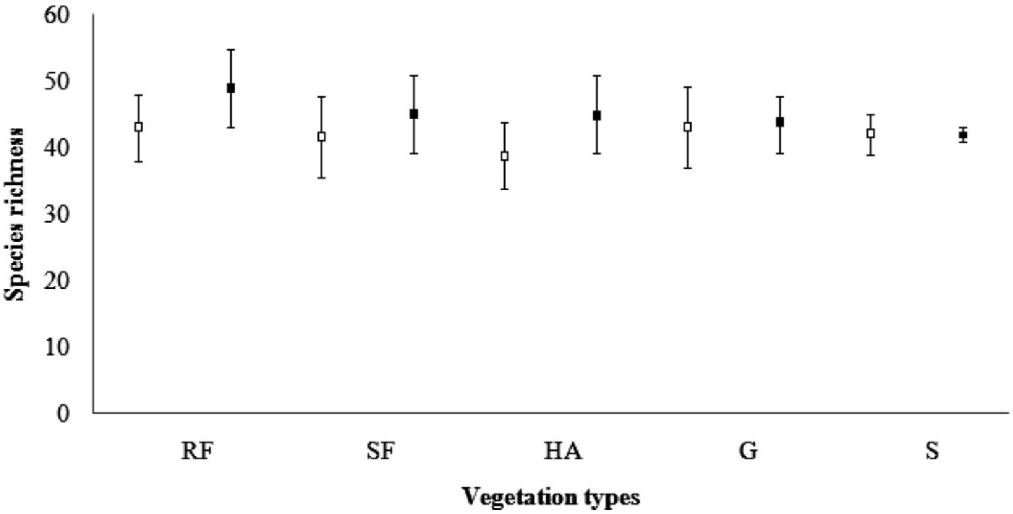

Figure 3.—Comparison of species richness values (± 95% confidence intervals) at the lowest number of individuals (136), derived from sample-based rarefaction curves (open squares) and individual-based rarefaction curves (filled squares). RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs.

for the infrequent species. Our results show that the partitioning pattern for the entire community mirrors those of infrequent and common species. This suggests that no group (infrequent or common species) is driving the patterns of the entire community in the El Vínculo NRP.

Beta diversity at each scale can be seen as the result of environmental heterogeneity in space and time, in combination with niche differences among species (Loreau 2000). Movements between spatial units, such as dispersal or migration, can lead to an increase in alpha diversity and therefore a decrease of beta diversity, due to a homogenizing effect (Loreau 2000). However, the spatial analysis conducted in this study demonstrated that spider communities in the natural park were not spatially autocorrelated, indicating that spatial heterogeneity in diversity among vegetation types (β_2) was not lowered due to a homogenizing effect. This is consistent with the results obtained by Klimek et al. (2008) with plant communities.

The partitioning of Simpson's index showed a contrasting pattern to that obtained with Shannon's index and species richness, since the alpha component was the largest contributor to gamma diversity (Fig. 5). These results are consistent with the results obtained by Wagner et al. (2000) and Chandy et al. (2006) for plants, Gering et al. (2003) for beetles, Stendera & Johnson (2005) for aquatic invertebrates and Summerville et al. (2006) for Lepidoptera. Thus, the partitioning suggests that the smaller scale of analysis (sampling units) is dominated by common species, which is directly related to the sensitivity of the Simpson's index to the abundance of these species. This demonstrates the importance of using different indices of diversity that consider diverse properties of the communities to understand in a more

Table 4.—Species richness and abundance per method. AHC= Aerial hand collection; B = Beating; GHC = Ground hand collection; BF = Berlese funnel litter extraction; PT = Pitfall traps.

