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Variación de los ensambles de arañas del sotobosque y su relación con la estructura de un bosque de niebla en el sureste de México.

TESIS
Presentada como requisito parcial para optar al grado de
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A mi familia, por ser los mejores maestros que he tenido en la vida, que siempre tuvieron la paciencia y estuvieron conmigo en todo momento, a quienes nunca han dejado de enseñarme, apoyarme y creer en mí, los mejores ejemplos de persistencia y trabajo.

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Introducción

El Bosque de Niebla (BN) es considerado uno de los ecosistemas más importantes del mundo, debido a su alta riqueza biológica y complejidad ecológica (Nadkarni y Wheelwright, 2000). En América, la mayoría de éstos bosques se distribuyen desde la Cuenca del Amazonas hasta México y generalmente presentan una distribución insular; por lo que, el área efectiva que ocupan es relativamente pequeña en comparación con otros ambientes (Aldrich, Hostettler y Van de Wed, 2000). Al igual que en otras regiones del continente, el BN mexicano presenta una distribución marcadamente residual, no solo por razones de su historia biogeográfica, sino en gran medida por el reciente cambio de uso de suelo para la agricultura de cultivos anuales o plantaciones de café (Gonzales-Espinoza, et al., 2012). Actualmente se estima que menos del 1% de la superficie nacional es ocupada por BN y cerca de la mitad ha sido alterada. El BN es considerado uno de los ecosistemas terrestres con mayor riesgo de desaparecer en el país (CONABIO, 2010).

Las comunidades forestales de BN en México se localizan sobre las montañas húmedas tropicales y subtropicales, desde los 1,500 a los 2,500 m de altitud al sur del paralelo 25° de latitud norte (Gual-Díaz y Rendón-Correa, 2014). Algunas de sus características incluyen: presencia constante de neblina, altos niveles de precipitación anual (500 a 6,000 mm), así como una vegetación perenne abundante, con árboles en diferentes estratos, abundantes helechos y gran variedad de plantas epífitas (Aguirre, 1992; Challenger, 1998; Wolf y Flamenco, 2003; Pérez, Tejada y Silva, 2010). Otra característica importante es la alta complejidad que presenta el estrato arbóreo, involucrando variaciones importantes en su composición, estructura y fenología

(Williams-Linera, 2003). Todas estas características remarcan heterogeneidad que presenta el BN en el país, por lo que se han aplicado diferentes terminologías para referirse a este sistema, destacando en las últimas décadas el de “Bosques Mesófilos de Montaña” (Rzedowski, 2006; véase una revisión reciente en Villaseñor, 2010).

La riqueza biológica de los BN mexicanos ha sido ampliamente reconocida. Su alta diversidad es un producto combinado de las variaciones climáticas y topográficas de su ubicación, además de su compleja historia geológica (Flores-Villela y Gerez, 1994). En términos generales, se ha estimado que cerca de 2,822 especies de plantas vasculares habitan en estos ecosistemas (10% de las especies conocidas para la flora mexicana), de las cuales 35% son endémicas (Villaseñor, 2010). Respecto a la fauna de vertebrados, el BN mexicano ocupa el segundo lugar en número de especies endémicas a Mesoamérica, con 298 (Flores-Villela y Gerez, 1994). En este sentido y dada su extensión territorial, es importante señalar que ningún otro tipo de vegetación en México contiene una densidad de especies tan alta (Gual-Díaz y Rendón-Correa, 2014).

La región montañosa de México, donde generalmente se localizan los BN, destaca entonces como una de las zonas más ricas en diversidad de todo el país. La Sierra Madre de Chiapas contiene el área más grande y continua de BN en el sureste de México (CONABIO, 2010). Sin embargo, el conocimiento sobre la ecología y diversidad de artrópodos en esta zona se encuentra sesgada hacia los órdenes más diversos de la clase Hexapoda como: Coleoptera, Lepidoptera, Hymenoptera y Diptera (Morón-Ríos y Morón, 2001; Ramos, 2001; Micó, Gómez y Galante, 2006; Chamé-Vázquez, Reyes-Castillo y Gómez, 2007; Rotheray, Hancock y Marcos-García, 2007; Balboa, 2010; Gómez y Morón, 2010). Para la clase Arachnida los trabajos realizados se limitan al orden Araneae y a la Reserva de la Biosfera del Volcán Tacaná (Ibarra-Núñez y Chamé-

Vázquez, 2009; Maya-Morales, 2010; Ibarra-Núñez, Maya-Morales y Chamé-Vázquez, 2011; Maya-Morales e Ibarra-Núñez, 2012; Maya-Morales, et al., 2012). El número de publicaciones sobre ecología y diversidad de arañas en los BN del resto del país es aún más limitado (Méndez-Castro y Rao, 2014)

Las arañas forman parte de los depredadores más abundantes en las redes tróficas de diversas comunidades terrestres (Greenstone, 1999), su taxonomía es relativamente bien conocida (Coddington y Levi, 1991), y su abundancia y distribución se encuentran ligadas a diversos atributos estructurales del hábitat (Corcuera, et al., 2008; Larrivée, et al., 2005; Larrivée y Buddle, 2010). En este sentido las arañas se han considerado como un buen modelo para estudios ecológicos (Cardoso, et al., 2010). Por otro lado, el efecto de la vegetación sobre las comunidades de arañas ha alcanzado un especial interés en las últimas décadas (Halaj, Ross y Moldenke, 1998; Jiménez-Valverde y Lobo, 2007; Corcuera, Jiménez y Valverde, 2008; Samu, et al., 2014). Sin embargo, la relación entre la estructura del bosque y sus ensambles de arañas aún no está claro. Por ejemplo, algunas prácticas de manejo intensivo, que homogenizan hábitats forestales en distintas zonas boreales, causan una disminución en la riqueza de especies y en la diversidad beta (Nimelä, 1997). En China, la diversidad de árboles afecta significativamente la estructura de los ensambles de arañas, pero no a la riqueza de especies (Schuldt, et al., 2012), contrario a lo reportado por Samu et al. (2014) quienes mencionan una fuerte relación positiva entre la riqueza de arañas y la riqueza de árboles en un bosque mixto de coníferas en Hungría. Finalmente, Schuldt, et al. (2008) no encontraron relación alguna entre la diversidad arbórea respecto a la de arañas en comunidades de bosques caducifolios en Alemania. Ricklefs (1987) señala que es necesario ampliar la información sobre los elementos que varían dentro de un mismo hábitat para obtener un mejor entendimiento de los procesos que explican los patrones de sus comunidades.

El presente estudio se realizó considerando que las arañas son sensibles a los cambios en la estructura de su hábitat a escalas finas, por lo que se esperaba que las variaciones espaciales y temporales que presentan los bosques de niebla en el sureste de México afectara la distribución de los ensambles de arañas del sotobosque. El objetivo de esta investigación fue analizar la variación espacio-temporal de los ensambles de arañas del sotobosque respecto a la variación estructural del bosque de niebla perenne de la zona núcleo I de la Reserva de la Biósfera El Triunfo en Chiapas, México. Para ello se determinó: 1) la composición y abundancia de las especies de arañas presentes en el sotobosque, 2) sus cambios espaciales y temporales en la riqueza de especies, la abundancia y la estructura de los ensambles y 3) el efecto de la estructura del bosque sobre los ensambles de arañas.

