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Source: Florida Entomologist, 99(2) : 248-256

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.099.0214

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Myrmecofauna (Hymenoptera: Formicidae) response to habitat characteristics of tropical montane cloud forests in central Veracruz, Mexico

*Miguel Á. García-Martínez, Dora L. Martínez-Tlapa, Gibrán R. Pérez-Toledo, Luis N. Quiroz-Robledo, and Jorge E. Valenzuela-González**

Abstract

Tropical montane cloud forests are characterized by a persistent cloud cover at the vegetation level. In central Veracruz, Mexico, these forests are found distributed in several small fragments with differing degrees of disturbance. In this changing ecosystem, the use of indicator groups has been proposed to assess disturbance effects on biodiversity. Ants may serve as bioindicators in various contexts, as they are social insects that have a high response capacity to environmental stimuli. In this study, the relationship of several environmental characteristics to ant diversity was measured in 5 fragments of tropical montane cloud forest in central Veracruz. In total, 5,270 individuals belonging to 75 species, 29 genera, 13 tribes, and 8 subfamilies were collected. The richness, diversity, and evenness increased significantly as a function of the structural complexity of the vegetation. In terms of composition and structure, the assemblages showed high heterogeneity between fragments. The similarity analyses showed high species complementarity between fragments, with a large proportion of unique species to each fragment. A high rate of species turnover is likely due to fragment isolation and its subsequent influence on habitat quality. However, the results demonstrated that overall, the remaining fragments of tropical montane cloud forest sheltered a large ant richness and diversity. In consideration of the observed habitat disturbances, it is necessary to implement measures that would allow for the conservation of the remaining fragments of cloud forest, as they represent an important reservoir of ant species and likely of other organisms as well.

Key Words: ant; fog forest; diversity; turnover; disturbance

Resumen

El bosque mesófilo de montaña es caracterizado por una persistente nubosidad a nivel de vegetación. En el centro de Veracruz, México, se compone por un conjunto de pequeños fragmentos con diferente grado de perturbación. Se ha propuesto evaluar los cambios en la biodiversidad causados por perturbaciones usando grupos indicadores. Las hormigas son insectos con una alta capacidad de respuesta bioindicadora en diferentes contextos. Se estudió la relación del ambiente y la estructura de la vegetación con la diversidad de hormigas asociada a cinco fragmentos de bosque mesófilo de montaña en el centro de Veracruz. En total se colectaron 5,270 individuos pertenecientes a 75 especies, 29 géneros, 13 tribus y ocho subfamilias. La riqueza, la diversidad y la equidad incrementaron significativamente en función de la complejidad estructural de la vegetación. Tanto en composición como en estructura, los ensambles muestran una alta heterogeneidad entre fragmentos. El análisis de similitud mostró una alta complementariedad entre ellos con una proporción importante de especies exclusivas en cada uno. El alto recambio de especies se debe posiblemente a la distribución aislada de los fragmentos y a la influencia de la calidad del hábitat. Los resultados obtenidos muestran que los fragmentos de bosque mesófilo de montaña que aún se conservan en la zona albergan una gran riqueza y diversidad de hormigas. Debido a la alta perturbación que se observa, es urgente la implementación de medidas que permitan y favorezcan la conservación de los pocos fragmentos que aún existen en la zona, puesto que representan un importante reservorio para las hormigas y muy probablemente también para otros organismos.

Palabras Clave: hormigas; bosque de niebla; diversidad; recambio; perturbación

Tropical montane cloud forest (TMCF) is a physiognomically heterogeneous floristic group, composed of species with diverse biogeographic affinities and characterized by a persistent cloud-cover that envelops its vegetation (Williams-Linera 2007). It is considered threatened throughout the world due to its limited and fragmented physical and climatological distribution at medium altitudes or mid-level mountainous ranges. It occupies 2.5% of the land surface area worldwide, although it is estimated that 44% of the original forest cover has been lost, mainly due to deforestation for agricultural purposes (Bruijnzeel et al. 2010).

In Mexico, TMCF is one of the most threatened ecosystems, occupying less than 1% of the national territory. Although it is highly diverse and offers important hydrological environmental services, it is estimated that more than 50% of the original area of TMCF has been deforested and converted to other land uses (Williams-Linera et al. 2002, 2015). Veracruz, Mexico, once had a high percentage of TMCF land cover, but currently most of this area has been converted to other land uses. The central mountainous region of this state is composed of several fragments with differing degrees of disturbance that are surrounded by secondary vegetation, coffee and sugarcane plantations,

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bean and corn crops, pastures, and human settlements (Williams-Linera et al. 2002, 2015).

The rapid changes endured by many ecosystems require the identification of sensitive organisms that can rapidly provide information on ecosystem conditions, alterations, or the potential restoration of an environment (Favila & Halffter 1997). In this sense, ants are an insect group that serve as good bioindicators due to their capacity to respond to changes in the environment in a wide range of contexts (Quiroz-Robledo & Valenzuela-González 1995; Bustos & Ulloa-Chacón 1997; Estrada & Fernández 1999). They are both abundant and diverse in tropical and subtropical regions of the world. Their ecological importance is due to their influence on diverse ecosystem processes and their associated presence/absence in relationship to certain plant or invertebrate communities (Hölldobler & Wilson 1990).

There are several studies on myrmecofauna associated with TMCF carried out in Brazil (Queiroz et al. 2013), Colombia (Bustos & Ulloa-Chacón 1997; Estrada & Fernández 1999), and Costa Rica (Longino & Nadkarni 1990; Schonberg et al. 2004). In Mexico, some comparisons have been carried out on the composition of ant communities between TMCF fragments and coffee plantations (Perfecto & Vandermeer 2002; Ramos-Suárez et al. 2002; Valenzuela-González et al. 2008).

However, the effects of the habitat characteristics that could potentially regulate ant assemblages in TMCF fragments have been little studied (Queiroz et al. 2013). Some studies have shown that an increase in the structural complexity of vegetation leads to an increase in ant diversity (Bustos & Ulloa-Chacón 1997; Ramos-Suárez et al. 2002; Schonberg et al. 2004). In the current study, we examined the relationship between several environmental characteristics with the alpha and beta diversity of ant assemblages within 5 fragments of TMCF in the central mountainous region of Veracruz, Mexico.

Materials and Methods

The study area is found in the central mountainous region of the state of Veracruz, Mexico, spanning an altitudinal range of 1,000 to 1,590 m asl (Fig. 1). The climate is humid temperate, and the average annual temperature is 18 °C. The annual precipitation varies from 1,500 to 2,000 mm. A hot–dry season exists from Mar to May, a warm–rainy season from Jun to Oct, and a cold–dry season from Nov to Feb. The soil is characterized as Andosol, with a volcanic origin and loamy texture (Williams-Linera et al. 2002, 2015).

