DANON CLEMES CARDOSO

DETERMINANTES DE COMUNIDADES DE FORMIGAS EM RESTINGA

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-graduação em Entomologia, para a obtenção do título de *Magister Scientiae*.

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Dr.ª Tathiana Guerra Sobrinho
(Co-orientadora)

Prof. José Henrique Schoereder
(Orientador)

Aos meus Pais, e
Aos meus Avôs, Tomazia e Hercílio (*in memoriam*).
Meus exemplos de vida e sabedoria.

Minuciosa formiga
não tem que se lhe diga:
leva a sua palhinha
asinha, asinha.
Assim devera eu ser
e não esta cigarra
que se põe a cantar
e me deita a perder.
Assim devera eu ser:
de patinhas no chão,
formiguinha ao trabalho
e ao tostão.
Assim devera eu ser
se não fora
não querer.

Alexandre O'Neill,
"Velha fábula em bossa nova"

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Resumo

CARDOSO, Danon Clemes, M.Sc., Universidade Federal de Viçosa, Julho de 2009. **Determinantes de comunidades de formigas em Restinga**. Orientador: José Henrique Schoereder. Co-orientadoras: Tathiana Guerra Sobrinho e Carla Rodrigues Ribas.

O litoral brasileiro apresenta aproximadamente 9.200 quilômetros de extensão, das quais 5.000 km são ocupados por ecossistema de Restinga. Este ecossistema é um conjunto de formações vegetacionais que se desenvolvem em dunas e cordões arenosos do período Quaternário dentro do domínio da Floresta Atlântica. As espécies de plantas que ocorrem em Restinga possuem elevada plasticidade, apresentando adaptações para seu desenvolvimento sob influência de vários fatores abióticos como: estresse hídrico, ventos, topografia e salinidade. Tais fatores condicionam a ocorrência e a distribuição das comunidades vegetais em ambientes de Restinga, e similarmente, devem influenciar a distribuição e a diversidade da fauna animal. O presente estudo teve por objetivo testar o pressuposto de que a riqueza de espécies de formigas aumenta com o aumento da distância em que se encontram em relação ao oceano e as seguintes hipóteses explicativas: (1) a riqueza de espécies de formigas aumenta com a riqueza de espécies de plantas, que por sua vez aumenta com a distância do mar; (2) a riqueza de espécies de formigas é diretamente proporcional a cobertura do solo por plantas e serapilheira; (3) a riqueza de espécies de formigas aumenta com a concentração de matéria orgânica no solo; (4) a riqueza de espécies de formigas diminui com o aumento da concentração de sal no solo; e (5) a riqueza de espécies de formigas responde positivamente à heterogeneidade espacial do ambiente. Além disso, nós testamos um segundo pressuposto de que diferentes fitofisionomias de Restinga possuem composição de espécies de formigas específicas. As coletas de formigas foram realizadas na Restinga herbáceo-arbustiva do Morro dos Conventos, em Araranguá (SC) utilizando armadilhas de solo. Foram instaladas 65 armadilhas distantes 10 metros entre si, em dois transectos do oceano para o continente. Em cada ponto amostral, foram coletadas as seguintes variáveis explicativas: riqueza de espécies de plantas, percentagem de cobertura vegetal e de serapilheira, concentração de matéria orgânica e sal no solo. No total, foram coletadas 71 espécies de formigas. Os resultados obtidos permitiram confirmar nossos dois pressupostos. Observamos que a riqueza de espécies de formigas está positivamente relacionada com a distância em que se encontram do mar, com a riqueza de espécies de plantas, cobertura vegetal e cobertura por serapilheira do solo. Além disso, observamos que diferentes fitofisionomias dentro da Restinga apresentam comunidades de formigas específicas, e que em geral, habitats próximos ou com condições ambientais semelhantes apresentaram maior similaridade quanto à composição de espécies. Esses resultados sugerem que a vegetação e os fatores ambientais condicionados por ela, podem ser os principais fatores determinando a riqueza e composição de espécies de formigas em Restinga.

Abstract

CARDOSO, Danon Clemes, M.Sc., Universidade Federal de Viçosa, July of the 2009. **Determinants of ant communities in Restinga**. Advisor: José Henrique Schoereder. Co-advisors: Tathiana Guerra Sobrinho and Carla Rodrigues Ribas.

The Brazilian coast presents approximately 9,200 kilometers, which 5.000 km of them are occupied by the Restinga ecosystems. This ecosystem is a set of vegetation formations that develop in sandy plains dating from the Quaternary, within the Atlantic Forest domain. The plant species that occur in Restinga have high plasticity, presenting adaptations for their development under the influence of various biotic and abiotic factors such as drought stress, wind, topography and salinity. These factors influence the occurrence and distribution of plant communities in the Restinga, and similarly, should influence the distribution and diversity of animals. The aim of this dissertation was to test the assumption that the species richness of ants increases with distance from the ocean, as well as the following hypotheses: (1) ant species richness increases with plant species richness, which in turn increases with distance from the sea, (2) ant species richness is proportional to soil cover by plants and litter; (3) ant species richness increases with soil organic matter concentration, (4) ant species richness decreases with soil salinity, and (5) the species richness of ants responds positively to spatial heterogeneity of the environment. Moreover, we tested a second assumption that the distinct Restinga phytophysiognomies have different ant species composition. The ants were sampled in herbaceous and shrubby Restinga of the Morro dos Conventos in Araranguá (SC) using pitfall traps. Sixty-five pitfall traps were placed 10 meters away from each other in transects disposed from the ocean to the continent. At each sampling point, were collected the following explanatory variables: plant species richness, percentage of vegetation cover and litter, concentration of organic matter and salt in soil. In total, we collected 71 species of ants. Our results have confirmed both assumptions. Ant species richness was related to distance from the sea, plant species richness, soil cover by plant and litter. Moreover, we observed that different vegetation types within Restinga have specific communities of ants, where habitats near or with similar environmental conditions had higher similarity among them. These results indicate that the vegetation and environmental factors affected by them are the main factors determining the ant species richness and composition in Restinga.

1. Introdução Geral

O litoral brasileiro apresenta aproximadamente 9.200 quilômetros de extensão, das quais 5.000 km são ocupados por ecossistema de Restinga (Villwock *et al.*, 2005). A Restinga é um ambiente geologicamente recente, inserido no Domínio da Mata Atlântica e constituído por dunas e cordões arenosos formados no Quaternário. Diferentes fitofisionomias ocorrem neste ecossistema, variando desde formações herbáceas, arbustivas fechadas ou abertas, até pequenas florestas com altura do dossel não ultrapassando 20 metros (Falkenberg, 1999). As espécies de plantas que ocorrem em Restinga possuem elevada plasticidade, apresentando adaptações para seu desenvolvimento sob influência de vários fatores abióticos como: estresse hídrico, ventos, topografia e salinidade (Maun, 1998; Griffiths & Orians, 2004; Griffiths, 2006).

Por não apresentam um banco de sementes persistente, apresentarem grande sensibilidade ao fogo e processo de recuperação mais lento do que outros ecossistemas, as Restingas são consideradas frágeis do ponto de vista ecológico (Salimon *et al.*, 2001; Teixeira *et al.*, 2005, Vieira *et al.*, 2008). Estes fatores, somados à sua localização geográfica, fazem das Restingas ambientes extremamente suscetíveis a perturbações antrópicas. As zonas costeiras do mundo estão entre os ambientes mais populosos (Croosland *et al.*, 2005). Atualmente no Brasil, mais de 42 milhões de pessoas residem no litoral. O que corresponde a uma densidade demográfica de 122,8 habitantes por quilômetro quadrado, cinco vezes maior do que a densidade média nacional (Brasil, 2005). Mesmo protegidos pela legislação brasileira, o qual se refere às Restingas como Áreas de Preservação Permanente (Brasil, 1999; 2002), estes ecossistemas vêm sofrendo acelerado processo de desmatamento e destruição devido à urbanização, especulação imobiliária e turismo. Estima-se que grandes proporções destes ecossistemas estejam sendo perdidos sem que haja conhecimentos acerca de sua composição e funcionamento (Rocha *et al.*, 2007).

Evidentemente, a perda da biodiversidade global é uma das maiores preocupações socioambiental, econômica e política. Os conhecimentos dos padrões da biodiversidade local são fundamentais e de grande importância ecológica para o desenvolvimento de programas racionais de conservação da diversidade biológica. Comumente, os insetos têm sido utilizados em estudos com propósitos à conservação e monitoramento da biodiversidade, como agentes indicadores da qualidade ambiental dos ecossistemas (Brown, 1997; King & Porter, 2005). Entre os insetos, as formigas são apontadas por muitos autores como bons bioindicadores (Andersen, 1997; Whitford *et al.*, 1999; Andersen, 2000; Alonso & Agosti, 2000; Delabie *et al.*, 2006), visto que estes organismos são amplamente distribuídos em diversos ecossistemas e são responsáveis por inúmeros processos ecológicos (Hölldobler & Wilson, 1990). As formigas ocorrem em todos os ecossistemas, com exceção apenas dos pólos. Além disso, desempenham papéis importantes na ciclagem dos nutrientes e apresentam diversas relações inter e intra-específicas. Desde modo, afetam o ecossistema como um todo (Hölldobler & Wilson, 1990; Farji-Brener & Silva, 1995). Além disso, as formigas são biologicamente e taxonomicamente bem conhecidas, de considerável facilidade de observação, coleta e identificação (Graham *et al.*, 2004), premissas básicas de um bom bioindicador ambiental (Brown, 1997).

De modo geral, as formigas são de grande importância ecológica devido à complexa rede de relações entre o ambiente abiótico e as relações biológicas em todos os níveis tróficos (Hölldobler & Wilson, 1990). Assim, sua diversidade local deve estar intrinsecamente relacionada com as características do ambiente, e consequentemente pode afetar a comunidade onde ocorrem de forma direta ou indireta. Dessa maneira, estudos sobre a comunidade de formigas em ecossistema de Restinga podem ser valiosos para ajudar no entendimento dos componentes que determinam a riqueza das espécies neste ecossistema. Além disso, o conhecimento sobre as comunidades de Restinga é importante para o estabelecimento de prioridades e planejamento de programas de conservação em Restinga, uma vez que a conservação deste ecossistema é pouco priorizada e a lei brasileira assegura a preservação apenas dos primeiros 300 metros de dunas, excluindo diversas fitofisionomias como marismas e mangues.

Diversos fatores tais como, condições físicas, micro-clima, recursos para nidificação e alimentação, somados às relações intra e interespecíficas são apontados como os principais responsáveis pela distribuição espacial das espécies (Tews *et al.*, 2004). A competição é levantada como o principal fator estruturador das comunidades, principalmente para comunidades de formigas (Hölldobler & Wilson, 1990). Assume-se que a competição interespecífica é forte entre as espécies que possuem grande similaridade morfológica e utilizam de modo semelhante os mesmos recursos (Gotelli & Ellison, 2002). Desde modo, são formadas hierarquias de dominância, onde espécies que exploram os recursos e condições de maneira mais eficiente excluem competitivamente outras espécies (Retana & Cerdá, 2000, Arnan *et al.*, 2007). No entanto, assumir a competição como o único fator delineando a distribuição das espécies é extremamente simplista, uma vez que muitos outros fatores podem afetar a distribuição das espécies de formigas, como capacidade de dispersão e necessidades intrínsecas por determinados recursos e condições (ver Ribas *et al.*, 2003). A vegetação deve ter um papel fundamental sobre a distribuição das espécies já que é o principal promotor da grande maioria dos fatores mencionados acima, principalmente em ambientes áridos ou semi-áridos (Wenninger & Inouye, 2008). Exceto pelo regime de chuvas, as dunas de Restinga são semelhantes aos ambientes de deserto, visto que possuem baixa retenção de água e grande variação de temperatura durante o dia, além de altos níveis de radiação solar (Franco *et al.*, 1984).

