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Dissertação de Mestrado

Fatores ambientais que estruturam a mirmecofauna nos Campos Sulinos

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Porto Alegre, janeiro de 2019

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"Even as empiricism is winning the mind,

transcendentalism continues to win the heart."

Edward O. Wilson

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Sumário

Resumo

Formigas são insetos sociais e sedentários, essa condição confere certas particularidades no estudo de comunidades ecológicas. Graças à sua organização em colônias, o grupo possui, de forma geral, capacidade de dispersão limitada. Assim, comunidades mirmecológicas respondem facilmente a fenômenos na escala local, tornando-as valiosos bioindicadores, especialmente em ecossistemas amplamente impactados pela ação humana, como os Campos Sulinos. O pastejo por gado bovino, atividade muito comum nesses ambientes, está intrinsecamente ligado à biodiversidade local. Por meio da seleção alimentar, bem como os demais efeitos ligados à sua presença (e.g. pisoteio, deposição de urina), o gado modifica o campo, gerando complexidade estrutural no ambiente. Seu efeito sobre a vegetação, por sua vez, pode acarretar em mudanças nos recursos e condições disponíveis para a mirmecofauna. É bem estabelecido em mirmecologia que comunidades de formigas se estruturam, ao menos em parte, devido a processos competitivos, que se dão usualmente pelo fenômeno da dominância ecológica. Entretanto, sabe-se também que a dominância em formigas é geralmente regulada pelas condições ambientais, que afetam o estabelecimento e expansão das colônias. Uma possível maneira de explicar como o ambiente estrutura as comunidades ecológicas é a metáfora dos filtros ambientais, em que uma espécie deve ser capaz de tolerar as condições de um determinado ambiente para que possa se estabelecer. Nesta perspectiva, o presente estudo busca compreender por meio da metáfora de filtros ambientais, como se estruturam comunidades mirmecológicas em campos do bioma Pampa no sul do Brasil. Verificamos se as condições ambientais: condição hidrológica, heterogeneidade ambiental, abertura de microhabitat e diversidade de recursos, eram preditoras da composição de espécies de formigas definida pelas abundâncias ou pelas incidências. Também testamos se as mesmas variáveis eram preditoras da riqueza e abundância total de formigas. Além disso, avaliamos se há segregação temporal das comunidades mirmecológicas entre os períodos diurno e noturno.

Palavras-chave: Filtro ambiental, estrutura de habitat, mirmecofauna, estruturação de comunidades, competição

Abstract

Ants are social and sedentary insects, such condition ensures some particularities in the study of ecological communities. Due to colony organization, ants have in general, low dispersibility. Thus, myrmecological communities usually respond to local scale phenomena, which make them valuable bioindicators, especially in highly human impacted ecosystems, such as *Campos Sulinos* grasslands. Cattle grazing is a very common activity in those environments, also intrinsically linked to local biodiversity. Through feeding selection behavior, as well as other effects due to its presence (e.g. trampling, urine deposition), cattle modifies the vegetation, generating structural complexity, which can lead to changes in conditions and resources available to myrmecofauna. In myrmecology, it is well established that ant communities assembly, at least in part, due to competition outcomes, which usually occur through ecological dominance phenomena. However, it is also known that dominance in ants is restricted to environmental conditions that, in general, constraints colony establishment and expansion. A possible way to explain how the environment contributes in assembly process is by using the environmental filter metaphor, in which a species must be able to tolerate given environmental conditions in order to establish. Therefore, through the environmental filter metaphor, the present study aims to understand myrmecological community assembly in grasslands of the *Pampa* biome in southern Brazil. We verified if environmental conditions: hydrological condition, environmental heterogeneity, microhabitat openness and resource diversity, are predictors of ants species composition defined by abundance and incidence. We tested as well, if the same variables are predictors of ants abundance and species richness. Further, we verified if there is temporal segregation between nocturnal and diurnal periods in those myrmecological communities.

Key-words: Environmental filter, habitat structure, myrmecofauna, community assembly, competition

Introdução geral

O que é estrutura de comunidade biológica? (breve histórico e aspectos teóricos)

Embora a palavra nicho (no contexto ecológico) tenha surgido muito cedo (Grinnell 1917), somente 40 anos depois Hutchinson (1957) criou a primeira definição de nicho como sendo propriedade do organismo, e sinteticamente, definiu-o como a distribuição do conjunto de necessidades e limitações de um organismo no ambiente. A partir dessa definição, Hutchinson (1959) propôs que a diversidade de espécies resultaria da ocupação de nichos distintos no ambiente, mas que no entanto, espécies diferentes poderiam compartilhá-los (competir). MacArthur & Levins (1967) seguindo esse preceito, propuseram que se duas ou mais espécies ocupassem nichos semelhantes, haveria um limite de similaridade entre esses nichos até o qual as espécies poderiam coexistir, partilhando dos mesmos recursos. No entanto, se fossem suficientemente semelhantes, seria aplicado o princípio de Gause (1934), nomeado por Hardin (1960) de princípio da exclusão competitiva, onde a melhor competidora entre as espécies eliminaria as demais.

Diamond (1975), diante da ideia de que as comunidades seriam resultantes da adequação das espécies ao ambiente, somada às interações entre elas, foi o primeiro a sugerir que haveria regras determinísticas para a estruturação de comunidades “assembly rules”. Essas regras definiriam padrões locais de organização espacial e trófica das comunidades a partir de processos ecológicos como competição, predação e ocupação de nichos. A partir das ideias de Diamond, surgiu o termo filtro ambiental, como uma metáfora para explicar a estruturação de comunidades em passos discretos (Bazzaz, 1991; Belyea & Lancaster, 1999; Noble & Slatyer, 1977; van der Valk, 1981; Woodward & Diament, 1991, Weiher & Keddy, 1999), onde haveria restrições que determinariam a organização observável das comunidades. Dessa forma, a partir de um pool de espécies regional, essas restrições (filtros) selecionariam aquelas espécies que pudessem superar os processos de dispersão, estabelecimento e interação.

Logo no início do século XXI, Chesson (2000), atendo-se às relações competitivas e à assimetria de nicho, contribuiu com o avanço no campo da estruturação de comunidades com uma teoria da coexistência, que seria regulada por dois tipos de mecanismos: 1) os estabilizadores, que aumentariam as interações negativas intraespecíficas, levando à autorregulação das competidoras superiores, permitindo uma estabilidade na coexistência das espécies competitivamente inferiores (e.g. particionamento de nicho), e 2) os equalizadores, que diminuiriam a diferença de *fitness* existente entre as espécies (e.g. coexistência mediada por predador). É importante ressaltar que o emprego do termo *fitness* não é o mesmo que se usa em estudos evolutivos (ao nível de indivíduo) mas, contextualmente atribuído às espécies para expressar as diferenças existentes na taxa de ocupação de nichos e reprodução.

No entanto, a utilização de modelos nulos (variação devida a estocasticidade) levaram Hubbell (2001) a contestar os padrões determinísticos da estruturação de comunidades. Em sua "teoria neutra unificada da biodiversidade e biogeografia", Hubbell sugere que todas as espécies seriam competidoras potencialmente iguais, e que a estruturação das comunidades poderia se dar por estocasticidade demográfica, em contraste com a teoria determinista de particionamento de nichos.

Com o advento da ecologia filogenética e funcional, passamos a analisar a estruturação de comunidades considerando o papel importante da história evolutiva e dos atributos funcionais, ajudando-nos a compreender a organização estrutural das comunidades biológicas e possíveis mecanismos causais. Segundo Peterson et al. (1999), comunidades nas quais os caracteres são estruturados filogeneticamente teriam conservatismo de nicho ecológico. Webb et al. (2002)

sugeriu que essas comunidades poderiam ser formadas por meio de dois processos distintos: 1) filtro ambiental, onde haveria a formação um padrão filogenético e funcional agregado, uma vez que todas as espécies seriam submetidas a uma mesma condição ecológica ou 2) exclusão competitiva, sob a qual se formaria um padrão disperso (filogenético e funcional), pois as espécies competiriam por nichos específicos, sendo sua proximidade relativa à função desempenhada. Entretanto, na ausência de conservantismo de nicho, filtros ambientais promoveriam a seleção de espécies menos aparentadas (filogeneticamente dispersas), uma vez que os caracteres não refletiriam na filogenia dos organismos, mas apenas em sua função (funcionalmente agregadas). Já a exclusão competitiva, em um cenário mais caótico, poderia dever-se a mais de um fator nesse caso: com seleção de espécies mais próximas devido a funções semelhantes (padrão filogenético agregado e funcional disperso) ou indiferente à filogenia (padrão aleatório da estrutura filogenética e funcional).

Nesta perspectiva, Menezes et al. (2016) em um artigo de revisão, afirmam que é preciso ter cautela ao inferir relações causais na estruturação de comunidades, pois essa estruturação pode ser dependente de escala geográfica, particularidades ambientais (e.g. intensidade de distúrbios no ecossistema, clima) e de vários fatores, tanto determinísticos (e.g. filogenéticos, funcionais, particionamento de nicho, competição) quanto estocásticos.

A estruturação da mirmecofauna: um problema complexo

Formigas são insetos sociais, e por essa razão respondem ao ambiente de forma muito diferente da maioria dos artrópodes de vida livre; o mesmo distúrbio que causaria uma extinção local por perda de indivíduos em outros organismos, não necessariamente extingue uma colônia de formigas (Lach et al. 2010; Read and Andersen 2000). Uma vez que há poucos indivíduos nas castas reprodutivas, a sobrevivência individual depende diretamente da sobrevivência da colônia (Lach et al. 2010; Wilson 2008). Nesta perspectiva, a organização em colônias torna as formigas verdadeiros superorganismos. Embora esse seja um dos aspectos mais interessantes em mirmecologia, pode ser também um dos mais problemáticos em ecologia.

Em uma revisão da literatura, Soares (2013) mostra que a competição interespecífica pode ser um dos fatores de maior importância na estruturação da mirmecofauna, uma vez que as colônias são sésseis, e geralmente dependentes de recursos semelhantes. Nesse contexto, através da competição, algumas espécies acabam estabelecendo dominância sobre outras (Lach et al. 2010). Além disso, a mirmecofauna dominante usualmente limita o sucesso de forrageamento de espécies competitivamente inferiores aos recursos locais, podendo afetar, como um todo, a estrutura da comunidade em um ambiente (Gibb 2005; Arnan et al. 2011). O efeito desse processo pode ser positivo (e.g. aumentando a riqueza de espécies ao criar nichos para as subordinadas; Andersen 2008), ou negativo (e.g. diminuindo a riqueza de espécies ao dominar, em grande escala, os recursos disponíveis; Hölldobler & Wilson 1990; Parr 2008). No primeiro caso, 1) as espécies dominantes podem ter nichos de ação mais específicos, exercendo uma dominância restrita à proximidade de suas colônias no ambiente (Stringer et al. 2007), ou 2) as espécies dominantes podem excluir as subdominantes (oportunistas que ocupam preferencialmente recursos menos valiosos) (Arnan et al. 2011) de forma que se criam nichos para espécies subordinadas. No segundo caso, as espécies envolvidas geralmente têm grande capacidade de recrutamento (chamam outros membros da colônia) ou são amplamente distribuídas e abundantes no ambiente, extinguindo localmente algumas das demais espécies por exclusão competitiva (Parr 2008).

