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Species composition and co-occurrence patterns of ant assemblages in *Coccoloba uvifera* shrubs of two sandy beaches

Composición de especies y patrones de coexistencia de ensamblajes de hormigas en *Coccoloba uvifera* de dos playas arenosas

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Abstract: Ants are one of the most important animal groups in terms of biomass and local abundance, and have been poorly studied in coastal dunes systems. The sea-grape shrub *Coccoloba uvifera* provides shelter and resources, such as nectar, fruits, "honey dew" of scale insects, and the leaf-litter supplies organic matter and retains humidity. The goal of this paper is to assess species composition and co-occurrence patterns of ant assemblages in sea-grape shrub formations along two sandy beaches in the northern coast of Western Cuba. There were determined, during the years 2017-2018, 21 ant species from 240 1x1m quadrats at Eastern Beaches and 13 species from 80 quadrats at Varadero Beach, for a total of 23 ant species. The most frequent species were *Wasmannia auropunctata*, *Pheidole megacephala* and *Paratrechina longicornis*. The predominant functional groups were the dominant omnivorous of ground and vegetation, and ground and vegetation opportunists. Both ant assemblages showed equivalent proportions of shared species and similar values in species richness and diversity. It was observed a nested general pattern of species composition across quadrats. Species co-occurrence and species combinations were less than expected by chance alone. The highest scores for negative interactions at the two beaches corresponded to the pair *Pheidole megacephala*-*Wasmannia auropunctata*, and for positive associations to the pair *Paratrechina longicornis* - *Dorymyrmex pyramicus* and *Paratrechina longicornis* - *Brachymyrmex obscurior*. It is concluded that both ant assemblages exhibited similar ecological structure.
Key words: Cuba, functional groups, negative associations, spatial nestedness.

Resumen: Las hormigas constituyen uno de los grupos animales más importantes en cuanto a biomasa y abundancia local y han sido poco estudiadas en sistemas de dunas costeras. El arbusto *Coccoloba uvifera* suministra refugio y recursos, tales como néctar, frutos, "miel de rocío" de insectos escamas, y la hojarasca suministra materia orgánica y retiene humedad. El objetivo de este estudio fue evaluar la composición de especies y patrones de coexistencia en ensamblajes de hormigas en dos playas arenosas de la costa norte del occidente de Cuba. Durante los años 2017-2018, se determinaron 21 especies de hormigas en 240 parcelas de 1x1m en Playas del Este y 13 especies en 80 parcelas en Playa Varadero, para un total de 23 especies. Las especies más frecuentes fueron *Wasmannia auropunctata*, *Pheidole megacephala* y *Paratrechina longicornis*. Los grupos funcionales predominantes fueron omnívoros-dominantes de suelo y vegetación, y oportunistas de suelo y vegetación. Ambos ensamblajes mostraron proporciones equivalentes de especies compartidas y valores similares en riqueza de especies y diversidad, pero sí en equitabilidad y proporción de la especie más frecuente. Se obtuvo un patrón general de anidamiento significativo de la composición de especies. El patrón de coexistencia y el número combinaciones de especies a través de las parcelas fueron menores que los esperados al azar. Las asociaciones espaciales negativas más intensas correspondieron al par *Pheidole megacephala*-*Wasmannia auropunctata*, y las asociaciones positivas más intensas a los pares *Paratrechina longicornis* - *Dorymyrmex pyramicus* y *Paratrechina longicornis* - *Brachymyrmex obscurior*. Se concluye que ambos ensamblajes exhibieron estructura ecológica similar.
Palabras clave: anidamiento espacial, asociaciones negativas, Cuba, grupos funcionales.

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Introduction

Ants constitute one of the most important animal groups in terms of biomass and local abundance (Brandão *et al.*, 2012; Widhiono *et al.*, 2016). The ants mediate key ecological processes, like nutrient cycling, mixing of organic matter, and soil enrichment and aeration (Folgarait, 1998; del Toro *et al.*, 2015). They also can play important roles as predators, defoliators, scavengers, decomposers, seed dispersers and pollen collectors (Brandão *et al.*, 2012; Kwong *et al.*, 2014). On the other hand, ants are among the most problematic invasive species (Bertelsmeier *et al.*, 2015a, b, 2016). They are capable to monopolize space, along with other resources, and thus displace native species, specially in insular areas (Miravete *et al.*, 2014; Roura-Pascual *et al.*, 2016). In addition, these insects are considered suitable bioindicators of habitat quality and environmental changes (Rivas *et al.*, 2014; Bharti *et al.*, 2016).

