

The Myrmecofauna (Hymenoptera: Formicidae) of the Macanao Semi-arid Peninsula in Venezuela: An Altitudinal Variation Glance

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Abstract

There are incomplete data about ant taxonomy and diversity in the Caribbean islands of Venezuela. In order to broaden myrmecological information in the Peri-Caribbean arid belt, ground-dwelling ant assemblage of the Macanao semi-arid peninsula (Margarita Island) was sampled with a Rapid Assessment Program (RAP). Two study sites on the northern slope of the peninsula were chosen, La Chica (LC) at 70 m of altitude and Cerro Macanao (CM) at 598 m of altitude. Sixty pitfall traps (30 per site) and 96 man-hours of manual collecting (48 man-hours per site) were employed. Overall, 40 species and 32 genera from eight subfamilies were recorded, twice the number of species previously reported for Margarita Island. Differences in ant species richness and structure were detected between both sites, with 31 species in CM and 25 species in LC. Such variations indicate that microclimatic conditions are more favorable in uplands than lowlands in Macanao. This situation may be attributed to the moisture gradient effect upon vegetation, and microclimatic conditions influenced by peninsular orography. Our findings corroborate that the pattern of higher diversity with higher altitude in arid zones also holds for the tropics, and suggest a continental origin for the Lesser Antilles ant fauna.

Keywords: Caribbean semideserts; Formicidae; Margarita island; Neotropics; Richness patterns; Species list

Introduction

Ants are an important group of insects in arid and semiarid environments with high species richness and a variety of morphological, physiological, and behavioral adaptations [1]. However, there is insufficient information about the taxonomy and ecology of this group in tropical semi-arid environments of the Americas, including the Peri-Caribbean arid belt [2-4]. Ant surveys in Caribbean islands have been developed since last four decades, showing very interesting but contradictory findings on ant species richness and endemism within and between islands [2]. A first comprehensive numbers of ant species in Venezuelan islands (Margarita, La Blanquilla, La Orchila and Las Aves) has been reported based on data from museum collection and non-systematic field work [2]. However, in that work only twenty ant species were recorded for Margarita Island, hinting an under-sampled myrmecofauna given the island's area and variety of habitats. Additionally, most of those records belong to mesic environments of the eastern region (Paraguachoa peninsula), while the ant fauna of the semi-arid western half (Macanao peninsula) have remained completely unknown. The Macanao peninsula contains a moisture gradient ranging from arid lowlands to less extreme environments at higher altitudes [5,6]. In this situation, ant fauna composition may vary according to environmental conditions and be differentiated into well-defined assemblages [7]. Therefore, ant richness and structure were evaluated with a Rapid Assessment Program (RAP) at two altitudinal sites in the Macanao semi-arid peninsula in order to assess ant composition in western Margarita Island (Venezuela), and increase myrmecological records for the Peri-Caribbean arid belt.

Study Area

The Macanao peninsula represents the western half of Margarita Island in northeastern Venezuela, with 330.7 km² of area and 700 m of elevation (10°56' - 11°05' N 64°10' - 64°24'W) [6]. The climate is semi-arid with an annual mean temperature of 27.4 °C and annual mean precipitation of 522 mm with peaks during July-August and November-January [5,6]. The vegetation varies from a few dry forests associated with intermittent water bodies and higher elevations, to thorn shrublands and cactus thickets at different elevations above sea level [6,8]. Two sites were chosen along an elevation gradient of 700 m in the northern slope of the peninsula. One site represents a xeric lowland habitat located 300 m from La Chica sand mine (70 m; 11°02'N, 64°15'W). The other site is near the summit of Cerro Macanao and represents a more mesic habitat (598 m; 11°00'N, 64°18'W). La Chica site, henceforth LC, spans a transition between low thorny shrubland and cactus thickets with a high proportion of bare ground areas. Canopy height varies from 0.3 to 4 m with species from Capparaceae, Theophrastaceae, and Cactaceae (columnar cacti) as dominant vegetative elements [6,8]. Cerro Macanao, henceforth CM, represents a high thorny shrubland, where bare ground is scarce and the canopy varies between 3 and 5 m with dominance of woody species from the Fabaceae and Boraginaceae families [6,8].