Dividido em dois capítulos apresentados na forma de artigos, o presente estudo investigou diferentes aspectos da ecologia de comunidades de formigas em Restinga. No primeiro capítulo são abordados diferentes fatores responsáveis pela riqueza de espécies de formigas em uma escala local. Testou-se o pressuposto de que a riqueza de espécies de formigas aumenta com o aumento da distância em que se encontram em relação ao oceano. A partir daí, testamos as seguintes hipóteses explicativas: (1) a riqueza de espécies de formigas aumenta com o aumento da riqueza de espécies de plantas, que cresce com o aumento da distância do mar; (2) a riqueza de espécies de formigas é diretamente proporcional à cobertura do solo por plantas e serapilheira; (3) a riqueza de espécies de formigas aumenta com o aumento da concentração de matéria orgânica no solo; (4) a riqueza de espécies de formigas diminui com o aumento da concentração de sal no solo; e (5) a riqueza de espécies de formigas responde positivamente à heterogeneidade ambiental.

No segundo capítulo, testamos o pressuposto de que diferentes fitofisionomias de Restinga possuem composições de espécies de formigas específicas, ou seja, que composição da comunidade de formigas responde à zonação da vegetação de Restinga.

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3. Capítulo I

Effects of distance from the sea, biotic and abiotic factors on ant communities in Brazilian coastal sand dunes.

Cardoso, D.C. and Schoereder, J.H.

Effects of distance from the sea, biotic and abiotic factors on ant community in Brazilian coastal sand dunes.

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Running heading: Restinga ant community structure

3.1 Abstract:

Species inhabiting Brazilian coastal sand dunes (Restingas) may feature a number of adaptations to their development and survival in these physical stressors environment. Selection of nesting site may depend on various factors. In the present study a survey was carried out to determine the pattern of sea distance, biotic and abiotic factors on the community structure of ground-dwelling ants in a Restinga ecosystem. We expected higher ant species richness in areas more distant from the sea and with complex vegetation structure than in open sandy soil areas closer to sea. A total of 71 ant species were collected in the survey from 21 genera into seven subfamilies. We found a positive relationship between ant species richness and sea distance, as well as a positive relationship between plant species richness and sea distance. Ant species richness was correlated with plant species richness, litter and vegetation coverage. Different factors of the environment associated to plant species richness may have influenced our results. Plant species richness and litter may have influenced the ant species richness by increasing the diversity and amount of resources, already plant density just allowing increasing the amount of resources. The vegetation may also provide the necessary environmental conditions by the creation of different microhabitats. Overall, our results showed the importance of plant species richness, litter and plant density as local processes determining the ant species richness in Restinga. However, since distinct species differ in their habitat requirements , we cannot ignore that the ant communities may be responding to independent factors acting on local and in other scales.

Key-words: Restinga, ant communities, resource availability, ant species richness, ant distribution, Formicidae.

3.2. Introduction

Within Brazil's coastal zone is characterized by a singular ecosystem the Atlantic Forest domain known as Restinga. The Atlantic Forest in Brazil, together with "Cerrado", is a biodiversity hotspot due to large species endemism and to the degree of threat. Nowadays only 7.5% of Atlantic Forest remains as primary vegetation (Myers *et al.*, 2000; Elias *et al.*, 2008). The Restinga is a particular ecosystem because it contains a great number of distinctive biological assemblages constrained by several environmental stresses such as water strain, wind, unsteady substrate, salt spray, soil salinity, burial and wave action (Maun, 1998). The majority of these factors are regulated by sea, which makes highly dynamic regimes the physical, chemical and biological processes (Croosland *et al.*, 2005).

The Restinga is a fragile ecosystem, due to the stronger abiotic factors that act on living communities (Comor *et al.*, 2008). This is aggravated by intense anthropogenic disturbances, since most of the world's population lives in Coastal zones. In Brazil, more than 42 million people live at the 342,000 km^{-2} of the Coastal zone (Brasil, 2005). Therefore, the Restinga has been suffering from the loss of biodiversity due to tourism and urbanization since the European colonization, more than 500 years ago (Falkenberg, 1999).

The loss of global biodiversity is a major socio-environmental and political concern (Santos & Medeiros, 2003; Diehl *et al.*, 2005). The understanding of the local biodiversity patterns is of high interest in conservation of natural ecosystems under anthropogenic pressure. The knowledge of species richness and patterns of distribution is fundamental to the development of a rational program for biological diversity conservation (Brown, 1997; Alonso & Agosti, 2000; Ribas & Schoereder, 2007).

Ants are among the most suitable groups of animals for characterization of the community, since they are diverse, very abundant and occur virtually in all ecosystems on Earth (Hölldobler & Wilson, 1990; King & Porter, 2005). Moreover, ants influence and are sensitive to biotic and abiotic processes where they occur, basic premises that make ants as faithful ecological indicators for monitoring environmental changes (Brown, 1997).

Many studies of plant species richness, composition and zonation are found for Restinga in the literature (Castellani *et al.*, 1995; Pereira *et al.*, 2001; Assis *et al.*, 2004; Scherer *et al.*, 2005; Martins *et al.*, 2008), whereas studies about their fauna are scarce. Many of these studies address the question of vegetation zonation led by several environmental stresses (Wilson & Sykes, 1999; Gilbert *et al.*, 2008). However, the ecological factors that determine these distributions are seldom discussed and were not tested on the Restinga fauna.

The ecology of communities studies the variations in the distribution of populations in different spatial and temporal scales, and attempts to explain the patterns that are responsible for it (Ricklefs & Schluter, 1993). Species richness and distribution may be influenced by many local and regional processes (Cornell & Lawton, 1992). However, the distinction among these spatial scales depends upon the species or taxon in question (Soares *et al.*, 2001). Competitive interactions, microclimatic conditions, the availability of resources and nesting site location are considered as major processes that determine ant species richness on local scale (Cornell & Lawton, 1992; Godfray & Lawton, 2001). Ant communities were reported to be highly interactive, because they show mutualistic interactions (Hölldobler & Wilson, 1990).

This interactivity has been demonstrated in several papers, in which species richness and composition have been associated in local scales with resource diversity, quantity, quality, and structural heterogeneity (Ribas *et al.*, 2003; Lassau & Hochuli, 2004; Vargas *et al.*, 2007; Wenninger & Inouye, 2008). Plant species richness, or density, is the main variable used in these studies as surrogate of conditions and resources. Nevertheless, species richness is not always correlated with habitat structural heterogeneity. For ants, higher biodiversity may be associated to areas with low complexity. This case was related for sandstone ridgetop woodland in Sydney, Australia (Lassau & Hochuli, 2004). In Restinga, few studies attempted to describe general patterns that determine local ant species richness in sand dune (Vargas *et al.*, 2007). Moreover, the Restinga ant fauna is little known (Silva, 2005).

The most distinct feature of Restinga is the vegetation zonation. The plant communities are spread in clusters due to progressive shifts of environmental stresses and the plant species that showed different tolerance to these stresses. Nevertheless, different authors diverge about the mechanisms affecting this zonation, and remain unclear which factors determine it (Wilson & Sykes, 1999; Maun & Perumal, 1999). The main goal of this study was to determine the relationship of ant species richness with seaward edge distances to inland Restinga, testing the assumption that ant species richness increase with distance from the sea. We hypothesized that: (1)

ant species richness increase with plant species richness, which also increase to inland restinga; (2) ant species richness is directly proportional to soil cover by plants and/or litter; (3) ant species richness increase with the concentration of organic matter; (4) ant species richness decreases with salt concentration in soil, and (5) ant species richness responds positively to structural heterogeneity of environment.

3.3. Materials and Methods

3.3.1. Study area

This study was conducted in herbaceous and shrubby Restinga of the Morro dos Conventos (28°56' S; 49°21' W) in Araranguá, Santa Catarina, Brazil. The climate, according to Köppen's climatic classification, is Cfa type with rain distributed throughout the entire year, without dry season. Average annual rainfall is 1269.3 mm and average annual temperature is 21.4 °C (Dufloth *et al.*, 2005).

The studied Restinga area has a length of approximately 6,5 km of coastline extending up to the limit with the estuary of Araranguá river. The Morro dos Conventos Restinga is a complex set of quaternary dunes composed predominantly by quartzipsamment soils (Dufloth *et al.*, 2005). The vegetation is represented by secondary formations of the "Dense Umbrophilous Forest" (Falkenberg, 1999). The plant community occurs in well delimited patches with shrubs and trees interspersed with shrubby and herbaceous patches that extend from the beach to the base of the dunes and reaching the top.

3.3.2. Sampling ants and identification

We sampled the ants between January and February 2008, using pitfall traps into two arbitrarily disposed 650 m-long transects from the sea to inland Restinga.

Pitfall traps consisted of plastic recipients 77 cm height and 119 cm diameter. Traps were filled with a solution of salt, water and detergent, to kill and conserve ants. In each transect we installed 65 pitfall traps (each representing one sample unit, n=130) distants 10 m from each. Pitfall traps remained in the field for 48 hours.

We sorted and identified the ants to genera with aid of identification keys by Bolton (1994) and Palacio & Fernandéz (2003). We adopted the classification proposed by Bolton (2003). We identified ants to species level whenever possible, using taxonomic keys and genera revision articles, or by comparisons with of the Formicidae reference collection of the Laboratório de Ecologia de Comunidades of Universidade Federal de Viçosa, where all voucher specimens were deposited.

3.3.3. Sampling explanatory variables

In each sampling unit, after removing the pitfall traps, we installed four quadrants of one m^2 subdivided into 25 quadrants of the 20x20 cm around each pitfall site. We took four measures to test our hypotheses: plant species richness, soil cover, soil salinity and organic matter concentration in the quadrants (Figure 1).

We estimated plant species richness as a surrogate of diversity of resource and environmental heterogeneity (Ribas *et al.*, 2003). We counted plant species in field, without comparison with any botanic collection. Since our goal was to test the relationship between plant and ant species richness, the taxonomic identity was not important. We measured the total plant species in each one of the four quadrants (1m^2) installed, counted each plant species in each quadrant just one time ever by same researcher.

Soil cover was estimated through number of sub-quadrants covered by plant (hereafter, plant density) and litter (hereafter, litter density) in all quadrants within each sampling unit. Because each sub-quadrant has a known area, we made conversion to a plant/litter percentage cover.

Organic matter (OM) was estimated from soil samples collected at 0-0.1 m deep in center of each quadrant in all sample units, measuring total concentration of organic matter in each soil sample. Soil salinity was determined from soil samples from the same depths as those sampled to determine organic matter, and was estimated by sodium (Na) concentration. All soil analyses were realized in the Laboratory of Soil Analysis Viçosa, Minas Gerais, Brazil.

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

We calculated the average of each estimate obtained in the four quadrants for each sampling unit. Coefficient of variation (CV) of plant and litter density was obtained for each sampling unit. CV was used as a surrogate of environmental heterogeneity for each sampling unit. Plant species richness was used too as a surrogate of environmental heterogeneity (Ribas *et al.*, 2003). Several studies about ant community structure have associated the ant species richness and composition to the structural heterogeneity of the environment (Ribas *et al.*, 2003; Lassau & Hochuli, 2004; Vargas *et al.*, 2007).

3.3.4. Statistical analyses

The assumption that the ant species richness increase with distance from the sea was analyzed adjusting two models: simple linear regression and simple quadratic regression, with Poisson error distribution. Ant species richness was the response variable, and distance from the sea was the explanatory variable. This second model was carried out because of the occurrence of sand dunes across the inland transect was observed. The suitability of the models was compared by their Akaike's Information Criterion (AIC) values (Crawley, 2007). We tested a sub-assumption to evaluate whether plant species richness increases to inland Restinga. Average plant species richness was used as response variable and distance from the sea as explanatory variable. This analysis was also carried out using the same models described above, with normal error.

