Article

Simple does not mean poor: grasslands and forests harbor similar ant species richness and distinct composition in highlands of southern Brazil

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Abstract: Several studies addressed ant communities in the dense Atlantic Forest that runs along the Brazilian coast. However, comparatively little is known about the mixed forests and grasslands that occur in the southern range of the Atlantic Forest domain. In this study we performed the first standardized assessment of ants in the forest-grassland mosaic found in the highlands of the state of Santa Catarina. We aimed to investigate and compare ant richness and composition between mixed forests and grasslands in the main mountain range of south Brazil. Ants were collected in two years with ground pitfalls, tree pitfalls and litter samples. Sixty ant species were recorded, resulting in 22 new records for "Planalto Serrano" region and three for the state of Santa Catarina: *Eurhopalothrix depressa*, *Pheidole radoszkowskii* and *Wasmannia williamsoni*. There was significant dissimilarity in ant species composition between grasslands and forests, but no difference in ant species richness, even considering the higher number of strata in mixed forests. Similar richness and low number of arboreal species suggest that this ant community is structured similarly to temperate ones. Both habitats presented a large proportion of exclusive species. The fact that species composition between grassland and forest areas differed, coupled with the similarity in species richness between habitats and the record of new ant species for the region, calls for strong conservation efforts in grasslands of southern Brazil, which still are little protected by conservation areas.
Keywords: Formicidae, Atlantic Forest, Araucaria Forest, PPBio da Mata Atlântica, Eurhopalothrix depressa, Wasmannia williamsoni.

Simples não significa pobre: campos e florestas abrigam riqueza similar e composições distintas de espécies de formiga em regiões altas do sul do Brasil

Resumo: Diversos estudos já foram realizados com comunidades de formigas nas regiões de Floresta Ombrófila Densa que ocorrem ao longo da costa do Brasil. Comparativamente menos é conhecido sobre as Florestas Ombrófilas Mistas e campos que ocorrem na parte meridional do domínio da Mata Atlântica. Neste estudo nós realizamos o primeiro levantamento padronizado de formigas no mosaico de florestas e campos que ocorre nas regiões altas de Santa Catarina. Nosso objetivo foi investigar e comparar a riqueza e composição de espécies entre florestas e campos na principal cordilheira do sul do Brasil. Formigas foram coletadas em dois anos com armadilhas de queda no solo e nas árvores, e com amostras de serapilheira. Sessenta espécies foram registradas, constituindo 22 novos registros para a região do Planalto Serrano e três para o estado de Santa Catarina: *Eurhopalothrix depressa*, *Pheidole radoszkowskii* e *Wasmannia williamsoni*. A composição de espécies diferiu significativamente entre florestas e campos, mas não houve diferença em riqueza de espécies, mesmo considerando o maior número de estratos nas florestas. Riqueza similar e pequeno número de espécies arbóreas sugere que esta comunidade é estruturada de modo semelhante às comunidades de regiões temperadas. Ambos os habitats apresentaram alta proporção de espécies exclusivas. O fato de que a composição foi diferente, somado à similaridade em riqueza de espécies entre habitats e ao registro de novas espécies, indica a necessidade de maiores esforços conservacionistas nos campos do Sul do Brasil, que ainda são pouco protegidos por unidades de conservação.
Palavras-chave: Formicidae, Mata Atlântica, Floresta de Araucária, PPBio da Mata Atlântica, Eurhopalothrix depressa, Wasmannia williamsoni.

Introduction

Brazil is one of the most biodiverse countries in the world, due to its high diversity of ecosystems, many containing a high number of endemic species (Lewinsohn & Prado 2003). The Atlantic Forest runs from northeast to south Brazil and its considered one of the world's eight main hotspots of biodiversity (Myers et al. 2000). It harbors a multitude of vegetation types under its domain, such as highland mixed forests on the southern border of its distribution (IBGE 2012). Highland mixed forests, or "*Araucaria* forests", are constituted by a mixture of tropical and temperate flora and are characterized by the occurrence of the endemic *Araucaria angustifolia* (Bertol.) Kuntze, one of the few gymnosperm trees native to Brazil (Gasper et al. 2013). However, in areas of high altitude, forests are sharply interrupted by grasslands patches, resulting in mosaics of variable habitat complexity (Klein 1978). Here, we define habitat complexity as the vertical variation in habitat physiognomy (August 1983). Forests can be considered habitats with higher degree of complexity in relation to grasslands, due to the presence of several strata (ground, litter, understory, canopy) and more heterogeneous distribution of abiotic conditions and resources.