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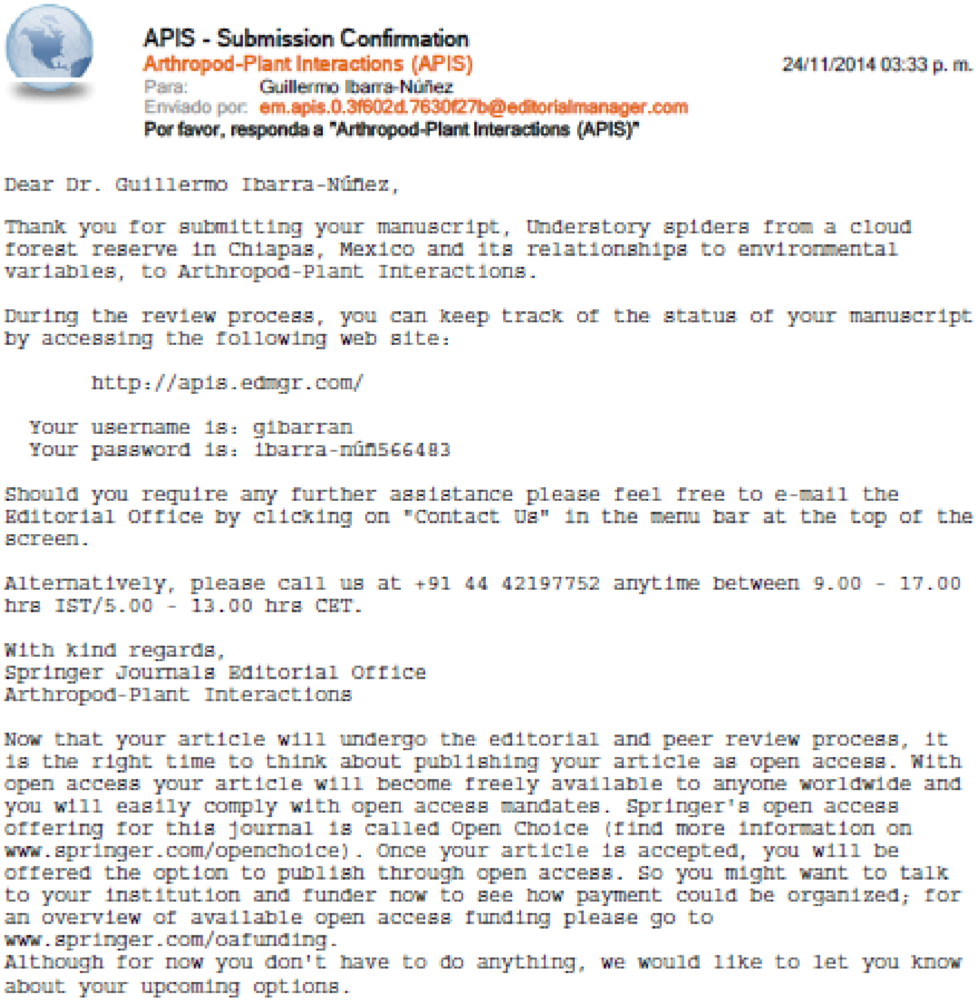

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Title page

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Abstract

Cloud forests have high ecological complexity, but their reduced area and exploitation by human communities, make them one of the most endangered ecosystems in Mexico. The spider assemblages of a cloud forest reserve in Chiapas, Mexico were studied to analyze the influence of environmental variables (e.g., forest stand structure, temperature and relative humidity). Also we characterized the temporal variation of these spider assemblages on the distribution, abundance, species richness and their structure. We sampling ten transects in order to recording spider assemblages, forest structure and climatic variables. Spider sampling were conducted during dry and rainy seasons. Forest structure data were recorded at the end of the study, except canopy cover that was registered at the end of each season. In spite of finding differences in forest stand among transects, only the density of seedlings showed a high correlation with spider abundance. Spider abundance was notoriously higher in the dry season. No effects of the environmental variables were detected on spider species richness, and assemblage structure. The most abundant families, Tetragnathidae, Theridiidae and Linyphiidae, were among the dominant families reported in other tropical cloud forests. The two latter were also the most diverse families. As complex ecosystems, tropical cloud forests seem to have complicated interactions with their arthropod inhabitants, further studies are needed to elucidate them.

Key words: Abundance, Araneae, biosphere reserve, species richness, forest structure.

Introduction

The cloud forest is considered one of the more important ecosystems in the world due to its biological richness and its high ecological complexity (Nadkarni and Wheelwright 2000). In the American continent, the cloud forest is distributed from the Amazon Basin to Mexico, generally with an insular distribution on the tops of mountains and consequently with a very small area in comparison with others ecosystems (Aldrich et al. 2000). In Mexico, the area occupied by cloud forest is less than 1% (including the Sierra Madre of Chiapas as the largest and continuous area), however about half of this has been altered, so it is considered one of the more endangered ecosystems in the country (González-Espinosa et al. 2012).

In Mexico, cloud forests are located from 1,500 to 2,500 m elevation, on humid tropical and subtropical mountains (Gual-Díaz and Rendón-Correa 2014). These forests are characterized by a continuous presence of clouds or mist at vegetation level that promotes a high annual precipitation (500 to 6 000 mm) and abundant evergreen vegetation with a high arboreal structure complexity that including: trees in several levels, covered with mosses, ferns and a variety of epiphytes (Williams 1991; Aguirre 1992; Challenger 1998; Wolf and Flamenco 2003). Mexican cloud forests are known for their high biological diversity, but the knowledge over arthropods diversity and their ecology is biased only on a few groups (Pérez et al. 2010). For example, many studies have been focused toward the largest Hexapoda orders such as: Coleoptera, Lepidoptera, Hymenoptera and Diptera (Morón-Ríos and Morón 2001; Ramos 2001; Micó, Gómez and Galante 2006; Chamé-Vázquez et al. 2007; Rotheray et al. 2007; Balboa 2010; García-Flores 2011). For the Araneae, the sixth more diverse global animal order, the studies conducted at the Mexican cloud forest are focused on Volcán Tacaná Biosphere Reserve located at south of Mexico (Ibarra-Núñez and Chamé-Vázquez 2009; Ibarra-Núñez et al. 2011; Maya-Morales and Ibarra-Núñez 2012; Maya-Morales et al. 2012), however, there is a little information about Araneae at the rest of cloud forest in Mexico.

Spiders are a good model taxa for ecological studies because they are abundant predators in forest ecological webs (Greenstone, 1999), their taxonomy is relatively well know (Coddington and Levi 1991), and their distribution and abundance are linked to structural attributes of the habitat (Larrivée et al. 2005; Larrivée and Buddle 2010). However, the effect of forest structure on spider assemblages is not yet clear. Intensive management practices that homogenize forest habitats cause a decline of species richness and beta diversity in several forest of North America (Nimelä, 1997). Woody plant diversity in China forests affects spider assemblage structure, but not species richness (Schuldt et al. 2012). Samu et al. (2014) found that spider richness was positively and strongly affected by tree species richness of deciduous-coniferous mixed forests in Hungary. However, Schuldt et al. (2008) found no general relationship among tree species diversity with diversity and abundance in spider communities of deciduous forest stands in Germany. This study analyzes the effect of forest structure on spider understory assemblages in a cloud forest from Chiapas, Mexico.

Materials and methods

Study area and sampling design

The study area was located at the El Triunfo Biosphere Reserve, Chiapas, Mexico (15° 39’ 48.4’’ to 15° 38’ 54.3’’ N, 92° 48’ 16.9’’ to 92° 48’ 38.5’’ W, 1,998 to 2,115 m elevation, Fig. 1). The climate is temperate humid with abundant rains in summer (from May to October) and with total annual precipitations of 3,500 mm and a mean annual temperature of 18°C (Morón-Ríos and Morón, 2001). The vegetal community corresponds to evergreen cloud forest that is mainly integrated by genera *Quercus, Matudea, Dendropanax* and *Hedyosmum* (Breedlove 1981; Long and Heath 1991). This study was conducted in 10 transects (five in the southern slope and five in northern slope) separated by at least 100 m among them (Fig. 1). The spider and forest structure sampling were conducted in each transect (20 x 40 m, Fig. 2).

Forest structure and climate variables

The forest structure was evaluated considering the species richness trees, stand structure (density and DBH: diameter at breast height of stems in several diametric classes; Fig. 2) and canopy cover. The canopy cover data was recorded at the end of each spider sampling seasons, because it may be influenced by season’s factors (Solórzano et al. 2010). Planar photograph method was used, with eight photographs per transect and season (Korhonen and Heikkinen 2009). Stand structure and tree species richness were recorded only once at the end of the study. The tree ferns and shrubs were considered because they are common elements of evergreen cloud forest (Williams 1991; Martínez-Camilo et al. 2012). All individuals were recorded according to size categories in nested plots (protocol modified from Olvera et al. 1996; Fig 2). Climate variables, such as temperature and relative humidity only were recorded since July 10th to August 24th 2014, because of logistic impediments. One data logger was located in each transect to record temperature and relative humidity on laps of 30 minutes between this period.