Nesse contexto, uma forma indireta de estruturação da mirmecofauna é a segregação temporal de nicho. Embora o fenômeno seja pouco estudado, há evidências empíricas de sua existência. Dáttilo et al. (2014) encontraram diferenças entre noite e dia na dinâmica de interações existentes em comunidades de formigas associadas a nectários extraflorais. Albretch & Gotelli (2001) constataram modificações na estrutura de coexistência da mirmecofauna entre os períodos noturno e diurno, embora restrito às estações quentes. Houadria et al. (2015) evidenciaram a presença de segregação temporal especializada em algumas espécies em regiões de floresta tropical. O fenômeno da segregação temporal das comunidades pode ser visto como indiretamente relacionado à competição interespecífica. Pois, se por um lado as espécies subordinadas seriam forçadas a modificar seu nicho em função das dominantes, por outro lado evitariam a interação competitiva exatamente por meio da segregação temporal.

No entanto, embora alguns autores sustentem a hipótese de que a estruturação das comunidades de formigas se dá principalmente por competição interespecífica (Ellwood et al. 2016; Parr 2008), outros sugerem que esta estruturação é resultado da seleção de habitat na fase de recrutamento local (formação de colônias), e não resultado de processos pós-estabelecimento (Andersen 2008), ou ainda, que pode ser estocástica (Ribas and Schoereder 2002). Nesse contexto, fatores ambientais do habitat agem como um filtro, limitando o estabelecimento e sobrevivência das espécies bem como suas interações (Andersen 2008). A estrutura de microhabitat (e.g. heterogeneidade) parece ser importante na determinação do sucesso de forrageamento das espécies (Gibb e Parr 2010); fatores como umidade e temperatura (e.g. mediada pelo relevo e de abertura de dossel do habitat) podem ter influências na composição de formigas devido a diferenças na tolerância ambiental das espécies (Pearce-Duvet et al. 2011). Além disso, em comunidades onde o processo competitivo não é acentuado, os recursos podem agir como filtros estruturando as comunidades (Ambretch et al., 2004). Fica claro, dessa forma, que o arranjo de comunidades em formigas é um fenômeno complexo e aparentemente contexto-dependente que, em escala local, parece depender de vários fatores, desde a relação das espécies com o ambiente (fatores abióticos) até relações interespecíficas (fatores bióticos), em diferentes escalas temporais, e em boa medida, dependente de fatores nem sempre mensuráveis (estocasticidade).

Contudo, é possível declarar que formigas são modelos muito úteis de estudo em ecologia de comunidades. Isso deve-se a três razões principais:

1) formigas têm capacidade de dispersão limitada, por essa razão, fenômenos na escala local podem apresentar relações causais com a estruturação das comunidades. Além disso, sua condição sedentária faz delas excelentes bioindicadores de distúrbios ambientais, ampliando seu valor em estudos de conservação

2) formigas apresentam nichos razoavelmente semelhantes (e.g. são organismos sociais, sedentários e de hábito alimentar usualmente generalista, cuja unidade de seleção é a colônia), o que pode facilitar, em boa medida, a inferência processos de competição (atual ou passada) como agentes estruturadores das comunidades mirmecológicas (Parr 2008; Andersen 2008; Arnan et al. 2011). Nesta perspectiva, por meio do fenômeno da dominância, é possível dialogar muito bem com as teorias ecológicas sobre organização de comunidades, encontrando explicações previsíveis a partir dos fenômenos observados;

3) formigas são cosmopolitas e têm sua taxonomia relativamente bem resolvida, sendo possível encontrá-las em quase qualquer ecossistema, desempenhando funções semelhantes (Lach et al. 2010).

O gado, o campo e a mirmecofauna

Nos campos do sul do Brasil, assim como em diferentes ecossistemas campestres ao redor do mundo, o pastejo por gado bovino é uma atividade econômica muito comum. Grandes pastadores são seletivos quanto sua alimentação no que se refere a fatores como: (1) qualidade do recurso, (2) palatabilidade da vegetação e (3) acessibilidade do recurso (Adler et al. 2001). Dessa forma, campos pastejados geralmente são campos heterogêneos com manchas de diferentes tipos de vegetação, sujeitas à preferência ou não do gado (e.g. manchas com campo alto, indicando rejeição pelo gado e manchas com campo baixo, indicando preferência), tal condição é mais acentuada em ambientes pouco pastejados.

Nesta perspectiva, o gado afeta a estrutura e a composição da vegetação campestre pela remoção de biomassa, do pisoteio e da deposição de urina (Adler et al. 2001; Pillar et al. 2009;Lezama and Paruelo 2016) podendo trazer mudanças nos recursos e condições do habitat para a mirmecofauna (Read and Andersen 2000; Calcaterra et al. 2010; Andersen 2018). Assim, embora sejam organismos usualmente generalistas, formigas de forma geral podem responder a flutuações na quantidade total de recursos (Andersen 1995; Hoffman 2010). Entretanto, visto que as interações dentro das comunidades mirmecológicas são restringidas por variáveis do habitat (Andersen 2008; Lach et al. 2010), é importante considerar que pode haver segregação de nicho entre as espécies de formigas, possivelmente correlacionada aos diferentes filtros ambientais (e.g. formas de vida de plantas, tipo de solo). Dessa forma, tal segregação poderia ser resultante tanto da seleção alimentar do gado, como também de características inerentes ao ambiente. Estruturação interna (tipo de solo, produtividade) e externa (ação do pastejo) são, em boa medida, efeitos indissociáveis em quaisquer ambientes sob regime de pastejo (Wang *et al.* 2018; Jing *et al.* 2014; Laliberté *et al.* 2013).

Nesse ecossistema heterogêneo, há um mosaico de distúrbios criados devido à seleção da vegetação pelo gado que varia desde áreas menos pastejadas até intensamente pastejadas. Essa configuração pode se manter durante anos, apresentando espécies vegetais adaptadas a esse regime de distúrbio, que de outra forma não sobreviveriam (Bugalho and Abreu 2008; Bencke 2009). No contexto da mirmecofauna, essa intrínseca relação gado-campo desses ecossistemas pode fornecer condições razoavelmente estáveis para as formigas, tanto relativas à complexidade (heterogeneidade) do habitat, quanto a variáveis derivadas como temperatura e sombreamento, importantes em seu processo de estruturação (Gibb e Parr 2010; Pearce-Duvet et al. 2011).

No entanto, é preciso cautela ao avaliar as relações da mirmecofauna com o pastejo. Andersen (2018), em uma recente revisão, afirma que a estruturação de comunidades mirmecológicas sob regime de distúrbio dá-se majoritariamente pela modificação na estrutura do ambiente. Dessa forma, é preferível que a avaliação dos efeitos nessas comunidades seja feita, não diretamente por meio do distúrbio como causa direta, mas dos efeitos do mesmo sobre a vegetação e/ou habitat. Além disso, o autor aponta a abertura de habitat, (e.g. dossel) como fator principal na modificação organizacional das comunidades mirmecológicas. No entanto, em menor escala, considerando um ambiente aberto, sob regime de distúrbios como nos Campos Sulinos, a pergunta que se faz é: que fatores e processos estariam estruturando a mirmecofauna? Em virtude da ausência de estudos sobre as formigas nesses ambientes, nossa compreensão a respeito desses fenômenos ainda é bastante limitada, oferecendo um vasto campo de pesquisa para a mirmecologia.

Objetivo

Geral

Analisar a estruturação das comunidades de formigas em ecossistemas campestres no bioma Pampa em uma área sujeita a distúrbio de pastejo de longa duração. Compreender aspectos de sua dinâmica ecológica em escala local, de forma a ampliar o conhecimento na área de estruturação de comunidades ecológicas, especialmente no que tange à mirmecologia.

Específicos

1) Testar quais variáveis do habitat constituem filtros ambientais importantes na estruturação da mirmecofauna.

2) Verificar se há segregação temporal (noite, dia) de nicho em comunidades de formigas dos campos do bioma Pampa.

Capítulo 1

(a ser submetido para a revista *Austral Ecology*)

Title

ENVIRONMENTAL FILTERS STABILITY AS DRIVER TO ANTS COMMUNITY ASSEMBLY IN SOUTHERN BRAZILIAN GRASSLANDS.

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Abstract

Ants are social organisms known to assembly through competition outcomes. However, despite the majority of studies investigate ant species interactions, environment plays an important role regulating the assembly process while constraint species establishment, as well as their coexistence, competition ability and dispersion. The Pampa biome in the region of *Campos Sulinos* is a highly human impacted ecosystem, which has cattle grazing as main economic activity. Cattle modifies the vegetation through trampling, alimentary selection and urine deposition, which possibly affect conditions and resources available to myrmecofauna. The importance of environmental filters in assembly process was measured through effects of environmental variables (hydrological condition, microhabitat heterogeneity, microhabitat openness and resource diversity) in ant species composition (abundance and incidence based) as well as species richness and total abundance. To do so, we used partial-RDA to investigate effects of environmental variables in ant species composition, and a series of Linear Models (LM) to test their influence on ant species richness and abundance. To better understand the relationship between plant and ant species composition, we perform a series of Mantel correlations between ant (incidence and abundance based) and plant composition (frequency based), in different hydrological conditions. Diurnal-nocturnal segregation was verified using a paired design, comparing ant species composition during day and night (incidence and abundance based). Permutational multivariate analysis of variance (constrained to pairs, 10000 permutations) was used to test for possible differences. Hydrological condition, microhabitat heterogeneity and resource diversity seem to be important environmental filters, contributing to community assembly process. Our results may be indicative that the effects of environmental filters depend on their stability when it comes to community assembly in those myrmecological communities. Hydrological condition, as well as

microhabitat heterogeneity are essentially different, but both are stable and long-term conditions in these grassland ecosystems, being important to dominant as well as subordinate ant species. Resource diversity, however, can be considered an environmental filter, since there is frequent plant species turnover, accounting strongly to subordinate ant species. We found evidence for temporal niche segregation in these ant communities, which we attribute to thermal tolerance-dominance tradeoff.

Introduction

Recent literature, in general, is focused on co-occurrence models and network analysis to infer mechanisms underlying ant community assembly (Tavella and Cagnolo 2018; Camarota *et al.* 2016; Fayle *et al.* 2015). Although these studies are useful and provide great insights on this topic, it is still a challenge to establish causal relationships or understand, at the community level, local ant-plant interactions. Despite the great bearing of interactions, especially competition, in assembly processes (Höldobler and Wilson 1990; Blütghen and Fiedler 2004; Lach et al 2010), it cannot explain alone all myrmecofauna-structuring phenomena. Considering habitat selection processes, we must keep in mind that, regardless of the interactions role, all ant species present in a community are under environmental constraints which they are able to tolerate, whereas selecting the best conditions to establish. These processes can be elucidated through the environmental filter metaphor. In order to establish in a community, a species must be able to surpass major abiotic factors (dispersion filter), habitat conditions (environmental filter), as well as species interactions (interactions filter) (Kraft et al. 2014; Cadotte and Tucker 2017). Few studies were capable still, to offer empirical evidence of ant community structure through environmental filters at the local scale considering hydrological condition (Hertzog et at. 2016), temperature (Pearce-Duvet et al. 2011), microhabitat selection (including other taxa; Lindsay and Cunningham 2009) and resources use (Sendoya *et al.* 2016). However, in most of the cases, environmental filters are used to explain regional patterns (Arnan et al. 2015; Donoso 2014, Wiescher et al. 2012), generally attributing local scale phenomena to species interaction outcomes.

