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WILLIAM DRÖSE

PADRÕES DE ORGANIZAÇÃO EM COMUNIDADES DE FORMIGAS NOS CAMPOS SULINOS E ECOSSISTEMAS ASSOCIADOS

PORTO ALEGRE
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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Doutor em Biologia Animal.

Área de concentração: Biodiversidade

Orientador: Prof. Dr. Milton de Souza Mendonça

Co-orientadora: Dra. Luciana Regina Podgaiski

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Aprovada em ____ de ____________ de 2019.

BANCA EXAMINADORA

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Profa. Dra. Sandra Cristina Müller (UFRGS)

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Prof. Dr. Leandro da Silva Duarte (UFRGS)

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Dr. Rogério Rosa da Silva (MPEG-UFPA)

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SUMÁRIO

RESUMO

Entender a distribuição de espécies em ecossistemas naturais e os processos envolvidos com estes padrões tem sido um tema cada vez mais importante devido a rápida perda e transformação de habitats atualmente. Com isso, é possível evitar potenciais perdas de espécies, funções ecológicas ou até mesmo histórias evolutivas de comunidades frente a mudanças climáticas e no uso da terra. O objetivo geral desta tese foi avaliar os padrões de organização de comunidades de formigas em ecossistemas campestres e florestais ao longo de toda distribuição dos Campos Sulinos no Sul do Brasil. Para isso, utilizei diferentes escalas espaciais e abordagens baseadas em diversidade taxonômica, atributos funcionais e relações filogenéticas de espécies de formigas. Os resultados obtidos para cada capítulo indicam que: (1) campos e florestas localizados em áreas de ecótonos são igualmente diversos quanto a riqueza de espécies e linhagens evolutivas de formigas, porém com distinta composição taxonômica entre ambientes (escala local) e regiões fisiográficas (escala regional); além disso, enquanto a filtragem ambiental explica os padrões em escala local, processos espaciais estão relacionados à escala regional; (2) diversidade taxonômica, funcional e filogenética de formigas seguem um clássico padrão latitudinal no Sul do Brasil, mas a variação interespecífica de tamanho de corpo mostra um padrão contrário (espécies menores em maiores latitudes); além disso, enquanto o aumento de precipitação e produtividade explicam a variação taxonômica e funcional, a diminuição da temperatura é o principal *driver* da diversidade filogenética; por fim (3) uma redução na porcentagem de cobertura florestal e na biomassa de serapilheira acumulada em florestas ripárias reduzem a diversidade de formigas, potenciais funções ecológicas e histórias evolutivas, indicando a importância da conservação destes ecossistemas. Os resultados desta tese contribuem com padrões de distribuição de espécies e descreve potenciais *drivers* e processos envolvidos. Além disso, do ponto de vista das formigas, tanto campos quanto florestas em mosaicos e maiores coberturas de matas ripárias devem ser preservadas.

Palavras-chave: Formicidae; campos naturais; ecótonos; matas ripárias; bioma Pampa; bioma Mata Atlântica; fogo; pastejo; diversidade taxonômica; diversidade funcional; diversidade filogenética; variáveis ambientais.

ABSTRACT

Understanding the species distribution in natural ecosystems and the processes behind these patterns has been an increasingly important issue due to the rapid habitat loss and transformation nowadays. Thus, it is possible to avoid potential loss of species, ecological functions or even evolutionary histories of communities to climate and land use change. The aim of this thesis was to evaluate the assembly patterns of ant communities in forest and grassland ecosystems throughout South Brazilian Grasslands. For this, I used different spatial scales and approaches based on taxonomic diversity, functional traits and phylogenetic relationships of ant species. The results obtained for each chapter indicated that: (1) forest and grassland habitats in ecotones are equally diverse in ant species richness and evolutionary lineages, but with distinct taxonomic composition between habitats (local scale) and physiographic regions (regional scale); furthermore, while environmental filtering explains the local scale patterns, spatial processes are related to the regional scale; (2) ant taxonomic, functional and phylogenetic diversity follows a classical latitudinal pattern in southern Brazil, and the interspecific variation in body size show the opposite pattern (lower size at highest latitudes); moreover, while the increase precipitation and productivity explain the taxonomic and functional variation, the decrease in temperature is the main driver of phylogenetic diversity; finally, (3) loss of the percentage of forest cover and leaf-litter biomass accumulated in riparian forests result in loss of ant diversity, potential ecological functions, and evolutionary histories, highlighting the importance of the conservation of these ecosystems. The results of this thesis contribute to species distribution patterns and describe potential drivers and processes involved. In addition, from the ants' point of view, both grasslands and forests in ecotones and larger riparian forest cover should be preserved.

Key words: Formicidae; natural grasslands; ecotones; riparian forests; Pampa biome; Atlantica Forest biome; fire; grazing; taxonomic diversity; functional diversity; phylogenetic diversity; environmental variables.

INTRODUÇÃO GERAL

Comunidades biológicas são dinâmicas e podem variar no tempo e no espaço (Rosenzweig 1995). Pesquisadores têm explorado padrões temporais e espaciais buscando entender qual o papel do ambiente e das interações como forças estruturadoras dos padrões de organização. Uma das abordagens teóricas por trás destes padrões é a das regras de montagem (*assembly rules*), proposta originalmente por Diamond (1975). Em suma, as regras de montagem estabelecem que um conjunto (*pool*) regional de espécies é definido com base em processos de migração, especiação e extinção. A partir deste *pool* regional, a capacidade de dispersão das espécies associada ao seu sucesso de estabelecimento (i.e. sob pressões bióticas e abióticas) pode definir um *pool* local de espécies (Diamond 1975; Zobel 1997; HilleRisLambers et al. 2012). Apesar de nem sempre ser uma tarefa fácil identificar os processos associados aos padrões de organização de comunidades (especialmente em se tratando de interações entre espécies), estes processos podem ainda estar atuando em diferentes escalas espaciais.

Dois principais tipos de processos são associados às regras de montagem: estocásticos e determinísticos. Processos estocásticos como a dispersão, especiação e a extinção são explorados mais intensamente na teoria neutra (Hubbel 2001). Esta teoria prediz que a organização de comunidades é determinada ao acaso e que independe de características funcionais e filogenéticas das espécies. Já os processos determinísticos são aqueles relacionados ao nicho das espécies, e podem ocorrer tanto por filtragem ambiental como por limitação de similaridade. Após a dispersão de uma determinada espécie, filtros ambientais são a primeira barreira enfrentada para que possa se estabelecer no novo ambiente. Ou seja, não basta apenas obter sucesso na capacidade de dispersar, mas esta espécie deve também superar as condições ambientais locais. Desta forma, a filtragem ambiental determina que espécies que compartilham características similares são capazes de se estabelecer e permanecer sob as mesmas condições abióticas (Kraft et al. 2015). Já a limitação de similaridade prediz que espécies ecologicamente similares não podem coexistir devido à maior probabilidade de competir pelos mesmos recursos (MacArthur & Levins 1967). Tanto processos estocásticos quanto determinísticos (bióticos e abióticos) podem estar relacionados e determinar a dinâmica de comunidades ecológicas (Chase & Myers 2011).

Estudos em biodiversidade têm sido amplamente explorados com tradicionais mensurações taxonômicas, em especial a riqueza de espécies. Apesar de representar uma métrica com alto poder comparativo entre diferentes táxons ou regiões de estudo, estes aspectos consideram as espécies de uma mesma comunidade como equivalentes (Podgaiski et al. 2011), ignorando, por exemplo, características funcionais e evolutivas. A diversidade funcional é uma forma de representar como as espécies estão refletindo suas respostas em relação ao ambiente, baseado em diferenças em seus atributos funcionais (Petchey & Gaston 2006). A diversidade filogenética representa a história evolutiva de uma comunidade com base nas relações de parentesco entre as espécies (Webb et al. 2002; Cavender-Bares et al. 2009). Atualmente, a organização de bancos de dados globais de espécies (e.g. GBIF 2019) é uma ferramenta que facilita a obtenção de características funcionais e de histórias evolutivas, possibilitando que mais pesquisas possam integrar estas abordagens. Utilizar uma abordagem funcional e filogenética em ecologia de comunidades pode facilitar a compreensão dos padrões de organização, demonstrando muitas vezes resultados que apenas aspectos taxonômicos não seriam capazes de predizer (Pausas & Verdú 2010).

Apesar dos maiores e mais completos bancos de dados animais contemplarem grupos de vertebrados, entre os insetos as formigas tem se destacado e vem crescendo rapidamente em relação a compilação de dados. *The Global Ant Biodiversity* (GABI –

Guénard et al. 2017) e *The Global Ants Database* (GLAD – Parr et al. 2017) são bases de dados que contam com a colaboração de pesquisadores de todo o mundo. Atualmente, GABI conta com mais de dois milhões de registros obtidos de mais de 9.400 publicações compiladas. Devido a estes trabalhos em equipe de compilações de dados taxonômicos, funcionais e filogenéticos de formigas, diversas pesquisas com análises de padrões globais têm sido publicadas, como padrões climáticos (Dunn et al. 2009; Jenkins et al. 2011), efeitos de distúrbios e mudanças climáticas (Gibb et al. 2018) e distribuição de histórias evolutivas (Economo et al. 2018). Além disso, o acesso a este tipo de informação possibilita que estudos de caso também possam utilizar estas abordagens. De fato, formigas desempenham papéis essenciais na dinâmica ecológica em ambientes naturais (Lach et al. 2010) e fornecem inúmeros serviços ecossistêmicos (Del Toro et al. 2012). Essas características do grupo fazem com que sejam amplamente utilizadas como modelo para o monitoramento de dinâmicas de ecossistemas naturais, distúrbios e mudanças no uso da terra (Underwood & Fisher 2006; Nemec 2014). Com as atuais taxas de mudança global, abordagens funcionais e filogenéticas podem complementar a compreensão das relações e do papel das formigas nos ecossistemas.

Ecossistemas campestres naturais estão distribuídos ao longo do Sul do Brasil, estendendo-se também para a Argentina e o Uruguai (Bilenca & Miñarro 2004). Estes ecossistemas formam paisagens com diferentes tipos florestais nos biomas Pampa e Mata Atlântica e são conhecidos como Campos Sulinos. Enquanto florestas ombrófilas mistas definem as paisagens com campos na região no Planalto Sul-Brasileiro, florestas estacionais e ciliares se distribuem ao longo das demais regiões fisiográficas do Sul do Brasil (Fig. 1). Estudos palinológicos demonstram que estes campos são ecossistemas relictos de um clima frio e seco, e que apenas recentemente a mudança para um clima mais quente e úmido fez com que ecossistemas florestais tenham se expandido (Behling et al. 2007; 2009). Com esta mudança, a acelerada expansão florestal sobre os campos tem se tornado um problema, levando a redução e fragmentação de áreas campestres. Uma forma de evitar a expansão florestal é manter o manejo contínuo de campos com fogo e pastejo, os quais inibem o desenvolvimento de espécies florestais na matriz campestre (Müller et al. 2012). Apesar de essenciais para a manutenção da alta diversidade campestre, estes distúrbios podem ter efeitos negativos para florestas, como o livre acesso do gado ao interior florestal, prejudicando o desenvolvimento do sub-bosque e a regeneração de espécies florestais. Debates recentes têm levantado estas questões da dinâmica campo-floresta no Sul do Brasil (Pillar & Vélez 2010; Luza et al. 2014; Overbeck et al. 2016; Carlucci et al. 2016). De qualquer maneira, diferentes estratégias devem ser adotadas para a manutenção e preservação destes mosaicos.

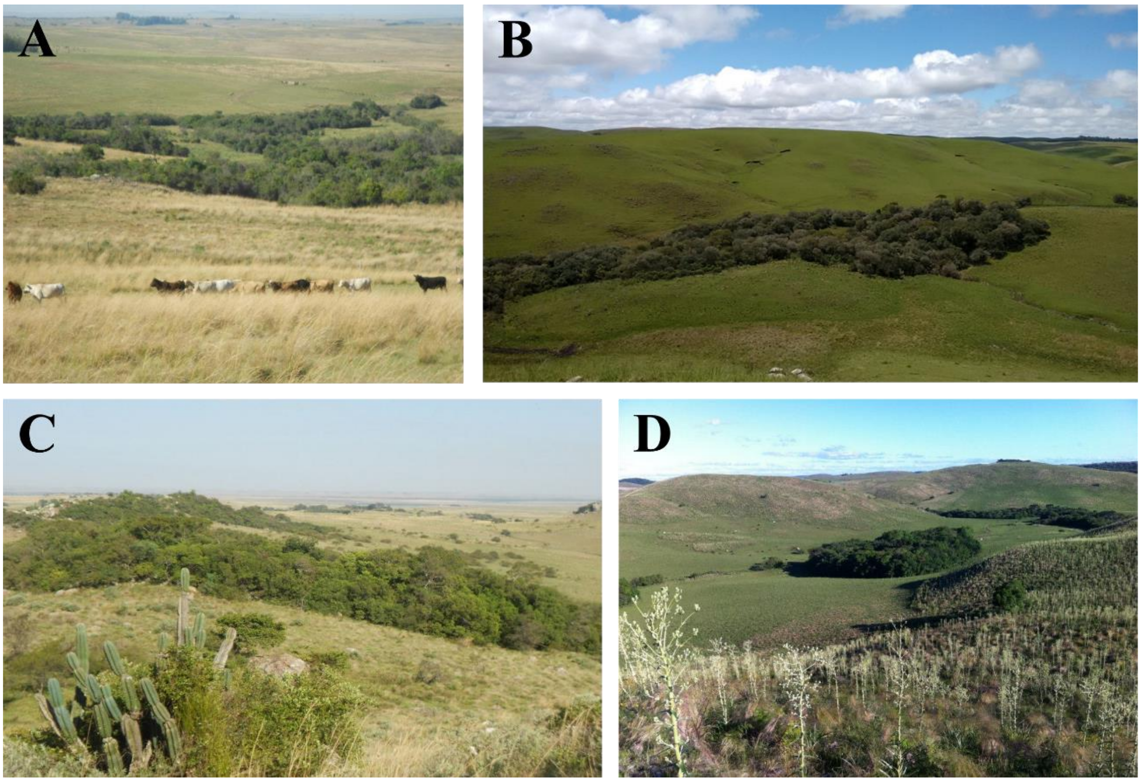

Figura 1. Paisagens campestres associadas a diferentes tipos florestais no Sul do Brasil. (A) Quaraí – RS; (B) Palmas – PR; (C) Santana da Boa Vista – RS; (D) Soledade – RS. Fotos: William Dröse e Luciana Podgaiski.

OBJETIVOS E ESTRUTURA DA TESE

O objetivo geral desta tese foi avaliar os padrões de organização em comunidades de formigas em ecossistemas campestres e florestais no Sul do Brasil. A tese está estruturada em três capítulos, os quais correspondem a artigos científicos formatados de acordo com as normas de periódicos internacionais.

- ✓ Capítulo I: neste capítulo exploramos potenciais preditores ambientais dos padrões das comunidades de formigas em ecótonos de campo-floresta no Rio Grande do Sul. Estes padrões são explorados tanto numa escala local quanto regional utilizando uma abordagem taxonômica e filogenética.
- ✓ Capítulo II: explorando uma escala espacial um pouco mais ampla, investigamos neste capítulo padrões latitudinais utilizando como modelo comunidades de formigas de serapilheira de ecossistemas ripários distribuídos nos estados do Rio Grande do Sul, Santa Catarina e Paraná. Além das abordagens taxonômica e filogenética, também exploramos aspectos funcionais destas comunidades.
- ✓ Capítulo III: utilizando os dados do mesmo projeto do capítulo anterior, investigamos neste terceiro capítulo a influência de variáveis locais de habitat e de estrutura da paisagem em matas ripárias no Sul do Brasil com enfoque para conservação destes ecossistemas.

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CAPÍTULO I

Local and regional drivers of ant communities in forest-grassland ecotones in South Brazil: A taxonomic and phylogenetic approach[1]

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Local and regional drivers of ant communities in forest-grassland ecotones in South Brazil: a taxonomic and phylogenetic approach

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Abstract

Understanding biological community distribution patterns and their drivers across different scales is one of the major goals of community ecology in a rapidly changing world. Considering natural forest-grassland ecotones distributed over the south Brazilian region we investigated how ant communities are assembled locally, i.e. considering different habitats, and regionally, i.e. considering different physiographic regions. We used taxonomic and phylogenetic approaches to investigate diversity patterns and search for environmental/spatial drivers at each scale. We sampled ants using honey and tuna baits in forest and grassland habitats, in ecotones distributed at nine sites in Rio Grande do Sul state, Brazil. Overall, we found 85 ant species belonging to 23 genera and six subfamilies. At the local scale, we found forests and grasslands as equivalent in ant species and evolutionary history diversities, but considerably different in terms of species composition. In forests, the soil surface air temperature predicts foraging ant diversity. In grasslands, while the height of herbaceous vegetation reduces ant diversity, treelet density from forest expansion processes clearly increases it. At a regional scale, we did not find models that sufficiently explained ant taxonomic and phylogenetic diversity based on regional environmental variables. The variance in species composition, but not in evolutionary histories, across physiographic regions is driven by space and historical processes. Our findings unveil important aspects of ant community ecology in natural transition systems, indicating environmental filtering as an important process structuring the communities at the local scale, but mostly spatial processes acting at the regional scale.

Introduction

Ants are extremely abundant and ecologically important organisms widespread through ecosystems worldwide [1]. Several mechanisms shape ant distribution patterns such as environmental conditions (i.e. that filter species or lineages according to habitat requirements), species interactions, historical and geographical factors (i.e. affecting dispersal) [2]. Indeed, depending on the spatial scale considered ants might show different distribution patterns (e.g. [3,4]). For example, at smaller or local scales, microclimatic variation [5,6], soil and vegetation characteristics [7-9] and interspecific competition [10,11] usually act on community assembly. At broad or regional scales, climate variables [12,13], altitude [14,15], latitude [16-18] and dispersal limitation [19,20] may explain most of the patterns. All these predictors, acting in isolation or interacting, play roles in ant community diversity and distribution patterns of evolutionary lineages [2].

Ecotones are zones where adjacent ecological systems co-occur in space, supporting unique ecological dynamics [21]. Their definition is scale-dependent, including from biomes or ecoregions, to landscape patches or vegetation communities [22]. An example of an ecotone widespread through the globe is the contact between grassland/savannas and forests. Such contrasting habitats differ in relation to several environmental characteristics and conditions, which select adapted species and evolutionary histories from the regional pool [23,24]. While forests may harbor species more associated with deep shade, moisture and buffered temperatures, grasslands, on the contrary, may favor shade-intolerant species and those more prone to microclimatic oscillations [25].

In South Brazil, the current warm and moist climate favors forest expansion processes over native grasslands in many physiographic regions, forming mosaic landscapes [26]. Fire and grazing have potential roles of controlling forest expansion without causing major damage to grasslands, but in ecotones where disturbances are low or even absent, the establishment and growth of shrubs and treelets, which are good light competitors, inhibits typical grassland plant diversity [27]. Here we aim to investigate ant community diversity patterns in this system, and search for potential drivers, considering local (different habitats: forests and grasslands) and regional scales (different physiographic regions over Rio Grande do Sul state).

Diversity patterns and their drivers are often explored in the context of the taxonomic identity of the species. In addition to the description of the taxonomic diversity (TD), the use of the evolutionary history (phylogenetic diversity - PD) and ecological traits (functional diversity - FD) of a community are useful to understand these patterns of distribution in a historical and ecological context. Taking into account that higher evolutionary diversification might result in higher functional diversification, recent studies have suggested that PD can be an effective proxy for FD, particularly in the absence of trait data (e.g. [28]). In the case of ant communities, PD and FD have been highly correlated as reported in many studies [20,29,30], meaning that the traits display phylogenetic signals, i.e. they are evolutionarily conserved. Therefore, PD can be a potentially useful tool to estimate functional diversity in ant communities. On the other hand, TD may not always converge with the patterns of PD and FD [30], e.g. when two communities with equal TD have different levels of functional redundancy and evolutionary histories, and then their information can be complementary. Here we used both TD and PD to explore ant diversity distributions patterns in forest-grassland ecotones. Based on the available literature, we elaborate some predictions.

Locally, we expect compartmented ant assemblages inhabiting forests and grasslands, but no detection of differences regarding species diversity between habitats, as reported similarly by Pinheiro et al. [31] and Klunk et al. [32] for the same region. As ants are thermophilic organisms, local temperature should positively influence the diversity of ant species found foraging [33]. In forests, structural properties such as leaf-litter depth should increase microhabitat complexity and thus support increased ant species diversity [8,34]. In grasslands, suppression or diminished disturbance frequency/intensity (e.g. fire and grazing), as measured by herbaceous vegetation height and shrub density, should reduce ant diversity [35], although tree densification through forest expansion may increase it due to the higher availability of resources [36].

Regionally, we expect distinct ant composition among physiographic regions of Rio Grande do Sul state [37], and since ants lack in efficient large-scale dispersal mechanisms [19,20], both environmental and spatial factors may contribute to this variation. Based on the water-energy dynamics hypothesis [38], regional temperature and precipitation patterns should positively affect ant diversity [12,13,18,39], while altitude affects it negatively [14,15].