The hypotheses to explain ant species richness patterns along distance from the sea were tested using multiple linear regressions, with Poisson distribution. We carried out a model in which ant species richness was the response variable and average of plant species richness, litter density, plant density, MO concentration (dag kg^{-1}) and Na concentration (mg/dm^3) within each sampling unit were used as explanatory variables, as well as each coefficient of variation (CV). Additionally, the interaction of plant species richness x plant density was included in the model because these variables might be correlated, since the increase in richness can result in increased vegetation cover, but not necessarily.

The complete model was simplified, when possible, excluding variables and verifying effects on deviance until the simples adequate model (Crawley, 2002). All analyses were carried out under R program (R Development Core Team, 2008) and followed by residual analyses to verify the suitability of the models and of the distributions of errors (Crawley, 2002).

3.4. Results

We collected 71 ant species, from 21 genera and seven subfamilies. Mymicinae was the most speciose subfamily, with 41 species, followed by Formicinae (13 species), Ponerinae (eight species) and Dolichoderinae (six species). The subfamilies Ecitoninae, Pseudomyrmecinae and Ectatomminae were the least speciose, with only one species each (Table 1).

We found a significant relationship between ant species richness and sea distance. The two models tested were significant. However, the quadratic model was more parsimonious ($\chi^2 = 15.954$; df =1; p<0.001, AIC value=639.25, Figure 2A). Furthermore, we also found a relationship between plant species richness and sea distance, only in the quadratic model ($F_{(2,\ 127)} = 12.793$; p<0.001, Figure 2B).

The hypotheses that ant species richness increase with plant species richness was accepted (χ^2= 66.067, df=1, p< 0.001, Figure 3A). Likewise, the hypotheses that the species richness is directly proportional to plant density (χ^2= 4.050, df=1, p= 0.04) and litter density (χ^2= 23.849, df=1, p< 0.001), was accepted (Figure 3B and 3C, respectively). However, we did not find significant relationship between ant species richness and OM (χ^2= 0.087, df=1, p= 0.769) and sodium (χ^2= 0.404, df=1, p= 0.525) concentrations. The interaction between plant species richness and plant density was not significant (χ^2=0.697, df=1, p=0.848), therefore, the two factors should act independently on ant species richness.

There was no significant relationship between ant species richness and the CV of plant density (χ^2=0.334, df=125, p= 0.563) and litter density (χ^2=0.806, df=123, p= 0.369).

3.5. Discussion

3.5.1. Ant fauna

The ant species collected in our work comprehend, to our knowledge, the first list of the myrmecofauna of southern Santa Catarina State (Table 1). Few studies have been conducted with ants in the State. Furthermore, most studies are concentrated in other ecosystems of Atlantic Forest, in the northern and western region (Silva & Silvestre, 2000; Lutinski & Garcia, 2005; Rosumek *et al.*, 2008). Studies in Restinga were carried out only in the central-east region (Bonnet & Lopes 1993).

The number of ants sampled in our study was smaller than the number of ant species collected in Rio de Janeiro Restinga (23º03' S; 44º03' W) with the same sampling methodology (pitfall traps), which sampled 92 ant species in total (Vargas *et al.*, 2007). However, that number was larger than the species richness presented in two studies of Rio Grande do Sul Beach (29º20' S; 49º43' W), which sampled 36 and 60 ant species, respectively (Diehl *et al.*, 2000; Diehl *et al.*, 2005). Indeed, the authors in the two last studies employed different types of sampling than used in our study, and consequently different sampling effort (Bestelmeyer *et al.*, 2000).

The genera *Pheidole*, *Solenopsis* (Myrmicinae) and *Camponotus* (Formicinae) were the richest in species. These genera, according to Wilson (1976), together with *Crematogaster*, represent the most diverse genera worldwide, presenting also a broad distribution and wide range of ecological adaptations. Species in these genera occur in most diverse habitat types. *Pheidole* for example, occurs from closed and humid to dry and open environments, such as sand dunes. Similar results in Restinga and in many other ecosystems were found (Leal, 2003; Sacchett & Diehl, 2004; Diehl *et al.*, 2005; Vargas *et al.*, 2007; Rosumek *et al.*, 2008).

The ant species sampled in Morro dos Conventos Restinga were more similar to the species collected (Bonnet & Lopes, 1993) in Joaquina Restinga (Florianópolis, SC) and also at Beaches in the neighboring Rio Grande do Sul State (Diehl *et al.*, 2000; Albuquerque *et al.*, 2005; Diehl *et al.*, 2005) than to ant species collected in Rio de Janeiro State (Vargas *et al.,* 2007). Only four species recorded were common among the Restingas of Rio de Janeiro and Santa Catarina States. This may evidence that regional scale factors are important on ant species richness and distribution in Brazilian Restinga. These ecosystems have undergone recent environmental disturbances in the last Quaternary. Glaciations in this period are a major historical factor shaping the patterns of spatial distribution of species due to the creation of isolated refuges (see Carnaval & Moritz, 2008; for a review).

3.5.2. Response of the Ant species to conditions and resources

In this work, we found that ant species richness increases with distance from the sea and similarly, this pattern has been also observed in plant species richness. The data found in our study agree with the idea that the plant species richness, which is a surrogate of environmental heterogeneity, is an important factor to structure ant communities in Restinga. This response was also observed for ants in studies in Brazilian savannas/"Cerrado" (Ribas *et al.*, 2003), Pantanal (Corrêa *et al.*, 2006), and "Caatinga" (Leal, 2003), where the number of ant species was higher in sites with more plant species richness. The relationship between habitat or resource heterogeneity and species richness has been reported for innumerable taxa (Tews *et al.*, 2004).

Several components associated to plant species richness may have influenced our results. The vegetation is the primary resource at food or shelter for most insects (Wenninger & Inouye, 2008), and this should not be different for ants. The relationship between the amount and variety of resource availability and fauna diversity is extensively accepted (Tews *et al.*, 2004). The process driving this pattern may be that the increase of primary producers in ecosystems may increase in the other trophic levels by bottom-up effect (Hunter & Price, 1992; Wenninger & Inouye, 2008).

Vegetation may represent a large variety of resources for ants. Ants can be direct consumers of seeds, nectar and foliage (e.g., leaf-cutting ants), or indirect consumers, using the plants as nesting sites or foraging area (Oliveira & Pie, 1998; Oliveira & Freitas, 2004). Besides, the amount and variety of resources should affect ants differently. Resource variety may support a larger number of ant *taxa* by interaction of plant-species specialists, whereas the amount of resources may offer support for more generalist ants (Ribas *et al.*, 2003, Wenninger & Inouye, 2008). We found a positive relationship between ant species richness and plant and litter density. In this way, apparently, plant species richness is the main structuring force of the ant communities in Restinga, because organic matter, supposedly another surrogate for resource, was not associated with ant species richness.

Many studies have addressed the importance of ants in the modification of soil properties (e.g., Cammeraat & Risch, 2008). Due to their burrowing activities, ants alter soil physical, chemical and biological processes. Therefore, ants may increase the diversity of soil organisms or change the structure of the detritivorous food web (Paris *et al.*, 2008). However, the soil properties should equally affect ant species richness, because most species are ground dwelling. In our study, we did not finding relationship between ant species richness and concentration of soil organic matter. However, Johnson (1998) suggested a relationship between soil and ant spatial distribution. This author found that mating queens of *Pogonomyrmex rugosus* and *P. barbatus* choose soils with higher fertility and moisture in the establishment phase. Conversely, Wagner *et al.* (2004) did not find similar relationship for *P. barbatus*. The knowledge about the effect of soil characteristics on ant communities is very limited. Soil properties different from organic matter may affect the ant communities. Some studies have indicated the importance of the proportion of sand in the soil on ant community diversity (Boulton *et al.*, 2005; Ríos-Casanova *et al.*, 2006).

Plant density, similarly to plant species richness, may increase the amount of resources, leading to a higher number of ant colonies, or still, relaxing interspecific competition and increasing ant species richness. High abundance of dominant ant species has been reported in open areas; whereas in environments with more vegetation, the number of dominant species is lower (Retana & Cerdá, 2000; Vasconcelos & Davidson, 2000). Similarly to plant density, litter density may also affect ant species richness by increasing resources and changing conditions. However, other studies did not find a positive relation between litter composition and ant species richness (Campos *et al.*, 2003; Vargas *et al.*, 2007; Muscardi *et al.*, 2008). The positive relationship found between litter coverage/density and ant species richness in this work may be an outcome of canopy created by arboreal and shrubby plant species in these habitats. Canopy cover decreases the temperature and increase moisture (see below), allowing the formation of persistent litter and creating the conditions for establishment of cryptic species that live in rotting wood and in leaf litter. Areas with litter in Restinga are scarce in herbaceous and open shrubby phytophysiognomies due to the strong wind regimes.

As mentioned above, the vegetation may also provide the necessary environmental conditions through the creation of microhabitats. In arid 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 & Hochulli, 2004; Vargas *et al.*, 2007). Plant species richness in subtropical and tropical climates increase soil moisture and decrease mean temperature, although these parameters vary along the day (Chen *et al.*, 2004). Higher temperatures are expected with upright sun. Besides, the temperature and moisture differ significantly between microhabitats in closed shrubs and open areas, as well as in different vertical strata of shrubby vegetation (Yu *et al.*, 2008). For Restinga, the temperature and moisture are closely associated with plant zonation. Franco *et al.* (1984), found that temperature decrease with vegetation complexity in one zonation from the sea to inland Restinga. In areas without vegetation, high temperatures were recorded even at a depth of -5 cm. Besides, the same authors observed that there was a great variation in temperature during the day in different local habitats, like other dry environments.

Another factor that might influence ant species richness is habitat heterogeneity. This factor is repeatedly reported as an important structuring force in arid and semi-arid environments (e.g., Wenninger & Inouye, 2008). Restinga can be divided into distinct communities depending on dune structure and unique species associations. Restinga is a desert-like ecosystem, with well-drained sandy soils and high solar incidences. Restingas usually have sparse vegetation cover and are characterized by patchiness comprised of shrubs and herbaceous plants, and the shift between open and cover sites may occur in very small scale (few meters). As the micro-climate in open and cover sites may differ significantly (Yu *et al.*, 2008), we believe that sites more heterogeneous would be richer in species. This is because, the covered micro-habitats shelter the heat-limited species and open micro-habitats leads to the increase of heat-tolerant species, a pattern well established for Mediterranean ecosystems (Retana & Cerdá, 2000). In this study, the Coefficient of Variation (CV) between sample units was accessed to evaluate the dissimilarity of soil cover (plant and litter density) among sample units as a measure of spatial habitat heterogeneity. We expected that higher CVs represent more 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 be applied for ant communities in Restinga. This may have occurred because sites with total cover have CV equal to zero, as well as sites with zero cover. Thus more homogeneous sites (overall soil cover) may have higher ant species richness due to the action of others variables, such as plant density, which has a significant relationship with ant species richness in this study. However, plant species richness may also be a surrogate of heterogeneity, and its relationship with ant species richness was positive.

In sand dunes coastline, most physical and chemical stressing factors are regulated by the sea (Croosland *et al.*, 2005). It is also largely accepted that the salt spray and salinity are the main factors governing vegetation zonation in coastal dunes (Maun & Perumal, 1999). Therefore, we expected that salinity would be an abiotic stressor for ground-dwelling ant communities. Interestingly, our results showed that salinity apparently has no effect on ant communities. Indeed, this factor can be explained by vegetation itself. Many authors have tested the effect of salt spray and salinity on plants, reporting that salt spray and salinity are not important environmental factors promoting coastal sand dune zonation (Maun, 1998; Maun & Perumal, 1999; Gilbert *et al.*, 2008). These authors attributed vegetation zonation in coastal areas to sand burial. Furthermore, salinity effects on plant communities apparently prevail in environments closer to the sea, the fore dunes (Wilson & Sykes, 1999).

This study demonstrates that ant species richness in Restinga is correlated with plant species richness and soil coverage at local scale. It is important to stress that the results and conclusion presented in this study where derived from a single Restinga sample area. However, since the Restinga studied area is not visually different from any other Restinga area in region, results obtained here can be applied to other sites. Future studies should explore additional habitats components, such as biotic interactions as determinants for ant species richness.

