Sociobiology 61(1): 35-42 (March, 2014) DOI: 10.13102/sociobiology.v61i1.35-42

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - ANTS

Trophic Guild Structure of a Canopy Ants Community in a Mexican Tropical Deciduous Forest

Gabriela Castaño-Meneses[1,2]

1 - Ecología y Sistemática de Microartrópodos, Depto de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, México, DF.

2 - Current Address: Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, Campus Juriquilla, Querétaro, México.

Article History
Edited by:
Jacques H. C. Delabie, UESC, Brazil
Received 27 July 2013
Initial acceptance 01 November 2013
Final Acceptance 14 November 2013

Keywords
Diversity, Chamela, Fogging, Species Richness

Corresponding author
Gabriela Castaño-Meneses
Ecología y Sistemática de Microartrópodos
Deptamiento Ecología y Recursos Naturales, Facultad de Ciencias, UNAM
Ciudad Universitaria, 04510
México, D. F.
Phone: (52) 55 56 22 49 02
E-mail: gabycast99@hotmail.com

ABSTRACT
Seasonality in tropical dry forest shows extreme changes in the physiognomy of forest as well the available resources in each season, thus, the composition and diversity of fauna inhabiting in that ecosystem show seasonal variations in answer to that changes. The ants constitute a very important element in the canopies of tropical forests, and there is few information about their communities in dry forest. In most of ecosystems, the general patterns of ant distribution show increase of their abundance during the wet season, but according with the characteristics of Chamela tropical dry forest in the Pacific Cost of Mexico, the great amount of epiphytes in the area can be an important resource to the ants, and the canopy can be an environment visited for different species of ants during the driest month. In order to study the seasonal variations in species richness, composition and diversity of ant canopy community in a tropical deciduous forest, seven fogging were performed in a watershed of the Chamela Biological Station, Jalisco State, Mexico, including dry and rainy season. A total of 5 563 ant specimens were collected belong to 46 morphospecies from 17 genera. The most species richness genera were *Camponotus* and *Cephalotes*, with 13 and 6 species respectively, and the most abundant ants were species of *Crematogaster, Tapinoma*, *Cephalotes* and *Camponotus* genera. Nevertheless dominant species were present during all the study, abundance show a great seasonality, with highest values during the dry season. The dominant guild in the canopy was the omnivorous in all study, but differences in guild trophic composition were recorded in each fogging. The ant community in the canopy of Chamela shows important seasonal variations in the composition and trophic guilds dominance, due conditions of this forest, that differences can be result of variations in the exploitation of resources along the year, and vertical migrations of ant species from soil and shrub layer to canopy in the tropical deciduous forest.

Introduction

In tropical regions, ants constitute one of the most abundant and diverse groups in canopies (Tobin, 1995; Davidson et al., 2003; Lach et al., 2010). In Peruvian forest canopy, Wilson (1987) found 135 ant species while in Budongo Forest, Uganda, Schulz and Wagner (2002) recorded 161 species; in the South part of Australia, ants represented about 48% of the total of arboricolous fauna (Andersen & Yen, 1992), while in Borneo constituted near 18% (Stork, 1987) and in New Caledonia close to 7% (Guilbert et al., 1995). Those variations are related with the habitat heterogeneity and the availability of resources, factors that affect the species richness and abundance of the communities, and in the case of tropical ants, they can exploit a great variety of resources that are provided directly or indirectly by several tree species with different phenologies (Ribas et al., 2003; Armbrecht et al., 2004).

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

The seasonality is a very important component of the ant communities structure in tropical forests (Basset et al., 2003), and in the tropical deciduous forest its importance increases considerably (Dirzo et al., 2011), due to the changes in the availability of resources and the ability of the organisms to use them according to their feeding habits. Thus, species composition of trophic guilds shows changes according to the season, due to trophic guilds that answer differently to environmental conditions modifiing the interactions between species and the composition of community (Meyer et al., 2010; Cook et al., 2011).

Into the tropical forest areas, the tropical dry forest ecosystems comprise more than 40% of surface area in the World, but these ecosystems show an important loss of forest area in recent years as a result of accelerated anthropogenic disturbance (Trejo & Dirzo, 2000; Dirzo et al., 2011).

There are few information about the importance of seasonality on the ant activity and structure of communities in the tropical dry forest (Neves et al., 2010), and in Mexico there are only records for the Atlantic Coast (Gove et al., 2005), but there are no studies in the Pacific Coast. The study of ant communities in canopies from Mexico is still unexplored, with a few notes about their abundance (Palacios-Vargas et al., 1999) or their importance as indicators of perturbation (Gove et al., 2005). Thus, in the present work, the temporal variation and the trophic guild distribution in the canopy ant community of Chamela, Jalisco, in the Pacific Cost of Mexico were analyzed in order to study the seasonal pattern shown by ants in this vegetation.

