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Linking Vegetation Structure and Spider Diversity in Riparian and Adjacent Habitats in Two Rivers of Central Argentina: An Analysis at Two Conceptual Levels

Mariana Griotti,[1,2] Christian Muñoz-Escobar,[3] and Nelson E. Ferretti[4]

[1]Instituto Argentino de Investigaciones de las Zonas Áridas IADIZA (CCT-CONICET), Av. A. Ruiz Leal s/n, Parque Gral. San Martín (5500), Mendoza, Argentina (mgriotti@mendoza-conicet.gob.ar), [2]Corresponding author, e-mail: mgriotti@mendoza-conicet.gob.ar, [3]Programa de Doctorado en Sistemática and Biodiversidad. Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Chile (christianmz@gmail.com), and [4]Centro de Estudios Parasitológicos y de Vectores CEPAVE (CCT-CONICET), Boulevard 120 s/n e/61 y 62, La Plata, Argentina (nferretti@conicet.gov.ar)

Abstract

The link between vegetation structure and spider diversity has been well explored in the literature. However, few studies have compared spider diversity and its response to vegetation at two conceptual levels: assemblage (species diversity) and ensemble (guild diversity). Because of this, we studied spider diversity in riparian and adjacent habitats of a river system from the Chacoan subregion in central Argentina and evaluated their linkage with vegetation structure at these two levels. To assess vegetation structure, we measured plant species richness and vegetation cover in the herb and shrub - tree layers. We collected spiders for over 6 months by using vacuum netting, sweep netting and pitfall traps. We collected 3,808 spiders belonging to 119 morphospecies, 24 families and 9 guilds. At spider assemblage level, SIMPROF analysis showed significant differences among studied habitats. At spider ensemble level, nevertheless, we found no significant differences among habitats. Concerning the linkage with vegetation structure, BIOENV test showed that spider diversity at either assemblage or ensemble level was not significantly correlated with the vegetation variables assessed. Our results indicated that spider diversity was not affected by vegetation structure. Hence, even though we found a pattern in spider assemblages among habitats, this could not be attributed to vegetation structure. In this study, we show that analyzing a community at two conceptual levels will be useful for recognizing different responses of spider communities to vegetation structure in diverse habitat types.

Key words: assemblage, ensemble, SIMPROF, BIOENV test, Chacoan subregion

In many ecological studies, an aspect of great interest has been to understand how diversity varies in a given system (Fauth et al. 1996). Several studies have applied a taxonomic approach (lists of species) by using abiotic factors (e.g., environmental or spatial factors) to explaining shifts in community structure across space and time (Göthe et al. 2013, Souffreau et al. 2015, Astor et al. 2017). However, the community structure can be described not only by its species diversity but also by functional traits of their species (McGill et al. 2006). Species diversity concept was denominated by Fauth et al. (1996) as assemblage (defined as "a taxonomically related group of species that occur together in space and time"), whereas functional group of species was regarded as ensemble ("a phylogenetically bounded group of species that use a similar set of resources within a community"; Fauth et al. 1996). Hence, in studying both species diversity (hereafter referred to as assemblage) and guild diversity (ensemble), are involved two different levels of analysis, which could

not necessarily respond in the same way to the influence of abiotic factors in an ecological system (Hatley and MacMahon 1980, Schulze and Fiedler 2003, Klingbeil and Willing 2010).

Spiders have been a good model for community ecology, as they are a diverse and widely distributed group of obligate predators that show multiple hunting strategies (Turnbull 1973, Wise 1993, Patrick et al. 1999, Toti et al. 2000). As such, their abundance and richness are helpful indicators of biodiversity in an ecological system as a whole (Willett 2001).

A major factor influencing spider diversity is vegetation structure. Many studies have shown a link between vegetation structure and spider diversity (Weeks and Holtzer 2000, Halaj et al. 2000, Hore and Uniyal 2008, Rubio et al. 2008, Bowden and Buddle 2010, Oguri et al. 2014, Gómez et al. 2016, amongst many others). Spiders make use of vegetation as a physical structure needed to support webs and as shelter to avoid predators. Thus, a structurally

complex habitat could lead to higher spider species diversity (Hatley and MacMahon 1980). Likewise, guild diversity is positively related with habitat structure: the more complex the habitats, more guilds will be found (Cardoso et al. 2011).

Particularly, riparian habitats have been defined as very complex habitats with distinct vegetation and soil characteristics (Malanson 1993). These ecosystems consist of ecotones between streams and adjacent terrestrial habitats and contain structurally complex vegetation as compared with the matrix of vegetation where they are located (Caradine 1998). Several studies have shown that riparian areas have unique spider composition (Laeser et al. 2005, Lambeets et al. 2008, Gallé and Schwéger 2014) as well as resource flows owing to emergence of aquatic insects, which are an important source of high energy for riparian web-building spiders (Kato et al. 2003, Marzak and Richardson 2007, Tagwireyi and Sullivan 2016). In effect, spiders inhabiting riparian areas are important terrestrial consumers that may depend both on terrestrial habitats as sites for supporting webs, and on emerging aquatic adult insects as prey.