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3.6. References

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3.7. Figures and Table

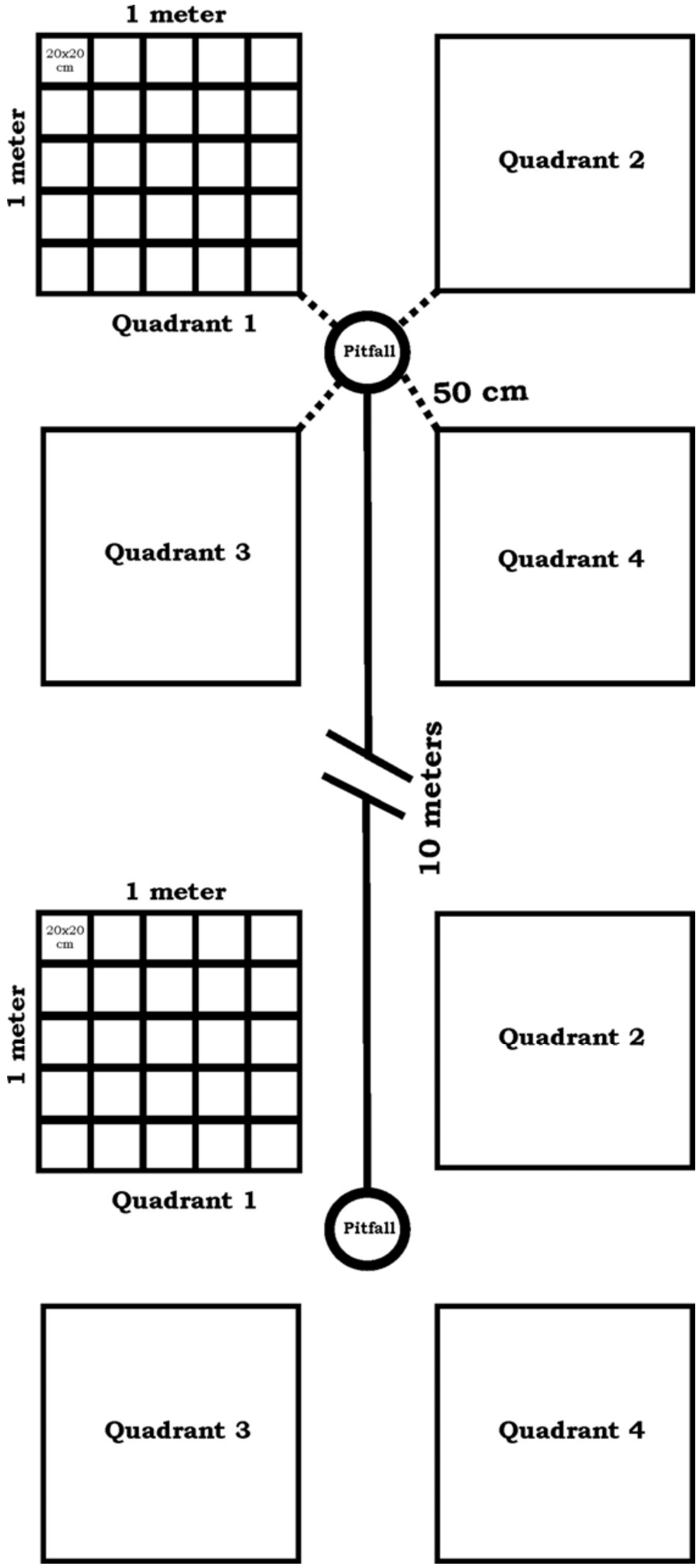

Figure 1 – Scheme of ant sampling design in Morro dos Conventos Restinga, Santa Catarina, Brazil. Overall, 65 pitfall traps in two transects were installed, 10 m from each.

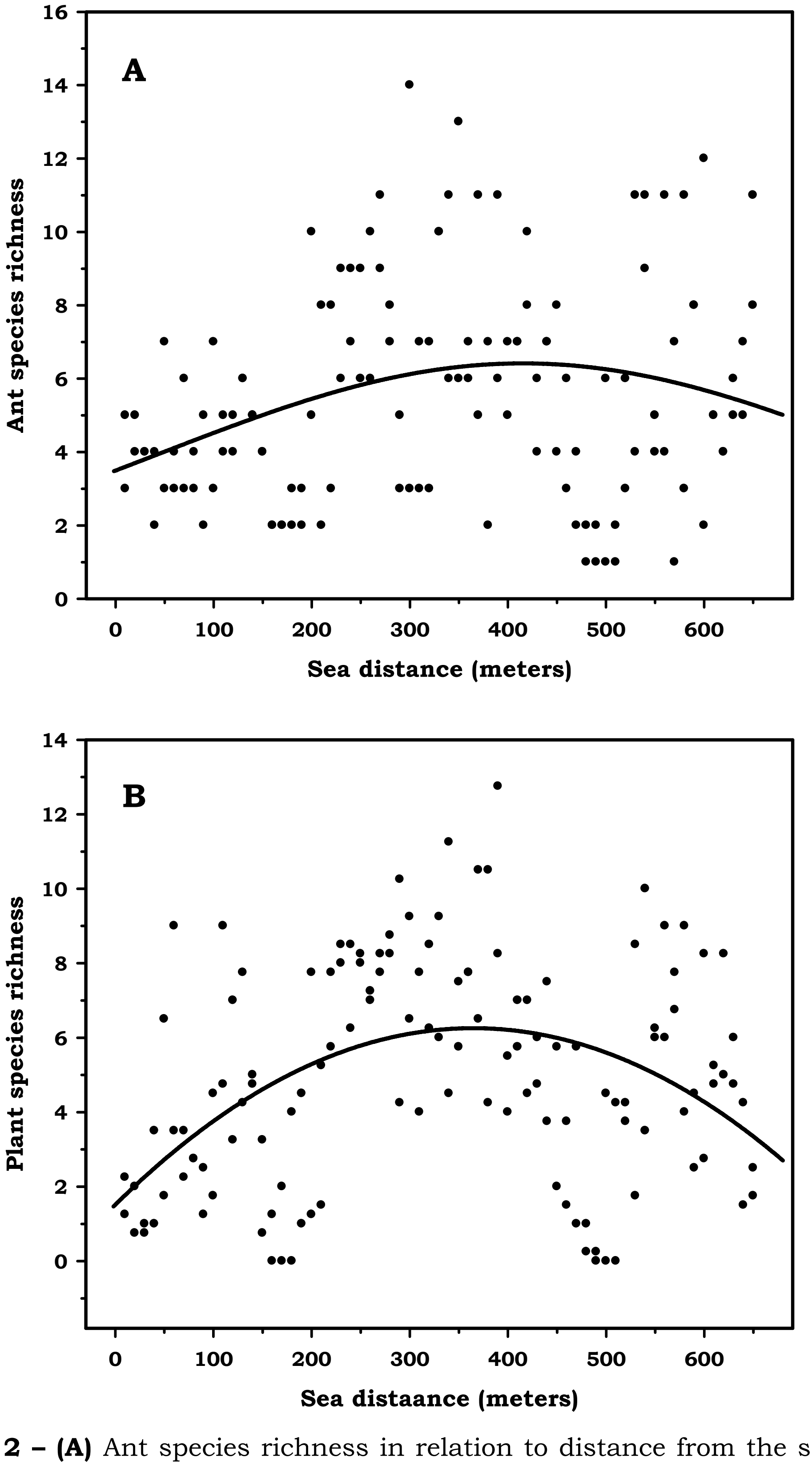

Figure 2 – (A) Ant species richness in relation to distance from the sea. (χ^2 = 15.954; *df* = 2; p<0.001) [y=exp(1.252+2.923e-03x-3.519e-06x^2)]. **(B)** Plant species richness in relation to distance from the sea. ($F_{(2,\ 127)}$ = 12.793; *p*<0.001) [y=1.516+2.601e-02x-3.568e-05x^2].

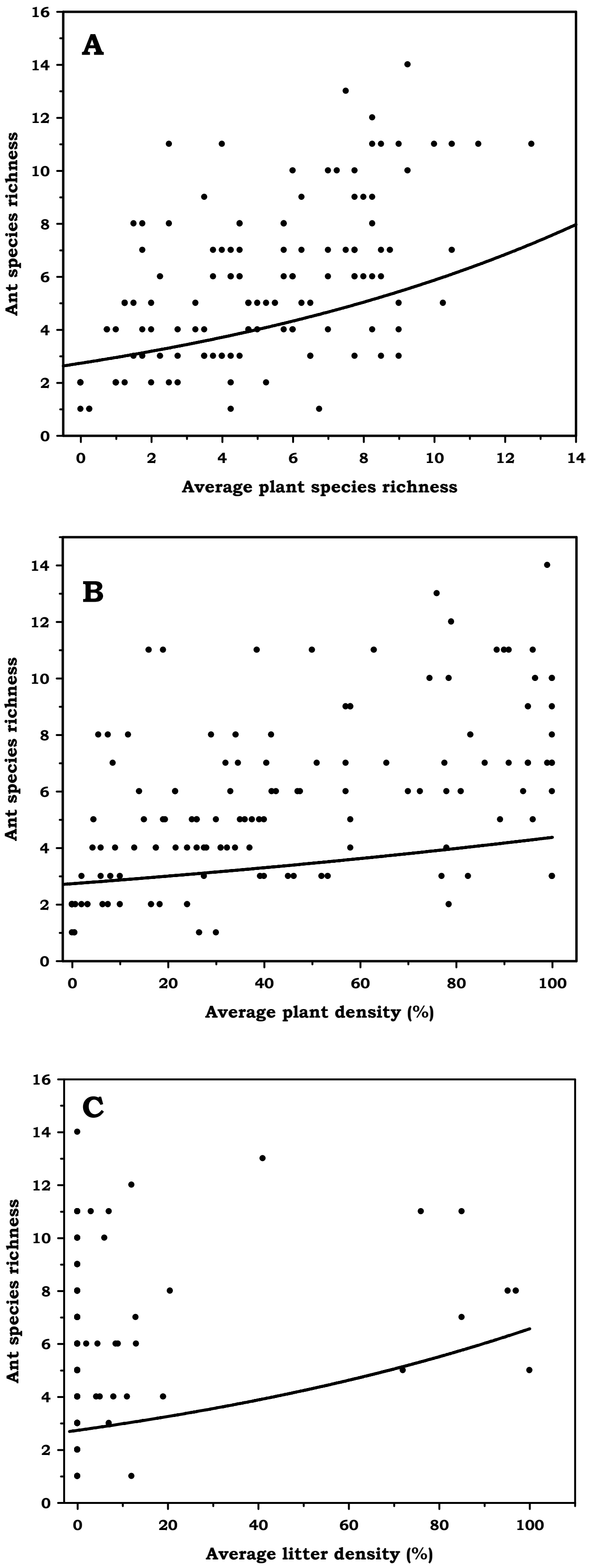

Figure 3 – Relationship between ant species richness and surrogates of resources and conditions and Restinga Morro dos Conventos. (A) Average plant species richness, y=exp(1.008611+0.076248x); (B) Average plant density, y=exp(1.008611+ 0.004686x); (C) Average litter density, y=exp(1.008611+ 0.008754x).

Table 1 – List of the ants collected at 50 m intervals of distance from the sea. Morro dos Conventos Restinga, Santa Catarina, Brazil.