Spider sampling and determination

The spider sampling was made monthly during six months, along two seasons: dry (from February to April) and rainy (from June to August) season. Four circular plots (5 m diameter) were established inside each transect (Fig. 2). Two sampling techniques were used: direct hand collecting and beating vegetation. These techniques were alternated per month and per sampling point for each transect. Hand collecting consisted in locate and catch spiders by hand or with a mouth aspirator, investing 15 min for low vegetation (from the ground surface to knees level) and 15 min for high vegetation (from the knees level to the maximum reach of the arm). Vegetation beating was realized with a sweeping net (30 sweeps to sample low vegetation) and with a stick and a collecting tray of 1 m^2 (30 stick hits to sample high vegetation). The sampling team included 4 to 5 collectors per event. The spiders were killed and preserved in 96% ethanol and later deposited in the Colección de Arácnidos del Sureste de México, at El Colegio de la Frontera Sur, Tapachula, Chiapas. Specimens were identified to genus or species level when were possible, not determined specimens were separated into morphospecies. Hereafter, the term species will refer to both determined and undetermined morphospecies.

Data analysis

An Analysis of Variance (ANOVA) test was applied to analyze differences in forest stand (the value of the whole vegetation's categories) among transects using *R* (R Development Core Team 2014). Before analysis, forest stand data were submitted to natural logarithm transformation. Differences on temperature and humidity among transects were tested by orthogonal contrasts with Bonferroni correction (45 comparisons). To evaluate the seasonal (fixed effect) and transect (random effect) differences over the canopy cover, a mixed model ANOVA was performed using the *lme4* package (Bates et al. 2014). Dot plot of model's intercepts with confidence limits was displayed only to visualize differences among transects. To analyze the similarity of stand structure and tree community structure (abundance per species) among transects, we computed Bray-Curtis similarity values (for each of these variables) to produce constrained cluster analysis by unweighted pair-group method average (UPGMA) algorithm in PAST 3.0 (Hammer and Harper 2014).

For analysis purposes, a spider sample corresponded to one point of transect per month (hand collecting or beating), so for each sampling month there were 40 spider samples, and the whole study counted with 240 samples. A mixed models ANOVA was performed in R to evaluate the seasonal (fixed effect) and transect (random effect) differences over spider abundance. The spider abundances data were submitted to a natural logarithm transformation.

Dot plot of model's intercepts with confidence limits was displayed to visualize differences among transects. To examine the inventory completeness (i.e. the species observed as a percentage of the Chao 1 estimator values), the estimated species richness was calculated using EstimateS (version 9.1, Colwell 2013). The Coleman (1981) method of individual-based rarefaction was used to investigate spatial and seasonal impacts on species richness based on the lowest number of individuals caught in all the samples compared. To analyze the similarity among transects for each season, and for the whole sampling (both seasons), we computed Bray-Curtis similarity values to produce constrained cluster analysis by UPGMA algorithm in PAST 3.0.

A multivariate generalized linear model (GLM) was performed to test the influence of environmental variables (forest structure categories plus humidity and temperature) on spider variables (abundance and species richness per transect). Variables were checked for normality before testing, but no transformation was needed. To test the influence of the environmental variables on assemblage's structure (abundance per species of whole study), a Canonical Correspondence Analysis (CCA) was performed. This ordination synthesizes the multidimensional variation of a group of variables (Zuur et al. 2007). For this analysis, we only used spider species with at least 20 sampled individuals (totaling 28 species) (Rodrigues et al. 2014). A Monte Carlo permutation test was applied to obtain the significance of the correlations among environmental variables and the spider assemblage's structure (1,000 permutations).

Results

Environmental variables

Forest stand ($F = 0.596$; df = 9; $P = 0.7963$) and relative humidity ($F = 2.78$; df = 9; $P = 0.0033$) do not differ among transects. In contrast, temperature differ significantly among them ($F = 3.22$; df = 9; $P = 0.0008$). Canopy cover differs significantly between seasons but not among transects ($X^2 = 20.57$; df= 1; P<0.0001). Stand structure classes (Fig. 3a) and tree community structure (Fig. 3b) showed clearly that transect 1 is very different respect to the rest. For other transects a higher similarity is observed between the two transects groups (transects 2 to 5, and 6 to 10).

Spiders

A total of 5,441 spiders were collected, including 749 adults and 4,692 immatures. Of these latter, 33 very young immatures could not be assigned to species or morphospecies. The other juveniles were deemed as distinct species based on a combination of somatic characteristics (*i.e.* spines and color pattern, proportion of several structures, form of abdomen, etc.) not shared with any other species. The diversity analyses consider 5,408 specimens (99.4% of the sampled specimens) representing 17 families, 52 genera, and 100 species (16 identified at species level and 84 morphospecies). The five most abundant families were Tetragnathidae (2,642 individuals), Theridiosomatidae (1,037), Theridiidae (721), Linyphiidae (312), and Araneidae (263), whereas the most diverse families were Theridiidae (29 species), Linyphiidae (15), Anyphaenidae (11) and Araneidae (10). *Anyphaena*, *Theridion* and *Araneus* were the most diverse genera (nine, five and five species respectively). Most genera (73%) comprised only one specie. The dominants species were *Leucauge simplex* and *Epeirotypus* sp.1 with 1,798 and 665 individuals respectively.

The inventory completeness of the whole study was 85%. When considering seasons and transects independently the completeness values were similar for both seasons (for dry season 75% and for rainy season 78%), but differed more among transects for the whole sampling (53 to 83%) and for each season (dry season 43 to 75% and rainy season 55 to 84%) (Table 1). Abundance differed between seasons and among transects ($X^2 = 134.52$; df= 1, $P<0.0001$, Fig. 4) with lowest values for the rainy season and for the transect 1 (Table 1). Rarefied richness values neither differ among transects nor between seasons (except for transect 9 when each transect is compared between seasons, Fig. 5b). On the other side, Bray-Curtis similarity values between seasons were low (0.446). The relationships among transects for spider community structure are summarized in Figure 6. In the South slope, transects 1 and 2 show strong differences respect to the rest (T3 to T5) during both seasons. This difference is stronger during the rainy season (Fig. 6b). The relationships among T3 to T5 were similar during both seasons and the whole study. In the North slope, T6 to T10 showed variable gradients of similarity among them along seasons and the whole study. In general the similarity values for dry season is relatively consistent with the general cluster analysis (Fig. 6c).

For the environmental variables tested in the multivariate GLM, only abundance of seedlings had a significant relationship with spider variables ($F= 5.961$, $P = 0.0307$, Table 2), especially with spider abundance. In the CCA, the first two axes (Fig. 7) explain the 32% (axis1) and 23% (axis 2) of total variability and the eigenvalues were low for the two axes (Table 3). The evaluated environmental variables are not significantly related to the variation found in the spider assemblages (for all axes, $P = 0.4635$). However, the most abundant species (*Leucauge simplex* and *Epeirotypus* sp.1) are associated with the North slope group of transects (T6 toT8 and T10). An association is observed for transects: T1 and T2 are positively correlated with both axes, T9 and T4 are positively correlated with axis 1 and negatively with axis 2, T3 and T5 are negatively correlated with both axes, and T6, T7, T8, and T10 are negatively correlated with axis 1 and positively with axis 2 (Fig. 7). The association among transects are relatively consistent with that observed in general cluster analysis (Fig. 6c), except for T4 and T9, that seem to be correlated in CCA.

Discussion

The observed spider species richness in this study is similar to values reported in other studies conducted in other cloud forest. For example, Maya-Morales et al. (2012) reported 94 species (juveniles included) for another cloud forest in Chiapas, Mexico and Sorensen (2003) recorded 114 species for understory (juveniles excluded) for a cloud forest in Tanzania. As in this study, other studies of spiders in Neotropical cloud forests consider only particular sub-assemblages. However, these studies differ from our in the number of observed species: 56 species reported for epiphytes in Veracruz, Mexico (juveniles excluded, Méndez-Castro and Rao 2014), 48 species of spiders soil in a preserved site in Chiapas, Mexico (juveniles included), and 151 species for understory and soil spiders of two sites (conserved and disturbed) of a cloud forest in Chiapas, Mexico (juveniles included, Ibarra-Núñez, Maya-Morales and Chamé-Vázquez 2011). Also, Theridiidae and Linyphiidae were among the most abundant and the richest species families in the other studies (Sorensen 2003; Maya et al. 2012). Maya and colleagues (2012) reported that Tetragnathidae was among the most abundant families in their study, with *Leucauge simplex* as the most abundant species in the dry season. Furthermore, as the other studies mentioned, the low percentage of identified species (16%) suggest a significant proportion of new species and therefore a high degree of endemism in this habitat.