Ants have been poorly studied in coastal dunes systems. These systems are affected from different sources of natural and anthropogenic disturbances, which include hurricanes, invasive species, global sea-level rise, urbanization, and inadequate management (Rojas *et al.*, 2014; Chen *et al.*, 2015). This scenario is also the case for Cuban sandy coastal dunes systems, specially those present in areas of intense human activity, like the beaches located northeast from Habana City, known as "Eastern Beaches"; and Varadero Beach, along the Northern coast of the Peninsula of Hicacos.

The typical Cuban sandy coastal vegetation is classified as "sandy coast vegetation complex" and is composed mainly by herbaceous species like *Sesuvium portulacastrum*, *Panicum amarum*, *Ipomea pes-caprae* and *Canavalia rosea* (Ricardo *et al.*, 2009; Álvarez and Ricardo, 2011). Another typical vegetable component of sandy coasts is the sea-grape, *Coccoloba uvifera*. This species grows, as a shrub formation, behind the herbaceous components of the vegetation complex (Ricardo *et al.*, 2009), representing thus a distinctive habitat, continuous or patchy, between the sandy beaches and other plant formations or urbanizations of different kinds.

As field observations suggest, the sea-grape shrubs represent a suitable habitat for ants, providing shelter and resources, such as nectar, fruits and Hemiptera known as "scale insects". These insects are attended by ants in demanding of the so called "honey dew", a sugar and amino acid-rich bodily secretion (Newton *et al.*, 2011). In addition, the sea-grape leaf-litter supplies organic matter and retains humidity. Sea-grapes shrubs are usually utilized by persons in pursuit of shadow. The resulting leftovers contribute to the proliferation of ants, mainly invasive ones, and other undesirable organisms, like flies ant rats.

The known Cuban ant fauna is composed by 168 species, belonging to 46 genera and nine subfamilies. The proportion of endemic species is 44.0% and of cosmopolitan species is 18.0% (Fontenla and Alfonso-Simonetti, 2018). Bertelsmeier *et al.* (2016) recognize 19 invasive ant species, and 10 of them are present in Cuba. Some of these species, like *Wasmannia auropunctata* and *Pheidole megacephala* are very abundant in Cuban agroecosystems and man-modified environments (Fontenla and Matienzo, 2011).

Ants are an ideal group for testing patterns of assemblage organization, because their assemblages tend to be organized by interspecific interactions (Wittman and Gotelli, 2011; Camarota *et al.*, 2016). Understanding the environmental drivers of community organization in natural ecosystems is of great importance, specially in those severely threatened (Silva *et al.*, 2017). In addition, visualizing the structure of ant communities may be useful for understanding the effects of urbanization and for evaluating the qualities of man-modified environments (Santos *et al.*, 2019).

The goal of this paper is to assess species composition and co-occurrence patterns of ant assemblages in sea-grape shrub formations along two sandy beaches in the northern coast of Western Cuba.

Materials and Methods

Ant sampling. The study was developed by sampling at 12 sites in Eastern Beaches and at four sites in Varadero Beach during the years 2017-2018. The sites were only a reference to locate the quadrats, the level at which the analyses were conducted. Sampling sites in Eastern Beaches were located between the coordinates 23° 10' 48.53"N, -82° 12' 15.35"W, and 23° 10' 26.88"N, -82° 05' 57.01"W. The sites in Varadero Beach were located between the coordinates 23° 09'17.68"N, -81° 14' 53.08"W, and 23° 12' 11.19"N, -81° 09' 10.09"W. The distance from the first site to the last site in Eastern Beaches was about 10 km, and the corresponding distance in Varadero Beach was about 11.5 km. The distance from the last site in Eastern Beaches to the first site in Varadero Beach was about 90 km (Fig. 1). The average annual temperature and rainfall in Eastern Beaches is 25.0 °C and 1272 mm, respectively (https://es.climate-data.org/location/874868/), which is similar to Varadero Beach, with 25.2 °C and 1264 mm respectively (https://es.climate-data.org/location/30137/).

There were established 20 randomly located 1X1m quadrats in each site, for a total of 240 quadrats at

