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Source: Florida Entomologist, 97(4) : 1443-1450

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.097.0419

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BIOTIC AND ABIOTIC FACTORS SHAPING ANT (HYMENOPTERA: FORMICIDAE) ASSEMBLAGES IN BRAZILIAN COASTAL SAND DUNES: THE CASE OF RESTINGA IN SANTA CATARINA

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Supplementary material for this article in Florida Entomologist 97(4) (2014) is online at http://purl.fcla.edu/fcla/entomologist/browse

ABSTRACT

Species inhabiting Brazilian coastal sand dunes (restingas) may feature a number of adaptations in their development and survival in these physical stressful environments. The present study determined the effect of biotic and abiotic factors on the assemblage of ground-dwelling ants in a sand dune ecosystem of the Santa Catarina coastal plain in Brazil. Both linear and quadratic models were significant, but the quadratic model fitted the obtained data better. Furthermore, we also found a relationship between plant species richness and distance from the ocean only by using the quadratic model. Ant species richness was correlated with plant species richness, litter and vegetation coverage. Different environmental factors associated with plant species richness may have influenced the ant species richness by increasing the diversity and amount of available resources. The vegetation may also offer protection from higher temperatures by providing shade, a humid microclimate and a source of water, which is a limiting factor in sand dune environments. Our results showed the importance of plant species richness, and soil cover by litter and plants as local characteristics determining ant species richness in sand dunes. Further studies should explore additional habitat components, such as biotic interactions, as determinants of ant species richness.

Key Words: species distribution; species richness; community ecology; Formicidae; restinga

RESUMO

Espécies que habitam a restinga apresentam adaptações para seu desenvolvimento e sobrevivência sob inúmeros fatores ambientais estressantes. A seleção de um habitat particular deve depender destes diversos componentes do ambiente físico, associado às interações biológicas. O presente estudo foi realizado na restinga herbáceo-arbustiva do Morro dos Conventos para determinar a influência da distância do oceano, fatores bióticos e abióticos sobre a comunidade de formigas de solo. Foram instaladas 65 armadilhas de solo em dois transectos arbitrários de 650 metros a partir do oceano em direção ao continente. Um total de 71 espécies de formigas foi amostrado. Os gêneros *Pheidole*, *Solenopsis* e *Camponotus* foram os gêneros mais representativos. Foi encontrada uma relação positiva entre distância do oceano e riqueza de espécies de formigas, bem como entre distância do oceano e riqueza de espécies de plantas. Das hipóteses testadas, apenas as que estavam relacionadas com a vegetação foram aceitas. A riqueza de espécies de formigas esteve relacionada com a riqueza de espécies de plantas e cobertura do solo. A riqueza de espécies de plantas pode ter influenciado o aumento da riqueza de espécies de formigas pelo aumento da variedade de recursos para consumo e nidificação. Além disso, a vegetação pode alterar as condições microclimáticas, com o aumento da umidade e diminuição da temperatura, fatores extremamente importantes em ambientes com alta incidência de radiação solar e altas taxas e evapotranspiração como a restinga. Esses resultados permitem sugerir a importância da vegetação, e os componentes ligados a ela, como fatores locais determinantes da riqueza de espécies de formigas em Restinga.

Palavras Chave: distribuição de espécies; riqueza de espécies; ecologia de comunidades; Formicidae; restinga

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The southern Brazilian coastland is mainly characterized by the Atlantic Forest domain, which is a complex of phytophysiognomies distributed according to topography, altitude and distance from the ocean. One of these physiognomies is the "restinga", defined as groups of plant communities under marine or riverine-marine influence living on salty sand soils, being considered edaphic communities because they depend more on the soil characteristics than on the climate. This is a peculiar ecosystem because it contains a great number of distinctive biological assemblages, constrained by several environmental stresses such as water stress, strong winds, unsteady substrate, salt spray, soil salinity, burial propensity, wave action, solar radiation and wide daily and seasonal fluctuations of temperature (Franco et al. 1984; Maun 2009). These factors make sand dunes a comparatively harsh environment, with severe limitations to the vegetation and fauna.