In central Argentina, there are several river systems that have been studied in terms of their macroinvertebrate, fish, and amphibian fauna (Vallania et al. 1996, Garelis and Bistoni 2010, Jofré et al. 2010, Calderón and Jofré 2011, Tripole et al. 2012), but little is known about their riparian arthropod communities. Hence, we studied spider diversity in riparian and adjacent habitats in two rivers from the Chacoan subregion in central Argentina, and performed a spatio-temporal evaluation of the link between vegetation structure and spider diversity at both assemblage and ensemble levels. These terms have been used imprecisely in many studies and are often prone to cause confusion or misuse within the field of community ecology. Thence, a clarification in the definitions of assemblage and ensemble terms will benefit ecology as a whole by allowing for an increased potential in cross-literature comparisons (Stroud et al. 2015). Following Fauth et al. (1996), we refer species diversity as assemblage and guild diversity as ensemble.

Given the little knowledge we have about whether spider assemblage and ensemble respond to vegetation structure in a similar way (Rubio et al. 2008, Almada et al. 2012, Lee et al. 2014), we compared spider diversity and their response to vegetation between different habitats at these two community levels. We therefore tested the following hypotheses: 1) spider assemblages and ensembles are similarly affected by vegetation structure. We expect our analyses show similar patterns at these both concept levels; and 2) riparian habitats have a distinct spider community compared with adjacent habitats. This research constitutes a contribution to the ecological knowledge of spider diversity in central Argentina and provides new species records for the country.

Materials and Methods

Study Site and Sampling

We carried out fieldwork in two rivers of the Quinto River basin, in the province of San Luis, Argentina. This area involves the Chacoan subregion (Morrone 2001, 2006), where grassland and highland forests predominate. Regarding spider fauna, this area is still understudied (Rubio et al. 2008, Ávalos et al. 2013, Ferretti et al. 2014). We selected two sampling sites—La Carolina (hereafter LC), in the upstream of the "Grande" River (−32.80436° S, −66.09763° W, 1,650 m asl), and Villa Salles (hereafter VS), in the downstream of the "Quinto" River (−33.83668° S, −65.23953° W, 429 m asl). We set four transects (100 m in length and 2 m in width) in habitats with different vegetation structure at each sampling site (Fig. 1).

Transects were located as follows: at LC: 1) Right and Left banks, vegetation typified by *Cortaderia* sp. and shrubs; 2) Mountain grassland, dominated by Poaceae (e.g., *Sporobolus pyramidatus* (Lam.) Hitchc. and *Stipa* spp.) and with no tree or shrub layers; 3) Poplar grove, exclusively composed of *Populus* sp. and sparse herbaceous ground cover. At VS: 1) Right and Left banks, typified by *Cortaderia* sp., *Tipha* sp., and grasses (Poaceae); 2) Tamarind islet, characterized by *Tamarix ramosissima* Ledeb.; and 3) Secondary forest, typified by grasses and woody species, such as *Prosopis* spp. and *Geoffroea decorticans* (Gillies ex Hook. and Arn.) Burkart.

Vegetation Measurements

To characterize vegetation structure, four vegetation variables were measured once (in October 2012) during the study. We estimated plant species richness and percent vegetation cover in herb and shrub - tree layers. To measure the herb layer, we used the Quadrat method (Coulloudon et al. 1999, Mostacedo and Fredericksen 2000). This method consists of visually estimating cover (percentage) and richness of herb species by using squares of one per one meter. Each square was set randomly along each transect, a total of 10 per transect. To measure the shrub - tree layer, we used the Transect method by estimating the vertical projection of each plant species (Mostacedo and Fredericksen 2000). Intercept distance (coverage) was recorded for each shrub and tree species that intercepted the virtual line along the transect and was expressed as percentage of the total length (100 m).

Spider Sampling

We collected spiders from along all transects, between October 2012 and February 2013 (three sampling dates: spring, early summer, and late summer). We used three sampling techniques: 1) vacuum netting, used to suck on vegetation, among rocks and cryptic shelters, for 1 min in a 1-m^2 quadrat. Each 1-min lasting suction event was considered a sampling unit, comprising a total of 10 per transect; 2) sweep netting, using an entomological net with rolling movements in a 1-m^2 quadrat on vegetation. Each 1-min duration tapping action was considered a sampling unit, comprising a total of 10 per transect; and 3) pitfall traps that consisted of plastic cups (12 cm in diameter and 14 cm in depth) buried at ground level. We placed 20 pitfall traps on each transect. They were kept open for 15 d in each sampling month with ethylene glycol as preservation liquid. Each pitfall trap was considered a sampling unit. Sampled spiders were identified using the keys published in Ramírez 1999, Ubick et al. 2005, Jocqué and Dippenaar-Schoeman 2006, and Grismado et al. 2014, among others. We used a morphospecies classification based on sexual morphology. Juvenile specimens were identified only to family taxonomic level. Thereafter, they were counted for analyses at ensemble level but not at assemblage level. To evaluate guild diversity, we followed the classification proposed by Días et al. (2010) and Cardoso et al. (2011).