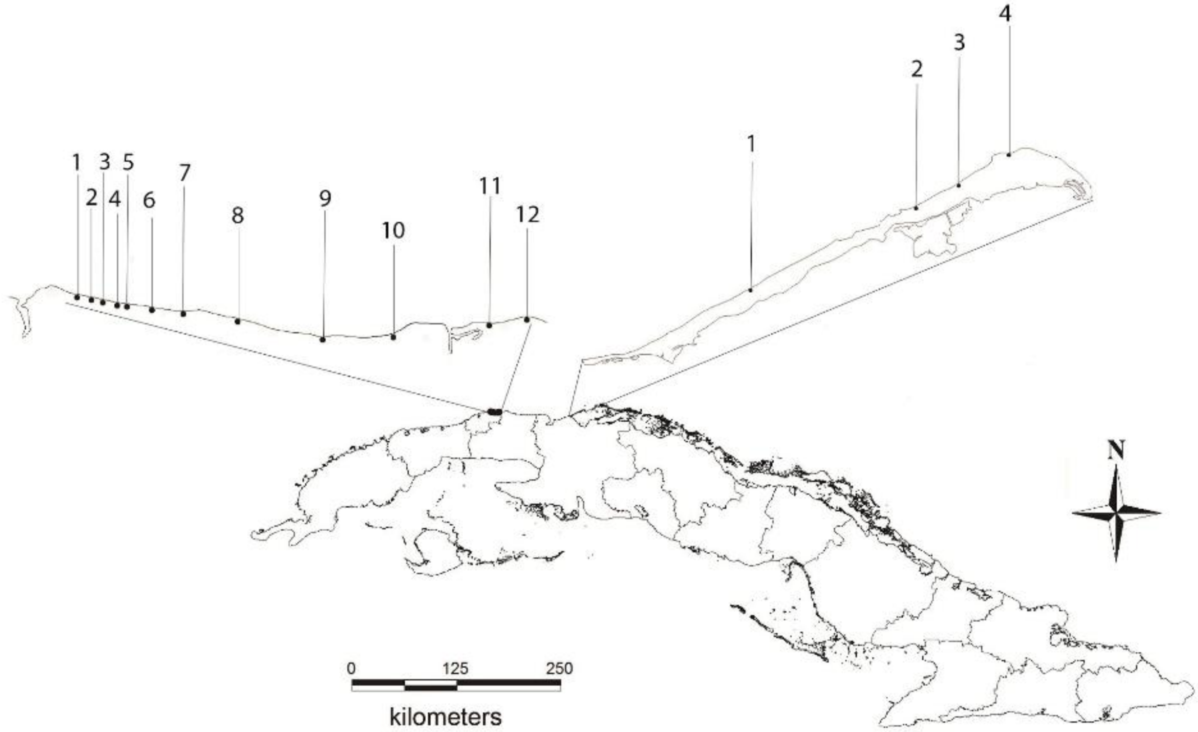

FIGURE 1. Left: Sampling sites at Eastern Beaches. 1. Tarará. 2. Mégano. 3. Pino Mar. 4. Tropicoco West. 5. Tropicoco East. 6. Caribe Hotel. 7. Atlántico Hotel. 8. Itabo. 9. Boca Ciega Cancha. 10. Guanabo. 11. Veneciana. 12. Brisas del Mar. Right: Sampling sites at Varadero Beach. 1. Street 52. 2. Aguas Azules Hotel. 3. Verde Hicaco Hotel. 4. Varahicaco Ecological Reserve.

FIGURE 1. Izquierda: Sitios de muestreo en Playas del Este. 1. Tarará. 2. Mégano. 3. Pino Mar. 4. Tropicoco Oeste. 5. Tropicoco Este. 6. Hotel Caribe. 7. Hotel Atlántico. 8. Itabo. 9. Boca Ciega Cancha. 10. Guanabo. 11. Veneciana. 12. Brisas del Mar. Derecha: sitios de muestreo en Playa Varadero. 1. Calle 52. 2. Hotel Aguas Azules. 3. Hotel Verde Hicaco. 4. Reserva Ecológica Varahicaco

Eastern Beaches and 80 quadrats at Varadero Beach. Each quadrat was separated from each other by at least five meters. In each quadrat, sea-grape litter and sandy soil were examined, as well as trunk and branches of sea-grapes up to 2.0 m high above the ground. Only species frequencies were taken into account as a surrogate for ant abundance. Incidence data, instead of number of individuals, avoids biases due to sampling near nests or trails (Croc *et al.*, 2014). The ant species were assigned to functional groups (Fontenla and Alfonso-Simonetti, 2018). For identification, specimens were compared at the ant collection of the Institute of Ecology and Systematic, Cuba.

Data analysis. The completeness of sampling effort across quadrats was assessed using two non-parametric species richness estimators: 1. Model (h) (ICE). It assumes that detection probabilities are hetererogeneous among species. 2. Model (th). It assumes that detection probabilities vary not only among species, but also among samples (quadrats). This analysis was conducted by the SPADE program (Chao and Shen, 2009).

The confidence limits (95.0%) of variables were computed by the adjusted percentile method with 9 999 bootstrapping replicates. Correlations were running by Spearman's rank-order correlation coefficient (rs). Statistical significance was assessed by 9999 random replicates of Monte Carlo permutation test. The program used was PAST 3.15 (Hammer, 2017).