Due to spiders form a hyperdiverse group, most surveys suffer some degree of undersampling. Cardoso (2009) considers three categories of completeness for overall sampling effort: the “reasonable” when about 50% of the species have been sampled, the “comprehensive” for a sampling of 70-80%, and the “exhaustive” inventory might reach 90-100%. In our study, we obtained a “comprehensive” completeness for the whole study and for each season. Respect to the values for the transects in each season only transect 2 in dry season obtained a value lower than 50% and the rest obtained of “reasonable” to “comprehensive” completeness percentage (Table 1).

A low similarity between seasons (0.446) with differences in similarity observed among transects per season (Fig. 5) and lower spider abundance values during the rainy season (mixed models ANOVA and Table 1) indicate a marked seasonal effect on spider assemblages. Other studies in montane tropical habitats that include a seasonal component, report a similar reduction of abundance in the rainy season (Pinkus et al. 2005; Maya-Morales et al. 2012, preserved site). However, since the study of spiders in cloud forest are little studied and since their life cycle and longevity are unknown, more studies are necessaries to elucidate the observed temporal variation.

Studies on Mexican cloud forests exposed a high degree of spatial and temporal heterogeneity (Challenger 1998; Rzedowski 2006; CONABIO 2010; Williams-Linera 2012; Gual-Díaz and Rendón-Correa 2014). Floristic and phenological studies over cloud forest around the refuge “El Triunfo” reported important spatial and temporal variations (Williams 1991; Pérez et al. 2010; Martínez-Camilo et al. 2012). In this study, differences on forest structure among transects were found, indicating a spatial heterogeneity (for stand classes and community structure) and a temporal fluctuation of canopy cover. Since most spiders are very sensitive to fine-scale habitat structure (Jiménez-Valverde and Lobo 2007; Corcuera et al. 2008; Foord et al. 2008), we expected that spider assemblages were affected by some spatial and climatic variables. The multivariate GLM only show a high correlation with tree seedlings, but other results show few spatial effects. Seedlings may shelter potential preys of spiders, provide refuges then again predators or unfavorable environmental conditions to the wandering spiders, or web supports to the orb-weaver spiders (Riechert and Gillespie 1986; Wise 1993; Samu et al. 1996; Corcuera 2008). Since we failed to detect any clear correlation between seedling and spider species, the seedling/spider abundance relation seem to be general. The most notably spatial effect was recorded in transects 1 which vegetation (abundance and composition) differ from the rest of transects and coincidently having the lowest similarity values for spider and tree assemblages. Nevertheless, the analysis did not detect a relationship of this spider assemblage with any of the included environmental variables. It is possible that other abiotic or biotic variables, not considered in this study, could have an important influence on spider assemblages. Transect 1 was located in the crest of a slope, where the wind blows more continuously and is stronger than in other transects (E. F. Campuzano, personal observation). This could affect the availability of adequate microhabitats (support of webs or refuges) or prey, and consequently limit the spider populations (Riechert and Gillespie 1986; Wise 1993; Samu et al. 1996). In general, the distribution of spider assemblages of this study was weakly explained by the environmental variables. Other studies about spider communities also have reported a weak response to environment variables on systems of high diversity (Sanzone et al. 2003; Schuldt et al. 2011; Rodrigues and Mendonça 2012; Rodrigues et al. 2014). It is possible that the spatial scale (and variables) at which the forest structure was evaluated was not relevant for the spider populations dynamic, since differences in spider assemblages and factors that explain its distribution in different forest ecosystems also depend on spatial scale considered (Larrivée and Buddle 2010; Schuldt et al. 2013). Sanzone and colleagues (2003) showed that proximity of stream affected the distribution of spiders along a gradient of distance. Since streams were present in the studied transects, this environmental variable may help to explain spider abundance.

In conclusion, this study show clear spatial and seasonal differences for the selected environmental variables in this cloud forest, but these variables could not explain the distribution of the understory spider assemblages. Another study that includes other environmental variables, such as wind speed or prey availability and attempts different spatial scales should be consider to explain the factors that have the most influence on the structure of spider communities in cloud forest. This is one of the first studies that an intensive sampling has been employed to investigate spider responses to forest structure and climate variables in Neotropical cloud forest. Tropical cloud forest is complex ecosystems, due to the high number of plants and animals that inhabit it, and interactions could be very intricate and not easy to elucidate. Besides, the results of this study are congruent with these of other studies in understory spiders in cloud forests, particularly for the patterns of dominant families in abundance and richness. Given the threatened conditions of cloud forest in the Neotropics, the results of this paper present some ideas for future research, in view that this knowledge will contribute for its conservation.

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Table 1 Abundance (n), observed species richness (S), estimated species richness with Chao 1 estimator (C1) and percent of completeness (Cs) for each transect, season, transect per season and totals

	Dry				Rainy				Total			
	n	S	C1	Cs	n	S	C1	Cs	n	S	C1	Cs
T1	188	36	70	52	121	25	32	78	309	43	78	55
T2	259	25	58	43	90	19	25	77	349	32	51	62
T3	323	41	75	55	191	32	38	84	514	50	74	67
T4	370	48	86	56	168	31	49	63	538	52	63	83
T5	428	43	67	64	203	38	70	55	631	57	83	69
T6	353	35	48	73	115	20	32	63	468	43	68	63
T7	478	46	61	75	135	25	32	77	613	51	64	79
T8	531	41	68	60	223	30	41	73	754	51	97	53
T9	499	41	68	60	193	38	52	73	692	54	68	80
T10	438	33	49	68	102	20	31	64	540	38	51	75
TOTAL	3867	91	121	75	1541	73	94	78	5408	100	117	85

Table 2 Multivariate general linear model for ambient variables (all categories of forest structure, species richness trees, temperature and humidity) influencing spider diversity variables (abundance and species richness) (bold tipe indicates significant relationships)

Factor	MS	*F*	*P*
Seedlings	4,401	5.961	**0.0307**
Juveniles-Trees	1.10E+04	0.054	0.9476
Small-Trees	1.02E+04	0.478	0.6338
Mid-Trees	1.07E+04	4.326	0.0598
Large-Trees	9,004	0.9713	0.4144
Small-Shrubs	9,123	2.985	0.1155
Large-Shrubs	1.02E+04	2.402	0.1606
Small-Tree ferns	8,975	4.091	0.0666
Large-Tree ferns	8,863	0.97	0.4248
Canopy cover	1.04E+04	0.522	0.6147
Temperature	8,554	1.429	0.3017
Humidity	1.10E+04	0.063	0.9392
Richness-Trees	7,046	2.047	0.1995

Table 3 Correlation coefficients from CCA among environmental variables and the first two ordination axes for spider species composition and corresponding *P* values.

Variables	Correlation	
	Axis 1	Axis 2
Temperature (Temp)	-0.7258	-0.2491
Humidity (Hum)	0.3497	0.0505
Seedlings (Seed)	-0.4576	-0.1284
Juveniles-Trees (Juv-T)	-0.2963	-0.0797
Small-Trees (Sma-T)	0.7117	0.1533
Mid-Trees (Mid-T)	-0.3762	0.4408
Large-Trees (Lar-T)	0.1856	0.3144
Small-Shrubs (Sma-Sh)	-0.093	-0.5379
Large-Shrubs (La-Sh)	-0.0514	-0.6285
Small-Tree ferns (Sm-TF)	-0.0802	0.396
Large-Tree ferns (La-TF)	-0.0288	-0.2233
Canopy cover (CC)	-0.3863	0.0225
Richness-Trees (S-Trees)	-0.1392	-0.3971
Eigenvalues	0.117	0.0848
P	0.1319	0.4376

Figure legends

Fig. 1 Location of sampling transects in El Triunfo Biosphere Reserve, Chiapas, México.

Fig. 2 Details of the spider and forest structure sampling. Spider sampling: circular plot; A: seedlings (<0.5 m height) in three plots of 2 m^2; B: juveniles (>0.5 m tall and <5 cm DBH) in three plots of 8 m^2; C: Shrubs and Tree ferns small sized (<1.5m tall) in one plot of 100 m^2 ; D: small, mid and large sized trees (small: 5-10 cm DBH; mid: 10-30 cm DBH; large: >30 cm DBH), shrubs and tree ferns large sized (>1.5m tall) in one plot of 400 m^2 (adapted from Olvera-Vargas et al. 1996).