The remarkable limitation imposed by such harsh environmental conditions is easily observed in a plant community (Wilson & Sykes 1999; Maun & Perumal 1999; Gilbert et al. 2008; Maun 2009). Plant assemblages are spread in clusters due to progressive shifts of environmental stresses and the plant species that showed different tolerances to these stresses (Maun 2009). Nevertheless, different authors hold divergent views on the mechanisms affecting this clustered distribution, although wind, burial propensity and soil characteristics are considered major structuring forces shaping plant distribution in sand dunes (Wilson & Sykes 1999; Maun & Perumal 1999; Gilbert et al. 2008). These factors, directly or indirectly, should also affect the fauna that occurs in these environments.

Various factors have been suggested as determinants of ant assemblages and several studies have addressed this issue (Retana & Cerdá 2000; Ribas et al. 2003; Coelho & Ribeiro 2006; Wenninger & Inouye 2008). Among these factors, competitive interactions, microclimatic conditions, the availability of resources and nesting site locations are considered as major influences that determine species richness at a local scale (Cornell & Lawton 1992; Godfray & Lawton 2001).

Ants are an important and diverse component of restingas (Vargas et al. 2007; Cardoso & Cristiano 2010). In Brazil, Vargas et al. (2007) sampled 92 ant species comprising 36 genera and 8 subfamilies in the restinga of Marambaia, state of Rio de Janeiro, while Cardoso & Cristiano (2010) sampled a total of 71 ant species in the restinga of Morro dos Conventos, state of Santa Catarina, comprising 21 genera and 7 subfamilies. Such differences in richness using the same sampling technique (pitfall traps) may reflect a species richness gradient of latitude, in which the diversity decreases with increasing latitude (Silva & Brandão 2014).

Several studies on plant and ant communities addressed predicted relationships between plant and ant diversity in different ecosystems (Ribas et al. 2003; Leal 2003; Corrêa et al. 2006), but this issue has not yet been extensively explored in sand dune environments. Vargas et al. (2007) found a positive correlation between ant and plant species richness in sand dune habitats, although they did not actually estimate plant species richness, but inferred this parameter from the literature. Moreover, other plant attributes like percentage of cover and soil attributes were not evaluated. Changes in ant species composition along different sand dune phytophysiognomies were found in the restinga of Morro dos Conventos (Cardoso et al. 2010). However, the ecological factors that determine these remarkable spatial distributions were not tested.

In this study, we analyzed the relationship of ant species richness with oceanward edge distances to inland sand dunes, testing the prediction that ant species richness, together with plant species richness, increases with distance from the ocean. We hypothesized that ant species richness increases with (1) plant species richness, (2) soil cover by plants or litter, and (3) the amount of soil organic matter; moreover that (4) ant species richness decreases with increasing salt concentration in the soil, and that (5) ant species richness responds positively to the heterogeneity of the environment.

Materials and Methods

Study Site

This study was conducted in the restinga of the Morro dos Conventos (S 28° 56' W 49° 21') in Araranguá, Santa Catarina State, Brazil. According to Köppen's (1984) classification the climate of the study site is a Cfa type with rain events distributed throughout the year, an average annual rainfall of 1,269.3 mm and average annual temperature of 21.4 °C (Dufloth et al. 2005).

The studied sand dune area is a transgressive dunefield-like type (Suppl. Fig. 1), which develops in a region of higher energy due to strong winds that blow large amounts of sand inland. Hence, the dunes increase in height from the ocean to inland with depressions created among them, where dense vegetation sheltered from the wind can develop. On dunes near the ocean, low plants occur in well delimited patches, mainly composed of herbaceous and rhizomatic species. The soil is sparsely covered, with predominance of open sandy areas. On the lee sides of dunes and on the earlier described depressions, the plants occur in well delimited patches, however, with dense herbaceous vegetation, with shrubs and shrubby patches extending from the last dune to the base of the next one. According to Falkenberg (1999),

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the southern dunefields can be divided into 3 main environments: (1) frontal dunes, (2) lagoons, marshes and pits and (3) internal dunes (as described in Cardoso et al. 2010).