A rarefaction test was applied to compare ant species richness between the two beaches. There were ran 1000 iterations with independent sampling to rarefy the larger assemblage down to the frequency level of the smaller, and checked if the observed species richness of the species poorer assemblage fell within the 95% confidence limit. This would mean that both assemblages do not differ significantly in species richness. This analysis was made by the program EcoSim version 7.0 (Gotelli and Entsminger, 2012).

Total beta dissimilarity was given by: $\beta to = b + c / a + b + c$, where *b* is the number of species exclusive of one beach; *c* is the number of species exclusive of the second beach, and *a* is the number of shared species between beaches. Beta dissimilarity was decomposed into species replacement plus differences in species richness ($\beta to = \beta re + \beta ri$). $\beta re = 2min(b,c)/a + b + c$. $\beta ri = [b-c] / (a+b+c)$. The relative importance of replacement was calculated as: $Tre = \beta re/\beta to$, and the relative importance of difference in species richness by: $Tri = \beta ri/\beta to$ (Tonial *et al.*, 2012; Podani y Schmera, 2016).

Based on the total frequency of species, it was calculated as a diversity index the "effective number of species" e^H, where *H* is the Shannon-Wiener index of entropy. The assemblages' frequency evenness was calculated as e^H/S, where *S* is the species richness of a beach (Jost, 2010; Aisling *et al.*, 2018). The frequency contribution of the most frequent species was specified by the Berger-Parker index. These indices were compared by running a permutation test of 10 000 random matrices PAST 3.15 (Hammer *et al.*, 2001).

Co-occurrence patterns across quadrats were analyzed by the C-score (checkerboard species pairs) and the number of unique species combinations. These indices were compared with the average simulated values from 5000 randomly assembled matrices by a swapping algorithm and the fixed-fixed model. The analyses were conducted with EcoSim 7.0 software. In addition, there were identified the species pairs that showed significant positive or negative spatial associations by applying the togetherness index with 1000 simulated distribution of the fixed-fixed null model. The program used was PAIRS (Ulrich, 2008).

A nested configuration is a pattern of spatial order where common species tend to occur in any sites, while rare species tend to occur only in the richest sites. The degree of nestedness was calculated with the NODF index, based in overlap and decreasing fill of the species in the matrix. It was applied the fixed-fixed null model with 1000 iterations using the NODF Program (Ulrich, 2010). Nestedness was calculated for the whole incidence matrix (NODFm), sites (NODFc) and species (NODFr). Site (quadrats) nestedness occurs when species present at species-poor sites are a subset of the species present at species-rich sites. Species nestedness occurs when the occurrences of species occupying few sites are a subset of the occurrences of species occupying more sites (Novak *et al.*, 2011).

The softwares mentioned above offer a standardized (z-transformed) effect size (SES), which expresses the direction and degree of deviation from the null model. SES values ≥ [2.0] point to statistical significance. If SES is positive indicates less co-occurrences, more unique combinations and more positive spatial associations than expected by chance alone, as well as absent of nestedness (segregation). If SES is negative indicates a higher co-occurrence, less unique species combinations and more negative spatial associations than expected by chance alone as well as nestedness (aggregation).

Results

There were observed 21 species in Eastern Beaches, and 13 species in Varadero Beach, for a total of 23 species between the two beaches (Supplementary material 1, 2). The 21 species observed in Eastern Beaches fell within 92.5%-93.3% of the estimated species richness for that locality, and the 13 species observed in Varadero Beach fell within 88.4%-89.0% of the expected species richness for that beach. According to these values, sampling effort was adequated in both beaches (Table 1). Species richness rarefaction pointed out that the confidence interval of Eastern Beaches showed values from 13 species (lower limit) to 19 species (upper limit). The 13 species observed at Varadero Beach fell within the lower limit of this interval. Therefore, the two beaches did not differ in species richness.

Table 1. Non-parametric richness estimators across quadrats in Eastern Beaches (EB) and Varadero Beach (VB). CVI: coefficient of variation of infrequent species. Confidence limits between parentheses.

Tabla 1. Estimadores de riqueza no paramétricos a través de cuadrantes en Playas del Este (EB) y Playa Varadero (VB). CVI: coeficiente de variación de especies poco frecuentes. Límites de confianza entre paréntesis

Richness estimators	EB	VB
CVI	0.38	0.67
Model (h) (ICE)	22.7 (21.3, 31.7)	14.7 (13.2, 25.8)
Model (th)	22.5 (21.2, 34.8)	14.6 (13.1, 30.9)

Myrmicinae was the species richest and most frequent subfamily at the two localities, followed by Formicinae. Most of the species with the highest frequency (above upper confidence limit) were common between the two localities, like *Wasmannia auropunctata*, *Pheidole megacephala* and *Paratrechina longicornis*. Total species frequencies were significantly correlated between the two assemblages (r_s= 0.72, pep= 0.0001). The cosmopolitan species represented 43.0% of the species richness and 69.4% of total assemblage frequency in Eastern Beaches, whereas comprised 54.0% of the species richness and 61.0% of total assemblage frequency in Varadero Beach. The dominant omnivorous of ground and vegetation, ground and vegetation opportunists, and arboreal functional groups, accounted to the highest frequency and species richness in the two beaches (Table 2).