Data Analysis

Vegetation richness and coverage of herb and shrub - tree layers were compared among sites (i.e., LC and VS) and habitats within sites (i.e., RB, LB, MG, PG, TI, and SF). For each vegetation variable, we calculated a Euclidean distance matrix of differences between every pair of observations (sampling units). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001a) was carried out to compare vegetation among habitats within sites. Each test was done using 50,000 permutations under Type III sum
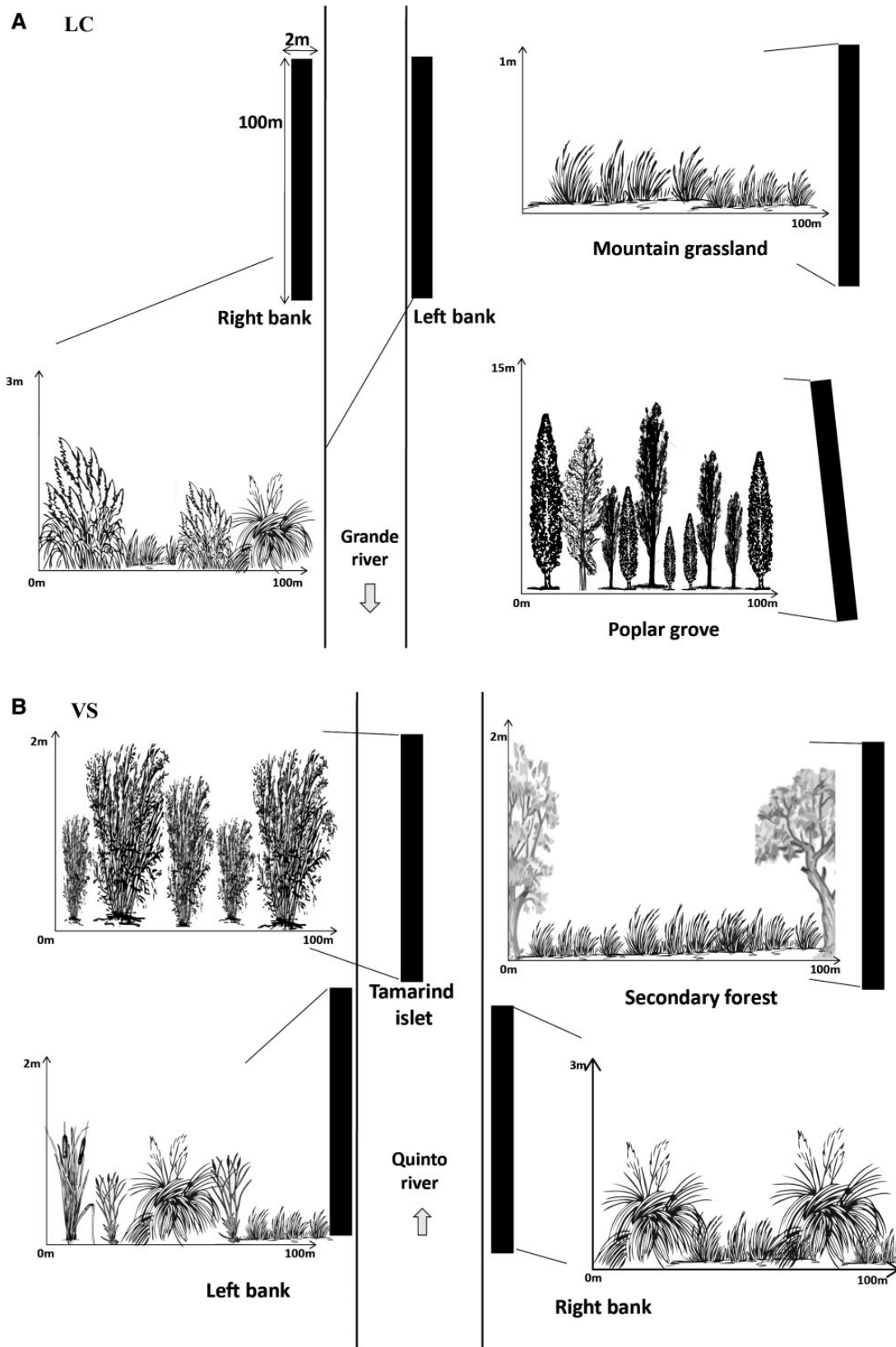
Fig. 1. Transects arrangement in La Carolina (LC) and Villa Salles (VS). The direction of the arrow shows the direction of the current. For each transect, characteristic profile vegetation is observed (plant height in axis y and length transect in axis x).

of squares (SS) and a reduced model to generate a permutated *F* statistic (pseudo-*F*) and *P*-value (Anderson 2001b). In cases of significant differences, pair-wise tests for all combinations of factors were conducted using the *t*-statistic (pseudo *t*-test; Anderson 2001a). For some terms in the analysis, there were not enough permutable units to get a reasonable test by permutation, so a *P*-value was obtained using a Monte Carlo (*P*(MC)) random sample from the asymptomatic permutation distribution (Anderson et al. 2008, Anderson 2001a) between each pair of plots (transects). To summarize spider diversity (at assemblage and ensemble levels) between habitats and sampling time (i.e., October, December, and February), we estimated richness (S), abundance (N), Pielou's evenness (J'), and Shannon's exponential (Exp H'; Jost 2006). These parameters were compared among habitats by using a PERMANOVA test. To analyze the spider assemblage and ensemble, data on species and guild abundance were log-transformed (x + 1) and evaluated by applying Bray–Curtis resemblance measure between each pair of plots (habitats; Clarke et al. 2006). A similarity profile test (SIMPROF) was carried out to test for differences in diversity between habitats and for sampling time nested within habitats. To visualize and contrast the main sources of variation in assemblage and ensemble structure, a nonmetric multidimensional scaling (nMDS) was performed as an ordination method (Kruskal 1964). We also evaluated the effect of geographic distance between habitats on spider diversity by implementing RELATE routine (Clarke and Gorley 2006). This analysis is a nonparametric version of the Mantel test, which estimates the relationship between two hemi-matrices (based on Bray–Curtis resemblance measures of species and guilds and geographical distance datasets) using Spearman's rank correlation. To evaluate the statistical significance of correlations, we used 50,000 randomizations. At last, to assess linkage between vegetation structure and spider diversity, the BIOENV routine was performed (Clarke and Ainsworth 1993). We used species and guild richness (S_{i-ii}), species and guild abundance (N_{i-ii}), species and guild Pielou's evenness (J'_{i-ii}), and species and guild diversity (exp H'_{i-ii}) as surrogate of spider diversity. The BIOENV procedure uses Spearman's rank correlation coefficients on resemblance matrices for both biotic (Bray–Curtis similarity) and vegetation structure (Euclidean distance) datasets (Clarke et al. 2008). Thus, iteratively this routine maximizes the rank correlation between spider variables and the "best" subsets of vegetation variables within the sample set (Clarke and Gorley 2006). All multivariate analyses were performed with PRIMER software v6.1.12 (Clarke and Gorley 2006) with PERMANOVA+ 1.0.2 add-on software (Anderson et al. 2008). To determine whether the sampling effort was appropriate, we constructed species accumulation curves for each sampling technique using the rarefaction method based on the number of individuals (Gotelli and Colwell 2001) with EstimateS software, version 8.0 (Colwell 2006). Voucher specimens were deposited in the Arachnid Collection of Universidad Nacional de San Luis and in the Arachnid Collection of the Instituto Argentino de Investigaciones de las Zonas Áridas (CAI, Susana Lagos Silnik).