Five fragments of TMCF (F1–F5) were selected, separated by distances varying from 7 to 30 km (Table 1; Fig. 1). F1 (90 ha) and F3 (31 ha) are both natural protected areas, and F2 (30 ha), F4 (19 ha), and F5 (10 ha) are private properties. These forest fragments are immersed within a matrix of forest, coffee plantations, pasture lands, row crops (mainly maize), and secondary vegetation in various degrees of recovery (Williams-Linera et al. 2002, 2015). Within the study area, the TMCF has been subjected to firewood collection, selective logging within the forest, and harvesting of epiphytes as non-timber forest products for ornamental and ceremonial purposes (Toledo-Aceves et al. 2014). In each fragment, the sampling was performed with 10 circular sampling units with a radius of 8 m and separated by 50 m.

To locally characterize the fragments, in each sampling unit the following attributes were recorded: 1) slope, using a PM-5/360 PC clinometer (Suunto, Co., Vantaa, Finland); 2) percentage of canopy cover, using a spherical, convex model A densitometer (Forestry Suppliers, Inc., Jackson, Mississippi); 3) percentage of soil covered by leaf litter, grass, and other herbaceous plants, including uncovered soil, in an area delimited by a square frame of 1 m^2; 4) soil compaction, using a hand-held penetrometer (JDBlab, Cochabamba, Bolivia); 5) species composition and richness of trees with a diameter at breast height (DBH) of ≥5 cm; and 6) DBH (measured at 1.3 m from the ground) and height of trees, using a Haga model altimeter (Forestry Suppliers, Inc., Jackson, Mississippi).

For collecting ants, in each sampling unit the following traps were set: 1) one subterranean trap; 2) two pitfall traps, with and without tuna bait; and 3) two traps in low-lying tree vegetation (1.5–2 m in height) with tuna or honey baits. The traps were recovered after 72 h of exposure in the field. Subterranean traps consisted of 250 mL plastic containers, each with a smaller 60 mL container inside containing tuna bait; the latter was glued to the bottom of the first. The larger container was half-filled with propylene glycol diluted in water (50%), and 3 mm wide perforations were made around the circumference, 2 cm above the level of propylene glycol. These traps were then placed 10 cm underground. Pitfall traps consisted of a 500 mL plastic container with a diameter of 5 cm. These containers were filled to one-fourth of their capacity with diluted propylene glycol and buried such that the opening was flush with the ground. In each sampling unit we placed 2 traps, 1 baited with tuna and 1 without bait. For the traps at vegetation level, honey-baited traps consisted of closed 100 mL plastic containers with 20 mL of honey. Perforations were made around the circumference of each container approximately 2 cm above the honey. Tuna-baited traps consisted of 150 mL plastic containers, each with a smaller 60 mL container inside, containing tuna as bait; the latter was glued to the bottom of the first. The larger container was half-filled with diluted propylene glycol and 3 mm wide perforations were made around the circumference. These traps were placed in tree trunks at heights between 1.5 and 2 m (Quiroz-Robledo & Valenzuela-González 1995).

In addition, a 1 m^2 quadrate of leaf litter was collected per sampling unit from the ground and sifted through a 1 cm^2 opening sieve. These leaf litter samples were processed in Winkler sacks for 72 h for extracting ants (Bestelmeyer et al. 2000).

The specimens were determined at the genus level following the key of Mackay and Mackay (1989) and several keys for species identification depending on the genus involved. Voucher specimens were deposited in the Entomological Collection of Instituto de Ecología A.C. in Xalapa, Veracruz, Mexico (IEXA; Reg. SEMARNAT: Ver. IN.048.0198).

Because the environmental variables did not fulfill the basic parametric assumptions, non-parametric Kruskal–Wallis tests were used for comparing attributes among fragments. To avoid collinearity, all variables were tested using Spearman's rank correlation coefficient. These analyses were carried out in the software R 3.1.1 (R Development Core Team 2014).

Species occurrences (i.e., the number of times that a given species was collected in a trap) were taken into account as proxies for relative ant abundance. Because the comparison of richness among assemblages is only ecologically appropriate for similar sampling completeness, the sample coverage ($\hat{C}n$) was calculated for each fragment. This value indicates the proportion of the statistical population that is represented by the captured species (Chao & Jost 2012) and is expressed by the following equation:

$$\hat{C}n = \left(1 + \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]\right) * 100$$

where n is the relative abundance of the sample, and f_1 and f_2 are singletons and doubletons, respectively. $\hat{C}n$ has values from 0 (minimal completeness) to 100 (maximum completeness). When completeness is close to 100% and similar among assemblages, richness values can be compared directly (details in Chao & Jost 2012). Values of $\hat{C}n$ were calculated using iNEXT and compared at their 95% confidence interval (Hsieh et al. 2013).

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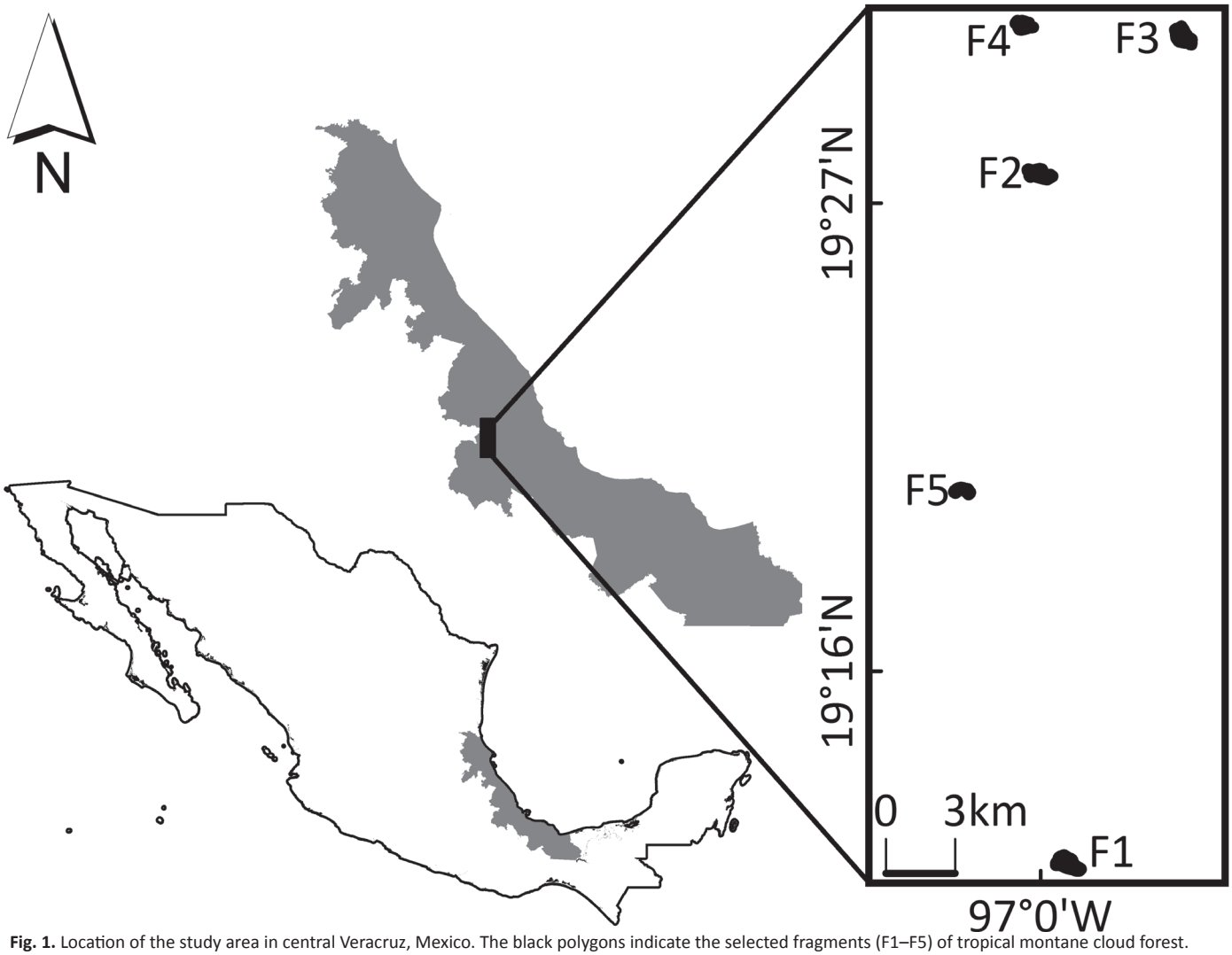