	AHC	GHC	B	BF	PT
Morphospecies	102	101	77	1	29
Unique morphospecies	33	31	20	1	15
Total specimens	2125	1788	801	18	407
Identifiable specimens	571	576	241	10	239
Sampling units	60	60	48	30	40
Identifiable specimens / sampling unit	9.52	9.60	5.02	0.33	5.98
Morphospecies / sampling unit	1.70	1.68	1.60	0.03	0.73
Singletons	27	33	30	0	8
Doubletons	21	21	21	0	9
Estimates					
ACE	123.97	135.25	110.66	1	35.27
ICE	139.72	141.21	126	1	35.91
Chao 1 ± SD	119.36 ± 8.74	126.93 ± 11.81	98.43 ± 10.22	1 ± 0.01	32.56 ± 3.36
Chao 2 ± SD	142.11 ± 17.29	135.78 ± 14.43	115.03 ± 16.57	1 ± 0.13	32.56 ± 3.36
Jackknife 1 ± SD	139.37 ± 6.87	140.33 ± 8.02	113.23 ± 7.03	1 ± 0.01	36.8 ± 2.86
Jackknife 2	158.99	157.14	131.8	1	36.07
Inventory completeness (%)	85.46	79.57	78.23	100	89.07

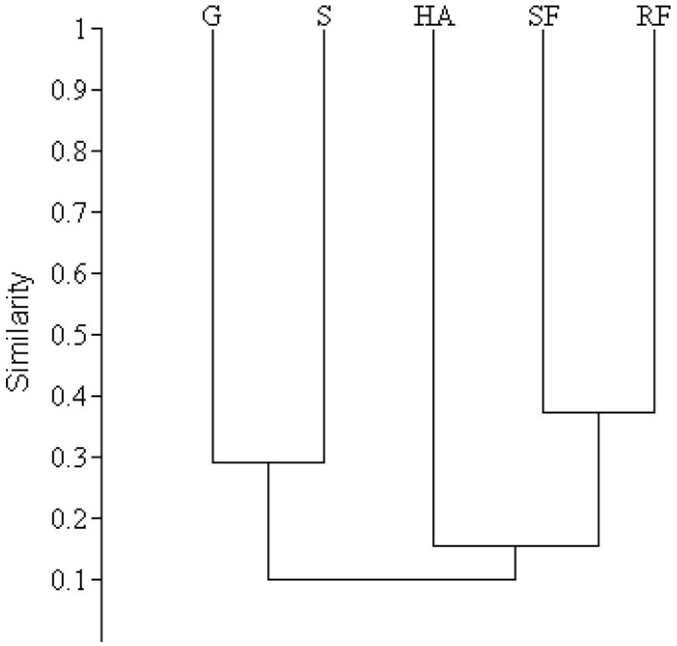

Figure 4.—Dendrogram showing clustering of five vegetation types at EL Vínculo NRP, based on Jaccard index of similarity. RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs.

Table 6.—Significance values for tests of actual diversity estimates from additive partitioning against null estimates from the PARTITION© 2.0 program. All values determined at the 0.05 level. + = significantly larger; – = significantly smaller; AHC = Aerial hand collection; B = Beating; GHC = Ground hand collection; PT = Pitfall traps; ns = not significant.

Group	Level	Richness	Simpson	Shannon
Entire community	β_2	+	+	+
	β_1	−	−	−
	α_1	−	+	−
Infrequent species	β_2	+	+	+
	β_1	−	−	−
	α_1	+	+	+
Common species	β_2	+	+	+
	β_1	−	−	−
	α_1	−	+	−
AHC	β_2	+	+	+
	β_1	−	−	−
	α_1	−	+	−
B	β_2	+	+	+
	β_1	−	−	−
	α_1	−	ns	−
GHC	β_2	+	+	+
	β_1	−	+	−
	α_1	−	−	−
PT	β_2	+	+	+
	β_1	−	−	−
	α_1	−	ns	−

objective way the contributions of the alpha and beta components to regional diversity (Gering et al. 2003).

Veech (2005) suggests that intraspecific aggregation is a common feature in different communities of arthropods. He states that this property should limit the mean alpha diversity of the communities to a level less than what it would be if individuals were randomly distributed among the communities, as a result enhancing beta diversity. This could be one of the explanations for the pattern observed in this investigation. However, we require a more detailed knowledge of the natural history of various species to test this hypothesis, as well as biotic and abiotic factors influencing the aggregation of conspecifics (Veech 2005).