Ant Sampling

Here we analyzed the richness and distribution of our previous ant sampling (Cardoso & Cristiano 2010) in relation to the distance from the ocean to inland restinga. Ants were sampled from Jan to Feb 2008 with pitfall traps installed along 2 transects from the ocean to inland sand dunes, crossing all physiognomies (frontal dunes occurred from 0 to 200 m; lagoons, marshes and pits from 200 to 450 m and internal dunes from 450 to 650 m, including tree habitats). The transects were 500 m distant from each other, oriented perpendicularly to the ocean, starting 10 m from the high tide level and ending at the ocean cliff that occurs in the region. Within each transect (640 m long), 65 sampling stations spaced 10 m from each other were established as recommended in the ALL protocol. Ants were identified to the species level whenever possible through taxonomic keys and genera revision articles or by comparison with the Formicidae reference collection of the Laboratório de Ecologia de Comunidades of the Universidade Federal de Viçosa, where all voucher specimens were deposited (details of ant sampling and identification can be obtained in Cardoso & Cristiano 2010).

Explanatory Variables

In each sampling station, after removing the pitfall traps, we installed 4 quadrats of 1 m^2 subdivided into 25 quadrats of 20 × 20 cm, in order to facilitate the whole 1 m^2 estimation of soil cover, around each pitfall. The sum of these four 1 m^2 quadrats was enough to sample the herbaceous and shrubby vegetation that occurs in the sand dunes. We measured plant species richness, soil cover, soil salinity and organic matter concentration in each 1 m^2 quadrat (Fig. 1).

We used plant species richness as a surrogate of resource diversity (Ribas et al. 2003). We estimated plant species richness by counting all plant morphospecies per quadrat. Thus, our estimate of plant species richness is the number of morphospecies occurring in 4 m^2. We estimated soil cover (number of filled sub-quadrats) by litter and/or plants in each quadrat by visually estimating a cover percentage and calculating the mean for each pitfall site. All variables were expressed as a mean of the 4 quadrats evaluated in each sampling station.

Organic matter (OM) was estimated from soil samples collected at 0-0.1 m depth in the center of each quadrat in all sampling units. Soil salinity was determined from soil samples obtained at the same depths as those sampled to determine organic matter quantity, and was estimated by sodium (Na) concentration. All analyses were performed in the soils laboratory of Viçosa (Laboratório de Solos Viçosa). OM concentration was determined by the Walkley-Black method, which