Fig. 1. Location of the study area in central Veracruz, Mexico. The black polygons indicate the selected fragments (F1–F5) of tropical montane cloud forest.

To compare the alpha diversity, diversity profiles were created for the orders $q = 0$, $q = 1$, and $q = 2$. The diversity of order zero (^0D) was represented by the number of observed species. Shannon's diversity of the first order (^1D) used the relative frequency of each species, thereby avoiding a favoring of rare or dominant species, and is equivalent to the exponential factor of the Shannon entropy index. The diversity of the second order (^2D) was equivalent to the inverse of the Simpson index, favoring dominant species within the assemblages (Jost et al. 2010). These calculations were performed in the SPADE software and considered to be significantly different when 95% confidence intervals did not overlap, whereas no differences were assumed when they did overlap at an $\alpha = 0.05$ (Chao & Shen 2010). The patterns in the distribution of abundances of the ant assemblages were represented with rank–abundance curves and were compared with paired Kolmogorov–Smirnov tests in the PAST software (Hammer et al. 2001).

The beta diversity was analyzed by comparing the similarity between fragments with the Sørensen similarity index (relates the number of shared species with the arithmetic mean of the species from all fragments). To represent the matrix of similarity, a cluster analysis was carried out with the UPGMA clustering method (Unweighted Pair Group Method with Arithmetic Mean). The cophenetic coefficient was calculated, which varies from zero to one, in order to establish what proportion of the structured similarity was explained by the dendrogram. A similarity profile analysis (SIMPROF) was used as a statistical means of confirming the generated clusters. These analyses were carried out in the PRIMER software, version 6.1.16 (Clarke & Gorley 2006; Licensed to: Miguel Ángel García Martínez; Type: Full single user; Product: FP6100; User number: Q388).

To test if there was an effect or contribution of the area (fragment size) on the species richness or sampling completeness, we calculated the Spearman's rank correlation coefficient. Three global Biota-Environment + Stepwise (BEST) tests were completed to select the optimum combination of environmental variables that would maximize the correlation with the richness, diversity, and evenness of the ant assemblages. The optimum combination of variables that explained the diversity was represented by a linkage tree analysis (LINKTREE). To validate if the clusters of diversity were significantly influenced by variations in environmental characteristics, a SIMPROF test was calculated. These analyses were carried out in the PRIMER program, version 6.1.16 (Clarke & Gorley 2006; Licensed to: Miguel Ángel García Martínez; Type: Full single user; Product: FP6100; User number: Q388).

Results

FRAGMENT CHARACTERIZATION

The percentage of canopy coverage ($H = 46.7$; $P < 0.001$) and the proportion of the soil covered by leaf litter ($H = 30.92$; $P < 0.001$) de-

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Table 1. Characteristics of the 5 fragments (F1–F5) of tropical montane cloud forest in central Veracruz, Mexico.

Characteristic	F1	F2	F3	F4	F5
Municipality	Huatusco	Coatepec	Xalapa	Tlalnelhuayocan	Ixhuacan
Elevation (m asl)	1,360	1,350	1,250	1,420	1,650
Latitude N	19.1897222°	19.4608333°	19.5116667°	19.5183333°	19.3369444°
Longitude W	96.9877778°	96.9972222°	96.9369444°	97.0041667°	97.0300000°
Area (ha)	90	30	31	19	10
Slope of terrain (°)	54.2 ± 13.7a	56.0 ± 7.3a	52.2 ± 4.4a	66.8 ± 1.9a	18.0 ± 8.0b
Leaf litter cover (%)	91.4 ± 7.1a	80.7 ± 12.6b	71.1 ± 19.3c	69.6 ± 14.6d	54.8 ± 27.1e
Herb cover (%)	8.3 ± 7.2a	15.0 ± 12.2a	8.3 ± 9.0a	11.2 ± 8.6a	2.0 ± 2.6b
Grass cover (%)	0.1 ± 0.3a	0.4 ± 1.1b	10.5 ± 9.8c	12.3 ± 11.4d	28.7 ± 32.8e
Bare ground cover (%)	0.1 ± 0.3a	3.7 ± 3.8b	10.0 ± 10.5c	6.8 ± 8.4d	14.3 ± 14.3e
Compaction (kg/m²)	5.3 ± 0.7a	8.9 ± 1.4b	10.1 ± 0.4c	13.1 ± 0.8d	15.6 ± 0.4e
Canopy cover (%)	91.1 ± 4.5a	87.6 ± 3.8b	78.7 ± 6.6c	65.8 ± 7.4d	46.8 ± 11.2e
No. plant species	24.0 ± 2.4a	22.0 ± 4.2a	17.0 ± 2.7b	17.0 ± 3.2b	16.0 ± 4.2b
Canopy height (m)	14.9 ± 1.0a	14.0 ± 1.1a	10.8 ± 1.0a	12.3 ± 0.5b	8.7 ± 0.6a
Basal area (m²/ha)	87.3 ± 28.5a	55.2 ± 10.9a	42.2 ± 9.5a	50.4 ± 7.9a	18.5 ± 4.2b
Tree density (individuals per ha)	1,340 ± 177.7a	1,200 ± 169.5a	1,140 ± 94.0a	1,190 ± 131.7a	620 ± 131.9b
Tree circumference (cm)	61.2 ± 7.8a	62.7 ± 10.1a	50.0 ± 5.6a	53.8 ± 1.6a	54.3 ± 5.4a

Means (± SE) in a row followed by different lowercase letters are significantly different ($P \leq 0.05$; Kruskal–Wallis and Mann–Whitney U tests).

creased significantly and continuously from sites F1 to F5 ($\rho = 0.94$; $P = 0.01$; Table 1). The percentage of uncovered soil ($H = 28.09$; $P < 0.001$), soil covered by grass ($H = 38.95$; $P < 0.001$), and soil compaction ($H = 35.38$; $P < 0.001$) also increased significantly in the same direction across the fragments ($\rho \geq 0.90$; $P = 0.01$). In the case of the slope of the terrain ($H = 23.91$; $P < 0.001$) and the percentage of soil covered by herbs ($H = 23.45$; $P < 0.001$), significant differences were observed only between F5 and all of the other fragments (Table 1), and these 2 variables were positively correlated ($\rho = 0.90$; $P = 0.01$).