It is important to recognize that differences in the area of the vegetation types did not involve changes in the richness of communities (Fig. 3). This is consistent with the findings of Whitmore (2000), who suggests that many other factors can influence the patterns of diversity in communities of spiders. Additionally, it is important to note that despite the high degree of isolation of the forests evaluated with respect to other fragments of Bs-T at Valle del Cauca province (Arcila 2007), and its small area compared to the highly intervened matrix, the composition of spider assemblages in these vegetation types is very different (Fig. 4), a pattern that seems to have no relation to rare species (Table 5), demonstrating the importance of protecting these areas for the conservation of the spider richness in the natural park.

Table 5.—Values of the Jaccard index of similarity for the five vegetation types. Index values in parentheses were generated after removing all singletons. RF = Riparian forest; SF = Secondary forest; HA = Highly disturbed area; G = Grasslands; S = Shrubs.

Vegetation type	SF	HA	G	S
RF	0.372 (0.452)	0.165 (0.194)	0.043 (0.049)	0.057 (0.061)
SF		0.145 (0.183)	0.079 (0.097)	0.118 (0.138)
HA			0.16 (0.198)	0.141 (0.165)
G				0.291 (0.328)

As expected, and in accordance with all previous studies (Coddington et al. 1991, 1996; Sørensen et al. 2002; Scharff et al. 2003; Cardoso et al. 2008, 2009), sampling methods directly influence the results. Here all methods, including the least productive, sampled unique species, which justifies the use of the broadest possible spectrum of collecting methods in spider inventories that aim to be complete (Scharff et al. 2003). We attribute the low productivity of the Berlese funnel litter extraction (Table 4) to the small amount of litter processed in each sampling unit. We believe that a larger quantity of litter would give better results. It is interesting to note that despite the different nature of the sampling methods used, the additive partitioning pattern for each one was very similar (Table 6), which supports the idea that beta diversity among vegetation types is the main component of spider diversity in the natural park, regardless of any data partitioning, at least at the level of sampling methods.

Many factors have been shown to influence the structure and composition of spider communities at multiple spatial scales, including intra- and interspecific competition, predation, spatial heterogeneity, environmental stability, availability of prey and productivity (Turnbull 1973; Uetz 1979; Greenstone 1984; Riechert & Gilliespie 1986; Marc et al. 1999; Shochat et al. 2004; Pinkus-Rendón et al. 2006). However, understanding the impact of these factors on diversity patterns in spider communities of the El Vínculo NRP requires much more detailed analysis in future research. The additive partitioning performed in this study suggests that factors related to a higher scale of analysis (vegetation types) such as topography, dominant tree species, land-use patterns and habitat heterogeneity could involve strong differences in the composition of spider assemblages but not in species richness. Additionally, our results indicate that the maintenance of a large variety of vegetation types, along with heterogeneous abiotic environmental conditions, can be an important tool for the conservation of spider richness due to the enhancement of beta diversity among vegetation types.