Both beaches shared 11 species. Species composition dissimilarity yielded a beta value of 52.2%. The difference in species richness component contributed the most to the dissimilarity value, with 34.8%. The replacement component contributed with 17.4%. The relative importance of difference in species richness was 66.7%, and the relative importance of replacement was 33.3%.

There were observed between 1-4 species across quadrats in Eastern Beaches and between 1-3 species in Varadero Beach (Supplementary material 1, 2), with similar mean species per quadrats. Both of the areas also showed similar values of species diversity (effective number of species). The main difference between species compositions were evenness and the frequency of the most frequent species. According to the confidence limits, the evenness in Varadero Beach assemblage was significantly higher than in Eastern Beaches. On the other hand, the contribution of the most frequent species in Eastern Beaches (*W. auropunctata*) was significantly higher than the contribution of the most frequent species in Varadero Beach (*P. megacephala*) (Table 3).

Species co-occurred less and there were less species combinations than expected by chance in both beaches, respectively. The values of the standard Effect Size were high for the two indexes, especially in Varadero Beach, with over nine standard deviations, either for the C-Score or for the species combinations (Table 4).

The pattern of species-pairs association among quadrats showed that four species pairs had significant negative association and five species pairs significant positive associations at Eastern Beaches. At Varadero Beach, six species pairs had a pattern of significant negative association, and four species pairs significant positive associations. The species pair *Pheidole megacephala-Wasmannia auropunctata* displayed the most intense negative spatial association in both beaches. These two species, along with *Paratrechina longicornis*, were mostly involved in negative spatial interactions. The species more frequently involved in positive associations in both places was *Brachymyrmex obscurior*. The most intense positive associations corresponded to the species pair *Paratrechina longicornis-Dorymyrmex pyramicus* at Eastern Beaches, and to *Wasmannia auropunctata-Camponotus planatus* at Varadero Beach (Table 5).

According to confidence limits and SES values, the whole incidence matrix and quadrat species composition showed a significant nested pattern in both of the beaches. On the contrary, species distribution per quadrats pointed to a segregated tendency (positive sign) in Varadero Beach, which was statistically significant in Eastern Beaches (Table 6).

DISCUSSION

The 23 ant species detected in the two beaches represent 14.0% of the Cuban myrmecofauna. In a sea-grape formation located in a more complex vegetation matrix, between a subcoastal forest and a rocky coast vegetation complex, Fontenla (1993) found 27 ant species in only 20 quadrats, but Increasing in ant species richness is expected with a corresponding increasing in vegetation structure complexity (Rojas *et al.*, 2014; García-Martínez *et al.*, 2015). Several of the recorded species are shared with other sandy systems elsewhere. Cupul-Magaña (2006) reports *Dorymyrmex pyramycus*, *Solenopsis geminata* and *Brachymyrmex obscurior* from Mexican Pacific coastal dunes, while Rojas *et al.* (2014) mention among the most frequent ants in Mexican Atlantic coastal dunes to *S. geminata* and *Camponotus planatus*.

With the exception of *Brachymyrmex obscurior*, the rest of the most frequent species in the two areas, the big-headed ant (*Pheidole megacephala*), the little red fire ant (*Wasmannia auropunctata*) and the long-horn crazy ant (*P. longicornis*), are cosmopolitan-invasive species (Wetterer, 2012, 2015; Bertelsmeier *et al.*, 2016). Other cosmopolitan ants are present in the beaches, such as *Monomorium pharaonis*, *Nylanderia bourbonica*, *Solenopsis geminata*, and *Tapinoma melanocephalum*. These ants have become also major ecological, agricultural or household pest species (Wetterer, 2015), but they are not very frequent in the studied environment.

The predominant functional groups are the dominant omnivorous of ground and vegetation, and the ground and vegetation opportunists. Opportunist species was the most diverse functional group across the dune systems in the north coast of the Gulf of Mexico. This is related to the ability of opportunist ants to withstand natural disturbance on coastal dunes, such as sand burial and strong winds (Chen *et al.*, 2015). In the sea-grape shrub habitat studied here, this last factor can be less intense, because of the sheltering of the sea-grape shrub itself, although this habitat is also affected by human intrusion, which frequently results in sand burial and disturbance of ant colonies. Predominance of dominant and opportunist species can be facilitated by a lack of any major change in vegetation (Underwood and Fisher, 2006), and by the relative homogeneity of the habitat (Croc *et al.*, 2014). Both evironmental conditions tipify the sea-grape habitat.