With regards to floristic composition, 549 individuals belonging to 49 species of woody plants, 36 genera, and 34 families were recorded. F1 and F2 were significantly richer than the other fragments (Fig. 2). For tree richness ($H = 18.10$; $P = 0.001$) and basal area per ha ($H = 18.33$; $P = 0.001$), significant differences were observed only between F5 and the rest of the fragments, and both variables were positively correlated ($\rho = 0.98$; $P = 0.01$). The DBH of the trees did not vary between fragments and was not correlated with any other variable. The average height of the canopy was significantly less in F4 compared with the other fragments and was not correlated with any of the other environmental variables.

DIVERSITY OF ANT ASSEMBLAGES

In total, 5,270 ants belonging to 75 species, 29 genera, 13 tribes, and 8 subfamilies were collected (Table 2). The greatest numbers of tribes, genera, and species were registered with the subfamily Myrmicinae. The *Pheidole* genus had the largest number of species (14), followed by *Camponotus* (7), *Stenamma* (6), *Nylanderia* and *Solenopsis* (5), *Leptothorax* (4), and *Carebara* and *Strumigenys* (3). *Adelomyrmex*, *Brachymyrmex*, *Cyphomyrmex*, *Labidus*, *Neivamyrmex*, *Odontomachus*, and *Ponera* were each represented by 2 species and the remaining 14 genera by only 1 species.

The most efficient sampling method, with respect to species number, was the leaf litter quadrats processed with Winkler sacks, and the least efficient were the honey- and tuna-baited traps (Table 2). Each method detected some species that others failed to detect, where at a maximum, 36 species (48% of the total richness recorded) were detected by a single sampling method. A comparison of the 6 methods used within the 5 fragments shows the differences among them (Table 2).

The average sample coverage was 92% (range: 86.6–95.5%). The overall sample coverage, considering the 5 fragments, was 96%. The richness of the fragments varied significantly between 21 and 37 species (Fig. 2; Table 2). The diversity profiles showed that the F1 ant assemblage was significantly richer, more diverse, and more equitable than the others (Fig. 3). The F2 assemblage was significantly richer, more diverse, and more equitable than the remaining 3 fragments. The F3, F4, and F5 had a similar richness, diversity, and evenness, as their confidence intervals at 95% overlapped.

The greatest frequency of captures was registered for F5 (138 captures), followed by F2 (102), F1 (96), F3 (86), and F4 (84). The distribution of the species abundance of F5 differed significantly from the other fragments ($D = 0.22$; $P < 0.05$; Fig. 4).

The dendrogram, based on the Sørensen similarity index, adjusted to 89% of the structure of the original data (Fig. 5). At the lowest level of similarity (31.1%), the myrmecofauna of F5 was significantly different from the rest of the sites ($\pi = 3.32$; $P = 0.03$). At 41.8%, without significant differences ($\pi = 2.02$, $P = 0.45$), 2 sub-groups were identified, one by F1 and F2 and the other by F3 and F4.

Of the total number of species, 55% were unique to a single fragment. The number of unique species was largest in F1 and F5, intermediate in F2 and F4, and smallest in F3 (Table 3). Twenty percent of the species were shared between 2 fragments, 16% between 3, 4% between 4, and only 5% were found in all of the fragments (*Camponotus atriceps* [Smith], *Labidus praedator* [Smith], *Pheidole nubicola* Wilson, and *Solenopsis geminata* [F.]).

MYRMECOFAUNA RESPONSES TO FRAGMENT CHARACTERISTICS

The global BEST test indicated an optimal relationship between the species richness and the canopy height, the slope of the terrain, and the percentage of soil covered by grasses ($\rho = 0.89$; $P = 0.02$). The species richness ($\rho = 0.66$; $P = 0.21$) or sampling completeness ($\rho = -0.3$; $P = 0.68$) was not related with fragment size. When fragment size was combined in an explanatory model with the environmental variables, it did not affect ant richness. The diversity was optimally related with canopy coverage, canopy height, and the percentage of the soil covered by leaf litter ($\rho = 0.90$; $P = 0.01$). The evenness was optimally related with the richness of woody species, tree abundance and basal area per ha ($\rho = 0.73$; $P = 0.19$). The LINKTREE analysis (Fig. 6) displayed a split ($R = 0.83$; $B\% = 94.1$) that was statistically significant ($\pi = 3.31$; $P =$

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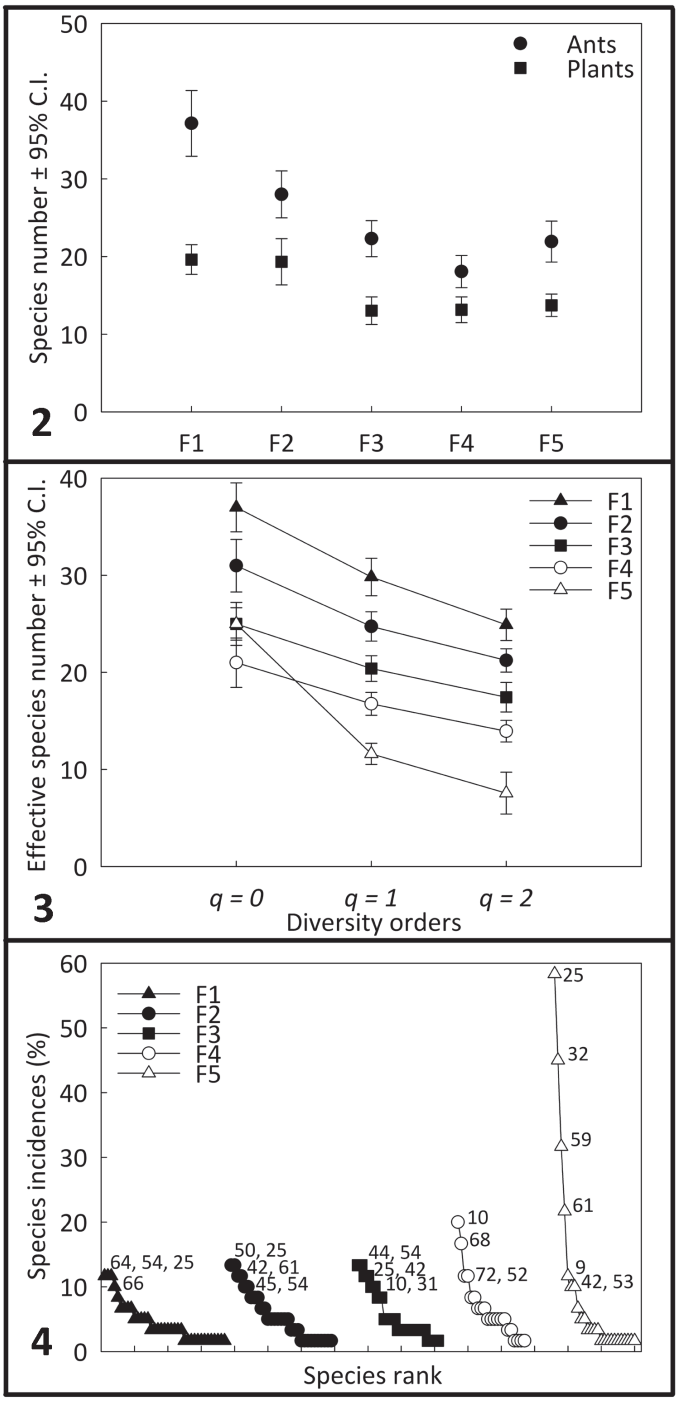