Material and Methods

The study was carried out in the Chamela Biological Station (ChBS) of the Instituto de Biología of Universidad Nacional Autónoma de México (UNAM). This is a natural reserve located at the Pacific Coast of Mexico, in the state of Jalisco (19°83'00"N 105°80'30"W; 150 m elevation). The rainy season, according to Bullock (1986), lasts four months, from July to October, with more than 50% of precipitation during September and October (García-Oliva et al., 2002). Mean annual precipitation and temperature are 788 mm and 24.68ºC, respectively (1977–2000; García-Oliva et al., 2002). Details of physical and biological parameters of the reserve have been compiled by Bullock (1988) and Noguera et al. (2002). The flora and vegetation structure of the forest have been described (Lott, 1985; Lott et al., 1987; Balvanera et al., 2002).

A total of seven fumigations were performed in order to sample the canopy. Fogging sessions were made using a Dyna fog machine. The sampling was performed during rainy and dry seasons from 1992 to 1994, in August and September 1992 (rainy season); May (dry season), July (rainy) and November (dry) 1993; and February and May 1994 (dry). Sampling sites were located in the watershed named 4A (Cervantes et al., 1988), where the tree layer was about 25 m tall. Dominant species in the area are *Guapira macrocarpa* (Miranda), *Celaenodendron mexicanum* Standl., *Lonchocarpus eriocarinalis* Micheli, *Lonchocarpus constrictus* Pittier, *Bursera instabilis* McVaugh & Rzed., *Tabebuia impetiginosa* (Mart.) Standl. and *Caesalpinia eriostachys* Benth., and tree density is about 2,686 ± 84 ind. ha^{-1} (Maass et al., 2002a). The average number of trees sampled in each plot was 30 ± 7 ind. In each occasion, a new plot of 100 m^2 was delimited and 50 plastic funnels with 50 cm of diameter were hung randomly in the shrub layer at 50 cm above floor forest at intervals of 50 cm. According to the number and area of the funnels, the biological material retained in each fogging comprises an area of 9.82m^2, and in total were sampled 68.7m^2 in the seven foggings. The average net primary productivity in the forest is 3.2 Mg $ha^{-1}y^{-1}$ (Martínez-Yrízar et al., 1996). The application of insecticide was between 04:00 and 06:00, using a solution of 3% of Resmethrin in kerosene solution. A total of 6L of solution was used in each application. After 5h of the insecticide application, the funnels were washed with 80% ethanol, in order to collect the specimens fell in them. The material was stored in plastic bottles with 1L capacity. The ant specimens obtained were isolated, quantified and identified as morphospecies. The specimens were deposited in Colección de Hormigas del Ecología y Sistemática de Microartrópodos (LESM), Facultad de Ciencias, UNAM. Only workers and soldiers were considered, because they are a better reference to sample canopy habitats (Wilson, 1987). According to their feeding habit preferences, the species were classified as omnivorous, predators, herbivorous, granivorous and nectarivorous (considered the consumption of extrafloral nectaries and hemipteran secretions; Byk & Del-Claro 2010, 2011).

The diversity index per fumigation was estimated by Shannon diversity index. Species richness, Pielou's evenness, and Simpson's dominance indices were also calculated for the study (Ludwing & Reynolds, 1988).

The effect of the season on the ant abundance was evaluated by a nested ANOVA test, nesting month collection within the corresponding season and significant differences were tested by *post hoc* Tukey's test (Zar, 1984). The Spearman correlation between precipitation and temperature and the diversity indices were calculated, as well as the correlation between ant density and the precipitation and temperature. Climatic data were obtained from the meteorological station of Chamela (http://www.ibiologia.unam.mx/ebchamela/www/clima.html). The analyses were performed using *Statistica* version 9.0 software (StatSoft, 2009).

Seasonal variations in the ant community composition were analyzed by ordination analysis through nonmetric dimensional scaling (NMDS), and similarity between groups was tested by a similarity analysis (ANOSIM), using 1000 permutations, following Clarke (1993) and Clarke and Green (1988). Analyses were performed using PAST software (Hammer et al., 2001).

Results

A total of 5,563 specimens belonging to 46 morphospecies belonging to 17 genera of ants were collected during the seven fumigations (Appendix 1). The average density of ants in the canopy was 81 ind/m^2, while the species ant density was 26 species/m^2. The Myrmicinae subfamily was the most diverse, represented by 21 morphospecies grouped in nine genera. The most abundant genus in the sampling was *Crematogaster*, with *Crematogaster crinosa* Mayr as the most abundant species, shown an average density of 26 ind/m^2 in the canopy, representing the 32% of the total. This genus is considered predominantly arboriculous.

The genus *Camponotus* was the most rich in morphospecies number, with 13 species, followed by *Pseudomyrmex* and *Cephalotes* (five each one). All of them are considered predominantly arboricolous.

The calculated diversity indices to the ant community in canopy show values relatively high, compared with other studies, and there are variations between fumigations (Table 1). The highest diversity values were found during the rainy months (August, September), except July, where the diversity and species richness recorded were the lowest during the study. The dominant ants were different in each fumigation, as show by Simpson's dominance index (Table 1; Fig 1). The species better represented in the canopy along the study were *C. crinosa*, *C. sumichrasti*, *Tapinoma melanocephalum* (Fabricius) and *Forelius kieferi* Wheeler (Fig 2), represent 77% of the total. The variation in the species richness, diversity and evenness show that there are high temporal variation in the ant canopy community in Chamela. The NMDS analysis shows the aggregation of September and July, nevertheless the other rainy month, August is located in the same quadrant with November, because both were the months with more species richness. There is an important note that during November, atypical rains fell in Chamela, with a higher amount of precipitation than in rainy months of the same year and in other years (http://www.ibiologia.unam.mx/ebchamela/www/clima.html).

