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ABUNDANCE AND RICHNESS OF ORB-WEB SPIDERS (ARACHNIDA: ARANEAE) IN A SECONDARY HIGH-ANDEAN FOREST OF COLOMBIA

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Abstract: We compared the species richness and abundance of orb-web spiders in a secondary high-Andean forest in Colombia in the dry and wet seasons at two altitudes (3100 and 3300 m a.s.l.). We identified six species, four belonging to Araneidae and two to Tetragnathidae. The abundance of Araneidae and Tetragnathidae decreased with increasing altitude, which was mainly due to the harsh climatic conditions (e.g. low temperature) which are in fact a limiting factor in the establishment and survival of spiders. Yet, the orb-web spider community appeared to be adapted to major variation in precipitation between the dry and wet season, with no significant change in spider abundance between these two periods. Apparently, disturbed forest, along with the high altitude, would explain the low number of spider species recorded in this study and high dominance observed of the genus *Chrysometa* (Tetragnathidae).
Key words: Araneae, Araneidae, Tetragnathidae, *Chrysometa*, biodiversity, high altitude ecosystems, Andes, Colombia.

Abundancia y riqueza de arañas orbiculares (Arachnida: Araneae) en un bosque alto andino secundario de Colombia
Resumen: Se comparó la riqueza de especies y abundancia de arañas orbiculares entre las estaciones seca y húmeda a dos altitudes (3100 y 3300 m.s.n.m.) en un bosque secundario alto andino en Colombia. Se identificaron seis especies, cuatro de Araneidae y dos de Tetragnathidae. La abundancia de Araneidae y Tetragnathidae disminuyó con el aumento de altitud, posiblemente debido a las duras condiciones climáticas (por ejemplo, baja temperatura), que son de hecho un factor limitante en el establecimiento y la supervivencia de las arañas. Sin embargo, la comunidad orbicular pareció adaptada a la variación en la precipitación entre la estación seca y húmeda, pues no se registró ningún cambio significativo en la abundancia de araña entre estos dos períodos. Aparentemente, un bosque perturbado, junto con la gran altitud, explicaría el bajo número de especies de arañas registrado en este estudio y alta dominancia observada del género *Chrysometa* (Tetragnathidae).
Palabras clave: Araneae, Araneidae, Tetragnathidae, *Chrysometa*, biodiversidad, ecosistemas de elevada altitud, Andes, Colombia.

Introduction

In spiders, a decrease in diversity and abundance with increasing altitude has been reported, although more complex patterns such as humpback relationships between species richness and altitude have also been found (Otto & Svensson, 1982; Greenstone, 1984; Olson, 1994; Chatzaki *et al.,* 2005; Lee *et al*., 2012; Foord & Dippenaar-Schoeman, 2016). In high altitude environments, abiotic factors are the principal components affecting the abundance and distribution of biota (Chatzaki *et al.,* 2005; Almeida-Neto *et al.,* 2006). Two main abiotic factors have been suggested to cause these patterns: climatic conditions and habitat heterogeneity. McCoy (1990) proposed that "ends are bad" to explain the low diversity on different groups of invertebrates (e.g. ants, spiders, parasitoids) in high altitude environments. According to McCoy (1990), the climatic severity and resource scarcity are the principal factors affecting the distribution of various groups of invertebrates. Probably, harsh conditions (e.g. low temperature) is the limiting factor that can explain the distribution of spiders at high altitude environments (Chatzaki *et al.,* 2005; Lee *et al.,* 2012; Foord & Dippenaar-Schoeman, 2016)

The decrease in habitat heterogeneity is another abiotic factor that affects spider richness and abundance (Greenstone, 1984; Riechert & Gillespie, 1986; Wise, 1993; Gunnarsson, 1996). The hypothesis of habitat heterogeneity mentions that the more complex the habitat, the more niches are available and, therefore, the greater the species richness (Tews *et al.,* 2004). Habitat structure and, more specifically, vegetation complexity, has been frequently recognized as one of the most important factors in determining the presence of spider species, as well as their richness and composition (Uetz, 1991; Wise, 1993). Therefore, vegetation type may be an important factor in determining spider associations due to their relationship to vegetation structure (Greenstone, 1984; Urones & Puerto, 1988). Then changes in habitat (e.g. forest fragmentation or loss, deforestation) can greatly affect the composition of the spider community because the local vegetation complexity decreases affecting the availability and variety of insect populations which affects spider community (Denno *et al.,* 2005; Prieto-Benítez & Méndez, 2011).