Figs. 2–4. Species richness, diversity profiles, and rank–abundance curves. **Fig. 2.** Comparison of the richness of woody plants at a sampling coverage of 90% and of ants at 85% coverage, among 5 fragments of tropical montane cloud forest in central Veracruz, Mexico. Statistical differences are considered when 95% confidence intervals do not overlap, whereas no differences are assumed when they do overlap, with an α = 0.05. **Fig. 3.** Diversity profiles of the ant assemblages of F1–F5 based on the equivalent species number. Statistical differences are considered when 95% confidence intervals do not overlap, whereas no differences are assumed when they do overlap, with an α = 0.05. **Fig. 4.** Rank–abundance curves of the ant assemblages of F1–F5. Total number of ant incidences in each fragment is 60 traps. Only those species with a relative abundance equal to or higher than 10% in a given fragment are shown. Ant species are numbered in accordance with Table 2.

0.02) between the F5 assemblage and the other sites. This division was distinguished by percentage of canopy cover (≤46.84%), percentage of soil covered by leaf litter (≤54.85%) and grass (≤2.05%), and slope of the terrain (≤16.1°). The successive division of the F3-F4 and F1-F2 assemblages was not significant.

Discussion

The total number of species and/or morphospecies collected in this study represented nearly 27% of the myrmecofauna registered for the state of Veracruz (Vázquez-Bolaños 2011). Approximately 10% of the identified species were new records for the state of Veracruz and 5% for Mexico (Quiroz-Robledo & Valenzuela-González 2010; García-Martínez et al. 2013). These results demonstrated that the TMCF fragments that still exist in the region serve as important refuges for ant diversity, some of which appear to restrict the ants' distribution to these types of environments.

Our results also showed the importance of environmental characteristics on the alpha, beta, and gamma diversity of the ant assemblages, and these results were not affected by fragment size. It has been shown that the characteristics particular to a fragment can favor or limit the availability of space, food, and nesting sites for various groups of insects (Bustos & Ulloa-Chacón 1997). Some investigations suggest that the vegetation structure generates habitat partitions where ants can distribute and organize themselves according to their specific requirements, without necessarily competing with one another (Oliveira et al. 2011; Landero-Torres et al. 2014b). Our results agree with those reported by other authors that indicate that a greater structural complexity of the habitat increased the availability of niches for local ant diversity (Ramos-Suárez et al. 2002; Schonberg et al. 2004; Queiroz et al. 2013).

The completeness of the sampling indicates that a significant portion of ant species that make up the assemblages were collected (>85% in all cases). The portion of the myrmecofauna that was not collected likely corresponds to that associated with tree species and the canopy (not sampled), as the large quantity of epiphytic plants increase the availability of micro-nesting sites (Hölldobler & Wilson 1990; Williams-Linera 2007; Toledo-Aceves et al. 2014). It is expected that the tree strata shelters species that rarely forage in the lowest strata and thus would only occasionally be collected in the soil.

The parameters used to measure the alpha diversity indicated that the 5 studied fragments represented a gradient of structural complexity of ant habitats. A high canopy increased the number of foliage strata, providing improved micro-climatic quality and availability of resources for ants and other arthropods (Oliveira et al. 2011). To the contrary, richness was negatively correlated with the slope of the terrain and the proportion of soil covered by grasses. These characteristics are indicators of the degree of disturbance of the fragments, as it has been demonstrated that forests with greater slopes are less susceptible to logging or clearing than forests with smaller slopes (Landero-Torres et al. 2014c; Luke et al. 2014).

Diversity may also be framed as a function of the coverage and height of the canopy, in addition to the proportion of the soil that is covered by leaf litter (Schonberg et al. 2004; Queiroz et al. 2013). Conditions such as the canopy coverage, soil coverage, vertical complexity, and abundance of leaf litter and organic matter in the soil can influence the availability of nesting and foraging sites for ants (Estrada & Fernández 1999).

An increase in the spatial heterogeneity of forest fragments can also result in an increase in the evenness of the ant assemblages that inhabit them (Bustos & Ulloa-Chacón 1997; Landero-Torres et al. 2014b,c). In our case, the rank–abundance curve of F5 differed significantly from the rest due to the dominance of *S. geminata* (Fig. 4). This species is

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Table 2. Myrmecofauna associated with fragments of tropical montane cloud forest in central Veracruz, Mexico. a) The individuals (occurrence frequency) of each species collected; b) the alpha diversity measures ±95% confidence intervals (95% C.I.), and different letters denote significant differences among fragments ($P < 0.05$); c) relative abundance of the species collected using each trap type.

