



RESEARCH ARTICLE - ANTS

Ant Communities along a Gradient of Plant Succession in Mexican Tropical Coastal Dunes

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Abstract

Most of Mexican coastal dunes from the Gulf of Mexico have been severely disturbed by human activities. In the state of Veracruz, the La Mancha Reserve is a very well preserved coastal community of sand dunes, where plant successional gradients are determined by topography. In this study we assessed species richness, diversity and faunal composition of ant assemblages in four plant physiognomies along a gradient of plant succession: grassland, shrub, deciduous forest and subdeciduous forest. Using standardized and non-standardized sampling methods we found a total of 121 ant species distributed in 41 genera and seven subfamilies. Grassland was the poorest site (21 species) and subdeciduous forest the richest (102 species). Seven species, with records in $\geq 10\%$ of samples, accounted 40.8% of total species occurrences: *Solenopsis molesta* (21.6%), *S. geminata* (19.5%), *Azteca velox* (14%), *Brachymyrmex* sp. 1LM (11.7%), *Dorymyrmex bicolor* (11.2%), *Camponotus planatus* (11%) and *Pheidole susannae* (10.7%). Faunal composition between sites was highly different. Nearly 40% of all species were found in a single site. In all sites but grassland we found high abundances of several species typical of disturbed ecosystems, indicating high levels of disturbance. A species similarity analysis clustered forests in one group and grassland and shrub in another, both groups separated by more than 60% of dissimilarity. Similarity of ant assemblages suggests that deciduous and subdeciduous forests represent advanced stages of two different and independent successional paths.

Introduction

Ants are social insects with important ecological functions. They influence ecosystems through soil bioturbation (Lobry de Bruyn & Conacher, 1990), predation of invertebrates (Gotwald, 1995) and mutualistic interactions with hundreds of plant species (Jolivet, 1996). Due to their high diversity, numerical and biomass dominance (Fittkau & Klinge, 1973, Brown, 2000) and sensitivity to environmental changes (Andersen, 1995), ants constitute an ideal group to inquire about patterns in community characterization. Coastal dunes are complex and very dynamic environments that have been shaped by biological and physical processes like water and wind action (McLachlan, 1991). Its high environmental heterogeneity is determined by distinct landforms and different plant communities (Martínez et al., 2004).

Ant communities from coastal environments have been

poorly studied. However, the importance of these ecosystems for conservation of ants has been recently recognized (Howe et al., 2010). Communities from temperate and tropical coastal ecosystems are markedly different. In general, ant communities from temperate marine coasts have a low number of species and, independently of the number of sites included in a given locality, the number of species never surpass two dozen. For example, Boomsma and De Vries (1980) in The Netherlands recorded only three species in sparsely vegetated sand dunes and grasslands, whereas studies in successional gradients from pioneer vegetation to mature forests carried out in Finland (Gallé, 1991) and Spain (Ruano et al., 1995), recorded 19 and 24 species respectively. In temperate dunes, species richness, abundance and equitability increases along vegetation succession, with higher values being found in sites with a more dense plant cover (Boomsma & Van Loon, 1982; Ruano et al., 1995). Positive correlations have also been observed between



composition of ant assemblages and a more complex habitat (Boomsma & Van Loon, 1982). These attributes of ant assemblages, however, are relatively independent of diversity and composition of vegetation, suggesting that in temperate coastal systems, plant succession stages are not coordinated with successional stages of ant communities (Gallé, 1991).

In tropical coastal dunes the number of ant species is more variable. Studies in comparable vegetation mosaics, recorded from 22 to 92 species in Cuba (Fontenla, 1993, 1994), Mexico (Durou et al., 2002), and Brazil (Bonnet & Lopes, 1993; Texeira et al., 2005; Vargas et al., 2007; Cardoso et al., 2010). In these systems species richness varies between habitats, with higher values being found in more complex and heterogeneous habitats (Fontenla, 1993; Durou et al., 2002; Vargas et al., 2007). Faunal composition is another attribute of tropical coast ant assemblages that strongly varies with the type of vegetation (Fontenla, 1993; Cardoso et al., 2010) and plant cover (Dorou et al., 2002).

Most of natural undisturbed coastal dunes of the Mexican littoral zone of the Gulf of Mexico have disappeared due to extensive farming management, human settlements and touristic activities (Moreno-Casasola, 2006). However, the state of Veracruz still harbors some well-preserved sites of coastal dunes that can enter inland up to 3 km. One of these sites is found within the Ecological Reserve of the Centro de Investigaciones Costeras La Mancha (CICOLMA). In the dunes of La Mancha environmental gradients related to the force of the wind, sand movement, and depth of water table (ultimate mediated by topography), determine the establishment of different plant communities (Moreno-Casasola & Vázquez, 2006). In this zone the vegetation follows a successional gradient, from pioneer plants and grasslands growing on the beach and young dunes, to deciduous and subdeciduous tropical forests established on older dunes. This last community constitutes the last remnant of this kind of forest in the Gulf of Mexico growing in sandy soils (Moreno-Casasola & Travieso, 2006).

Several studies of ants have been conducted at La Mancha, including numerous aspects of plant-ant interactions (Rico-Gray, 1989, 1993; Mehlreter et al., 2003), evaluation of some invasive ants (Fragoso & Rojas, 2009), records in checklists (Rojas 2001, 2011) and taxonomical studies (Mackay et al., 2004). So far, no studies characterize the complete ant community in any vegetation type of this site have been published.

The main objective of our study was to describe the ant communities of La Mancha in four types of vegetation that represent a gradient of plant succession on coastal dunes. Communities were characterized considering species richness, diversity, abundance and species composition. We hypothesized that richness and diversity would increase along the vegetation successional gradient; that each stage will have different faunal composition, and that differences will be higher between early and late successional stages.

Material and methods

Study area

The study area is located at the Centro de Investigaciones Costeras La Mancha (CICOLMA) in the coast central region of Veracruz State (96°22'40" W; 19°36'00" N) with an altitudinal range of 0-80 m elevation. The CICOLMA field station covers a total area of 83 ha. The zone is geologically young, shaped by Miocene volcanic activity and by Quaternary deposits (Geissert, 1999). The weather is characterized by an annual average temperature of 25°C and an annual precipitation of 1500 mm, with the large amount of rains (78%) occurring during the rainy season of June-September. Soils are unstructured luvic and calcaric arenosols (Travieso & Campos, 2006).