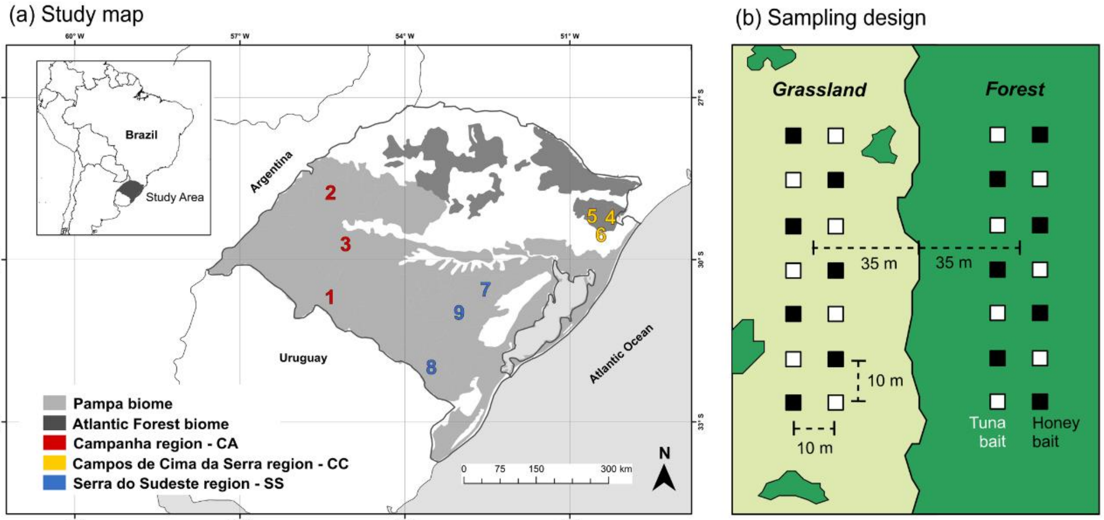
Materials and methods

Ethics Statement

Permission to carry out this study in private lands was granted by landowners; sites within conservation units had authorization granted by the Environmental Secretariat of Rio Grande do Sul state (SEMA, Brazil).

Study area and design

We studied forest-grassland ecotones along nine sites in Rio Grande do Sul state, Brazil. Grasslands occur on areas in both the Atlantic Forest and Pampa biomes and form mosaic landscapes with forests [40]. The sites sampled belong to three different physiographic regions: (i) Campanha, (ii) Campos de Cima da Serra and (iii) Serra do Sudeste (henceforth CA, CC and SS, respectively) (Fig 1a). The nearest sites were about 36 km apart (Cambará do Sul and Jaquirana municipalities) and the most distant sites (Cambará do Sul and Santana do Livramento municipalities) were about 553 km apart. The physiographic regions differ in terms of climate, vegetation, soil types and biotic evolutionary histories. The climate is Cfb type in the CA and SS regions, according to the Köppen climate classification. Only CC and the high altitude sites in SS are classified as Cfa type climate [41]. There is an environmental temperature gradient across the three regions, decreasing from southwest to northeast (i.e. from CA to CC) (see S3 Table). Mean altitude in sites sampled at CA is 185 m, while at CC it is 883 m and at SS 240 m.



(a) Study map

(b) Sampling design

(c) Physiographic regions

Fig 1. Map of the study sites and types of forest-grassland ecotones from different physiographic regions. (a) Forest-grassland ecotones sampled in nine localities belonging to three different physiographic regions of Rio Grande do Sul state, Brazil: Campanha region (red numbers: 1-Santana do Livramento; 2-Santo Antônio das Missões; 3-São Francisco de Assis), Campos de Cima da Serra region (yellow numbers: 4-Cambará do Sul; 5-Jaquirana; 6-São Francisco de Paula) and Serra do Sudeste region (blue numbers: 7-Encruzilhada do Sul; 8-Herval; 9-Santana da Boa Vista). (b) Sampling design with bait points. (c) Different physiognomies of forest-grassland ecotones sampled.

Each studied site was delimited by a 2 x 2 km grid where we selected two forest-grassland ecotones at least 1 km from each other. The sole exception was one site from the CC region, where we studied only one ecotone (totaling 17 ecotones). Ecotones from each physiographic region are formed by different natural grassland types associated with specific forest remnants: CA region – Deciduous Seasonal Forest and Sand and Soil Shallow Grasslands; CC region – Mixed Ombrophilous Forest and Highland Grasslands; and SS region – Semideciduous Seasonal Forest and Shrub Grasslands [40,42] (Fig 1c). At each ecotone, we sampled ant communities in both forests and grasslands.

Ant sampling design

We carried out ant sampling during Summer 2013 (January and February). In each forest-grassland ecotone we established one parcel (10 x 70 m) inside each habitat (i.e. predominantly forest and predominantly grassland). Each parcel was 35 m apart from the edge between habitats, and about 70 m from each other. In each parcel we placed fourteen baited sample points (seven with honey and seven with tuna fish in oil) over paper cards (10 x 10 cm), 10 m from each other (two rows of seven baits), left to attract ants for 1 hour (Fig 1b). After this, ants on each bait were stored in plastic bags with ethyl acetate and then preserved in 80% ethanol. All ant individuals were taken to Laboratório de Ecologia de Interações (LEIN) in Universidade Federal do Rio Grande do Sul (UFRGS) for further processing.

Ant genera identification was based on dichotomous keys [43]. Specific literature was used for species classification, and direct comparisons were done with specimens in scientific ant collections in LEIN and the Entomological Collection Padre Jesus Santiago Moure of the Universidade Federal do Paraná (DZUP). Morphospecies determination followed the standard practice of LEIN, where vouchers are deposited.

Environmental and spatial variables

At the local scale, we recorded soil surface air temperature (ºC) and air moisture (%) at the moment of ant sampling in both forests and grasslands. We used two data loggers (HOBO Pro V2 Temp/RH Onset) per parcel recording data at each 5 min for one hour. Habitat structure variables were collected at each habitat independently, according to their physiognomy. In forest parcels, we evaluated leaf-litter depth (cm) and canopy openness (%) at three equidistant points 30 m from each other (one point at 5 m, one at 35 m and another at 65 m on parcel). In grassland parcels we measured herbaceous vegetation height (cm) and shrub and tree density (amount of branches and leaves touching a 1.5 m height pole at 10 cm radius) also at three equidistant points. All local predictor variables at each parcel (forest and grassland) were averaged among the points, and are available in S1 and S2 Tables, respectively.

At the regional scale, we considered two categories of environmental variables: climate and geomorphometry. Data were extracted for the nine sampling sites. Climate variables (annual mean temperature, temperature seasonality, minimum temperature of coldest month, annual precipitation and precipitation seasonality) were obtained from WorldClim - Global Climate Data (http://www.worldclim.org) [44]. Temperature and precipitation seasonality summarizes the monthly variation during the year. Mean altitude of each site was used as a geomorphometry variable, obtained from Shuttle Radar Topographic Mission data available from the CIAT-CSI database [45]. Descriptions of all sites in terms of their regional predictor variables are available in S3 Table.

Some predictor variables might be highly correlated and influence the analysis. We used the Variance Inflation Factor (VIF) to detect multicollinearity among environmental variables [46]. We calculated VIF for all predictors, for both scales, and selected only those with VIF ≤ 3, which indicate insignificant multicollinearity [47,48]. Thus, for local scale analysis, air moisture was removed (S4 Table), and for regional scale analysis, minimum temperature of the coldest month and mean altitude were removed (S5 Table). VIF values were calculated with the *fmsb* package in *R* [49].

Finally, the spatial matrix was arranged from geographical coordinates (latitude and longitude) of one central point between ecotones on each site (S6 Table). This matrix was transformed into spatial data by the Principal Coordinates of Neighbor Matrices method (PCNM) [50]. Five PCNM vectors were generated using the *pcnm* function of the *vegan* package [51].

Data analysis

For the local scale analysis, we searched for predictors of ant communities in forests and grasslands separately. Thus, we had 17 sampling units of forest and 17 of grassland. At the regional scale, we considered the site (data from two ecotones) as a sampling unit, totaling nine samples. All analyses presented here were implemented in the *R* software environment [49].

Ant phylogenetic tree

Currently, there is no complete species-level ant phylogeny available. We considered phylogenetic relationships among ant genera from the phylogeny of Moreau & Bell [52] and complemented this database with the phylogenetic relationships within Myrmicinae proposed by Ward et al. [53]. These two publications with time-calibrated phylogeny were used to build a phylogenetic tree for the ant communities found in the present study. We built this tree at genus-level in the software Phylocom 4.2 [54]. Then, all species were inserted in this tree as polytomies. After that, we randomly generated 1000 potential trees considering the relationships among species within each genus as phylogenetic uncertainty in the software Sunplin [55] (see an example of one of the 1000 phylogenetic trees in S1 Appendix).

Taxonomic and phylogenetic diversity

We characterized the taxonomic diversity for each forest and grassland (local scale), and each site (regional scale) using species richness (the number of species in each habitat or site) and species diversity (Simpson index), henceforth *S* and *D*, respectively. Phylogenetic diversity was calculated with Faith’s phylogenetic diversity (*PD*) and Rao’s quadratic entropy (*PR*, which is equivalent to the Simpson index). *PD* was the sum of branch lengths of the phylogenetic tree linking all the species represented in each community [56] and *PR* was calculated considering phylogenetic distance among species in each habitat or site weighted on the proportion of the occurrences of ant species [57]. We used these two metrics because *PD* is not an abundance (or occurrence) weighted index, while *PR* is (as is *D*). We calculated *PD* and *PR* for the 1000 phylogenetic trees generated by randomization (as described above) and used the mean value of these metrics for each habitat or site in further analyses. *PD* was calculated with the *picante* package [58] and *D* and *PR* with *SYNCSA* [59].

Taxonomic and phylogenetic composition

Principal Coordinates Analysis (PCoA) based on the Bray-Curtis index among sampling units was used for the ordination of species taxonomic composition in forests and grasslands (local scale) and sites (regional scale). We used the *Adonis* function (permutation-based multivariate analysis of variance) with 9,999 permutations to examine differences between habitats (local scale) and physiographic regions (regional scale).

To explore ant phylogenetic composition between habitats (local scale) and physiographic regions (regional scale), we performed an analysis of Principal Coordinates of Phylogenetic Structure (*PCPS*) [60]. *PCPS* analysis represents the variation in phylogenetic composition across environmental gradients with eigenvectors (ordination vectors – *PCPS*). This method has already been applied to different taxonomic groups with relatively well-established phylogenetic relationships among species, such as birds [61], amphibians [62] and plants [63-65], and it is briefly described below.

First, the matrix with phylogenetic patristic distance between species (matrix **D**) is transformed into a matrix with pairwise phylogenetic similarities between species (matrix **S**). Then, the phylogenetic weights of taxa are calculated by fuzzy weighting [66] through standardization by the marginal totals within the columns of matrix **S**, generating the matrix **Q**. The matrix **Q** considers the phylogenetic relationships among the taxa, reflecting the evolutionary history shared between one taxon compared with all others [67]. Then, the matrix **Q** is finally multiplied by the matrix of species occurrences by communities (matrix **W**) to generate the matrix of phylogeny-weighted species composition (matrix **P**). *PCPS* vectors are extracted through Principal Coordinates Analysis (*PCoA*) based on matrix **P**, resulting in eigenvectors that describe the variation of phylobetadiversity across environmental gradients. *PCPS* is able to capture phylobetadiversity patterns from both basal and more terminal nodes associated with specific communities [67]. Ultimately, the phylobetadiversity pattern found is tested against null models (*taxa shuffle*) based on permutations of phylogenetic relationships among species (9,999 permutations) while species composition is kept the same across the communities. Thus, a significant probability value of *taxa shuffle* means that the association between species distribution and environmental gradients is structured by the phylogenetic relationships among species. More details about these procedures can be accessed in [67].

In our study, we performed *PCPS* analysis for each of the 1000 ant phylogenetic trees generated by randomization (previously described). We then presented the proportion of significant/non-significant *PCPS* (i.e. n-trees out of 1000 trees that returned $p \leq 0.05$) and discussed the results. This is the first time that the analysis of Principal Coordinates of Phylogenetic Structure has been applied to explore phylobetadiversity of data while treating the relationships among species within each genus as phylogenetic uncertainty. We used the *vegan* package for PCoA and *Adonis* function, and the *PCPS* package for PCPS analysis [68].

Local predictors

First we tested whether metrics of taxonomic and phylogenetic diversity differ between habitat types (17 units of forests and 17 units of grasslands) through generalized linear mixed models (GLMMs). At this scale, habitat type was used as a fixed factor and site (nine units) was used as a random factor (y ~ habitat type + (1|site)). We assumed a Poisson distribution for *S* and Gaussian distributions for *D*, *PD* and *PR* metrics fitted with the *fitdist* function in the *fitdistrplus* package (based on maximum likelihood estimation) [69]. We applied ANOVA to test the significance and obtained the χ^2 and *p*-values for each model.

We also fitted GLMMs with the same data distribution to test the responses of taxonomic and phylogenetic metrics to the local environmental variables in each habitat separately. We selected the model(s) that best explained the patterns based on the Akaike's information criterion corrected for small samples (AICc) [70]. For each response variable, we applied the complete additive model (with all variables), simple models with interaction (only between two variables), and the null models (y ~ 1 + (1|site)). The models with ΔAICc ≤ 2 were considered viable to explain the observed patterns. Additionally we calculated the conditional coefficient of determination $R^2_{(c)}$ for the selected models. The conditional R^2 represents the variance explained by both fixed and random factors [71]. All selected models were submitted to residual analysis to evaluate the adequacy of the error distribution. GLMMs were performed using the *glmer* function for *S* and *lmer* function for *D*, *PD* and *PR*, both with the *lme4* package [72]. The model selections based on AICc criteria and the conditional R^2 were implemented with the *MuMIn* package.

To verify whether environmental variables might be influencing species composition, we performed a forward selection analysis based on redundancy analysis (RDA) for forests and grasslands, separately. To reduce the effect of rare species, singletons (i.e. species with only one occurrence) were removed from this analysis [73]. Variables with $p \leq 0.05$ were selected as significant to explain the variation in ant composition. Forward selection was performed with the *vegan* package.

Regional predictors

At the regional scale, we used the mean value of the metrics between each forest-grassland ecotone for each site, totaling nine values. We did this since one site from the CC region had only one ecotone studied. In addition, each regional variable was obtained on a site level and not on an ecotone level (data from WorldClim). Then, we first tested whether metrics of taxonomic and phylogenetic diversity differ among physiographic regions using GLMMs as previously above. In these models, we used the region as a fixed factor while the sites were entered as a random factor (y ~ region + (1|site)). We apply the same distribution errors for each metric from the local scale and obtained the χ^2 and p-values. When a model showed significant differences, we performed Tukey post-hoc tests for comparisons among means with the *multcomp* package [74].

Subsequently, we evaluated the responses of taxonomic and phylogenetic metrics to regional environmental variables. To select the most suitable models we applied Akaike's information criterion corrected for small samples (AICc) as previously described for the local scale, considering the complete additive model, simple models with interaction, and the null model for each metric separately.

For ant taxonomic composition, we applied a forward selection analysis based on RDA following exactly the same procedures as explained for the local scale. Further, we verified whether, besides environmental variables, spatial variables also influenced species composition at the regional scale through partitioning analysis. For this, we submitted the PCNMs matrix also to forward selection. Then, we performed a variation partitioning analysis dividing the contribution of the total variance of species composition into four fractions, and tested their significance: [a] the component only explained by the environment (independent of the spatial variation); [b] the component explained by the environment that is also spatially structured (spatially structured environmental filtering); [c] the component explained only by space (independent of the environmental variation); and [d] the residual variation [75]. The variation partitioning analysis was carried out with the *varpart* function in the *vegan* package.

Results

Ant fauna

We sampled 10,906 ants, belonging to six subfamilies, 23 genera and 85 morphospecies (S2 Appendix). The richest subfamilies were Myrmicinae (46 spp.) and Formicinae (19 spp.), and the richest genera were *Pheidole* (18 spp.), *Camponotus* and *Crematogaster* (nine spp. each) and *Brachymyrmex* (eight spp.). *Pheidole radoszkowskii* Mayr, 1884, *Pheidole* nr. *pubiventris* Mayr, 1887 and *Solenopsis invicta* Buren, 1972 were the most frequent species (66, 65 and 35 occurrences, respectively). Sixty species were sampled in forests and 63 in grasslands. Twenty-two species were exclusive of forests while 25 were exclusive of grasslands. The SS region had the most ant species (53 spp.), followed by CA (48 spp.) and CC (40 spp.). Overall, 27 singletons were collected.

Taxonomic and phylogenetic diversity

Taxonomic and phylogenetic metrics did not differ between forests and grasslands (*S*: $\chi^2 = 0.27$, $p = 0.61$; *D*: $\chi^2 = 0.38$, $p = 0.54$; *PD*: $\chi^2 = 0.009$, $p = 0.93$; *PR*: $\chi^2 = 0.09$, $p = 0.76$). However, we found specific local variables explaining these metrics at each habitat. In forests, we found a positive relationship between soil surface air temperature and *S* ($R^2_{(c)} = 0.27$, Fig 2a), *D* ($R^2_{(c)} = 0.49$, Fig 2b), *PD* ($R^2_{(c)} = 0.51$, Fig 2c) and *PR* ($R^2_{(c)} = 0.67$, Fig 2d), meaning that sites with higher temperatures in the sampling moment also presented higher taxonomic and phylogenetic diversity (Table 1).

Table 1. Best-supported models (GLMMs) in forests.

Distribution	Response variable	Model	AICc	ΔAICc	df	Weight	$R^2_{(c)}$
Poisson	Species richness (*S*)						
		MTF	86.1	0.0	3	0.455	0.27
Gaussian	Simpson index (*D*)						
		MTF	-50.9	0.0	4	0.619	0.49
Gaussian	Faith's PD (*PD*)						
		MTF	218.8	0.0	4	0.729	0.51
Gaussian	PhyRao (*PR*)						
		MTF	-38.6	0.0	4	0.420	0.67

Best-supported models with ΔAICc ≤ 2 retained in forest habitats from forest-grassland ecotones in South Brazil. MTF-Soil Surface Air Mean Temperature of Forests (ºC).

In grasslands, we found *S* ($R^2_{(c)} = 0.27$, Fig 2e), *D* ($R^2_{(c)} = 0.31$) and *PR* ($R^2_{(c)} = 0.14$) negatively related to herbaceous vegetation height, and *S* ($R^2_{(c)} = 0.20$), *D* ($R^2_{(c)} = 0.75$, Fig 2f) and *PD* ($R^2_{(c)} = 0.82$) positively associated with tree density (Table 2). Furthermore, we also found, as possible models, herbaceous vegetation height combined with tree density explaining *S* ($R^2_{(c)} = 0.34$), *D* ($R^2_{(c)} = 0.64$) and *PD* ($R^2_{(c)} =$

0.85, Fig 2g and 2h). That is, grasslands with taller herbaceous vegetation presented lower numbers of ant species and phylogenetic diversity while grasslands with higher tree density increased ant taxonomic and phylogenetic diversity. *PR* was the only metric where the null model was selected (Table 2).

Table 2. Best-supported models (GLMMs) in grasslands.

Distribution	Response variable	Model	AICc	ΔAICc	df	Weight	$R^2_{(c)}$
Poisson	Species richness (*S*)						
		HVE	89.1	0.0	3	0.268	0.27
		TRD	90.0	0.9	3	0.173	0.20
		HVE + TRD	90.3	1.1	4	0.154	0.34
Gaussian	Simpson index (*D*)						
		TRD	-45.3	0.0	4	0.278	0.75
		HVE	-44.7	0.6	4	0.202	0.31
		HVE + TRD	-43.9	1.5	5	0.133	0.64
Gaussian	Faith's PD (*PD*)						
		HVE + TRD	215.1	0.0	5	0.418	0.85
		TRD	215.8	0.7	4	0.288	0.82
Gaussian	PhyRao (*PR*)						
		Null Model	-49.4	0.0	3	0.336	Null
		HVE	-48.3	1.1	4	0.197	0.14

Best-supported models with ΔAICc ≤ 2 retained in grassland habitats from forest-grassland ecotones in South Brazil. HVE-Herbaceous Vegetation Height (cm); TRD-Tree Density.

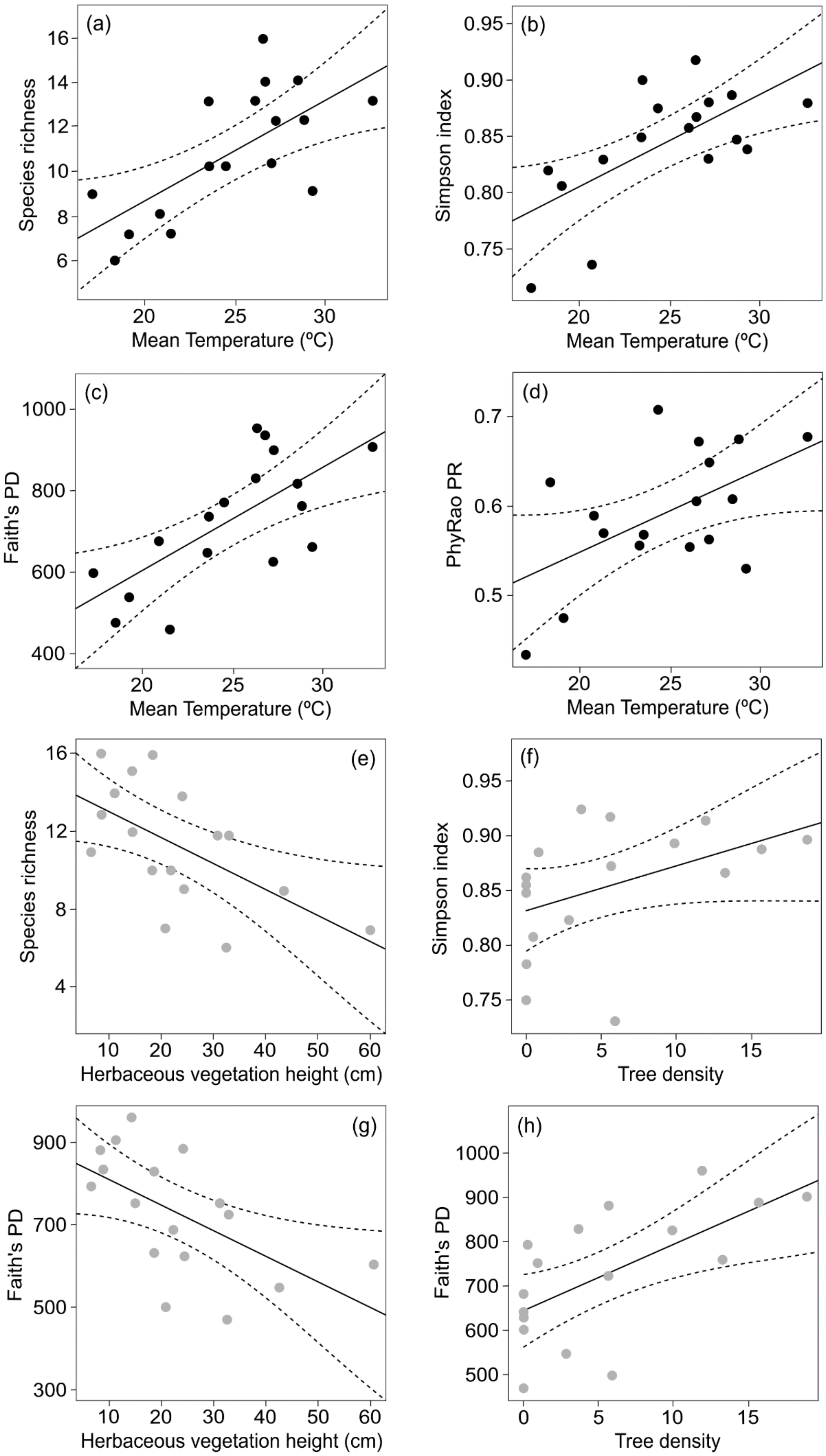

(a)
Species richness
6
8
10
12
14
16
20
25
30
Mean Temperature (ºC)
(b)
Simpson index
0.75
0.80
0.85
0.90
0.95
20
25
30
Mean Temperature (ºC)
(c)
Faith's PD
400
600
800
1000
20
25
30
Mean Temperature (ºC)
(d)
PhyRao PR
0.5
0.6
0.7
20
25
30
Mean Temperature (ºC)
(e)
Species richness
4
8
12
16
10
20
30
40
50
60
Herbaceous vegetation height (cm)
(f)
Simpson index
0.75
0.80
0.85
0.90
0.95
0
5
10
15
Tree density
(g)
Faith's PD
300
500
700
900
10
20
30
40
50
60
Herbaceous vegetation height (cm)
(h)
Faith's PD
500
600
700
800
900
1000
0
5
10
15
Tree density

Fig 2. Relationship between local variables and ant taxonomic and phylogenetic metrics in forest-grassland ecotones in South Brazil. The best generalized linear mixed models (ΔAICc = 0.0) using sites as a random factor: (a) to (d) plots represent relationships in forests (black dots) and (e) to (h) plots represent relationships in grasslands (grey dots).