Spiders are usually classified based on hunting strategies and predatory habits, such behaviors range from active search and ambushing prey ("sit and wait") to the use of various types of traps (e.g. orb-webs) (Uetz, 1977; Foelix, 2011; Elias *et al.,* 2011; Cardoso *et al.,* 2011). Orb web spiders are one of the most diverse and abundant guilds, representing from 15% to over 50% of total richness and abundance in tropical (Basset, 1991; Silva & Coddington, 1996; Brescovit *et al.,* 2004; Villadiego *et al.,* 2013) and subtropical forest environments (Avalos *et al.,* 2009). In Colombia, patterns of species richness and abundance in orb-web spiders have been

little studied (Muñoz-Acevedo, 2013). Barriga (1995) and Cepeda & Flórez (2007) recorded in the Andean region of Colombia a decrease in the abundance and richness of species of spiders, mainly of the family Araneidae, with the increase of altitude. On the other hand, unlike other spiders, Tetragnathidae appears to increase in abundance and species richness at high altitudes. Several factors have been shown to influence the community composition of orb-web spiders, including the humidity of the microhabitat, change in altitude and rainfall and the availability of flying insects (Blanco-Vargas *et al.,* 2003; Cabra-García *et al.,* 2010a, b; Peñaloza−Villadiego *et al*., 2013). However, most of these studies were performed in Andean forests (1000–2800 m a.s.l.) with very few studies being conducted in high altitude ecosystems, such as high-Andean forests (2800–3300 m a.s.l.). In these ecosystems, Romo & Flórez (2008) registered that both availability of prey and the plant structures used to support and fix webs may influence the composition of orb-web spiders.

Thus, the present study aimed to document species richness and abundance of orb-web spiders along an altitudinal gradient in high Andean forests. Specific objectives of this study were to: (1) survey orb-web spiders in a secondary high-Andean forest; (2) assess whether the abundance and richness of orb-web spiders varies between periods of higher and lower rainfall and at two different altitudes; and (3) evaluate whether spider species use similar plant species in a secondary high-Andean forest.

Material and methods

Study area

This study was carried out in the Municipal Forest Reserve of Cogua (RFMC; 5° 4' 35"N, 74° 00' 00" W) that covers an area of 500 ha (Zambrano, 1995), and is located in the Quebra Honda region, in the eastern part of the Páramo de Guerrero, Cundinamarca, Colombia. The average annual temperature is 10.5°C, and annual average precipitation of 1046 mm with a bimodal rainfall regime (Zambrano, 1995). In the forest reserve, vegetation typically occurs as patches in different stages of regeneration (Montenegro & Vargas, 2008a). This vegetation mosaic is the result of land uses (mainly agriculture) previous to the designation as a reserve (León, 2002; León *et al.,* 2008). Actually, the RFMC extends over an altitude range of 2970 to 3650 m, which corresponds to high-Andean forest to Páramo ecosystems. There are several fragments of forest within the reserve, dominated by trees of 8 to 10 m high with abundant epiphytes and lacking an understory except for a low stratum of grasses and mosses (León *et al.,* 2008). The main tree species that dominate these fragments are *Brunellia colombiana*, *Clusia multiflora*, *Weinmannia rollottii, W. tomentosa, Persea ferruginea, Drimys granadensis, Shefflera bogotensis*, *Gaiadendron punctatum* and *Escallonia myrtilloides* (León et al., 2008). However, their abundances are low in the reserve compared with bushy plant species like *Tibouchina grossa* (Montenegro & Vargas 2008a, b).