Grasslands occurring in highlands of southern Brazil are considered a remnant of the Glacial, Early and Mid-Holocene period, when the cold weather favored grasslands instead of forests (Behling & Pillar 2007). Nowadays, forests have been slowly expanding over grasslands, but these persist because of a complex set of drivers (Silva & Anand 2011). Even though grasslands are considered important sources of regional biodiversity, they are frequently neglected on the conservation agenda (Overbeck et al. 2007, Overbeck et al. 2015). In addition, out of the few studies about conservation biology directed to grasslands in the highlands of southern Brazil, most have addressed the protection of endemic grassland plants (e.g. Overbeck et al. 2007). Less works called attention to animal species, which also occur as endemic in grasslands around the world (Bond & Parr 2010). Thus, surveys of arthropods richness and abundance can provide interesting data about the value of such grasslands for the conservation of animal diversity (Albuquerque & Diehl 2009, Azcárate & Peco 2012, Rosado et al. 2012, Diehl et al. 2014).

Ants are an important component of most terrestrial ecosystems, showing high richness and abundance, and displaying many ecological associations with plants and other animals (Ness et al. 2010). Because ant colonies are sessile, habitat structure is fundamental to determine food resources and availability of nesting sites (Blüthgen & Feldhaar 2010), which results in ants being highly dependent on microhabitat conditions. Indeed, this strong relationship imply that ant species composition can be dissimilar between distinct phytophysiognomies that co-occur at the same site, such as in forest-grassland mosaics (Gibb & Parr 2010).

Several studies addressed ant communities in the dense Atlantic Forest that runs along the Brazilian coast (a.k.a. Atlantic Forest *stricto sensu* or Atlantic Rainforest; e.g. Silva & Lopes 1997, Freitas et al. 2014, Silva & Brandão 2014). Comparatively little is known about highland mixed forests and grasslands (Ulysséa et al. 2011), which only recently started to be systematically investigated (Pinheiro et al. 2010, Dröse et al. 2017, Franco & Feitosa 2018). We contributed to fill this knowledge gap with the first standardized assessment on the

forest-grassland mosaic found in the highlands of the state of Santa Catarina, as a part of the "Programa de Pesquisa em Biodiversidade (PPBio) da Mata Atlântica" (Atlantic Forest Research Program on Biodiversity). Additionally, we compared ant species composition and richness between mixed forest and grasslands patches, with the hypothesis that ant distribution would be affected by habitat structure, thus leading to distinct assemblages coexisting in this mosaic.

Methods

1. Study Area

Fieldwork was carried out in "Parque Nacional de São Joaquim (PNSJ)" (28°8'53.07"S and 49°36'34.61"O), a national park which lies on the "Serra Geral" formation, the main mountain range of southern Brazil. The geology of this region is a result of volcanic sheds of basaltic lava that started ~127 million years ago (Milani et al. 2007). The climate in the region is Cfb following Köppen's classification (Alvares et al. 2014), with mean annual precipitation ~1,400 mm and mean annual temperature ~14ºC (Fernandes & Omena 2015). On winter, temperatures commonly fall below 0ºC with occasional occurrence of snow (Nimer 1989).

The PNSJ has a total area of 49,300 ha and it is within the Atlantic Forest domain. Altitude of sampled plots ranged from 1,462 m to 1,671 m. Samples were collected in two vegetation types, namely mixed forest ("Floresta Ombrófila Mista Alto-Montana") and grassland ("Campos do Planalto"). Grasslands are predominantly covered by a dense layer of herbaceous stratum, with occasional shrub patches and small isolated trees. Mixed forests have a canopy height of ~8 m, with emergent *Araucaria angustifolia* trees typically reaching 13 m (Rafael Barbizan Sühs, personal communication).