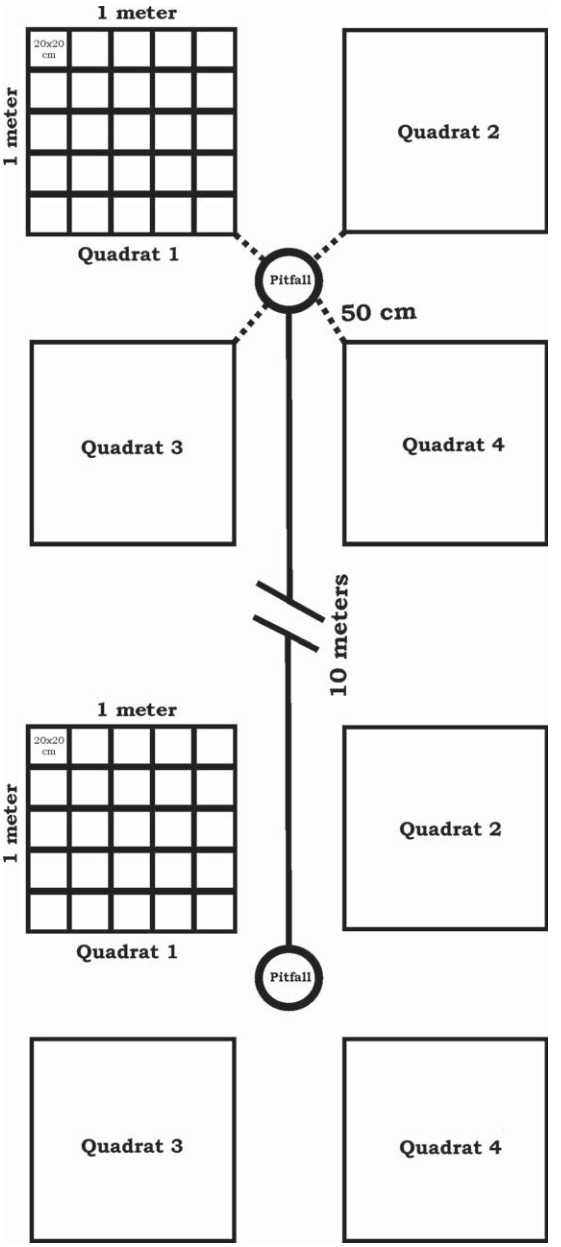


Fig. 1. Scheme of ant sampling design in Morro dos Conventos restinga, Santa Catarina, Brazil (not drawn to scale). Overall, 65 pitfall traps were installed in each of the 2 transects, pitfalls were 10 m distant from each other.

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uses chromic acid to measure the oxidizable organic carbon in a soil sample. Na concentration was determined by flame photometry with an acid extractor.

We used plant species richness, soil cover (plant and litter) and organic matter concentration as surrogates of resources and conditions available to the ants. Plant species richness and soil cover by litter or vegetation have been described in the literature as determining factors of ant diversity (Vargas et al. 2007). We used Na concentration as an estimate of abiotic stress for ants and plants, since Na+ is the second most abundant ion in oceanwater and is the main component of soil salinity (Munns 2005).

We used the coefficient of variation (CV) of soil cover by plant and litter as well as plant species richness as a surrogate of environmental heterogeneity for each sampling unit. Plant species richness was also used as a surrogate of environmental heterogeneity (Ribas et al. 2003).

Statistical Analyses

The assumption that ant species richness increases with distance from the ocean was analyzed by adjusting 2 models: simple linear regression and simple quadratic regression, both with Poisson error distribution. The latter model was carried out after the residual analysis, which indicateded that the linear model may not be the better fit to the obtained data. Similarly, the quadratic model was also fitted for plant species richness, although the linear model also produced a fairly good fit. The suitabilities of the linear and quadratic models were compared by their Akaike's Information Criterion (AIC) values (Crawley 2007). The initial analyses were carried out with the 2 transects as co-variables, because we did not know a priori whether the response of ants were similar in the 2 transects. Because the interaction between ant response and transect was not significant (P = 0.39), we assumed that the responses were similar and subsequent analyses were carried out by grouping the results of the 2 transects.

We tested a sub-assumption to evaluate whether plant species richness increases toward inland sand dunes, using the same models described above, with normal error, because the averages of plant species richness of the 4 quadrants were used.

The hypotheses to explain ant species richness patterns along the gradient of increasing distance from the ocean were tested by multiple linear regressions with Poisson distribution. We carried out a model in which ant species richness was the response variable, and the means of plant species richness, litter cover, plant cover, OM concentration (percentage of weight) and Na concentration (mg/l) within each sampling unit were used as explanatory variables, as well as each coefficient of variation (CV). Additionally, the interaction factor "plant species richness × plant density" was included in the model because these variables might be correlated, since the increase in plant richness may result in increased vegetation cover.