Table 1. Parameters of the ant canopy community in Chamela, Jalisco, Mexico. S = Species richness; H'= Shannon diversity index; J´= Pielou's evenness; 1/D = Simpson's dominance index

Fumigation	S	H'	J´	1/D
August-1992	26	2.02	0.62	4.2
September- 1992	17	2.13	0.75	6.3
May-1993	17	1.68	0.59	3.4
July-1993	16	1.16	0.42	1.8
November-1993	29	1.58	0.47	2.8
February-1994	19	1.59	0.54	1.5
May-1994	22	1.34	0.43	2.5
Total	46	1.99	0.52	4.8

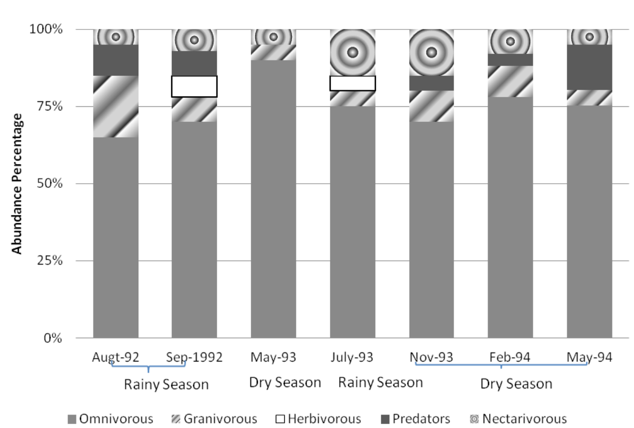

Fig 1 Temporal variation in canopy ant community composition in Chamela, Jalisco. Numbers on the lines indicate the number of species included in Others in each sampling.

The two samplings from May are grouped, showing similar composition. The ANOSIM test indicated that the observed community in the sampling months was significantly different (global R = 0.64).

The date of collection is an important factor in the structure of the community of ants in the canopy of Chamela. The nested ANOVA test showed a significant effect of the season on the ant density in the canopy ($F = 8.45$; df = 5, 343; $p<0.005$), and *post hoc* Tukey's test showed differences between the fumigations performed in July and May in relation to the other months ($p<0.05$). A possible reason for which July showed a difference with the other rainy months is that it is the month of the begining of the rains, and the conditions can differ regarding August and September, in the middle of the rainy season.

The ant density in the canopy was higher during the dry months' fumigations (May and February). Density average during rainy months it was 73 ind/m^2, while in the dry months was 92 ind/m^2. Nevertheless there was not a significant correlation between density of ants and the precipitation recorded during the months of fumigation ($r = -0.35$, df=5; $p>0.05$),

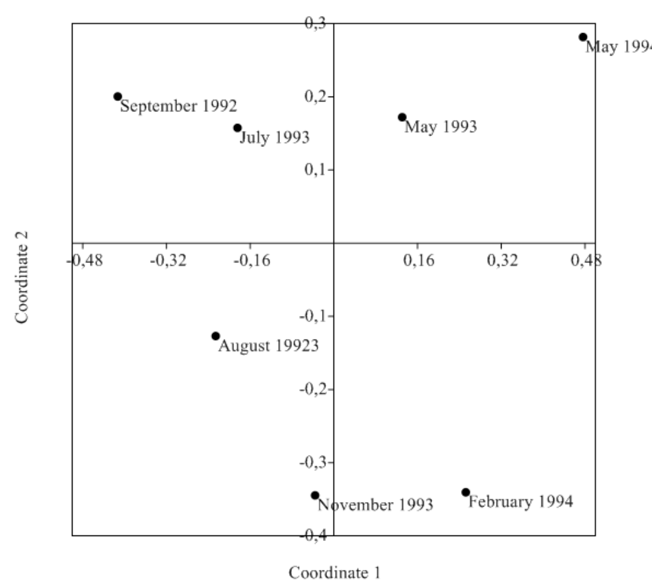

Fig 2 Non-metric multidimensional scaling ordination (NMDS) in two-dimensions of the canopy ant community inhabiting in a tropical dry forests in Chamela, Jalisco, Mexico. Ordination was based on Bray-Curtis dissimilarity index. Stress = 17%.

neither with the temperature (r =-0.17, df = 5; p >0.05; Table 2).

In relation to the trophic guilds of ants found in canopy of Chamela, five guilds were recorded: omnivorous, predators, herbivorous, granivorous and nectarivorous. Omnivorous was the dominant guild in the canopy, representing about 60% of the species founded, followed by granivorous and predators (Fig 3). The trophic guilds distribution was different during the fumigations, and some guilds were found only during the fumigations performed in rainy months, as the case of the herbivorous. Predators increased its abundance during the rainy months while omnivorous increased during the dry months (Fig 3). That pattern produce differences in ant composition along the year, due the variations of feeding habits and the capability of the ant species to use different resources.