Ant Survey and Analysis

Ant composition and relative abundance were sampled using pitfall traps and direct collection at each site during August 2008. Three 120 m linear transects were randomly located and separated by at least 20 m of distance at each site. Along each transect 10 pitfall traps (12 m spacing) were installed, totalizing 30 traps per site and 60 traps for the peninsula (ten traps x three transects x two sites). The traps were

plastic containers (7.5 cm diameter, 9.3 cm deep) filled with 150 ml of preservative solution of ethanol (70%), monoethylene glycol (11%), and a few drops of liquid soap [9]. All traps were operated simultaneously for ca. 72 h (three continuous days). Additionally, diurnal walks were carried out at each site in order to complement the pitfall survey. We employed 8 hours of active search in ground and vegetation per two days. A total effort of 48 hours and 96 hours of direct collecting was accomplished for each site and the peninsula, respectively (8 hrs/man×3 men×2 days×2 sites). Ants were sorted to species or morphospecies using taxonomic keys for the Neotropical region [10]. Voucher specimens were deposited in the Museo del Instituto de Zoología Agrícola (MIZA), Universidad Central de Venezuela, Aragua, Venezuela.

Species richness was calculated as the total number of species captured in the 60 traps, as well as 30 traps at each site. Estimates 8.2 software was used for calculating second order Chao index (Chao2) and Incidence-based Coverage Estimator (ICE) from data in traps [11]. All estimations used incidence data and 100 randomizations of sample order. Variation in ant composition and abundance between sites was explored using a multivariate frequency plot (MFP), a little routine in R software that permits generating a plot of species count per sample. Species scores were calculated from a Principal Components Analysis or PCA (log-transformed data), and are represented as circles in a two axis plane. Circle diameter is proportional to species abundance of the counts (species scores). Each circle was arranged according to its importance at each pitfall trap along the ordinate axis, while both, species and samples, are arranged in order to maximize the grouping of both along the abscissa axis. The MFP was performed using the Vegan package in R 2.13.1 [12,13].

Ant species were assigned to general groups and guilds based on a functional classification used by Pérez-Sánchez et al. [3]. Each category is based upon field observations and published behavioral data for some neotropical species [3,4,14]. Differences in guild composition among sites were analyzed using the functional similarity index (S_f) [14]. Likewise, in order to explore microhabitat conditions between sites, bare ground proportion and foliage height profiles (FHP) were measured with a thin 2.5 m long rod placed vertically at each trap location, recording the presence/absence of bare ground, leaf litter layer thickness (three measure points), and number of plant contacts at different heights: herbaceous stratum (0-30 cm), shrub stratum (30-150 cm), and tree stratum (> 150 cm) [15]. We calculated the Mann-Whitney U Statistic for comparing leaf litter data (n=30), while FHP data were analyzed through a 4×3 (sites×height-levels) contingency and chi square estimation ($\alpha=0.05$).

Results

Overall, 40 species, 22 genera and eight subfamilies were collected with Myrmicinae as the diverse subfamily (Table 1). Of the 40 species recorded, 31 were collected by traps and nine were added through direct collection (Table 1). Based on trapping effort, richness indexes estimate at least 37 species for the peninsula, even though Chao2 confidence boundaries suggest that 13 species eluded capture (Table 1). Considering the maximum Chao2 value (53), the total richness recorded through both methods represents 76% of the total peninsular myrmecofauna. The ant assemblage in CM was richer than LC according to the traps, and manual collecting added seven and eight records to reach 31 and 26 species, respectively (Table 1). In both cases, the total observed richness matched Chao2 and ICE estimated values (Table 1). Nevertheless, ant assemblages from both sites showed

variations in composition and abundance (Figure 1). LC showed three times the total abundance recorded in CM (Table 1 and Figure 1). The numerically dominant species were *Pheidole sp. R1* in CM and *Crematogaster rochai* in LC, while species of *Bachymyrmex*, *Prionopelta*, and *Rogeria* showed low frequency in traps (Figure 1 and Table 1). Species such as *Paratrechina longicornis*, *Acromyrmex octospinosus* and *Prionopelta sp.* were exclusively from LC, but *Ectatomma tuberculatum*, *Pheidole sp. R1*, *Brachymyrmex sp. 1* and almost all ponerines were only collected in CM (Figure 1 and Table 1).