In the forest reserve two altitudes were chosen for this study: 3100 m a.s.l. and 3300 m a.s.l. At each altitude, we established a single plot of 0.5 ha. The two delimited plots in the reserve are in altered condition due to land use (mainly agriculture) in previous years. In these plots, the typical vegetation included the grass *Calamagorstis* (Poaceae), a common plant in regenerating ecosystems. This plant represented approximately 55% to 65% of the vegetal cover within the two plots (Figure 1A). The remaining percentage were represented by patches in different regeneration states covered by other plants that could be found in low abundance in the plot: *Weinmannia tomentosa*, *Tibouchina grossa, Hesperomeles, Prunus*, some patches of *Chusquea* and the tree *Escallonia myrtilloides* (Escalloniaceae) (Figure 1C) which tends to be common in the high-altitude ecosystems of the tropics (Hernández-Camacho & Sánchez, 1992).

Collection of orb web spiders

The collections of individuals were made in January (dry period, monthly mean rainfall 16.6 mm) and April (wet period, monthly mean rainfall 96.6 mm) of 2010 during 15 days of field work per month. At each altitude, we established a single plot of 0.5 ha. In each plot 10 collection points were randomly placed. At each collection point, we used manual collection and vegetation beating. One-hour sampling effort was allocated for manual collection, while 30 min sampling effort was allocated for vegetation beating (Coddington *et al.,* 1991). We considered as unit of sampling the total time devoted by a person to collection combining these two techniques. All 10 collection points into the two delimited areas were sampled during the morning (8:00-10:00 h) and evening (21:00-23:00 h). All collected spiders were preserved in 70% ethanol. Only adults were identified to species. Voucher specimens were deposited in the Arachnida collection at the Instituto Butantan, São Paulo, Brazil (Curator: A.D. Brescovit).

Data analysis

Abundance of orb-web spiders

To asses if there were significant differences in the abundance of spiders between the wet and dry seasons and between the two altitudes (3100 and 3300 m a.s.l.), we applied a two-way ANOVA, once the normality and the homogeneity of variances of the data had been tested. The 10 points within each plot were used as replicates in this analysis.

Richness of orb-web spiders

To estimate the richness of orb-web spiders we used the species accumulation curve proposed by Jiménez-Valverde & Hortal (2003). We made a curve for each station and altitude. The 10 sampling points per season and altitude were used as a sampling effort. To generate the species accumulation curve values, we used the program EstimateS version 9.1.0 (Colwell 2013). The empirical accumulation curve was adjusted to the function of Clench to calculate the asymptotic value of the curve. The models were fitted to the data through nonlinear regression using the Simplex and Quasi-Newton algorithm (Jiménez-Valverde & Hortal, 2003; Jiménez-Valverde & Lobo, 2007). To reduce the effect of adding samples to the curve we randomized them 100 times into the software. After that, we used the program Statistica version 13.2 (Statsoft 2016) to generate the graphic of the curve in each altitude and season.

In addition, to compare species composition between wet and dry seasons and between altitudes, we used two-way PERMANOVA analysis, once the uniformity of data dispersion had been tested. Given the strong differences in the absolute abundance of spider species, the data were log transformed before analysis (Anderson *et al*., 2006).

We used Gower dissimilarity in the PERMANOVA test. For these statistical analyses, we used package vegan in R version 3.2.5 (R Core Team, 2016), with 1000 permutations