Sampling sites were established on four different successional stages of coastal dune vegetation: grassland, shrub, deciduous forest and subdeciduous forest (Fig 1). Grasslands and shrubs are found in semi stabilized dunes, with grasslands being found in upper dry parts of the dunes and shrubs on humid depressions, where water table is higher. Tropical forests grow over stabilized dunes with subdeciduous forests being established on flat sites or sites with level relief, and deciduous forests located on more steep sites (Moreno-Casasola & Travieso, 2006).

Grassland (G), (Fig 1A) - With a plant cover of nearly 40%, this community includes grasses and short shrubs that alternate with open spaces of bare sand. Common species are *Trachypogon plumosus* (Humb. & Bonpl. ex Willd.) Nees, *Andropogon glomeratus* (Walter) B.S.P. and *Chamaecrista chamaecristoides* (Colladon) Greene (Moreno-Casasola & Travieso, 2006).

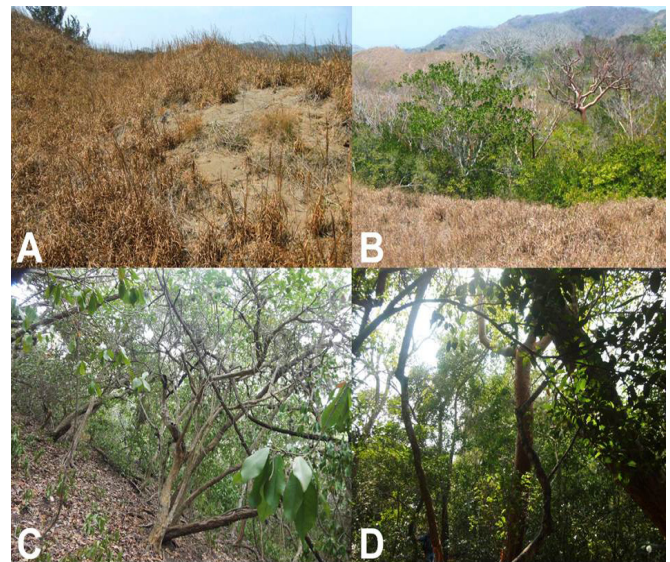


Fig 1. La Mancha plant physiognomies sampled in this study. A – Grassland, B – Shrub, C – Deciduous forest, D – Subdeciduous forest.

Shrub (S), (Fig 1B) - Medium size (2-3 m high) closed canopy shrub with a plant cover of 80% and with some isolated trees. Predominant species are shrubs *Randia laetevirens* Standl., *Pluchea odorata* (L.) Cass. and *Mimosa chaetocarpa* Brandeg. (Moreno-Casasola & Travieso, 2006).

Deciduous forest (DF), (Fig 1C) - Trees reach 12m height, with many deciduous species. Most common species are *Bursera simaruba* (L.) Sarg., *Coccoloba barbadensis* Jacq. and *Ocotea cernua* (Nees) Mez. The understory stratum is dominated by *Crossopetalum uragoga* (Jacq.) Kuntze, *Chiococca alba* (L.) Hitchc. and *Randia aculeata* L.; grasses and herbs are almost absent (Castillo, 2006).

Subdeciduous forest (SF), (Fig 1D) - The canopy (>20m height) is dominated by *Brosimum alicastrum* Sw., *Ficus cotinifolia* Kunth, *Cedrela odorata* L. and *Enterolobium cyclocarpum* (Jacq.) Griseb., whereas the lower canopy (6-15 m) is characterized by *Erithroxylum havanense* Jacq., *Nectandra salicifolia* (Kunth) Nees and *Ocotea cernua*. The species *Crossopetalum uragoga*, *Schaefferia frutescens* Jacq. and *Hippocratea celastroides* Kunth predominate in the shrub stratum (Castillo, 2006).

Ant sampling

Our sampling was performed only in one plot per vegetation type (no replicates); however we consider that the amount of traps and eight different sampling methods made this study valid for site comparisons.

Standardized sampling (SS). Sampling of grassland, deciduous forest and subdeciduous forest was performed during 1992 whereas shrub was sampled two years later (1994). In each site, a 20x20m (400m²) plot was delimited and located at least 30m inside the respective vegetation type; the plot was a grid each five meters. Sampling was made in the dry (May) and rainy (October) seasons. A total of 588 samples were obtained, using the following standardized sampling methods:

Pitfall traps (based on Greenslade, 1964) (200 traps) - In each site and plot 25 plastic container traps were set at distances of five meter intervals in a grid pattern. Each container, with a volume of 250 ml and a diameter of 8 cm, was buried at ground level and filled 3/4 with 70% ethanol and a small quantity of commercial detergent. Traps remained in the field five days.

Subterranean baits (200 baits) - Following the same grid pattern, 25 subterranean baits were set in each site and plot. Each bait was buried at 20-30 cm depth, inside a plastic vial of 5 ml volume and with several holes in the walls (Mackay & Vinson, 1989); tuna fish and a mixture of honey and oatmeal were used as bait. Traps were left buried for 48 hours.

Surface baits (72 baits) (see Bestelmeyer et al., 2000) - In each site and plot nine surface (three per row) baits were placed along three parallel rows separated 10 meters. In each row baits were separated 10 m each. A teaspoon of bait (the same type used in subterranean sampling) was placed within a

10cm diameter plastic Petri dish, deposited aboveground and left for 5 hours (from 10:00 to 15:00 h). Attracted ants were collected at one hour intervals.

Arboreal baits (70 baits) - This method was used only in the two forests, because trees were nonexistent or very scarce in G and S plots, respectively. Baits (same type used in former methods) were placed inside plastic containers of 150ml and tied at 1.5m height in different tree species with a minimal diameter of 20cm. Baits were left for 5 hours (from 10:00 to 15:00h); attracted ants were collected at one hour intervals. Twenty arboreal baits were placed in DF and 15 in SF.

Leaf-litter samples (30 samples) (see Bestelmeyer et al., 2000) - This method was used in all sites except G, where no litter stratum was found. In each site five samples of litter (1m²) were collected and processed with Berlese funnels until the litter was dry. Samples were taken from the center and two meters inside the four corners of each plot.

Hand sampling (16 samples) - In all sites, search and capture of ants was performed by two persons during 4h (8 hours per site). Sampling included vegetation (epiphytes, foliage and hollow stems) and soil (litter, first centimeters of soil and within and under decaying logs).