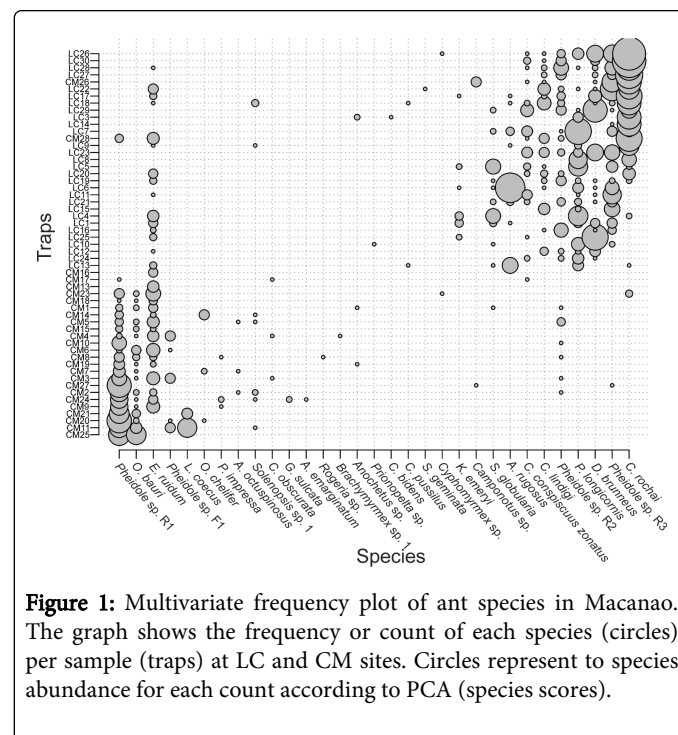


Figure 1: Multivariate frequency plot of ant species in Macanao. The graph shows the frequency or count of each species (circles) per sample (traps) at LC and CM sites. Circles represent to species abundance for each count according to PCA (species scores).

Subfamily	Sites		
	LC	CM	Guilds*
Dolichoderinae			
<i>Dorymyrmex brunneus</i>	336	1	GD
Formicinae			
<i>Brachymyrmex sp. 1</i> (AM)	-	1	LVS
<i>Brachymyrmex admotus</i>	-	HC	LVS
<i>Camponotus bidens</i>	1	-	SARM
<i>Camponotus conspicuus zonatus</i>	48	3	PC
<i>Camponotus lindigi</i>	57	7	PC
<i>Camponotus sp.</i>	HC	7	PC
<i>Paratrechina longicornis</i>	338	-	OP
Pseudomyrmicinae			
<i>Pseudomyrmex boopis</i>	HC	HC	AP
<i>Pseudomyrmex c.f. elongatus</i>	HC	-	AP
<i>Pseudomyrmex simplex</i>	HC	-	AP