As social sedentary organisms, ants can be resistant to disturbances at the local scale (Hölldobler and Wilson 1990; Lach *et al.* 2010). Besides, it is unlikely that well established mature colonies would exclude each other due to competitive outcomes, since these processes usually occur in the recruiting and establishing phases of new colonies (Andersen 2008). Nevertheless, considering post-colonization processes, more specifically the dominance hierarchy, Arnan *et al.* (2011) formulate the interstitial hypothesis, which works just as a stabilizing mechanism (Chesson 2000), where subordinate ant species can survive in environments under high behavioral dominance condition, once dominant ants play an important role assuring subordinate survivorship, as they open ecological niches, controlling subdominant ant populations which usually compete for secondary resources sources. Gaps in niche availability can be from different natures though; Dátillo et al. (2014) found temporally partitioned (day and night) ecological dynamics of ant-plant interactions at small spatial scales despite the high similarity in incidence-based ant species composition. However, their study in Brazilian *Cerrado* was restricted to focal plants with extrafloral nectaries, which directly infer competition as structuring driver. Such approach constraints our inference to competition outcomes when there is evidence that ant community assembly is not always due to competitive interactions (Ibarra-Isassi and Sendoya 2016; Ribas and Schoereder 2002).

Ants (Formicidae) are a cosmopolite and dominant group, thus closely related to disturbing processes in natural and semi-natural ecosystems (Lach *et al.* 2010; Andersen 2018). Ants are considered a good model for community assembly studies due to some inherent features. 1) Similar niche: which implies relatively similar responses to designed explanatory variables, especially when it comes to colony organization. 2) Known responses to human disturbances: readiness to infer effects of land use at the local scale, usually associated with grassland ecosystems (Folgarait 1998; Ribas et al. 2012; Fowler et al. 2014). However, there are no clear patterns for ant community structuring under grazing-mediated environmental constraints. Cattle farming under extensive grazing management is one of the most important economic activities in the southern

Brazil grasslands, known as *Campos Sulinos* (Overbeck *et al.* 2007; Pillar *et al.* 2009). Grazing has shaped these ecosystems for almost 400 years through cattle feeding selection behavior (Adler *et al.* 2001), thus grazed natural grasslands ecosystems offer a great opportunity to study myrmecofauna organization under these conditions by asking the following questions:

1) Which environmental drivers are assembling ant communities through environmental filtering processes?

2) Are there differences in the composition of ant foraging during the day and the night periods, which could potentially infer temporal niche segregation of communities?

Specifically, for the first goal we evaluated if ant species composition (incidence and abundance-based), richness and abundance are modified by grassland hydrological condition, microhabitat heterogeneity, microhabitat openness, potential resource diversity (indicated by plant species richness), as well as plant species composition. Hydrological condition can be considered a major abiotic condition which ants, as sedentary organisms, must surpass in order to establish. As cattle is present in those environments, vegetation structure can keep its physiognomy over years, granting a reasonably stable condition that possibly modifies ant community assembly.

For the second goal, we considered incidence and abundance-based species composition matrices of ant individuals. Due to the known duality thermal tolerance-dominance in ants (Bestelmeyer 2000), we believe there will be niche segregation through a modification in species composition lead by changes in temperature between diurnal and nocturnal periods.

Methods

Study area

The study was conducted during summer, between December 2017 and January 2018, in Estância Cinco Salsos, Aceguá municipality, Rio Grande do Sul state, - Brazil (31°39'10.70" S - 54°10'9.01"W, 150 m a.s.l.), in typical natural grassland (Campos) ecosystem in south Brazil (Overbeck et al. 2007). The climate is *Cfa* (humid subtropical) under Köppen climate classification, with hot summers, cool winters and no dry season.

Experimental design

We sampled ant assemblages within the paddocks of a cattle grazing management experiment. The experiment aims to evaluate the long-term effect of grazing regimes (continuous, rotational, deferred grazing) on the grassland ecosystem, including livestock productivity. The whole experiment occupies 160 ha and is replicated into three blocks (Figure 1C). The blocks are the replicated experimental units of three different grazing managements, each with ca. 17 ha (Figure 1D). In this experiment, plant communities are annually sampled using 285 permanent plots systematically located 75 m each other in a grid arrangement covering the whole experiment. Each plot measures 1.6 m x 0.2 m and contains eight sub-plots (0.2 m x 0.2 m) where vegetation data have been obtained (Figure 2). For this study we selected 108 of these plots and set them as sampling units. They were chosen to be equally distributed among the experimental blocks in order to assure a good spatial representation for the description of ant assemblages and habitat characteristics.

Previous studies in the same experimental area indicate that different grazing treatments do not induce changes in local ant assemblages (David 2016 – unpublished data). Therefore, it is not our intention to compare them through, nor evaluate their direct influence on the myrmecological communities; our interests here are on the indirect effects of grazing on microhabitat conditions mediated by vegetation change (Hoffman 2010; Andersen 2018), which is naturally variable within each experimental unit.

Of particular importance for our analysis of ant assemblages, the selected 108 sampling units were distributed into two distinct hydrological conditions: 1) dry environment (DE): areas with no flood, even during rainy periods, these areas are usually hilltops, slightly higher than those around them, allowing water outflow; 2) humid environment (HE): areas subjected to partial flooding in some months of the year, usually located in lowlands. Among the 108 sampling units, 57 were in DE and 51 were in HE, proportion that was purposely kept inside each experimental block. All the study was conducted in summer, when there is no water accumulation in the experimental area due to elevated temperature and longer sunshine period, so that all sampling units were dry during the course of the sampling.

Description of ant assemblages

Ants were sampled using baitless pitfall traps, which consisted in falcon tubes (50 ml) containing 15 ml of alcohol at 80%. In each sampling unit we placed three pitfall traps, and they were positioned at a maximum of 1.2 m apart each other and about 0.2 m from the sampling unit border (Figure 2B) in order to assure a good representation of the myrmecofauna of each sampling unit. These traps remained 72 hours open in the field, and then were brought to the laboratory for processing. Whenever possible we identified the sampled ants to the level of species; if not possible, morphospecies were identified to the level of genus, but for the sake of simplicity, henceforth we refer to these as ant “species”. To accurately identify the sampled ants, we used as reference the myrmecological collection from the Laboratory of Ecological Interactions at Universidade Federal do Rio Grande do Sul (UFRGS), the collection is a taxonomical reference to identify ants from *Campos Sulinos* region.

Plant data

Vegetation data were obtained during the annual vegetation sampling of the grazing management experiment, which described each 1.6 x 0.2 m sampling unit by the frequency (0 to 8) of plant species, as well as by vegetation height mean and variance (Figure 2A). For this, the data were organized in a matrix containing the frequency of each plant species per sampling unit (Matrix $\mathbf{W_p}$), which was also separated for DE or HE sampling units (Matrices $\mathbf{W_{pd}}$ and $\mathbf{W_{ph}}$ respectively). We obtained as well, plant species richness per sampling unit, as a measure of potential resource diversity (i.e. diversity of flowers, seeds, leaves). In order to obtain microhabitat physical parameters, we measured, in each sub-plot, the mean vegetation height as a proxy for microhabitat openness (i.e. the higher the grassland vegetation, the smaller the microhabitat openness, higher vegetative structures, just as tussocks, usually allow lower solar incidence on the soil surface), and calculated height standard deviation as a surrogate for microhabitat heterogeneity (i.e. the higher the standard deviation, the higher the microhabitat heterogeneity; Figure 2A).

Ant species composition matrices

To evaluate environmental filter effects, the data on the ant assemblages described in the 108 sampling units were used to build two composition matrices, one containing incidence-based (matrix $\mathbf{W}_{\mathbf{ai}}$), and the other containing standardized abundance of each ant species per sampling unit (matrix $\mathbf{W}_{\mathbf{aa}}$). These were as well separated for DE (matrices $\mathbf{W}_{\mathbf{aid}}$ and $\mathbf{W}_{\mathbf{aad}}$) and HE (matrices $\mathbf{W}_{\mathbf{aih}}$ and $\mathbf{W}_{\mathbf{aah}}$). For this analysis, sampling units with diurnal/nocturnal segregated pitfalls (see next section) had their ant data summed up (i.e. since they are equivalent to the other pitfalls in the relation area x exposition time).

Diurnal-nocturnal segregation

To explore nocturnal-diurnal segregation, we used 36 among the 108 sampling units, half in dry environments and the other half in humid ones. In each of these sampling units, instead of three, six pitfall traps were placed. During daylight (from 5:30 am to 8:30 pm) three pitfall traps were exposed (total of 15 hours/day); the other three traps were exposed during the night (from 8:30 pm to 5:30 am; nine hours/day), which was achieved by exchanging their lids during twilight (8:00 pm – 9:00 pm) and dawn (5:00 am – 6:00 am) (Figure 3), obtaining in this way a paired design. With the data, two species composition matrices were built, one using incidence data in each sampling unit and period (matrix $\mathbf{W}_{\mathbf{adni}}$) and the other the standardized abundance of ants in each sampling unit and period (matrix $\mathbf{W}_{\mathbf{adna}}$).

Why abundance and pitfalls?

There is a well-established literature about why myrmecologists usually avoid the use of abundance-based species composition to describe ecological patterns. Melbourne (1999) suggests that habitat structure can cause bias in ant abundance using pitfall traps. Gotelli et al. (2011) verified that the number of captured ant individuals can be biased by trap proximity to the nest, or nature of species foraging. All the discussion is around the fact that, in myrmecology, the selection unit will always be the colony, not the individuals (Hölldobler and Wilson 1990; Gotelli et al. 2011), which turns into a challenge the understanding of species diversity through the abundance of captured foraging individuals. However, we decided to take the risk of considering abundances for two main reasons: 1) the size of our total sampled area is relatively large, as well as the number of sampling units, so that it seems mathematically unlikely to create a bias through nest proximity; the latter in this case may only add noise for pattern detection. 2) Abundance data can grant useful information on myrmecofauna organization under disturbances that modify habitat structure and may lead to changes in local scale environmental filters, modifying local ant species abundance (Arnan et al. 2013).

Melbourne (1999) found that, for the same area, pitfall traps detected differences in relative abundances of ant species according to experimental changes in habitat structure, and called it sampling bias. However our intention in the present study is to evaluate if and how those changes in habitat structure (environmental filters) modify myrmecofauna, which just made the pitfall trap sampling sensible to answer our questions, besides allowing us to make comparisons between abundance and incidence-based compositions.

We expect that a comparison of the outcomes of incidence and abundance-based composition patterns could provide information about which species are affected by environmental filters. We consider four possible scenarios (Figure 3): A) double response (both abundance and incidence-based ant species's composition respond to the analyzed factor). B) Double negative (neither abundance nor incidence-based composition respond). C) Incidence response only (the analyzed effect seems to not affect dominant species or the proportion in which they occur, but changes subordinate species, since all ant species have the same weight in the matrix). D) Abundance response only (the analyzed effect seems to affect only the proportion of present species, including the dominants, but not which species are actually present).

Data analyses

We used partial distance-based redundancy analysis (partial-RDA) and tested their significance using permutation tests (10.000 permutations). In one analysis we analyzed incidence data $\mathbf{W}_{ai}$, thus utilizing Jaccard dissimilarity as distance metric. In another, we used abundance data $\mathbf{W}_{aa}$, with Bray-Curtis dissimilarity as distance metric. Matrix $\mathbf{W}_{aa}$ was previously standardized by sampling unit total (Figure 6). Both models used ant species composition matrices as response variable, and as explanatory variables: hydrological condition (binary), vegetation height, vegetation height standard deviation and plant species richness. In both partial-RDAs, block was used as conditional variable (Matrix $\mathbf{Y}$).