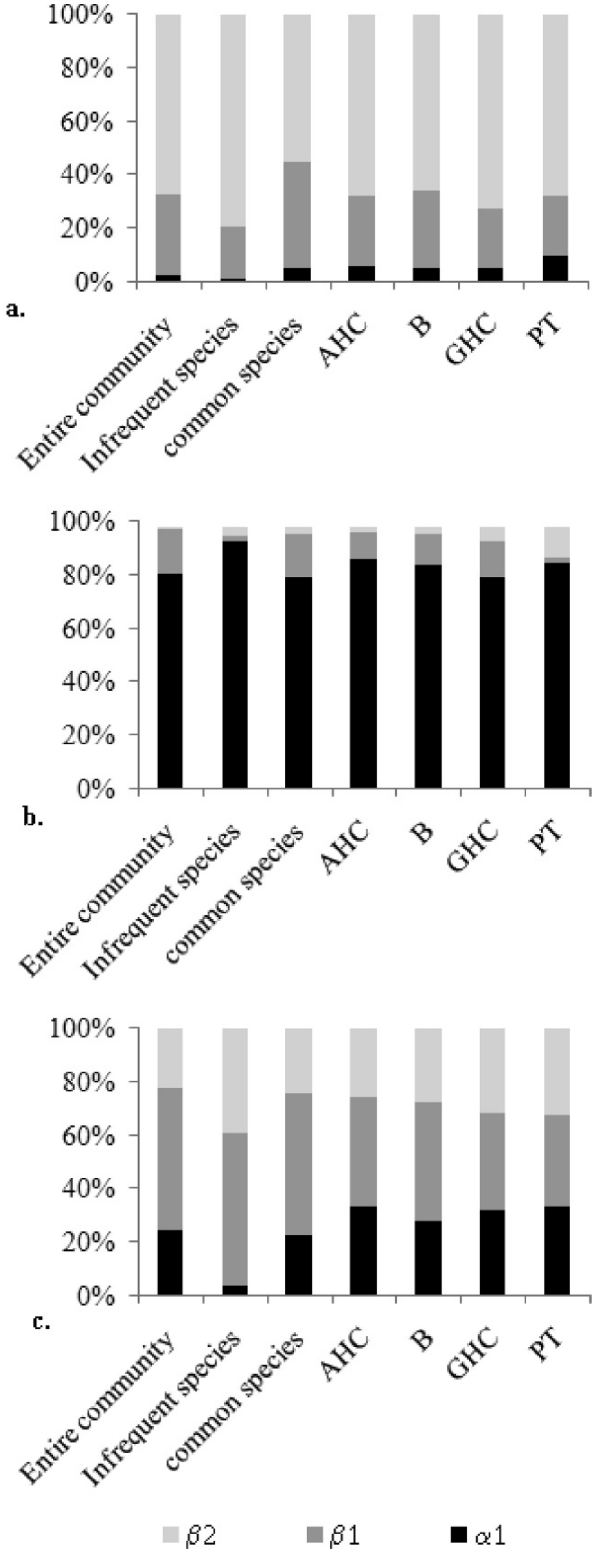

Figure 5.—Additive partitioning of (a) species richness, (b) Simpson's index, and (c) Shannon's index at NRP El Vínculo, following a hierarchical sampling design of two spatial scales: sampling units and vegetation types. AHC = Aerial hand collection; B = Beating; GHC = Ground hand collection; PT = Pitfall traps.

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Appendix 1.—Species, morphospecies and number of identifiable spiders collected in Natural Regional Park El Vínculo, Colombia. RF = Riparian forest; SF = Secondary forest; G = Grasslands; S = Shrubs; HA = Highly disturbed area.