Discussion

According to the results of Palacios-Vargas et al. (1999), ants represent the 0.5% of the total arthropods collected by fogging in Chamela, and the pattern of abundance differs of the observed in other groups, as springtails, where the highest abundances were found during rainy season, while ants showed higher abundances in the dry season. The canopy of Chamela showed a particular phenology, because leaves of tree species fall during dry season, but there are many tree species that are in flowering in this season (Bullock & Solís-Magallanes, 1990; Bullock, 2002), and that constitute important resources for many arthropods, including ants. Furthermore, there is a high density and diversity of epipythes in the area (Lott & Atkinson, 2006). These epiphytes can be exploited by ants, and constitute an important refuge during the dry season, due to their capacity to accumulate detritus and water. In epiphytes and branches of trees in Chamela there are important accumulation of organic matter, with amounts higher in the canopy than in the soil (Maass et al., 2002b), and an important phase of the decomposition cycle is developed in the canopy, and many groups of invertebrates can live in that environment, such as Collembola (Palacios-Vargas & Gómez-Anaya, 1993; Palacios-Vargas et al., 1998; Palacios-Vargas & Castaño-Meneses, 2003) that can be potential preys to some groups of ants as *Strumigenys* and *Neivamyrmex* (Brown, 1959; Bolton 1999).

In the present study the most abundant genus in the canopy was *Crematogaster*, an ant genus considered as arboricolous and is frequently found in high populations in rainy forest, different studies show that it represents more than 44% of the total collected arthropods (Basset et al., 1992), and in Thailand is the genus with the highest species richness in the canopy of dominant deciduous tree *Elateriospermum tapos* Blume (Jantarit et al., 2009). The two species of the genus *Crematogaster* found in Chamela (*C. crinosa* and *C. sumichrasti* Mayr) are probably not competitors, nevertheless both are considered as arboricolous, even the first though can be found in the shrub layer and soil in the forest (Castaño-

Table 2. Spearman correlation coefficient between the diversity index with precipitation and temperature monthly average (N = 7) in the canopy of Chamela Biological Station, Chamela, Jalisco, Mexico. H'= Shannon diversity index, S = Species richness, J' = Pielou's evenness index, ns= no significant at α=0.05.

Index	Precipitation	Temperature
H'	0.23 ns	0.38 ns
S	-0.34 ns	0.23 ns
J'	0.27 ns	0.32 ns

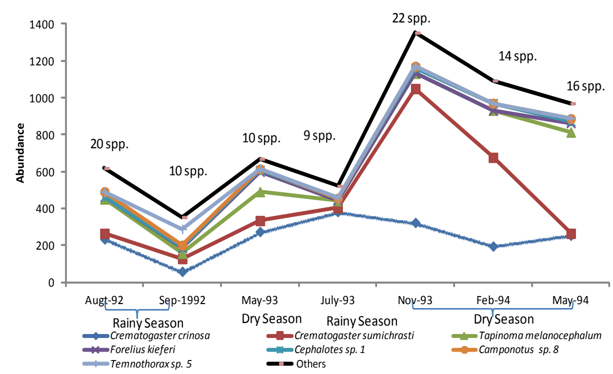

Fig 3 Temporal variation of trophic guilds of ants from the canopy of Chamela, Jalisco, Mexico.
Percentage of ant species from canopy of Chamela included in each trophic guild. N=46. Average percent of each guild: omnivorous: 60%; granivorous: 17%; herviborous: 2%; predators: 14%; nectarivorous: 7%.

Meneses, 2008; Castaño-Meneses et al., 2009). This species has been recorded as very abundant in the upland forest in Peru (Wilson, 1987).

Genera as *Cephalotes*, *Pseudomyrmex* and *Camponotus* were also abundant and species richness in canopy of Chamela. Dominance of that genera has been recorded in different tropical canopies around the World (Wilson, 1987; Guilbert & Casevitz-Weulersse, 1997; Watanasit et al., 2005), thus the composition and dominance in tropical dry forest is similar to the found in tropical rainy forest.

The presence and abundance of *T. melanocephalus* in canopy of Chamela is remarkable, because this is considered as tramp ant species or invasive. In Mexico, *T. melanocephalus* has been reported in canopies of rain forest in Chiapas, associated to orchids (Damon & Pérez-Soriano, 2005), as well in epiphytes from Panama rain forest (Stuntz et al., 2003). This species has one of the widest distribution ranges for any ant species, and its origin has been discussed (Wilson & Taylor, 1967), but, in general. consensus suggests *T. melanocephalum* origin in the Old World tropics, and recent studies indicate that it is most probably originated in the Indo-Pacific (Wetterer, 2009). Nevertheless ,there are some evidence that support the hypothesis of the Neotropical origin of *T. melanocephalum* (Wetterer, 2009), and the presence of alated females in samples of canopy of Chamela, as well the similar seasonal pattern of this species with the other abundant species considered as arboricolous, can be an evidence to support this hypothesis, or well suggest the success of this ant colonizing the forest.