2. Field Procedures

Two field campaigns were conducted during summer, one in March 2014 and other in February 2015. Sampling was carried out on a rectangular grid of 5 × 1 km with 10 plots, 1 km apart from each other (Figure S1 in Supplementary information). Each plot was 250 m long and followed the isocline of the ground. This design follows the RAPELD method for biodiversity surveys (Magnusson et al. 2005), implemented in the "PPBio Mata Atlântica". Five sampling points were established at each plot, 50 m apart from each other, totaling 50 sampling points. Nineteen sampling points were located in grasslands (n_g) and 31 in forests (n_f).

Ants were sampled with up to three methods, depending on the habitat structure of each sampling point (see Figure S2 in Supplementary information for detailed schematics). Ground pitfall traps were installed on all sampling points and retrieved after 48 hours. Each pitfall trap consisted on 300 ml plastic cups with diameter of 7.2 cm, buried at ground level, with a solution of water, detergent and salt as killing agent. Arboreal pitfalls followed the same design and were tied to trees at 1.5 m high, only in sampling points where there was at least one tree with more than 15 cm of diameter at breast height (DBH). Because of the low number of ants collected on arboreal pitfall traps in 2014, we added sardine baits to these traps in 2015. Additionally, in all sample points with accumulated leaf litter, we collected 1 m² of

it, three meters away from the ground pitfall. The litter was sifted on the field and later placed into Winkler extractors for 48 hours. Tree pitfalls and litter samples were collected mainly in forests, but also in a few grassland points whenever isolated trees/litter were available. All collected material was stored in ethanol 95%.

3. Laboratory Procedures

For each sample, ants were initially sorted to morphospecies and at least one individual per morphospecies was mounted on paper triangles fixed in entomological pins. Ants were identified at genus level according to Palacio & Fernández (2003). Species were identified with taxonomic keys and further compared with reference collections and AntWeb images (AntWeb 2017). Genus and species names were updated with Bolton (2017). When no taxonomic resources were available, they remained as morphospecies. All species identifications were revised by taxonomists of the "Laboratório de Sistemática e Biologia de Formigas" (Universidade Federal do Paraná) (see Acknowledgements). Voucher specimens are deposited in the reference collection of the "Laboratório de Biologia de Formigas" (ECZ, Universidade Federal de Santa Catarina).

The sources used for species-level identification were: *Acromyrmex* – Gonçalves (1961); *Anochetus* – Fernández (2008); *Eurhopalothrix* – Longino (2013a); *Gnamptogenys* – Lattke et al. (2007); *Heteroponera* – Arias-Penna & Fernández (2008); *Linepithema* – Wild (2007); *Neivamyrmex* – Watkins (1976); *Octostruma* – Longino (2013b); *Oxyepoecus* – Albuquerque & Brandão (2004), Albuquerque & Brandão (2009); *Pachycondyla* – Fernández (2008); *Strumigenys* – Bolton (2000); *Trachymyrmex* – Mayhé-Nunes & Brandão (2005); *Wasmannia* – Longino & Fernández (2007).

New species records were checked against the most recent checklist for Santa Catarina (Ulysséa et al. 2011) and the literature published afterwards.

4. Data Analysis

Data from the two field campaigns were merged for each sample point. We excluded from quantitative analyses data from one plot that was relocated between years. Therefore, the effective number of sampling points used in the analyses was 45, 19 in grassland (n_g) and 26 in forest areas (n_f), including 45 ground pitfalls ($n_g = 19$, $n_f = 26$), 29 tree pitfalls ($n_g = 6$, $n_f = 23$) and 27 litter samples ($n_g = 1$, $n_f = 26$).