	Vegetation types					
Taxon	RF	SF	G	S	HA	Total
Anyphaenidae						
Wulfila sp. 1	3	12	0	0	2	17
Anyphaenidae sp. 1	0	0	2	0	14	16
Anyphaenidae sp. 2	0	0	1	0	0	1
Anyphaenidae sp. 3	0	0	0	2	2	4
Araneidae						
Acacesia hamata Hentz 1847	0	0	11	0	3	14
Acacesia tenella L. Koch 1871	1	1	1	0	0	3
Alpaida leucogramma White 1841	0	0	19	0	0	19
Alpaida truncata Keyserling 1865	1	0	0	0	0	1
Argiope argentata Fabricius 1775	0	1	6	4	3	14
Cyclosa sp. 1	0	1	0	0	7	8
Cyclosa sp. 2	0	0	1	0	0	1
Cyrtophora citricola Forsskål 1775	0	0	3	0	0	3
Edricus spiniger O. Pickard-Cambridge 1890	2	3	0	0	0	5
Eriophora ravilla C.L. Koch 1844	2	0	2	0	4	8
Eriophora sp. 1	0	0	0	2	0	2
Eustala fuscovittata Keyserling 1864	0	0	4	0	4	8
Eustala sp. 1	0	0	0	0	1	1
Eustala sp. 2	0	0	0	2	0	2
Eustala sp. 3	0	0	3	0	0	3
Gasteracantha cancriformis Linnaeus 1758	0	0	4	3	15	22
Gea heptagon Hentz 1850	0	0	8	2	0	10
Mangora melanocephala Taczanowski 1874	11	0	0	0	19	30
Mastophora dizzydeani Eberhard 1981	0	0	0	0	1	1
Metazygia octama Levi 1995	1	0	0	0	0	1
Metazygia sp. 1	0	0	0	0	2	2
Metepeira sp. 1	0	0	5	0	0	5
Micrathena horrida Taczanowski 1873	3	1	0	0	3	7
Pronous pance Levi 1995	0	1	0	0	0	1
Scoloderus cordatus Taczanowski 1879	0	1	0	0	0	1
Verrucosa sp. 1	0	0	4	0	6	10
Wagneriana undecimtuberculata Keyserling 1865	0	0	0	0	1	1
Witica crassicaudus Keyserling 1865	3	0	0	0	0	3
Clubionidae						
Clubionidae sp. 1	0	3	0	0	0	3
Corinnidae						
Castianeira sp. 1	0	0	0	1	0	1
Mazax sp. 1	0	0	6	2	0	8
Mazax sp. 2	0	0	1	0	2	3
Trachelas sp. 1	0	0	0	0	1	1
Ctenidae						
Ctenus sp. 1	0	1	0	0	0	1
Ctenus sp. 2	0	1	0	0	0	1
Ctenidae sp. 1	2	1	0	0	0	3
Ctenidae sp. 2	0	4	0	1	0	5
Ctenidae sp. 3	3	1	0	0	0	4
Ctenidae sp. 4	0	1	0	0	0	1
Cybaeidae						
Cybaeus sp. 1	0	10	0	0	0	10
Deinopidae						
Deinopis sp. 1	0	0	1	1	1	3
Dictynidae						
Lathys sp.1	2	2	0	0	2	6
Lathys sp.2	0	1	0	1	0	2
Dictynidae sp. 1	0	2	1	0	0	3
Dictynidae sp. 2	1	2	0	0	0	3

Appendix 1.—Continued.

	Vegetation types					
Taxon	RF	SF	G	S	HA	Total
Dipluridae						
Ischnothele caudata Ausserer 1875	0	0	0	0	16	16
Gnaphosidae						
Gnaphosidae sp. 1	0	0	1	1	0	2
Hahniidae						
Hahniinae sp. 1	0	0	15	6	3	24
Hersiliidae						
Ypypuera sp. 1	34	28	0	0	0	62
Linyphiidae						
Dubiaranea margaritata Millidge 1991	0	0	0	0	23	23
Erigoninae sp. 1	20	5	4	6	20	55
Erigoninae sp. 2	1	4	0	0	0	5
Erigoninae sp. 3	0	0	0	0	23	23
Erigoninae sp. 4	2	0	0	0	0	2
Erigoninae sp. 5	2	0	0	0	2	4
Erigoninae sp. 6	0	1	0	0	0	1
Novafrontina uncata F.O. Pickard-Cambridge 1902	38	0	0	0	46	84
Linyphiinae sp. 1	2	9	0	0	0	11
Linyphiinae sp. 2	4	0	0	0	0	4
Linyphiinae sp. 3	0	0	0	3	0	3
Linyphiinae sp. 4	0	0	0	2	0	2
Linyphiinae sp. 5	0	0	0	2	0	2
Linyphiidae sp. 1	2	0	0	0	0	2
Lycosidae						
Aglaoctenus sp. 1	5	16	0	0	0	21
Allocosa sp. 1	15	0	0	0	2	17
Hogna sp. 1	0	0	9	2	0	11
Hogna sp. 2	0	0	2	0	0	2
Hogna sp. 3	0	0	13	2	0	15
Hogna sp. 4	0	0	1	2	0	3
Hogna sp. 5	0	0	4	2	0	6
Trochosa sp. 1	0	1	0	4	76	81
Mimetidae						
Mimetus sp. 1	5	48	0	0	0	53
Miturgidae						
Cheiracanthium inclusum Hentz 1847	0	0	4	3	0	7
Teminius hirsutus Petrunkevitch 1925	0	0	7	8	0	15
Mysmenidae						
Calodipoena sp.	0	0	0	0	1	1
Microdipoena guttata Banks 1895	0	1	1	1	0	3
Nephilidae						
Nephila clavipes Linnaeus 1767	0	0	0	0	3	3
Ochyroceratidae						
Ochyrocera sp. 1	23	19	0	0	0	42
Oonopidae						
Ischnothyreus sp. 1	0	0	10	0	1	11
Heteroonops sp. 1	0	0	3	2	0	5
Oonops sp. 1	0	1	0	0	0	1
Orchestina sp. 1	0	0	2	0	1	3
Oxyopidae						
Hamatilawa sp. 1	2	5	0	0	0	7
Oxyopes salticus Hentz 1845	0	0	4	0	2	6
Oxyopes sp. 1	0	6	0	0	0	6
Oxyopes sp. 2	0	1	0	0	0	1
Peucetia rubrolineata Keyserling 1877	0	0	0	3	3	6
Philodromidae						
Tibellus sp. 1	0	0	0	0	1	1