Studies developed in New Caledonia using fogging, recorded 27 species and 14 genera of ants in the canopy (Guilbert & Casevitz-Weulersse, 1997). In the tropical rain forest of Peru, Wilson (1987) recorded 135 species and 40 genera of ants, while in Australia there is a great variation, with records of 37 species in the North region (Majer, 1990), to 102 species in the South (Andersen & Yen, 1992). Species richness recorded in the canopy of Chamela shown values between rainy forest and temperate forest, according with different studied performed in that canopies vegetation, nevertheless different sampling methods has been used (Wilson, 1959; Schonberg et al., 2004; Bos et al., 2007; Jaffe et al., 2007). The genera composition recorded in all canopies is similar in different studies.

The forest canopy can support high populations of organisms which had been recorded in tropical rain forest (Longino & Nadkarni, 1990; Paoletti et al., 1991). It has been proposed that the arboricolous fauna estimation can give a good estimation of the total species in the World (Erwin, 1983; Ødegaard, 2000; Longino et al., 2002). Ants can exploit a great variety of resources due the diversity of their feeding habits. The distribution of trophic guilds was different during the fumigations. That produced differences in ant composition along the year, due the variations of feeding habits and the capability of the ant species to use different resources. The domination of omnivorous is frequent in many ecosystems, including the canopy, and in environments with limited resources (Rojas 2001), due to the specialized feeding habits characteristic of environments with diversity of resources (Lévieux, 1977).

Although no significant correlations were found in the study between abundance, species richness and diversity with precipitation and temperature, these results must be viwed with caution, because the data were collected in atypical climatic conditions recorded during the studied period, as the great precipitation amount in November.

The results show that the ant community in the canopy of Chamela is diverse and have important changes in functional composition along the time. The diversity of trophic guilds showed that the ecosystem present a high productivity supporting different trophic levels in communities of ants and other faunistic groups.

Acknowledgements

This project was supported by IN2078/91 DGAPA-UNAM coordinated by Dr. José G. Palacios-Vargas (Science Faculty, UNAM). The field work was developed with the help of Alfonso Pescador Rubio, José Antonio Gómez Anaya, Alex Cadena Carrión and Alicia Rodríguez Palafox (†). Drs. José G. Palacios-Vargas, Betty Benrey, Alfonso Pescador, Zenón Cano, Francisco Villalobos, Norma García-Calderón, Victor Rico-Gray and Patricia Rojas gave invaluable suggestions on a first draft of manuscript. Two anonymous reviewers and Dr. Jacques Delabie gave invaluable suggestions to improve the manuscript.

References

Andersen, A.N. & Yen, A.Y. (1992). Canopy ant communities in the semi-arid mallee region of Northwestern Victoria. Australian Journal of Zoology, 40: 205-214. doi:10.1071/ZO9920205

Armbrecht, I., Perfecto, I. & Vandermeer, J. (2004). Enigmatic biodiversity correlations: ant diversity responds to diverse resources. Science 304: 284-286. doi: 10.1126/science.1094981

Balvanera, P., Lott, E., Segura, G., Siebe, C. & Islas, A. (2002). Patters of β-diversity in a Mexican tropical dry forest. Journal of Vegetation Science 13:145–158.

Basset, Y., Aberlenc, H.P. & Delvare, B. (1992). Abundance and stratification of foliage arthropods in lowland rainforest of Cameroon. Ecological Entomology, 17: 310-318. doi: 10.1111/j.1365-2311.1992.tb01063.x

Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (2003). Arthropods of Tropical Forest. Spatio-temporal dynamics and resource use in the canopy. Cambridge: Cambridge University Press, 474 p.

Bolton, B. (1999). Ant genera of the tribe Dacetonini (Hymenoptera: Formicidae). Journal of Natural History, 33: 1639-1689. doi: 10.1080/002229399299798

Bos, M.M., Steffan-Dewenter, I., Tscharntke, T. (2007). The contribution of cacao agroforest to the conservation of lower canopy ant and beetle diversity in Indonesia. Biodiversity and Conservation, 16: 2429-2444. doi: 10.1007/s10531-007-9196-0

Brown, W.L. (1959). A revision of the dacetine ant genus *Neostruma*. Breviora, 107: 1-13. http://hdl.handle.net/10199/1881

Bullock, S.H. (1986). Climate of Chamela, Jalisco and trends in the South coastal region of Mexico. Archives for Meteorology, Geophysics and Bioclimatology, Series B, 36: 297-316. doi: 10.1007/BF02263135

Bullock, S.H. (1988). Rasgos del ambiente físico y biológico de Chamela, Jalisco, México. Folia Entomológica Mexicana.,77: 5-17.

Bullock, S.H. (2002). La fonología de plantas en Chamela. In Noguera, F.A., Vega-Rivera, J.G. García-Aldrete, A.N. & Quesada-Avendaño, M. (Eds.), Historia Natural de Chamela (pp. 491-498). México: Instituto de Biología, UNAM.

Bullock, S.H. & Solís-Magallanes, J.A. (1990). Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica, 22: 22-35.