Parameters and ant species	F1	F2	F3	F4	F5
a) Species abundance					
Subfamily Dolichoderinae Forel					
Tribe Leptomyrmecini Emery					
1. *Azteca velox* Forel					4 (1)
2. *Forelius damiani* Emery					3 (1)
3. *Linepithema* cf. *dispertitum* (Forel)					3 (1)
Subfamily Dorylinae Leach					
Tribe Dorylini Leach					
4. *Eciton burchellii* (Westwood)	15 (3)	3 (3)			
5. *Labidus coecus* (Latreille)	349 (3)			3 (3)	
6. *Labidus praedator* (Smith)	36 (3)	54 (3)	10 (2)	3 (3)	184 (6)
7. *Neivamyrmex rugulosus* Borgmeier	2 (2)				
8. *Neivamyrmex sumichrasti* (Norton)	73 (4)	1 (1)			
Subfamily Ectatomminae Emery					
Tribe Ectatommini Emery					
9. *Gnamptogenys strigata* Norton		3 (3)	5 (2)	2 (2)	8 (7)
Subfamily Formicinae Latreille					
Tribe Camponotini Forel					
10. *Camponotus atriceps* (Smith)	8 (2)	20 (3)	16 (5)	20 (12)	3 (3)
11. *Camponotus claviscapus* Forel	1 (1)				
12. *Camponotus* cf. *elevatus* Forel					2 (2)
13. *Camponotus linnaei* Forel					2 (1)
14. *Camponotus* sp. 1					2 (1)
15. *Camponotus* sp. 2				2 (1)	
16. *Camponotus striatus* (Smith)					4 (1)
Tribe Lasiini Ashmead					
17. *Acropyga exsanguis* (Wheeler)		1 (1)			
Tribe Plagiolepidini Forel					
18. *Brachymyrmex depilis* Emery	17 (3)	4 (4)		16 (4)	
19. *Brachymyrmex musculus* Forel	1 (1)	16 (2)			
20. *Myrmelachista zeledoni* Emery	1 (1)				
21. *Nylanderia austroccidua* (Trager)	8 (4)	1 (1)			
22. *Nylanderia* sp. 1		7 (3)	11 (1)		
23. *Nylanderia* sp. 2	1 (1)				
24. *Nylanderia* sp. 3				17 (4)	
25. *Nylanderia steinheili* Forel	21 (7)	53 (7)	62 (7)		30 (13)
Subfamily Myrmicinae Lepeletier					
Tribe Attini Smith					
26. *Apterostigma pilosum* Mayr					1 (1)
27. *Cyphomyrmex minutus* Mayr		21 (1)			
28. *Cyphomyrmex wheeleri* Forel			2 (1)		
29. *Pheidole biconstricta* Mayr	38 (2)				
30. *Pheidole flavens* Roger		23 (3)	6 (2)		
31. *Pheidole mooreorum* Wilson			8 (7)		1 (1)
32. *Pheidole nubicola* Wilson	6 (2)	42 (6)	38 (8)	24 (7)	35 (19)
33. *Pheidole oaxacana* Wilson		132 (1)	41 (2)		
34. *Pheidole protensa* Wilson	9 (2)				
35. *Pheidole punctatissima* Mayr	4 (2)				
36. *Pheidole scabriventris* Wilson		10 (1)	2 (2)		2 (2)
37. *Pheidole* sp. 1	1 (1)		127 (3)		
38. *Pheidole* sp. 2	16 (1)				
39. *Pheidole ursus* Mayr	1 (1)				
40. *Pheidole* cf. *spadonia* Wheeler					2 (1)
41. *Pheidole titanis* Wheeler		18 (5)	2 (2)	2 (1)	
42. *Pheidole xiston* Mayr	27 (7)	129 (8)	77 (6)		13 (6)
43. *Rhopalothrix weberi* Brown & Kempf					1 (1)

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Table 2. (Continued) Myrmecofauna associated with fragments of tropical montane cloud forest in central Veracruz, Mexico. a) The individuals (occurrence frequency) of each species collected; b) the alpha diversity measures ±95% confidence intervals (95% C.I.), and different letters denote significant differences among fragments ($P < 0.05$); c) relative abundance of the species collected using each trap type.

Parameters and ant species	F1	F2	F3	F4	F5
44. *Strumigenys brevicornis* Mann	1 (1)		62 (8)	15 (5)	
45. *Strumigenys crementa* (Bolton)	2 (1)	15 (6)	16 (3)		
46. *Strumigenys* sp.				13 (3)	
Tribe Crematogastrini Forel					
47. *Crematogaster* sp.	3 (3)				
48. *Leptothorax aztecus* (Wheeler)					2 (2)
49. *Leptothorax* sp. 1	2 (2)				
50. *Leptothorax* sp. 2		17 (7)			
51. *Leptothorax* sp. 3				1 (1)	
52. *Temnothorax striatulus* (Stitz)	2 (2)	1 (1)		7 (5)	
Tribe Solenopsidini Forel					
53. *Adelomyrmex silvestrii* (Menozzi)					4 (3)
54. *Adelomyrmex tristani* (Menozzi)	27 (7)	5 (5)	37 (6)		
55. *Carebara* sp. 1	9 (1)		11 (2)		
56. *Carebara* sp. 2	23 (2)				
57. *Carebara* sp. 3		7 (1)			
58. *Solenopsis* cf. *conjurata* Wheeler					4 (4)
59. *Solenopsis geminata* (F.)	1 (1)	3 (3)	6 (2)	1 (1)	2051 (35)
60. *Solenopsis* sp. 1	9 (1)	38 (4)			24 (2)
61. *Solenopsis* sp. 2		208 (8)			192 (27)
62. *Solenopsis* sp. 3	4 (4)	1 (1)			
Tribe Stenammini Ashmead					
63. *Stenamma excisum* Branstetter		1 (1)			
64. *Stenamma felixi* Mann	17 (6)				
65. *Stenamma* cf. *lobinodus* Branstetter		11 (5)			
66. *Stenamma nonotch* Branstetter	17 (5)			30 (4)	
67. *Stenamma pelophilum* Branstetter	5 (2)		22 (3)	51 (3)	
68. *Stenamma stictosomum* Branstetter	2 (1)		1 (1)	263 (10)	
Subfamily Ponerinae Lepeletier					
Tribe Ponerini Lepeletier					
69. *Leptogenys longata* (Buckley)			1 (1)		
70. *Odontomachus laticeps* Roger			3 (3)	2 (2)	1 (1)
71. *Odontomachus yucatecus* Brown		2 (2)			
72. *Ponera exotica* Smith				22 (7)	
73. *Ponera pennsylvanica* Buckley			4 (2)	3 (3)	
Subfamily Proceratiinae Emery					
Tribe Proceratiini Emery					
74. *Discothyrea horni* Menozzi		2 (2)			
Subfamily Pseudomyrmecinae Smith					
Tribe Pseudomyrmecini Smith					
75. *Pseudomyrmex gracilis* (F.)	4 (4)		5 (5)	8 (3)	
Total individuals captured	763	849	575	505	2,578
b) Alpha diversity measures ±95% C.I.					
Observed species richness	37 ± 2.52a	31 ± 2.71b	25 ± 2.21c	21 ± 2.55c	25 ± 1.67c
Sampling completeness (%)	86.67 ± 5.94a	90.25 ± 5.13a	95.58 ± 4.29a	95.29 ± 4.30a	92.29 ± 3.60a
c) Species collected using each trap type					
Subterranean traps	9	6	4	2	4
Baited pitfall traps	11	7	7	4	7
Pitfall traps	2	7	6	7	9
Winkler sacks	17	16	18	11	19
Honey-baited traps	8	4	1	5	8
Tuna-baited traps	6	8	2	2	8