Taxa	**0-50**	**60-100**	**110-150**	**160-200**	**210-250**	**260-300**	**310-350**	**360-400**	**410-450**	**460-500**	**510-550**	**560-600**	**610-650**
DOLICHODERINAE													
Dorymyrmex brunneus					X								
Dorymyrmex pyramicus	X	X	X	X	X	X	X	X		X	X	X	X
Linephitema leucomelas													X
Linepithema humile					X		X	X	X				
Linepithema iniquum													X
Linepithema neotropicum		X	X	X	X	X	X	X	X	X	X	X	X
ECITONINAE													
Labidus coecus													X
FORMICINAE													
Brachymyrmex cordemoyi	X	X	X	X	X	X	X	X	X	X	X	X	X
Brachymyrmex pr. *obscurior*					X	X	X	X		X	X	X	
Camponotus trapezoideus												X	
Camponotus melanoticus				X	X	X	X	X	X		X	X	
Camponotus punctulatus											X		
Camponotus blandus			X	X		X	X	X	X	X	X	X	X
Camponotus crassus					X	X	X	X	X				
Camponotus pr. *cameranoi*	X	X	X	X			X			X	X	X	X

Taxa	**0-50**	**60-100**	**110-150**	**160-200**	**210-250**	**260-300**	**310-350**	**360-400**	**410-450**	**460-500**	**510-550**	**560-600**	**610-650**
Camponotus rufipes	X	X	X	X	X	X	X	X	X				
Myrmelachista gallicola								X					
Paratrechina pr. *fulva*	X			X	X	X	X	X	X	X			
Paratrechina sp. 1					X						X	X	X
Paratrechina sp. 3									X				
MYRMICINAE													
Acromyrmex (Moellerius) sp. 4								X					
Acromyrmex ambiguus	X		X										
Acromyrmex balzani								X					
Acromyrmex pr. *laticeps*					X	X		X				X	X
Acromyrmex sp. 7								X	X				
Acromyrmex striatus	X	X	X	X	X	X			X		X	X	X
Crematogaster moelleri												X	
Crematogaster sp. 2												X	
Cyphomyrmex rimosus			X		X		X	X				X	X
Cyphomyrmex strigatus						X						X	
Monomorium pharaonis				X									
Mycetophylax morschi		X	X	X	X	X	X	X			X	X	X
Mycetophylax simplex	X		X	X									
Pheidole (gr. Flavens) sp. 05								X				X	X

Taxa	**0-50**	**60-100**	**110-150**	**160-200**	**210-250**	**260-300**	**310-350**	**360-400**	**410-450**	**460-500**	**510-550**	**560-600**	**610-650**
Pheidole sp. 01	X	X	X	X	X					X	X		X
Pheidole sp. 02			X	X	X	X	X	X	X			X	
Pheidole sp. 03					X	X	X	X	X	X	X	X	X
Pheidole sp. 04					X		X				X	X	X
Pheidole sp. 06													X
Pheidole sp. 07						X	X				X		
Pheidole sp. 13												X	X
Pheidole sp. 14													X
Pheidole sp. 15					X	X		X	X				
Pheidole sp. 16					X								
Pheidole sp. 17												X	
Pogonomyrmex naegelli			X	X	X	X	X	X	X				
Solenopsis saevissima	X	X	X	X	X	X	X	X	X	X			
Solenopsis sp. 2		X	X	X	X	X	X	X	X	X	X		X
Solenopsis sp. 3				X	X	X	X	X	X		X	X	X
Solenopsis sp. 4											X	X	X
Solenopsis sp. 6			X	X									
Solenopsis sp. 8						X	X	X			X	X	
Solenopsis sp. 9		X	X		X	X	X	X	X		X	X	X
Strumigenys crassicornis													X

Taxa	**0-50**	**60-100**	**110-150**	**160-200**	**210-250**	**260-300**	**310-350**	**360-400**	**410-450**	**460-500**	**510-550**	**560-600**	**610-650**
Strumigenys denticulata						X							
Strumigenys louisianae						X			X				
Trachymyrmex holmgreni					X				X				
Trachymyrmex iheringi						X					X		X
Wasmannia affinis													X
Wasmannia auropunctata	X	X	X	X	X	X	X	X	X	X	X	X	X
Wasmannia sulcaticeps							X					X	X
ECTATOMMINAE													
Gnamptogenys striatula												X	X
PONERINAE													
Hypoponera foreli													X
Hypoponera pr. *opaciceps*					X			X					
Hypoponera reichenspergeri													X
Hypoponera sp. 4												X	
Hypoponera sp. 6									X				
Odontomachus chelifer							X					X	X
Pachycondyla harpax												X	
Pachycondyla striata					X	X	X						X
PSEUDOMYRMECINAE													
Pseudomyrmex pr. *laevivertex*												X	

4. Capítulo II

Ant community composition and its relationship with phytophysiognomies in a Brazilian Restinga.

Cardoso, D.C. and Schoereder, J.H.

Ant community composition and its relationship with phytophysiognomies in a Brazilian Restinga.

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4.1. Abstract

In this study the composition of ant communities was compared in four adjacent phytophysiognomies in Morro dos Conventos Restinga, in Brazil. Ant species were sampled with pitfall traps. Overall, 71 ant species were collected. Ant species composition differed between phytophysiognomies. Our results suggest that environments were more similar in the adjacent than in the more distant phytophysiognomies, which is similar to the vegetation zonation and gradient sea-inland Restinga. Thirteen species determined more than 50% of the dissimilarity between phytophysiognomies. *Solenopsis saevissima* was the species that contribute more to phytophysiognomic distinction, followed by *Pheidole* and *Camponotus* species. The ants of these genera are among the most abundant genera in the World, due to their mega diversity, wide distribution and abundance. The type of vegetation is one of the main factors affecting the composition of ant communities in Restinga. The role of plants is linked to the availability of resources and conditions and they may determine ant assemblage composition and different interactions occurring in Restinga.

Keywords: Ant community, Community composition, Formicidae, Phytophysiognomies, Restinga, Sand dunes.

4.2. Introduction

The Brazilian Atlantic Coastline is very extensive, and presents a range of vegetation types with conspicuous changes across landscapes (Cerqueira, 2000). *Restinga* is a common name of coastal sandy open vegetation covered predominantly by herbaceous and shrubby plants, which occur along the Brazilian coastline. This ecosystem develops in marine deposits of quaternary origin, within the Atlantic Forest domain. The vegetation that comprises these environments plays a key role on the stability of the sand dunes and on its biodiversity (Kuki *et al.*, 2008).

The most distinctive feature of Restinga is its vegetational gradient across coastal dunefields from the sea to inland, named as *vegetation zonation* (Maun, 2009). Distinct phytophysiognomies compose the Restinga, varying from areas with scarce vegetation near the sea, to inland areas with shrubby and tall thicket. Near the ocean the physical stressors are harshest and the plant community is characterized mainly by creeping grasses and herbs with rhizomatous and stoloniferous growth. In inland dunefields a decrease of the physical stressors occurs and the forest and shrubby vegetation develops in areas sheltered by larger dunes (Maun, 2009).

The plant species that occur in Restinga, as well as in many other Atlantic Forest ecosystems, show phenotypic variation, possessing several adaptations for their development under physical stress conditions. Among this stressors, soil salinity, burial, salt spray, wind and unconsolidated soils, are important (Maun, 1998).

Habitat structure and complexity are important aspects affecting animal community in more diverse environments (Tews *et al.*, 2004). More complex habitats may be divided into distinct niches that culminate in higher species richness (Finke & Snyder, 2008). Besides, other authors point competition as a major factor determining animal assemblage structure (MacArthur, 1958; Connell, 1961). Abiotic factors, such as microclimate, soil properties, wind and others, may also influence communities over different geographic scales (Spiesman & Cumming, 2008). Biotic factors, such as competition, predation, and other interactions between species, are more prone to influence communities on a local scale (Ricklefs & Schluter, 1993). In arid and semi-arid environments, abiotic factors, rather than biotic interactions, such as moisture and ground temperature, may have greater influence on local communities (Rojas & Fragoso, 2000; Vargas *et al.*, 2007; Luque & López, 2007; Wenninger & Inouye, 2008). Restinga is a desert-like ecosystem, with large temperature variation, bare patches of a well-drained sandy soil and high solar incidence (Franco *et al.*, 1984).

The relationship between plant species richness and fauna biodiversity was extensively investigated in many studies in distinct environments (e.g., Wenninger & Inouye, 2008). However, few studies have attempted to examine shifts in species composition between local habitats types within a particular ecosystem (Hill *et al.*, 2008). Nevertheless, studies on plant species composition are found in the literature for Restinga (Castellani *et al.*, 1995; Pereira *et al.*, 2001; Assis *et al.*, 2004; Scherer *et al.*, 2005; Martins *et al.*, 2008), although studies about its fauna are very scarce (Silva, 2005). The species composition reflects a combination of ecological and historical processes at local level (Philippi *et al.*, 1998). As abiotic and biotic processes differentially affect species composition, their understanding can provide information on how these processes act on local communities. Generally, species-specific demands are the key to successful conservation actions, although actions focused on one species may not benefit other species (Caughley, 1994). Thus, the knowledge on how species composition or assemblages of species react to changes in habitats may be of fundamental importance for the definition of conservation priorities.

Ants are among the most suitable groups of animals for community characterization, since they are diverse, very abundant and occur virtually in all ecosystems on Earth (Hölldobler & Wilson, 1990; King & Porter, 2005). Moreover, ants influence and are sensitive to biotic and abiotic processes, basic premises to make them reliable ecological indicators for monitoring environmental changes (Brown, 1997).

This study investigates the relationship between vegetation zonation and ant community composition. Our hypothesis is that the ant community composition differs between habitats across a gradient from sea to inland continent. Therefore, we expect that different phytophysiognomies have different ant community compositions.

4.3. Material and Methods

4.3.1. Study area

This study was conducted in herbaceous and shrubby Restinga of the Morro dos Conventos (28º56’16”S and 49º21’25”W) in Araranguá, Santa Catarina, Brazil. The climate, according to Köppen’s climatic classification, is Cfa type with rain distributed throughout the entire year, without dry season. Average annual rainfall is 1269.3 mm and average annual temperature is 21.4 ºC (Dufloth *et al.*, 2005).

The area studied has a length of approximately 6.5 km of coastline extending up to the estuary of Araranguá river. The Morro dos Conventos Restinga is a complex set of quaternary dunes composed predominantly by Quartzipsamment soils (Dufloth *et al.*, 2005). The vegetation is represented by secondary formations of “Dense Umbrophilous Forest” (Falkenberg, 1999). The vegetation occurs in defined zones in well delimited patches, with shrubs and trees interspersed with shrubby and herbaceous patches. This classification was taken from floristic and phytosociologic data, and modified of the proposed by Falkenberg (1999). The four phytophysiognomic environments that occur in Morro dos Conventos Restinga are described below.

4.3.2. Phytophysiognomies

In this work we adopted a simplified classification of Restinga vegetation (Falkenberg, 1999), because it is more adequate for the Restingas of Santa Catarina State. The phytophysiognomies occur across a gradient extending from the sea backshore to inland Restinga (Figure 1).

Frontal Dunes (FD): Low plants, mainly composed of herbaceous and rhizomatic plants. The soil is sparsely covered, with predominance of open sandy areas. The plant community, disposed in patches, is scarce and widespread and more influenced by the sea (Figure 2, A).

Lagoons, marsh and pits (LMP): This area has the more extensive topographic depressions, with grassland, herbaceous and shrubby vegetation generally not higher than one meter tall. Lagoons and marshes of different sizes occur, formed temporally by rainfall or persistent, due to the conditions of the groundwater level (Figure 2, B).

Internal Dunes (ID): Comprehend stable, semi-stable and mobile dunes with vegetation more exuberant but not higher than 1.5 meters tall. Herbaceous, shrubby and arboreal species may occur. In this landscape, little lagoons may also occur among dunes (Figure 2, C).

Restinga Forest (RF): It shows arboreal, shrubby and herbaceous strata, with more litter on the ground, and higher plant species richness. The vegetation is usually 1-15 meters tall, reaching 20 meters. It occurs in depressions, sand slopes, stable and semi-stable dunes in extensive or brushwood forests (Figure 2, D).