At the regional scale, we found significant differences among regions for *S* (χ^2 = 15.6, $p = 0.05$, Fig 3a) and *PD* (χ^2 = 605.4, $p < 0.001$, Fig 3b), with ecotones from the SS region exhibiting more ant species and phylogenetic diversity than the CC region. At this scale, we did not find suitable models using our regional environmental variables to explain ant diversity. Only null models met the model selection criteria (Table 3).

Table 3. Best-supported models (GLMMs) at regional scale.

Distribution	**Response variable**	**Model**	**AICc**	**ΔAICc**	**df**	**Weight**	**$R^2_{(c)}$**
Poisson	Species richness (*S*)						
		Null Model	53.2	0.0	2	0.527	Null
Gaussian	Simpson index (*D*)						
		Null Model	-35.9	0.0	3	0.775	Null
Gaussian	Faith's PD (*PD*)						
		Null Model	113.9	0.0	3	0.846	Null
Gaussian	PhyRao (*PR*)						
		Null Model	-23.3	0.0	3	0.825	Null

Best-supported models with ΔAICc ≤ 2 retained in forest-grassland ecotones at the regional scale in South Brazil.

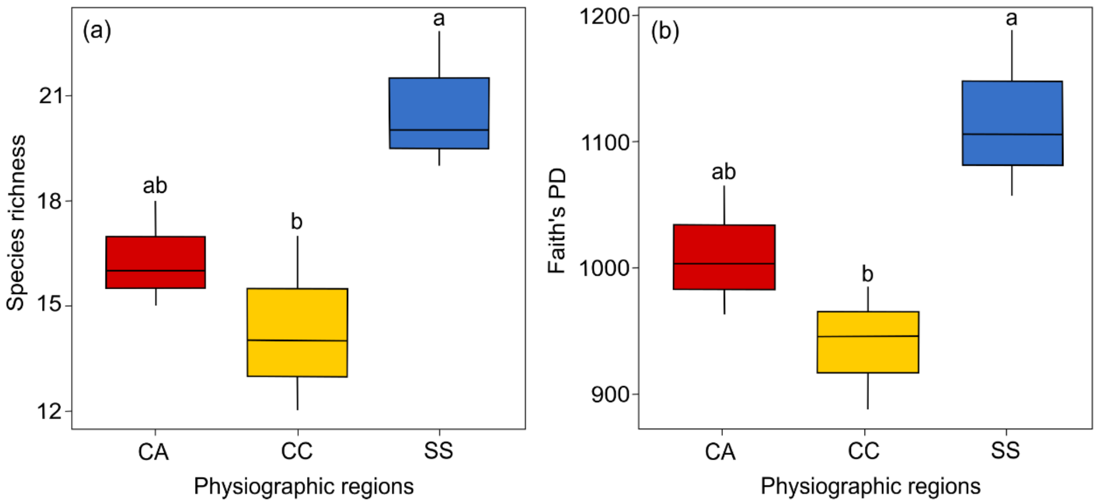


Fig 3. Boxplot showing ant species richness and phylogenetic diversity among physiographic regions in South Brazil. Forest-grassland ecotones from the SS region had more (a) ant species and (b) phylogenetic diversity than the CC region. Different regions of Rio Grande do Sul state: Campanha region - CA (red boxes), Campos de Cima da Serra region - CC (yellow boxes) and Serra do Sudeste region - SS (blue boxes). Tukey post-hoc tests (a) CA:CC ($p = 0.50$); CA:SS ($p = 0.11$); CC:SS ($p = 0.02$) and (b) CA:CC ($p = 0.34$); CA:SS ($p = 0.13$); CC:SS ($p = 0.01$).

Taxonomic and phylogenetic composition

Ant taxonomic composition was clearly different between forests and grasslands with 28% of the variation explained by the first two PCoA axes (Adonis: F = 2.67, $p < 0.01$, Fig 4a). However, we did not find differences in ant phylogenetic composition based on all 1000 phylogenetic trees permuted in PCPS analysis ($p_{(taxa\ shuffle)} > 0.05$ for all 1000 phylogenetic trees). The forward selection did not retain any local environmental variables associated with species composition either in forests or grasslands, only the habitat variable.

At the regional scale, we found differences in ant taxonomic composition among different physiographic regions (52% of the variation explained by the first two PCoA axes; Adonis: F = 2.35, $p < 0.01$, Fig 4b), but we also did not find differences in phylogenetic composition ($p_{(taxa\ shuffle)} > 0.05$ for all 1000 phylogenetic trees). The forward selection retained only annual mean temperature affecting ant taxonomic composition (df = 1, AIC = 54.838, F = 1.84, $p = 0.02$).

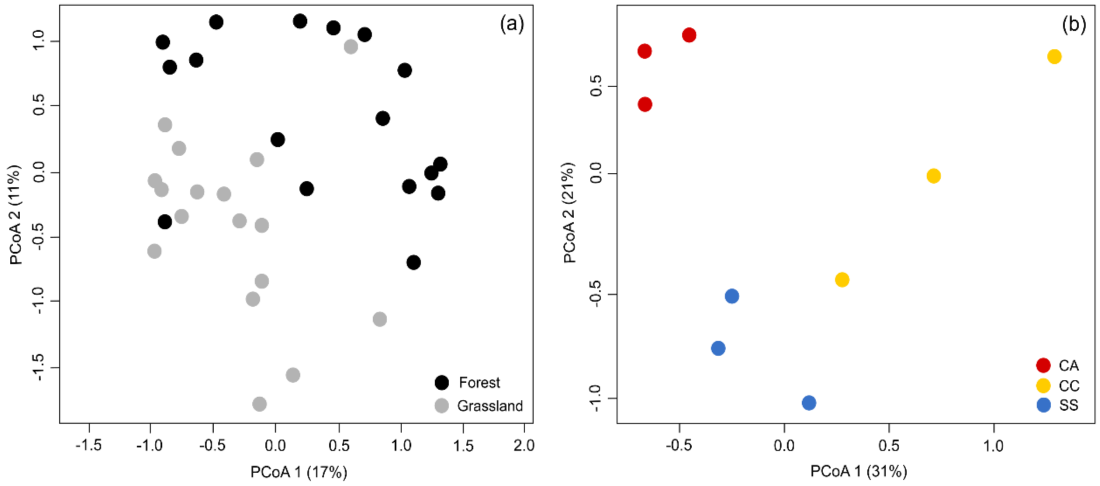


Fig 4. Ordination diagrams of ant species composition. (a) Principal Coordinates Analysis (PCoA) of forest-grassland ecotones based on ant species composition (frequency matrix) with Bray-Curtis similarity index. Black dots represent forest sampling sites and grey dots grasslands sampling sites. (b) PCoA at the regional scale with nine sites belonging to three physiographic regions. Different regions of Rio Grande do Sul state: Campanha region - CA (red dots), Campos de Cima da Serra region - CC (yellow dots) and Serra do Sudeste region - SS (blue dots).

After submitting all five PCNM vectors to forward selection, only two were retained: PCNM 2 (df = 1, AIC = 54.803, F = 1.87, $p = 0.01$) and PCNM 1 (df = 1, AIC = 54.283, F = 1.94, $p = 0.02$). Thus, variation partitioning analysis was carried out with only one environmental and two spatial variables. Overall, environmental and spatial variables explained 27% of the variation in ant taxonomic composition, i.e. 73% was unexplained (residuals). Of the 27% explained, 6% was purely environmental, 18% purely spatial and 3% spatially structured environmental variation. However, the purely environmental proportion was not significant, i.e. the variation in ant composition found among physiographic regions is largely due to spatial effects (Table 4).

Table 4. Variation partitioning analysis.

Fractions of variation	R^2	R^2_{ajd}	F	*p*
[a+b] Environmental + shared	0.21	0.09	1.84	0.02
[b+c] Spatial + shared	0.40	0.20	2.03	0.001
[a+b+c]	0.54	0.27	1.98	0.001
[a] Only environmental		0.06	1.53	0.12
[b] Environment spatially structured		0.03		
[c] Only spatial		0.18	1.84	0.01
[d] Residual		0.73		

Variation partitioning showing the relative influence of environmental variables [a] (only annual mean temperature), spatial variables [c] (PCNM 1 and 2), spatially structured environmental [b] and residual variation [d] on ant taxonomic composition in forest-grassland ecotones in South Brazil.

Discussion

At a local scale, our study did not show differences in ant diversity between adjacent grasslands and forests, corroborating both Pinheiro et al. [31] and Klunk et al. [32] for South Brazil, even when more than one stratum (ground, leaf litter and arboreal) is considered (as discussed by Klunk et al. [32]). Overall, studies have showed open ecosystems such as grasslands/savannas harboring higher ant diversity than forests in ecotones or landscape mosaics, for many regions of the world (e.g. [76-78]). In

Brazilian neotropical savannas this pattern also seems to occur, as showed by Camacho & Vasconcelos [79]. Mirroring the distinct forest and grassland plant communities, we found distinct ant communities in these habitats [76-78]. Despite short distances between sampling sites in different habitats (about 70 m), environmental filtering probably sort those species more adapted to or with a higher advantage when inhabiting each specific habitat [24]. We did not detect differences in ant phylogenetic composition between forest and grasslands, suggesting that no specific lineages evolved or have adapted to each environment in this region along its evolutionary history.

Within forests, we found the ground surface temperature as a driver of the local foraging ant diversity (both taxonomic and phylogenetic). This means that at higher temperatures during the day, or on hotter days, more forest ant species and ant lineages are actively exploring the environment. Ants are poikilothermic organisms, so their temperature depends on the surrounding environment, which determines their metabolic rates and foraging speed [80]. Closed-canopy habitats, such as forests, are typically shaded and cooler than open-canopy ecosystems (in our study, grasslands: mean 29.9ºC with max 36.2ºC; forests: mean 24.8ºC with max 32.7ºC), in addition to offering buffered microclimate conditions to the biota [81]. Thus, forests and grasslands may present ant species with different thermal niches [82], with forest ant communities more sensitive to the daily thermal oscillation in comparison to grassland species. Further studies should clarify this topic in detail with experiments and field observations.

In grasslands, ant diversity was driven by habitat structural properties. The diversity of ant species and evolutionary histories decreased with the height of herbaceous vegetation. Tall grassland vegetation usually characterizes ecosystems with low levels of disturbances (e.g. grazing and fire), where the biomass of a few dominant plant species, standing dead mass and a dense litter layer accumulates [27,83]. In this system, plant functional groups such as forbs (i.e. plants that typically present attractive resources to fauna) may be outcompeted by the dominant tussock grasses and disappear below them, decreasing the total local plant diversity. This process gradually modifies natural habitat characteristics and could decrease ant diversity due to habitat simplification and reduction in resource diversity [84]. In Neotropical Brazilian savannas (Cerrado biome), where fire helps to maintain biodiversity, fire suppression results in severe reduction of both plant and ant species (27% and 35% respectively [35]).

Another possible explanation for the negative relation between ant diversity and the height of herbaceous vegetation is the alteration of ant competitive interactions at the community level according to the grassland disturbance levels [85]. A relief in disturbance intensity (i.e. leading to taller vegetation) might trigger negative competitive interactions among ants, decreasing species coexistence. On the contrary, moderate or intense grazing (i.e. leading to shorter vegetation) might allow greater ant diversity by diminishing the dominance of particular species, as discussed by Moranz et al. [86] for tallgrass prairies from central North America. Furthermore, if we assume ant phylogenetic diversity as a potential proxy for ant functional diversity [20,29,30], our results are likely to indicate a decline of the ecological functions performed by ants in tall homogeneous grasslands.

Interestingly, we also found tree density on grasslands promoting ant species and phylogenetic diversity. The establishment of trees over the grass matrix progressing from the forest/grassland edge represents a classical forest expansion process [87]. Such process can clearly amplify habitat environmental/spatial heterogeneity, and thus the availability of ecological niches and resources for ants, affecting the dominance hierarchy [36]. By locally changing grassland environmental conditions at the ground level (e.g. solar incidence), it is plausible to expect treelet density allows species with different requirements to coexist [88], i.e. both forest and grassland-prone species. Similarly to our considerations on the correlations between vegetation height and grassland management, forest expansion processes usually take place on non-grazed or slightly grazed grasslands [87]. Knowledge about the responses of South Brazilian ant communities to grassland management and their relation with specific plant structures is strongly limited [37] and an intensive research effort on this topic is needed.

At a regional scale, we detected distinct ant species composition among ecotones in the three different physiographic regions in South Brazil (CA, CC and SS), which was mostly structured by space. Similarly, Arnan et al. [20] found spatial effects assembling ant communities across western and central Europe. Differences in ant species composition in South Brazilian grasslands were already reported for the CC region compared to the SS and CA regions by Dröse et al. [37]. However, we did not detect patterns in ant phylogenetic composition among the physiographic regions, indicating no divergence in specific ant lineages at this scale. Taxonomic differences, but not phylogenetics, indicate that macroscale variations in ant communities in South Brazil are primarily at the species rather than genus or subfamily level. Ant species can be strongly affected by spatial variables because of the low mobility and dispersal capacity of gynes [19]. Also, besides this limitation, different historical processes and landscape features may contribute to community dissimilarity [89]. In our study, higher altitudes and formation of gorges (CC region) and valleys (SS region) may have acted as dispersal barriers, increasing ant species dissimilarity among regions, but not affecting widespread ant lineages. Ultimately, although many studies report the water-energy dynamic hypothesis as elucidating ant macroscale patterns [12,13,18,38,39], the environmental variables considered in this study did not explain our regional patterns.

This can be attributed to (i) the omission of important spatially structured environmental variables (e.g. landscape habitat loss [84]), or even (ii) low site replication at the regional scale (n=9) that could be increasing the probability of committing Type II errors. Furthermore, stochastic processes might be at play in structuring these ant communities, meaning that species with similar ecological traits are allocated to the physiographic regions mostly by ecological drift and dispersal [19,20].

The standardized baiting sampling employed in this study provided fast and low cost surveys of ant communities from 34 forests and grasslands throughout a geographic extent of more than 553 km traveled in less than two months in the southernmost part of Brazil. This rapid ant assessment presented sufficient resolution to detect taxonomic and phylogenetic patterns in forest-grassland ecotones across different regions. Nevertheless, we cannot rule out completely that baiting may be leading to a biased assessment of communities in cases when behaviorally dominant ant species impede lonely or subordinate species from reaching the bait [90,91]. In this context, cryptic (confined to litter and soil) and rare ant species and lineages associated with forest or grassland habitats could have been underestimated in this study, hiding some patterns (e.g. phylogenetic composition). However, we do not have sufficient field evidence and knowledge about the species pool in this region to suggest this to be at work. In the Cerrado biome, pitfall traps and winkler extractions collected more ant species than sardine baits in forest and savanna physiognomies [92]. Despite that, baiting was as efficient as the other sampling methods to detect differences in species composition between physiognomies, indicating it to be adequate for studies comparing distinct habitats or conditions.

Conclusions

Our study unveils important aspects of ant community assembly and drivers in natural forest-grassland ecotones in South Brazil, considering taxonomic and phylogenetic perspectives, and may serve as a reference to other studies in these ecological transition systems worldwide. Here we showed that forests and grasslands are similar regarding ant diversity at ground level, but considerably different in terms of species composition (but not phylogenetic). In forests, the soil surface air temperature predicts foraging ant diversity. In grasslands, the height of herbaceous vegetation reduces ant diversity while treelet density from forest expansion processes clearly increases it. At a regional scale, space explained the most of the variance in species composition, and no environmental variables sufficiently explained ant diversity patterns at this scale. These results call for attention to the importance of these natural habitats and their biodiversity. All different habitat physiognomies from different regions of southern Brazil should warrant equally distributed conservation efforts to maximize biodiversity, but special care should be devoted to grasslands that are currently under major threat of conversion to other land use types.

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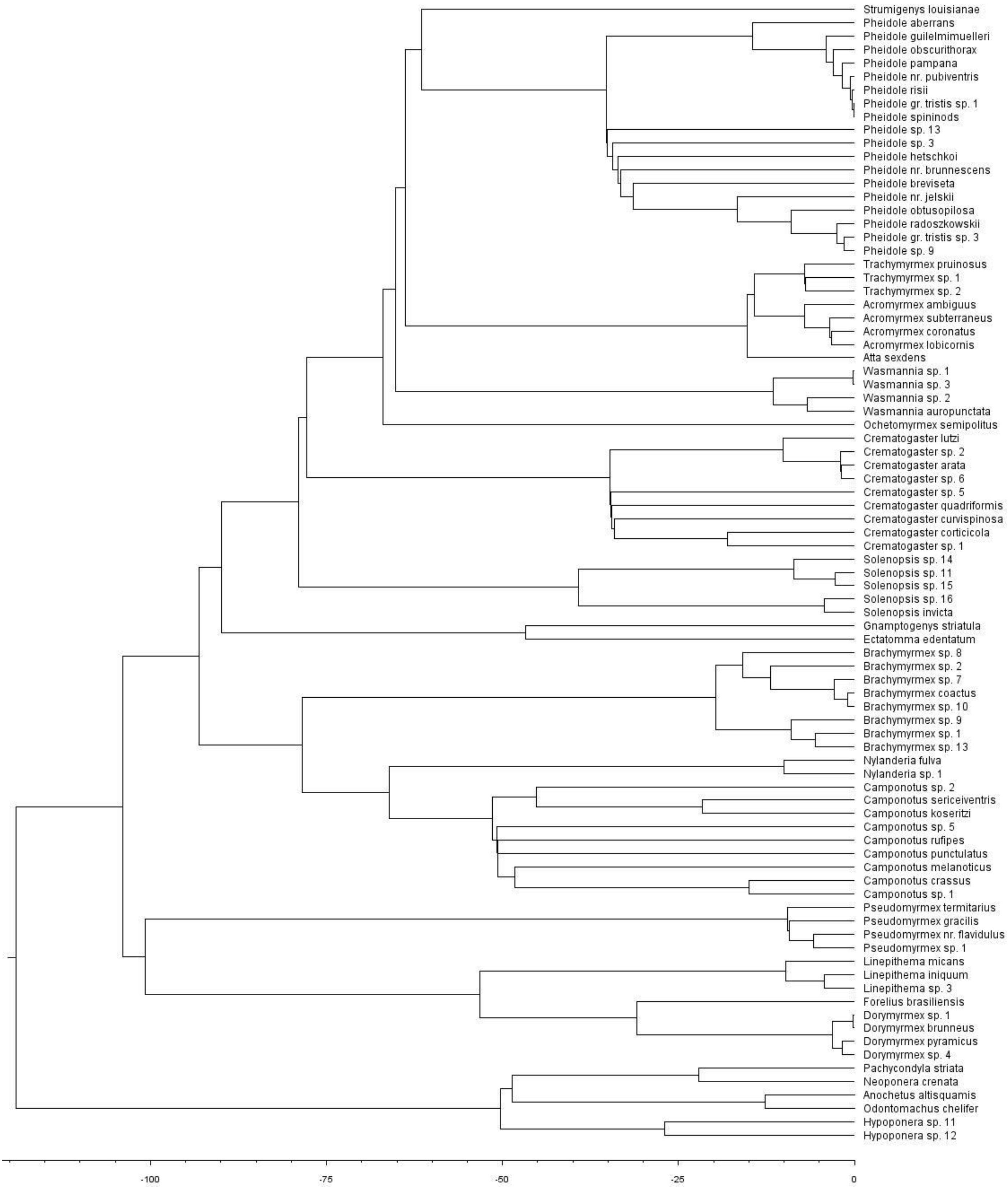
S1 Appendix. Phylogenetic tree from the 85 ant species collected in forest-grassland ecotones in South Brazil. An example of one of the 1000 phylogenetic trees built in the software Sunplin considering the relationships among species as phylogenetic uncertainly. Scale bar in millions of years before the present.



S2 Appendix. List of ant species recorded in forest-grassland ecotones in South Brazil. Numbers represent the total number of occurrences in the three physiographic regions (CA-Campanha; CC-Campos de Cima da Serra; SS-Serra do Sudeste) and habitats (F-forest; G-grassland). *New record to Rio Grande do Sul state, Brazil.