Appendix 1.—Continued.

Taxon	Vegetation types					
	RF	SF	G	S	HA	Total
Pholcidae						
Metagonia sp. 1	6	2	0	0	0	8
Waunana sp. 1	4	0	0	0	0	4
Pisauridae						
Thaumasia argenteonotata Simon 1898	0	0	0	3	10	13
Salticidae						
Beata sp. 1	0	0	0	0	2	2
Lyssomanes bitaeniatus Peckham & Wheeler 1889	7	12	0	0	0	19
Lyssomanes jemineus Peckham & Wheeler 1889	0	0	0	0	3	3
Lyssomanes sp. 1	0	0	0	0	1	1
Lyssomanes sp. 2	0	0	0	0	1	1
Mexigonus sp. 1	0	2	0	0	0	2
Thiodina sp. 1	3	4	0	0	8	15
Zygoballus sp. 1	0	0	1	0	0	1
Salticidae sp. 1	0	0	2	0	0	2
Salticidae sp. 2	0	0	0	2	0	2
Salticidae sp. 3	0	0	0	0	1	1
Salticidae sp. 4	0	3	0	0	0	3
Salticidae sp. 5	4	12	0	12	11	39
Salticidae sp. 6	4	2	0	0	0	6
Salticidae sp. 7	2	0	0	0	0	2
Salticidae sp. 8	1	0	0	0	0	1
Salticidae sp. 9	0	0	0	0	2	2
Salticidae sp. 10	2	0	0	0	0	2
Salticidae sp. 11	1	0	0	0	0	1
Salticidae sp. 12	2	0	0	0	0	2
Salticidae sp. 13	6	0	0	0	0	6
Salticidae sp. 14	0	0	0	0	2	2
Scytodidae						
Scytodes sp. 1	0	0	0	0	5	5
Senoculidae						
Secoculus canaliculatus F.O. Pickard-Cambridge 1900	8	2	0	0	3	13
Sparassidae						
Sparassidae sp. 1	0	0	0	24	2	26
Sparassidae sp. 2	0	0	1	0	0	1
Tetragnathidae						
Chrysometa sp. 1	10	6	0	0	3	19
Dolichognatha sp. 1	8	4	0	0	0	12
Leucauge sp. 1	0	0	0	0	4	4
Plesiometa sp. 1	0	0	3	0	0	3
Theraphosidae						
Pamphobeteus sp. 1	0	1	0	0	0	1
Theridiidae						
Anelosimus sp. 1	0	5	4	2	0	11
Anelosimus sp. 2	8	1	0	0	0	9
Anelosimus sp. 3	2	0	0	0	0	2
Anelosimus sp. 4	0	0	5	2	0	7
Anelosimus sp. 5	2	0	0	0	0	2
Anelosimus sp. 6	0	1	0	0	2	3
Anelosimus sp. 7	2	0	0	0	0	2
Anelosimus sp. 8	0	0	10	0	0	10
Argyrodes elevatus Taczanowski 1873	0	0	0	2	2	4
Argyrodes weyrauchi Exline & Levi 1962	0	0	0	0	1	1
Coleosoma acutiventer Keyserling 1884	2	0	0	0	0	2
Dipoena sp. 1	0	1	0	0	0	1
Dipoena sp. 2	0	2	0	0	0	2
Dipoena sp. 3	16	27	2	2	0	47
Dipoena sp. 4	0	0	0	5	0	5
Dipoena sp. 5	0	2	1	0	1	4
Dipoena sp. 6	0	0	0	2	0	2