Table 2. Species frequencies, general distribution (GD) and functional groups (FG). Frequencies in Eastern Beaches (FEB), frequencies in Varadero Beach (FVB). Endemic species (E), cosmopolitan species (C). LCF: leaf-cutting fungus growers. GVO: ground and vegetation opportunists. ARB: arboreal specialists. NCF: non- leaf-cutting fungus growers. OHS: open- habitat specialists. PSP: “poneroids” specialist predators. PEP: large ponerines epigaeic predators. DOM: Ground and vegetation dominant omnivores.

Tabla 2. Frecuencia de especies, distribución general (GD) grupos funcionales (FG). Frecuencias en Playas del Este (FEB), frecuencias en Playa Varadero (FVB). Especies endémicas (E), especies cosmopolitas (C). LCF: cortadoras de hojas cultivadoras de hongos. GVO: oportunistas de suelo y vegetación. ARB: especialistas arbóreos. NCF: cultivadoras de hongos no cortadoras de hojas. OHS: especialistas de habitats abiertos. PSP: “poneroides” depredadores especializados. PEP: depredadores ponerinos grandes epigéicos. DOM: omnívoros dominantes de suelo y vegetación

Species	Subfamily	FEB	FVB	GD	FG
Atta insularis	Myrmicinae	3		E	LCF
Brachymyrmex obscurior	Formicinae	27	25		GVO
Camponotus conspicuus	Formicinae	1			GVO
Camponotus planatus	Formicinae	11	14		ARB
Cardiocondyla emeryi	Myrmicinae	7	11	C	GVO
Cephalotes varians	Myrmicinae	1			ARB
Cyphomyrmex minutus	Myrmicinae	4		C	NCF
Dorymyrmex pyramicus	Dolichoderinae	29	3		OHS
Hypoponera opaciceps	Ponerinae		1	C	PSP
Monomorium floricola	Myrmicinae	2		C	GVO
Monomorium pharaonis	Myrmicinae		2	C	GVO
Nylanderia bourbonica	Formicinae	1		C	GVO
Odontomachus insularis	Ponerinae	2	2		PEP
Odontomachus ruginodes	Ponerinae	1			PEP
Paratrechina longicornis	Formicinae	34	20	C	GVO
Pheidole megacephala	Myrmicinae	44	35	C	DOM
Platytyrea punctata	Ponerinae	2			PEP
Pseudomyrmex cubensis	Pseudomyrmicinae	37	8		ARB
Pseudomyrmex pallens	Pseudomyrmicinae	6	4		ARB
Pseudomyrmex pazosi	Pseudomyrmicinae	3		E	ARB
Solenopsis geminata	Myrmicinae	25	1	C	DOM
Tapinoma melanocephalum	Dolichoderinae	2		C	GVO
Wasmannia auropunctata	Myrmicinae	155	19	C	DOM
Total frequency		397	145		
Mean frequency		19.7	11.2		
Confidence limits		(7.5, 34.4)	(5.7, 17.1)		

Table 3. Interval of species richness by quadrats, coefficient of variation (CV). ENS: effective number of species. Confidence limits between parentheses. Eastern Beaches (EB), Varadero Beach (VB).

Tabla 3. Intervalos de riqueza de especies por cuadrantes. Riqueza promedio de especies (mean), coeficiente de variación (CV) límites de confianza entre paréntesis Playas del Este (EB), Playa Varadero (VB)

Indices	EB	VB
Species quadrats	1-4	1-3
Mean	1.6 (1.5-1.7)	1.8 (1.6, 1.9)
CV	46.9 (43.5, 50.6)	41.3 (35.2, 47.0)
Observed ENS	8.3	8.3
Expected ENS	8.5-8.6 (4.6, 12.3)	8.8-8.8 (5.3, 12.2)
Evenness	0.39 (0.36, 0.47)	0.64 (0.59, 0.78)
Berger-Parker	0.39 (0.35, 0.44)	0.24 (0.19. 0.31)

Species replacement contributes more to beta dissimilarity across different vegetation types (Silva *et al.*, 2017). The component that contributes more to beta dissimilarity in these ant assemblages is difference in species richness, whose relative importance is twice as much as that of the species replacement component. This pattern of dissimilarity should be expected across plots in homogeneous habitats.

The assemblages showed very similar frequency proportion of shared species and diversity. Structural differences in species composition between the beaches are centered in evenness and dominance values. Varadero Beach exhibits the highest evenness and lowest dominance index. Its most frequent species, *Pheidole megacephala* has a lesser proportional frequency that his similar in Eastern Beaches, *Wasmannia auropunctata*. In general terms, the presence of *W. auropunctata* is associated with a low evenness of ant communities, as a result of the great population density that this species is able to reach (Wauters *et al*, 2016), which matches the situations observed here.