Non standardized sampling (NSS). It refers to any sample of ants obtained out of the SS protocol by hand sampling.

Ants were identified to genus level using Bolton (1994); species were determined using specialized publications and revisions or by comparison with reference material from the ant collections of W.P. Mackay and the Laboratorio de Invertebrados del Suelo (INECOL, Xalapa). Voucher specimens of all species were deposited in the latter Collection. Nomenclature follows Bolton et al. (2007).

Data analysis

Seasonality - Differences in the number of species captured in rainy and dry season were analyzed with parametric t-test for dependent samples (when normality was fitted) and nonparametric Wilcoxon matched pair test. Analyses were performed for each site and the following SS methods: pitfall traps, subterranean baits, surface baits and arboreal baits. All these tests were performed using STATISTICA (Statsoft, 1999). Seasonality differences for a given site (SS + NSS samples) were compared considering 95% confidence intervals derived from rarefaction curves (Mao Tau, EstimateS program version 9, Colwell, 2013).

Abundance - In order to avoid over estimation of those species with large foraging areas or legionary habits, abundance was calculated as presence/absence data (occurrence) from SS samples. For a given species, abundance was calculated as frequency of occurrence ($FO = \frac{n_i}{N} \times 100$, where n_i is the number of samples where species i was found, and N is the total number of samples). The number of occurrences in samples was considered as an indirect measure of the relative

abundance of each species in each site (Gottelli & Colwell, 2011) and can be used to estimate abundance distribution of species along gradients (Andersen, 1997).

Species richness and diversity - Considering SS data, species accumulation curves were generated as rarefaction curves (Mao Tau) and compared to estimated richness (Chao 2 estimator) (Gotelli & Colwell, 2011) using EstimateS program (version 9, Colwell, 2013). Diversity was calculated using Shannon and Simpson indices; differences between vegetation types were evaluated using the t-tests of Hutcheson (1970) and Brower et al. (1998) for, respectively, Shannon and Simpson indices. These analyses were performed using PAST program (version 3, Hammer et al., 2001).

Similarity - Similarity of the four sites was calculated following two approaches. In the first one a hierarchical similarity analysis of sites was made with the presence/absence data (SS and NSS sampling) of each species in each site (121 species per four sites). Variables were associated and clustered using Kulczinski index (incidence-based) and UPGMA, respectively and represented as a similarity dendrogram; these analyses were performed using PATN software (Belbin, 1989). Incidence-based Sorensen index was also calculated for comparative purposes. In the second approach we used FO of each species obtained from SS sampling. The resultant species per site matrix (97 x 4) was analyzed using the Morisita-Horn index (abundance-based), from EstimateS (version 9, Colwell, 2013).

Vertical distribution - Each species was assigned to one

of the following vertical categories: soil only, vegetation only, both. Assignment was made considering the more frequent localization of nests (personal observations) and by consulting natural history information available in current literature.

Results

Considering that no significant differences in number of species were found between dry and rainy seasons for all sites and sampling methods, except for pitfall trap data from G and SF (see Table 1), and that similar numbers of species were collected during dry and rainy seasons (78 and 77 species, respectively) our results correspond to clumped data from both seasons. In the four sites 121 ant species of 41 genera and seven subfamilies were found. With the standardized sampling 97 species (80.2 % of total) were obtained from 1440 species occurrences from all sites; the remaining 24 species were captured using non standardized sampling. Subfamilies with more species were Myrmicinae (57 species) and Formicinae (23); the genera with more species were *Camponotus* (16 species), *Pheidole*, *Pseudomyrmex* (14 each), *Solenopsis* and *Crematogaster* (5 each) (Appendix 1).

The following seven species, with records in $\geq 10\%$ of samples, accounted for 40.8% of total species occurrences: *Solenopsis molesta* (21.6%), *S. geminata* (19.5%), *Azteca velox* (14%), *Brachymyrmex* sp. 1LM (11.7%), *Dorymyrmex bicolor* (11.2%), *Camponotus planatus* (11%) and *Pheidole susanna* (10.7%). Twenty eight species (23%) were repre-

Table 1. Average values and standard deviations (in brackets) in the number of ant species found in dry (x_d) and rainy (x_r) seasons at La Mancha with four standardized sampling methods (SS). The last column shows values (and 95% confidence intervals) including all species in dry (N_d) and rainy (N_r) seasons collected by SS and non-standardized methods, NSS. Significant differences between seasons are in bolds (ns = no significant differences).

	Pitfall (t-test)	Subterranean (Wilcoxon)	Superficial (t-test)	Arboreal (Wilcoxon)	SS + NSS
Grassland	$X_d=3$ (1.6) $X_r=1.6$ (1.3) n=25 $P=0.0007$	$X_d=0.52$ (0.59) $X_r=0.6$ (0.65) n=25 ns	$X_d=2.3$ (1) $X_r=2.1$ (1.3) n=9 ns	Not used	$N_d=14 \pm 5.1$ $N_r=10 \pm 3.6$
Shrub	$X_d=6.2$ (1.7) $X_r=6.4$ (2.5) n=25 ns	$X_d=0.16$ (0.37) $X_r=0.2$ (0.41) n=25 ns	$X_d=3.8$ (1.5) $X_r=3.8$ (1.3) n=9 ns	Not used	$N_d=29 \pm 6.3$ $N_r=38 \pm 8.4$
Deciduous forest	$X_d=2.7$ (1.6) $X_r=2.5$ (1.3) n=25 ns	$X_d=0.88$ (0.53) $X_r=0.80$ (0.41) n=25 ns	$X_d=4.1$ (1.7) $X_r=4.7$ (1.7) n=9 ns	$X_d=1.9$ (1.1) $X_r=2$ (1) n=20 ns	$N_d=26 \pm 8.5$ $N_r=34 \pm 8.6$
Subdeciduous forest	$X_d=2.5$ (1.7) $X_r=4.2$ (1.5) n=25 $P=0.001$	$X_d=0.36$ (0.76) $X_r=0.44$ (0.58) n=25 ns	$X_d=3.8$ (1.9) $X_r=3.2$ (1.6) n=9 ns	$X_d=1$ (0.8) $X_r=2$ (1.6) n=15 ns	$N_d=50 \pm 8.8$ $N_r=44 \pm 9.5$

sented only by a single record.