Ant species composition	**CA**		**CC**		**SS**	
	F	**G**	**F**	**G**	**F**	**G**
Dolichoderinae						
Dorymyrmex brunneus Forel, 1908	0	5	0	0	0	0
Dorymyrmex pyramicus (Roger, 1863)	0	1	0	0	0	0
Dorymyrmex sp. 1	0	0	0	0	0	1
Dorymyrmex sp. 4	0	0	0	0	0	2
Forelius brasiliensis (Forel, 1908)	0	0	0	0	0	1
Linepithema iniquum (Mayr, 1870)	0	0	1	0	15	7
Linepithema micans (Forel, 1908)	1	7	5	10	0	1
Linepithema sp. 3	0	0	0	0	0	2
Ectatomminae						
Ectatomma edentatum Roger, 1863	1	7	0	0	1	0
Gnamptogenys striatula Mayr, 1884	7	0	1	0	6	3
Formicinae						
Brachymyrmex coactus Mayr, 1887	0	0	0	0	0	3
Brachymyrmex sp. 1	1	4	0	0	1	17
Brachymyrmex sp. 2	0	0	0	0	1	4
Brachymyrmex sp. 7	0	0	1	9	0	0
Brachymyrmex sp. 8	1	0	5	0	5	0
Brachymyrmex sp. 9	0	0	1	0	0	0
Brachymyrmex sp. 10	3	4	2	1	5	3
Brachymyrmex sp. 13	0	0	0	0	1	1
Camponotus crassus Mayr, 1862	21	4	0	5	0	0
Camponotus koseritzi Emery, 1888	0	0	0	0	2	1
Camponotus melanoticus Emery, 1894	0	2	1	1	0	0
Camponotus punctulatus Mayr, 1868	0	0	0	6	2	11
Camponotus rufipes (Fabricius, 1775)	10	10	0	5	0	1
Camponotus sericeiventris (Guérin-Méneville, 1838)	2	0	0	0	0	0
Camponotus sp. 1	0	4	0	0	3	0
Camponotus sp. 2	0	0	0	7	4	12
Camponotus sp. 5	0	1	0	0	0	0
Nylanderia fulva (Mayr, 1862)	13	14	0	1	2	1
Nylanderia sp. 1	0	1	4	1	6	4
Myrmicinae						
Acromyrmex ambiguus (Emery, 1888)	0	0	0	0	0	1
Acromyrmex coronatus (Fabricius, 1804)	0	1	0	0	0	0
Acromyrmex lobicornis (Emery, 1888)	0	0	0	2	0	0
Acromyrmex subterraneus (Forel, 1893)	4	3	2	0	2	2
Atta sexdens (Linnaeus, 1758)	1	1	0	0	0	0
*Crematogaster arata** Emery, 1906	2	0	0	0	0	0
Crematogaster corticicola Mayr, 1887	1	0	0	0	6	2
*Crematogaster curvispinosa** Mayr, 1862	0	1	0	0	0	0
*Crematogaster lutzi** Forel, 1905	0	0	2	0	0	0
Crematogaster quadriformis Roger, 1863	1	10	0	3	1	9
Crematogaster sp. 1	0	2	0	0	0	1

Crematogaster sp. 2	0	1	0	0	0	2
Crematogaster sp. 5	1	0	0	0	0	0
Crematogaster sp. 6	0	1	0	0	0	0
Ochetomyrmex semipolitus Mayr, 1878	1	0	0	0	0	0
Pheidole gr. *tristis* sp. 1	6	0	0	2	15	10
Pheidole gr. *tristis* sp. 3	1	3	0	0	0	0
Pheidole aberrans Mayr, 1868	0	0	0	0	0	1
Pheidole breviseta Santschi, 1919	3	10	8	2	7	2
Pheidole nr. *brunnescens* Santschi, 1929	2	4	0	0	0	0
*Pheidole guilelmimuelleri** Forel, 1886	0	0	0	0	1	0
Pheidole hetschkoi Emery, 1896	0	0	1	0	1	0
Pheidole nr. *jelskii* Mayr, 1884	0	0	0	3	0	4
Pheidole obscurithorax Naves, 1985	0	1	0	0	0	0
Pheidole obtusopilosa Mayr, 1887	1	3	1	3	2	11
Pheidole pampana Santschi, 1929	2	2	5	7	5	5
Pheidole nr. *pubiventris* Mayr, 1887	7	0	28	2	19	9
Pheidole radoszkowskii Mayr, 1884	25	14	0	2	10	15
Pheidole risii Forel, 1892	0	0	0	0	4	2
Pheidole spininods Mayr, 1887	0	0	0	0	0	2
Pheidole sp. 3	4	4	0	0	4	6
Pheidole sp. 9	0	0	0	1	0	0
Pheidole sp. 13	0	0	0	0	1	0
Solenopsis invicta Buren, 1972	3	15	1	8	2	6
Solenopsis sp. 11	0	1	0	7	0	7
Solenopsis sp. 14	0	1	6	4	13	6
Solenopsis sp. 15	0	0	0	0	3	0
Solenopsis sp. 16	1	0	0	0	0	0
Strumigenys louisianae Roger, 1863	1	0	0	0	0	0
Trachymyrmex pruinosus (Emery, 1906)	0	0	0	1	0	0
Trachymyrmex sp. 1	0	0	0	0	1	0
Trachymyrmex sp. 2	0	0	0	0	2	0
Wasmannia auropunctata (Roger, 1863)	2	3	0	0	1	4
Wasmannia sp. 1	0	0	1	6	2	1
Wasmannia sp. 2	1	0	0	0	0	0
Wasmannia sp. 3	0	0	1	0	0	0
Ponerinae						
Anochetus altisquamis Mayr, 1887	0	0	1	0	0	0
Hypoponera sp. 11	0	0	0	1	0	0
Hypoponera sp. 12	0	0	3	0	0	0
Neoponera crenata (Roger, 1861)	0	0	2	0	0	0
Odontomachus chelifer (Latreille, 1802)	0	0	0	0	1	0
Pachycondyla striata Smith, 1858	8	0	1	1	11	1
Pseudomyrmecinae						
Pseudomyrmex nr. *flavidulus* (Smith, 1858)	0	0	0	1	0	1
Pseudomyrmex gracilis (Fabricius, 1804)	1	0	0	0	0	0
Pseudomyrmex termitarius (Smith, 1855)	0	0	0	1	0	0
Pseudomyrmex sp. 1	5	1	0	0	2	1
Total species	**48 species**		**40 species**		**53 species**	

S1 Table. Local environmental variables sampled in forests from forest-grassland ecotones in Rio Grande do Sul state, Brazil. COP-Canopy Openness (%); LIT-Litter Depth (cm); MOF-Air Moisture of Forests (%); MTF-Soil Surface Air Mean Temperature of Forests (ºC).

Physiographic region	Sites	Ecotone	COP	LIT	MOF	MTF
Campanha	Santana do Livramento	A	14.24	2.06	68.42	23.52
		B	11.87	1.67	59.05	26.10
	Santo Antônio das Missões	A	13.00	2.12	69.10	27.22
		B	11.57	1.68	67.49	27.24
	São Francisco de Assis	A	9.90	4.43	78.28	20.81
		B	9.22	0.81	63.63	24.43
Campos de Cima da Serra	Cambará do Sul	A	14.29	4.68	86.23	19.13
		B	22.60	2.06	88.93	17.09
	Jaquirana	A	10.79	1.62	76.27	21.44
		B	10.77	2.12	58.50	26.65
	São Francisco de Paula	A	-	-	-	-
		B	8.44	5.68	77.86	18.42
Serra do Sudeste	Encruzilhada do Sul	A	11.96	1.68	60.76	29.33
		B	10.38	2.00	65.23	28.55
	Herval	A	15.83	2.37	71.59	26.51
		B	12.29	2.75	71.18	23.56
	Santana da Boa Vista	A	12.60	1.62	63.61	28.82
		B	30.09	2.31	55.05	32.69

S2 Table. Local environmental variables sampled in grasslands from forest-grassland ecotones in Rio Grande do Sul state, Brazil. HVE-Herbaceous Vegetation Height (cm); MOG-Air Moisture of Grasslands (%); MTG-Soil Surface Air Mean Temperature of Grasslands (ºC); SHD-Shrub Density; TRD-Tree Density.

Physiographic region	Sites	Ecotone	HVE	MOG	MTG	SHD	TRD
Campanha	Santana do Livramento	A	24.23	60.23	26.98	39.37	0
		B	14.33	51.33	36.05	7.87	11.87
	Santo Antônio das Missões	A	20.66	50.67	36.17	3.37	5.87
		B	30.76	61.65	34.96	6.37	13.25
	São Francisco de Assis	A	14.86	58.80	26.78	0	0.87
		B	21.73	50.99	31.91	1.37	0
Campos de Cima da Serra	Cambará do Sul	A	32.26	53.54	28.16	24.62	0
		B	11.06	79.23	18.64	7.87	18.75
	Jaquirana	A	18.23	74.14	20.45	2.50	0
		B	42.00	45.28	34.04	0	2.87
	São Francisco de Paula	A	-	-	-	-	-
		B	59.86	56.55	29.52	8.37	0
Serra do Sudeste	Encruzilhada do Sul	A	6.50	59.31	32.57	4.75	0.25
		B	8.56	65.83	28.49	1.25	9.87
	Herval	A	32.40	64.88	30.31	28.87	5.62
		B	23.90	65.56	27.17	24.12	15.62
	Santana da Boa Vista	A	18.36	62.82	30.36	10.12	3.62
		B	8.33	51.32	35.84	4.75	5.62

S3 Table. Regional variables obtained from WorldClim (V1 to V5) and Shuttle Radar Topographic Mission (V6) to three different physiographic regions from Rio Grande do Sul state, Brazil. V1-Annual Mean Temperature (ºC); V2-Temperature Seasonality (ºC); V3-Minimum Temperature of Coldest Month (ºC); V4-Annual Precipitation (mm); V5-Precipitation Seasonality (%); V6-Mean Altitude (m).

Physiographic region	Sites	V1	V2	V3	V4	V5	V6
Campanha	Santana do Livramento	18.5	443.5	6.9	1588	10	279
	Santo Antônio das Missões	21.1	393.9	9.8	1907	12	113
	São Francisco de Assis	19.0	407.9	8.1	1876	9	162
Campos de Cima da Serra	Cambará do Sul	14.6	286.1	6.3	1876	10	979
	Jaquirana	16.0	291.0	7.2	2048	9	836
	São Francisco de Paula	14.9	301.6	6.6	1957	8	835
Serra do Sudeste	Encruzilhada do Sul	18.1	345.8	8.9	1616	10	382
	Herval	17.4	389.8	6.7	1340	12	244
	Santana da Boa Vista	19.6	360.3	10.1	1577	12	93

S4 Table. Variance inflation factor (VIF) table with local environmental variables sampled in (a) forests and (b) grasslands from forest-grassland ecotones in Rio Grande do Sul state, Brazil. Bold numbers means multicollinearity between variables (VIF > 3). COP-Canopy Openness (%); LIT-Litter Depth (cm); MOF-Air Moisture of Forests (%); MTF-Soil Surface Air Mean Temperature of Forests (ºC); HVE-Herbaceous Vegetation Height (cm); MOG-Air Moisture of Grasslands (%); MTG-Soil Surface Air Mean Temperature of Grasslands (ºC); SHD-Shrub Density; TRD-Tree Density.

(a)

	COP	LIT	MOF	MTF
COP				
LIT	1.012			
MOF	1.001	1.439		
MTF	1.053	1.445	**4.683**	

(b)

	HVE	MOG	MTG	SHD	TRD
HVE					
MOG	1.085				
MTG	1.009	**3.039**			
SHD	1.051	1.024	1.038		
TRD	1.074	1.201	1.008	1.000	

S5 Table. Variance inflation factor (VIF) table with regional variables obtained to three different physiographic regions from Rio Grande do Sul state, Brazil. Bold numbers means multicollinearity between variables (VIF > 3). V1-Annual Mean Temperature (ºC); V2-Temperature Seasonality (ºC); V3-Minimum Temperature of Coldest Month (ºC); V4-Annual Precipitation (mm); V5-Precipitation Seasonality (%); V6-Mean Altitude (m).

	V1	V2	V3	V4	V5	V6
V1						
V2	2.341					
V3	**3.052**	1.087				
V4	1.091	1.378	1.006			
V5	1.632	1.199	1.385	1.617		
V6	**7.507**	**3.642**	1.881	1.432	1.686	

S6 Table. Geographical coordinates obtained from one central point between ecotones in each site.

Physiographic region	Sites	Latitude	Longitude
Campanha	Santana do Livramento	-30.719103	-55.512003
	Santo Antônio das Missões	-28.530828	-55.423558
	São Francisco de Assis	-29.628075	-55.137556
Campos de Cima da Serra	Cambará do Sul	-29.164836	-50.057197
	Jaquirana	-29.016753	-50.395103
	São Francisco de Paula	-29.483322	-50.204753
Serra do Sudeste	Encruzilhada do Sul	-30.561036	-52.562158
	Herval	-32.093058	-53.621503
	Santana da Boa Vista	-30.932525	-53.023883

CAPÍTULO II

Geographical gradients in leaf-litter ant diversity and body size in riparian forests from South Brazilian grasslands[2]

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Geographical gradients in leaf-litter ant diversity and body size in riparian forests from South Brazilian grasslands

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Running title: Geographical gradient on leaf-litter ants

Abstract

1. Latitudinal and altitudinal gradients are classic ecological patterns of biodiversity investigated worldwide. However, understanding the predictors underlying these patterns is still a challenge.

2. We sampled leaf-litter ant species in riparian forests at 12 sites in South Brazil to investigate geographical gradients and potential environmental predictors. Here, we used interspecific variation of body size and a triple approach with taxonomic, functional and phylogenetic diversity (TD, FD, and PD respectively). Geographic variables investigated were latitude and altitude and environmental predictors used are related to energy, water, and primary productivity.

3. We recorded 120 leaf-litter ant species. TD, FD, and PD follow the classical latitudinal pattern, and the interspecific variation in mean body size show the opposite pattern. Ant diversity and ecological traits diversity were positively correlated with precipitation and productivity. That is, higher species diversity and potential ecological functions were found with decreasing latitude and increasing precipitation and productivity. PD showed an unusual pattern with mean annual temperature: more ant lineages were found in lower temperatures. Mean body size had not environmental variables associated.

4. Our results for ant diversity and functional traits corroborate the expected pattern for forest-associated ant species with precipitation in the Neotropical region, showing that the latitudinal gradient can be considered an indirect factor affecting ant community assembly. Possibly, the facilitated dispersion and colonization due to the proximity with more forest patches may explain our pattern with more ant lineages at sites with lower temperature. Finally, body size follows a contrary latitudinal pattern, but temperature was not responsible for this pattern.

Key words: species diversity; functional diversity; phylogenetic diversity; altitude; latitudinal gradient.

Introduction

Patterns of species diversity and their correlation to biogeography, particularly altitude and latitude, have been investigated worldwide (Stevens 1989, 1992; Rohde 1992; Roy et al. 1998; Hillebrand 2004). Biological community assembly along latitudinal and altitudinal gradients may be driven by climatic and other environmental characteristics, as well as biotic interactions and stochastic processes (McCain & Grytnes 2001; Willig et al., 2003). However, understanding these gradients of biodiversity and potential predictors associated has been and still is a challenge. Several hypotheses were proposed to explain these geographic patterns, that can be summarized in: (i) temperature and energy – metabolic theory (e.g. Allen et al., 2002); (ii) water-energy dynamics (e.g. Hawkins et al., 2003); (iii) productivity (e.g. Mittelbach et al., 2001); (iv) area size (e.g. Rosenzweig, 1995) and (v) the mid-domain effect (e.g. Colwell et al., 2004). Based on these hypotheses, independent of the process or variable associated with geographic gradients, it is supposed that higher species diversity will be found at lowest latitudes and altitudes (McCain & Grytnes 2001; Willig et al., 2003).

Ecogeographic rules are applied to biogeography patterns of species variation (intra or interspecific), especially with latitude. Bergmann's rule is one of the most tested ecogeographic rules (e.g. Meiri & Dayan 2003; Vinarski 2014). It states that body size is inversely proportional to temperature, and due to this, body size may increase with latitude (Bergmann 1848). That is, larger animals have smaller surface area in relation to body volume, then these organisms conserve heat more efficiently (expected pattern to be found at highest latitudes); smaller animals have higher surface area in relation to body volume, lose heat more easily, and are expected to be found at lowest latitudes. In the past, Bergmann's rule was commonly tested with endothermic organisms because they are more efficient to maintain a constant body temperature compared with ectothermic species (Vinarski 2014). However, recent studies have reported that ectothermic organisms follow the Bergmann’s rule patterns (e.g. Osorio-Canadas et al. 2016; Bernadou et al. 2016). For instance, a global data set on ant body size show a negative relationship with temperature (Gibb et al. 2018). Understanding body size distributions and their relationship with ecological processes and ecosystem services may contribute with current practical issues, as climate change and anthropic disturbances (Sheridan & Bickford 2011; Gibb et al. 2018).

Ants are organisms with widespread distribution in most terrestrial ecosystems (Hölldobler & Wilson 1990; Folgarait 1998), and geographical patterns as well as environmental variables associated with ant diversity have been explored for this group in recent years, both at the regional and continental/global scale. For instance, while is expected that body size of ants increase with elevation (Bernadou et al., 2016), ant diversity is reduced (Szewczyk & McCain; 2016), and it is especially due to decreases in temperature (Sanders et al., 2007; Reymond et al., 2013). Similarly, while ant body size increase with latitude (Cushman et al., 1993, Gibb et al. 2018), ant diversity decreases (Dunn et al., 2009; Jenkins et al., 2011), following the classical latitudinal pattern (Willig et al., 2003). Recently, studies have showed that this high number of ant species and evolutionary lineages present at the tropics is due to diversification time (tropical conservatism hypothesis – TCH) and not to diversification rate (diversification rate hypothesis – DRH) (Pie, 2016; Economo et al., 2018). That is, regions outside the tropics, mainly the northern hemisphere, are diversifying at similar rates than regions in the tropics. Furthermore, warmer and wetter regions are expected to have more ant species than warmer and drier or cooler regions (Weiser et al., 2010; Jenkins et al., 2011). Finally, as a surrogate of water-energy balance, areas with high plant productivity may increase ant diversity (Kaspari et al., 2000; Paknia & Pfeiffer, 2012; but see also Sanders et al., 2007).

Although many studies had investigated geographical patterns on ant communities, most of them only address taxonomic diversity – TD (e.g. species richness). Recently, the use of other biodiversity metrics have been increased, as ecological and historical approaches to understand ant assemblage diversity use ecological traits (functional diversity – FD) and phylogenetic trees (phylogenetic diversity – PD). For instance, ant functional diversity may increase with productivity and vegetation type (Arnan et al., 2014) and decrease with altitude (Reymond et al., 2013), whereas ant phylogenetic diversity is more clustered in high latitudes (Economo et al., 2018) and elevations (Machac et al., 2011; Smith et al., 2014). If functional traits are evolutionarily conserved, i.e. they present phylogenetic signal, a strong correlation between FD and PD would be expected (Webb et al., 2002). Tucker et al. (2018) showed that including more traits to calculate FD strongly increases its correlation with PD. Exploring more diverse biodiversity aspects in ecological studies is an important and necessary point, which may result in different and better explanations for detected processes and patterns.

Here we investigated geographical patterns in leaf-litter ant communities from riparian forest. Specifically, we explored patterns in taxonomic, functional and phylogenetic diversity, and interspecific body size variation (Bergmann's rule), considering the distribution region of South Brazilian Grassland ecosystems. However, there is a particular geographic characteristic in this region: mean altitude above sea level increases markedly with decreasing latitude (see Fig. 1). Due to the high negative correlation (r = -0.799, $p < 0.001$) and the fact that we do not have a complete altitudinal gradient, we specifically investigated in this study the latitudinal gradient in ant communities. We ask if ant diversity and interspecific variation in body size would be assembly in a (i) latitudinal gradient, and (ii) which potential environmental variables might be beyond these patterns. We chose three main environmental variables related to classical hypothesis: (i) mean annual temperature (energy hypothesis), (ii) annual precipitation (water-energy dynamics) and (iii) annual actual evapotranspiration (AET) (productivity hypothesis). Although the opposite latitudinal pattern was recorded for ant communities in Neotropical region (Silva & Brandão, 2014; Vasconcelos et al., 2018), we expect found the classical latitudinal gradient with annual precipitation related. If the temperature is the main driver of body size (with an inverse pattern: larger body in colder regions) and we have a strong positive correlation between latitude and temperature, we expect find the opposite latitudinal pattern (larger body size at lowest latitudes), and mean annual temperature as the main predictor of body size.

Materials and Methods

Study Area

We performed standardized sampling in riparian forests at 12 sites in South Brazil (Fig. 1). Sites sampled in the southern range (latitude 28º33’ and above) belong to Pampa biome, while the more northern sites (latitude 28º51’ and below) belong to Atlantic Forest biome. Seven sites were sampled in the Pampa biome and five sites in the Atlantic Forest biome. Riparian forests sampled are localized in natural grassland matrices with livestock grazing. These forest habitats are important natural environments offering several ecosystem services such as providing clean water and flood control, serving as a unique habitat for many species or as natural corridors to biodiversity (Naiman et al., 2010). In open ecosystems, as grasslands and savannas, riparian forest may represent the only arboreal species in the region.