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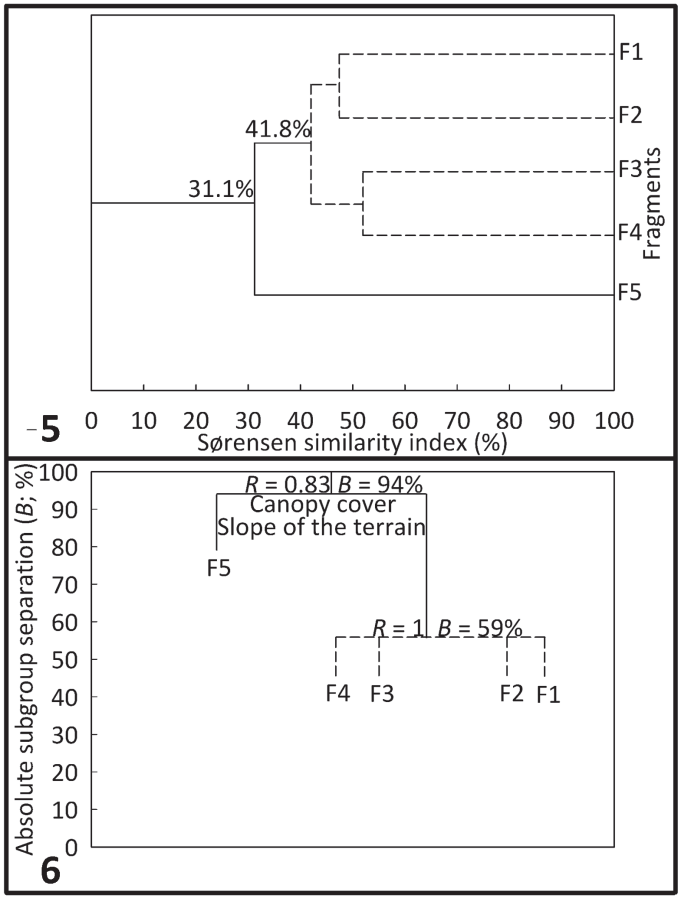

Figs. 5 and 6. Results from cluster and linkage tree analyses. **Fig. 5.** Dendrogram of hierarchical standardized clustering based on the Sørensen similarity index of the studied fragments. The cophenetic correlation coefficient of the cluster is 0.89. The dendrogram displays with continuous lines the divisions for which the SIMPROF test rejects the null hypothesis (where assemblages in that group have no further structure to explore) and with dashed lines the groups of assemblages not separated (at $P < 0.05$) by SIMPROF. **Fig. 6.** Linkage tree analysis (LINKTREE) showing divisive clustering of fragments (F1–F5) from species compositions constrained by inequalities on one or more environmental variables. Only binary partitions of uncorrelated environmental variables are shown in the cluster. The dendrogram displays with continuous lines the divisions for which the SIMPROF test rejects the null hypothesis (where assemblages in that group have no further structure to explore) and with dashed lines the groups of assemblages not separated (at $P < 0.05$) by SIMPROF.

a very abundant generalist and opportunistic ant in the disturbed and open habitats within the study region (Valenzuela-González et al. 2008; Landero-Torres et al. 2014a–c). The dominance of this species in F5 is mainly due to the low percentage of canopy cover, which generates a micro-climate that is thermically favorable in comparison with other fragments (Table 1). Another possible explanation could be related to spatial factors, such as the shape and location of F5, which is a 100 m wide × 1,000 m long linear strip that is located in a matrix of coffee plantations. For these reasons, it could be inferred that it is permeable to typical species from neighboring habitats, in this case *S. geminata* from nearby coffee plantations.

With regards to species composition, the cluster and LINKTREE analyses showed a gradient of structural complexity in the vegetation and the slope of the terrain, separating the more simplified fragment (F5) from the rest of the fragments (Figs. 5 and 6). The grouping of the remaining fragments responded to a gradient of canopy height, separating F1 and F2 on one side and on the other F3 and F4, although without significant differences between them. These results support the hypothesis put forth by Rocha-Ortega & Favila (2013), as our results also indicated that the beta diversity is influenced by environmental filters in each fragment that limit or favor the establishment of certain species of ants in them.

The high species turnover between the 5 ant assemblages that were sampled was due to the high proportion of species that were unique to each fragment (55% of the total). Due to the high beta diversity between the studied assemblages, these unique species contributed independently to the regional gamma diversity. Although some fragments possessed a low richness of ants, species were found within those fragments that are not found anywhere else (Quiroz-Robledo & Valenzuela-González 2010; García-Martínez et al. 2013).

Finally, our results indicate that the remaining TMCF fragments in central Veracruz continue to shelter an important diversity of myrmecofauna. The richness, diversity, and evenness of ant assemblages responded positively to increasing structural complexity of habitats. Changes in local characteristics of TMCF increased the effective number of ant assemblages in the studied region. This high heterogeneity among sites suggests that the maintenance of even highly disturbed fragments can play a strategic role in the conservation of the myrmecofauna and probably of other organisms in the severely transformed landscape of the region. As the TMCF in central Veracruz has suffered extensive transformations and currently exists only as remnant fragments, occupying less than 10% of its original area (Williams-Linera et al. 2002), a regional conservation approach is required to value and preserve the high beta diversity among remaining TMCF fragments. These fragments are the final reservoirs of the high biodiversity of the once continuous forest in this region.

Table 3. Number of species exclusive to each fragment (diagonal value), number of species shared between fragments (values above diagonal values) and Sørensen similarity index (values below diagonal values).

Fragments	F1	F2	F3	F4	F5
F1	**13**	16	14	12	7
F2	47	**8**	14	8	10
F3	45	50	**2**	12	10
F4	41	31	52	**5**	6
F5	22	35	40	26	**13**

Acknowledgments

We are grateful to Magda Gómez-Columna and Víctor Vasquez-Reyes for field assistance in ant sampling and to Javier Tolome-Romero and Claudia Gallardo-Hernández for field assistance in plant species sampling and determination. We thank the 3 anonymous reviewers for their valuable comments and suggestions to improve the manuscript. The manuscript was translated by Allison Marie Jermain. Funding was provided by the Instituto de Ecología A.C. through the strategic project "Biodiversidad del Jardín Botánico-Santuario Bosque de Niebla" INECOL-20035-30890 and project 902-11-10204 to Jorge E. Valenzuela-González.

References Cited

Bestelmeyer BT, Agosti D, Alonso LE, Brandao C, Brown W, Delabie JH, Silvestre R. 2000. Field techniques for the study of ground-dwelling ant: an overview, description, and evaluation, pp. 122–144 *In* Agosti D, Majer J, Alonso LE, Schultz T [eds.], Ants: Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, Washington, District of Columbia.

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Bruijnzeel LA, Kappelle M, Mulligan M, Scatena FN. 2010. Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world, pp. 691–740 *In* Bruijnzeel LA, Scatena FN, Hamilton L [eds.], Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, London, United Kingdom.