To evaluate possible ant-plant interactions we performed Mantel tests between ant species composition and plant species composition, using on one side ant standardized abundance or incidence-based matrices $\mathbf{W}_{aa}$, $\mathbf{W}_{ai}$, and on the other side plant frequency matrix $\mathbf{W}_{p}$. The distance metrics used were respectively Bray-Curtis and Jaccard dissimilarities to ant species composition and Bray-Curtis dissimilarity to plants frequency-based composition. We performed also the same analyses to evaluate if these relationships were any different by considering dry and humid hydrological conditions separately ($\mathbf{W}_{aid}$ x $\mathbf{W}_{pd}$; $\mathbf{W}_{aad}$ x $\mathbf{W}_{pd}$; $\mathbf{W}_{aih}$ x $\mathbf{W}_{ph}$; $\mathbf{W}_{aah}$ x $\mathbf{W}_{ph}$).

In order to test if ant species richness and total raw abundance were influenced by the parameters of hydrological condition (binary), vegetation height, vegetation height standard deviation and plant species richness, we performed a set of linear models, using second order correction of Akaike Information Criterion (AICc) to select the most suited model. AICc was used instead of the primary order AIC because it is recommended to mathematically small number of sampling units (as usual in biological sciences) (Burnham and Anderson 2002). Residual distributions were evaluated using *fitdistrplus* R package (R core team 2018). However, ant species richness residuals conform a Gaussian distribution, whereas ant abundance residuals were fitted to normal using a scalar transformation (square root) in the original variable, such that there was no need to use a different link function. We tested separately two sets of models: (1) using ant species richness as response variable, and different combinations of the above-cited parameters as explanatory variables; (2) using the square root of ants total raw abundance (which has normal distribution) as response variable, and different combinations of the above-cited parameters as explanatory variables (Table 6). In both sets, the models with the lowest AICc were selected, unless the ΔAICc was less than 2, in which case, the simpler model was used. The most suited models were used to obtain the significance of the variables as well as their explanatory power.

To test diurnal-nocturnal segregation. We performed two Permutational Multivariate Analysis of Variance (PERMANOVA, 10000 permutations; Pillar and Orlóci 1996) evaluating if ant assemblage composition was affected by temporal niche segregation outcomes. Permutations were restricted to within sampling units, which kept the paired design. For the first analysis, we used standardized abundance-based matrix $\mathbf{W}_{\mathbf{adna}}$ as response variable, using Bray-Curtis dissimilarity as distance metric. $\mathbf{W}_{\mathbf{adna}}$ was standardized by sampling unit total in the corresponding period (diurnal, nocturnal), avoiding in this way the effect of diurnal-nocturnal sampling time asymmetry on total abundances. For the second test, use used incidence matrix $\mathbf{W}_{\mathbf{adni}}$ as response variable, using Jaccard's dissimilarity as distance metric.

All the analyses were performed using *default, fitdistrplus* and *vegan* packages from R software (R core team, 2018), as well as MULTIV software (Pillar 2006, available at http://ecoqua.ecologia.ufrgs.br/MULTIV.html) to perform PERMANOVA.

Results

General data

We identified 44 ant morphospecies, distributed in 18 genera (Table 1). From a total of 7777 captured individuals, *Pheidole* (53.8%), *Solenopsis* (22.2%) and *Camponotus* (7.3%) were the most abundant. *Solenopsis invicta* (Buren 1972) was the most frequent ant species, being captured in 76% of the sampling units. We identified 147 plant species, distributed in 94 genera (Table 2). *Steinchisma hians* (Poaceae) was the most frequent plant species, occurring in 97.2% of the sampling units, followed by *Axonopus affinis* and *Paspalum notatum*, with 95.3% and 89.8% of sampling unit occurrence.

Environmental filters

Ant species composition was significantly correlated to hydrological condition as well as to microhabitat heterogeneity considering both incidence (F=4.45, $p<0.05$; F=1.88, $p<0.05$) and standardized abundance (F= 2.75, $p<0.05$; F=3.17, $p<0.05$) partial-RDA models. Nonetheless, for resource diversity, incidence- and abundance-based responses differed. According to our analysis, we found no evidence that microhabitat openness and resource diversity (plant richness) were related to standardized abundance-based composition (Figure 6A, Table 3). However, when using incidence data, we found a significant relationship with resource diversity (F=1.63, $p<0.05$) (Figure 6B, Table 3), though the possible effects are confounded with hydrological condition. Dry and humid hydrological conditions presented a high number of shared ant species (33; Figure 8).

However, there are more exclusive species in dry environments (eight) than in humid environments (three).

Mantel correlation between ant (incidence based) and plant species composition was significant ($r=0.24$, $p<0.05$). However, when considering different hydrological conditions, just humid environments presented statistically significant correlation ($r=0.169$, $p<0.05$; Table 4). Our analyses were not able to detect any correlations between ant species composition (standardized abundance-based) and plant species composition.

Regarding the relations of factors and ant species richness, among the six models considered, two were equally suited according to AICc (Table 6). As we have proposed, we used the simpler model (m6), which considered as explanatory variables: (1) hydrological condition (binary, opposed to DE); (2) plant species richness (resource diversity). Regarding the relations of factors and square rooted ant total abundance, among the four models considered, two models were equally suited. We selected the simpler model (ma4), which considered only hydrological condition (binary, opposed to DE) as explanatory variable.

Mean ant species richness was higher in DE than in HE ($F_{1,104}=45.9$, $p<0.05$, $r^2=0.437$; Figure 7B). Ant species richness presented a positive relationship with resource diversity ($F_{1,104}=11.06$, $p<0.05$, $r^2=0.106$; Figure 7A). Ants total abundance was higher in DE than in HE as well ($F_{1,104}=57.8$, $p<0.05$, $r^2=0.54$).

Diurnal-nocturnal segregation

Ants species composition differed between diurnal and nocturnal periods by considering both incidence- ($F=17.5$, $p<0.05$) and abundance-based ($F=3.23$, $p<0.05$) composition.

Discussion

A clear conceptual framework for ant community assembly under disturbance is lacking (Andersen 2018). Our results help advancing in predicting the effects of environmental filters on ant assemblages and on understanding the assembly processes behind the patterns we observed in the studied grasslands, which are managed under grazing. Our results show that hydrological condition, microhabitat heterogeneity, and resource diversity seem to be environmental filters affecting the structure of myrmecological communities at the local scale. Further, myrmecofauna nocturnal-diurnal niche segregation seems to be important for ant community assembly in these ecosystems.

Hydrological condition

Few studies have evaluated the effects of flooding structuring ant community assembly in open environments. Hertzog et al. (2016) investigated effects of inundation in grassland ant communities widely dominated by a single species (*Lasius niger*, more than 90% of the sampled ants). The authors detected no evidence of change in ant species richness and abundance in areas before and after a great single event of flooding (caused by a natural disaster). They attributed their results to the high resistance of local ant species to disturbances. However, in our study, myrmecofauna presented a considerably higher diversity. Besides, although there are no permanent flooded environments, flooding is seasonal and relatively common in our study area, being a long-term condition to local myrmecofauna. Different from Hertzog et al. (2016), we did find differences in ant species richness, abundance and composition (incidence and abundance-based) between areas with distinct hydrological conditions (dry and humid environments). Similar patterns were described for Amazonian arboreal ant communities, which have water regime as a long-term condition, modifying ant species composition across floodable and non-floodable environments (Mertl et al. 2009). In this perspective, our study is the first to investigate water regime as a long-term ecological filter in grasslands ecosystems. In fact, our results suggest that hydrological condition seems to be important structuring factor for ant assembly in such environments. This is relevant for the comprehension of flooding dynamics in those ecosystems, especially considering that floodable grasslands are common, and widely converted to human activities (e.g. inundated rice crops) in south Brazil *campos* grassland (Guadagnin et al. 2009). We may attribute such change in those myrmecological communities to the social sedentary habit of ants. As most of these organisms reside permanently in sessile colonies (Lach et al. 2010) environmental filters, such as hydrological condition, may be constraining colonization processes as well as resources gathering (Chen 2016). In this perspective, it is impossible to the species to keep a non-nomad lifestyle without adaptations that keep colony structure and, or make them able to use those areas for foraging (LeBrun *et al.* 2011).

Our study showed a significant correlation between ant (incidence–based) and plant composition in humid environments. Those areas usually have a different vegetation structure, with predominance of perennial *Cyperaceae* species (Boldrini 2009) and relative homogeneity, which may be a result of environmental filtering linked to the hydrological condition, leading humid environments to be less diverse in plant species. Considering ants as a generalist group (in terms of resource use; Hölldobler and Wilson 1990), it is unlikely that the correlations between ant and plant composition would be linked to species-specific relationships. However, despite the apparent homogeneity, minor differences in the length of the flooding periods may be critical for both plant and ant species. Therefore, microvariation in hydrological condition within humid habitat may be a common cause structuring not just ants, but all the present species, which may explain the correlation found for ant-plant composition.

Microhabitat heterogeneity

Our results suggest that myrmecofauna seems to assembly differentially according to microhabitat heterogeneity (variation in vegetation height). Differences in habitat complexity might cause changes in the nature of available niches for ants (e.g. homogeneous environments favor different species than heterogeneous ones; Lassau and Hochiuli 2004; Gibb and Parr 2010). Moreover, habitat heterogeneity could limit ant interspecific interactions, which often provide empty niches for less representative species (subordinate), even considering environments with high level of behavioral dominance (Andersen 2008). In our study, we believe that microhabitat heterogeneity works as a double-edge sword, whereas it is not correlated to mean ant species richness, suggesting that ant assemblages may be able to withstand the same number of species in environments with different degrees of complexity, apparently constraining the establishment of some of them in both, homogeneous and heterogeneous environments, which also explains incidence-based composition differences.

Resource diversity

Most of the myrmecofauna is represented by a few dominant ant species in our study, so that, standardized abundance-based composition is unlikely to detect changes in subordinate species. However, abundance-based composition can provide us useful information allowing us to detect patterns of organization that contrast to the ones revealed by incidence-based data, especially concerning species representativeness (dominance) in ant communities. Indeed, we found a relatively high correlation between ant composition (incidence-based) and plant composition, as well between ant composition (incidence-based) and resource diversity. The non-responsive abundance-based composition can possibly be an indicative of a dominant myrmecofauna which is not related to resource diversity (Figure 3). In this perspective, a possible explanation is that dominant ants may be affected by resource abundance only, not necessarily quality. Consequently, according to our predictions, we can possibly infer that resource diversity is an environmental filter that affects mostly less representative (subordinate) ant species. Hence, those ant species may be occupying interstitial niches (Arnan et al. 2011), possibly using temporary plant resources (whereas annual plant species turnover, due to the seed bank, produces variation in species richness seasonally; García 2009).

A matter of time

Despite the complexity of myrmecofauna structuring under the studied environmental conditions, there is a pattern suggesting some processes shaping ant community assembly in these grassland ecosystems. Our results suggest that myrmecofauna seems to assemble in concern to **environmental filter duration.** Andersen (2018) summarily proposed the idea that chronic (long-term) disturbances upon myrmecological communities can affect more intensively ant assembly than short-term ones. This is especially true when considering long-term fire regimes (Parr et al. 2004; Maravalhas and Vasconcelos 2014), forest canopy openness (Dolek et al. 2009) or even water regimes (Ribas and Schoereder 2007; Mertl et al. 2009). In this perspective, we add some thoughts about the ecological filters tested.

First, as an abiotic factor, hydrological condition is a seasonal, but permanent effect in those ecosystems, especially for ants, that are social sedentary organisms. Therefore, in order to establish in humid environments, they must be able to surpass, or at least forage under the prevailing water regime as well as tolerate most of the conditions imposed by it (e.g. seasonal flooding, less resource diversity). Second, although it seems counterintuitive, microhabitat heterogeneity can be considered in these environments, as a long-term condition due cattle feeding selection behavior. Some perennial plant species such as *Baccharis spp. and Eryngium horridum* are taller in comparison to the rest of the vegetation, and are not usually consumed by cattle, generating heterogeneous vegetation patches that are kept over years (Bugalho and Abreu 2009; Rodrigo Baggio, personal communication). Thirdly, but not less important, resource diversity (plant species richness) seems to be a short-term environmental filter due to seasonal plant species variation, being important to less representative ant species dynamics.