We calculated species frequency (number of records divided by total number of sampling points, calculated separately for each habitat) using presence-absence data, which is preferred to represent ant abundance (Longino 2000). To compare species richness between grassland and forest samples, we fitted curves of interpolation and extrapolation of Hill numbers to the split dataset, following the method developed by Chao et al. (2014) with order q = 0, which is the Hill number where there is zero weight for species abundances and thus stands for species richness. We built curves for ground pitfalls (the sampling method shared for all sampling points) and for all methods combined, which represents the sum of the strata available at each sample point. Interpolation and extrapolation curves were calculated with the R package "iNEXT" (Hsieh et al. 2016) and 95% confidence intervals were estimated based on 1000 permutations. Comparison of confidence intervals was used to test for species richness differences between vegetation types. We compared curves both within the observed

range of data and after extrapolating up to 50 sampling units within each vegetation type. Interpolated curves are important to smooth sampling effects in unbalanced designs as ours, while extrapolation allows the use of all sample units, and point out the expected behavior of the curves if a larger proportion of the community were sampled (Colwell et al. 2012).

To visualize differences in ant species composition among sampling points, we ran a Principal Coordinate Analysis (PCoA), using the package "vegan" (Oksanen et al. 2016). The PCoA was based on Jaccard similarities, using only ground pitfall records. To test the differences in composition between the two habitats, we calculated a Generalized Linear Model for multivariate response data (GLM_{mv}) using the package "mvabund" (Wang et al. 2012). The GLM_{mv} allows for choosing a family for the distribution of residuals. For species presence-absence data, the best option is to use the binomial distribution because it accounts for data with both lower and upper boundaries. Choosing an adequate distribution has the advantage that the GLMmv avoids confounding differences in location (true differences in species composition) and dispersion (differences due to changes in beta diversity; Wang et al. 2012). Specifically, the GLM_{mv} has been shown to be more reliable to point out only location differences than traditional approaches, such as permutational multivariate analysis of variance – PERMANOVA, which can point out significant differences because of either location, dispersion, or even both patterns (Wang et al. 2012). Because GLM_{mv} are more specific in terms of what their results tell, we can also be more confident in answering more specific questions, here whether there are differences in species composition, not beta diversity, between grassland and forest. We analyzed all data in R, version 3.3.2 (R Core Team 2016).

Results

We recorded 60 ant species belonging to nine subfamilies and 23 genera. Our survey adds 22 new species to the "Planalto Serrano" region list, including three new to Santa Catarina territory: *Eurhopalothrix depressa*, *Pheidole radoszkowskii* and *Wasmannia williamsoni*. Forty-six species were sampled in forests and 34 in grasslands (Table 1). Twenty-six species were exclusive to forests (56% of the total for this vegetation), while 14 were exclusive to grasslands (41%). The most frequent species in mixed forest was *Heteroponera dentinodis* (relative frequency = 0.81), followed by *Oxyepoecus crassinodus* (0.73). In grassland, the most frequent species was *Pheidole* sp.5 (0.68), followed by *Camponotus rufipes* (0.53). Compared to ground pitfalls (40 spp.) and litter samples (42 spp.), tree pitfalls collected fewer species (11 spp.), and only two species were exclusively recorded by this method.

The interpolation curves based only on ground pitfalls showed a higher number of observed species in grasslands (Figure 1). However, with extrapolation, the curves tend to overlap, suggesting no actual difference between vegetation types. This richness equivalence is highlighted when we added data from leaf litter and tree pitfalls. With pooled data from all strata, the curves were similar and confidence intervals largely overlapped (Figure 2).

The GLM_{mv} results showed a difference in species composition between grasslands and forests (Wald-value = 4.159; p = 0.034). Most sampling points were separated in two groups corresponding to the two habitats, although there were intermediate sites that shared species from both habitats (Figure 3).

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Table 1. Ant species recorded in "Parque Nacional de São Joaquim", southern Brazil. Frequencies represent number of records relative to number of sample points for each habitat (grasslands = 19, forest = 26). For methods, it is indicated whether the species was recorded or not with the method.