Results

Vegetation Structure

The results of PERMANOVA indicated significant differences in herb cover and richness among habitats within sites (Tables 1 and 2). Shrub - tree cover and richness variables were not significantly different among habitats.

Table 1. Results of PERMANOVA from differences in the vegetation structure among sites (LC and VS) and habitats within site, using type III sums of squares based on 50,000 permutations of residuals under a reduced model

Source	df	Vegetation variables			
		Herb cover		Herb richness	
		Pseudo-*F*	*P*(MC)	Pseudo-*F*	*P*(MC)
Site	1	0.19185	0.675	0.12	0.747
Habitat (site)	6	26.198	<0.001	31.406	0.0002
Residuals	72				
Total	79				
		Shrub/tree cover		Shrub/tree richness	
		Pseudo-*F*	*P*(MC)	Pseudo-*F*	*P*(MC)
Site	1	2.075 e^{-3}	0.965	2.1429	0.191
Habitat (site)	6	1.0669	0.390	0.51724	0.793
Residuals	72				
Total	79				

P(MC): *P* value using Monte Carlo algorithm; df—degree of freedom.

Table 2. Summary of paired *t*-tests among habitats within sites (LC and VS) on vegetation variables with significant differences

Within site "LC"			Within site "VC"		
		Herb cover			
Groups	*t*	*P*(MC)	Groups	*t*	*P*(MC)
LB, RB	0.26189	0.7957	LB, RB	2.2324	0.0388
LB, GL	0.66078	0.5198	LB, TI	0.52623	0.607
LB, PG	8.5404	0.00002*	LB, SF	3.4108	0.0033*
RB, PG	16.58	0.00002*	RB, SF	0.92309	0.37
MG, PG	29.364	0.00002*	TI, SF	4.3231	0.0003*
		Herb richness			
Groups	*t*	*P*(MC)	Groups	*t*	*P*(MC)
LB, RB	1.4343	0.1698	LB, RB	0.38983	0.7067
LB, MG	6.057	0.0002*	LB, TI	2.4004	0.0264*
LB, PG	7.1945	0.0002*	LB, SF	1.369	0.1898
RB, MG	7.9643	0.0002*	RB, TI	2.0397	0.0562
RB, PG	8.7857	0.0002*	RB, SF	0.72058	0.4797
MG, PG	12.696	0.0002*	TI, SF	3.5857	0.0018*

LC, La Carolina: LB, left bank; RD, right bank; MG, mountain grassland; PG, poplar grove; VS, Villa Salles: TI, tamarind islet; SF, secondary forest. An asterisk indicates significant differences (*P* < 0.05).

Spider Composition

We collected 3,808 spiders belonging to 119 morphospecies and 24 families (Supp. Table 1 [online only]). Juveniles represented 63.89% of the total collected. Lycosidae and Linyphiidae were the dominant families (34.5% and 15.41%, respectively). These families showed the highest species richness (15 and 21 morphospecies, respectively). Of the remaining 24 families, two (Theraphosidae and Pholcidae) were represented by singletons. *Allocosa* sp2 (Lycosidae) was the most abundant species in pitfall traps (265 individuals), whereas *Sphecozone* sp 3 (Linyphiidae) and Ara-sp1 (Araneidae) were the most abundant in vacuum net and sweep net, respectively. *Glenognatha australis* and *Nothiophantes* sp. are new records for Argentina. We identified nine guilds (Table 3). Ground hunter was

Table 3. Relative abundance of the guilds in different habitats throughout sampling period