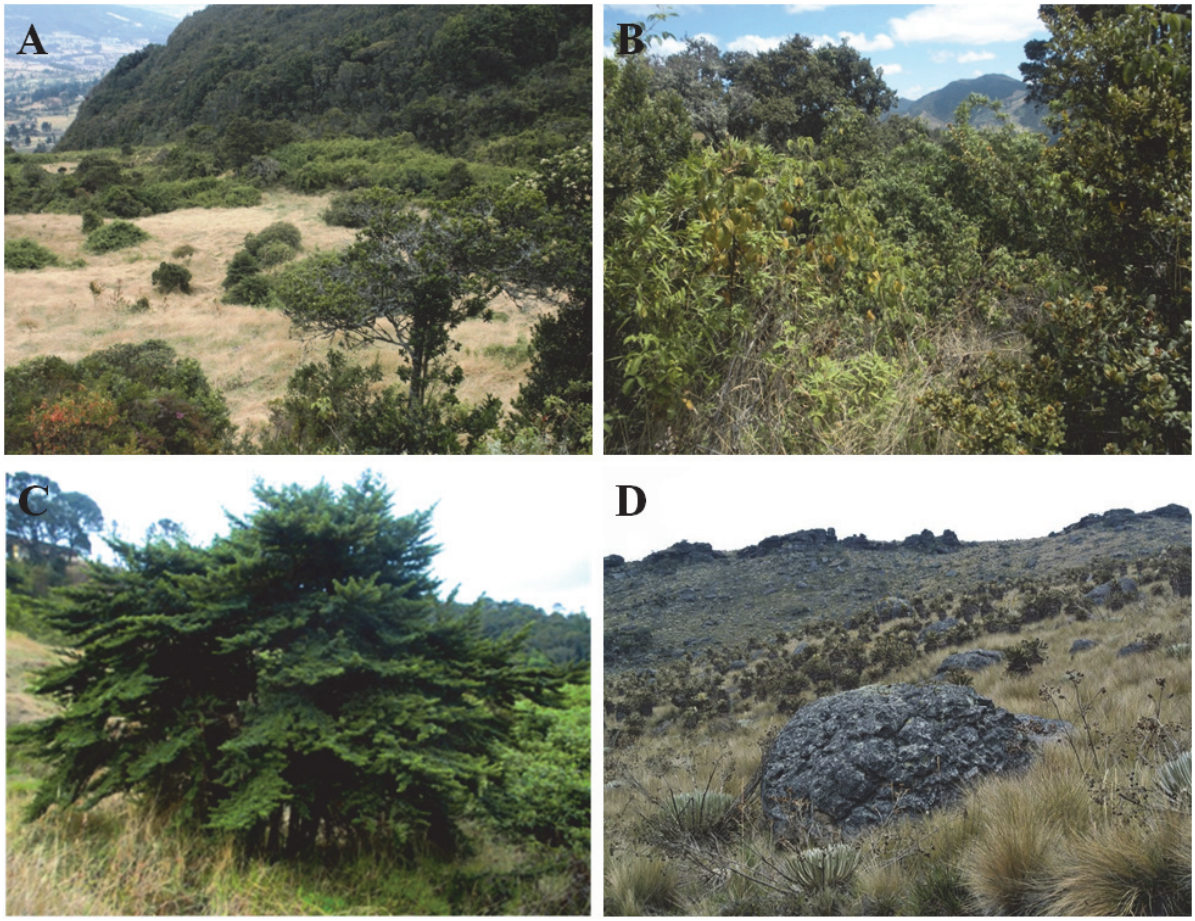


Fig. 1. Forest reserve in the Cogua town, Cundinamarca, Colombia. **A**) Panoramic view at an altitude of 3100 m a.s.l.; **B**) Vegetation present in the altitude of 3100 m a.s.l.; **C**) *Escallonia myrtilloides* (Escalloniaceae), a species representative of the forest reserve; **D**) Páramo ecosystem vegetation at an altitude of 3300 m a.s.l. Photo D by Lina Maria Peña.

Table I. Absolute and relative abundance of adult orb-web spiders divided by altitude and season (Wet and Dry) present in the RFMC, Cogua town, Cundinamarca, Colombia. Ta: Total Abundance; Ra: relative Abundance

Species	Wet season				Dry season			
	3100 m a.s.l.		3300 m a.s.l.		3100 m a.s.l.		3300 m a.s.l.	
	Ta	Ra	Ta	Ra	Ta	Ra	Ta	Ra
Araneidae								
Zygiella x-notata (Clerck, 1757)	22	7.02%	32	17.97%	33	10.12%	48	31.57%
Ocrepeira sp.	4	1.27%	10	5.61%	7	2.14%	15	9.86%
Araneus bogotensis (Keyserling, 1864)	4	1.27%	1	0.56%	10	3.06%	1	0.65%
Eustala sp.	0	0%	1	0.56%	0	0%	1	0.65%
Tetragnathidae								
Chrysometa zelotypa (Keyserling, 1864)	272	86.90%	125	70.22%	261	80.06%	80	52.63%
Leucauge sp.	11	3.51%	99	5.05%	15	4.60%	7	4.60%
Total	**313**		**178**		**326**		**152**	