Species	Habitat		Method		
	Grassland	Forest	GP	TP	LL
Acromyrmex crassispinus (Forel, 1909)		0.27	+		+
Anochetus altisquamis Mayr, 1887		0.08	+		+
Brachymyrmex sp.1		0.19	+		+
Brachymyrmex sp.2	0.11	0.12	+		+
Camponotus alboannulatus[†] Mayr, 1887		0.12		+	+
Camponotus crassus[†] Mayr, 1862	0.16		+		
Camponotus fastigatus[†] Roger, 1863	0.32		+		
Camponotus melanoticus[†] Emery, 1894	0.21	0.12	+	+	+
Camponotus rufipes (Fabricius, 1775)	0.53	0.35	+	+	+
Camponotus sp.	0.05			+	
Crematogaster sp.1		0.12			+
Crematogaster sp.2		0.08		+	+
Crematogaster sp.3	0.11		+		
Crematogaster sp.4	0.05			+	
Crematogaster sp.5		X			+
Discothyrea sp.		0.04			+
Eurhopalothrix depressa[‡] Ketterl, Verhaagh e Dietz, 2004		0.08			+
Gnamptogenys striatula[†] Mayr, 1884	0.42		+		
Heteroponera dentinodis[†] (Mayr, 1887)		0.81	+		+
Hypoponera sp.1		0.69	+		+
Hypoponera sp.2	0.05	0.27			+
Hypoponera sp.3		0.19			+
Linepithema angulatum[†] (Emery, 1894)	0.11		+		
Linepithema gallardoi[†] (Brèthes, 1914)	0.37	0.23	+		+
Linepithema micans (Forel, 1908)	0.21	0.27	+		+
Myrmelachista gallicola[†] Mayr, 1887		0.04			+
Neivamyrmex hetschkoi[†] (Mayr, 1886)		X			+
Neivamyrmex punctaticeps[†] (Emery, 1894)		X			+
Nylanderia sp.		0.08	+		+
Octostruma rugifera[†] (Mayr, 1887)		0.04			+
Oxyepoecus crassinodus[†] Kempf, 1974		0.73	+	+	+
Oxyepoecus plaumanni[†] Kempf, 1974		0.04			+
Oxyepoecus vezenyii[†] (Forel, 1907)		0.31			+
Pachycondyla striata Smith, 1858	0.26	0.08	+		
Pheidole aberrans[†] Mayr, 1868	0.05		+		
Pheidole avia[†] Forel, 1908		X			+
Pheidole radoszkowskii[‡] Mayr, 1884	0.21		+		
Pheidole rosae[†] Forel, 1901	0.21	0.04	+		+
Pheidole aff. *lutzi*	0.11	0.04	+	+	
Pheidole sp.1		0.31	+		+
Pheidole sp.3	0.16	0.35	+		+
Pheidole sp.4		0.12	+		+
Pheidole sp.5	0.68	0.23	+		+

Continued Table 1.

Species	Habitat		Method		
	Grassland	**Forest**	**GP**	**TP**	**LL**
Pheidole sp.9	0.05	0.04	+		
Pheidole sp.11	0.16	0.08	+		+
Pseudomyrmex termitarius (Smith, 1885)		0.12		+	+
Solenopsis sp.1	0.16	0.69	+		+
Solenopsis sp.2	0.16	0.12	+		+
Solenopsis sp.4	0.05		+		
Solenopsis sp.5		X			+
Solenopsis sp.6		0.04		+	
Solenopsis sp.7	0.16	0.08	+	+	+
Solenopsis sp.8	0.05		+		
Strumigenys louisianae[†] Roger, 1863	0.05		+		
Strumigenys aff. *louisianae*	0.11	0.04	+		+
Trachymyrmex holmgreni[†] Wheeler, 1925	0.05		+		
Trachymyrmex sp.	0.05		+		
Wasmannia affinis[†] Santschi, 1929	0.05	0.65	+		+
Wasmannia auropunctata[†] (Roger, 1863)	0.11	0.04	+		+
Wasmannia williamsoni[‡] Kusnezov, 1952	0.16	0.04	+		+
TOTAL	34	46	40	11	42