Byk, J. & Del-Claro, K. (2010). Nectar and pollen-gathering *Cephalotes* ants provide no protection against herbivory: a new manipulative experiment to test ant protective capabilities. Acta Ethologica, 13: 33-38. doi: 10.1007/s10211-010-0071-8

Byk, J. & Del-Claro, K. (2011). Ant-plant interaction in the Neotropical savanna: direct beneficial effects of extrafloral nectar on ant colony fitness. Population Ecology, 53: 327-332. doi: 10.1007/s10144-010-0240-7

Castaño-Meneses, G. (2008). Estructura de la comunidad edáfica de hormigas en la selva baja caducifolia de Chamela, Jalisco, México. In Estrada-Vanegas, E.G. (Ed.), Fauna de Suelo I. Micro, meso y macrofauna (pp. 133-140). Texcoco: Colegio de Postgraduados.

Castaño-Meneses, G., Benrey, B. & Palacios-Vargas, J.G. (2009). Diversity and temporal variation of ants (Hymenoptera: Formicidae) from Malaise traps in a tropical deciduous forest. Sociobiology, 54: 633-645.

Cervantes, L., Domínguez, R. & Maass, M. (1988). Relación lluvia-escurrimiento en un sistema pequeño de cuencas de selva baja caducifolia. IIngeniería hidráulica en México II 1: 30-41.

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology, 18: 117-143. doi: 10.1111/j.1442-9993.1993.tb00438x

Clarke, K.R. & Green, R.H. (1988). Statistical design and analysis for a "biological effects" study. Marine Ecology Progres Series, 4: 213-226.

Cook, S.C., Eubanks, M.D., Gold, R.E. & Behmer, S.T. (2011). Seasonality directs contrasting food collection behavior and nutrient regulation strategies in ants. PLoS One 6: e25407. doi: 10.1371/journal.pone.0025407. (accessed date: 23 May, 2012).

Damon, A. & Pérez-Soriano, A. (2005). Interaction between ants and orchids in the Soconusco region, Chiapas, Mexico. Entomotropica 20: 59-65.

Davidson, D.W., Cook, S.C., Snelling, R.R. & Chua, T.H. (2003). Explaining the abundance of ants in lowland tropical rainforest canopies. Science 300: 969-972. doi: 10-1126/science.1082074

Dirzo, R., Young, H.S., Mooney, H.A. & Ceballos, G. (2011). Seasonally dry tropical forest. Ecology and Conservation. Washington: Island Press, 400 p.

Erwin, T.L. (1983). Beetles and other insects of tropical forest canopies at Manaus, Brazil, sampled by insecticidal fogging. In Sutton, W.L., Whitmore, T.C. & Chadwick, A.C. (Eds.), Tropical rain forest: ecology and management (pp. 59-79). Oxford: Blackwell Scientific Publications.

García-Oliva, F., Camou, A. & Maass, M. (2002). El clima de la región central de la costa del Pacífico mexicano. In Noguera, F.A., Vega-Rivera, J.H., García-Aldrete, A.N. & Quesada-Avendaño, M. (Eds.), Historia Natural de Chamela (pp. 3-10). Distrito Federal: Instituto de Biología, UNAM.

Gove, A.D., Majer, J.D. & Rico-Gray, V. (2005). Methods for conservation outside of formal reserve systems: the case of ants in the seasonally dry tropics of Veracruz, Mexico. Biological Conservation, 126: 328-338. doi: 10.1016/j.biocon.2005.06.008

Guilbert, E. & Casevitz-Weulersse, J. (1997). Caractérisation de la myrmécofaune de la canopée de forêts primaires de Nouvelle-Calédonie échantillonnée par fogging. In Najt, J. & Matile, L. (Eds.), Zoologia Neocaledonica, Vol. 5. (pp. 357-368). París: Mémoires du Muséum National d'Historie Naturelle.

Guilbert, E., Baylac, M. & Najt, J. (1995). Canopy arthropod diversity in New Caledonian primary forest sampled by fogging. Pan-Pacific Entomology, 71: 3-12.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001). PAST: Paleontological statistics software package for education and data analysis. Paleontología Electrónica, 4: 9.[7-11-2013]. Available at http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Jaffe, K., Horchler, P., Verhaagh, M., Gómez, C., Sievert, R., Jaffe, R. & Morawez, W. (2007). Comparing the ant fauna in a tropical and a temperate forest canopy. Ecotropicos, 20: 74-81.

Jantarit, S., Wattanasit, S. & Sotthibandhu, S. (2009). Canopy ants on the briefly deciduous tree (*Elateriospermum tapos* Blume) in a tropical rainforest, southern Thailand. Songklanakarin Journal of Science and Technology, 31: 21-28.

Lach, L., Parr, C.L. & Abbott, K.L. (2010). Ant ecology. Oxford: Oxford University Press, 402 p.

Lévieux, J. (1977). La nutrition des fourmis tropicales: V. Éléments de synthèse. Les modes d'exploitation de la biocoenose. Insects Sociaux, 24: 235-260. doi: 10.1007/BF02232743

Longino, J.T. & Nadkarni, N.M. (1990). A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. Psyche, 97: 81-94. doi: 10.1155/1990/36505

Longino, J.T., Coddington, J. & Colwell, R.K. (2002). The ant fauna of a tropical rain forest: estimating species richness three different ways. Ecology, 83: 689-702. doi: 10.1890/0012-9658(2002)083[0689:TAFOAT]2.0.CO;2

Lott, E.J. (1985). Listados florísticos de México. III La Estación de Biología Chamela, Jalisco. México: Instituto de Biología, UNAM, 47 p.