and with a significance level of 0.05. Later, we used a similarity percentage (SIMPER) analysis to know which spider species were responsible for similarity/dissimilarity between altitudes and seasons based on Bray-Curtis distance. For this analyses we used the software PAST (Paleontological Statistics Software) version 1.0 (Hammer *et al*., 2001).

Similarity in plant use by orb-web spiders

In the field, we recorded the identity of the plant species on which each spider was collected. When the substrate was not a living plant, it was coded as "dry twigs". To assess the similarity of plants used as substrate of the spider webs, a Non-Parametric Multidimensional (NMDS) Ordination was performed. Spider abundance data in each registered plant were log-transformed to downplay the effect of the rare species. NMDS ordination was based on the Bray–Curtis distance measure, and a maximum number of 100 random starts were used to search for a stable solution. For these statistical analyses, we used the package Vegan of R.

Results

Richness and abundance of orb-web spiders

From 3861 orb-web spiders collected, 25% (969) were adult spiders. Adults belonged to six species, four Araneidae and two Tetragnathidae. Tetragnathidae was the most abundant family, with 780 individuals being collected during our study (80.4% of all individuals). The two most abundant species were *Chrysometa zelotypa* (Keyserling, 1883), and *Zygiella x-notata* (Clerck, 1757) (Table I).

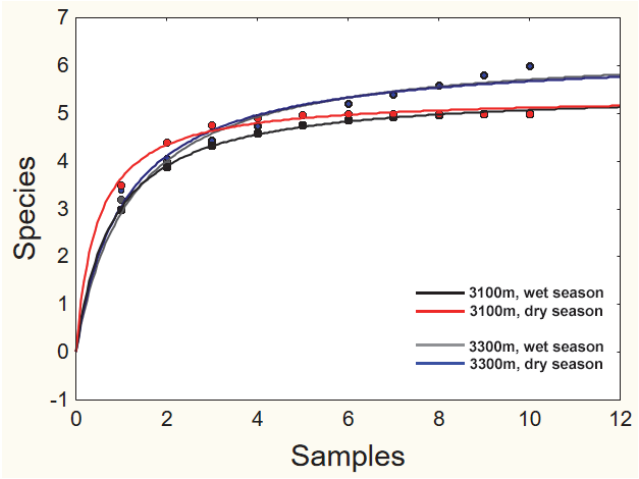


Figure 2. Species accumulation curves adjusted to the Clench function, of the orb-web spider species in RFMC, Cogua, Cundinamarca, Colombia.

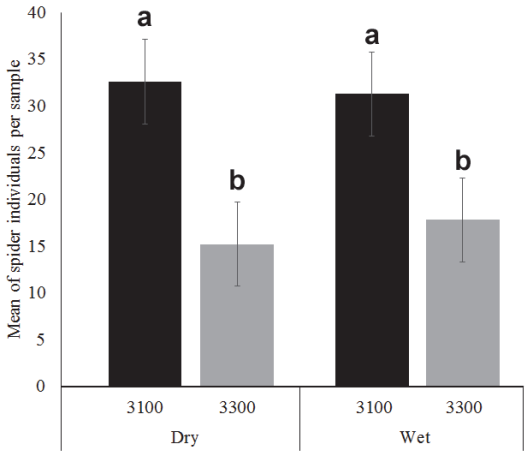


Figure 3. Mean number of orb-web spiders per sample recorded at two elevations in in two climatic periods (wet and dry), RFMC, Cundinamarca, Colombia. Different letters indicate significant differences between values. The vertical bars indicate standard error. N = 10 in al cases.