X = the species was recorded only on the plot removed from quantitative analyses. GP = ground pitfall traps. TP = tree pitfall traps. LL = leaf-litter samples.
[†] = new records for the Planalto Serrano region. [‡] = new records for the state of Santa Catarina.
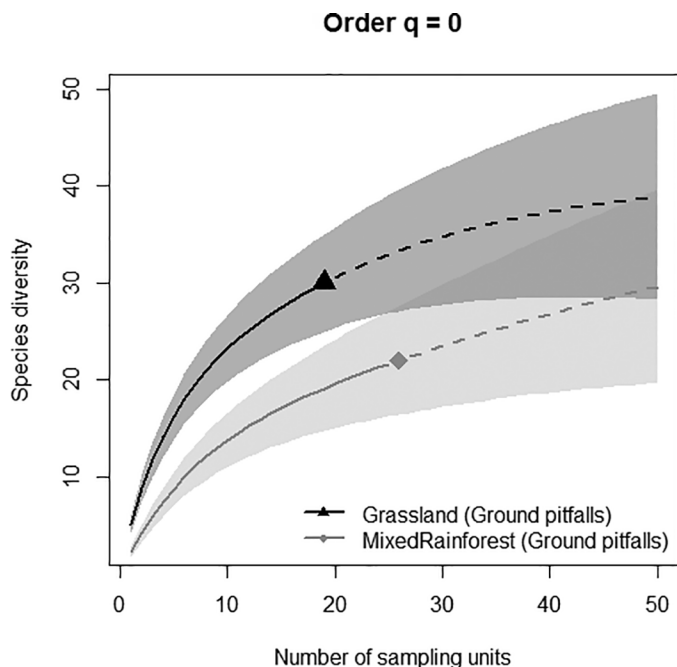

Figure 1. Interpolation, extrapolation and 95% confidence intervals of species richness in grassland and forest, using data from ground pitfall traps. Interpolation – solid lines; extrapolation – dashed lines.
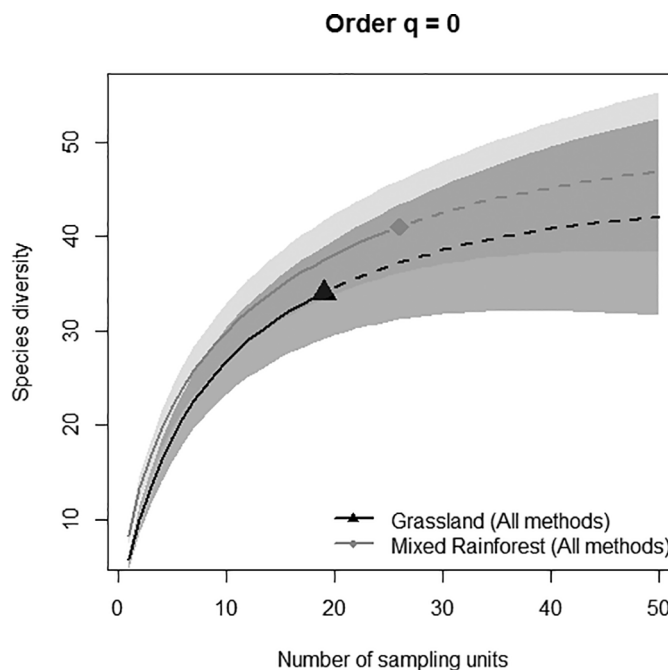

Figure 2. Interpolation, extrapolation and 95% confidence intervals of species richness in grassland and forest, using pooled data from all sampling methods. Interpolation – solid lines; extrapolation – dashed lines.
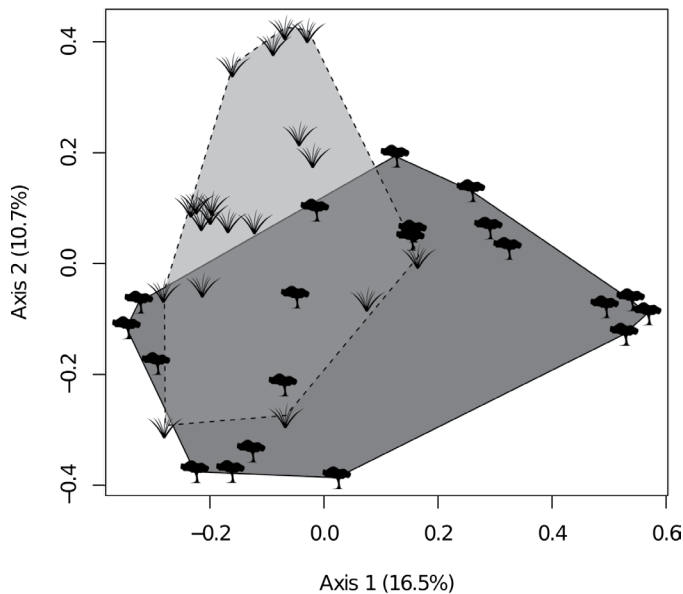
Figure 3. Principal Coordinate Analysis showing the dissimilarity of ant species composition between sites on grasslands or forests using data from ground pitfalls. Lines indicate convex hulls encompassing sites from each type of habitat (forests – solid line; grasslands – dashed line).