The complete model was simplified by excluding non-significant variables until the minimal adequate model (Crawley 2002) was attained. All analyses were carried out under the R program (R Development Core Team 2010) and followed by residual analyses to verify the suitability of the models and of the distributions of errors (Crawley 2002). The significance of the models was assessed by Chi-square distribution when using Poisson distribution and by F distribution when using normal errors, according to the suggestions in Crawley (2002).

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Results

Suppl. Fig. 2 illustrates how the 71 ant species are distributed in relation to the distance from the ocean. Some species have been collected only in sampling stations closer to the ocean, while other species only occurred in the most distant sites, e.g. *Labidus coecus*. We observed a discontinuity in species distribution between 200 and 250 m from the ocean (Suppl. Fig. 2 and Suppl. Table 1). Some species of *Pheidole* and all species of Ponerinae only occurred in sites more than 200 m distant from the ocean. Moreover, other Myrmicinae, such as *Strumigenys*, only occurred in habitats distant from the ocean and sheltered by dunes with some shrubby or arboreal plants. On the other hand, 3 species, *Acromyrmex ambiguus*, *Mycetophylax simplex* and *Pheidole* sp. 1, were sampled only in sites within the first 200 m and appear to be restricted to open areas in sand dune environments. *Mycetophylax morschi* was found both near and far from the ocean, nesting in open and shaded sites. A similar pattern was observed for *Acromyrmex striatus*, which was not sampled only in 3 distance points (Suppl. Fig. 2). Only 4 species, *Dorymyrmex pyramicus*, *Linepithema neotropicum*, *Brachymyrmex cordemoyi* and *Wasmannia auropunctata*, were present along the entire gradient from the ocean to inland restinga. The most common plant species occurring near the ocean were *Ipomoea pescaprae*, *Blutaporum portulacoides* and *Spartina ciliata*, while *Hydrocotyle bonariensis* and *Gamochaeta americana* were commonly recorded after 250 m from the ocean.

We found a significant relationship between ant species richness and distance from the ocean. Both linear (AIC = 645.68) and quadratic models were significant, but the quadratic model fit the obtained data better (χ^2 = 15.95, P < 0.001, AIC =

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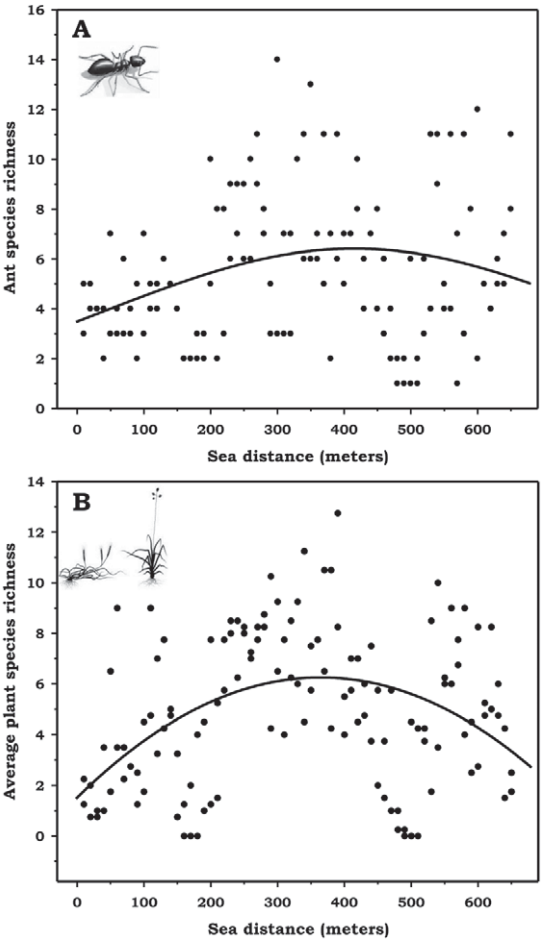


Fig. 2. Relationship between ant and plant species richness and distance from the sea in Morro dos Conventos sand dune (A) Ant species richness in relation to distance from the sea ($\chi^2 = 15.95$; $P < 0.001$). (B) Average plant species richness in relation to distance from the sea ($F_{(2, 127)} = 12.79$; $P < 0.001$).