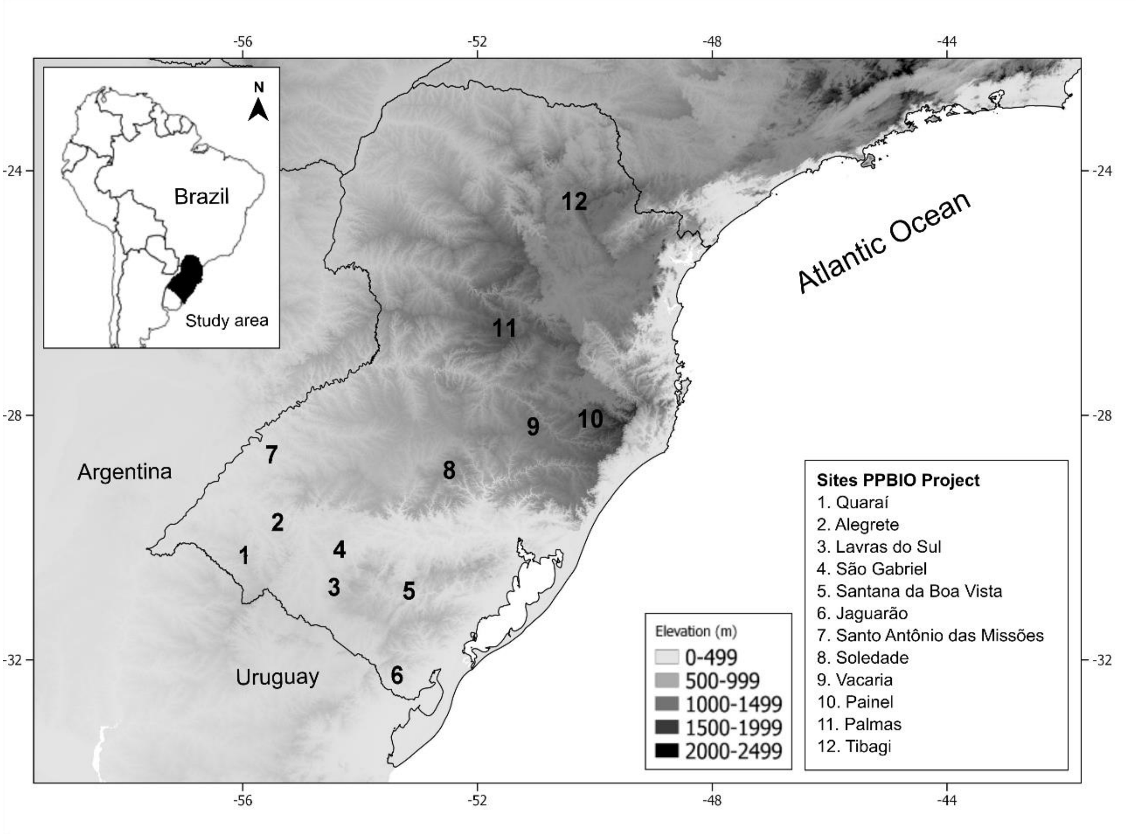

Figure 1. Map of study area showing the sites distribution and the latitudinal and altitudinal gradients in South Brazil.

The sites in our study encompass 08º20’ of latitude (about 913 km apart) and 05º47’ of longitude (about 621 km apart). Average altitude in these sites ranged from 92 to 1,241 m a.s.l. (Jaguarão and Palmas municipalities, respectively). There is a negative correlation between latitude and altitude (r = -0.799, p < 0.01), where the high altitudes are found in the lowest latitudes (northern region of this study). Mean annual temperature at the sites are positively correlated with latitude (r = 0.659, p = 0.02, Fig 2a) and negatively with altitude (r = -0.955, p = 0.01, Fig 2b). Annual precipitation is weakly related to latitude, in a negative relationship (r = -0.515, p = 0.06, Fig 2c) and not correlate with altitude (r = 0.438, p = 0.15, Fig 2e). Plant productivity (AET) follows a latitudinal gradient of negative correlation (r = -0.731, $p < 0.01$, Fig 2e), but not altitudinal (r = 0.321, p = 0.30, Fig 2f). More details about geographical and environmental variables are available in Table S1.

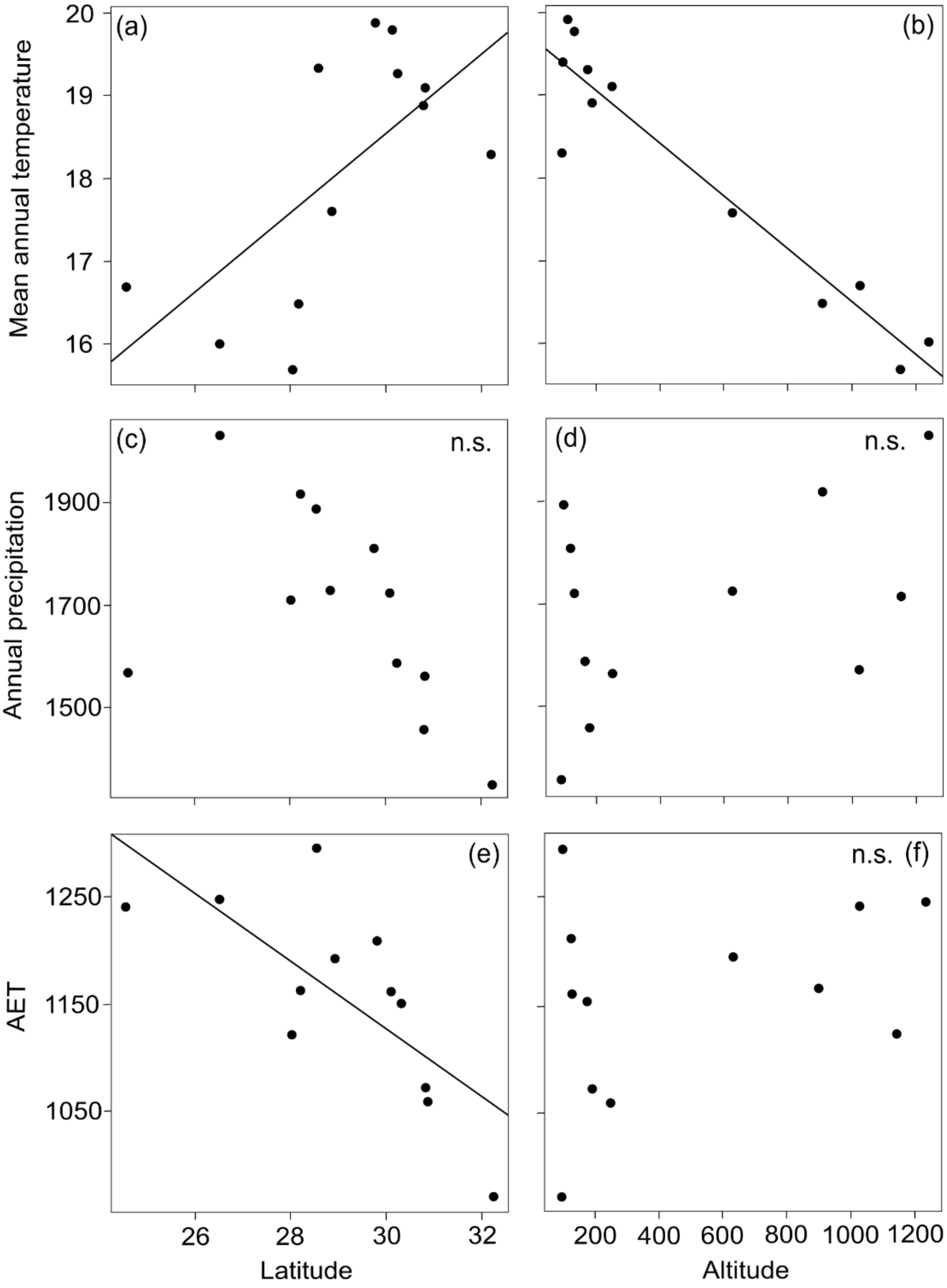

Figure 2. Simple correlation between geographical and environmental variables: mean annual temperature against (a) latitude and (b) altitude; annual precipitation against (c)

latitude and (d) altitude; plant productivity (AET) against (e) latitude and (f) altitude. n.s. (non-significant).

Sampling Design

At each site, we sampled three riparian forests (totaling 36 forests) between October 2013 and May 2016. We established in each riparian forest a 100 m line with five equidistant sampling points, and about 5 m far from the river. At each sampling point, during the day and under dry weather, we collected two samples of leaf-litter with a 30 cm radius circular sampling. These two circular samples at each point were pooled, forming a single sampling unit. Leaf-litter from each sample unit was sifted through a coarse mesh screen of 1 cm grid size to remove and separate the largest fragments from the ants. Ant individuals were stored at the Laboratório de Ecologia de Interações (LEIN) in Universidade Federal do Rio Grande do Sul (UFRGS).

Ant genera identification was based on Baccaro et al. (2015). Ant species identification was done with specific literature and direct comparisons with specimens in scientific ant collections in LEIN and the Entomological Collection Padre Jesus Santiago Moure of the Universidade Federal do Paraná (DZUP). Vouchers are deposited in ant collections of LEIN and DZUP.

Ant Functional Data

To estimate ant functional diversity, we considered morphological traits. We measured at least one ant individual per sample unit (the two circular leaf-litter samplings) from each species. Only minor workers were measured due to the polymorphism of some species. We selected six ant morphological traits to describe ecological functions in leaf-litter habitat: (i) Weber's (mesosoma) length; (ii) hind femur length; (iii) mandible length; (iv) scape length; (v) compound eye length and (vi) interocular distance.

(i) Weber's length was used as a proxy for total body length (Weiser & Kaspari, 2006); ant species with larger bodies can explore and forage environments with open conditions, while species with smaller bodies can access finer grains in closed habitats (e.g. leaf-litter in forests) (Silva & Brandão 2010; Gibb & Parr, 2013).
(ii) Femur length is also related to habitat complexity; longer legs are associated with simple and/or planar environments (Gibb & Parr, 2013; Parr et al. 2017).
(iii) Mandible length is related to predation; ants with longer mandibles are expected to be predators; longer mandibles = larger preys (Silva & Brandão 2010; Parr et al. 2017).
(iv) Scape length represents sensory abilities (e.g. pheromone); longer scapes may be more efficient to follow pheromone trails (Weiser & Kaspari, 2006).
(v) Eye length is associated with abilities to search food; it is mainly related to predator species (Silva & Brandão, 2010; Parr et al. 2017).
(vi) Interocular distance can influence the visual of predators species (Silva & Brandão, 2010).

All traits were divided by Weber's length to control for relative body size measurement. Exploring Bergmann's rules, we also used Weber's length as a measure to represent the body size of each species (Weiser & Kaspari, 2006).

Ant Phylogenetic Data

Currently, a full species-level phylogeny is not available for ants. The worldwide phylogenetic hypothesis proposed by Moreau & Bell (2013) considering all extended subfamilies and genera is the best approach thus far. After this publication, other authors proposed to resolve the phylogenetic relationships within some subfamilies (also genus-level), as for Myrmicinae, the larger subfamily of Formicidae (Ward et al., 2015). Therefore, we used these two publications (Moreau & Bell, 2013; Ward et al., 2015) with time-calibrated phylogeny to build a genus-level phylogenetic tree for the species recorded in our study with Phylocom 4.2 software (Webb et al., 2008). All leaf-litter ant species recorded were inserted in this tree as polytomies. Then, we used the software Sunplin (Martins et al., 2013) to generate randomly 1000 potential trees considering the relationships among species within each genus as phylogenetic uncertainty. We provide an example of one of the 1000 phylogenetic trees in Appendix S1.

Phylogenetic Signal in Morphological Traits

To verify phylogenetic signal in the ant morphological traits measured, we used Pagel's λ (Pagel, 1999), which assumes a Brownian motion (BM) model of trait evolution. We calculated the significance of signal using a likelihood ratio test based on the minimum values to estimate the probability that the observed λ value differs from the null λ of zero. The *lambda* values computed can range from 0 to 1, with values close or equal to 0 meaning absence of phylogenetic signal, while values close or equal to 1 mean phylogenetic signal present in the traits. The λ values were calculated for each morphological trait in each one of the 1000 phylogenetic trees with the *phylosig* function in the *phytools* package (Revell, 2012).

Ant diversities

To describe ant taxonomic (TD), functional (FD) and phylogenetic (PD) diversity we calculated Simpson index, Functional Rao and Phylogenetic Rao quadratic entropy, respectively. This approach is able to compare these diversity components in the same mathematical framework (Bello et al. 2010). We calculated Simpson index based on occurrences of ant species. FD consider trait distance among species while PD consider the phylogenetic distance, both weighted on the proportion of the occurrences of ant species. We used the 1000 phylogenetic trees generated by randomization to calculate the mean value of PD. All metrics were calculated with SYNCSA package in R (Debastiani & Pillar 2012).

Geographic and Environmental Variables

To describe geographic patterns in leaf-litter ant communities, we selected latitude and mean altitude (elevation above sea level). We determined the latitude coordinates of all the sites from the central point among the three sampled riparian forests. Mean altitude of each site was obtained from Shuttle Radar Topographic Mission data available at CIAT-CSI database (Jarvis et al. 2008). For environmental data, we chose three variables related with specific hypotheses as explained above. Mean annual temperature and annual precipitation were obtained from WorldClim - Global Climate Data (http://www.worldclim.org) (Hijmans *et al*., 2005) at 1 km² resolution. Furthermore, as a measure of water-energy balance closely associated with plant productivity, we used the annual actual evapotranspiration (AET). AET was obtained from Global High Resolution Soil-Water Balance at CGIAR-CSI database also at 1 km² resolution (Trabucco & Zomer, 2010).

Data analysis

For the purpose of this study, we considered the 12 sites as sampling units. For this, we pooled ant data from the three riparian forests at each site. Geographic and environmental variables were obtained also at the site scale. All variables were converted to Z-scores (*scale* function in the R software environment) prior to analysis (R Development Core Team, 2018).

Regarding the geographical gradients, we decided to consider only latitude in further analysis due to the high negative correlation with altitude ($r = -0.799$, $p < 0.01$). Another criterion to use latitude was because we did not evaluate sites in an elevational gradient (e.g. along with a mountain range). Mean annual temperature, annual precipitation, and annual actual evapotranspiration did not show a high correlation among them and were maintained in the analysis.

To evaluate the responses of ant taxonomic (TD), functional (FD) and phylogenetic (PD) diversity and the interspecific variation in body size to the geographic and environmental variables, we performed generalized linear mixed models (GLMMs). We used the sampling month (i.e. categorical variable describing the month that samples occurred, independently of the year) as a random factor to avoid a temporal bias in the results. We assumed a Gaussian distribution for TD, FD, PD, and body size fitted with the *fitdist* function in the *fitdistrplus* package, based on maximum likelihood estimation (Delignette-Muller & Dutang 2015).

First, we tested the responses of ant diversities and body size to latitudinal gradient. To identify the models that best explain the patterns, we used the Akaike's information criterion corrected for small samples (AICc) (Burnham & Anderson 2002). For each response variable (TD, FD, PD, and body size), we applied the latitudinal model (y ~ latitude + (1|sampling month)) and the null model (y ~ 1 + (1|sampling month)). We considered that models with ΔAICc $\leq$ 2.0 are equally viable to explain the observed patterns. Selected models were submitted to residual analysis to evaluate the adequacy of the error distribution. For each selected models, we calculated the conditional coefficient of determination $R^2_{(c)}$. The conditional R^2 represents the variance explained by both fixed and random factors (Nakagawa & Schielzeth, 2013).

Subsequently, we evaluated the responses of ant diversities and body size to environmental variables. Here, we considered the complete additive model, simple models with interaction, and the null model for each response variable separately. We also calculated the conditional coefficient of determination $R^2_{(c)}$ to each selected model and submitted to residual analysis to evaluate the adequacy of the error distribution. We performed GLMMs using the lmer function with the lme4 package (Bates et al. 2015). The model selections based on AICc criteria and the conditional R^2 were implemented with the MuMIn package.

Results

We recorded 120 leaf-litter ant species/morphospecies from 30 genera (Appendix S2). Eight subfamilies were sampled in our study, but only three represent more than 90% of all species: Myrmicinae (60.83%), Ponerinae (16.67%) and Formicinae (15%). *Pheidole* was the richest genus (26 species), followed by *Hypoponera* (15) and *Solenopsis* (13). The number of ant species sampled per site ranged from 13 (Lavras do Sul – Rio Grande do Sul state) to 43 (Tibagi – Paraná state).

We found TD (ΔAICc = 1.2), FD (ΔAICc = 0.3), and PD (ΔAICc = 0.0) negatively correlated with latitude (Fig. 3a, 3b, 3c), following the classical latitudinal pattern. That is, more ant species diversity, functional trait diversity and evolutionary lineages were found at lowest latitudes. Interspecific variation in mean body size also had latitude as a viable model to explain the observed pattern (ΔAICc = 1.7). Mean body size ranged from 0.31 to 4.30 mm and decreases with latitude (Fig. 3d). The null model also was selected to TD, FD, and mean body size variation (Table 1).

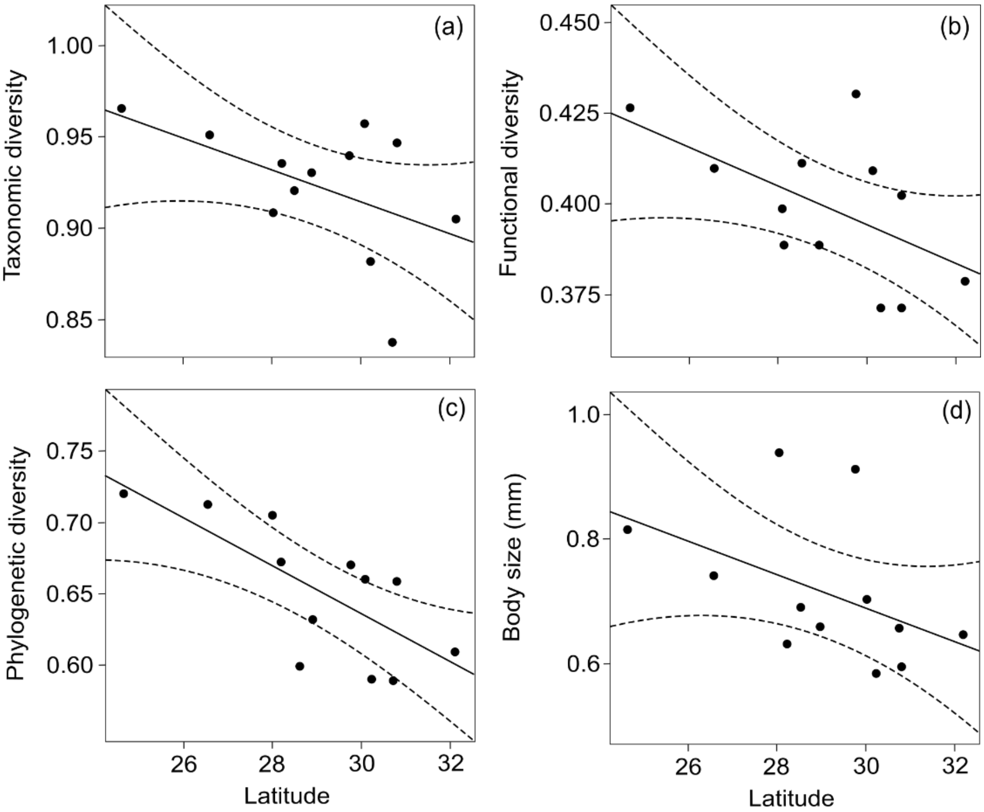

Fig 3. Relationship between latitude and leaf-litter ant diversities and body size in riparian forests in South Brazil. Generalized linear mixed models using the sampling month as a random factor: (a) taxonomic, (b) functional, (c) phylogenetic and (d) body size. Hatched lines represent the 95% confidence boundaries.

Table 1. Best-supported models (GLMMs) with Gaussian distribution and ΔAICc ≤ 2 retained to test geographic gradients (latitude) in diversities and body size of leaf-litter ant communities in South Brazil.

Response variable	Model	AICc	delta	df	Weight	$R^2_{(c)}$
Taxonomic diversity (TD)						
	Null	-38.0	0.0	3	0.640	Null
	LAT	-36.9	1.2	4	0.360	0.34
Functional diversity (FD)						
	Null	-52.0	0.0	3	0.530	Null
	LAT	-51.8	0.3	4	0.470	0.33
Phylogenetic diversity (PD)						
	LAT	-35.5	0.0	4	0.905	0.56
Body size						
	Null	-9.2	0.0	3	0.70	Null
	LAT	-7.5	1.7	4	0.30	0.24

We found annual precipitation (ΔAICc = 1.2; Fig. 4a) and plant productivity (ΔAICc = 2.0; Fig. 4b) positively correlated with ant species diversity (TD). For the FD, we found plant productivity as the best-selected model (ΔAICc = 0.0). That is, sites with higher plant productivity had higher ant functional diversity (Fig. 4c). PD was negatively correlated with mean annual temperature (ΔAICc = 0.0; Fig. 4d), meaning that sites with lower annual temperature had higher ant evolutionary lineages. Finally, we did not find suitable models using our environmental variables to explain the interspecific variation in mean body size. All minimum adequate models are available in the Table 2.