Discussion

1. New regional records

Santa Catarina is one of the few Brazilian states with a recent checklist of ant species recorded in its territory (Ulysséa et al. 2011). The "Planalto Serrano" region, where the PNSJ is located, was deemed as a research priority, with only 12 species recorded at the time (Ulysséa et al. 2011). The great number of new ant species in "Planalto Serrano" recorded here mainly is a result of this lack of knowledge, but also can be related to the complementarity of our sampling effort. The combination of pitfalls and leaf litter collection on the ground is strongly advised for biodiversity assessments (Alonso & Agosti 2000, Bestelmeyer et al. 2000, King & Porter 2005, Lopes & Vasconcelos 2008), since the first method catch larger and more active species (Sabu et al. 2011), while the second is efficient to sample smaller and less active ants, including cryptic species (Fisher 1999). Finally, our sampling effort in grasslands sites, a poorly surveyed physiognomy until now in Santa Catarina, is another important source of those new records, a trend that is increasingly highlighted in other grasslands surveys of South Brazil recently published (Pinheiro et al. 2010, Rosado et al. 2012, Dröse et al. 2017, Franco & Feitosa 2018).

With regard to the new records for the state of Santa Catarina, this is only the third known record for *Eurhopalothrix depressa*, previously found once in mixed forest, further south of our location, and once in dense Atlantic Forest (Ketterl et al. 2004). Considered a highly distinctive species of the genus (Longino 2013a), these few records suggest rarity and endemic distribution inside the Atlantic Forest domain. Little information is available about its biology, but most representatives of the genus are predators inside the leaf litter, where they are more often recorded (Longino 2013a). *Wasmannia williamsoni* is considered a grassland-associated species (Cuezzo

et al. 2015), and indeed we found it more often in this vegetation. Although the previous authors suggested it to be a relict endemic lineage of the central region of Argentina, it was found in the Pampa region of southern Brazil (Rosado et al. 2012), and our record expands its distribution by 600 km further north. Finally, *Pheidole radoszkowskii* is a widespread species – or species complex – found all over the Neotropical region (Wilson 2003). Contrary to *E. depressa*, this record is likely result of the taxonomic uncertainty associated with most species of *Pheidole*.

2. Species richness and composition

A positive relationship between species richness and habitat complexity often is found in tropical and subtropical ant communities (Majer et al. 1997, Vasconcelos & Vilhena 2006, but see Lassau & Hochuli 2004). In lowland forests with higher canopy and strong presence of epiphytes, arboreal ants largely contribute to forest richness (Vasconcelos & Vilhena 2006, Neves et al. 2013). However, this relationship might be found even when only the ground stratum is considered (Andersen 1986). The ground of a forest can be considered more complex and heterogeneous (Farji-Brener et al. 2004) than a grassland because of a litter layer with variable depth, more heterogeneous distribution of plants in the understory, and availability of tree-related resources (e.g. fallen fruits). In our study, ant richness was similar between habitats. This similarity was observed both when we compared pitfalls, and when we added data from other strata, which are characteristic of forests (leaf-litter, vegetation). A shift on the complexity-richness trend is common in temperate latitudes or high altitudes, where ant richness decline in shaded forests and increase in open habitats (Seifert 2007, Longino et al. 2014). Ants are thermophilic animals (Pie 2016) and, below a certain threshold, less species are able to tolerate low insolation and temperature inside forests. Even considering only grasslands, a decrease in species richness might be observed with altitude (Dröse et al. 2017). Thus, although most species we found also occur in dense Atlantic Forest, the community is organized differently, and some species change their behavior accordingly. This might be the case for *Gnamptogenys striatula* and *Pachycondyla striata*, two species very common inside lowland forests (Lattke 1995, Rosumek et al. 2008, Medeiros & Oliveira 2009), which shifted their occurrence mainly to open areas in our study site.