Effect of seasonality and altitude on spider richness and abundance

All species were present at all altitudes, except for *Eustala* which was only recorded at the altitude 3300m (Table I). The accumulation curves of the four inventories (two season and two altitudes) indicated inventories very close to completion (Figure 2; Table II). Clench´s function estimates indicate that between 78 and 93% of the fauna have been collected in the Forest Reserve (Table II).

Table II. Values obtained from the adjustment to the Clench function of the species accumulation curve.

Season	Alt.	Species observed	Asymptotic richness	R^2	Slope	%recorded fauna
Dry	3100	5	5.36	0.97	0.02	93%
	3300	6	6.26	0.96	0.05	79%
Wet	3100	5	5.49	0.99	0.03	90%
	3300	6	6.38	0.97	0.06	78%

All species were recorded in both seasons. No significant differences were recorded between wet and dry season in abundance (ANOVA: $F_{1, 36} = 0.019$; $p = 0.891$; Figure 3) or composition (PERMANOVA: $F = 1,15$; $R^2 = 0.02$; d.f. = 36; $p = 0.365$) of orb-weaver spiders. The most abundant species was *Chrysometa zelotypa*, representing 80.85% and 71.33% of individuals in the wet and dry seasons, respectively. The most abundant Araneidae species was *Zygiella x-notata*, representing 10.99% and 16.94% of individuals in the wet and dry seasons, respectively (Table I).

Significantly more spider individuals were collected at 3100 than at 3300 m.a.s.l. (ANOVA: $F_{1, 36} = 10.643$; $p = 0.002$; Figure 3, Table I). The relative abundance of species significantly differed between the two altitudes (PERMANOVA: $F = 5.68$; $R^2 = 0.13$; d.f. = 36; $p = 0.0001$), with six species being recorded at the higher altitude (3300 m a.s.l.) and five being recorded at the lower altitude (3100 m a.s.l.). All species excepting *Eustala* sp. contributed to these differences (Table III). *C. zelotipa*, *Leucauge* sp. and *Araneus bototensis* were more abundant at 3300 m, while *Z. x-notata* and *Ocrepeira* sp. were more abundant at 3100 m (Table III). No interactions between altitude and season in the abundance and composition was registered (ANOVA interaction: $F_{1,36} = 0.16$; $p = 0.68$; PERMANOVA interaction: $F = 0.37$; $R2 = 0.008$; d.f.= 36; $p = 0.789$).

Table III. Results of the similarity percentage (SIMPER) analysis of the orb-web spider community between altitudes registered in RFMC, Cogua town, Cundinamarca, Colombia.

Species	Contribution %	Average abundance	
		3100 m.a.s.l	3300 m.a.s.l
Chrysometa zelotypa	69.88	27.2	10.3
Zygiella x-notata	14.45	2.79	4
Leucauge sp.	6.59	1.37	0.8
Ocrepeira sp.	4.59	0.579	1.25
Araneus bogotensis	3.92	0.737	0.1
Eustala sp.	0.55	0	0.1

Orb-web spiders substrate

Most spiders were collected on *Calamagrostis* sp. plants, followed by *E. myrtilloides* L.f. (Table IV). The NMDS ordination had a stress value of 0.14, indicating a stable solution. This ordination showed that *Leucage* sp. and *Ocrepeira* sp. were related to *Chusquea*, *Eustala* sp. to *Tibouchina* and *A. bogotensis* to *Rubus* (Figure 4). *Calamagrostis*, *Escallonia*, *Prunus*, the four *Baccharis* species and dry twigs were utilized as web support by most spider species and thus clumped at the center of the ordination diagram (Figure 4).