Diurnal-nocturnal segregation

Although environmental filtering processes can shape ant community assembly through space, time seems to be a reasonable factor through which species can present niche segregation. This process can be so strong in some myrmecological communities that nocturnal-specialist ants are somewhat common (Bestelmeyer 2000; Houadria et al. 2015). Indeed, we found differences between diurnal and nocturnal periods when it comes to ant composition, considering both incidence and abundance-based.

As our results suggest, there is a great disparity in the representativeness of some ants as *Pheidole sp.4* and *Pheidole sp.1* morphospecies, and the well-known fire ant *Solenopsis invicta* compared to the rest of the myrmecofauna. Such species occupied most of the traps, with many foraging individuals in each one, representing almost 50% of sampled ants. Previous studies in the same area using bait traps also showed a high representativeness of those same species (David, 2016 – unpublished data). This evidence may be a clue for a defined dominance hierarchy, at least numerical. Bestelmeyer (2000) suggested that there must be a negative relationship between thermal tolerance and dominance in ants, so that, in low temperatures it may be possible to found more available niches to subordinate species, once the dominant become less active.

Therefore, temporal segregation seems to be important to ant community assembly in southern Brazil grasslands. Considering the evidence of dominance phenomena in those communities, it is possible to understand the potential reasons for such organization. It is still necessary, however, to clarify if the species turnover observed is the outcome of nocturnal specialist species (that never actually compete with dominant species, by using only nocturnal period to foraging), or of actual competition outcome due to interactions with dominant species, which would suggest a community molded in competition basis, commonly presenting sub-dominant ant species that have their distribution conditioned to dominance hierarchy.

Conclusion

It is undoubtable the importance of environmental conditions in shaping biological communities. Using the environmental filter metaphor, myrmecologists must rethought what environmental variables represent actual constraints to myrmecological assembly. Through this study, we revealed empirical evidence that long-term environmental conditions play an important role as filters structuring ant communities, although short-term conditions could shape rare or subordinate species dynamics. Myrmecofauna seems to assemble according to temporal segregation in those environments, which was expected due to evidence of a dominance hierarchy, even so, more studies are necessary to really assume competition as the reason for such pattern. Last, we proposed myrmecologists should consider, besides incidence, fluctuations in the number of individuals foraging in the environment as well, which complementary can grant us useful information on ant community assembly.

Considerações finais

O presente estudo é pioneiro em estruturação de comunidades de formigas nos Campos Sulinos. Foi desafiador, ao passo que instigante, desvendar os processos ecológicos responsáveis por perfazer um fenômeno tão importante e do qual tão pouco se conhece para esse bioma. Nesta perspectiva, este trabalho garante uma contribuição ímpar para a mirmecologia, ao passo que explora a organização das comunidades de formigas sob uma ótica não de intensidade, mas de tempo de efeito e estabilidade das variáveis ambientais sobre a mirmecofauna. Revisitando a metáfora dos filtros ambientais, observamos que, ao passo que os efeitos tornam-se de longo prazo, eles passam a ter um maior peso na estruturação dessas comunidades, o que faz total sentido quando se considera a eusocialidade das formigas. O superorganismo de Edward O. Wilson, para além da comunicação, possui uma capacidade própria dos *Hymenopera* sociais, o sedentarismo.

Estudos atuais em mirmecologia usualmente abreviam esse importante passo na estruturação de comunidades mirmecológicas, assumindo a capacidade de espécies que coexistem de suportar o ambiente comum a elas. Embora este pensamento não esteja, de forma alguma, errado ele é limitante para dialogar com outras áreas da ecologia. Não obstante alguns trabalhos de redes de interações consigam de certa forma serem mais multidisciplinares e contribuírem para a compreensão das relações ecológicas, esses pecam por restringirem-se a pequenos sistemas, ou pela utilização de dados não intercambiáveis com outras escalas de estudo. A interação com o ambiente é a base organizacional de qualquer comunidade biológica, fornecendo informações importantes em diversos níveis, desde a biologia das espécies, até como fins de conservação. Para as formigas, isso torna-se ainda mais acentuado, pois são organismos sedentários e de organização estável, cuja interação com o ambiente precisa ser um espelho dessa condição, abarcando as flutuações e nuances da sazonalidade, clima e, em boa medida, distúrbios de longo prazo.

Os Campos Sulinos, uma região de potencial valor mirmecológico

O bioma Pampa é o menos protegido do Brasil, pois apresenta a menor representatividade no Sistema Nacional de Unidades de Conservação (SNUC). Apenas 0,4% da área continental brasileira nesse bioma é protegida por unidades de conservação, 3,3% de sua área total, com uma meta estabelecida para 2020 de 17% (MMA, 2016). Além disso, a exploração econômica do Pampa ao longo dos anos tem promovido o estabelecimento de pastagens cultivadas, agricultura e silvicultura, que implicam na supressão da vegetação nativa campestre, enquanto que a atividade pastoril de produção pecuária sobre campos nativos permite conservar a biodiversidade típica desses ecossistemas (Pillar & Lange 2015). Em uma perspectiva ecológica, formigas são organismos que toleram distúrbios de curto prazo, interagindo bem, dessa forma, com atividades econômicas de caráter sustentável. A pecuária, quando boas práticas de manejo são adotadas, pode funcionar como mantedor dos ecossistemas campestres do Sul do Brasil, sendo a total ausência de distúrbios, considerada problemática nesse aspecto (Dresseno & Overbeck, 2013; Overbeck et al, 2007; Pillar & Vélez, 2010) se tornando por essa razão, imprescindível aliar conservação da biodiversidade e sistemas de produção de alimentos no bioma Pampa.

Dessa forma, a mirmecofauna pode servir como boa indicadora de alterações problemáticas para a estrutura das comunidades e por extensão, para a conservação de ecossistemas. Estudos como este, que levam em consideração o ambiente sob regime de distúrbio como forma de estruturação, ampliam nosso conhecimento sobre a dinâmica antrópica nesses locais. Uma informação importante nesse aspecto é que, os Campos Sulinos, englobando os campos da Argentina, Paraguai e Uruguai, são ambientes muito peculiares para a mirmecologia, uma vez que são o berço das espécies de formigas com maior potencial invasivo até então conhecidas.

Supreendentemente ou não, na qualidade de espécies nativas, não são uma ameaça para o bom funcionamento de seus ecossistemas de origem. Apesar da relevância dessa informação, ela é negligenciada em diversos aspectos. Ao passo que pouco se sabe sobre a ecologia desses organismos nos Campos Sulinos, os mesmos são cada dia mais impactados pela ação humana. A degradação desses ambientes impossibilita-nos conhecer a dinâmica natural da mirmecofauna local. Nessa perspectiva, perdem-se informações essenciais para a conservação, não só desses ecossistemas, mas para ecossistemas do mundo inteiro.

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Tabelas e Figuras

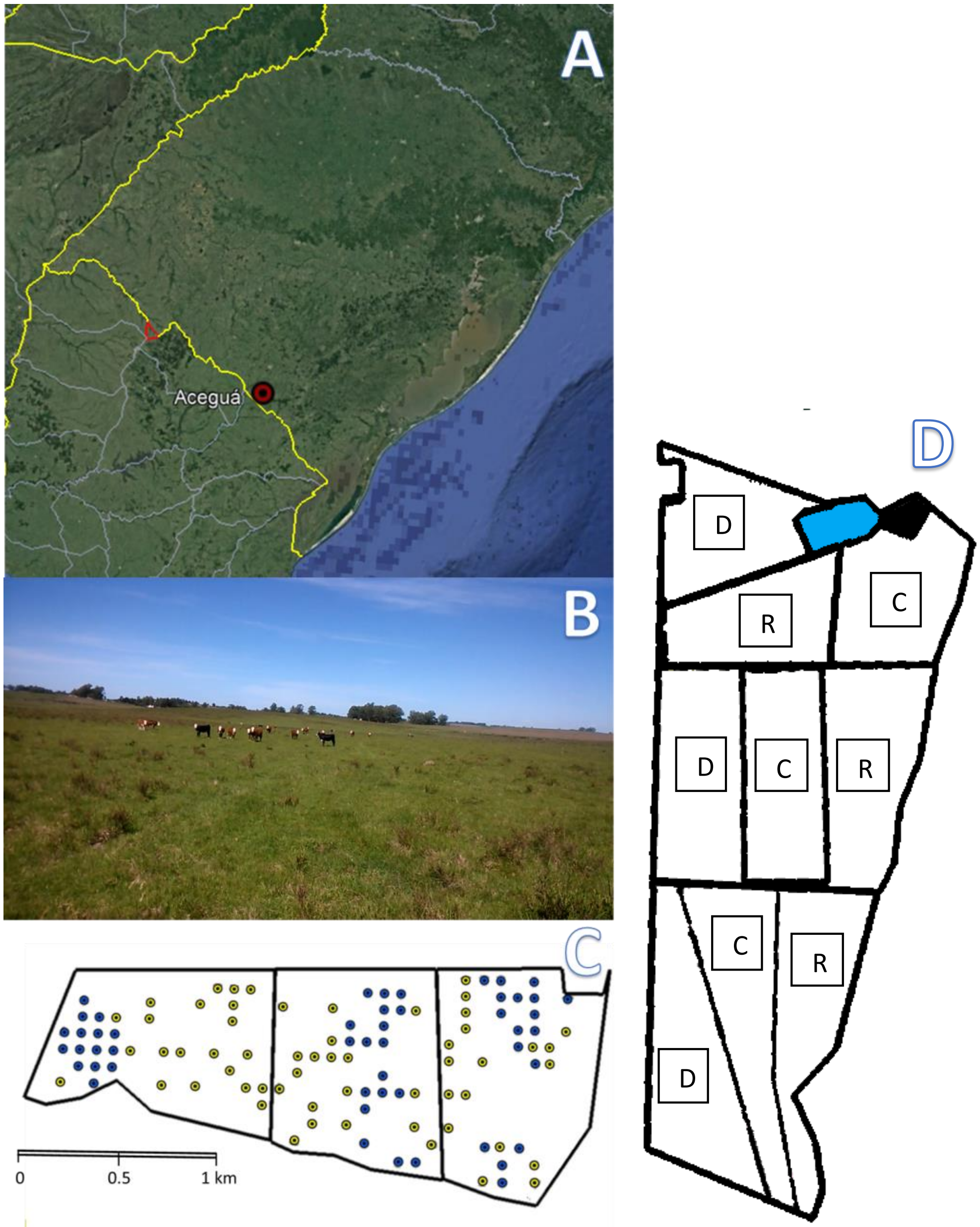

Figure 1: A) Study location – Aceguá municipality – Rio Grande do Sul / Brazil; B) Semi-natural grasslands physiognomy; C) Experimental design, black lines delimit the three blocks of the experiment, yellow points represent dry environment sampling units, blue points represent humid environment sampling units. D) Experimental units (D: grazing deferment treatment,
R: rotational grazing treatment, C: continuous grazing treatment), blue colored area represents a water body.