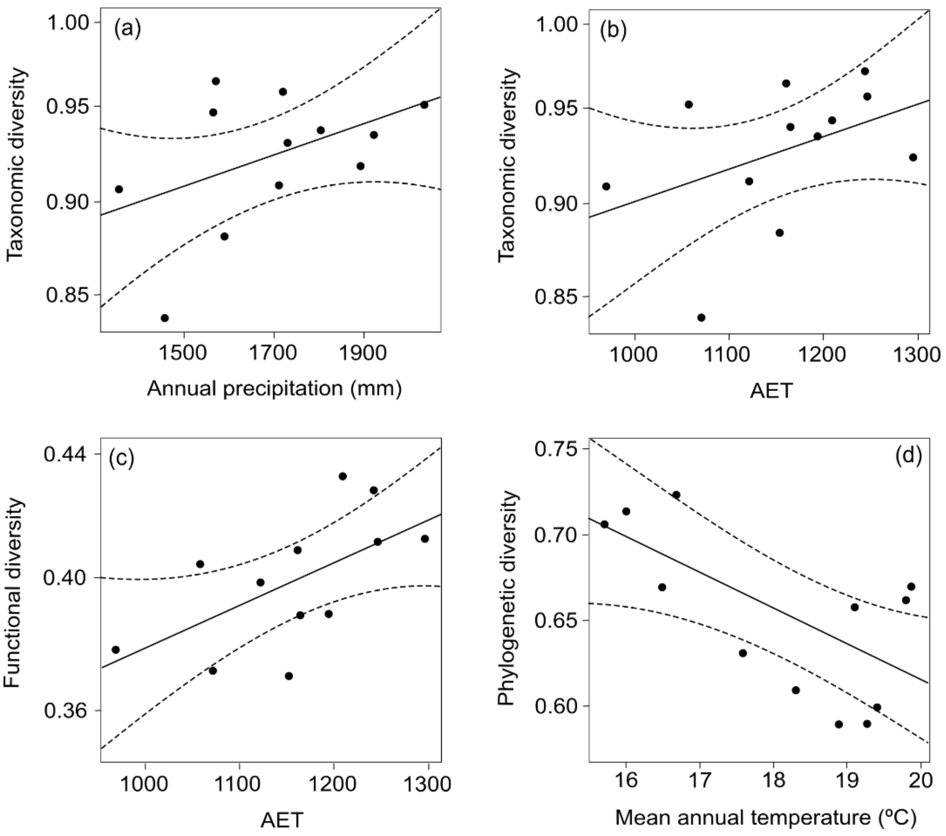

Fig 4. Relationship between environmental variables and leaf-litter ant diversities in riparian forests in South Brazil. Generalized linear mixed models using the sampling month as a random factor: (a) annual precipitation and (b) plant productivity (AET) with ant taxonomic diversity; (c) plant productivity (AET) with ant functional diversity; (d) mean annual temperature with ant phylogenetic diversity. Hatched lines represent the 95% confidence boundaries.

Table 2. Best-supported models (GLMMs) with Gaussian distribution and ΔAICc ≤ 2 retained to test environmental variables in diversities of leaf-litter ant communities in South Brazil. MAT – mean annual temperature; PRE – annual precipitation; AET – annual actual evapotranspiration.

Response variable	Model	AICc	delta	df	Weight	$R^2_{(c)}$
Taxonomic diversity (TD)						
	Null	-38.0	0.0	3	0.481	Null
	PRE	-36.8	1.2	4	0.263	0.23
	AET	-35.8	2.0	4	0.161	0.30
Functional diversity (FD)						
	AET	-52.9	0.0	4	0.481	0.39
	Null	-52.0	0.9	3	0.314	Null
Phylogenetic diversity (PD)						
	MAT	-33.0	0.0	4	0.577	0.45

Ultimately, we found all metrics significantly and positively correlated: TD x FD (r = 0.77, $p < 0.001$), TD x PD (r = 0.71, $p < 0.001$) and FD x PD (r = 0.67, $p = 0.02$). Moran's λ showed a strong and significant phylogenetic signal in the six morphological traits measured, meaning that all measured traits are phylogenetically conserved in our leaf-litter ant communities (Appendix S3).

Discussion

Our results show that diversity metrics of ant communities are following the classic latitudinal gradient in South Brazil. However, the null model also was selected as a minimum adequate model for TD and FD. This result suggests that there are other factors structuring ant taxonomic and functional diversity in riparian forests in South Brazilian grasslands, for instance, stochastic processes as dispersal and ecological drift (Mezger & Pfeiffer, 2011; Arnan et al., 2015). However, communities at lowest latitudes have more species diversity, potential ecological functions and lineages of ants, and these results agree with ours predicts. Global patterns have shown that there is a latitudinal effect in increasing ant species richness towards the equator, both northern and southern hemispheres (Dunn et al., 2009; Jenkins et al., 2011). In the Neotropical region, two studies have reported the opposite latitudinal pattern considering ant species richness (Silva & Brandão, 2014; Vasconcelos et al., 2018), but we explained and discussed this topic in more details below.

Regarding the potential environmental variables involved with geographical patterns of ant diversity, only TD had the null model as the best-selected model. This means that possibly unmeasured variables may be better predictors of ant taxonomic diversity at the latitudinal gradient in South Brazil. However, we also found TD positively correlated with annual precipitation and AET and, FD positively correlated with AET. That is, higher ant diversity and potential ecological functions are found with decreasing latitude and increasing precipitation and productivity. These results agree with our hypotheses of water availability and plant productivity (Hawkins et al., 2003; Mittelbach et al., 2001). Regions with more productive environments and higher precipitation rates are expected to support more resources to fauna, reducing interspecific competition and allowing species with different forages strategies and functional traits coexist. In arid regions, for instance, more productive environments (and consequently with more rainfall) harbor higher ant species richness (e.g. Paknia & Pfeiffer, 2012). However, there is a particular pattern in Australian arid savanna where the high ant diversity is maintained with aridity (Andersen et al., 2015). Differently from ant fauna associated with rainforest in Neotropical region, Australian savanna ant fauna reflect the evolutionary history of arid-adapted species there. Our results of leaf-litter ant species in riparian forests corroborate the strong association between rainfall and forest-associated ant species in Brazilian Cerrado (Vasconcelos et al., 2018). An interesting further research issue could investigate if ant fauna from South Brazilian grasslands follow the same pattern from forest-associated species in the Neotropical region or resemble the Australian arid savanna fauna. We suggested it because while savannas from Brazilian Cerrado are younger than forests, grasslands in South Brazil are older than southern forests (Behling et al., 2009).

Two studies have showed the opposite latitudinal gradient to ant species richness in the Neotropical region. That is, ant richness increased with increasing latitude. Our results are contrary to this latitudinal pattern, but consistent with the increase ant diversity with precipitation. Sites with more ant species in Silva & Brandão (2014) and Vasconcelos et al. (2018) are in the same latitude ranges than our study, either in Brazilian Atlantic Forest or Cerrado (latitude range between 24 and 27º in the three studies). Although we did not evaluate ant species richness, we found higher ant diversity, potential ecological functions and evolutionary histories in this region. All these results highlight that forest-associated ant fauna (either in riparian forests surrounded by grasslands, rainforests or savannas) in the Neotropical region is driven, indeed, by precipitation and plant productivity.

Although we showed a latitudinal gradient for ant phylogenetic diversity, we found an unusual pattern for environmental predictor associated. More ant lineages were found in sites at lowest latitude, but also with lower temperature. This is not a common pattern for many taxa, especially thermophilic organisms, as the ants. While at a local scale days or periods hotter are expected to find more ant species and lineages foraging (Dornhaus, 2010; Dröse et al., 2019), regions or gradients hotter at a broad scale are expected to show high ant diversity (Sanders et al., 2007; Dunn et al., 2009; Reymond et al., 2013). Based on that, we would expect an opposite latitudinal pattern for ant phylogenetic diversity since the sites at lowest latitudes in our study have the higher altitudes and, consequently, lower temperatures. Then, we propose an alternative explanation. The ant evolutionary history diversities at lowest latitudes (i.e. northern sites) may be related to the influence by patches size or amount of natural forests. In the

Atlantic Forest region, riparian forests surrounded by grasslands matrices has more forest patches at the landscape scale. It might be favoring ant species forest-associated in riparian ecosystems by dispersion among forest patches, increasing the chance to colonize, while ant species in Pampa biome might have a poor chance of dispersing and colonizing the riparian forests. This explanation is based on metacommunity (Leibold et al., 2004) and island biogeography theories (MacArthur & Wilson, 1967): the number of species is lower in islands of reduced size and distant from the mainland. Furthermore, forests in the southernmost part of Brazil are younger than grasslands (ca. 3,210 years since beginning the forest expansion on grasslands) (Behling et al., 2009). Differences in evolutionary time of these riparian forests compared to sites closer or inside the Atlantic Forest also could explain more ant lineages found in this region.

Investigating geographic gradient and environmental variables associated with interspecific variation of mean body size, we found an opposite latitudinal pattern, but not predictors explaining it. We expected this opposite gradient due to the Bergmman's rule state that smaller species tend to occur in warm regions (Bergmann, 1848), and we have a strong positive relationship between latitude and temperature. However, suitable models were not selected with our environmental variables to explain interspecific variation. Indeed, studies investigating body size variation in insects can be highly variable and depends of the taxa analyzed or the study design (Shelomi, 2012; Vinarski 2014). We argue that the absence of potential predictors explaining body size in our study can be due to: (i) unmeasured environmental variables, even though body size responses are commonly based on mean annual temperature and annual precipitation; (ii) methodology and scale may be not adequate to capture the complete interspecific variation of body size; and (iii) the small range in mean annual temperature between southern and northern sites (minimum value: 15.7ºC; maximum value: 19.9ºC). Data compilation with different studies and representing a large range of annual temperature might show results more precise in body size variation and potential predictors of this pattern.

Ultimately, although we found a strong phylogenetic signal in all morphological traits measured, FD and PD showed different responses to the geographic gradient. We expected similar results to FD and PD, especially if ant species more closely related share morphological traits more similar (as was in this case). Other studies with ant communities also have been found functional traits phylogenetically conserved, but not always congruent in results with PD (e.g. Arnan et al., 2017; Arnan et al., 2018). However, we cannot go deep into this topic because specific relationships among diversity facets were not explored in our study. Nevertheless, these different patterns highlight the importance of exploring biological communities through different components of diversity. In a rapidly changing world, efforts to biodiversity protection and conservation should consider integrative approaches (Devictor et al., 2010).

Conclusions

Our study uses results from sampling in riparian forests surrounded by grasslands from throughout South Brazil to identify potential drivers of a geographical gradient of leaf-litter ant communities. We found specific patterns associated with ant diversities and body size. Ant taxonomic, functional and phylogenetic diversity increase with decreasing latitude, while the interspecific variation in mean body size showed the opposite pattern (smaller size at highest latitudes). Ant species diversity and ecological traits diversity increase with precipitation and plant productivity at the latitudinal gradient. These results agree with the origin of the forest-associated fauna in the Neotropical region, a contrary pattern to evolutionary histories of arid-adapted ant fauna in Australian savannas. Ant phylogenetic diversity showed a contrary pattern with mean annual temperature: more ant lineages were recorded at lowest latitudes, but with lower temperatures. We believe that this unusual pattern is due to the proximity to the higher amount of forest patches in the Atlantic Forest region at lower latitudes, and it might facilitate the chance of dispersing and colonizing in riparian forests. Ultimately, as we expected, body size follows a contrary latitudinal pattern decreasing with increase latitude, but our hypothesis to temperature explaining this pattern was not corroborated. Our study highlights the importance to consider multiple approaches in biodiversity, especially to understand patterns and processes related in shaping community ecology along geographic and environmental gradients.

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Author contributions

LRP and MMJ coordinated the project; WD and LRP conducted field work and data sampling; WD identified the ants, measured morphological traits, analyzed the data, prepared the illustrations and wrote the original draft; LRP and MMJ reviewed and wrote the final draft. All authors have approved the manuscript and there are no conflicts of interest.

Supporting information

Appendix S1. Phylogenetic tree from the 120 leaf-litter ant species collected in riparian forests in South Brazil.

Appendix S2. Leaf-litter ant species recorded in riparian forests in South Brazil.

Appendix S3. Phylogenetic signal in ant morphological traits.

Table S1. Geographical and environmental variables obtained to 12 sites from South Brazil.

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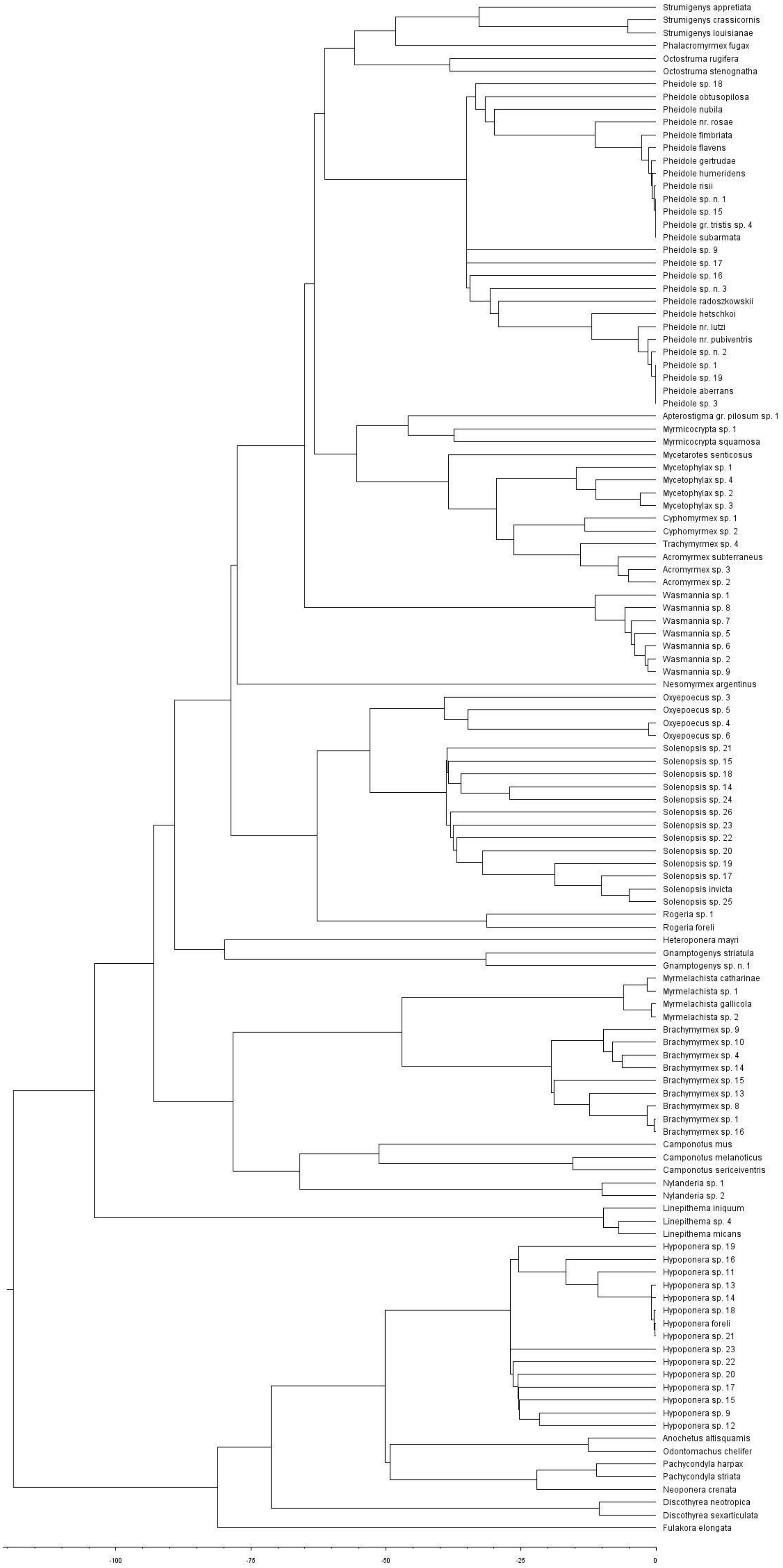
S1 Appendix. Phylogenetic tree from the 120 leaf-litter ant species collected in riparian forests in South Brazil. An example of one of the 1000 phylogenetic trees built in the software Sunplin considering the relationships among species as phylogenetic uncertainly. Scale bar in millions of years before the present.



S2 Appendix. Leaf-litter ant species recorded in riparian forests in South Brazil. Numbers represent the total number of occurrences at each site. Sites from Pampa biome (A-Alegrete; B-Jaguarão; C-Lavras do Sul; D-Quaraí; E-Santana da Boa Vista; F-Santo Antônio das Missões; G-São Gabriel) and Atlantic Forest biome (H-Soledade; I-Vacaria; J-Painel; K-Palmas; L-Tibagi).

Ant species	**Sites sampled**											
	Pampa biome							**Atlantic Forest biome**				
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**
Amblyoponinae												
Fulakora elongata (Santschi, 1912)	0	0	0	0	0	0	1	0	2	0	0	1
Dolichoderinae												
Linepithema iniquum (Mayr, 1870)	0	1	0	0	0	0	0	0	0	0	0	0
Linepithema micans (Forel, 1908)	0	1	0	0	2	0	0	0	1	0	1	2
Linepithema sp. 4	0	1	0	0	2	0	0	0	0	0	0	0
Ectatomminae												
Gnamptogenys striatula Mayr, 1884	0	0	0	0	0	0	0	0	0	0	0	3
Gnamptogenys sp. n. 1	0	0	0	0	0	0	0	1	1	0	1	0
Formicinae												
Brachymyrmex sp. 1	0	0	1	0	0	0	0	0	0	0	0	0
Brachymyrmex sp. 4	1	0	0	0	0	0	0	0	0	0	0	0
Brachymyrmex sp. 8	0	0	0	0	0	1	0	14	3	1	0	0
Brachymyrmex sp. 9	0	0	0	0	0	0	0	0	0	0	3	0
Brachymyrmex sp. 10	4	2	0	1	3	0	1	0	0	1	1	0
Brachymyrmex sp. 13	0	0	0	0	0	0	0	1	0	0	0	0
Brachymyrmex sp. 14	0	2	2	2	3	1	1	1	1	0	0	0
Brachymyrmex sp. 15	0	0	0	0	0	0	0	0	0	0	5	2
Brachymyrmex sp. 16	1	0	8	2	4	3	5	0	0	0	0	0
Camponotus melanoticus Emery, 1894	1	0	0	0	0	0	0	0	0	0	0	0
Camponotus mus Roger, 1863	0	0	0	0	0	2	0	0	0	0	0	0
Camponotus sericeiventris (Guérin-Méneville, 1838)	0	0	0	0	0	1	0	0	0	0	0	0
Myrmelachista catharinae Mayr, 1887	0	0	0	0	0	0	0	2	0	0	2	0
Myrmelachista gallicola Mayr, 1887	0	0	0	0	0	0	0	0	0	0	0	1
Myrmelachista sp. 1	0	0	0	0	0	0	0	0	0	0	2	0
Myrmelachista sp. 2	1	0	0	0	0	0	0	0	0	0	0	0
Nylanderia sp. 1	0	4	0	1	4	4	1	0	0	0	0	0
Nylanderia sp. 2	0	0	0	0	0	0	4	0	1	1	5	1
Heteroponerinae												
Heteroponera mayri Kempf, 1962	0	0	0	0	1	0	0	2	1	0	0	1
Myrmicinae												
Acromyrmex subterraneus (Forel, 1893)	0	0	0	0	0	0	1	0	1	2	0	0
Acromyrmex sp. 2	0	0	0	0	0	0	0	0	0	0	1	0
Acromyrmex sp. 3	0	0	1	0	0	0	0	0	0	0	0	0
Apterostigma gr. *pilosum* sp. 1	0	0	0	0	0	0	2	0	0	0	0	0
Cyphomyrmex sp. 1	0	0	0	0	0	0	3	0	0	0	0	4
Cyphomyrmex sp. 2	0	0	0	0	0	0	0	0	0	0	0	1
Mycetarotes senticosus Kempf, 1960	0	0	0	0	0	0	0	0	0	0	0	1
Mycetophylax sp. 1	0	0	0	0	0	0	1	3	0	0	1	0
Mycetophylax sp. 2	0	0	0	0	1	0	0	2	0	0	0	0

Mycetophylax sp. 3	0	0	0	0	0	0	0	0	0	1	0	0
Mycetophylax sp. 4	1	0	0	0	0	2	0	0	0	0	0	0
Myrmicocrypta squamosa Smith, 1860	1	0	0	0	0	0	0	0	0	0	0	0
Myrmicocrypta sp. 1	2	0	0	0	0	0	0	0	0	0	0	0
Nesomyrmex argentinus (Santschi, 1922)	0	0	0	0	0	0	2	0	0	0	1	0
Octostruma rugifera (Mayr, 1887)	0	0	0	0	2	0	3	0	1	0	0	4
Octostruma stenognatha Brown & Kempf, 1960	0	0	0	0	0	1	0	3	1	0	0	2
Oxyepoecus sp. 3	0	0	0	0	0	0	0	1	0	0	0	1
Oxyepoecus sp. 4	0	0	0	0	0	0	0	0	1	0	0	0
Oxyepoecus sp. 5	0	0	0	0	0	0	0	0	4	0	1	0
Oxyepoecus sp. 6	0	4	0	0	1	0	0	0	0	0	0	0
Phalacromyrmex fugax Kempf, 1960	0	0	0	0	0	0	0	0	0	1	0	0
Pheidole gr. *tristis* sp. 4	0	0	0	0	0	0	0	1	0	0	2	2
Pheidole aberrans Mayr, 1868	0	0	0	0	1	0	0	0	0	0	0	0
Pheidole fimbriata Roger, 1863	1	0	0	0	0	0	0	0	0	0	0	0
Pheidole flavens Roger, 1863	0	0	0	0	0	0	0	1	2	1	1	0
Pheidole gertrudae Forel, 1886	0	0	0	0	0	0	0	0	0	0	0	4
Pheidole hetschkoi Emery, 1896	0	0	0	0	0	0	0	2	0	0	0	0
Pheidole humeridens Wilson, 2003	2	0	0	0	2	0	2	1	0	0	0	0
Pheidole nr. *lutzi* Forel, 1905	0	0	0	0	0	0	0	0	0	0	2	0
Pheidole nubila Emery, 1906	5	2	0	1	1	0	0	0	0	0	0	0
Pheidole obtusopilosa Mayr, 1887	0	0	0	0	0	0	1	0	0	0	0	0
Pheidole nr. *pubiventris* Mayr, 1887	0	3	3	0	1	0	5	2	1	2	3	3
Pheidole radoszkowskii Mayr, 1884	3	2	0	3	1	3	1	0	0	0	0	0
Pheidole risii Forel, 1892	0	5	0	0	4	0	7	3	1	0	2	0
Pheidole nr. *rosae* Forel, 1901	0	0	0	0	0	0	0	0	1	0	0	1
Pheidole subarmata Mayr, 1884	3	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp. n. 1	0	2	0	0	2	1	0	8	0	0	0	0
Pheidole sp. n. 2	0	0	0	0	0	0	0	0	0	0	1	2
Pheidole sp. n. 3	0	0	0	0	0	0	0	0	0	0	0	2
Pheidole sp. 1	1	0	0	0	0	0	0	0	0	0	0	0
Pheidole sp. 3	5	14	12	10	12	7	6	4	7	0	0	2
Pheidole sp. 9	0	0	0	0	0	0	1	0	0	0	0	1
Pheidole sp. 15	1	0	0	0	0	0	2	1	0	0	0	0
Pheidole sp. 16	0	0	0	0	0	0	0	0	0	0	0	7
Pheidole sp. 17	0	0	0	0	0	0	0	0	1	0	4	0
Pheidole sp. 18	0	0	0	0	0	0	0	2	0	0	0	0
Pheidole sp. 19	0	0	0	0	0	2	0	0	0	0	0	0
Rogeria foreli Emery, 1894	0	0	0	0	0	0	2	0	0	0	0	0
Rogeria sp. 1	0	0	0	0	0	0	2	0	0	0	0	0
Solenopsis invicta Buren, 1972	0	0	0	0	0	0	1	0	1	0	1	0
Solenopsis sp. 14	7	4	1	4	5	2	7	9	5	3	3	2
Solenopsis sp. 15	0	0	0	0	2	0	0	0	0	0	0	2
Solenopsis sp. 17	0	0	0	0	0	0	0	0	0	0	0	2
Solenopsis sp. 18	0	0	0	0	0	0	0	2	0	0	0	1
Solenopsis sp. 19	0	0	0	0	0	1	0	0	0	0	0	0
Solenopsis sp. 20	1	10	6	5	7	8	10	5	4	4	7	7
Solenopsis sp. 21	0	2	0	0	0	0	2	0	0	0	0	0
Solenopsis sp. 22	0	0	0	0	0	1	0	0	0	0	0	0