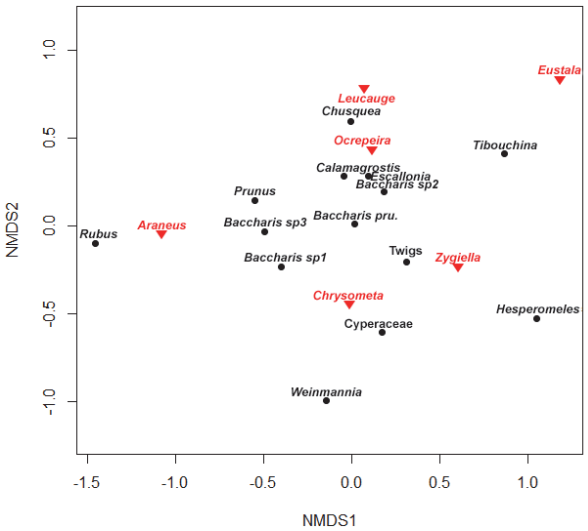


Figure 4. Non-metric multidimensional scaling (NMDS) ordination of the substrate plants in relation to the occupancy by six orb-web spider species in a high Andean forest in RFMC, Cundinamarca, Colombia. In red spider species, in black plant species.

Table IV. Plants used as web support and total abundance of orb-web spiders on each plant species in RFMC, Cogua town, Cundinamarca, Colombia.

Plant species	Spider species						Total
	Araneus bogotensis	*Chrysometa zelotypa*	*Eustala* sp.	*Leucauge* sp.	*Ocrepeira* sp.	*Zygiella x-notata*	
Asteraceae							
Baccharis prunifolia (Kunth)	2	24	-	1	1	19	47
Baccharis sp. 1	7	16	-	-	-	9	32
Baccharis sp. 2	-	2	-	1	1	2	6
Baccharis sp. 3	1	5	-	1	-	-	7
Poaceae							
Calamagrostis sp.	-	515	-	16	3	5	539
Chusquea sp.	-	10	-	10	1	1	22
Cyperaceae							
Cyperaceae sp.	-	8	-	-	-	1	9
Escalloniaceae							
Escallonia myrtilloides (L.f.)	1	121	-	12	27	80	241
Rosaceae							
Hesperomeles sp.	-	-	-	-	-	1	1
Prunus sp.	4	11	-	-	2	1	18
Rubus sp.	1	-	-	-	-	-	1
Melastomataceae							
Tibouchina grossa (L.f.)	-	3	2	1	-	6	12
Cunoniaceae							
Weinmannia tomentosa (L.f.)	-	2	-	-	-	-	2
Dry twigs	-	21	-	-	1	10	32

=

Discussion

The results of this study showed a negative effect of increasing altitude on the abundance of Araneidae and Tetragnathidae, although these results should be taken cautiously, due to the pseudoreplication involved in sampling ten points per plot. Bosmans *et al.* (1986) and Chatzaki *et al.* (2005) registered similar altitudinal patterns in the distribution of spider communities in European mountains. Bosmans *et al.* (2005) and Chatzaki *et al.* (2005) suggest that the tolerance to high mountain harshness is probably the filtered that can explain the pattern observed in these spiders. Differences in habitat structure (Jiménez-Valverde & Lobo, 2007; Romo & Flórez, 2008) are a non-exlusive explanation. Usually, species abundance and richness decline at high altitudes, such as for plants (Hartmut *et al.,* 1990; Stevens, 1992), which represent a critical substrate for fixing orb-weaver spider webs. Web spider abundance is generally limited by the number of structures available for fixing webs (e.g., branches of plants) (Rypstra, 1986; Rao & Poyyamoli, 2001; Elias *et al*., 2011). In our study, more spiders were found on *Calamagrostis* sp., which was more abundant at lower altitudes (personal obs. at 3100 m a.s.l.). Similar results were recorded in a high Andean forest (Romo & Flórez, 2008) and humid tropical forest in Colombia (Ferreira-Ojeda *et al.,* 2009), in which most spiders were collected on herbaceous and shrubby vegetation types. This type of vegetation is generally favorable for the establishment of orb-web spiders, because of the high architectural complexity of the plants (Blanco-Vargas *et al.,* 2003; Souza & Martins, 2005; Romo & Flórez, 2008). Thus, our results suggest that plant composition could be critical for the establishment of orb-web spiders because the plants are one of the available substrates for fixing webs (Souza & Martins, 2005; Jiménez-Valverde & Lobo, 2007).