High values of the checkerboard index, combined with fewer species combinations than expected by chance, point to a restricted coexistence pattern of species across quadrats. Like in this study, stable environments have been associated with significant negative species interactions (Ulrich *et al.*, 2012) or checkerboard segregation (Fayle *et al.*, 2015). This kind of spatial pattern suggests that assemblages are structured mainly by strong species interactions or habitat constraints (Ulrich and Gotelli, 2007). Ant assemblage structure at small or local spatial scale is regulated mainly by interspecific interactions (Olivier *et al.*, 2014; Silva *et al.*, 2017). Chen *et al.* (2016) assert that dominant ant species tend not to occur together in the same patch due to competition for resources. This spatial pattern is coherent with these results.

Table 4. C-Score and species combinations (Combo). Eastern Beaches (EB), Varadero Beach (VB). Observed Index (OI). Mean of simulated indexes (MSI). Error probability (p). Standard Effect Size (SES).

Tabla 4. C-Score y combinaciones de especies (Combo). Playas del Este (EB), Playa Varadero (VB). Observed Index (OI). Promedio de índices simulados (MSI). Probabilidad de error (p). Efecto de Tamaño Estandarizado (SES)

Indices	EB	VB
C-Score		
OI	196.3	84.6
MSI	180.9	77.2
p (OI<= MSI)	1.0	1.0
p (OI>=MSI)	0.0	0.0
SES	7.4	9.9
Combo		
OI	62	22
MSI	71.3	40.9
p (OI<= MSI)	0.02	0.0
p (OI>=MSI)	0.99	1.0
SES	-3.2	-9.5

Negative spatial interactions must be more evident between dominant/invasive species, which usually show non-random mutually exclusive distributions (Sanders *et al.*, 2007; Chen *et al.*, 2016). This kind of distribution are observed in this study mainly between dominant-invasive species, like *Pheidole megacephala* and *Wasmannia auropunctata*. This species-pair exhibits the highest negative SES values in both beaches. These ants are aggressive species (Holway *et al.*, 2002; Armbrecht and Ulloa-Chacon, 2003) that have been observed displaying mutually exclusive distributions (Xerdá *et al.*, 2011; Bertelsmeier *et al.*, 2015b) or mosaic patterns of dominant ant species (Franken and Gasnier, 2010). These two species, along with *Paratrechina longicornis*, are involved in most of the negative interactions, and thus they do not tend to overlap their spatial distribution across quadrats, either among themselves or with other species.

Table 5. Species pairs co-occurrence. Negative sign indicates significant negative co-occurrence and viceversa. S1 and S2: number of occurrences of the first and the second species, respectively. Com: common occurrences. Obs: observed value. Exp: expected value. LCL: lower confidence limit, UCL: upper confidence limit. SES: Standard Effect Size. *Wau: Wasmannia auropunctata. Pme: Pheidole megacephala. Plo: Paratrechina longicornis. Dpi: Dorymyrmex pyramicus. Sge: Solenopsis geminata. Cem: Cardiocondyla emeryi. Ppal: Pseudomyrmex pallens. Bob: Brachymyrmex obscurior. Cpl: Camponotus planatus.*

Tabla 5. Co-incidencia de pares de especies. Signo negativo indica co-incidencia negativa y viceversa. S1 and S2: número de incidencias de la primera y segunda especie, respectivamente. Com: incidencias comunes. Obs: valor observado. Exp: valor esperado. LCL: límite inferior de confianza, UCL: límite superior de confianza. SES: Efecto de Tamaño Estandarizado. *Wau: Wasmannia auropunctata. Pme: Pheidole megacephala. Plo: Paratrechina longicornis. Dpi: Dorymyrmex pyramicus. Sge: Solenopsis geminata. Cem: Cardiocondyla emeryi. Ppal: Pseudomyrmex pallens. Bob: Brachymyrmex obscurior. Cpl: Camponotus planatus*