Dorylinae				
<i>Labidus coecus</i>	-	46	NO	
<i>Labidus praedator</i>	HC	-	NO	
<i>Neivamyrmex</i> sp.	HC	-	NO	
Amblyoponinae				
<i>Prionopelta</i> sp.	1	-	SCP	
Ectatomminae				
<i>Ectatomma ruidum</i>	43	115	GD	
<i>Ectatomma tuberculatum</i>	-	HC	GD	
<i>Gnamptogenys sulcata</i>	-	5	SCP	
Ponerinae				
<i>Anochetus emarginatus</i>	-	1	LEP	
<i>Anochetus</i> sp.	2	2	LEP	
<i>Odontomachus bauri</i>	-	9	LEP	
<i>Odontomachus chelifer</i>	-	81	LEP	
<i>Pachycondyla impressa</i>	-	4	LEP	
Myrmicinae				
<i>Acromyrmex octuspinosus</i>	HC	3	CO	
<i>Acromyrmex rugosus</i>	317	-	CO	
<i>Cephalotes pusillus</i>	2	HC	CE	
<i>Crematogaster obscurata</i>	-	3	SARM	
<i>Crematogaster rochai</i>	2026	248	SARM	
<i>Cyphomyrmex</i> sp. (rimosus complex)	1	1	CA	
<i>Kalathomyrmex emeryi</i>	14	-	CA	
<i>Pheidole</i> sp. F1 (fallax complex)	-	11	GD	
<i>Pheidole</i> sp. R1 (radoszkowskii complex)	-	521	GD	
<i>Pheidole</i> sp. R2 (radoszkowskii complex)	81	20	GD	
<i>Pheidole</i> sp. R3 (radoszkowskii complex)	258	48	GD	
<i>Pheidole transversostriata</i>	HC	HC	GD	
<i>Rogeria</i> sp.	-	1	LVS	
<i>Solenopsis geminata</i>	1	HC	GD	
<i>Solenopsis globularia</i>	46	1	GD	
<i>Solenopsis</i> sp. 1	4	6	LVS	
<i>Trachymyrmex</i> sp.	Total	-	HC	CA
Number of individuals in traps	4717	3575	1142	
Number of species in traps	31	18	24	
Total number of species	40	26	31	

Chao2	35 (32-53)	24 (19-58)	29 (25-49)	
ICE	37	26	29	

Table 1: Ants of the Macano semi-arid peninsula, Margarita Island, Venezuela. Species list, abundance (number of workers) and guilds recorded in the two field sites. HC indicates species collected by manual techniques. Chao2 and ICE indicate the Chao second order and Incidence-based Coverage Estimator results. Values in parenthesis indicate confidence boundaries of Chao2 estimator.* Guilds abbreviations means: AP: Agile Pseudomyrmecines; CE: Cephalotines; LD: Large Dolichoderines; SAMR: Small Arboreals of Massive Recruitment; LC: Leaf Cutters; CA: Cryptic Attines; NO: Nomads; GD: Ground Dominants; PC: Patrol Camponotines; OP: Opportunists; LEP: Large Epigaeic Predators; SCP: Specialized Cryptic Ponerines; LVS: Litter and Vegetation Specialized; and SCPR: Specialized Cryptic Predators.

All ant species were sorted into a functional structure divided in three general sets, three trophic groups and 12 guilds (Table 2). Epigaeic ants were the most important component (73%), followed by arboreal (18%) and hypogaic ants (10%; Table 2). The omnivorous Ground Dominants represents the most important guild (29%) in the epigaeic ants (Table 2). Agile Pseudomyrmecines, Small Arboreals of Massive Recruitment, and Litter and Vegetation Specialized guilds were well represented in the arboreal and hypogaic groups, respectively (Table 2). The total number of guilds showed no significant variation between sites, with 12 guilds recorded in LC and 11 guilds in CM; however, the number of species within guilds varied between sites (Table 2). The most diverse guilds in LC site were Ground Dominants (7 spp.) and Agile Pseudomyrmecines (3 spp.); while Ground Dominants (10 spp.), Large Epigaeic Predators (5 spp.), and hypogaic guilds (4 spp.) were more diverse in CM site (Table 2). Predator and Opportunist guilds were poorly represented in LC (2 spp.), and the latter guild absent in CM (Table 2). The Sf showed a 73% of resemblance between guild structures of both sites.

Guilds		LC	CM	Peninsula
Arboreal (stem-dwelling)		6 (23%)	4 (13%)	7 (18%)
Small Arboreals of Massive Recruitment		2	2	3
Cephalotines		1	1	1
Agile Pseudomyrmecines		3	1	3
Epigaeics (ground-dwelling)		19 (73%)	23 (74%)	29 (73%)
Fungivores	Leaf Cutters	2	1	2
	Cryptic Attines	2	2	3
Omnivores	Ground Dominants	7	10	10
	Patrol Camponotines	3	3	3
	Opportunists	1	0	1
Predators	Large Epigaeic Predators	1	5	5
	Specialized Cryptic Ponerines	1	1	2

	Nomads	2	1	3
	Hipogaeics (litter-dwelling)	1 (4%)	4 (13%)	4 (10%)
	Litter and Vegetation Specialized	1	4	4
	Total number of species	26	31	40
	Number of guilds	12	11	12

Table 2: Number and relative importance of species within the ant guild structure at each field site and the whole peninsula.