Out of all orb-web spiders registered in this study, Tetragnathidae was the most abundant family in this type of ecosystem. Araneidae is regarded as one of the most cosmopolitan families, containing a high number of genera (Coddington & Levi, 1991; Schoeman & Jocqué, 1997; Romo & Flórez, 2008). However, in our study, only four species were recorded. In parallel, fewer individuals were recorded from this family when compared with Tetragnathidae. This observation agrees with another study in high-Andean forest in Cordillera Oriental, where Tetragnathidae was also reported as the most abundant family (Cepeda & Flórez, 2007). They also mention the possibility of an ecological replacement of Araneidae by Tetragnathidae since this last family is more abundant in high Andean forests (Romo & Flórez, 2008).

Our results confirm that *C. zelotypa* (Tetragnathidae) occupied the high-altitude ecosystems surveyed in this study. Similar results were obtained in other ecosystems of similar elevation (mountains of Pico da Neblina and Serra do Tapirapecó, Amazonas State, Brazil) in which the high abundance of species from this genus were found (Nogueira *et al.,* 2011). Thus, this genus may be broadly adapted to the environmental conditions of the study area, facilitating easier establishment compared to other species that have specific habitat preferences.

Interestingly, the abundance and richness of Araneidae and Tetragnathidae spider families did not change between wet and dry seasons. This spider community may be adapted to changes in precipitation in high altitude ecosystems. Similar results were recorded by Blanco-Vargas *et al.,* (2003) in an oak (*Quercus humboldtii*) and riparian forests of the Colombian Andes where the spider community was not influenced by precipitation changes in the studied region. Consequently, other conditions, such as food availability or vegetation structure may be critical parameters for establishment (Borges & Brown, 2001; Jiménez-Valverde & Lobo, 2007). In similar studies of other ecosystems at different altitude, there is no clear consensus whether the spider community is influenced by climatic conditions, because statistical tests corroborating this relationship for these variables are not available (Blanco-Vargas *et al.,* 2003; Sudhikumar *et al.,* 2005; Dias *et al.,* 2006; Ferreira-Ojeda *et al.,* 2009; Escorcia *et al.,* 2012).

The NMDS ordination revealed that individuals from the Araneidae family primarily inhabited plant with spaced

branches like the plant *E. myrtilloides*. This family of spiders is highly selective regarding the substrate on which it constructs webs (Valderrama, 1996; Schoeman & Jocqué, 1997), requiring open spaces for the proper attachment of vertical webs (Robinson, 1981; Valderrama, 1996; Foelix, 2011). This requirement is fulfilled by *E. myrtilloides*, which tends to grow with about 1 m separation between plants, providing space for the placement of webs. On the other hand, the only spider species associated with *Tibouchina grossa* plant was the genus *Eustala*. This spider usually fixes its webs on dead branches of the trees (Levi, 1977; Llinas-Gutiérrez & Jiménez, 2004). In southeastern Brazil, Souza *et al.* (2015) also recorded two species of *Eustala* associated with the dry parts of plants. This indicates that leafy plants are not the best substrates for this spider and at the time of the spider capture, *T. grossa* presented several dry branches without leaves offering a good substrate for *Eustala*.

Finally, altered forests differ widely from primary forests in habitat complexity. As a consequence, the structure, diversity and dynamics of arthropod community are also changed (Floren *et al.,* 2001). This factor along with the high altitude would explain the low number of spider species recorded in this study and high dominance observed in the genus *Chrysometa*. Similar results of high dominance in disturbed forest by a few species of spiders have been recorded by Floren & Deeleman-Reinhold (2005) and in ant species by Floren & Linsenmair (2001). Apparently, the strong change in habitat structure causes a decrease in species already established and improved the conditions for generalist species which could become dominant (Magura *et al.,* 2004, 2010).

In conclusion, the abundance of Araneidae and Tetragnathidae decreased with increasing altitude in our study area. This could be due to the harsh climatic conditions (e.g. low temperature) or to differences in plants for web construction, two limiting factors in the establishment and survival of spiders. Yet, the orb-weaver community did not show major changes in richness or abundance in relation to seasonal variation in precipitation. Our results on orb-web spider community composition at high altitude secondary forests should be compared with those at pristine forests to better understand the effect of altitude on orb-web spiders.

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