Solenopsis sp. 23	0	0	0	0	0	0	2	0	0	0	0	0
Solenopsis sp. 24	0	2	1	3	1	1	3	0	1	1	0	0
Solenopsis sp. 25	0	0	0	0	0	2	0	0	0	0	0	0
Solenopsis sp. 26	0	0	0	0	1	0	5	0	0	0	0	0
Strumigenys appretiata (Borgmeier, 1954)	0	0	0	1	0	0	0	0	2	0	0	0
Strumigenys crassicornis Mayr, 1887	0	0	0	0	0	0	0	0	0	0	0	2
Strumigenys louisianae Roger, 1863	1	0	2	1	4	6	1	2	0	0	1	3
Trachymyrmex sp. 4	0	0	0	0	1	0	0	0	0	0	0	0
Wasmannia sp. 1	0	0	0	0	5	0	3	0	0	0	0	0
Wasmannia sp. 2	1	0	0	1	2	2	2	0	0	0	0	2
Wasmannia sp. 5	0	0	0	0	0	0	0	0	0	0	1	0
Wasmannia sp. 6	0	0	0	0	2	0	0	0	0	0	0	4
Wasmannia sp. 7	0	0	0	1	0	0	1	0	0	0	0	0
Wasmannia sp. 8	0	0	0	0	0	0	0	7	6	0	5	3
Wasmannia sp. 9	0	0	1	0	0	0	0	0	0	0	0	0
Ponerinae												
Anochetus altisquamis Mayr, 1887	0	0	0	2	0	0	0	0	0	0	0	0
Hypoponera foreli (Mayr, 1887)	0	0	0	0	1	0	0	0	0	0	0	2
Hypoponera sp. 9	0	0	0	0	0	0	0	1	0	0	0	0
Hypoponera sp. 11	0	2	2	0	0	0	0	1	4	5	1	9
Hypoponera sp. 12	0	0	0	0	0	0	0	0	0	0	0	2
Hypoponera sp. 13	0	0	0	0	0	0	0	0	0	0	2	0
Hypoponera sp. 14	4	0	0	0	0	0	0	0	0	0	0	2
Hypoponera sp. 15	1	0	0	0	2	0	2	4	0	1	4	1
Hypoponera sp. 16	0	0	0	0	0	0	0	0	0	0	0	8
Hypoponera sp. 17	0	0	0	0	0	0	0	0	0	2	2	1
Hypoponera sp. 18	0	0	0	0	0	0	0	0	0	0	0	3
Hypoponera sp. 19	0	0	0	0	0	0	0	0	0	0	3	0
Hypoponera sp. 20	0	0	0	0	0	0	1	0	0	0	0	0
Hypoponera sp. 21	0	0	0	0	0	0	5	0	0	0	0	0
Hypoponera sp. 22	1	3	1	0	1	0	0	0	0	0	0	0
Hypoponera sp. 23	2	0	0	1	1	0	4	0	0	0	0	0
Neoponera crenata (Roger, 1861)	0	1	0	0	0	0	0	0	0	1	0	0
Odontomachus chelifer (Latreille, 1802)	2	0	0	0	0	1	0	0	0	0	0	0
Pachycondyla harpax (Fabricius, 1804)	1	0	0	0	0	0	0	0	0	0	0	1
Pachycondyla striata Smith, 1858	0	0	0	0	1	0	1	0	0	1	0	2
Proceratiinae												
Discothyrea neotropica Bruch, 1919	0	0	0	0	1	0	0	0	1	0	0	0
Discothyrea sexarticulata Borgmeier, 1954	0	0	0	0	0	0	0	0	0	0	0	3
Species richness	**26**	**20**	**13**	**16**	**34**	**21**	**38**	**28**	**26**	**16**	**30**	**43**

S3 Appendix. Phylogenetic signal in ant morphological traits. Phylogenetic signal (lambda and *p* values) calculated using Pagel's λ for each of the 1000 phylogenetic trees in morphological traits obtained from 120 leaf-litter ant species collected in riparian forests in South Brazil.

Morphological trait	**lambda**	***p* value**
Weber's (mesosoma) length	0.94	<0.001
Hind femur length	0.70	<0.001
Mandible length	0.86	<0.001
Scape length	0.77	<0.001
Compound eye length	0.85	<0.001
Interocular distance	0.79	<0.001

Table S1. Geographic and environmental variables obtained to 12 sites from South Brazil. Geographical variables: latitude (LAT) and mean altitude (ALT). Environmental variables: mean annual temperature (MAT), annual precipitation (PRE), and annual actual evapotranspiration (AET).

Biome	**Site**	**Sampling date (m/y)**	**LAT**	**ALT**	**MAT**	**PRE**	**AET**
Pampa	Alegrete	Oct/2013	29.77263	119	19.9	1811	1209
Pampa	Jaguarão	Jan/2014	32.24465	92	18.3	1351	969
Pampa	Lavras do Sul	Apr/2014	30.79011	185	18.9	1457	1071
Pampa	Quaraí	Oct/2013	30.29503	169	19.3	1588	1153
Pampa	Santana da Boa Vista	Dec/2013	30.83803	248	19.1	1564	1058
Pampa	Santo Antônio das Missões	Nov/2013	28.53752	98	19.4	1891	1296
Pampa	São Gabriel	Feb/2014	30.10739	133	19.8	1721	1160
Atlantic Forest	Painel	Apr/2015	28.00690	1154	15.7	1711	1122
Atlantic Forest	Palmas	Jan/2016	26.51664	1241	16.0	2036	1246
Atlantic Forest	Soledade	Nov/2013	28.87856	633	17.6	1726	1193
Atlantic Forest	Tibagi	May/2016	24.55090	1024	16.7	1568	1242
Atlantic Forest	Vacaria	Apr/2015	28.18144	905	16.5	1918	1164

CAPÍTULO III

Forest cover and leaf-litter biomass predict taxonomic, functional and phylogenetic diversity of ant communities in riparian ecosystems in South Brazilian grasslands[3]

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Forest cover and leaf-litter biomass predict taxonomic, functional and phylogenetic diversity of ant communities in riparian ecosystems in South Brazilian grasslands

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Abstract

Habitat loss and fragmentation are processes that are increasing rapidly with land use intensification. In South Brazil, conversion of natural ecosystems is threatening both forest and grassland habitats. Furthermore, disturbances as fire and grazing play a key role in grasslands management, but they may not be favorable for associated forest ecosystems. Here we investigated leaf-litter ant communities in riparian forests and their relationships with local habitat and landscape structure. We sampled 36 riparian forests in 12 sites throughout South Brazilian grasslands. Overall, 120 ant species were recorded belonging to 30 genera. We found riparian ecosystems with less forest area and less leaf-litter biomass had lower ant diversity, potential ecological functions, and shorter evolutionary histories. Landscape structure (i.e. natural forest and anthropic area cover) did not explain ant community patterns. Our results highlight the importance of riparian forests in South Brazilian grasslands. Protecting large riparian areas can amplify ant species diversity and linages performing different potential ecological functions in these ecosystems. Likewise, riparian forests with more leaf-litter also have increased ant diversities. Considering the amount of leaf-litter as a proxy to forest and understory quality, the presence of cattle may be affecting the regeneration and development of forest species. Landscapes with forest-grassland mosaics in South Brazil need different conservation strategies. Based on our results, we suggest fencing forests to avoid cattle access into the forests without excluding livestock grazing in natural grasslands in South Brazil.

Keywords: habitat loss, fragmentation, grazing, fire, management.

1. Introduction

Land use intensification has modified natural landscapes worldwide, leading to biodiversity loss, and affecting important ecosystem services and functions (Chapin et al. 2000). Two main processes are involved in biodiversity changes from natural habitats surrounded by human-modified areas: habitat loss and fragmentation (Fahrig 2003; Fischer and Lindenmayer 2007; Fahrig 2017). These processes modify species diversity and composition at different spatial scales. For example, locally, edge effects and variables associated with vegetation and microclimate may be responsible for biodiversity patterns, while size and distance of natural patches may affect biodiversity through species aggregation and dispersal limitation at a landscape scale (Tscharntke et al. 2012). Understanding species distribution in natural habitats, as well as potential predictors of environmental change, could help us minimize biodiversity loss by maintaining landscapes with a balance between natural and human-managed ecosystems.

Riparian ecosystems are important environments associated to watercourses in different landscapes. These habitats are recognized as natural biodiversity corridors (Gray et al., 2018) and provide several ecosystem services, especially those related to water dynamics (Naiman et al., 2010). The degradation of riparian zones may result in strong environmental changes, such as variation in microclimate and soil properties, hydrological dynamics (e.g. flood control), and litter input from vegetation (Naiman et al., 2010). In Brazil, the current Forest Code states that riparian ecosystems must be protected (Permanent Preservation Areas – PPA) and defines some protection categories: e.g. streams with less 10 m wide must have on either side 30 m of protected riparian forests (Brasil, 2012). However, recent studies have reported that these PPA categories should be wider than predicted by the law, both for fauna (Pereira et al. 2019) and to preserve water quality (Valera et al. 2019). Riparian forests surrounded by human-modified areas (e.g. agriculture) usually have their width reduced, which results in lower biodiversity (Fernández et al. 2014; García-Martínez et al. 2015).

Insects are considered useful indicators of environmental changes. Specifically, ants are organisms that perform important roles in species interactions and ecological processes (Lach et al. 2010; Del Toro et al. 2012). Ants are widely distributed in terrestrial ecosystems, and have been used for monitoring natural and modified habitats at different scales. For example, leaf-litter diversity and biomass may increase ant diversity through more food and nesting resources variety (Queiroz et al. 2013; Souza-Campana et al. 2017). Canopy openness variation may change microclimatic conditions, as well as resource quality, decreasing ant diversity (Neves et al., 2013). The availability of natural habitats enhance ant diversity in natural (García-Martínez et al. 2017) and production areas (e.g. silviculture and agriculture) (Solar et al. 2016). Ants in riparian ecosystems have shown associations with vegetation structure (Johnson et al. 2014), riparian zone width (Ives et al. 2011) and surrounding non-riparian habitats (Gray et al. 2015). Most studies have used ant taxonomic diversity to understand patterns and processes, especially species richness. Ecological functions and evolutionary aspects of Neotropical ant species are poorly explored yet.

South Brazilian grasslands, also named *Campos* or *Campos Sulinos*, are distributed in Pampa and Atlantic Forest biomes. These natural grasslands form landscapes with forests (deciduous and semi-deciduous seasonal forests and mixed ombrophilous forest), which are expanding over grasslands due to the present day climate in South Brazil (warm and moist) (Behling and Pillar 2008). Disturbances as fire and grazing can control this forest expansion process over grasslands. Furthermore, fire and grazing are essential to maintain high biodiversity in grasslands, reducing competition with dominant species (e.g. tussocks) and increasing diversity of grasses and forbs (Overbeck et al. 2005; 2007). Although these disturbances are very important to natural grasslands dynamics, livestock grazing may be prejudicial to forest habitats in the countless ecotones and mosaics throughout South Brazil. For example, the cattle accesses the forest interiors searching for water and/or shelter and, consequently, trample leaf-litter and feed on tree saplings (Carlucci et al. 2016). This can impede regeneration of forest species, reducing the structure and resources available to forest biota. Riparian forests in South Brazil have suffered with cattle in their interiors because these habitats are highly surrounded by grasslands in private properties that normally have high livestock grazing intensities. Another factor is the rapid change of grasslands into human-modified areas, especially agriculture and silviculture (Andrade et al. 2015; Oliveira et al. 2017), reducing natural areas and leading to biodiversity loss (Staude et al. 2018).

Here we explored leaf-litter ant community patterns and their relation to local habitat and landscape structure in riparian forests within a typical grassland matrix in South Brazil. Specifically, we expect decreasing ant diversity with reductions of riparian forest area and with natural forested area distribution at the landscape level (García-Martínez et al. 2017; Ahuatzin et al. 2019; Solar et al. 2016), and also with the amplification of surrounding anthropic areas (Assis et al. 2018). We expect decreasing ant diversity in riparian forests with less leaf-litter biomass (Queiroz et al. 2013) and higher canopy openness (Neves et al. 2013), using these variables as a proxy of internal forest quality. We investigated these patterns with taxonomic, functional and phylogenetic approaches. Our expectations with decreasing ant diversity may also mean species homogenization; increased ecological similarity among sites; and a reduced number of evolutionary linages able to coexist under these conditions.

2. Material and methods

2.1. Study area

Our 12 sampling sites were spread along South Brazilian grasslands (Fig. 1a). Grasslands in this region are distributed over the Pampa and Atlantic Forest biomes. These ecosystems form landscapes with different types of forest: mixed ombrophilous forest, deciduous and semi-deciduous seasonal forest (Overbeck et al. 2007; Boldrini 2009). In the Pampa biome, there are large grassland areas, and forests are mostly associated with rivers and slope conditions. In the Atlantic Forest, landscapes with forest-grassland ecotones are widespread (Boldrini 2009). We sampled seven sites in the Pampa biome and five sites in the Atlantic Forest biome. South Brazilian grasslands are in the humid subtropical zone. According to the Köppen criteria, the climate in the Pampa biome is classified as Cfa type (with hot summers) while Atlantic Forest biome is Cfb (with temperate summers) (Alvares et al. 2013).

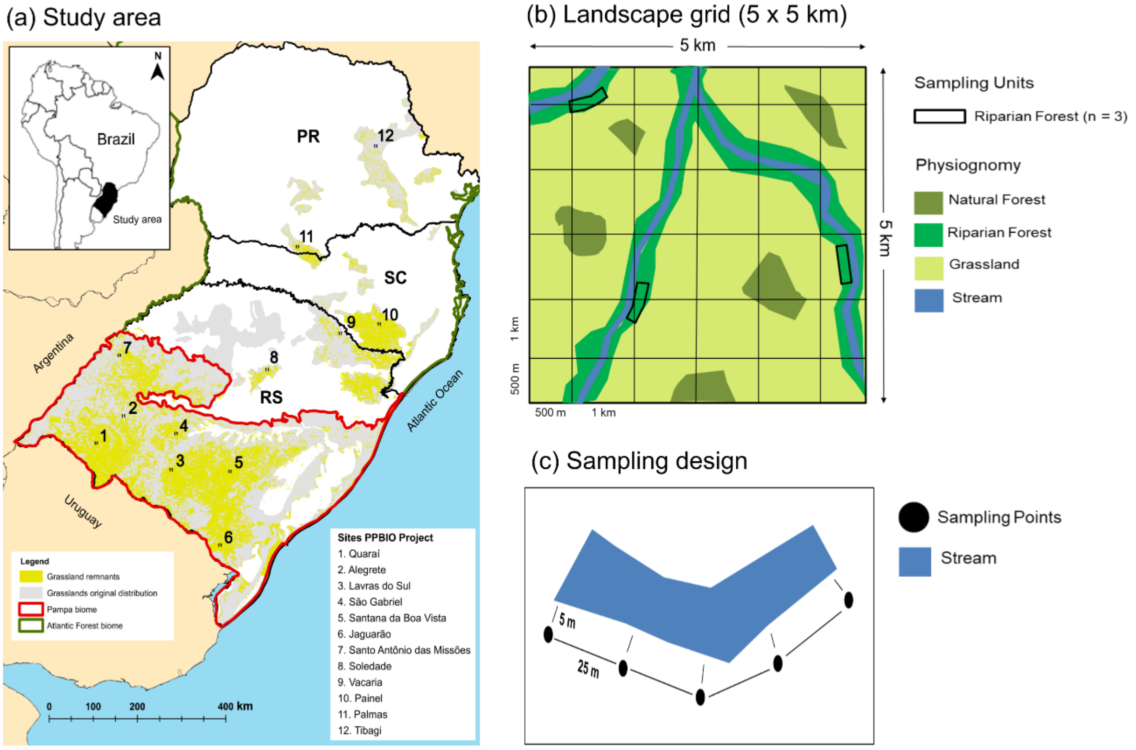

Fig. 1. Map of the study sites and sampling design of riparian forests in South Brazilian grasslands. (a) Riparian forests sampled in 12 sites belonging to Pampa and Atlantic Forest biomes. (b) Landscape grid (5 x 5 km) that represents one site with three riparian forests sampled. (c) Sampling design with leaf-litter points.

2.2. Ant sampling

At each site was delimited by a 5 x 5 km grid where were selected three riparian forests (summing 36 units) from different streams (Fig. 1b). All the riparian forests sampled are surrounded by natural grasslands with livestock grazing as the main management applied (most particular properties). We carried out ant sampling between October 2013 and May 2016 during the day and under dry weather. At each riparian forest, we established a 100 m line with five equidistant sampling points (25 m), and about 5 m far from the river (Fig. 1c). We collected two samples of leaf-litter with a 30 cm radius circular sampling at each sampling point. These two circular samples at each point were pooled, forming a single sampling unit. To separate the ants from the largest fragments of leaf-litter, each sample unit was sifted through a coarse mesh screen of 1 cm grid size. Ant individuals were stored at the Laboratório de Ecologia de Interações (LEIN) in Universidade Federal do Rio Grande do Sul (UFRGS).

Ants were identified to genus level based on Baccaro et al. (2015). The species were identified through comparisons with ant species deposited in the entomological collection at the LEIN and at the Entomological Collection Padre Jesus Santiago Moure of the Universidade Federal do Paraná (DZUP). Voucher specimens are deposited at the LEIN and DZUP.

2.3. Local habitat and landscape structure

At the local scale, we sampled variables to represent habitat structure and resource availability for ants: leaf-litter biomass, canopy openness and percentage of riparian forest cover. After all ant individuals were removed, leaf-litter from the two samples with a 30 cm radius circular sampling was dried at 60ºC for 72 h, and then weighed with a precision balance. We estimated canopy openness using hemispherical photographs of the canopy taken with a camera equipped with a fisheye objective lens. The camera was positioned adjacent to each sampling point and at 1.5 m above ground level. We used the Gap Light Analyser 2.0 software to analyze the images (Frazer et al. 1999). We calculated the percentage of riparian forest cover within a 200 m radius buffer from the central point in the 100 m line at each 36 forests. We used a 200 m buffer based on literature (e.g. García-Martínez et al. 2017 and references) and to represent a variable at a local scale, and not landscape scale (Ahuatzin et al. 2019).

At the landscape scale, we calculated the percentage of natural forested area and anthropic areas (i.e. crops, tree plantations, and urban areas) within the 5 x 5 km grid. We used a land cover map for southern Brazil based on Landsat 5 satellite images (from 2009).

We used the Variance Inflation Factor value (VIF) (Dormann et al. 2013) to test the multicollinearity among the variables (for both local and landscape scale). We defined VIF value ≤ 3 as an indicator of insignificant multicollinearity (Zuur et al. 2007; Akinwande et al. 2015). All variables in both scales showed VIF ≤ 1.04 and were considered to further analysis.

2.4. Ant functional data

Here we used morphological traits to estimate ant functional diversity. We measured at least one individual per species in each sampling point (the two circular leaf-litter samplings pooled). For instance, whether a species is present in all sampling points in a riparian forest, at least five individuals of this species were measured. Due to some species and genera are polymorphic, we measured only the minor works.

Based on the literature, we chose traits related to leaf-litter habitat and that could be functional to ant species (Weiser & Kaspari, 2006; Silva & Brandão 2010; Gibb & Parr, 2013): (1) Weber's length, used as a proxy to body size; (2) hind femur length; (3) mandible length; (4) scape length; (5) compound eye length and (6) interocular distance. All traits were divided by Weber's length to control for relative body size measurement.

2.5. Ant phylogenetic data

We built a complete phylogeny at the genus level for the ant species recorded in this study using the software Phylocom 4.2 (Webb et al. 2008). Phylogenetic relationships among these ant genera were based on Moreau and Bell (2013) and Ward et al. (2015). We inserted the species recorded in this study in the complete phylogeny as polytomies. Then, we randomly generated 1000 potential trees considering the relationships among species within each genus as phylogenetic uncertainty in the software Sunplin (Martins et al. 2013).

2.6. Ant diversities

To consider a comparative approach, we used Simpson index for taxonomic diversity (TD) and the Rao quadratic entropy index for functional (FD) and phylogenetic (PD) diversity (Bello et al. 2010). Simpson index was calculated considering the occurrences of ant species in the communities. FD was calculated considering trait distance and PD considering phylogenetic distance among species in each riparian forest and site weighted on the proportion of the occurrences of ant species. We calculated PD for the 1000 phylogenetic trees generated by randomization and used the mean value of this metric for each riparian forest and site. TD, FD, and PD were calculated with SYNCSA package in R (Debastiani & Pillar 2012).