639.25; Fig. 2A). Furthermore, we also found a relationship between plant species richness and distance from the ocean, only using the quadratic model ($F_{2, 127} = 12.793$, $P < 0.001$; Fig. 2B).

The hypothesis that ant species richness increases with plant species richness was accepted ($\chi^2 = 66.07$, $P < 0.001$; Fig. 3A). Likewise, the hypotheses that ant species richness is directly proportional to the amount of soil cover by plants ($\chi^2 = 4.05$, $P = 0.04$) and to the amount of soil cover by litter ($\chi^2 = 23.85$, $P < 0.001$) were also accepted (Figs. 3B and 3C, respectively). However, we did not find significant relationships between ant species richness and OM ($\chi^2 = 0.09$, $P = 0.77$) nor soil sodium ($\chi^2 = 0.40$, $P = 0.52$) concentrations. The interaction between plant species richness and plant cover was not significant ($\chi^2 = 0.70$, $P = 0.85$), therefore, the 2 factors should act independently on ant species richness (detailed information is available in the Suppl. Table 2).

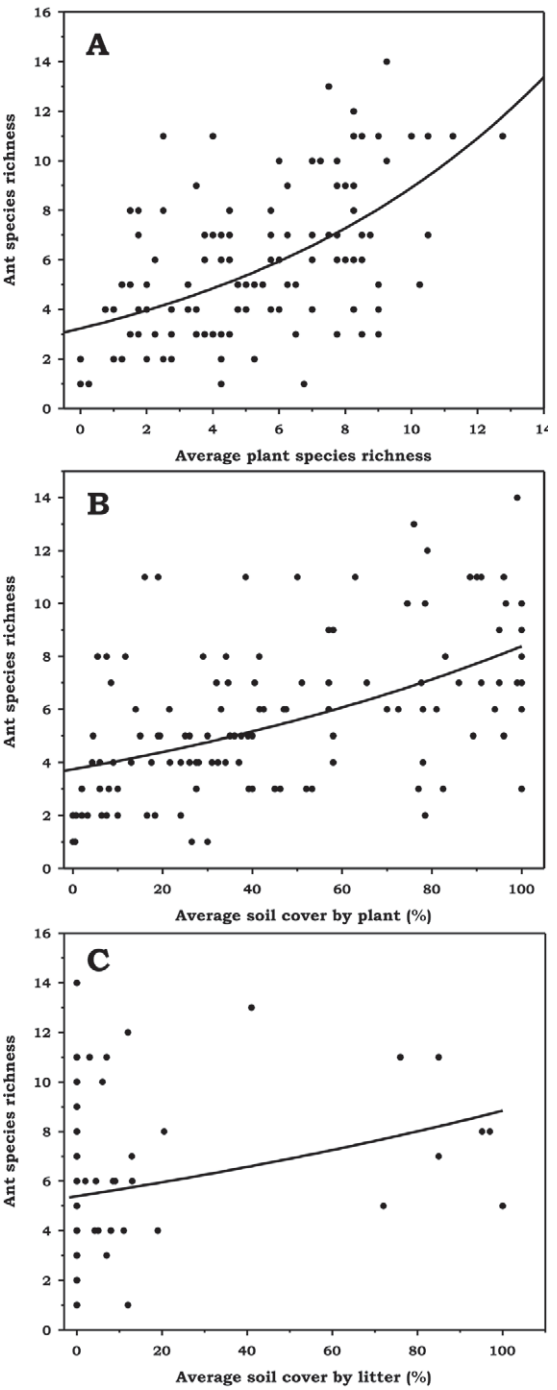


Fig. 3. Relationship between ant species richness and surrogates of resources and conditions in Morro dos Conventos restinga. (A) Average plant species richness, (B) Average soil cover by plant, (C) Average soil cover by litter.