Species richness - When considering only standardized sampling (SS), G was the site with the lowest species richness (15 species) whereas SF forest was the richest (62). DF and S presented an intermediate value of richness (42 species each). Estimates of expected species richness for each site (Chao2 richness estimator) showed that G was the best sampled site (77% of expected number of species), followed by SF and DF (64 and 59%, respectively). S turned to be the worst sampled site (56%) (Fig 2 and Table 2). When species captured with non-standardized sampling (NSS) are added, sites followed the same order of species richness, although percentages of increase varied for each site. Species richness values of G and SF were closer to those predicted by Chao2 index, even exceeding the estimated total number of species (Table 2).

Abundance - The lowest number of occurrences was found in G (197, 13.7% of total). S was the site with the highest number of occurrences (454, 31.5% of total); however, only with pitfall traps data was this value significantly different from the other sites (ANOVA, $F_{3,196}=52.88, P < 0.0001$, Tukey HSD test; $X_S = 6.30, SE_S = 0.31; X_G = 2.34, SE_G = 0.22; X_{DF} = 2.60, SE_{DF} = 0.21; X_{SF} = 3.32, SE_{SF} = 0.25$). The two forests showed intermediate occurrences values (deciduous: 393, 27.3%; subdeciduous: 396, 27.5%).

On the basis of the five most abundant species from each site (Table 3) communities were very different. Noteworthy in G these five species, characterized by the presence of three *Dorymyrmex* species, were not found in the two forests. All

though *Dorymyrmex* sp. aff. *flavus* and *D. bicolor* appear also in S, they have lower abundances. In G and S these five species accounted for 82.7% and 45.8% of species occurrences, respectively. In DF this group represented 56.5%, with the arboreal *Azteca velox* the more abundant species. In SF forest this group includes only ground ants which accounted 47.7%, with four of these species characteristic of disturbed places. *Solenopsis geminata* and *S. molesta* always appear in S, DF and SF among the five more abundant species.

Diversity - As expected, lower and higher diversity values were respectively observed in G and SF; however, diversity in S was higher than in DF (Shannon and Simpson indices, Table 4). In paired comparisons, all sites significantly differ in Shannon and Simpson indices (Table 5), excepting differences between S and SF with Simpson index. Rank abundance plots (Fig 3) also indicate that G was the less diverse assemblage (higher slope and shorter line) and that SF was the more diverse. Even that S and DF forest had the same number of species (SS sampling) the curve of S had a less steep slope indicating a higher evenness in the abundance of their species. Long curves observed in SF, DF and S reflect presence of many species with very low abundances.

Faunal composition - Appendix 1 (SS and NSS data) show the list of all species found at La Mancha, suggesting at first glance strong differences in faunal composition between sites. A similarity analysis of species presence/absence (Kulczynski index) clustered forests in one group and G and S in another, both groups being separated by more than 60%

Table 2. Observed (SS and SS+NSS) and estimated (Chao2) species richness of ants in the four sites. SS= standardized sampling; NSS= non standardized sampling.

	SS	SS+NSS	Chao2
Grassland	15	21	19.5
Shrub	42	47	74.7
Deciduous forest	42	50	70.9
Subdeciduous forest	62	102	96.3
Total	97	121	

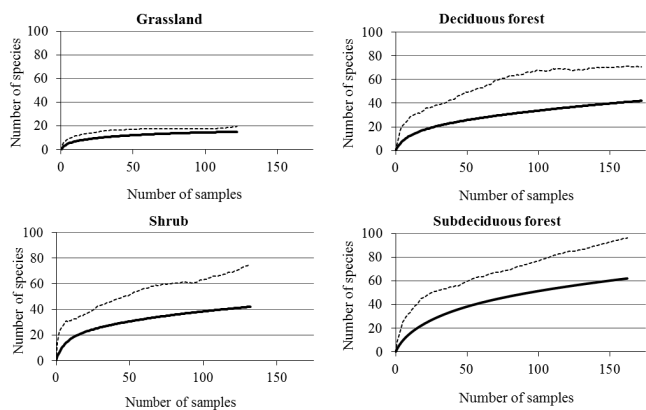


Fig 2. Species accumulation curves of ant species for each site. Solid lines correspond to rarefaction curves (Mao Tau) of observed species richness; dashed lines correspond to Chao2 predicted species richness.

Table 3. Abundance expressed as percentage of occurrences in samples (FO) of the five most important ant species in each site (in bold). FO values of these species in the other sites are shown for comparison; a dash means absence of species. G = Grassland; S = Shrub; DF = Deciduous forest; SF = Subdeciduous forest.

	G (N=122)	S (N=132)	DF (N=172)	SF (N=162)
<i>Azteca velox</i>	-	5.3	40.7	3.7
<i>Dorymyrmex bicolor</i>	42.6	10.6	-	-
<i>Dorymyrmex smithi</i>	22.9	-	-	-
<i>Dorymyrmex</i> sp. aff. <i>flavus</i>	10.6	0.7	-	-
<i>Forelius pruinosus</i>	19.7	15.1	-	-
<i>Brachymyrmex</i> sp. 1	37.7	9.1	5.1	0.6
<i>Camponotus planatus</i>	1.6	13.6	22.7	3.7
<i>Monomorium ebeninum</i>	-	43.9	-	-
<i>Pheidole punctatissima</i>	-	-	1.2	23.4
<i>Pheidole</i> sp. 11LM	-	23.5	-	5.5
<i>Pheidole</i> sp. 5LM	-	-	18.6	1.8
<i>Pheidole susannae</i>	-	5.3	-	34.6
<i>Solenopsis molesta</i>	0.8	29.5	30.8	21.0
<i>Solenopsis geminata</i>	8.2	39.4	16.3	15.4
<i>Tetramorium spinosum</i>	-	21.2	-	-
<i>Wasmannia auropunctata</i>	0.8	-	7.0	22.2

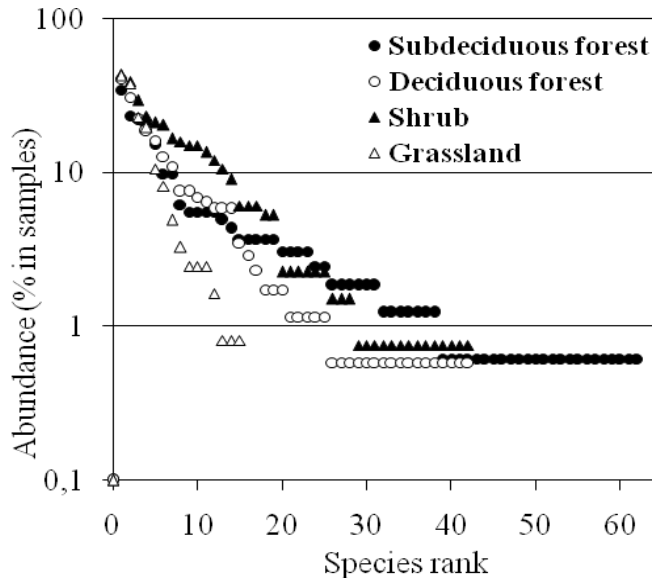


Fig 3. Rank-abundance plot of ant species in each site. Abundance is expressed on a log scale.