4.3.3. Ant sampling

The sampling of ants was carried out between January and February 2008 in the above described phytophysiognomies, using pitfall traps disposed along two transects installed from the sea to inland Restinga. Transects cross the whole extension of all phytophysiognomies.

The pitfall traps consisted of plastic recipients, 77 cm height and 119 cm diameter. The traps were filled with a solution of salt, water and detergent, to kill and conserve the ants. In each 650 m transect a set of 65 pitfalls traps (each representing one sample unit) were installed, distanced 10 m from each other. No baits were used to attract the ants and the traps remained in the field for 48 hours.

The ants collected were sorted and identified to genera level with the identification keys of Bolton (1994) and Palacio & Fernandéz (2003). The classification proposed by Bolton (2003) was used to the subfamilies. The ants were identified to species level whenever possible through taxonomic keys and genera revisions 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.

4.3.4. Statistical analyses

For the analysis of composition, we investigated the spatial differences in ant assemblages in the four phytophysiognomies of Restinga, through multivariate analysis with the program Past (Hammer, 2001). In a first step we plotted a two dimensional map with a non-metric multidimensional scaling (NMDS). The data that generated such map were a binary matrix (ant species absence or presence), and the dissimilarity were calculated by Bray-Curtis index of dissimilarity. The Bray-Curtis index is the more appropriate for multivariate statistic because it is less affected by the numbers of rare species in the samples (Krebs, 1999).

The second step was a one-way Analysis of Similarity (one way ANOSIM), performed by 10,000 permutations. This analysis establishes whether there were significant differences of species composition between phytophysiognomies through the comparison of the differences among the average rank similarities between samples within a phytophysiognomy and between samples in distinct phytophysiognomies. This analysis results in an R statistic, which is the measure of dissimilarity between sites. Values of R close to zero indicate low dissimilarity while values of R closer to 1 indicate high dissimilarity (Clarke & Green, 1988). The ANOSIM was also calculated using the similarity index of Bray-Curtis and each R-value has a corresponding p-value.

Finally, we carried out the similarity percentage test (SIMPER). This test allows determining which species contribute more to discriminate between different assemblages, i.e. which species were good discriminators of the differences in composition among sites (Clarke, 1993). The SIMPER analysis gives the percentage of the dissimilarity between sites (phytophysiognomies), presenting the percentage of contribution of each species to this dissimilarity. The Bray-Curtis index was also used here (Clarke, 1993).

4.4. Results

In all sampled phytophysiognomies, we collected 71 ant species, from 21 genera and seven subfamilies. Myrmicinae was the most speciose subfamily, with 41 species, followed by Formicinae (13 species), Ponerinae (eight species) and Dolichoderinae with six species. The Subfamilies Ecitoninae, Pseudomyrmecinae and Ectatomminae were the least speciose with only one species every (Appendix 1).

Ant species composition differed among phytophysiognomies (General ANOSIM, R=0.4633, p<0.0001, Figure 3). The ANOSIM comparisons between each pair of phytophysiognomies are shown in Table 1. The phytophysiognomies were more similar to the adjacent ones than to more distant ones. The SIMPER test also confirmed that more distant phytophysiognomies are more dissimilar (Table 2). However, the stress value of the NMDS ordination was 0.22 and there are recommendations that the stress values should be lower than 0.2, because data above this value could be difficult to interpret (Clarke, 1993). Nonetheless, according to this author, these guidelines are over-simplistic because stress tends to increase with increasing numbers of samples (Clarke, 1993). To determine this, a further test was carried out removing points in the first three phytophysiognomies, and the values of stress gradually decreased.

Table 3 shows the ant species that contributed more for the dissimilarity indicated by SIMPER for all phytophysiognomies combined. The 13 species listed in Table 3 determined more than 50% of the dissimilarity between the phytophysiognomies.

4.5. Discussion

Our data support the hypothesis that the composition of species of ants respond to vegetation zonation. At least three distinct groups were formed and the R-values support this grouping: (i) Frontal Dunes (FD), (ii) Lagoon, marsh and pits (LMP) and (iii) Restinga Forest (RF). The Internal Dunes showed a tendency for separation, but had a low R value in comparison to Frontal Dunes and an intermediate value compared to Lagoons, marsh and pits. Thus, it appears that the Internal Dunes ant fauna is a pool of the last two phytophysiognomies. Several characteristics occurring in FD and LMP are recurrent in ID, such as the species of the flora and physical and chemical environment. The sand dunes that occur in FD are also common in ID; environments similar to those of LMP are formed in ID. Likewise, ants displayed a similar trend, and most species present in the FD occurred also in ID. *Acromyrmex striatus*, *Pogonomyrmex naegelli* and *Camponotus cameranoi,* are examples of these. According to the ANOSIM analysis, FD and ID were more similar than ID and LMP (Table 1). Therefore, our results indicate that the composition of ant communities was correlated to the phytophysiognomies.

Daniel (2006) studied the phytosociology and floristic of herbaceous and shrubby Restinga of the Morro dos Conventos, and found that plant species occurred in patches, with restrict species occurring in determined habitats and anywhere else. This response was attributed to environmental factors, such as topography and groundwater level. Likewise, the ant species composition displayed a similar trend. The same pattern was also found in arid and semi-arid deserts in Mexico (Rojas & Fragoso, 2000; Wenninger & Inouye, 2008).

The vegetation is a main factor affecting the composition and structure of the ant communities in dry environments (Rojas & Fragoso 2000, Wenninger & Inouye, 2008). The role of plants on ants and many others insect communities is linked to the availability of resources and conditions (Ribas *et al.*, 2003; Leal 2003; Vargas *et al.*, 2007). In fact, vegetation determines the assemblage composition and the interactions occurring there, because each species has its intrinsic needs of resources and conditions (Carroll & Jazen, 1973; Ribas & Schoereder, 2002). Therefore, changes in the structure of plant communities should result in changes of composition of organisms living on it. Our results support this hypothesis.

Acromyrmex striatus is an example of the above hypothesis. This species is a fungus-growing ant of the Attini tribe, foraging on grasses and small herbaceous vegetation, preferentially in open habitats (Lopes, 2005). Accordingly, *A. striatus* was more common (see mean abundance, Table 3) at sites with sparse vegetation and open areas, in FD and ID, which display similar environments, than in LMP, which has dense vegetation and few open areas. Furthermore, *A. striatus* was completely absent in RF, which lacks open areas.

Similarly, *Mycetophylax simplex* was sampled only in FD. Albuquerque *et al.* (2005), studying the patterns of distribution of this species in Restinga found that the spatial arrangement of their nests were primarily determined by physical characteristics of the environment, because this species was never found in habitats other than Restinga open dunes. These authors explain that the occurrence of this ant species is possibly determined by the conditions and availability of resources rather than by competition.

Although the interespecific interactions cannot be completely over-considered, there are evidences against the competition as a general patterning force (Ribas & Schoereder, 2002; Andersen, 2008) for example, the co-occurrence of ants described as behavioral dominants. Moreover, it was empirically demonstrated by Ribas & Schoereder (2002) that competition may not be the unique process structuring ant assemblages.

Furthermore, competition may be weak in Restinga if dominant ants occur in patches (Andersen, 2008). In this case, the absence of dominant ants in some sites would open space for the occurrence of other non-dominant species. This would occur because dominant species do not occur in all areas in phytophysiognomy, and thus the occurrence of the species must be actually guided by variations in conditions and resources. Thus, the above pattern suggests that species-sorting mechanisms (Andersen, 2008) provide important structuring forces through local niche partitioning in Restinga. Andersen

(2008) proposes that distinct ant foundress queens, similarly as plant recruitment processes, choose randomly a suitable habitat and hold it once the colony is established. Hence, we expect that small changes in local conditions, such as the increase of open areas, would allow the establishment of species (i.e. *Acromyrmex striatus* and *Mycethopylax simplex* that occur only in uncovered soils). This has been observed for *Pogonomyrmex badius*, which build their nests deep in the soil, and their establishment is affected by the level of water table (Tschinkel, 2004). Likewise, the invasive argentine ant *Linephitema humile* is strongly affected by soil type (Way *et al.*, 1997).

Other studies also show changes in ant species composition among different habitat types (Lassau & Hochuli, 2004; Lassau *et al.*, 2005; Hill *et al.*, 2008; Barrow & Parr, 2008). Although these authors reported that the differences may be an outcome of interactions, mainly resource competition, we think that competition may not be the only factor to explain our results. Moreover, ant assemblage in arid and semi-arid environments was reported to be the outcome of negative interspecific interactions among heat-intolerant ants, which are dominants, and heat-tolerant ants, which are subordinates (Retana & Cerdá, 2000). However, other authors have reported that this distinction is not the result of competition, and believe that this may be a result of a temporal niche partitioning due to species microclimate preference (Kronfeld-Schor & Dayan, 2003).

Overall, 13 species contributed to 50.43% of the difference among phytophysiognomies, and *Solenopsis saevissima* was the ant species that better explains the habitat distinction. This species is highly prevalent in LMP and FD habitat, less abundant in ID and absent in RF. *Camponotus rufipes* showed a similar trend, with higher prevalence in LMP and absence in RF. These species were expected to be very common since they are *taxa* with generalist behavior (Silvestre *et al.*, 2003). According to Wilson (1976) *Camponotus*, *Solenopsis* and *Pheidole* form the most abundant genera of the world. These species have underground nests with a large amount of individuals that forage actively in mass. In addition, some species of these genera are extremely aggressive in interspecific interactions (Silvestre *et al.*, 2003). The presence of some ant species in given habitats is possibly related to their specific needs, and gives some valuable information regarding their biology.

Only six ant species were ubiquitous in Morro dos Conventos Restinga, occurring in all phytophysiognomies studied here. *Brachymyrmex cordemoyi* was the most abundant. This genus is characterized by an omnivore habit in respect to alimentary behavior, besides nesting in several sites and avoiding aggressive interspecific interactions (Delabie *et al.*, 2000; Silvestre *et al.*, 2003). The wide range of occurrence of this small and omnivore ant species have also been observed in Mexico Deserts (Rojas & Fragoso, 2000).

Confirming the hypotheses that vegetation is the main factor determining local composition and diversity in Restinga ecosystems, cryptic species were sampled only in environments that provide habitats favorable to their demands for foraging and nesting. Species of the *Hypoponera*, *Strumigenys*, *Gnamptogenys* genera occurred only in LMP, RF and few in ID, as well as *Trachymyrmex* and *Cyphomyrmex*. The former are species with specialized behavior of foraging and nesting. They have small colonies with limited number of individuals living in litter. The latter use organic matter, faeces and decomposing animals to cultivate in moist litter habitats their "garden" or "sponge" of the symbiontic fungus on which they feed (Silvestre *et al.*, 2003). In Morro dos Conventos Restinga, the litter is very scarce due to the absence of arboreal and shrubby plant species in some phytophysiognomies, for example, Frontal Dunes. Furthermore, these environments are under strong winds that impair the formation of a persistent litter. Not only in Restinga, but in Caatinga biome where the litter is also scarce, the distribution and diversity of these species is extremely limited (Leal, 2003). According to some authors (Soares & Schoereder, 2001; Theunis *et al.*, 2005), litter ants have not a territorial behavior, suggesting that habitat suitability, rather than competition, is the main force structuring leaf litter ant assemblages.

The response of the ant communities to particular habitat types has been demonstrated to be related to vegetation complexity, both negatively (Lassau & Hochuli, 2004) and positively (Lassau *et al.*, 2005; Hill *et al.*, 2008). However, the relationship between local-community diversity and assemblage composition may be influenced by factors acting at other scales. Spiesman & Cumming (2008) studying ant communities in northern Florida found that ant community composition was significantly influenced by simultaneous processes acting from local to regional scales. As abiotic and biotic processes differentially affect species composition, their understanding can provide information on how these processes act on local communities. Our study showed the importance of phytophysiognomies in the determination of ant species composition at local scale in Restinga. Moreover, the changes in species composition found for the gradient from the sea to inland stand out the importance of studies about species composition for conservation priorities, mainly in these ecosystems. Restinga has not been adequately prioritized in conservation strategies (Vieira *et al.*, 2008), and the Brazilian law of protection of these environments prioritizes only the first 300 meters from the sea shoreline, which covers just one of the phytophysiognomies studied here.