Species pairs	S1	S2	Com	Obs	Exp	LCL	UCL	SES
Eastern Beaches								
Wau-Pme	155	44	2	0.006	0.093	0.053	0.121	-4.88
Wau-Plo	155	34	8	0.033	0.081	0.052	0.112	-3.51
Wau-Dpi	155	29	6	0.026	0.068	0.047	0.094	-3.16
Pme-Plo	44	34	0	0.000	0.052	0.011	0.094	-2.23
Wau-Sge	155	25	19	0.104	0.067	0.043	0.091	2.73
Pme-Cem	44	6	4	0.054	0.013	0.000	0.041	3.36
Pme-Ppal	44	6	4	0.054	0.011	0.000	0.040	3.53
Dpi-Plo	28	34	10	0.131	0.038	0.012	0.077	5.41
Dpi-Bob	29	27	8	0.107	0.032	0.000	0.066	4.34
Varadero Beach								
Pme-Plo	35	20	0	0.000	0.116	0.052	0.219	-2.84
Pme-Wau	35	19	0	0.000	0.123	0.075	0.197	-3.17
Pme-Cpl	35	14	0	0.000	0.092	0.041	0.166	-2.35
Wau-Bob	19	25	0	0.000	0.101	0.023	0.188	-2.41
Wau-Plo	19	20	0	0.000	0.093	0.026	0.176	-2.22
Plo-Cpl	20	14	0	0.000	0.075	0.029	0.159	-1.91
Plo-Bob	20	25	13	0.391	0.101	0.046	0.215	7.01
Plo-Cem	20	11	5	0.169	0.054	0.000	0.132	2.96
Cem-Bob	11	25	7	0.223	0.066	0.000	0.153	3.79
Wau-Cpl	19	14	13	0.488	0.055	0.000	0.127	10.81

The observed mutual spatial exclusion pattern by several species-pairs might be a consequence of competition for resources in the homogeneous environment represented by the sea-grape shrub formation. On the other hand, subordinate species can coexist with dominant species (Wittman and Gotelli, 2011; Castracani *et al*., 2014). This assertion is also consistent with these results, since most of the positive interactions are displayed among opportunist species, such as *Brachymyrmex obscurior*, *Cardiocondyla emeryi*, *Dorymyrmex pyramicus*, and *Paratrechina longicornis,* or between a dominant species (*Wasmannia auropunctata*) and a habitat specialist (*Camponotus planatus*).

In nested assemblages, common species tend to occur in all sites and rare species in the richest sites (Ricotta and Pavoine, 2015). This tendency is observed in both ant assemblages, where the majority of the quadrats (with only one species) are occupied by the most frequent and abundant species, like *Wasmannia auropunctata* or *Pheidole megacephala*. Nestedness is to be expected in sites within a homogeneous area (Ulrich *et al*., 2009), and across temporarily stable sites (Ulrich *et al*., 2012), which is also coherent with the characteristics of the studied sea-grape formations.

Nestedness is a pattern of aggregated species co-occurrence; therefore, negative interactions

TABLE 6. Nestedness values across quadrats. NODFt: total matrix. NODFc: species quadrats composition. NODFr: species distribution across quadrats. Obs: observed value. Sim: mean of simulated indexes. LCL: lower confidence limit, UCL: upper confidence limit. SES: Standard Effect Size.

TABLA 6. Valores de anidamiento a través de cuadrantes. NODFt: matriz total. NODFc: composición de especies en cuadrantes. NODFr: distribución de especies a través de cuadrantes Obs: valor observado. Sim: promedio de valores simulados. LCL: límite inferior de confianza. UCL: límite superior de confianza. SES: Efecto de Tamaño Estandarizado

Index	NODFobs	NODFsim	LCL (%)	UCL (%)	SES
Eastern Beaches					
NODFt	27.6	29.3	28.9	29.6	-9.3
NODFc	27.7	29.4	29.1	29.8	-9.5
NODFr	13.0	10.1	8.1	12.0	3.1
Varadero Beach					
NODFt	19.1	21.7	20.2	22.8	-4.0
NODFc	19.1	21.9	20.4	22.9	-4.1
NODFr	15.9	15.1	12.1	18.9	0.52

decreases the matrix nestedness (Ulrich *et al.*, 2009). Nestedness (aggregation) and negative co-occurrences (segregation) represent alternatives patterns, but the same matrix can show both assemblage attributes (Ulrich and Gotelli, 2007; Ulrich *et al.*, 2009). This configuration is present in the species distribution component across quadrats, being a tendency in Varadero Beach and a significant pattern in Eastern Beaches.

Several of the most frequent species, such as *Wasmannia auropunctata*, *Pheidole megacephala* and *P. longicornis*, are involved in most of the negative interactions, and thus they do not tend to overlap their spatial distribution across quadrats, either among themselves or with other species. These interactions yield a segregated pattern of spatial distribution of species across quadrats, no matter the significant degree of nestedness of the whole incidence matrix and quadrat species composition.

In summary, the ant assemblages are characterized by high frequency of widespread dominant and opportunist species. Species richness and diversity are not significant different. Co-occurrence patterns are driving mainly by negative spatial interactions, especially between dominant-invasive species. It can be concluded that both ant assemblages exhibit similar ecological structure with significant nested pattern for the whole matrix of species incidence and species composition across quadrats.

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