of dissimilarity (Fig 4). Similar results were obtained when similarity was calculated with Sorensen index (Table 5). Conversely, the Morisita-Horn index indicated a higher similarity of DF and SF with S, leaving G as an isolated site. The number of species considered in Morisita analysis was lower, because abundance data was obtained from standardized sampling only (Table 5).

Table 4. Ant diversity of the four sites studied obtained with two diversity indices. Data from standardized sampling (SS).

	Shannon (H')	Simpson (1/D)
	Mean (SD)	Mean (SD)
Grassland	2.06 (0.06)	6.09 (0.04)
Shrub	3.06 (0.04)	16.30 (0.09)
Deciduous forest	2.89 (0.05)	12.29 (0.09)
Subdeciduous forest	3.35 (0.06)	17.92 (0.17)

Site specificity - At La Mancha 48 ant species (ca. 40% of total) were found in a single site. SF had the largest number of exclusive species (39, 32.2%), whereas DF and S had four exclusive species each (3.3%) and G only one species (0.8%). In contrast number of ubiquitous species (those found in all sites) was very low. Only six species (5%) were found in the four vegetation types: *Brachymyrmex* sp. 1LM, *Camponotus planatus*, *C. atriceps*, *Cyphomyrmex rimosus*, *Solenopsis geminata* and *S. molesta* (Appendix 1).

Vertical distribution - Soil-nesting species (69, 57%) dominated over plant-nesting species (48, 40%), with only four species nesting in both strata (3%) (Appendix 1). Five species in G were plant-nesting ants, but were low in abundance, and always captured with pitfall traps and soil baits; the remaining species (17, 76%) were soil dwellers. In S, very similar numbers of species nesting in soil (23, 49%) and vegetation (22, 47%) were found, with two species nesting in both strata (4%). A similar situation was observed in DF, 23

species (46%) nesting in soil, 25 (50%) in vegetation and two species (4%) in both strata. Finally SF forest had, respectively, 56 (55%) and 42 (41%) soil and plant-nesting species, with four species (4%) inhabiting both strata.

Discussion

In order to capture as many species as possible, ant communities were sampled in two seasons. Sampling was not designed with the aim to compare seasonal patterns.

Accordingly, we conducted some statistical tests to confirm that all the SS data can be grouped. In general no significant differences were observed between rainy and dry season in the amount of species per sampling method and by site, excepting pitfall traps of G and SF. This can be explained by the dependence of this method on the foraging activity of ants (Bestelmeyer, 2000).

Total species richness - The number of ant species en-

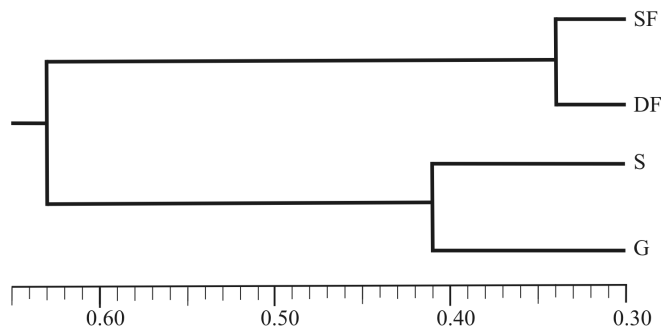


Fig 4. Similarity between sites in function of presence/absence of ant species. Scale shows values of dissimilarity (Kulczynski index). G = grassland, S = shrub, DF = deciduous forest, SF = subdeciduous forest.

countered in the four vegetation types studied at La Mancha was notably high, considering the relatively small area of the reserve (83ha, Moreno-Casasola & Monroy, 2006). Moreover, this number of species (121) make up nearly 34% of the total number of species recorded in the state of Veracruz (Rojas, 2011) and 13.7% of all Mexican ant species (Vázquez-Bolaños, 2011). Comparatively, similar studies completed in tropical coastal ecosystems recorded lower values of species richness. For example in the Brazilian "restinga" Cardoso et al. (2010) reported 71 species along one transect of 6.5 km length, whereas Vargas et al. (2007) recorded 92 species; similarly in Mexico Durou et al. (2002) found 96 species. The highest values found at La Mancha can be explained because our study included two well-developed tropical forests. In spite that Vargas et al. (2007) also sampled a tropical forest, their ant richness values were still lower than in La Mancha.

Species richness and diversity along the vegetation gradient - The four studied sites represent a successional plant gradient established on sand dunes, which also entails the stabilization of dunes. Accordingly, the grassland with 21 ant species and low diversity values, represent the first stage in dune succession and it is the less complex environment with

Table 5. Species similarity values between grassland (G), shrub (S), deciduous forest (DF) and subdeciduous forest (SF), calculated with three indices. Diversity differences between sites are also indicated: †= significant differences ($P < 0.005$) comparing Simpson index (Brower et al., 1998). *= Significant differences ($P < 0.01$) comparing Shannon index (Hutcheson, 1970).

	Kulczynski	Sorensen	Morisita-Horn
G vs S†*	0.41	0.50	0.25
G vs DF†*	0.76	0.20	0.09
G vs SF†*	0.65	0.19	0.05
S vs DF†*	0.63	0.37	0.39
S vs SF*	0.49	0.44	0.34
DF vs SF†*	0.34	0.58	0.37

only herbaceous vegetation alternating with areas of bare sand. In addition no litter layer exists and temperature differences between high and low cover sites can be up to 11°C (Moreno-Casasola & Travieso, 2006); thus scarcity of nesting sites for ants is not only restricted to vegetation, but also occurs in the soil. Non structured sandy soils represent an unstable substrate for ants, and they would need to frequently reconstruct nest chambers and galleries (Lubertazzi & Tchinkel, 2003). The higher diversity and number of species (42) in the shrub zone, the second successional stage, can be explained by the presence of both herbs and bushes. These strata produce a litter layer that, even scarce as it was, offers suitable microsites for the arrival and settlement of more ant species.