Lott, E.J., Bullock, S.H. & Solís-Magallanes, J.A. (1987). Floristic diversity and structure of upland and arroyo forests in coastal Jalisco. Biotropica, 19: 228–235.

Lott, E.J. & Atkinson, T.H. (206). 13. Seasonally dry tropical forests: Chamela-Cuixmala, Jalisco, as a focal point for comparison. In Pennington, R.T., Lewis, G.P. & Ratter, J.A. (Eds.), Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation (pp. 315-342). Florida: CRC Press.

Ludwing, J.A. & Reynolds, F.F. (1988). Statistical ecology: a primer on methods and computing. New York: Wiley Interscience Publishers, 368 p.

Maass, J.M., Jaramillo, V., Martínez-Yrízar, M., García-Oliva, F., Pérez-Jiménez, A., & Sarukhán, J. 2002. Aspectos funcionales del ecosistema de selva baja caducifolia en Chamela, Jaslico. In Noguera, F.A., Vega-Rivera, J.H., García-Aldrete, A.N. & Quesada-Avendaño, M. (Eds.), Historia Natural de Chamela (pp. 525-542). México: Instituto de Biología, UNAM.

Maass, J.M., Martínez-Yrízar, A., Patiño, C. & Sarukhán, J. (2002b). Distribution and annual net accumulation of above-ground dead phytomass and its influence on throughfall qua-lity in a Mexican tropical deciduous forest ecosystem. Journal of Tropical Ecology, 18: 821-834. doi: 10.1017/S0266467402002535

Majer, J.D. (1990). The abundance and diversity of arboreal ants in Northern Australia. Biotropica, 22: 191-199.

Martínez-Yrízar, A., Maass, J.M., Pérez-Jiménez, L.A. & Sarukhán, J. (1996). Net primary productivity of a tropical deciduos forest ecosystem in Wester Mexico. Journal of Tropical Ecology, 12: 169-175. doi: http://dx.doi.org/10.1017/S026646740000938X

Meyer, K.M., Schiffers, K., Münkemüller, T., Schädler, M., Calabrese, J.M., Basset, A., Breulmann, M., Duquesne, S., Hidding, B., Huth, A., Schöb, C. & van de Voorde, T.F.J. (2010). Predicting population and community dynamics: the type of aggregation matters. Basic and Applied Ecology, 11: 563-571. doi: 10.1016/jbaae.2010.08.001

Neves, F.S., Braga, R.F., Do Espírito-Santo, M.M., Delabie, J.H.C., Fernandes, G.W. & Sánchez-Azofeifa, G.A. (2010). Diversity of arboreal ants in a Brazilian tropical dry forest: effects of seasonality and successional stage. Sociobiology, 56: 1-18.

Noguera, F.A., Vega-Rivera, J.H., García-Aldrete, A.N. & Quesada-Avendaño, M. (2002). Historia Natural de Chamela. México: Instituto de Biología, UNAM, 568 p.

Ødegaard, F. (2000). How many species of arthropods? Erwin's estimate revised. Biological Journal of the Linnean Society, 71: 583-597. doi: 10.1111/j.1095-8312.2000.tb01279.x

Palacios-Vagas, J.G. & Castaño-Meneses, G. (2003). Seasonality and community composition of springtails in Mexican forest. In Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L. (Eds.), Arthropods of Tropical forest (pp. 159-169). Cambridge: Cambridge University Press.

Palacios-Vargas, J.G. & Gómez-Anaya, J.A. (1993). Los collembolan (Hexapoda: Apterygota) de Chamela, Jalisco, México. Distribución ecológica y claves. Folia Entomologica Mexicana, 89: 1-34.

Palacios-Vargas, J.G., Castaño-Meneses, G. & Gómez-Anaya, J.A. (1998). Collembola from the canopy of a Mexican tropical deciduous forest. Pan-Pacific Entomologist, 74: 47-54.

Palacios-Vargas, J.G., Castaño-Meneses, G. & Pescador, A. (1999). Phenology of canopy arthropods of a tropical deciduous forest in wetern Mexico. Pan-Pacific Entomologist, 75: 200-211.

Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H. & Benzing, D.H. (1991). Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. Journal of Tropical Ecology, 7: 373-383. doi: 10.1017/S0266467400005654

Ribas, C.R., Schoereder, J.H., Pic, M. & Soares, S.M. (2003). Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. Austral Ecology, 28: 305-314. doi: 10.1046/j.1442-9993.2003.01290.x

Rojas, P. (2001). Las hormigas del suelo en México: diversidad, distribución e importancia (Hymenoptera: Formicidae). Acta Zoologica Mexicana, 1: 189-238.

Schonberg, L.A., Longino, J.T., Nadkarni, N.M., Yanoviak, S.P. & Gering, J.C. (2004). Arboreal ant species richness in primary forest, secondary forest, and pasture habitats of a tropical montane landscape. Biotropica, 36: 402-409. doi: 10.1111/j.1744-7429.2004.tb00333.x

Schulz, A. & Wagner, T. (2002). Influence of forest type and tree species on canopy ants (Hymenoptera: Formicidae) in Budongo Forest, Uganda. Oecologia, 133: 224-232. doi: 10.1007/s00442-002-1010-9

StatSoft. (2009). Statistical user guide: complete statistical system StatSoft. Oklahoma.