Fig. 3 Cluster analysis of transects based in Bray-Curtis similarity of a) forest stand classes, and b) tree species abundance.

Fig. 4 Mixed models ANOVA dot plot with confidence limits per transects.

Fig. 5 Comparison of species richness by individual-based rarefaction (Coleman 1981) based in the lowest number of individuals caught in all the sample. a) All transects rarefied for each season (sample) and b) each transect (sample) rarefied between seasons.

Fig. 6 Cluster analysis of transects based in Bray-Curtis similarity among spider assemblages structure of transects by season and general. a) Dry season, b) rainy season, and c) general.

Fig. 7 Ordination (first two axes) from a Canonical Correspondence Analysis of spider species assemblage (only spiders with n>20 individuals) in El Triunfo Biosphere Reserve cloud forest. Factors included are eleven vegetation structure variables (*Seed* Seedlings, *Juv-T* Juveniles-Trees, *Sma-T* Small-Trees, *Mid-T* Mid-Trees, *Lar-T* Large-Trees, *Sma-Sh* Small-Shrubs, *La-Sh* Large-Shrubs, *Sm-TF* Small-Tree ferns, *La-TF* Large-Tree ferns, *S-Trees* Richness-Trees and *CC* Canopy cover) and two ambient variables (*Temp* Temperature and *Hum* Humidity). Dots represent transects, and triplot is expanded twice. Spider species code can be found on “Appendix”.

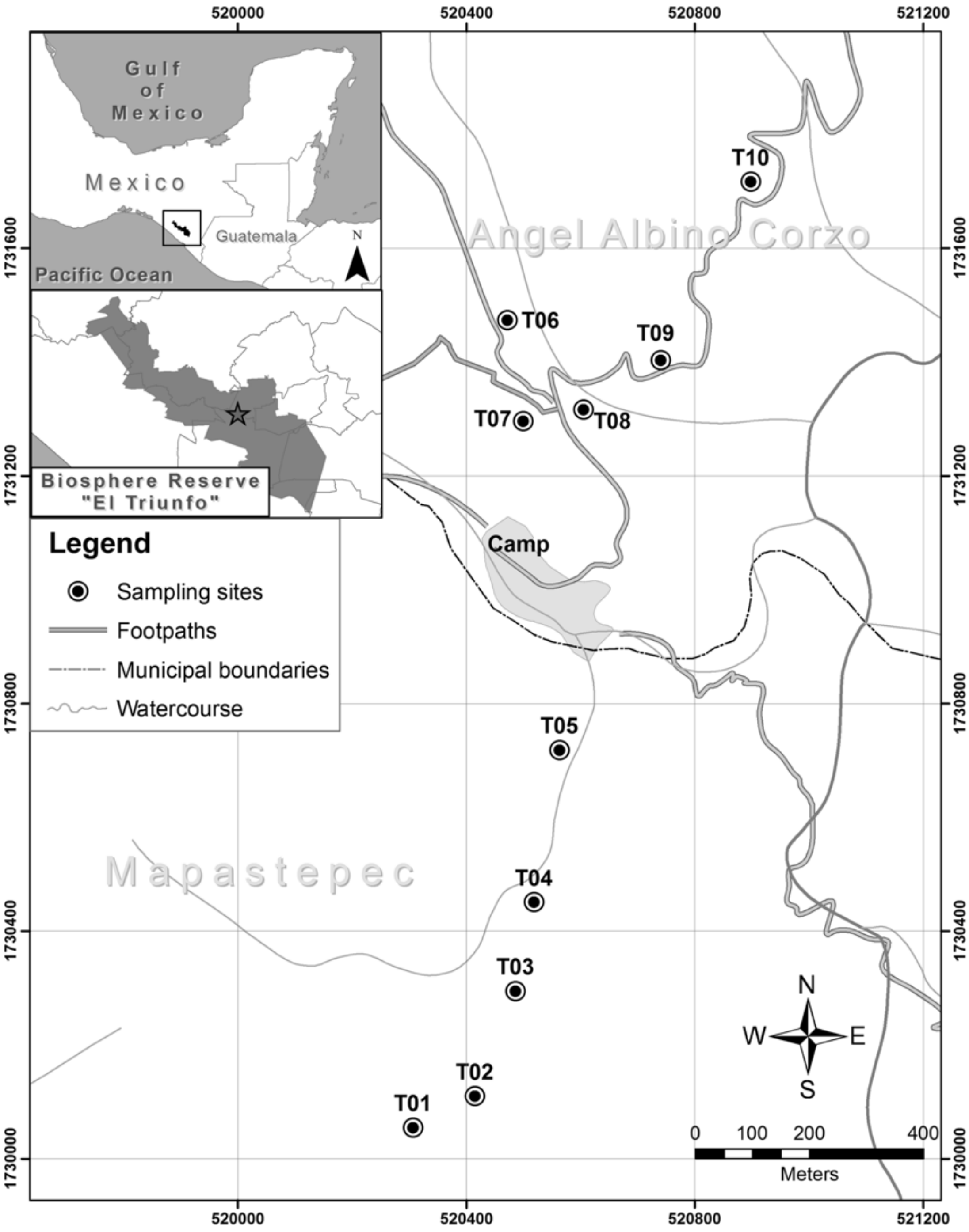
520000
520400
520800
521200
1731600
1731200
1730800
1730400
1730000
Gulf of Mexico
Mexico
Guatemala
Pacific Ocean
N
Biosphere Reserve "El Triunfo"
Legend
Sampling sites
Footpaths
Municipal boundaries
Watercourse
Angel Albino Corzo
Mapastepec
Camp
T01
T02
T03
T04
T05
T06
T07
T08
T09
T10
N
W
E
S
0
100
200
400
Meters