The two forests correspond to last successional stages, and although they have a well-developed arboreal, bush and litter strata, their plant diversity and environmental conditions are not the same (Castillo, 2006) as was indicated by ant diversity and species richness. By being located in upper and steep places of stabilized dunes, deciduous forest is more exposed to wind, with a higher water runoff, and is consequently dryer. This translates into less plant cover, smaller tree height and fewer epiphytes. Conversely the subdeciduous forest is located in a more humid flat and wind protected place; this causes a higher plant cover, taller trees and more epiphytes (Novelo, 1978). Correspondingly, the more stable subdeciduous forest harbor twofold ant species richness (102 species) than the stressed deciduous forest (50).

It is widely recognized that in most of habitats, plant communities determine the physical structure of environment and therefore have a strong influence over the distribution and interactions of animal species (Lawton, 1983; Rosenzweig, 1995; Tews et al., 2004). Several studies completed in temperate coastal dunes (Boomsma & Van Loon, 1982; Dauber and Wolters, 2005) and in tropical Brazilian “restinga” (Vargas et al., 2007) have shown that more heterogeneous environments correspond to late successional stages and harbor a more diverse fauna and a higher species rich ant communities. In general all of these studies conclude that this pattern is due to the higher amount of microhabitats and microclimates that in turn produces more availability of food and nest sites. The results

of this study partially support our original hypothesis related to an increase of ant species richness along the plant successional gradient (G→S→DF→SF). Sites with the lower and higher species richness were, respectively, G and SF; however no significant differences in species richness were observed between the intermediate gradient stages, with estimated richness (Chao 2) very similar in S and DF, and even higher in the former. Diversity values showed also the same pattern.

On the basis of these results we propose that plant succession at La Mancha has not been unidirectional, but that two independent paths have occurred after the development of shrubs from grasslands: the first path would be the successional change of shrubs into deciduous forest (S→DF) in more stressed environmental conditions; alternatively the second path would be the change of shrubs towards subdeciduous forest (S→SF) in more stable environments.

Faunal composition - Through coastal plant succession, faunal composition of ant assemblages varies between temperate and tropical ecosystems. In temperate sites, species assemblages are very similar across vegetation physiognomies, as it has been shown by studies in coastal dunes (Gallé, 1991; Ruano et al., 1995) and grasslands (Zorilla et al., 1986; Dauber & Wolters, 2005). Independently of the successional stage, ant assemblages from these sites have not shown different number of species; instead the abundances of each species changes across the gradient. On the other hand, ant communities from tropical ecosystems show larger differences across vegetation successions. At La Mancha, the four studied vegetation types presented different species assemblages as has been observed in other coastal dune vegetation studies (Fontenla, 1993; Durou et al., 2002; Cardoso et al., 2010).

Considering its faunal composition the studied sites were divided into two separated groups. The first group included sites of earlier stages of succession (G and S) whereas the second one grouped the two forests (DF and SF) corresponding to late successional stages. From the point of view of vegetation, at La Mancha grasslands and shrubs also comprises a well differentiated group from deciduous and subdeciduous forests, sharing only 14% of plant species (Castillo & Travieso, 2006). Ant membership in the first group was defined by the share of eight species typical of dry environments, in spite of differences in the number of species. Among them *Dorymyrmex bicolor* and *Forelius pruinosus* are well adapted to xeric conditions and nest and forage on the soil of sunny sites, especially in grasslands (Shattuck, 1992). *Tetramorium spinosum* was another shared species widely distributed in arid zones of Mexico, that also nest in exposed soil (Rojas & Fragoso, 1994). Although they nest only in S, other shared species such as *Atta cephalotes* and *Crematogaster crinosa* were found foraging in both G and S habitats; this foraging strategy has been also recorded in other coastal environments, where ants living in adjacent forests use dunes and beaches as foraging areas (Ruano et al., 1995). The remaining two species shared by G and S were *Pseudomyrmex brunneus* and *P. ejectus* which

have been reported occurring sympatrically and nesting in dead twigs of woody and herbaceous plants (Ward, 1985). We were unable to find nests of these species, but we observed them foraging in soil and plants at both sites. It remains to be demonstrated whether or not these species are adapted to live in harsh environments. Each site, nevertheless, has some exclusive species. Whereas G has only one unique species, the abundant ant *Dorymyrmex smithii* which nests under dead stems of grasses, S had four exclusive species (*Neivamyrmex rugulosus*, *Nesomyrmex wilda* and two unidentified *Pheidole*), all very low in abundance.

The second group clustered both forests on the basis of 27 shared species (see Appendix 1). The presence of a well-developed arboreal stratum determines that more than 50% of these species nest in trees.

In spite of their faunal similarities, both forests were separated by species richness and by the amount of exclusive species. While SF contained 39 exclusive species (38% of their 102 species), in DF only four species (all low abundant) were exclusive (8% of their 50 species). Thus, ant fauna of DF can be considered as an impoverished subset of SF with more microhabitats available to ants.

Interestingly in all sites, but G, ants typical of disturbed environments were found in high abundances. This was the case of *Solenopsis molesta*, a generalist soil-nesting species (Mackay & Mackay, 2002), *S. geminata*, commonly found in disturbed ecosystems of the Neotropics, and which have been found even penetrating tropical forests (Risch & Carroll, 1982; Taber, 2000), and *Pheidole susannae* which has been reported in disturbed habitats throughout the Neotropics (Wilson, 2003).

Unexpectedly, the higher number of ant species associated to disturbance was recorded in SF, currently considered as a functional forest in the last stages of succession (Castillo, 2006). An explanation of this finding could be related that in the past botanists recognized this site as a strongly disturbed secondary forest (Novelo, 1978); moreover Gomez-Pompa (as cited in Paradowska & Moreno-Casasola, 2006) suggests that presence of useful trees is an indication that this forest underwent high disturbances in the past, even being used as orchard by prehispanic people.

Vertical distribution - Our results showed that 97% of species were found associated with a single vertical stratum (soil or vegetation) in agreement with other studies which show a high vertical segregation in ants (Bruhl et al., 1998; Yanoviak & Kaspari, 2000). In the three sites with developed plant strata, vertical segregation was nearly 50%. Considering that in our sampled forests canopy ants were under-sampled, this proportion should change once a detailed sampling of canopy is undertaken. Remarkably, the only four species found nesting both in soil and vegetation were tramp and/or invasive species: *Paratrechina longicornis*, *Pheidole punctatissima*, *S. geminata* and *Tetramorium bicarinatum* (Kempf, 1972; McGlynn, 1999; Wetterer, 2009).