Stork, N.E. (1987). Guild structure of arthropods from Bornean rain forest trees. Ecological Entomology, 12: 69-80. doi: 10.1111/j.1365-2311.1987.tb00986.x

Stunts, S., Linder, C., Linsenmair, K.E., Simon, U. & Zotz, G. (2003). Do non-myrmocophilic epiphytes influence community structure of arboreal ants? Basic and Applied Ecology, 4: 363-374. doi: 10.1078/1439-1791-00170

Tobin, J.E. (1995). Ecology and diversity of tropical forest canopy ants. In Lowman, M.D. & Nadkarni, N.M. (Eds.), Forest canopies (pp.129-147). San Diego: Academic Press.

Trejo, R.I. & Dirzo, R. (2000). Deforestation of seasonally dry tropical forest towards its northern distribution: a national and local analysis in Mexico. Biological Conservation, 94: 133-142. doi: 10.1016/S0006-3207(99)00188-3

Watanasit, S., Tongjerm, S. & Wiwatwitaya, D. (2005). Composition of canopy ants (Hymenoptera: Formicidae) at Ton Nga Chang Wildlife Sactuary, Songkhla Province, Thailand. Songklanakarin Journal of Science and Technology, 27: 665-673.

Wetterer, J.K. (2009). Worldwide spread of the ghost ant, *Tapinoma melanocephalum* (Hymenoptera: Formicidae). Myrmecological News, 12: 23-33.

Wilson, E.O. (1959). Some ecological characteristics of ants in New Guinea rain forest. Ecology, 40: 437-447.

Wilson, E.O. (1987). The arboreal fauna of Peruvian Amazon Forest: a first assessment. Biotropica 19: 245-251.

Wilson, E.O. & Taylor, R.W. (1967). Ants of Polynesia. Pacific Insects Mongraphs, 14: 1-109.

Zar, J.H. (1984). Biostatistical Analysis. Second Edition. New Jersey: Prentice Hall, 718 p.

Appendix 1 - Monthly and total abundance of ants collected by fogging at the canopy of Biological Station Chamela. 1 = August 1992, 2 = September 1992, 3 = May 1993, 4 = July 1993, 5 = November 1993, 6= February 1994, 7 = May 1994.

Subfamily	**Species**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**Total**
Amblyoponinae	*Stigmatomma* sp.	1							1
Dolichoderinae	*Forelius keferi* Wheeler, 1934	12	30	160	3			50	255
	Tapinoma melanocephalum (Fabricius, 1793)	20	30	110	40	84	255	550	1071
Ecitoninae	*Neivamyrmex chamelensis* Watkins, 1986		5	4				1	10
Formicinae	*Brachymyrmex* sp. 1				10	15			25
	Brachymyrmex sp. 2					1			1
	Camponotus sp. 1	7				3	13		23
	Camponotus sp. 2	1	2						3
	Camponotus sp. 4	14	10	2	10	20	4	6	64
	Camponotus sp. 5					3	2		5
	Camponotus sp. 6			2		3	4		9
	Camponotus sp. 8	28	10	6	2	10		14	70
	Camponotus sp. 9					1		2	3
	Camponotus sp. 10	4							4
	Camponotus sp. 12	10			2				12
	Camponotus sp. 13					2			2
	Camponotus sp. 14			20	10	13	10		53
	Camponotus sp. 15					13	1		14
	Camponotus sp. 16							3	3
Myrmicinae	*Acromyrmex* sp.		1		1				2
	Carebara sp.		1						1
	Cephalotes sp. 1	15	5	9	8	30	39	1	107
	Cephalotes sp. 2	1		7			5		13
	Cephalotes sp. 3					14			14
	Cephalotes sp. 4	1		7		11		8	27
	Cephalotes sp. 5							1	1
	Cephalotes sp. 7					2			2
	Crematogaster crinosa Mayr, 1862	236	60	280	383	326	200	258	1743
	Crematogaster sumichrasti Mayr, 1870	189	70	60	20	730	481	10	1560
	Temnothorax sp. 2			4			7	5	16
	Temnothorax sp. 3					4			4
	Temnothorax sp. 4	13		1	7	12		5	38
	Temnothorax sp. 5		90	1	2	3		2	98
	Pheidole sp. 1	6	1			1	3		11
	Pheidole sp. 5	5							5
	Pheidole sp. 6	3				2			5
	Pheidole sp. 7	12		1				1	14
	Solenopsis geminata (Fabricius, 1804)	22	30		22	30	49		153
	Strumigenys sp. 2	1				2			3
	Strumigenys sp. 3	14						30	43
Ponerinae	*Pachycondyla* sp.	2	2			13	2	2	21
Pseudomyrmecinae	*Pseudomyrmex* sp. 1	3	3		1	2			9
	Pseudomyrmex sp. 2	4				2	2	2	10
	Pseudomyrmex sp. 3	6		5	2	1	12	6	32
	Pseudomyrmex sp. 4						6	2	8
	Pseudomyrmex sp. 5						2	1	3