Fig. 1

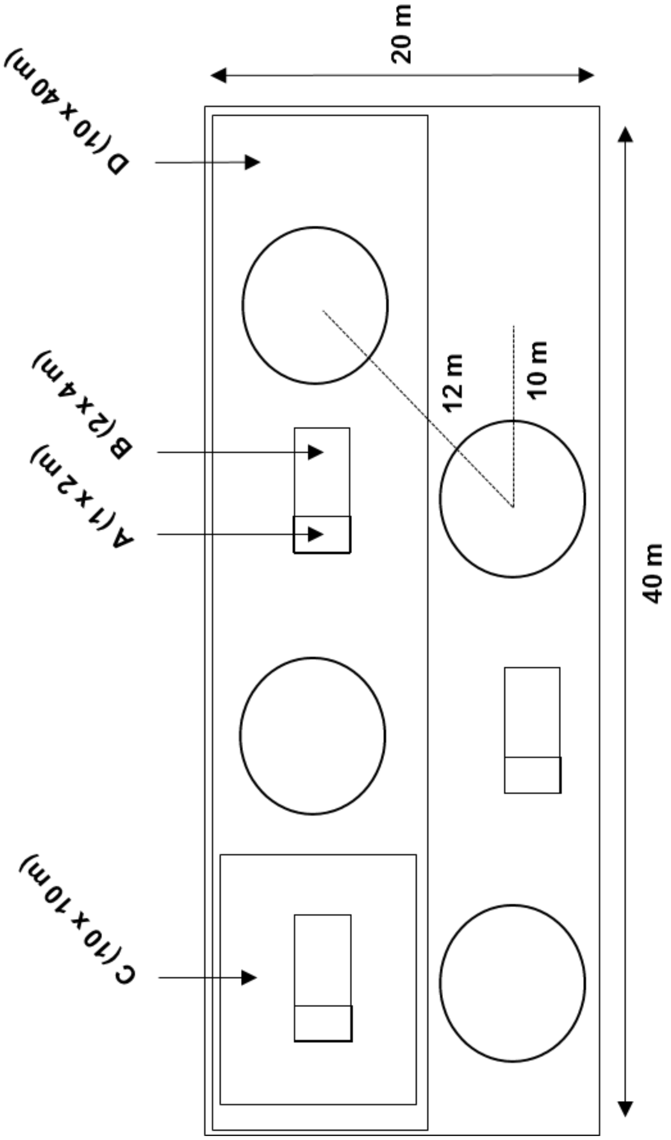

Fig. 2

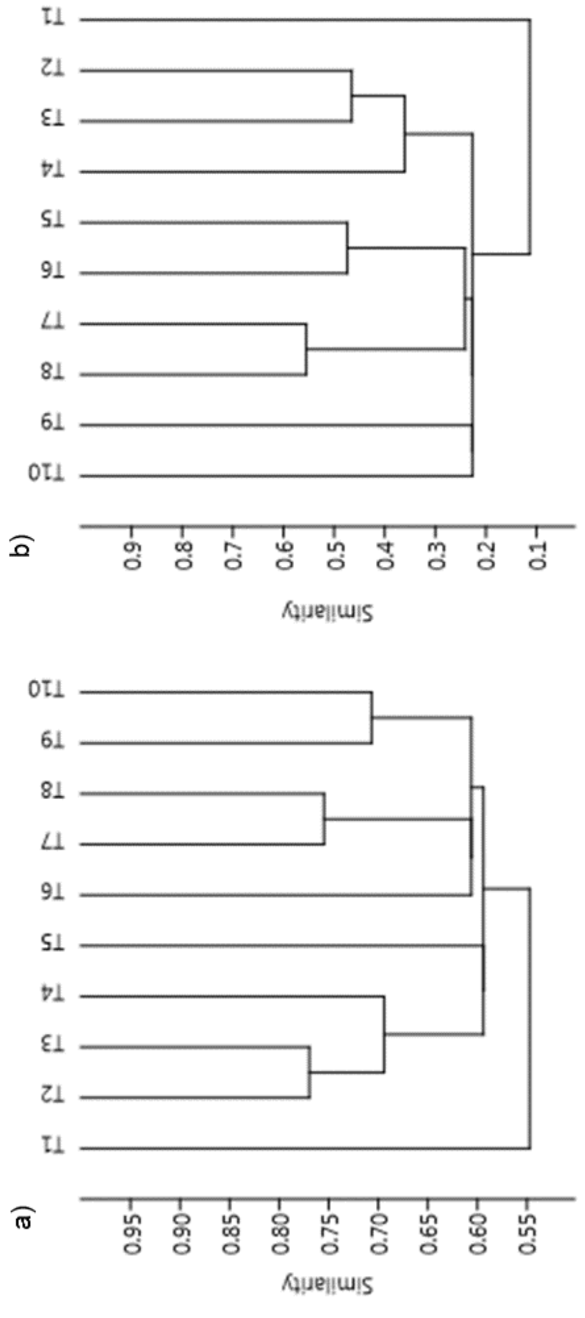
a)
Similarity
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
T1
T2
T3
T4
T5
T6
T7
T8
T9
T10
b)
Similarity
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
T1
T2
T3
T4
T5
T6
T7
T8
T9
T10

Fig. 3

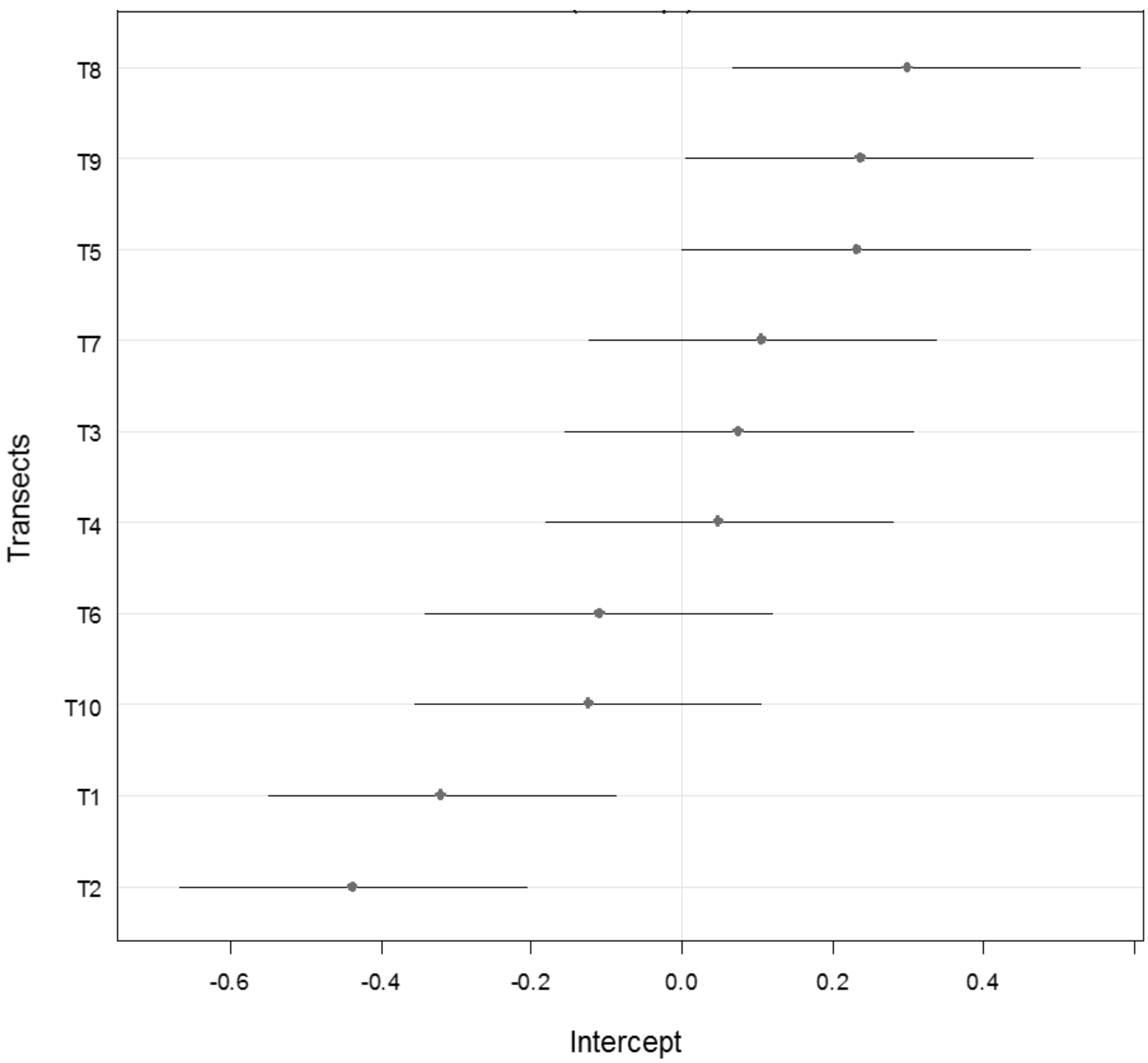
T8
T9
T5
T7
T3
T4
T6
T10
T1
T2
Transects
-0.6
-0.4
-0.2
0.0
0.2
0.4
Intercept