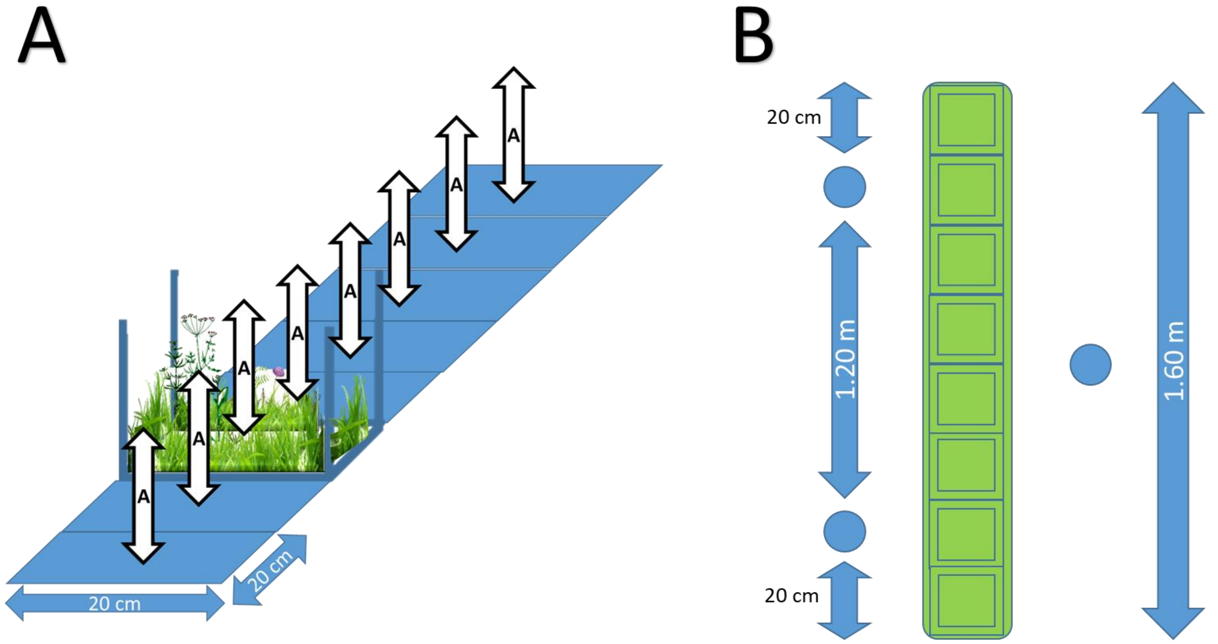

Figure 2: Sampling unit design - A) Plant sampling design: vegetation data were obtained in 0.2 m x 0.2 m sub-plots inside each plot (sampling unit). Habitat openness was obtained measuring mean vegetation height calculated based on height measures (A) taken at the center of each sub-plot (eight measures per plot). Vegetation heterogeneity was measured by the standard deviation values of vegetation height in each plot; B) Ant sampling design: pitfall traps (blue circles) were positioned at a maximum of 1.20 m apart each other, and a minimum of 20 cm from the sampling unit border. The length of the entire sampling unit was 1.60 m.

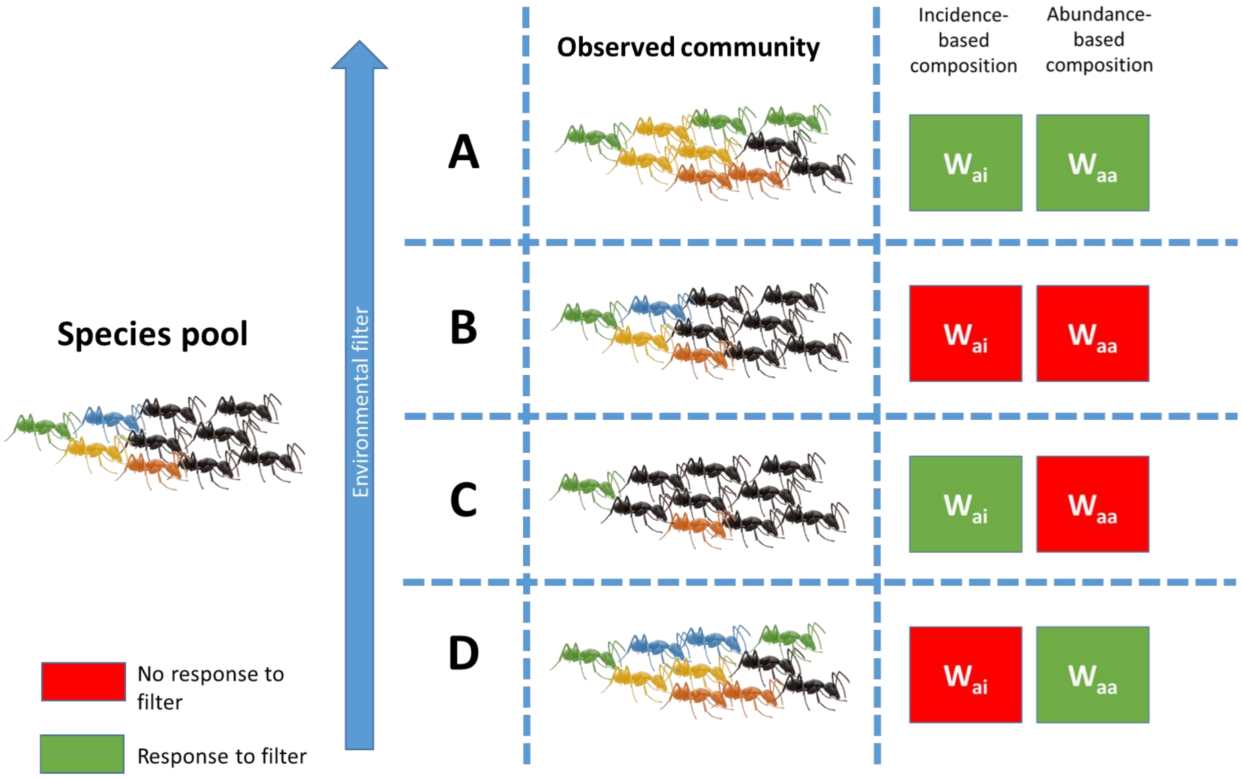

Figure 3: Community predictions based in incidence and abundance-based matrices contrast: A) Double response – Environmental factor affects myrmecofauna for both incidence- and abundance-base species composition. B) Double negative – Environmental factor does not affect ant communities. C) Incidence response – Environmental factor affects only incidence-based species composition, thus mostly affects some less representative (subordinate) ants, while dominant species have their abundances unaffected. D) Environmental factor affects only abundance-based species composition, with no effect on incidence-based species composition.

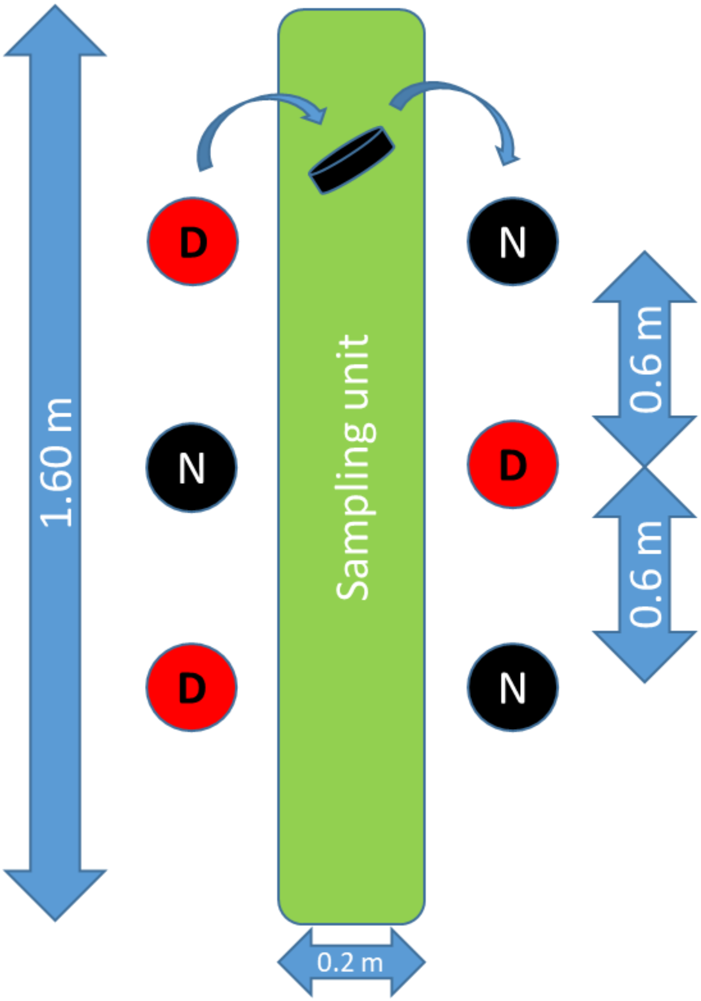

Figure 4: Sampling scheme for diurnal-nocturnal segregation experiment: D) red circles represent diurnal pitfalls, N) black circles represent nocturnal pitfalls – lids were changed during twilight and dawn, such as diurnal pitfalls remained closed during the night and opened during the day, while nocturnal pitfalls remained opened during the night and closed during the day.

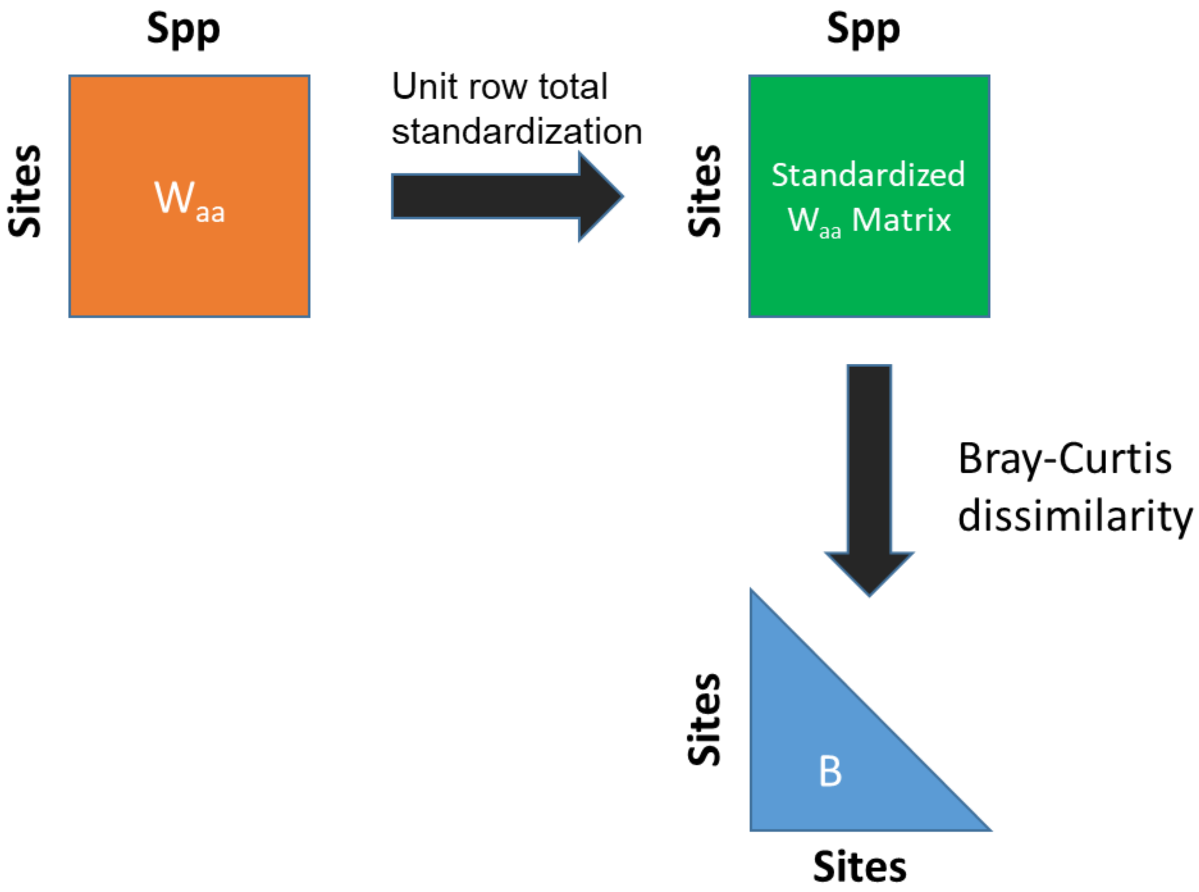

Figure 5: Multivariate transformation - unit row total standardization of Matrix $\mathbf{W_{aa}}$ before partial-RDA analysis. All standardized matrices in this study used the same transformation method.