A similar environmental effect reduces richness and abundance of arboreal-nesting ants in temperate habitats (Benson & Harada 1988, Blüthgen & Feldhaar 2010). Arboreal nests are more subject to temperature fluctuations along the year, particularly the harsh winter, which few species are able to withstand. In our site, arboreal pitfalls had low effect in total richness. In the mixed forest, only two species were found exclusively in arboreal pitfalls, all others also occurring on the ground. With pitfalls located at 1.5 m high, it is expected to find several ground species which climb up trees to forage. However, the low efficiency of the pitfalls and lack of exclusive species suggests a relatively small arboreal community. In grasslands, it was also observed that few species occur exclusively in vegetation (Dröse et al. 2017). Most plants in this habitat do not provide proper nesting sites above the ground, and these would be even more affected by cold temperatures.

While richness was similar, our results indicate that grassland and forest habitats maintain different ant assemblages. This division was confirmed by the GLM_{mv}, although it was not very strong (see axis values in Figure 3) and composition overlapped at many points. Two-thirds of the species were exclusive to one habitat, which accounted for about half of the total for each habitat. This finding agrees with the idea that ants have close relationships with vegetation structure, and, consequently, with microhabitat conditions and resources available, such as nesting sites and nutritional supplies (Rico-Gray & Oliveira 2007, Blüthgen & Feldhaar 2010, Gibb & Parr 2010). Indeed, most studies comparing ant species composition between different ecosystems found great dissimilarities (Marques & Del-Claro 2006, Vasconcelos & Vilhena 2006, Vasconcelos et al. 2008, Groc et al. 2014).

3. Concluding remarks

Here we assessed the ant community in highlands of the state of Santa Catarina, and showed that grasslands and forests harbor similar richness, yet distinct ant species composition. This work joins recent studies that assessed ant communities in the grassland/mixed forest mosaics of the southern Atlantic forest (Pinheiro et al. 2010, Dröse et al. 2017, Franco & Feitosa 2018). Our results provide insights on the drivers of community organization, and suggest that the combination of relatively high latitude and altitude gives to the ant community some features of temperate habitats, thus distinct from the dense Atlantic Forest and from most Brazilian ecosystems. Such patterns might be context-dependent, and more factors could be involved in the distribution of the biodiversity in this ecosystem, e.g. edge effects (Pinheiro et al. 2010). Nevertheless, we suggest that these grasslands and forests are equally relevant for biodiversity conservation. We call special attention to grasslands, because they are frequently neglected in conservation programs (Overbeck et al. 2015), a conclusion shared by the aforementioned recent studies in the same ecosystem. While grasslands occupy nearly 13.7 million ha in Brazilian territory, less than 0.5% of the ecosystem is within protected areas (Overbeck et al. 2007). As highlighted by some authors, managed grasslands lead to different plant and ant assemblages, and more research is necessary to effectively protect the biodiversity linked with those habitats (Azcárate & Peco 2012). Even though the issues in conservation status of plant species have been raised for over a decade (Overbeck et al. 2007), more recently attention has also been called for arthropod diversity in similar ecosystems around the world (Littlewood et al. 2012).

Supplementary material

The following online material is available for this article:
Figure S1 - Map of the sample grid established in "Parque Nacional de São Joaquim". The rectangular line shows the main trails of the 5x1 km grid. Red lines indicate 250 m plots, which follow the isocline of the ground. The thick yellow line shows the limits of the protected area.
Figure S2 - Schematic representation of the sample design.

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Author Contributions

Cristian Luan Klunk: Contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Eduardo Luís Hettwer Giehl: Contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Benedito Cortês Lopes: Substantial contribution in the concept and design of the study; contribution to data analysis and interpretation; contribution to critical revision, adding intellectual content.

Frederico Rottgers Marcineiro: Contribution to data collection; contribution to critical revision, adding intellectual content.

Félix Baumgarten Rosumek: Substantial contribution in the concept and design of the study; contribution to data collection; contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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