Bustos H, Ulloa-Chacón P. 1997. Mirmecofauna y perturbación en un bosque de niebla neotropical (Reserva natural Hato Viejo, Valle del Cauca, Colombia). Revista de Biología Tropical 45: 259–266.

Chao A, Jost L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93: 2533–2547.

Chao A, Shen T. 2010. SPADE (species prediction and diversity estimation). http://chao.stat.nthu.edu.tw/softwareCE.html (licensed access).

Clarke K, Gorley R. 2006. User Manual/Tutorial. PRIMER-E Ltd., Plymouth, United Kingdom.

Estrada C, Fernández C. 1999. Diversidad de hormigas (Hymenoptera: Formicidae) en un gradiente sucesional del bosque nublado (Nariño, Colombia). Revista de Biología Tropical 47: 189–201.

Favila ME, Halffter G. 1997. The use of indicator groups for measuring biodiversity as related to community structure and function. Acta Zoológica Mexicana 72: 1–25.

García-Martínez MA, Valenzuela-González JE, Martínez-Tlapa DL, Quiroz-Robledo LN. 2013. New ant species (Hymenoptera: Formicidae) records for Veracruz State and Mexico. Southwestern Entomologist 38: 661–666.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: paleontological statistics software for education and data analysis. Paleontología Electrónica 4: 1–9.

Hölldobler B, Wilson E. 1990. The Ants. Harvard Belknap, Cambridge, United Kingdom.

Hsieh TC, Ma KH, Chao A. 2013. iNEXT Oonline: Interpolation and Extrapolation (Version 1.0) [Software].]. http://chao.stat.nthu.edu.tw/blog/software-download (last accessed 13 Mar 2016).

Jost L, DeVries P, Walla T, Greeney H, Chao A, Ricotta C. 2010. Partitioning diversity for conservation analyses. Diversity and Distribution 16: 65–76.

Landero-Torres I, García-Martínez MÁ, Galindo-Tovar ME, Leyva-Ovalle LO, Lee-Espinosa HE, Murguía-González J, Negrín-Ruiz J. 2014a. Diversidad alfa de la mirmecofauna del área natural protegida Metlac de Fortín, Veracruz, México. Southwestern Entomologist 39: 541–553.

Landero-Torres I, García-Martínez MÁ, Galindo-Tovar ME, Leyva-Ovalle OR, Lee-Espinosa HE, Murguía-González J, Negrín-Ruiz J. 2014b. Un cultivo ornamental de heliconias como reservorio de la mirmecofauna nativa: un caso de horticultura tropical en el centro de Veracruz, México. Southwestern Entomologist 39: 135–146.

Landero-Torres I, Madrid-Ñeco I, Valenzuela-González JE, Galindo-Tovar ME, Leyva-Ovalle OR, Murguía-González J, Lee-Espinosa HE, García-Martínez MÁ. 2014c. Mirmecofauna de tres agroecosistemas ornamentales con diferente manejo y un remanente de selva en Ixtaczoquitlán, Veracruz, México. Southwestern Entomologist 39: 783–796.

Longino JT, Nadkarni NM. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a Neotropical montane forest. Psyche 97: 81–93.

Luke SH, Fayle TM, Eggleton P, Turner EC, Davies RG. 2014. Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. Biodiversity and Conservation 23: 2817–2832.

Mackay WP, Mackay E. 1989. Clave de los géneros de hormigas en México (Hymenoptera: Formicidae), pp. 1–82 *In* Quiroz-Robledo LN, Garduño-Hernández LMP [eds.], Memorias del II Simposio Nacional de Insectos Sociales, Sociedad Mexicana de Entomología, Morelos, Mexico.

Oliveira M, Lucia T, Morato E, Amaro M, Marinho C. 2011. Vegetation structure and richness: effects on ant fauna of the Amazon–Acre, Brazil (Hymenoptera: Formicidae). Sociobiology 57: 243–267.

Perfecto I, Vandermeer J. 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Conservation Biology 16: 174–182.

Queiroz ACM, Ribas CR, França FM. 2013. Microhabitat characteristics that regulate ant richness patterns: the importance of leaf litter for epigaeic ants. Sociobiology 60: 367–373.

Quiroz-Robledo L, Valenzuela-González J. 1995. A comparison of ground ant communities in a tropical rainforest and adjacent grassland in Los Tuxtlas, Veracruz, Mexico. Southwestern Entomologist 20: 203–213.

Quiroz-Robledo LN, Valenzuela-González JE. 2010. First record of the ant *Rhopalothrix weberi* (Hymenoptera: Formicidae: Myrmicinae) for Mexico. Florida Entomologist 93: 319–320.

R Development Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org (last accessed 11 Mar 2016).

Ramos-Suárez M, Morales H, Ruiz-Montoya L, Soto-Pinto L, Rojas-Fernández P, Monro A, Peña M. 2002. ¿Se mantiene la diversidad de hormigas con el cambio de bosque mesófilo a cafetales? Revista de Protección Vegetal 12: 17–30.

Rocha-Ortega M, Favila ME. 2013. The recovery of ground ant diversity in secondary Lacandon tropical forests. Journal of Insect Conservation 17: 1161–1167.

Schonberg LA, Longino JT, Nadkarni NM, Yanoviak SP, Gering JC. 2004. Arboreal ant species richness in primary forest, secondary forest, and pasture habitats of a tropical montane landscape. Biotropica 36: 402–409.

Toledo-Aceves T, García-Franco J, Williams-Linera G, MacMillan K, Gallardo-Hernández C. 2014. Significance of remnant cloud forest fragments as reservoirs of tree and epiphytic bromeliad diversity. Tropical Conservation Science 7: 230–243.

Valenzuela-González J, Quiroz-Robledo L, Martínez-Tlapa D. 2008. Hormigas (Insecta: Hymenoptera: Formicidae), pp. 107–122 *In* Manson RH, Hernández-Ortíz V, Gallina S, Mehltreter K [eds.], Agroecosistemas cafetaleros de Veracruz: biodiversidad, manejo y conservación, Instituto de Ecología–Instituto Nacional de Ecología, Veracruz, Mexico.

Vásquez-Bolaños M. 2011. Lista de especies de hormigas (Hymenoptera: Formicidae) para México. Dugesiana 18: 95–133.

Williams-Linera G. 2007. El bosque de niebla del centro de Veracruz: ecología, historia y destinos en tiempos de fragmentación y cambio climático. CONABIO–Instituto de Ecología, Veracruz, Mexico.

Williams-Linera G, Manson RH, Isunza-Vera E. 2002. La fragmentación del bosque mesófilo de montaña y patrones de uso del suelo en la región oeste de Xalapa, Veracruz, México. Madera y Bosques 8: 73–89.

Williams-Linera G, López-Barrera F, Bonilla-Moheno M. 2015. Estableciendo la línea de base para la restauración del bosque de niebla en un paisaje periurbano. Madera y Bosques 21: 89–101.

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