Guilds	Sampling technique	Relative abundance (%)							
		LC				VS			
		LB	RB	MG	PG	LB	RB	TI	SF
Ground hunters		54.68	57.31	61.54	11.52	53.09	42.83	73.42	49.54
Trachelidae	PF-SN								
Corinnidae	PF-SN								
Gnaphosidae	PF-SN								
Lycosidae	PF-SN-VN								
Scytodidae	PF								
Ctenidae	PF								
Ambush hunters		0.99	4.68	10.41	0.26	1.92	5.14	2.86	7.87
Philodromidae	PF-SN-VN								
Thomisidae	PF-SN-VN								
Sheet web weavers		19.21	7.02	3.62	46.60	27.51	30.19	16.16	13.66
Amaurobiidae	PF								
Amphinectidae	PF								
Hahniidae	PF								
Linyphiidae	PF-SN-VN								
Space web weavers		1.48	4.68	8.60	10.21	2.77	0.86	0	8.33
Dictynidae	PF								
Nesticidae	PF								
Pholcidae	PF								
Theridiidae	PF-VN								
Titanoecidae	PF								
Orb web weavers		7.88	4.68	4.07	15.18	10.02	9.64	1.23	1.39
Araneidae	PF-SN-VN								
Tetragnathidae	PF-SN-VN								
Sensing web weavers		0	0	0	0	0	0	0	0.23
Theraphosidae	PF								
Specialists		0	0	0.90	0	0.21	4.07	0.41	9.49
Zodariidae	PF-VN								
Aerial hunters		13.79	18.71	2.26	16.23	2.35	3.64	3.68	0.93
Anyphaenidae	PF-SN-VN								
Aerial runners		1.97	2.92	8.60	0	2.13	3.64	2.25	8.56
Salticidae	PF-SN-VN								
Oxyopidae	PF-SN								
Total		100	100	100	100	100	100	100	100

Sampling technique with which each guild was captured is specified. LC, La Carolina: LB, left bank; RD, right bank; MG, mountain grassland; PG, poplar grove; VS, Villa Salles: TI, tamarind islet; SF, secondary forest; PF, pitfall; SN, sweep net; VN, vacuum net.

the most dominant guild in all habitats except in the poplar grove (LC). In this habitat, the guild of sheet-web weavers predominated.

Spider Assemblage

The results of PERMANOVA from differences on spider species richness (S_i), species abundance (N_i), species evenness (J'_i), and species exponential Shannon (exp H'_i) parameters showed no significant differences among habitats on either of the sampling sites. Comparisons among sampling months were significantly different on S_i, N_i, and exp H'_i parameters. Differences among sites were significantly different only in S_i and N_i parameters (Table 4). On the other hand, the results of SIMPROF showed six clusters (Fig. 2). In LC, riparian habitats and mountain grassland were not significantly different (Pi = 1.72, P = 0.38, cluster f). Poplar grove formed a group dissimilar to the remaining habitats (cluster b). In VS, riparian habitats and tamarind islet shared a similar spider species composition (Pi = 1.39, P = 0.16, cluster e). Likewise, no significant differences were observed between secondary forest and left bank-October sampling (Pi = 1, P = 0.75, cluster d).

Spider Ensemble

The results of PERMANOVA showed differences between habitats in guild richness (S_{ii}) and between sampling months in guild abundance (N_{ii}; Table 5). Comparisons among sampling months were significantly different on guild abundance too. On the other hand, SIMPROF analyses showed no significant differences among habitats (SIMPROF Pi = 1, P = 0.089; Fig. 3).

Effect of Geographic Distance Between Transects on Spider Diversity

RELATE test based on Bray–Curtis (BC) similarity matrix showed that geographic distance had a direct effect on the similarity of spider assemblages (Rho = 0.686, P < 0.05) and ensembles (Rho = 0.497, P = 0.01).

Linkages Between Vegetation Structure and Spider Diversity

The BIOENV results showed that spider diversity at both assemblage and ensemble levels were not significantly correlated with the vegetation variables assessed (Table 6). Nevertheless, a significant

Table 4. Results of PERMANOVA from differences in spider species richness (S), species abundance (N), species evenness (J'), and exponential Shannon index species (exp H') among sites (LC and VS), sampling months (October, December, and February), and habitats within site, using type III sums of squares based on 50,000 permutations of residuals under a reduced model

Source	df	Spider assemblage			
		Species richness (S_i)		Species abundance (N_i)	
		Pseudo-F	P(MC)	Pseudo-F	P(MC)
Site	1	34.048	0.0008*	9.2107	0.0222*
Month	2	12.206	0.0015*	8.5599	0.0045*
Hábitat (site)	6	0.59034	0.7308	1.3738	0.2963
Residuals	12				
Total	23				
		Species evenness (J'_i)		Exponential Shannon (exp H'_i)	
		Pseudo-F	P(MC)	Pseudo-F	P(MC)
Site	1	2.052	0.2036	4.0596	0.09
Month	2	1.8055	0.2048	4.6304	0.0328*
Hábitat (site)	6	2.9647	0.0508	1.4063	0.2936
Residuals	12				
Total	23				

P(MC): P value using Monte Carlo algorithm; df—degree of freedom. An asterisk indicates significant differences ($P < 0.05$).

correlation was observed between vegetation structure and guild richness (rho = 0.714, $P = 0.01$). The cover and richness of the herb layer and shrub - tree richness were the main variables that contributed to this linkage.

Rarefaction Curves of Species and Morphospecies
These curves showed that vacuum netting and sweep netting techniques did not reach an asymptotic behavior with the capture effort employed, whereas pitfall trapping showed a closer approach to an asymptote (Fig. 4). Of the total spiders captured, 83.3% were with pitfall trapping, 10.4% with sweep netting, and 6.3% with vacuum netting.