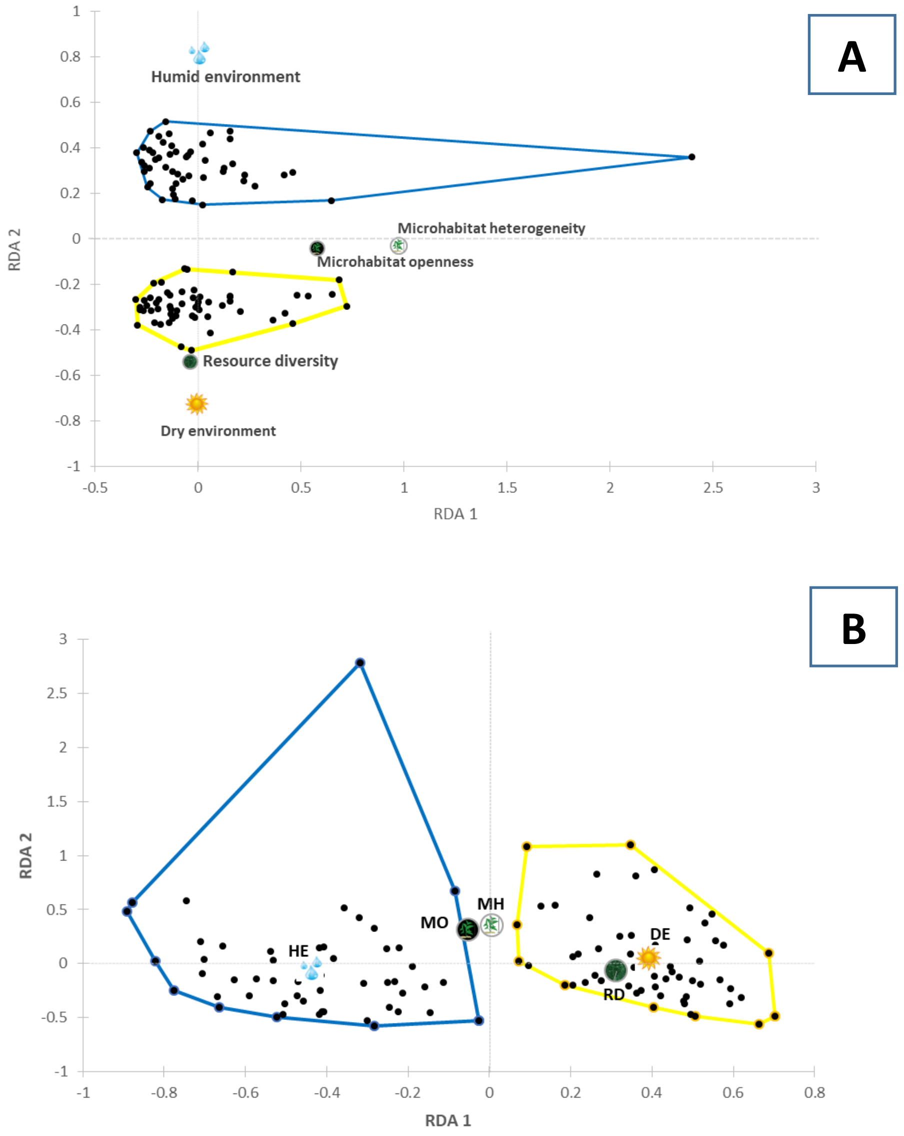

Figure 6: Partial-RDA biplot using hydrological condition, microhabitat openness (vegetation height) and heterogeneity (vegetation height standard deviation), and resource diversity (plant species richness) as explanatory variables and (A) standardized abundance-based and (B) incidence-based species composition as response variable. Black points represent sampling units in the bi-dimensional space. Plotted explanatory variables: (HE) humid environment, (DE) dry environment, (MO) microhabitat openness, (MH) microhabitat heterogeneity, (RD) resource

diversity. Blue and yellow polygons represent, respectively, humid and dry environment sampling units.

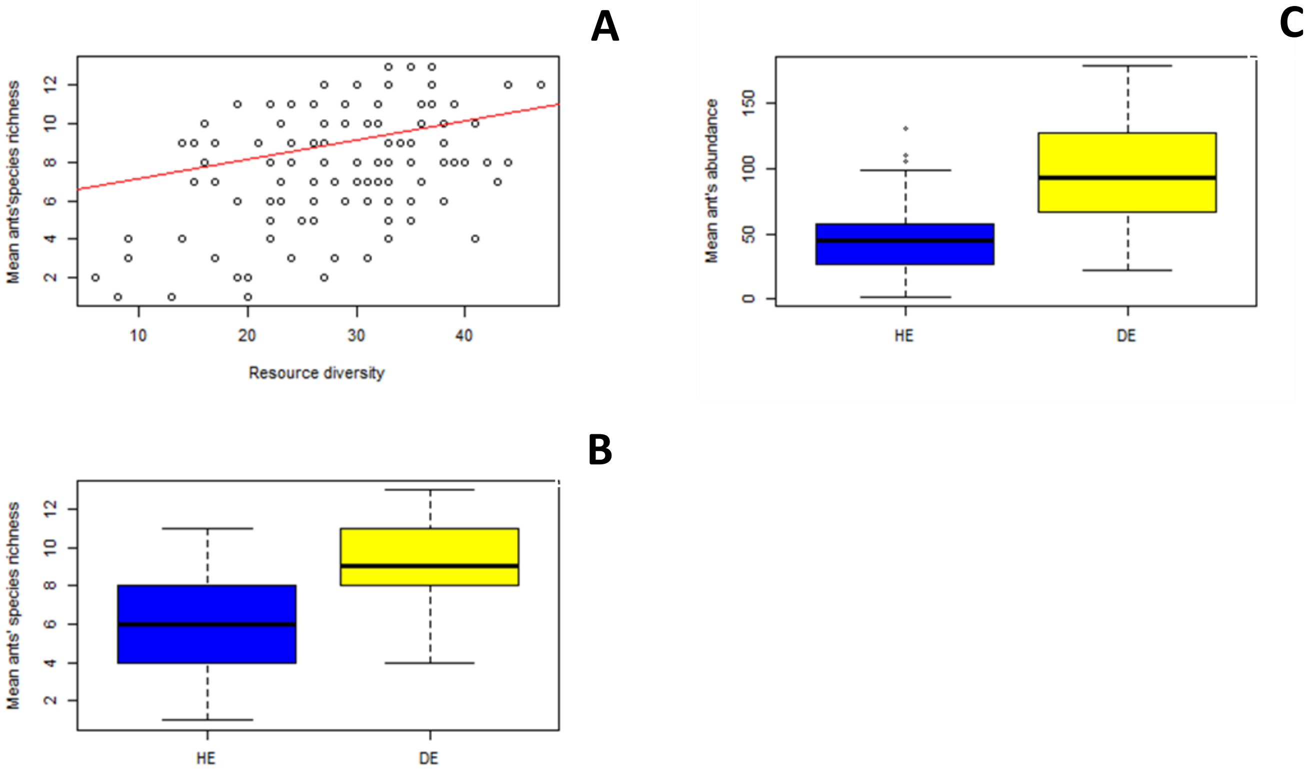

Figure 7: Myrmecofauna relationships to environmental filters: A) Mean ant species richness versus resource diversity; B) Mean ant species richness in different hydrological conditions; C) Mean ant abundance in different hydrological conditions.

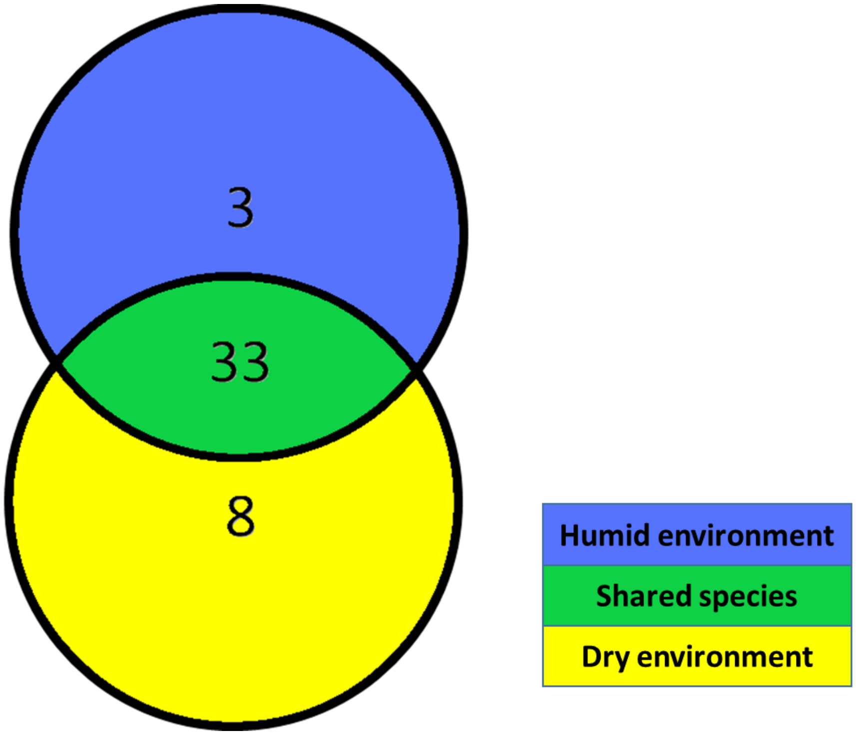

Figure 8: Venn's diagram - Number of ant species shared between both hydrological conditions. In blue: humid environments HE, in brown: dry environments DE.

Table 1: List of ant species and their representativeness inside the community and sampling units. Data are ordered by total number of individuals of each species. (*su*) = Sampling units

Species	Total number of individuals	Total species %	Frequency (total occurrence in *su*)
Pheidole sp. 4	1509	19.40	65
Solenopsis invicta	1271	16.34	83
Pheidole sp. 1	1008	12.96	54
Pheidole sp. 6	770	9.90	34
Pheidole sp. 2	481	6.18	45
Cyphomyrmex sp. 1	415	5.34	62
Pheidole sp. 3	330	4.24	41
Camponotus sp. 2	310	3.99	47
Camponotus sp. 1	223	2.87	41
Solenopsis sp. 1	202	2.60	35
Acromyrmex sp. 2	195	2.51	21
Acromyrmex sp. 1	188	2.42	31
Brachymyrmex sp. 1	179	2.30	66
Solenopsis sp. 4	117	1.50	19
Pheidole sp. 5	87	1.12	8
Solenopsis sp. 5	74	0.95	13
Solenopsis sp. 3	51	0.66	24
Crematogaster sp. 1	47	0.60	10
Nylanderia sp. 1	40	0.51	16
Wasmannia sp. 3	34	0.44	6
Gracilidris pombero	31	0.40	16
Wasmannia sp. 2	30	0.39	6
Camponotus sp. 4	27	0.35	6
Linepithema sp. 1	23	0.30	9
Wasmannia sp. 1	20	0.26	10
Tapinoma sp. 1	16	0.21	5
Solenopsis sp. 6	15	0.19	5
Trachymyrmex sp. 1	14	0.18	11
Acromyrmex sp. 3	12	0.15	4
Brachymyrmex sp. 2	11	0.14	7
Brachymyrmex sp. 3	8	0.10	5
Wasmannia sp. 4	6	0.08	4
Dorymyrmex sp. 1	6	0.08	2
Camponotus sp. 6	5	0.06	2
Anochetus sp. 1	4	0.05	4

Camponotus sp. 3	4	0.05	3
Acromyrmex sp. 4	4	0.05	2
Nylanderia sp. 2	3	0.04	1
Camponotus sp. 5	2	0.03	2
Ectatomma sp. 1	1	0.01	1
Hypoponera sp. 1	1	0.01	1
Linepithema sp. 2	1	0.01	1
Neivamyrmex sp. 1	1	0.01	1
Pheidole sp. 7	1	0.01	1

Table 2: List of plant species and their representativeness inside the community, sampling units and sampling units sub-plots. Data are ordered by percentage of sampling units occupied. (*su*) = Sampling units.