Appendix 1.—Continued.

Taxon	Vegetation types					
	RF	SF	G	S	HA	Total
Episinus sp. 1	10	12	0	2	21	45
Episinus sp. 2	3	3	0	0	0	6
Euryopis sp. 1	0	0	1	2	1	4
Euryopis sp. 2	0	0	0	0	3	3
Euryopis sp. 3	0	0	0	0	1	1
Faiditus caudatus Taczanowski 1874	4	0	0	0	29	33
Faiditus cochleaformus Exline 1945	0	0	0	0	1	1
Meotipa sp. 1	0	0	0	0	2	2
Paratheridula perniciosa Keyserling 1886	0	0	2	0	0	2
Phycosoma altum Keyserling 1886	0	32	0	0	0	32
Theridion sp. 1	2	2	0	0	3	7
Theridion sp. 2	19	0	0	0	0	19
Theridion sp. 3	2	0	0	0	0	2
Theridion sp. 4	8	0	0	0	0	8
Tidarren haemorrhoidale Bertkau 1880	5	1	0	0	32	38
Tidarren sp. 1	0	0	0	0	1	1
Tidarren sp. 2	0	0	0	0	1	1
Theridiidae sp. 1	0	0	2	0	0	2
Theridiidae sp. 2	2	0	0	0	0	2
Theridiidae sp. 3	2	2	0	0	0	4
Theridiidae sp. 4	2	1	0	0	0	3
Theridiidae sp. 5	0	1	0	0	0	1
Theridiidae sp. 6	2	2	0	0	0	4
Theridiidae sp. 7	0	0	0	2	0	2
Theridiidae sp. 8	0	1	0	0	0	1
Theridiidae sp. 9	14	2	0	0	1	17
Theridiidae sp. 10	0	0	0	0	2	2
Theridiidae sp. 11	0	0	0	0	6	6
Theridiidae sp. 12	0	0	1	0	0	1
Theridiosomatidae						
Theridiosoma sp. 1	0	4	0	0	0	4
Theridiosoma sp. 2	2	0	0	0	0	2
Theridiosoma sp. 3	1	0	0	0	0	1
Thomisidae						
Misumena sp. 1	0	0	0	0	3	3
Misumena sp. 2	3	3	6	2	1	15
Misumena sp. 3	0	0	0	0	3	3
Misumenops sp. 1	2	0	0	0	2	4
Tmarus sp. 1	0	0	0	0	2	2
Tmarus sp. 2	0	0	0	0	2	2
Tmarus sp. 3	0	0	0	0	3	3
Tmarus sp. 4	0	0	0	0	3	3
Tmarus sp. 5	2	5	0	0	2	9
Tmarus sp. 6	2	0	0	0	0	2
Thomisidae sp. 1	0	0	1	0	0	1
Titanoecidae						
Titanoeca sp. 1	0	0	1	0	0	1
Uloboridae						
Miagrammopes sp. 1	1	23	0	0	0	24
Philoponella sp. 1	4	11	0	2	0	17
Philoponella sp. 2	0	5	0	0	0	5
Philoponella sp. 3	0	7	0	0	0	7
Uloborus sp. 1	0	0	1	0	5	6
Zodariidae						
Zodariidae sp. 1	0	1	0	0	0	1
Total	382	402	207	136	510	1637