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There was no significant relationship between ant species richness and the CV of the amount of soil cover by plant (χ^2 =0.33, P = 0.56) and the amount of soil cover by litter (χ^2 = 0.81, P = 0.37).

Discussion

Our study revealed the same pattern of ant and plant species richness in relation to the distance from the ocean. There were remarkable changes in ant species richness and species occurrence among distances from the ocean. Some species such as *L. coecus,* only occurred in those habitats between 250 and 650 m from the ocean, where the proportion of soil cover was higher. Interestingly, only 4 species, *D. pyramicus*, *L. neotropicum*, *B. cordemoyi* and *W. auropuncutata*, were present along the entire gradient from the ocean to inland restinga. These species are characterized by an opportunist and generalist foraging and nesting habits (Armbrecht & Ulloa-Chacón 2003; Wild 2009). Yet, *Acromyrmex ambiguus*, *Mycetophylax simplex* and *Pheidole* sp. 1 only occurred in open habitats near the ocean from 10 to 200 m. The former is a leaf-cutter ant that generally harvests grasses, which is the most common widespread plant occurring on dunes near the ocean. *Mycetophylax simplex* has been reported to be endemic of the Atlantic coastal sand dunes (Cardoso et al. 2012), nesting only in open dune habitats.

The habitats more distant from the ocean support more and different species. The data found in our study agree with the ideas that the diverse plant species are important sources of nutrition and microhabitat requirements for insects, and thus plant species richness is an important factor in structuring ant assemblages in sand dunes. This response was also observed for ants in studies in other Brazilian ecosystems, such as savannas ("cerrado"; Ribas et al. 2003), Pantanal (Corrêa et al. 2006), and "caatinga" (Leal 2003), where plant species richness and ant species richness were also positively correlated. Nevertheless, the quadratic correlation between ant and plant species richness and distance from the ocean pointed to a particular pattern that may be linked with the heterogeneous landscape of sand dune ecosystems and resurgence of dunes and open areas. The sheltered areas protected by the first dunefields harbor more plant species, and therefore support more ant species. Soil areas covered with dense vegetation stretch inland until new open areas and dunes arise again (see Supplementary material 3). These new open dune areas lead to a decrease in ant species due to the harsh physical microhabitat generated, which is supported by a restricted number of plant species. Furthermore, these new sets of dunes can afford a new wind sheltered area, which may allow other and more species to occur. This is clearly observed in our study area (see Figs. 2 and 3); at around 400 m, the open dune environment starts again and the number of species decreases, whereas this number increases again around 550 m, after the second set of dunes.

Several components associated with plant species richness may have influenced our results. Vegetation is the primary food or shelter resource for most insects (Wenninger & Inouye 2008), and directly or indirectly this should not be different for ants. The process driving this pattern may be the increase of primary producers (either biomass or diversity) in ecosystems, increasing the availability of energy to the other trophic levels through bottom-up effects (Hunter & Price 1992; Wenninger & Inouye 2008). Besides being a minority of highly specialized predators species, ants in general are omnivores and opportunistic feeders and are considered as the dominant primary consumers in most habitats (Hölldobler & Wilson 1990). Ants can directly consume seeds/fruits, nectar, food bodies and foliage (used by leaf-cutting ants as a substrate for the fungus they feed on), or indirectly use plants as nesting sites or foraging place (Oliveira & Pie 1998; Oliveira & Freitas 2004). A richer variety of resources may support a larger number of ant taxa by interaction of plant-species specialists, whereas the amount of resources may offer support for generalist ants (Ribas et al. 2003; Wenninger & Inouye 2008). Our results also showed a positive relationship between ant species richness and the amount of soil covered by plant litter. Thus, more distant habitats were richer but also more abundant in resources, and thus may support more ants by providing a greater variety and amount of resources and microhabitats.