2.7. Data analysis

We separated the data in two groups for the purpose analyses: (i) local habitat variables, and (ii) landscape structure variables. Variables both at a local and landscape scale were standardized by Z-score transformation using *scale* function in R. At a local scale, we used the 36 riparian forests as sampling units. At the landscape scale, we pooled the three riparian forests and considered the sites (12 units).

Here we used Generalized Linear Mixed Models (GLMMs) to evaluate the responses of ant taxonomic (TD), functional (FD) and phylogenetic (PD) diversity to local habitat and landscape structure variables. Gaussian error distribution was used to fit the effect of local habitat variables on the TD, FD, and PD, based on maximum likelihood estimation (Delignette-Muller & Dutang 2015). We selected the best models using the Akaike's information criterion (AICc – Burnham & Anderson 2002). First, to evaluate local habitat structure (leaf-litter biomass, canopy openness, and riparian forest cover) we used the sites as a random factor in the models. Then, we applied the complete additive model (with all variables), simple models with interaction (only between two variables), and the null models (y ~ 1 + (1|site)). We considered as plausible models those with ΔAICc ≤ 2. Selected models were submitted to residual analysis to evaluate the adequacy of the error distribution. For the landscape structure variables, we follow the same procedures for the local habitat considering simple additive models and with interaction between natural forested and anthropic areas, and the null model for each metric separately. Here, we entered the sampling month as a random factor (i.e. categorical variable describing the month that samples occurred, independently of the year). For both local and landscape scale, the conditional $R^2_{(c)}$ explaining the variance by both fixed and random factors, were calculated (Nakagawa & Schielzeth, 2013). GLMMs were performed using the lmer function with the lme4 package (Bates et al. 2015). The model selections based on AICc criteria and the conditional R^2 were implemented with the MuMIn package.

3. Results

3.1. Ant diversity

Including all 36 riparian forests, we recorded eight subfamilies, 30 genera and 120 leaf-litter ant species (Table S1). The genera *Pheidole* and *Solenopsis* were recorded in all 36 riparian forests, while *Mycetarotes*, *Neoponera*, *Phalacromyrmex*, *Rogeria* and *Trachymyrmex* were recorded in only one riparian forest. The number of species per sampling point ranged from 0 to 12 ± 2.79 SD and the number of species per riparian forest varied from 4 to 28 ± 6.5 SD. Functional diversity calculated from the six ant morphological traits (Weber's length, hind femur length, mandible length, scape length, compound eye length and interocular distance) ranged from 0.26 to 0.44 ± 0.03 SD. Phylogenetic diversity obtained from the mean of 1000 phylogenetic trees ranged from 0.49 to 0.72 ± 0.06 SD.

3.2. Environmental description

The average leaf-litter biomass at the 36 riparian forests was 57.33 ± 14.73 g (min: 33.51 g; max: 104.61 g) and the average canopy openness was 8.54 ± 2.36 % (min: 3.1 %; 13.88 %). Riparian forest cover was 37.5 ± 11.78 % (min: 12.88 %; max: 67.73 %). The average natural forest area at the landscape scale was 7.71 ± 5.05 %

(min: 1.55 %; max: 19.04 %) and anthropic areas were 23.04 ± 17.44 % (min: 1.38 %; max: 55.53 %).

3.3. Local and landscape predictors

We found a positive relationship between riparian forest cover and TD ($R^2_{(c)}$ = 0.42), FD ($R^2_{(c)}$ = 0.35) and PD ($R^2_{(c)}$ = 0.23). That is, riparian forests with higher cover in a 200 m buffer had more ant diversity, potential ecological functions and longer evolutionary histories. Leaf-litter biomass was positively associated with PD ($R^2_{(c)}$ = 0.22). Furthermore, we found additive models with riparian forest cover and leaf-litter biomass explaining TD ($R^2_{(c)}$ = 0.48), FD ($R^2_{(c)}$ = 0.39) and PD ($R^2_{(c)}$ = 0.28), as well as the interaction between these two predictors explaining TD ($R^2_{(c)}$ = 0.51) and FD ($R^2_{(c)}$ = 0.40). Canopy openness was not selected by the model selection criteria. We present the relationships of simple models between these two predictors and ant taxonomic, functional and phylogenetic diversity in Figure 2, and all models selected in Table 1.

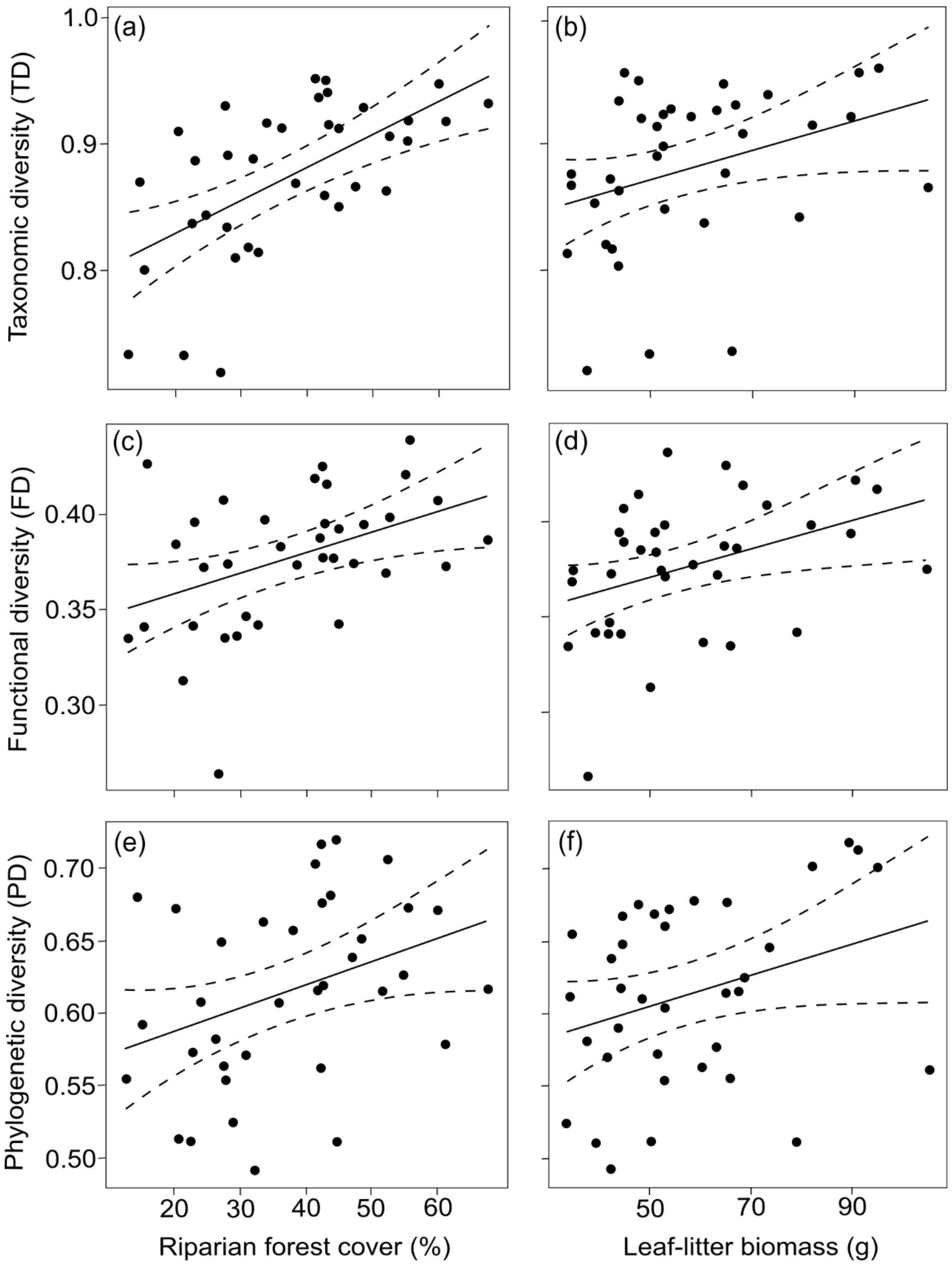

Fig. 2. Relationship of simple models (GLMMs) between riparian forest cover and leaf-litter biomass with ant taxonomic (a ; b), functional (c ; d) and phylogenetic (e ; f) diversity in riparian forests in South Brazil. Hatched lines represent confidence intervals (95%).

Table 1. Best-supported models (GLMMs) with ΔAICc ≤ 2 retained to test local habitat variables in leaf-litter ant communities of riparian forests in South Brazilian grasslands. LFL – leaf-litter biomass (g); RFC – percentage of riparian forest cover (%).

Distribution	Response variable	Model	AICc	delta	Df	Weight	$R^2_{(c)}$
Gaussian	Taxonomic diversity (TD)						
		LFL + RFC	-107.4	0.0	5	0.318	0.48
		LFL * RFC	-106.1	1.3	6	0.167	0.51
		RFC	-106.0	1.4	4	0.158	0.42
Gaussian	Functional diversity (FD)						
		LFL + RFC	-137.8	0.0	5	0.293	0.39
		LFL * RFC	-137.2	0.6	6	0.216	0.40
		RFC	-136.1	1.7	4	0.123	0.35
Gaussian	Phylogenetic diversity (PD)						
		LFL + RFC	-93.6	0.0	5	0.209	0.28
		RFC	-93.2	0.3	4	0.176	0.23
		LFL	-92.1	1.5	4	0.101	0.22

At the landscape scale, percentage of natural forests and anthropic areas were not selected as potential predictors of leaf-litter ant species. Only the null model was selected for ant taxonomic, functional and phylogenetic diversity (Table 2).

Table 2. Best-supported models (GLMMs) with ΔAICc ≤ 2 retained to test landscape structure in leaf-litter ant communities of riparian forests in South Brazilian grasslands.

Distribution	Response variable	Model	AICc	delta	df	Weight	$R^2_{(c)}$
Gaussian	Taxonomic diversity (TD)						
		Null Model	-38.0	0.0	3	0.620	Null
Gaussian	Functional diversity (FD)						
		Null Model	-52.0	0.0	3	0.797	Null
Gaussian	Phylogenetic diversity (PD)						
		Null Model	-31.0	0.0	3	0.681	Null

4. Discussion

Our results provide empirical support for the importance of riparian forests in South Brazilian grasslands. The accelerated land-use changes in this region, especially over grasslands, have been reducing natural habitats and fragmenting landscapes, endangering local biodiversity of associated ecosystems as well. We showed that leaf-litter ant communities respond to riparian forest cover and leaf-litter biomass, suggesting that habitat quantity and characteristics, that could reflect more conserved forests, can affect species diversity, their potential ecological functions, and evolutionary histories.

We found riparian ecosystems with less riparian forest area leading to loss of ant diversities. Species-area relationships (SAR) state that larger areas tend to support a larger number of species (Connor and McCoy 1979). These SAR patterns are not stochastic but mirror the ecological, evolutionary and geographical context of species (Drakare et al. 2006). Larger areas have more habitat types, increasing resources and niche diversity to support more species (Connor and McCoy 1979). Likewise, larger areas also have higher probabilities of colonization and speciation, reducing competition and probabilities of extinction (MacArthur and Wilson 1967; Hubbell 2001). Riparian forests are frequently formed by linear strips of vegetation and surrounded by different ecosystems. Especially in the Pampa biome, these forests are surrounded by grasslands, or even human-modified landscapes, and may represent disconnected habitats. These landscape characteristics can affect ant dispersal rates, favoring homogenization of species composition. Although the current Brazilian Forest Code assures at least 30 m of protected riparian forest on each side for small streams (less 10 m wide), for bats it is not enough to maintain some species and functional groups in the Amazonian forest (Pereira et al. 2019). Our results suggest that streams with a larger cover of riparian forests, at least in a 200 m buffer, are effective to support more ant species and lineages performing potential different ecological functions in South Brazilian grasslands.

Riparian forests with less leaf-litter biomass had lower ant diversities. An increase in leaf-litter diversity (e.g. twigs with different widths and lengths for nesting; Souza-Campana et al., 2017) creates conditions for more species and different compositions (Armbrecht et al., 2004). Studies have reported different characteristics of leaf-litter associated with more ant species in natural forests or modified habitats, such as weight (Queiroz et al., 2013), heterogeneity (Queiroz et al., 2017) and biomass (Solar et al., 2016). Although more biomass does not necessarily result in higher leaf-litter diversity (e.g. different shapes and types of leaves, sizes of twigs), the increase in volume might result in more spatial structure, allowing for ant species coexistence. Likewise, the correlation with FD and PD also show that different ant species and lineages are playing different ecological roles in leaf-litter, resulting in diverse ecosystem services (Del Toro et al. 2012). Leaf-litter ant communities in Neotropical forests are morphologically and ecologically specialized due to a combination of characteristics, such as microhabitat distribution, morphological traits and specialized habits (Silva and Brandão 2010). Our results highlight the importance of the leaf-litter layer in forest habitats to maintain not only ant species richness and diversity but also ecological functions and distinct evolutionary histories of ant fauna.

South Brazilian grasslands are highly endangered due to land use intensification and consequently reduced remnant areas. Indeed, the Pampa biome, the largest expanse of grasslands in Brazil, has the higher Conservation Risk Index, at least 2.3 times as large as other Brazilian biomes (Overbeck et al. 2015). A recent study has shown that landscapes with less grassland cover had lower plant taxonomic and phylogenetic diversity and, in a cascading effect, a reduction in 50% of ant richness in South Brazilian grasslands (Staude et al. 2018). The conversion of natural grasslands by human activities modify landscapes and affect other natural ecosystems associated.

However, another problem for South Brazilian grasslands concern the management of these habitats. This is especially due to the negative view of fire held until now by the non-scientific public and the lack of knowledge on the importance of grazing for these habitats. Disturbances as fire and grazing play a key role in grasslands, structuring diversity patterns, species composition, and ecosystem functioning (e.g. Milchunas et al. 1998; Bond et al. 2005; van Klink et al. 2015). Furthermore, there is a challenge for landscape management in mosaics of forest-grasslands in this region. These different habitats need different conservation strategies (Overbeck et al. 2016). On one hand, fire and grazing are essential to maintain grassland biodiversity and to control forest expansion over these habitats. On the other hand, fire can enter the forest causing damage and cattle can affect forest interiors by trampling and feeding on tree saplings and reducing understory structure (Carlucci et al. 2016). Riparian forests in southern Brazil need to be protected from fire and grazing without damaging grassland dynamics associated with the absence of these disturbances.

Here we found riparian ecosystems with less riparian cover and less leaf-litter biomass presenting loss of ant diversity, potential ecological functions, and evolutionary lineages. These results imply that the protection degree of riparian forests in South Brazil must be improved to support higher biodiversity, and that riparian forests degraded by livestock grazing and human activities should be restored. Furthermore, we recommend avoiding cattle access to the riparian forests building a fence or similar structure. This action could maintain cattle in the grasslands (in which it plays an important role), allow the regeneration of forest species and develop understory and forest structure, increasing the available resources (e.g. leaf-litter) to biodiversity without the presence of disturbances.

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CONSIDERAÇÕES FINAIS

O atual cenário global de rápida transformação e perda de ambientes naturais nos estimula a entender como as espécies estão distribuídas no espaço, o quanto elas podem variar em seus diferentes aspectos biológicos e quais fatores podem ser responsáveis por esses padrões. O objetivo geral desta tese foi abranger estes aspectos utilizando diferentes ecossistemas, escalas espaciais e propriedades biológicas das comunidades de formigas no Sul do Brasil.

Como padrões gerais, demonstro no **Capítulo I** que campos naturais e florestas em áreas de ecótonos são igualmente ricos e diversos em número de espécies e linhagens evolutivas de formigas. No entanto, a composição de espécies presentes em cada um destes ambientes é distinta. Avaliando uma escala espacial mais ampla, evidencio diferenças na composição de espécies de formigas entre três regiões fisiográficas do Rio Grande do Sul, mas nenhuma diferença em relação as relações filogenéticas entre as espécies destas regiões. Também demonstro que os ecótonos de campo e floresta da região da Serra do Sudeste tem maior número de espécies e linhagens evolutivas do que os ecótonos dos Campos de Cima da Serra.

Explorando aspectos em uma ampla escala regional das comunidades de formigas, demonstro no **Capítulo II** que tanto a diversidade de espécies, a funcionalidade e a história evolutiva destas comunidades seguem um clássico padrão latitudinal no Sul do Brasil. Ou seja, conforme avançamos em direção aos trópicos um maior número de espécies e linhagens de formigas que potencialmente desempenham diferentes funções ecológicas pode ser encontrado.

Em relação às variáveis ambientais envolvidas com estes padrões, no **Capítulo I** relato que um maior número de espécies e linhagens de formigas foi coletada em florestas com uma maior temperatura no momento da coleta. Este é um padrão já esperado, uma vez que as formigas são organismos ectotérmicos e seu metabolismo e atividade dependem das condições do ambiente. No entanto, também encontrei neste capítulo variáveis ambientais ainda pouco documentadas na literatura. Enquanto áreas campestres com uma maior altura da vegetação herbácea afetam negativamente as formigas, uma maior densidade de árvores nestas áreas tem um efeito positivo. Como estes campos estão localizados em áreas de transição com ambientes florestais, discuto que estes resultados podem ser reflexo da ausência ou da baixa intensidade manejo destas áreas. No **Capítulo II** demonstro que uma maior diversidade de espécies e de potenciais funções ecológicas no gradiente latitudinal seguem um aumento na precipitação e produtividade primária. Dois estudos na região Neotropical (Silva & Brandão 2014; Vasconcelos et al 2018) relatam um padrão latitudinal contrário para as comunidades de formigas, porém também seguindo um gradiente de precipitação e produtividade. Ainda neste capítulo, apenas a diversidade de linhagens evolutivas de formigas não foi explicada por estas variáveis. Encontrei uma maior diversidade filogenética relacionada com menores temperaturas. Este não é um resultado esperado e documentado na literatura, porém discuto que as áreas amostradas em menores latitudes neste estudo também apresentam as maiores altitudes. Além disso, estas áreas estão mais próximas de manchas e remanescentes florestais do que as áreas mais ao Sul no bioma Pampa, o que poderia facilitar o sucesso na dispersão e colonização por diferentes linhagens de formigas.

Por fim, abordando aspectos de conservação, no **Capítulo III** eu evidencio que ecossistemas ripários com uma menor cobertura (em um raio de 200 metros) e com menos biomassa de serapilheira acumulada no solo reduzem a diversidade de espécies de formigas, linhagens evolutivas coexistindo e de potenciais funções ecológicas que estas desempenham. Com estes resultados ressalto a importância de evitar o acesso do gado ao interior destas matas, evitando a degradação de espécies arbóreas e do sub-bosque, o que poderia resultar em menor estrutura da vegetação e recursos para outras espécies.

Os resultados desta tese contribuem para entender padrões de distribuição de espécies em diferentes escalas espaciais, corroborando outros estudos, mas também evidenciando aspectos ainda pouco explorados, como é o caso dos padrões ecológicos de formigas em áreas campestres. Apesar de numerosas pesquisas com vegetação nos campos do Sul do Brasil, o estudo destes ecossistemas ainda é incipiente quando comparado a ecossistemas florestais, especialmente em relação aos insetos e outros invertebrados. As respostas destes organismos às dinâmicas dos distúrbios pelo fogo e pastejo, essenciais para manter a alta biodiversidade destes campos, podem contribuir para entender os processos de regeneração e resiliência após o manejo. Assim como os resultados que obtive no **Capítulo I**, variáveis ambientais que podem ser exploradas como *proxies* para estes distúrbios (e.g. estrutura da vegetação: altura, variância, biomassa) devem ser exploradas em futuras pesquisas com invertebrados. Resultados destas pesquisas também auxiliam para que futuros planos de manejo destas áreas possam ser aplicados. Debates recentes tentam definir as melhores estratégias para o manejo e conservação destes mosaicos campo-floresta. Do ponto de vista das formigas, tanto campos quanto florestas são altamente diversos e possuem distinta composição, o que sugere que ambos ecossistemas devem ser levados em conta em áreas prioritárias para conservação no Sul do Brasil.

Uma possível limitação desta tese foi o baixo número de unidades amostrais em escala regional. Com base na experiência com os dados e resultados que obtive, sugiro que futuros trabalhos utilizem um maior número amostral possível para avaliar padrões e processos em largas escalas espaciais. Apesar de evidenciar potenciais preditores e processos atuando em escala regional, o número de unidades amostrais dos dois primeiros capítulos (nove unidades amostrais no **Capítulo I** e doze unidades amostrais no **Capítulo II**) podem ter contribuído para (i) a ausência de variáveis ambientais explicando os padrões dos ecótonos entre as diferentes regiões fisiográficas, e (ii) os modelos nulos também selecionados como potenciais preditores nos gradientes latitudinais de diversidade. Contudo, administrar pesquisas e experimentos regionais não é uma tarefa fácil, em muitos casos tornam-se caros e envolvem limitações logísticas mais do que esperadas para a cobertura de áreas geográficas mais amplas.

Há uma enorme necessidade de se criar estratégias sustentáveis para a preservação e conservação de ecossistemas naturais em todo o mundo. Mas para que isso aconteça, um passo inicial é conhecer a biodiversidade dos ecossistemas de interesse. Além das contribuições no contexto ecológico descrevendo padrões e processos que governam as comunidades estudadas, esta tese também contribui com conhecimento das espécies de formigas nos Campos Sulinos e ecossistemas florestais associados. Por fim, também apresento sugestões concretas para o manejo conjunto de ecossistemas campestres e florestais. Cercar florestas com o intuito de evitar o acesso do gado ao seu interior, mantendo a atividade pastoril nos campos, pode ser uma boa estratégia inicial para preservação destes ecossistemas. No entanto, um aprimoramento e uma combinação com outros aspectos práticos de manejo ainda são necessários. Por exemplo, em propriedades rurais onde florestas estão associadas aos campos com pastejo, estes ambientes podem servir de abrigo aos animais, fornecendo sombra em dias quentes, ou mesmo água fresca de córregos e riachos. Debates neste sentido têm ocorrido recentemente (Pillar & Vélez 2010; Luza et al. 2014; Overbeck et al. 2016; Carlucci et al. 2016) e são essenciais para a manutenção e preservação destas paisagens naturais na região Sul do Brasil.