Higher proportions of bare ground were detected in LC site (~30%) than CM habitat (~13%). The leaf litter layer showed significant differences, being higher in CM than LC ($U=249.5$; $p=0.003$). Vegetation vertical structure (FHP) showed differences between sites, and according to the standardized residuals, such variations occur only at tree and herbaceous strata ($\chi^2=27.05$; d.f.=2, $p<0.05$). The number of foliage contacts in trees was higher in CM, while foliage contacts at herbaceous stratum was higher in LC.

Discussion

Ant richness in Macanao is similar to other insular Neotropical locations, but lower than continental xeric environments [3,4,15,16]. This situation may be attributed to the biogeographical insularity features of Macanao peninsula, with its connection to the rest of the island (Paraguachoa peninsula) is restricted to 18 km long and ~20 km wide isthmus of marine zone with mangrove and semi-arid vegetation (La Restinga). Such isolation and Macanao's size may imply reduced resource and habitat options in relation to a bigger land mass, besides a colonization rate of new species (immigration) lower than the extinction rate, leading to an impoverished regional pool of species compared with mainland locations [3,17]. Contrarily to the Greater Antilles the presence of endemic species in Macanao could not be verified, and species composition is characterized by widespread Neotropical elements commonly found in semiarid environments of Venezuela [3,4]. Biogeographic and paleoclimatic evidence suggest connections between Margarita Island and the mainland during Mid to Late Pleistocene due to a 120 m sea level decline [18,19]. This scenario might explain ant composition similarities between Macanao and continental environments, the apparent lack of endemism, and the presence of ants that reproduce with non-alate queens (e.g. Dorylinae species and *Anochetus emarginatus*). Hence, our results support [2] comments on the absence of endemism and continental origin of the Lesser Antilles myrmecofauna.

The variation in ant species richness and structure between both study sites could be related to habitat conditions imposed by altitudinal variation [7]. Given the topography and geographic situation of Macanao, trade winds extract moisture from the lowlands, ascend the northern slopes and release it at higher elevations [5]. This effect generates a humidity gradient that favors temperature changes (0.5 °C decrease per 100 m increase) and modulates habitat conditions from xeric lowlands to more mesic environments at higher elevations [5,6]. Microhabitat measurements, richness differences, dominant species presence, and guild composition show an altitudinal variation of myrmecofauna that support these arguments. There are three general patterns that describe richness variation in relation to altitude changes [17]: i) the altitudinal hypothesis that describes a decrease in

species richness with elevation [20]; ii) the unimodal pattern, which holds maximum species richness at intermediate elevations [21,22]; and iii) the pattern that describes an increase of species richness with elevation proposed for arid regions and partially found in others environments [7,23]. Our results match the last pattern (iii) due to CM (598 m) showing higher species richness than LC (70 m). In the arid environments of Macanao the increase in altitude not only means augmented precipitations but a buffering of high temperatures as well [5,6]. Such changes may support higher levels of primary production and favor lessened levels of physiological stress for ants [7,20,21].

This work is an important contribution to the knowledge of ant composition in the Peri-Caribbean arid belt, in which we detect at least 20 more species than those previously reported for the whole of Margarita Island [2]. Although no ant endemism is reported in Macanao, the capture of several distinct species closely related to *Pheidole radozskowski* suggests such a possibility for the peninsula or at least for Margarita Island as a whole. The variations in ant fauna composition and structure, as well as differences in vegetation complexity among study sites, indicate that microclimatic conditions are more favorable in Cerro Macanao (598 m) than La Chica (70 m). This situation may be explained by the moisture gradient effects on habitat heterogeneity at each site. Our findings corroborate that the pattern of higher diversity with higher altitude in arid zones also holds for the tropics, and suggest a continental origin for the Lesser Antilles ant fauna, including direct terrestrial connections.

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