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4.7. Figures and Tables

Figure 1 – Schematic drawing of the profile Morro dos Conventos Restinga with the four phytophysiognomies sampled in this study.

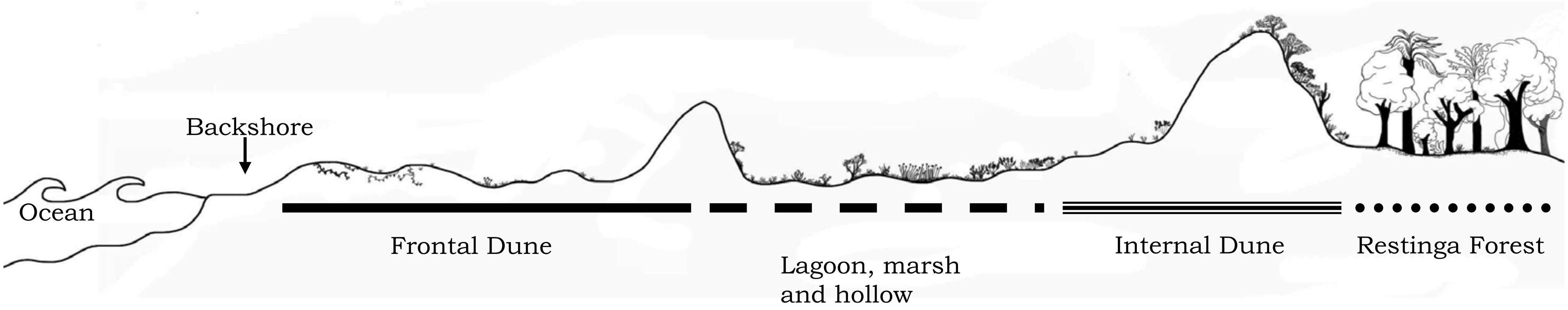

Figure 2 – Pictures of the four habitat types occurring along the studied gradient: frontal dunes (A), lagoons, marsh and pits (B), internal dunes (C) and restinga forest (D).

Figure 3 – Non-metric multidimensional scaling ordination for ground-dwelling ant species composition in Morro dos Conventos Restinga. RF (◆) = Restinga Forest, ID (■) = Internal Dune, LMP (●) = Lagoon, marsh and pits, FD (▲) = Frontal Dune. Stress value= 0.22

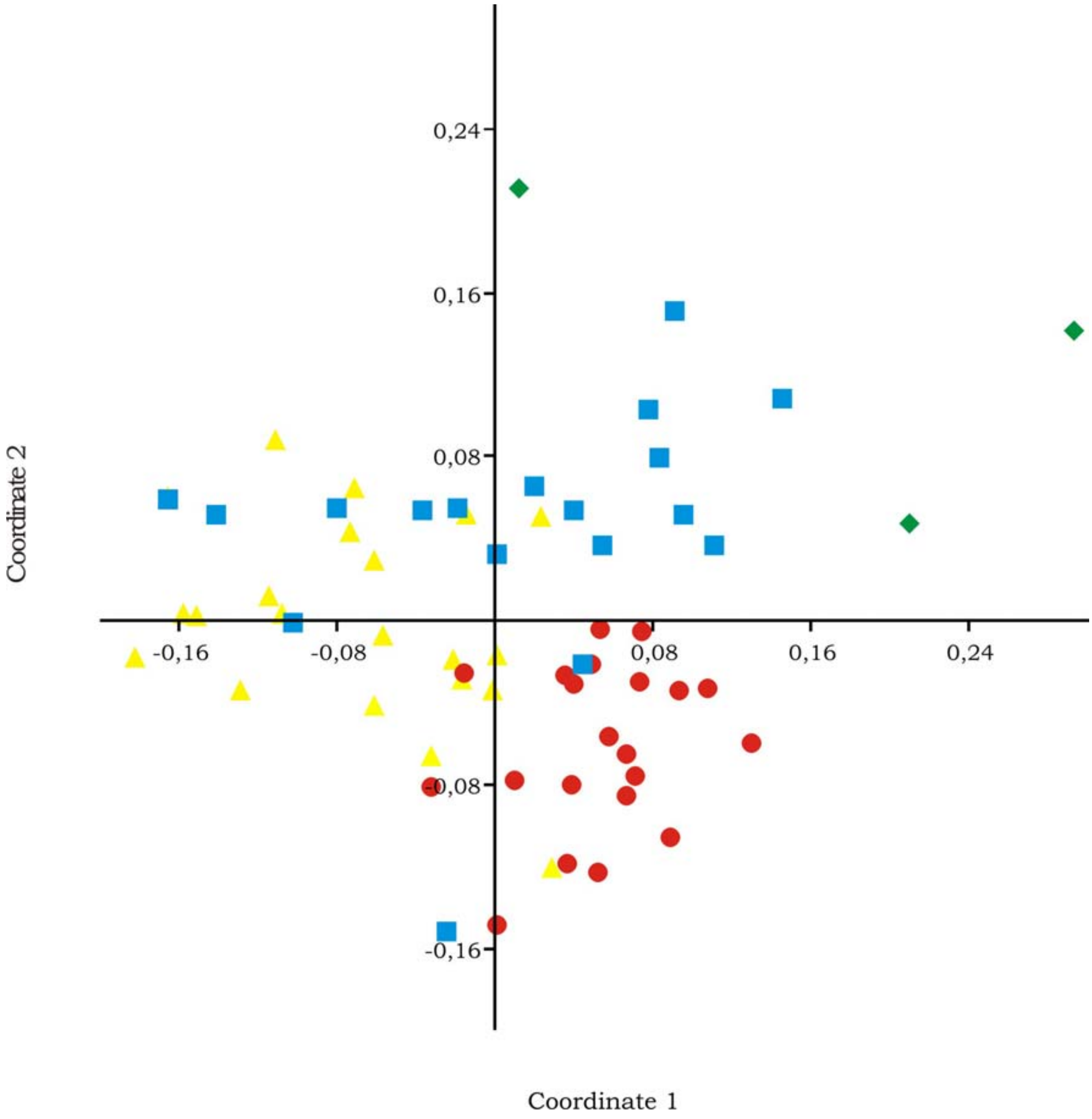

Table 1 – The ANOSIM comparisons of the ant species composition at the four phytophysiognomies in Morro dos Conventos Restinga.

	Frontal Dunes	**Lagoon, swamp and pits**	**Internal Dunes**	**Restinga Forest**
Frontal Dunes	-	0.531 (p<0.001)	0.211 (p<0.001)	0.93 (p<0.001)
Lagoon, swamp and pits		-	0.4716 (p<0.001)	0.9611 (p<0.001)
Internal Dunes			-	0.5377 (p<0.001)
Restinga Forest				-

Table 2 – The SIMPER dissimilarity between phytophysiognomies.

	Frontal dunes	**Lagoon, marsh and pits**	**Internal dunes**	**Restinga Forest**
Frontal Dunes	-	71.93 %	68.06 %	92.33 %
Lagoon, marsh and pits		-	73.63 %	89.23 %
Internal Dunes			-	85.25 %
Restinga Forest				-

Table 3 – Ant list contribution to average dissimilarities between the phytophysiognomies determined by SIMPER at Morro dos Conventos Restinga, Santa Catarina, Brazil. FD = Frontal Dune, LMP = Lagoon marsh and pits, ID = Internal Dune, RF = Restinga Forest.

Taxon	**Contribution**	**Cumulative %**	**Means abundance**			
			FD	**LMP**	**ID**	**RF**
Solenopsis saevissima	3.344	4.547	0.636	0.818	0.0556	0
Camponotus rufipes	3.249	8.965	0.364	0.909	0.0556	0
Pheidole sp. 01	3.19	13.3	0.682	0	0.389	0.333
Dorymyrmex pyramicus	3.052	17.45	0.909	0.318	0.611	0
Brachymyrmex cordemoyi	2.949	21.46	0.455	0.727	0.5	0.333
Linepithema neotropicum	2.888	25.39	0.5	0.591	0.722	0.333
Pheidole sp. 03	2.883	29.31	0.0455	0.636	0.5	0.333
Wasmannia auropunctata	2.849	33.19	0.455	0.591	0.389	0
Solenopsis sp. 2	2.784	36.97	0.318	0.591	0.389	0
Camponotus blandus	2.751	40.72	0.364	0.455	0.5	0
Mycetophylax morschi	2.505	44.12	0.182	0.318	0.556	0
Pogonomyrmex naegelli	2.386	47.37	0.0909	0.682	0.0556	0
Pheidole sp. 02	2.254	50.43	0.136	0.591	0.0556	0
Camponotus pr. *cameranoi*	2.12	53.32	0.364	0.0455	0.333	0.333
Brachymyrmex pr. *obscurior*	2.053	56.11	0	0.409	0.389	0
Solenopsis sp. 9	1.947	58.75	0.182	0.364	0.222	0
Paratrechina pr. *fulva*	1.938	61.39	0.136	0.5	0.0556	0
Acromyrmex striatus	1.937	64.02	0.318	0.0909	0.278	0
Camponotus melanoticus	1.788	66.46	0.0455	0.455	0.222	0
Solenopsis sp. 3	1.713	68.78	0.0455	0.318	0.167	0.667
Odontomachus chelifer	1.588	70.94	0	0.136	0.278	1
Cyphomyrmex rimosus	1.34	72.77	0.0455	0.273	0.111	0.333
Mycetophylax simplex	1.249	74.46	0.273	0	0	0
Camponotus crassus	1.19	76.08	0	0.364	0	0
Linepithema humile	1.095	77.57	0.0455	0.273	0	0
Pachycondyla striata	0.9816	78.91	0.0455	0.136	0	0.667
Solenopsis sp. 8	0.9622	80.21	0	0.136	0.222	0
Pheidole sp. 15	0.8798	81.41	0.0455	0.227	0	0
Paratrechina sp. 1	0.8491	82.57	0	0.0455	0.222	0.333
Pheidole sp. 04	0.8272	83.69	0	0.136	0.111	0.333
Pheidole (gr. Flavens) sp. 05	0.826	84.81	0	0.0455	0.111	0.667
Acromyrmex pr. *laticeps*	0.7172	85.79	0	0.136	0.0556	0.333
Solenopsis sp. 4	0.6075	86.62	0	0	0.167	0.333
Trachymyrmex iheringi	0.6041	87.44	0	0.0455	0.111	0.333