Fig. 4

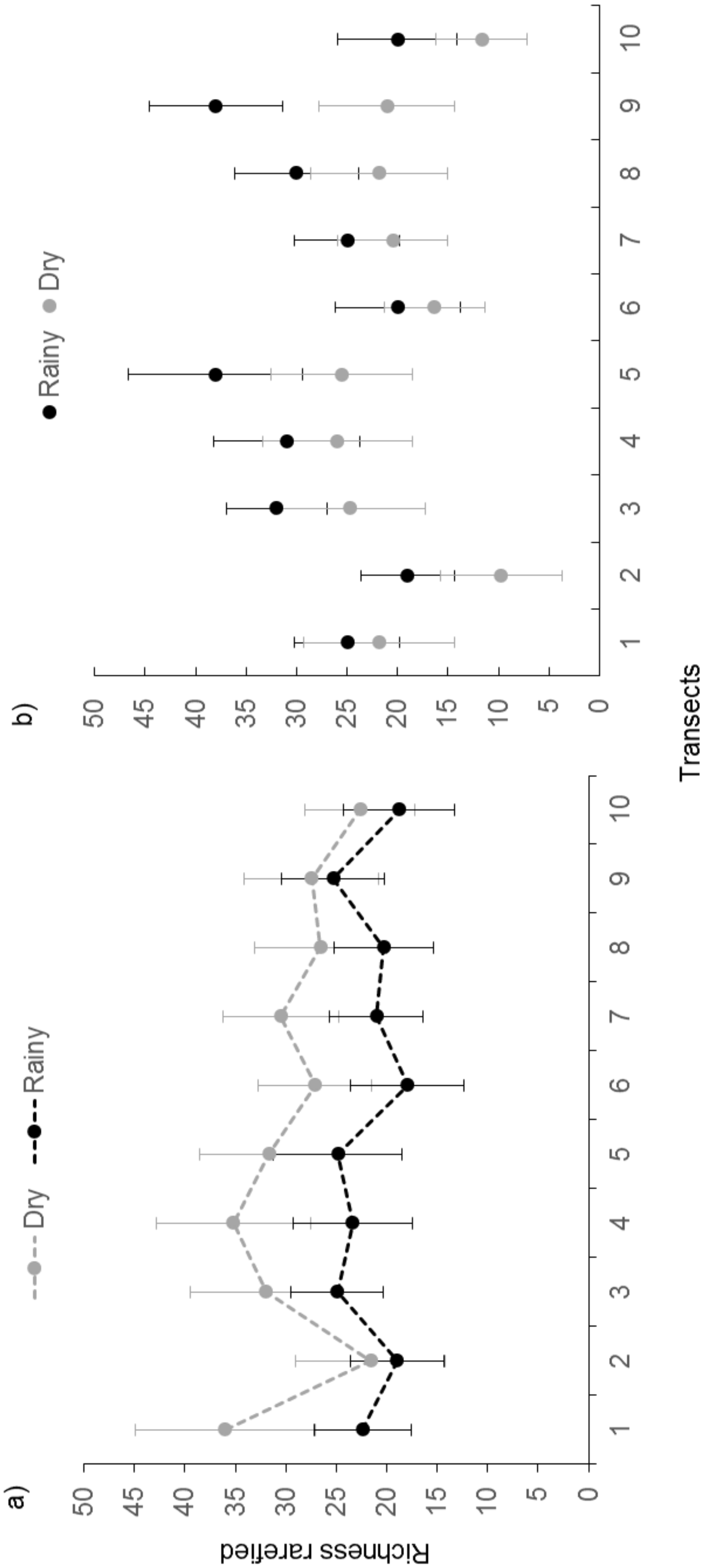a)
Dry
Rainy
Richness rarefied
50
45
40
35
30
25
20
15
10
5
0
1
2
3
4
5
6
7
8
9
10
b)
Rainy
Dry
50
45
40
35
30
25
20
15
10
5
0
1
2
3
4
5
6
7
8
9
10
Transects

Fig. 5

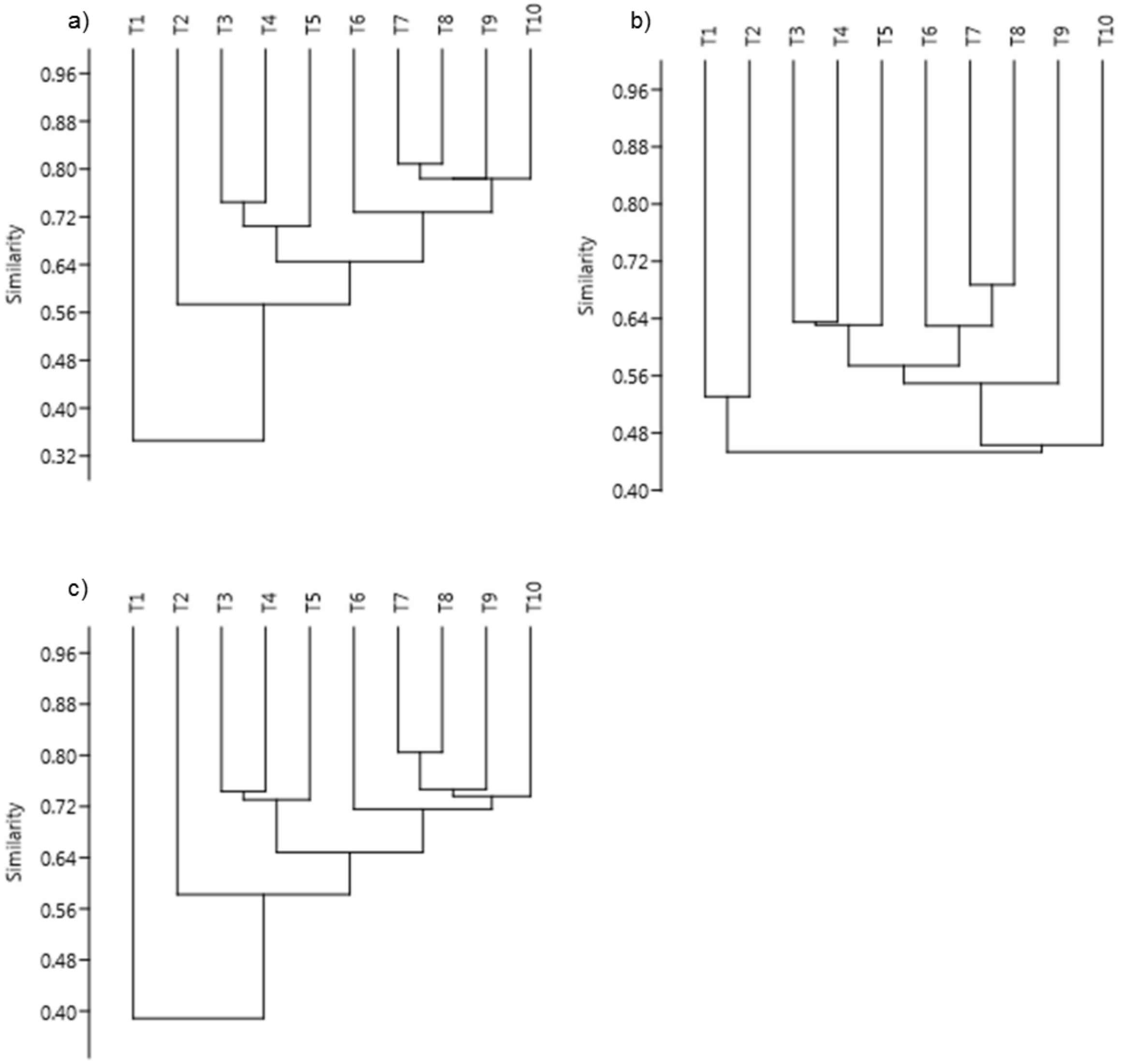
a)
T1
T2
T3
T4
T5
T6
T7
T8
T9
T10
Similarity
0.96
0.88
0.80
0.72
0.64
0.56
0.48
0.40
0.32
b)
T1
T2
T3
T4
T5
T6
T7
T8
T9
T10
Similarity
0.96
0.88
0.80
0.72
0.64
0.56
0.48
0.40
c)
T1
T2
T3
T4
T5
T6
T7
T8
T9
T10
Similarity
0.96
0.88
0.80
0.72
0.64
0.56
0.48
0.40