Species	Frequency of occurrence in the *su* sub-plots	Total number of sampling units occurred	% of *su* occupied
Steinchisma hians	677	105	97.22
Axonopus affinis	686	103	95.37
Paspalum notatum	713	97	89.81
Rhynchospora megapotamica	613	93	86.11
Mnesithea selloana	611	89	82.41
Paspalum dilatatum	394	80	74.07
Bothriochloa laguroides	261	67	62.04
Chaptalia piloselloides	220	67	62.04
Danthonia montevidensis	292	66	61.11
Dichondra sericea	348	65	60.19
Chevreulia sarmentosa	314	64	59.26
Chaptalia exscapa	250	64	59.26
Piptochaetium montevidense	317	63	58.33
Stenandrium dulce	245	63	58.33
Evolvulus sericeus	292	57	52.78
Cuphea glutinosa	159	54	50.00
Eryngium echinatum	206	53	49.07
Paspalum plicatulum	180	53	49.07
Richardia stellaris	197	52	48.15
Chascolytrum subaristatum	176	51	47.22
Baccharis ***trimera***	182	50	46.30
Richardia humistrata	209	49	45.37
Hypoxis decumbens	192	48	44.44
Plantago myosurus	147	46	42.59
Eryngium nudicaule	207	45	41.67
Soliva sesselis	164	45	41.67
Stipa setigera	217	41	37.96
Setaria parviflora	148	41	37.96
Eragrostis neesii	171	40	37.04
Andropogon ternatus	156	39	36.11
Carex phalaroides	139	39	36.11
Sisyrinchium micranthum	126	39	36.11
Polygala linoides	107	36	33.33
Galactia marginalis	132	35	32.41

Piptochaetium stipoides	110	34	31.48
Herbertia lahue	98	34	31.48
Eleocharis viridans	167	29	26.85
Trifolium polymorphum	115	29	26.85
Oxalis brasiliensis	78	27	25.00
Briza minor	93	26	24.07
Juncus capillaceus	87	26	24.07
Eryngium horridum	74	26	24.07
Sporobolus indicus	108	25	23.15
Galium richardianum	76	25	23.15
Gamochaeta americana	69	23	21.30
Pterocaulon alopecuroides	51	23	21.30
Nothoscordum montevidense	51	22	20.37
Aristida venustula	71	21	19.44
Chascolytrum poomorphum	65	21	19.44
Sisyrinchium platense	61	20	18.52
Chaptalia runcinata	59	20	18.52
Acmella bellidioides	49	19	17.59
Dichondra macrocalyx	46	19	17.59
Glandularia selloi	64	18	16.67
Schizachyrium microstachyum	61	18	16.67
Hypochaeris megapotamica	35	18	16.67
Apium leptophyllum	46	22	16.31
Juncus microcephalus	41	17	15.74
Dichanthelium sabulorum	61	16	14.81
Fimbristylis autumnalis	56	16	14.81
Axonopus argentinus	42	16	14.81
Oxalis perdicaria	37	16	14.81
Vulpia bromoides	32	16	14.81
Symphyotrichum squamatum	25	15	13.89
Aristida murina	69	14	12.96
Scutelaria racemosa	54	14	12.96
Agalinis communis	33	13	12.04
Carex sororia	54	11	10.19
Aristida uruguayensis	39	11	10.19
Plantago tomentosa	22	11	10.19
Leersia hexandra	62	10	9.26
Cynodon dactylon	57	10	9.26
Baccharis coridifolia	31	10	9.26
Juncus tenuis	34	9	8.33
Pfaffia tuberosa	27	9	8.33
Lolium multiflorum	25	8	7.41
Oxalis eriocarpa	13	8	7.41

Turnera sidoides	12	8	7.41
Hypochaeris chillensis	10	8	7.41
Luziola peruviana	39	6	5.56
Pennisetum clandestinum	25	6	5.56
Trachypogon molle	23	6	5.56
Kyllinga odorata	19	6	5.56
Nassela charruana	15	6	5.56
Marsilea ancylopoda	23	5	4.63
Eleocharis montana	22	5	4.63
Chascolytrum rufum	18	5	4.63
Desmanthus tatuhyensis	14	5	4.63
Scoparia montevidensis	14	5	4.63
Melica brasiliana	13	5	4.63
Hydrocotyle exigua	12	5	4.63
Conyza primulifolia	11	5	4.63
Aspilia montevidensis	10	5	4.63
Dorstenia brasiliensis	6	5	4.63
Agrostis hygrometrica	12	4	3.70
Phyla nodiflora	12	4	3.70
Eragrostis plana	9	4	3.70
Nothoscordum bivalve	9	4	3.70
Berroa gnaphalioides	6	4	3.70
Eragrostis lugens	6	4	3.70
Adesmia bicolor	17	3	2.78
Stylosanthes montevidensis	10	3	2.78
Mecardonia tenella	9	3	2.78
Paspalum lepton	7	3	2.78
Gratiola peruviana	4	3	2.78
Calamagrostis viridiflavescens	13	2	1.85
Trifolium argentinus	9	2	1.85
Chascolytrum brizoides	7	2	1.85
Facelis retusa	6	2	1.85
Jarava plumosa	6	2	1.85
Polygala molluginifolia	5	2	1.85
Lippia turnerifolia	3	2	1.85
Skeptrostachys arechavaletanii	3	2	1.85
Verbena montevidensis	3	2	1.85
Agrostis montevidensis	2	2	1.85
Senecio brasiliensis	2	2	1.85
Chascolytrum uniolae	7	1	0.93
Nierembergia riograndensis	6	1	0.93
Trachypogon montufari	6	1	0.93
Desmodium incanum	5	1	0.93

Kyllinga brevifolia	5	1	0.93
Galium hirtum	4	1	0.93
Gennaria sp.	4	1	0.93
Eragrostis airoides	3	1	0.93
Eryngium sanguisorba	3	1	0.93
Glandularia montevidensis	3	1	0.93
Cerastium humifusum	2	1	0.93
Conyza bonariensis	2	1	0.93
Eragrostis bahiensis	2	1	0.93
Herbertia pulchella	2	1	0.93
Aristida circinalis Lindm	1	1	0.93
Polygonum punctatum	1	1	0.93
Schizachyrium tenerum	1	1	0.93
Solanum commersonii	1	1	0.93

Table 3: Summary of partial redundancy analyses outcomes - effects of environmental filters in ant species composition, conditioned by the block. Asterisks indicate significant P-values.

Response variable	Environmental variable	Explanatory power (%)	*F*	p value	Conditional
Ant species composition Matrix $\mathbf{W}_{aa}$ (standardized abundance)	Hydrological condition	2.73	2.75	0.001*	Block (**Y**)
	Vegetation height standard deviation	3.14	3.17	0.006*	
	Vegetation height	0.92	0.92	0.575	
	Plant species richness	1.23	1.23	0.179	
Ant species composition Matrix $\mathbf{W}_{ai}$ (incidence)	Hydrological condition	4.42	4.45	0.001*	
	Vegetation height standard deviation	1.86	1.88	0.002*	
	Vegetation height	0.95	0.96	0.521	
	Plant species richness	1.62	1.63	0.027*	

Table 4: Summary of Mantel correlation outcomes – correlation coefficients between ant and plant composition matrices and respective p-values. DE: dry environment, HE: humid environment. Asterisks indicate significant P-values.

Matrix 1	Matrix 2	Correlation value r	p value
Ants total composition matrix $\mathbf{W_{ai}}$ (incidence)	Plants total composition matrix (frequency) $\mathbf{W_p}$	0.2418	0.001*
Ants HE composition matrix $\mathbf{W_{aih}}$ (incidence)	Plants HE composition matrix (frequency) $\mathbf{W_{ph}}$	0.169	0.008*
Ants partial DE composition matrix $\mathbf{W_{aid}}$ (incidence)	Plants DE composition matrix (frequency) $\mathbf{W_{pd}}$	0.105	0.08
Ants total composition matrix (standardized abundance) $\mathbf{W_{aa}}$	Plants total composition matrix (frequency) $\mathbf{W_p}$	0.07565	0.061
Ants HE composition matrix (standardized abundance) $\mathbf{W_{aah}}$	Plants HE composition matrix (frequency) $\mathbf{W_{ph}}$	0.07507	0.125
Ants DE composition matrix (standardized abundance) $\mathbf{W_{aad}}$	Plants DE composition matrix (frequency) $\mathbf{W_{pd}}$	0.03987	0.231

Table 5: Summary of permutational multivariate analysis of variance (PERMANOVA) outcomes nocturnal/diurnal segregation of ant communities. Response variable matrices contain both nocturnal and diurnal composition.

Response variable	Explanatory variable	F	Explanatory power (%)	p value
Ant species abundance-based composition $\mathbf{W}_{adna}$	Period (nocturnal-diurnal)	3.24	30.02	0.0007
Ant species incidence-based composition $\mathbf{W}_{adni}$	Period (nocturnal-diurnal)	17.59	80.98	0.0024

Table 6: Linear model selection (based on second order Akaike information criterion, AICc): selection – (A) refers to species richness response variable models, (B) refers to raw abundance response variable models. [Selections were tested separately]; **bold** and (*) indicate most suited models according to AICc.

Model	Response variable	Explanatory variables	AICc	Selection A
m6	Ant species richness	Hydrological condition Resource diversity	**502.199***	A
m5	Ant species richness	Hydrological condition Resource diversity Microhabitat heterogeneity	**502.874***	A
m1	Ant species richness	Hydrological condition Microhabitat heterogeneity Microhabitat openness Resource diversity	505.066	A
m4	Ant species richness	Hydrological condition	510.8794	A
m3	Ant species richness	Hydrological condition Microhabitat heterogeneity	512.3493	A
m2	Ant species richness	Hydrological condition Microhabitat heterogeneity Microhabitat openness	514.2633	A
m0	Ant species richness	Intercept (null model)	544.8201	A
Model	**Response variable**	**Explanatory variables**	**AICc**	**Selection B**
ma4	Ant raw abundance	Hydrological condition	**466.33***	B
ma3	Ant raw abundance	Hydrological condition Microhabitat heterogeneity	**466.94***	B
ma2	Ant raw abundance	Hydrological condition Microhabitat heterogeneity Microhabitat openness	468.22	B
ma1	Ant raw abundance	Hydrological condition Microhabitat heterogeneity Microhabitat openness Resource diversity	470.42	B
ma0	Ant raw abundance	Intercept (null model)	511.31	B