Taxon	**Contribution**	**Cumulative %**	**Means abundance**			
			FD	**LMP**	**ID**	**RF**
Gnamptogenys striatula	0.5621	88.2	0	0	0.0556	0.667
Pheidole sp. 13	0.5101	88.89	0	0	0.111	0.333
Solenopsis sp. 6	0.5009	89.58	0.136	0	0	0
Wasmannia sulcaticeps	0.466	90.21	0	0.0455	0.0556	0.333
Hypoponera pr. *opaciceps*	0.4489	90.82	0.0455	0.0909	0	0
Trachymyrmex holmgreni	0.4277	91.4	0	0.136	0	0
Pheidole sp. 07	0.4252	91.98	0	0.0909	0.0556	0
Acromyrmex sp7	0.323	92.42	0	0.0909	0	0
Acromyrmex ambiguus	0.3133	92.85	0.0909	0	0	0
Acromyrmex (Moellerius) sp. 4	0.3047	93.26	0	0.0909	0	0
Cyphomyrmex strigatus	0.2804	93.64	0	0.0455	0.0556	0
Strumigenys louisianae	0.2753	94.02	0	0.0909	0	0
Hypoponera foreli	0.2433	94.35	0	0	0	0.333
Pheidole sp. 14	0.2433	94.68	0	0	0	0.333
Pheidole sp. 06	0.2433	95.01	0	0	0	0.333
Wasmannia affinis	0.2171	95.3	0	0	0	0.333
Hypoponera reichenspergeri	0.2171	95.6	0	0	0	0.333
Monomorium pharaonis	0.2034	95.87	0.0455	0	0	0
Labidus coecus	0.1963	96.14	0	0	0	0.333
Strumigenys crassicornis	0.1963	96.41	0	0	0	0.333
Linephitema leucomelas	0.1963	96.68	0	0	0	0.333
Linepithema iniquum	0.1963	96.94	0	0	0	0.333
Acromyrmex balzani	0.1943	97.21	0	0.0455	0	0
Paratrechina sp. 3	0.1817	97.45	0	0.0455	0	0
Hypoponera sp. 6	0.1707	97.69	0	0.0455	0	0
Crematogaster sp. 2	0.1527	97.89	0	0	0.0556	0
Camponotus trapezoideus	0.1527	98.1	0	0	0.0556	0
Pheidole sp. 16	0.1524	98.31	0	0.0455	0	0
Crematogaster moelleri	0.1455	98.51	0	0	0.0556	0
Pheidole sp. 17	0.1455	98.7	0	0	0.0556	0
Pseudomyrmex pr. *laevivertex*	0.1455	98.9	0	0	0.0556	0
Pachycondyla harpax	0.1455	99.1	0	0	0.0556	0
Strumigenys denticulata	0.1377	99.29	0	0.0455	0	0
Dorymyrmex brunneus	0.1377	99.47	0	0.0455	0	0
Hypoponera sp. 4	0.1331	99.66	0	0	0.0556	0
Camponotus punctulatus	0.1277	99.83	0	0	0.0556	0
Myrmelachista gallicola	0.1256	100	0	0.0455	0	0

Appendix 1 – List of ant species collected in each phytophysiognomy in Morro dos Conventos Restinga, Santa Catarina, Brazil.

Taxa	**Frontal Dune**	**Lagoon, march and pits**	**Internal Dune**	**Restinga Forest**
DOLICHODERINAE				
Dorymyrmex brunneus		**X**		
Dorymyrmex pyramicus	**X**	**X**	**X**	
Linephitema leucomelas				**X**
Linepithema humile	**X**	**X**		
Linepithema iniquum				**X**
Linepithema neotropicum	**X**	**X**	**X**	**X**
ECITONINAE				
Labidus coecus				**X**
FORMICINAE				
Brachymyrmex cordemoyi	**X**	**X**	**X**	**X**
Brachymyrmex pr. *obscurior*		**X**	**X**	
Camponotus trapezoideus			**X**	
Camponotus melanoticus	**X**	**X**	**X**	
Camponotus punctulatus			**X**	
Camponotus blandus	**X**	**X**	**X**	
Camponotus crassus		**X**		
Camponotus pr. *cameranoi*	**X**	**X**	**X**	**X**
Camponotus rufipes	**X**	**X**	**X**	
Myrmelachista gallicola		**X**		
Paratrechina pr. *fulva*	**X**	**X**	**X**	
Paratrechina sp. 1		**X**	**X**	**X**
Paratrechina sp. 3		**X**		
MYRMICINAE				
Acromyrmex (Moellerius) sp. 4		**X**		
Acromyrmex ambiguus	**X**			
Acromyrmex balzani		**X**		
Acromyrmex pr. *laticeps*		**X**	**X**	**X**
Acromyrmex sp. 7		**X**		
Acromyrmex striatus	**X**	**X**	**X**	
Crematogaster moelleri			**X**	
Crematogaster sp. 1			**X**	
Cyphomyrmex rimosus	**X**	**X**	**X**	**X**
Cyphomyrmex strigatus		**X**	**X**	

Taxa	**Frontal Dune**	**Lagoon, march and pits**	**Internal Dune**	**Restinga Forest**
Monomorium pharaonis	**X**			
Mycetophylax morschi	**X**	**X**	**X**	
Mycetophylax simplex	**X**			
Pheidole sp. 01	**X**		**X**	**X**
Pheidole sp. 02	**X**	**X**	**X**	
Pheidole sp. 03	**X**	**X**	**X**	**X**
Pheidole sp. 04		**X**	**X**	**X**
Pheidole (gr. Flavens) sp. 05		**X**	**X**	**X**
Pheidole sp. 06				**X**
Pheidole sp. 07		**X**	**X**	
Pheidole sp. 13			**X**	**X**
Pheidole sp. 14				**X**
Pheidole sp. 15	**X**	**X**		
Pheidole sp. 16		**X**		
Pheidole sp. 17			**X**	
Pogonomyrmex naegelli	**X**	**X**	**X**	
Solenopsis saevissima	**X**	**X**	**X**	
Solenopsis sp. 2	**X**	**X**	**X**	
Solenopsis sp. 3	**X**	**X**	**X**	**X**
Solenopsis sp. 4			**X**	**X**
Solenopsis sp. 6	**X**			
Solenopsis sp. 8		**X**	**X**	
Solenopsis sp. 9	**X**	**X**	**X**	
Strumigenys crassicornis				**X**
Strumigenys denticulata		**X**		
Strumigenys louisianae		**X**		
Trachymyrmex holmgreni		**X**		
Trachymyrmex iheringi		**X**	**X**	**X**
Wasmannia affinis				**X**
Wasmannia auropunctata	**X**	**X**	**X**	
Wasmannia sulcaticeps		**X**	**X**	**X**
ECTATOMMINAE				
Gnamptogenys striatula			**X**	**X**
PONERINAE				
Hypoponera foreli				**X**
Hypoponera pr. *opaciceps*	**X**	**X**		

Taxa	**Frontal Dune**	**Lagoon, march and pits**	**Internal Dune**	**Restinga Forest**
Hypoponera reichenspergeri				**X**
Hypoponera sp. 4			**X**	
Hypoponera sp. 6		**X**		
Odontomachus chelifer		**X**	**X**	**X**
Pachycondyla harpax			**X**	
Pachycondyla striata	**X**	**X**		**X**
PSEUDOMYRMECINAE				
Pseudomyrmex pr. *laevivertex*			**X**	
TOTAL	**28**	**46**	**42**	**27**

5. Considerações Finais

Os resultados do presente trabalho confirmam a importância da vegetação como um dos fatores determinantes da riqueza e distribuição de espécies (Ribas *et al.*, 2003; Vargas *et al.*, 2007; Wenninger & Inouye, 2008). Especialmente em ambientes áridos e semi-áridos, onde padrões muito semelhantes aos encontrados em nosso estudo são apresentados por Rojas & Fragoso (2000) para o deserto de Mapimí no México, tal importância se faz notar. Embora estes autores utilizem dados da literatura sobre a vegetação da área de estudo para as comparações, a relação encontrada em nosso trabalho é empiricamente demonstrada e confirmada pelo estudo florístico e fitossociológico de Daniel (2006) para a Restinga do Morro dos Conventos.

O pressuposto de que a riqueza de espécies de formigas aumenta com a distância do mar foi aceito, bem como a relação entre a distância do mar e a riqueza de espécies de plantas. Embora bem conhecida, a relação entre distância do oceano e riqueza de plantas, para o nosso conhecimento, não havia ainda sido testada estatisticamente através de dados quantitativos.

Nossa hipótese de que a riqueza de espécies de formigas responde a riqueza de espécies de plantas também foi aceita, bem com a hipótese da relação entre a densidade vegetal e de serapilheira (cobertura do solo) e a riqueza de espécies de formigas. Embora a riqueza de espécies de plantas e a densidade vegetal não tenham sido correlacionadas, os três fatores podem ter influenciado a riqueza de espécies de formigas por meio de dois processos envolvendo condições e recursos. Riqueza e densidade vegetal podem representar aumento de recursos disponíveis, tais como fontes alimentares e locais para nidificação. Assim, maior quantidade de recursos poderia refletir em um maior número de espécies generalistas. Já riqueza de espécies de plantas pode influenciar o aumento de espécies especialistas pelo aumento da variedade de recursos (Ribas *et al.*, 2003). De outro modo, o aumento da riqueza e da densidade vegetal direta ou indiretamente condiciona a ocorrência de espécies através da criação de microhabitats adequados. Isto parece ser verdade para ambientes de Restinga, uma vez que variações na temperatura e umidade mudam significativamente em locais completamente abertos (dunas) em comparação a locais extremamente fechados (mata de restinga) (Franco *et al.*, 1984; Yu *et al.*, 2008).

Embora atribuído como um dos principais fatores influenciando a riqueza e distribuição de espécies de plantas (Wilson & Sykes, 1999; Maun &

Perumal, 1999), a salinidade não se mostrou como um fator importante sobre a riqueza de espécies de formigas. Mesmo sendo um dos fatores limitantes do desenvolvimento de plantas em Restinga, a concentração de sal parece não ser o principal fator responsável pela zonação vegetacional destes ambientes. O soterramento, causado pela erosão e regimes de ventos vêm sendo indicado como o principal fator determinante da zonação da vegetação em ambientes costeiros, bem como em ambientes lacustres (Maun, 1998; Maun & Perumal, 1999; Gilbert *et al.*, 2008).

O regime de ventos e o soterramento são fatores abióticos que de maneira pouco provável afetam a riqueza e a distribuição de espécies de formigas. Embora considerados organismos modulares (Andersen, 2008), as formigas são organismos altamente móveis, podendo realizar a migração de toda a colônia para outros locais mais favoráveis, caso necessário. No entanto, por serem os principais responsáveis pelo zoneamento da vegetação, estes fatores influenciam a distribuição de espécies de formigas de maneira indireta. Isto pode ser verdade uma vez que nós encontramos que a composição da comunidade de formigas responde a zonação vegetal da Restinga.

Nossos resultados sugerem que fitofisionomias distintas apresentam composições particulares de espécies de formigas. Assim, fitofisionomias mais próximas entre si ou mais semelhantes quanto à composição de espécies de plantas e condições ambientais (áreas abertas ou fechadas) apresentam maior similaridade do que ambientes mais distantes ou mais diferentes. A composição mudou ao longo do gradiente vegetacional, que varia do oceano para o interior do continente. Evidentemente, diferentes fatores podem estar influenciando a distribuição das espécies entre as diferentes fitofisionomias, e a vegetação provavelmente é o principal fator determinando este padrão.

Além disso, nossos resultados evidenciam uma preferência de determinadas formigas por diferentes tipos vegetacionais. Como descrito por outros autores (Fowler & Claver, 1991; Lopes, 2005), espécies como *Acromyrmex striatus* são espécies que nidificam especialmente em locais abertos e com alta incidência de luz solar. Esta espécie ocorreu apenas em áreas de dunas abertas, bem como as espécies *Mycetophylax simplex* e *Mycetophylax morschi.* Além disso, estas duas últimas espécies também são descritas como espécies essencialmente de dunas de Restinga do Atlântico Sudeste (Diehl-Fleig *et al.*, 2007; Kliengenberg *et al.,* 2007). Estes autores ressaltam que estas duas espécies ocorrem simpatricamente no conjunto de dunas frontais, onde *M. simplex* ocorrem no conjunto de dunas mais próximas à praia, sem sobreposição de distribuição. A despeito disto, nossos dados evidenciam que colônias de *M. morschi* estão presentes nas Restingas do Atlântico Sul e também podem ocorrer nas dunas mais próximas da praia.

Os dados obtidos com o presente estudo contribuem para o entendimento dos processos ecológicos envolvidos sobre os padrões de ocorrência e distribuição de espécies de formigas em Restinga. Além disso, fornecem informações para o uso em programas de planejamento e ocupação de áreas remanescentes de Restinga. Como, de modo geral, as Restingas são ambientes geologicamente recentes e geomorfologicamente distinto, estudos em outras escalas são interessantes para o entendimento da contribuição de fatores biogeográficos sobre a riqueza e distribuição das comunidades de formigas em ambientes costeiros.

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