Discussion

In this study, Linyphiidae and Lycosidae were the most abundant spiders, consistent with the findings of other authors (Bell 1993, Alford 2003, Aakra 2004). These families are the most common in pitfall traps. Several studies have demonstrated that Lycosidae is a dominating group in a wide range of environments and particularly scarce in densely forested habitats (Weeks and Holtzer 2000, Jocqué and Alderweireldt 2005). Jogar et al. (2004) observed that this family prefers habitats where plant cover is higher and older (Jogar et al. 2004). However, in our study, their predominance could not only be owing to their natural dominance but also because the sampling effort applied with pitfall traps was higher than that made with the other methods.
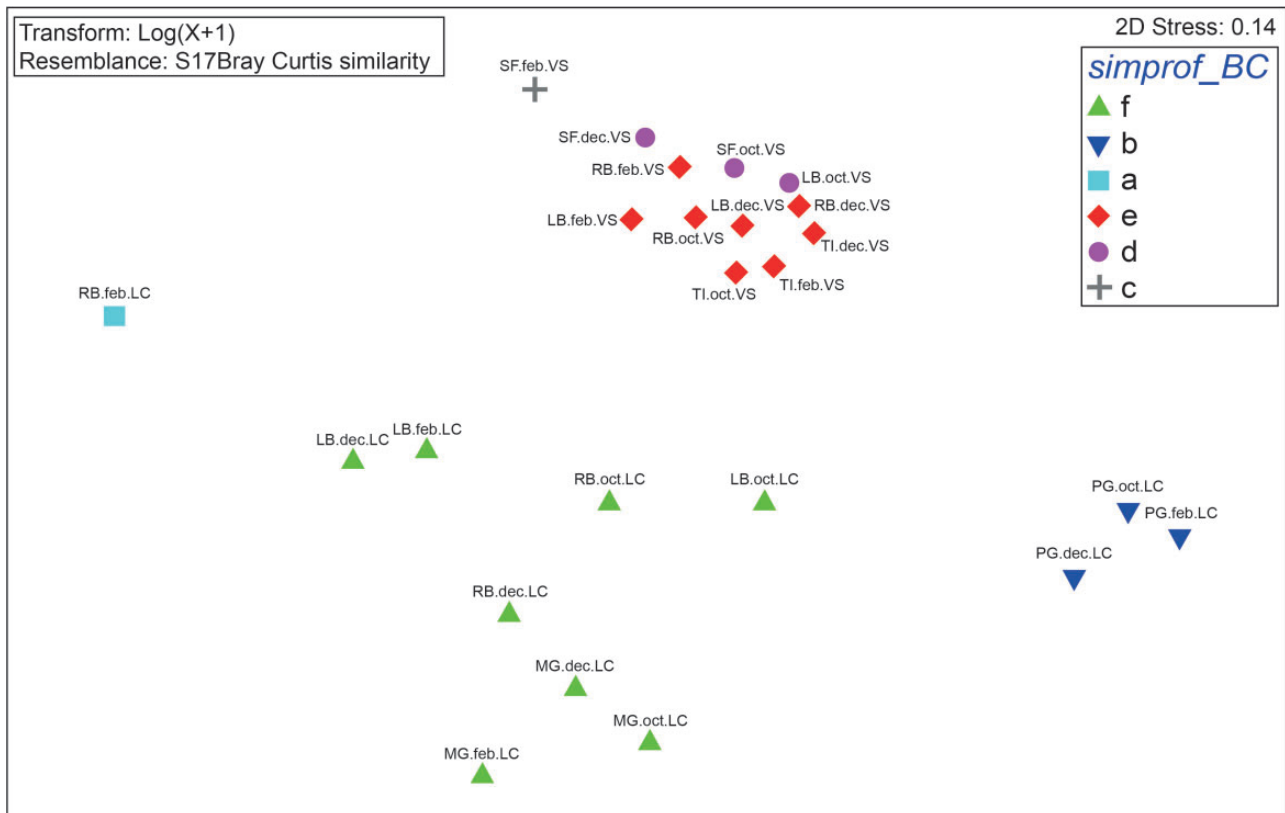

Fig. 2. Two-dimensional multidimensional scaling ordination plot of spider assemblages between sites and months (stress values = 0.14). a–f symbols represent significant differences between groups as identified by SIMPROF test (Bray–Curtis resemblance).

Table 5. Results of PERMANOVA from differences in spider guild richness (S), guild abundance (N), guild evenness (J'), and exponential Shannon index guild (exp H') among sites (LC and VS), sampling months (October, December, and February), and habitats within site, using type III sums of squares based on 50,000 permutations of residuals under a reduced model

Source	df	Spider ensemble			
		Guild richness (S_{ii})		Guild abundance (N_{ii})	
		Pseudo-*F*	*P*(MC)	Pseudo-*F*	*P*(MC)
Site	1	2.4545	0.1661	18.57	0.0046*
Month	2	0.66102	0.5338	13.809	0.0008*
Habitat	6	2.9831	0.0494*	2.3079	0.1026
Residuals	12				
Total	23				
		Guild evenness (J'_{ii})		Exponential Shannon (exp H'_{ii})	
		Pseudo-*F*	*P*(MC)	Pseudo-*F*	*P*(MC)
Site	1	1.3007	0.2977	0.2355	0.6459
Month	2	0.97553	0.4039	1.4695	0.2677
Habitat	6	1.156	0.3879	2.0743	0.1321
Residuals	12				
Total	23				

P(MC): *P* value using Monte Carlo algorithm; df—degree of freedom. An asterisk indicates significant differences (*P* < 0.05).