The influence of microhabitats promoted by plant distribution might explain the occurrence of some cryptic species like S*trumigenys crassicornis, S. denticulata* and *S. louisianae,* which occurred only in areas between 300-400 and 600-650 m from the ocean. These areas are more shaded by shrubby and arboreal vegetation, which also allows the formation of a litter layer. Areas covered with litter in sand dunes in herbaceous and open shrubby phytophysiognomies are scarce due to the strong wind.

In open environments, moisture and temperature effects are of great importance and can exert a strong influence on insect distribution (Wenninger & Inouye 2008). This is because temperature and soil moisture are positively associated with vegetation structure (Franco et al. 1984; Lassau & Hochuli 2004; Vargas et al. 2007) and differ significantly between microhabitats in closed shrubs and open areas (Yu et al. 2008). The ants sensitive to moisture and temperature will then be restricted to areas between 200 to 400 m and 500 to 650 m. On the other hand, thermophilic ants, such as Dolichoderinae, occurred mainly in open and dune areas between 0 and 200 m and 400 to 550 m.

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In this study, the coefficient of variation (CV) among sampling units was used to evaluate the dissimilarity of soil cover (by plant and litter) among sampling units as a measure of spatial habitat heterogeneity. We expected that higher CVs represent heterogeneous sample units, and that these sites would support more ant species. Surprisingly, ant species richness was not associated with spatial habitat heterogeneity. This result indicates that the pattern established for Mediterranean ground ant communities (Retana & Cerdá 2000), and also found for ant communities in other semi-arid ecosystems (Andersen 1992; Albrecht & Gotelli 2001), may not apply to ant assemblies in sand dunes. This may have occurred because sites with total cover have a CV equal to zero, just as sites with zero cover have a CV of zero. Thus, homogeneous sites (overall soil cover) may have higher ant species richness due to the action of others variables, such as plant cover, which has a significant relationship with ant species richness in this study.

In sand dune coastlines, most physical and chemical stress factors are regulated by the ocean. It is largely accepted that salt spray and soil salinity are the main factors determining vegetation distribution in coastal dunes (Maun & Perumal 1999). Therefore, we expected that salinity would be an abiotic stressor for ground-dwelling ants. Interestingly, our results showed that salinity has no effect on ant assemblages. Indeed, many authors who tested the effect of salt spray and salinity on plants have reported that salt spray and salinity are not important as environmental factors promoting coastal sand dune distribution (Maun 1998; Maun & Perumal 1999; Gilbert et al. 2008). These authors attributed vegetation distribution in coastal areas to sand burial. Furthermore, salinity effects on plant assemblages apparently prevail in environments closer to the ocean, i.e., the fore dunes (Wilson & Sykes 1999).

Soil properties should equally affect ant species richness, because most species are ground dwellers. In our study, we did not find a relationship between ant species richness and concentration of soil organic matter. Some studies have indicated the importance of the proportion of sand in the soil on ant diversity. Boulton et al. (2005) found higher ant abundance and species richness in habitats with soils that have a high percentage of sand than in habitats with less percentage of sand. These results could explain our findings, indeed sand was the major proportion of the soil in restinga. Thus, plant species richness and soil cover by plant and litter seem to be the main structuring forces shaping the ant assemblage in sand dune environments. Forthcoming studies should uncover other habitat components, such as biotic interactions, underpinning ant communities on sand dunes.

Acknowledgments

We thank Camila O. Arent, Rafaela G. Clemes and Maykon P. Cristiano for assistance in field sampling. Thanks also to Rodrigo Feitosa for the identification confirmation of the ant species. This research was part of the M. Sc. thesis of the first author and was supported by the Brazilian research agencies CAPES and CNPq. José H. Schoereder was supported by a CNPq grant and Danon C. Cardoso was supported by a CAPES grant.

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