Fig. 6

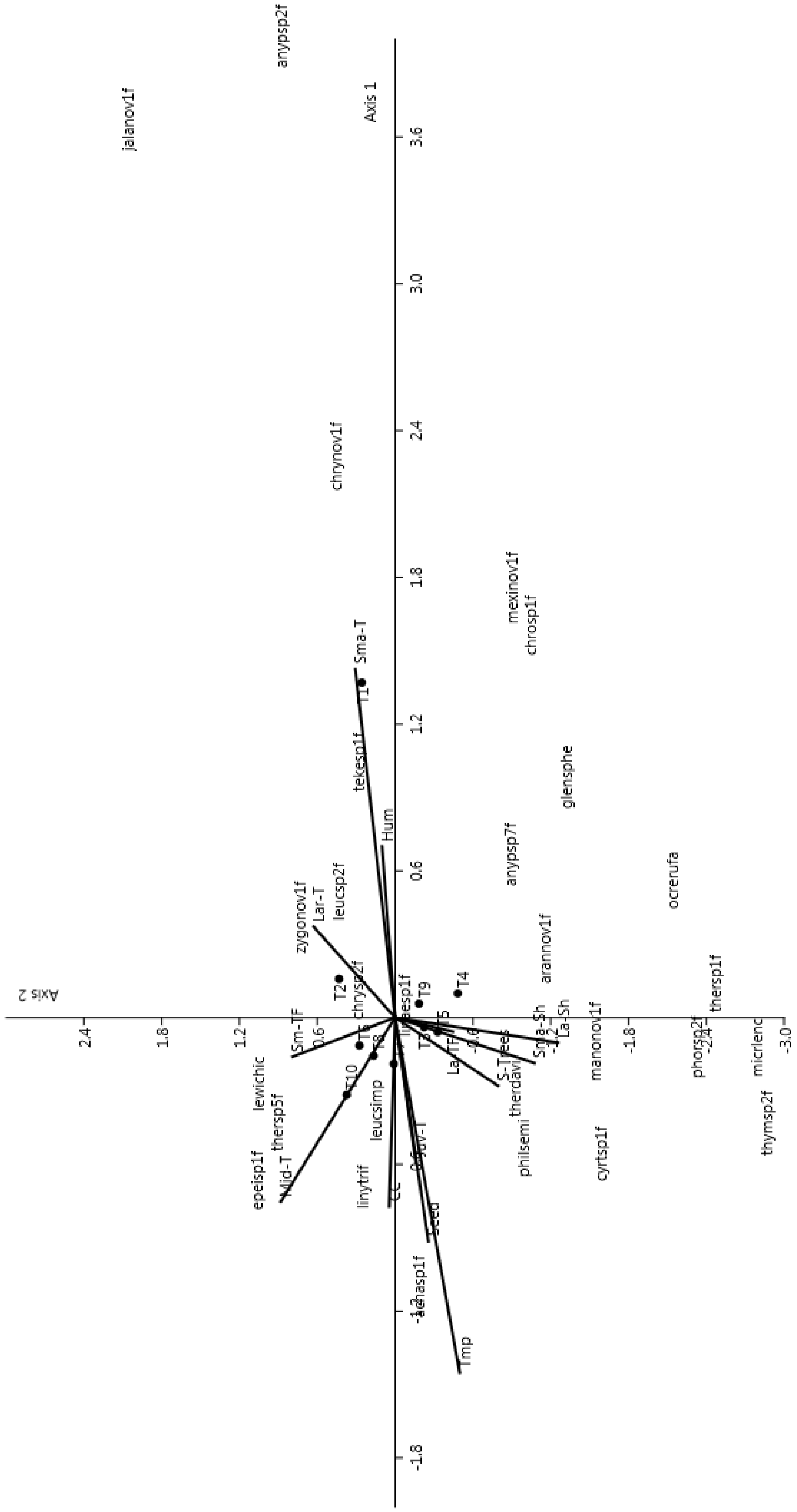
Axis 1
Axis 2
3.6
3.0
2.4
1.8
1.2
0.6
-0.6
-1.2
-1.8
-2.4
-3.0
jalanov1f
anypsp2f
chrynov1f
mexinov1f
chrosp1f
Sma-T
T1
tekesp1f
glensphe
Hum
anypsp7f
ocrerufa
leucsp2f
Lar-T
zygonov1f
arannov1f
thersp1f
T2
chrysp2f
T9
T4
Sm-TF
T6
T8
T10
lewichic
thersp5f
epeisp1f
Mid-T
leucsimp
linytrif
CC
Juv-T
Seed
achasp1f
Tmp
T3
T5
La-TF
S-Trees
Sma-Sh
La-Sh
therdavi
philsemi
manonov1f
cyrtsp1f
phorsp2f
micrlenc
thymsp2f

Fig. 7

Appendix

List of spider species and abundance per transect used in canonical correspondence analyses for understory spider in El Triunfo Biosphere Reserve cloud forest.

Code	Species	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	Total
achasp1f	*Achaearanea* sp.1	0	0	8	0	3	1	0	6	2	4	24
anypsp2f	*Anyphaena* sp.2	8	0	1	0	2	0	3	5	2	0	21
anypsp7f	*Anyphaena* sp.7	5	1	5	7	14	9	3	4	9	4	61
arannov1f	*Araneus* sp.1	4	3	15	6	17	1	6	10	8	5	75
chrosp1f	*Chrosiothes* sp.1	3	2	1	8	2	0	0	7	0	0	23
chrynov1f	*Chrysometa* sp.1	80	38	20	36	35	39	23	53	58	11	393
chrysp2f	*Chrysometa* sp.2	4	6	3	6	5	3	3	14	15	9	68
cyrtsp1f	*Cyrtognatha* sp.1	0	0	0	5	5	3	3	4	3	0	23
epeisp1f	*Epeirotypus* sp.1	3	78	67	41	55	68	65	121	38	129	665
glensphe	*Glenognatha spherella*	22	14	41	35	42	8	17	20	38	8	245
jalanov1f	*Jalapyphantes* sp.1	28	16	9	4	3	6	2	1	3	13	85
leucsimp	*Leucauge simplex*	34	85	145	132	170	183	242	272	272	233	1768
leucsp2f	*Leucauge* sp.2	6	23	4	3	30	9	5	18	8	3	109
lewichic	*Lewisepeira chichinautzin*	1	1	4	1	1	8	2	0	1	2	21
linaesp1f	Linyphiidae sp.1	1	1	1	3	2	3	2	1	4	3	21
linytrif	*Linyphia trifalcata*	2	3	13	1	25	21	26	32	10	10	143
manonov1f	*Manogea* sp.1	0	0	1	3	6	4	3	0	12	2	31
mexinov1f	*Mexigonus* sp.1	19	7	21	29	4	10	12	7	14	4	127
micrlenc	*Micrathena lenca*	1	0	16	14	22	1	6	4	3	1	68
ocrerufa	*Ocrepeira rufa*	0	0	0	2	1	2	0	0	30	0	35
philsemi	*Philoponella semiplumosa*	0	0	1	8	1	1	6	11	0	0	28
phorsp2f	*Phoroncidia* sp.2	0	3	7	3	19	1	1	1	3	1	39
tekesp1f	*Tekellina* sp.1	14	1	2	6	2	5	21	9	21	8	89
therdavi	*Theridiosoma davisi*	8	12	50	72	38	18	56	55	33	30	372
thersp1f	*Theridion* sp.1	1	2	9	30	22	3	13	9	30	2	121
thersp5f	*Theridion* sp.5	7	24	9	12	25	33	31	33	22	33	229
thymsp2f	*Thymoites* sp.2	0	1	10	17	17	0	8	3	3	2	61
zygonov1f	*Zygoballus* sp.1	4	7	4	5	3	1	8	16	4	4	56
	Total	255	328	467	489	571	441	567	716	646	521	5001

Conclusiones

1. Se registraron un total de 5,441 arañas colectadas en 240 muestras (749 adultos y 4,692 inmaduros) pertenecientes a 17 familias, 52 generos, 16 especies y 84 morfoespecies. *Leucauge simplex* (Tetragnathidae) y *Epeirotypus* sp.1 (Theridiosomatidae) fueron las especies más abundantes. Las familias Theridiidae, Tetragnathidae y Linyphiidae fueron dominantes en abundancia y riqueza, como en otros estudios realizados en bosques de niebla tropicales (Sorensen, 2003; Maya et al., 2012).
2. En general, los valores de eficiencia de muestreo (50-80%, rasonable a comprensible *sensu* Cardoso, 2009), demuestran que se obtuvo un buena representación de la composición de especies que habitan este bosque.
3. El bosque de niebla perenne de la zona núcleo I de la Reserva de la Biósfera El Triunfo presentó diferencias espaciales (estructura del bosque) y temporales (covertura del dosel), indicando un grado de heterogeneidad semejante al observado en otros bosques de niebla del sureste del país (Challenger, 1998; Williams-Linera, 2003; Rzedowski, 2006; CONABIO, 2010, Villaseñor, 2010).
4. La riqueza y abundancia de los ensambles de arañas presentaron diferencias temporales y espaciales, indicando un cierto grado de heterogeneidad. Sin embargo, las variables ambientales consideradas en el estudio no explican dicha heterogeneidad.
5. Para comprender mejor la distribución de los ensambles de arañas del sotobosque y su relación con las características del bosque de niebla, se sugiere considerar la inclusión de otras escalas espaciales y variables ambientales distintas a las evaluadas en la presente investigación.

6. Los resultados obtenidos en la presente investigación contribuyen al conocimiento de la dinámica del bosque de niebla perenne en la zona núcleo 1 de la Reserva de la Biósfera el Triunfo.

7. Dado el estado actual de vulnerabilidad que presentan estos ecosistemas terrestres, el conocimiento generado a partir de la presente investigación puede contribuir a mejorar la planeación para su conservación.

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