In relation to spider assemblages, we found differences between studied habitats. The spider assemblage of the poplar grove (LC) was different from that in the rest of habitats, whereas spider assemblages occurring along riverbanks (left and right) of LC, and in the mountain grassland (LC) were similar. In contrast, all habitats of VS (left and right banks, tamarind islet, and secondary forest) showed a similar spider species composition. This found pattern at assemblage level is in accord with vegetation structure analyses: Poplar grove (LC) was significantly different from all other habitats, whereas riverbanks (left and right) of LC, and mountain grassland (LC) were similar in herb cover and richness variables. In VS, only secondary forest was different from left bank and tamarind islet on herb cover and richness. Nevertheless, at spider ensemble level, we found that guild diversity was similar in all studied habitats. Our results show that spider species and guild diversity among dissimilar habitats respond in a different way. The results obtained here counter previous findings on studies linking species diversity and vegetation structure at assemblage and ensemble levels. For example, Lee et al. (2014) found nonsignificant differences between spider species diversity and species guild between types of rice fields. In contrast, Rubio et al. (2008) observed that species and guild diversity of spider were different between contiguous habitats (hygrophilous woodland and savannah parkland), indicating that the vegetation structure may have an influence on the spider diversity. In this study, however, we found that neither spider assemblages nor ensembles were affected
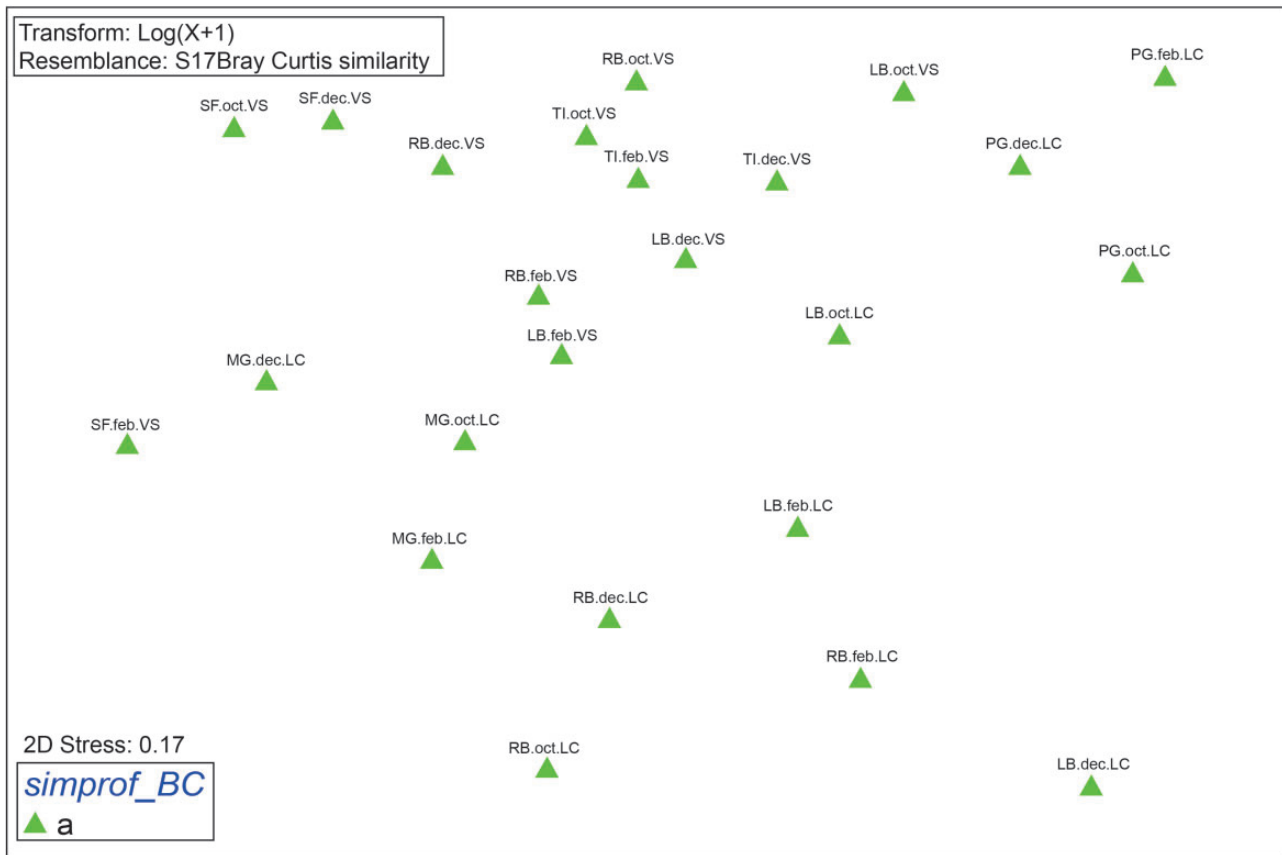

Fig. 3. Two-dimensional multidimensional scaling ordination plot of spider ensembles between sites and months (stress values= 0.17).

Table 6. BIOENV results showing the Spearman correlation coefficient (Rho) between vegetation variables and spider diversity

Vegetation variables	Vs	Best subset	Rho (Spearman)	P
1 cover herb layer	Assemblages (species composition)	1,3,6	0.591	0.105
2 sd cover herb layer	Ensembles (guild composition)	1,2,4,6	0.594	0.061
3 richness herb layer	Species richness (S)	1,6	0.227	0.548
4 sd richness herb layer	Guild richness (S)	1,2,4,6	0.714	0.014*
5 cover shrub/tree layer	Species abundance (N)	6	0.05	0.888
6 richness shrub/tree layer	Guild abundance (N)	5	0.216	0.563
	Species evenness (J')	1,5	0.132	0.74
	Guild evenness (J')	1	0.533	0.166
	Species diversity (exp H')	6	0.762	0.052
	Guild diversity (exp H')	5,6	0.133	0.743