Conclusions

Ant communities of tropical coastal environments have been, compared to other ecosystems, poorly studied in spite of their fragility and high risk of change due to climate change. In Mexico this is the first study that characterized ant communities in this kind of ecosystem. Considering that this country will probably be greatly affected in the future by climate change (International Panel for Climate Change [IPCC], 2013), we expect that patterns obtained in this study will constitute a base line to evaluate future changes. Although no continuous plant studies have been conducted in forests and shrubs, information is available on the changes that have occurred in dune grasslands over the last 20 years (Alvarez-Molina et al., 2012). This period of time corresponds to the time elapsed since we sampled these ant communities. Considering that after 20 years dune grasslands have a higher cover and more plant species typical of shrubs (Alvarez-Molina et al., 2012), we expect to find a similar trend in ant communities.

We can also anticipate that no large changes will be observed in the two forests, as far as it seems that both ecosystems represent advanced stages in a successional process (Castillo, 2006). Changes in abundance of invasive ants however, could significantly influence species richness as it has been observed in other ecosystems (McGlynn, 1999). In this regard the recent record of tramp species *Monomorium pharaonis* (pers. obs.) should be monitored. Considering that SF harbor more than 84% of ant species richness of La Mancha, and that it constitutes the last remnant of subdeciduous forest in the Mexican gulf coasts (Moreno-Casasola & Travieso, 2006) monitoring should be focused mainly at this site.

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Appendix 1. Number of records in samples of each ant species in the four sites studied at La Mancha. The total number of samples are included in brackets. *= species captured with non-standardized sampling (NSS). v= nesting in vegetation; s= nesting in soil; vs= nesting in vegetation and soil.

Species list	Grassland (N=122)	Shrub (N=132)	Deciduous forest (N=172)	Subdeciduous forest (N=162)
Dolichoderinae				
<i>Azteca forelii</i> Emery, 1893 v	0	0	*	*
<i>Azteca velox</i> Forel, 1899 v	0	7	70	6
<i>Dolichoderus diversus</i> Emery, 1894 v	0	0	1	*
<i>Dolichoderus lutosus</i> (Smith, 1858) v	0	3	2	3
<i>Dorymyrmex bicolor</i> Wheeler, 1906 s	52	14	0	0
<i>Dorymyrmex smithi</i> Cole, 1936 s	28	0	0	0
<i>Dorymyrmex</i> sp. aff. <i>flavus</i> s	13	1	0	0
<i>Forelius pruinosus</i> (Roger, 1863) s	24	20	0	0
Ectatomminae				
<i>Ectatomma ruidum</i> (Roger, 1860) s	0	0	0	2
Ecitoninae				
<i>Eciton burchelli parvispinum</i> Forel, 1899 s	0	0	0	*
<i>Labidus coecus</i> (Latreille, 1802) s	0	0	0	1
<i>Labidus praedator</i> (Smith, 1858) s	0	0	0	*
<i>Neivamyrmex opacithorax</i> (Emery, 1894) s	0	0	3	0
<i>Neivamyrmex pilosus</i> (Smith, 1858) s	0	0	0	*
<i>Neivamyrmex rugulosus</i> Borgmeier, 1953 s	0	*	0	0
<i>Neivamyrmex swainsoni</i> (Shuckard, 1840) s	0	0	0	1
<i>Nomamyrmex esenbeckii wilsoni</i> (Santschi, 1920) s	0	*	0	1
Formicinae				
<i>Acropyga smithii</i> Forel, 1893 s	0	0	0	*
<i>Brachymyrmex heeri</i> Forel, 1874 s	0	*	*	0
<i>Brachymyrmex</i> sp. 1LM s	46	12	10	1
<i>Brachymyrmex</i> sp. 2LM s	0	0	0	2
<i>Camponotus atriceps</i> (Smith, 1858) v	3	8	1	*
<i>Camponotus cerberulus</i> Emery, 1920 v	0	0	0	*
<i>Camponotus claviscapus</i> Forel, 1899 v	0	0	0	*
<i>Camponotus coloratus</i> Forel, 1904 v	0	1	0	*
<i>Camponotus coruscus</i> (Smith, 1862) v	0	0	0	1
<i>Camponotus etiolatus</i> Wheeler, 1904 v	0	0	1	*
<i>Camponotus excisus</i> Mayr, 1870 v	0	0	0	1
<i>Camponotus linnaei</i> Forel, 1886 v	0	3	2	3
<i>Camponotus mucronatus hirsutinasus</i> Wheeler, 1934 v	0	3	13	*
<i>Camponotus novogranadensis</i> Mayr, 1870 v	0	0	19	4
<i>Camponotus planatus</i> Roger, 1863 v	2	18	39	6
<i>Camponotus sericeiventris</i> (Guerin-Meneville, 1838) v	0	0	1	7
<i>Camponotus conspicuus sharpi</i> Forel, 1893 v	0	0	0	*
<i>Camponotus zoc</i> Forel, 1879 v	0	0	0	*
<i>Camponotus</i> sp. 1LM v	0	1	1	0
<i>Camponotus</i> sp. 2 LM v	0	1	0	*
<i>Myrmelachista skwarrae</i> Wheeler, 1934 v	0	0	1	*
<i>Nylanderia steinheili</i> (Forel, 1893) s	0	8	22	1
<i>Paratrechina longicornis</i> (Latreille, 1802) sv	1	20	0	*
Myrmicinae				
<i>Atta cephalotes</i> (Linnaeus, 1758) s	4	21	0	0
<i>Atta mexicana</i> (Smith, 1858) s	0	0	0	4
<i>Cephalotes minutus</i> (Fabricius, 1804) v	0	3	0	5
<i>Cephalotes scutulatus</i> (Smith, 1867) v	0	*	10	*
<i>Cephalotes umbraculatus</i> (Fabricius, 1804) v	0	0	10	1
<i>Crematogaster corvina</i> Mayr, 1870 v	0	0	1	0
<i>Crematogaster crinosa</i> Mayr, 1862 v	*	27	0	0
<i>Crematogaster curvispinosa</i> Mayr, 1862 v	0	0	4	1
<i>Crematogaster torosa</i> Mayr, 1870 v	0	0	1	3
<i>Crematogaster</i> sp. aff. <i>curvispinosa</i> v	0	0	0	1
<i>Cyphomyrmex costatus</i> Mann, 1922 s	0	0	0	*