Sd, standard deviation.
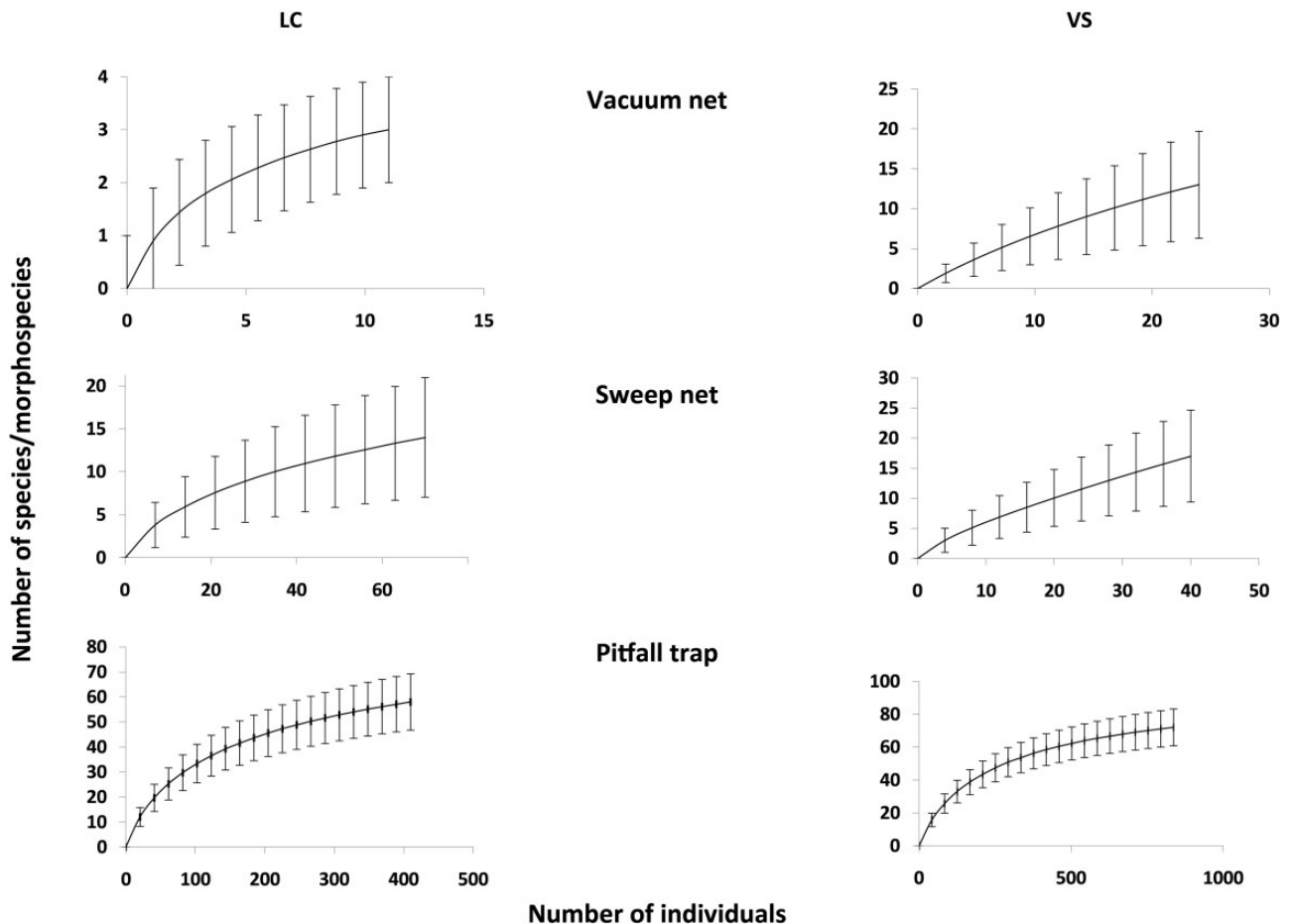An asterisk indicates significant differences ($P < 0.05$).

Fig. 4. Species and morphospecies rarefaction curves based on number of individuals captured during the study period for each sampling unit in separately sampling technique in La Carolina (LC) and Villa Salles (VS).

by the set of vegetation variables measured. Thereby, even though we found a pattern at assemblage level, it could not be attributed to the structure vegetation. Several authors have suggested that spider guilds would not be influenced by vegetation structure (Duffey 1966, 1974; Lopes Rodriguez and Mendonça 2012), and a possible explanation could be that spiders, being unspecialized predators, are generally independent of particular vegetation types and exist in more than one type of environment.

Concerning spider diversity on riparian banks, families such as Tetragnathidae, Corinnidae, and Nesticidae were found only along riverbanks. These families have been reported as riparian spiders before (Döbell et al. 1990, Akamatsu et al. 2004, Tagwireyi and

Sullivan 2016). Nevertheless, spider diversity on riverbanks was not different from that in adjacent habitats.

We therefore can explain found similarities by geographic distance, which had a direct effect on spider diversity (at assemblage and ensemble levels), with spider diversity being more similar when geographically closer. These results are consistent with the findings of Barton et al. (2017) and Rodriguez-Artigas et al. (2016), who by using the Mantel test, obtained significant correlations between the spatial proximity of studied sites and corresponding spider assemblages.

In this study, we show that analyzing a community at two conceptual levels will be useful to recognize different responses of spider communities in diverse habitat types. In addition, we contribute to the knowledge of spider diversity in a river system of the Chacoan subregion.

Acknowledgments

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