<i>Cyphomyrmex rimosus</i> (Spinola, 1851) s	*	8	13	6
<i>Megalomyrmex silvestri</i> Wheeler, 1909 s	0	0	0	*
<i>Monomorium ebeninum</i> Forel, 1891 s	*	58	0	*
<i>Monomorium floricola</i> (Jerdon, 1851) v	0	0	0	16
<i>Mycetosoritis hartmanni</i> (Wheeler, 1907) s	0	0	1	0
<i>Mycocepurus curvispinosus</i> Mackay, 1998 s	0	0	0	3
<i>Mycocepurus smithii</i> (Forel, 1893) s	0	0	*	6
<i>Myrmicocrypta</i> sp. s	0	0	0	1
<i>Nesomyrmex echinatinodis</i> (Forel, 1886) v	0	2	0	*
<i>Nesomyrmex wilda</i> (Smith, 1943) v	0	1	0	0
<i>Pheidole punctatissima</i> Mayr, 1870 sv	0	0	2	38
<i>Pheidole susannae</i> Forel, 1886 s	0	7	*	56
<i>Pheidole</i> sp. 1LM s	0	0	1	9
<i>Pheidole</i> sp. 2LM s	0	0	2	2
<i>Pheidole</i> sp. 3LM s	0	0	11	2
<i>Pheidole</i> sp. 4LM s	0	0	32	3
<i>Pheidole</i> sp. 5LM s	0	0	0	1
<i>Pheidole</i> sp. 6LM s	0	2	0	1
<i>Pheidole</i> sp. 7LM s	0	16	0	0
<i>Pheidole</i> sp. 8LM s	0	0	*	*
<i>Pheidole</i> sp. 9LM s	0	1	0	0
<i>Pheidole</i> sp. 10LM s	0	31	0	9
<i>Pheidole</i> sp. 11LM s	0	0	0	9
<i>Pheidole</i> sp. 12LM s	0	0	2	0
<i>Rogeria belti</i> Mann, 1922 s	0	0	*	1
<i>Rogeria cuneola</i> Kugler, 1994 s	0	0	0	*
<i>Sericomyrmex aztecus</i> Forel, 1855 s	0	0	0	9
<i>Solenopsis molesta</i> (Say, 1836) s	1	39	53	34
<i>Solenopsis geminata</i> (Fabricius, 1804) sv	10	52	28	25
<i>Solenopsis isopilis</i> Pacheco & Mackay, 2013 s	0	0	1	10
<i>Solenopsis</i> sp. aff. <i>azteca</i> s	0	0	0	*
<i>Solenopsis</i> sp. s	0	0	0	*
<i>Strumigenys boneti</i> Brown, 1959 s	0	0	6	*
<i>Strumigenys eggersi</i> Emery, 1890 s	0	0	0	*
<i>Strumigenys elongata</i> Roger, 1863 s	0	0	0	1
<i>Strumigenys louisianae</i> Roger, 1863 s	0	1	0	1
<i>Strumigenys ludia</i> Mann, 1922 s	0	0	0	2
<i>Strumigenys nigrescens</i> Wheeler, 1911 s	0	0	0	*
<i>Temnothorax subditivus</i> (Wheeler, 1903) s	0	2	3	*
<i>Tetramorium bicarinatum</i> (Nylander, 1846) sv	*	0	0	*
<i>Tetramorium simillimum</i> (Smith, 1851) s	*	0	0	*
<i>Tetramorium spinosum</i> (Pergande, 1896) s	*	28	0	0
<i>Trachymyrmex intermedius</i> (Forel, 1909) s	0	0	0	1
<i>Trachymyrmex</i> sp. aff. <i>saussurei</i> s	6	22	0	6
<i>Wasmannia auropunctata</i> (Roger, 1863) s	1	0	12	36
<i>Xenomyrmex panamanus</i> (Wheeler, 1922) v	0	0	1	1
Ponerinae				
<i>Hypoponera nitidula</i> (Emery, 1890) s	0	0	1	5
<i>Hypoponera opacior</i> (Forel, 1893) s	0	1	0	5
<i>Hypoponera</i> sp. aff. <i>vana</i> s	0	0	*	5
<i>Odontomachus brunneus</i> (Patton, 1894) s	0	0	0	*
<i>Odontomachus laticeps</i> Roger, 1861 s	0	0	0	1
<i>Pachycondyla crenata</i> (Roger, 1861) v	0	0	0	1
<i>Pachycondyla harpax</i> (Fabricius, 1804) s	0	0	3	8
<i>Pachycondyla stigma</i> (Fabricius, 1804) s	0	1	0	*
<i>Pachycondyla villosa</i> (Fabricius, 1804) v	0	0	*	16
<i>Platythyrea punctata</i> (Smith, 1858) s	0	0	0	*
Pseudomyrmeciinae				
<i>Pseudomyrmex boopis</i> (Roger, 1863) s	0	0	0	1
<i>Pseudomyrmex brunneus</i> (Smith, 1877) v	3	3	0	0
<i>Pseudomyrmex cubaensis</i> (Forel, 1901) v	0	1	0	3
<i>Pseudomyrmex ejectus</i> (Smith, 1858) v	3	3	0	0

<i>Pseudomyrmex elongatulus</i> Dalla Torre, 1892 v	0	1	1	1
<i>Pseudomyrmex ferrugineus</i> (Smith, 1877) v	0	0	1	2
<i>Pseudomyrmex gracilis</i> (Fabricius, 1804) v	0	0	1	1
<i>Pseudomyrmex ita</i> (Forel, 1906) v	0	1	0	*
<i>Pseudomyrmex oculatus</i> (Smith, 1855) v	0	0	0	*
<i>Pseudomyrmex seminole</i> Ward, 1985 v	0	0	0	1
<i>Pseudomyrmex simplex</i> (Smith, 1877) v	0	1	0	*
<i>Pseudomyrmex spiculus</i> Ward, 1989 v	0	0	1	*
<i>Pseudomyrmex tenuissimus</i> (Emery, 1906) v	0	1	5	*
<i>Pseudomyrmex</i> sp. (<i>pallens</i> group) v	0	*	0	2