

# Ant and tenebrionid beetle assemblages in arid lands: Their associations with vegetation types in the Patagonian steppe



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## ABSTRACT

Arid environments have long been perceived as simple and homogeneous ecosystems, but slight differences in precipitation, topography and soil attributes result in a variety of distinct plant associations. The availability of different vegetation types leads to a non-uniform distribution of resources and abiotic conditions, which may affect the spatial distribution of their associated fauna. Here we describe a study, in the San Jorge Gulf district of Patagonia, where we tested the relationships between ant and tenebrionid diversity and composition and discrete vegetation types in an area where invertebrate fauna is poorly known. We captured 5019 individuals, from 13 to 21 species, of ants and tenebrionids, respectively. We found differences in composition of ants and tenebrionids among the vegetation types, with unique ant composition on peladales and subshrub steppes, and distinct tenebrionid assemblages in all vegetation types. Our results show that ants and darkling beetles responded differently to vegetation type. Because both taxa are key components of arid environment fauna, it is important to consider vegetation heterogeneity when developing management plans to conserve biological diversity and ecological functions in these environments.

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## 1. Introduction

The relationship between environmental heterogeneity, and species composition and diversity has become a central topic in ecology, evolution and biogeography (Stein and Kreft, 2015). Although environmental heterogeneity is a common feature in natural systems, until recently, its importance has been overlooked. In particular, arid lands were often viewed as simple and structurally homogeneous systems until some decades ago, when more detailed ecological studies revealed high levels of temporal and spatial heterogeneity (Polis, 1991). At the landscape scale, vegetation in dry-lands is not continuous in space, mainly due to slight differences in precipitation, topography and soil attributes, resulting in a variety of distinct plant arrangements (Bisigato et al., 2009). The availability of different vegetation types (e.g., shrub steppes, subshrub steppes, grass steppes) is especially important for animals in this kind of environments with high climatic and resource fluctuations, as they provide shelter, food and suitable abiotic

conditions (e.g., Heatwole, 1996; Whitford, 2002). The increasing intensity of human activity in arid regions tends to increase bare soil at the expense of vegetation (Bainbridge, 2007), which could indirectly affect animal assemblages. Thus, a better knowledge of the associations between vegetation types and animal species in these regions is crucial for biodiversity conservation (Dufour et al., 2006).

Among the fauna of arid and semiarid environments, ants and beetles are dominant in terms of biomass and abundance (Polis, 1991; Claps et al., 2008). They also stand out as being involved in many ecological processes, such as predation, organic matter consumption, soil nutrient cycling, pollination, seed dispersal, plant anti-herbivore defense, and food for vertebrates (Flores, 1998; Andersen et al., 2004; Sackmann and Farji-Brener, 2006; Rico-Gray and Oliveira, 2007; Lach et al., 2010). Both ants and beetles are taxonomically diverse, occupy a wide range of microsites and also consume varied food resources (Borrer et al., 1989; Hölldobler and Wilson, 1990). Since they are key components of arid environments, it is important to know how they are influenced by changes in the spatial heterogeneity of vegetation. This knowledge allows us to predict how human disturbances are likely to influence

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diversity and distribution of ants and beetles, and ultimately their impacts on a range of ecosystem processes.

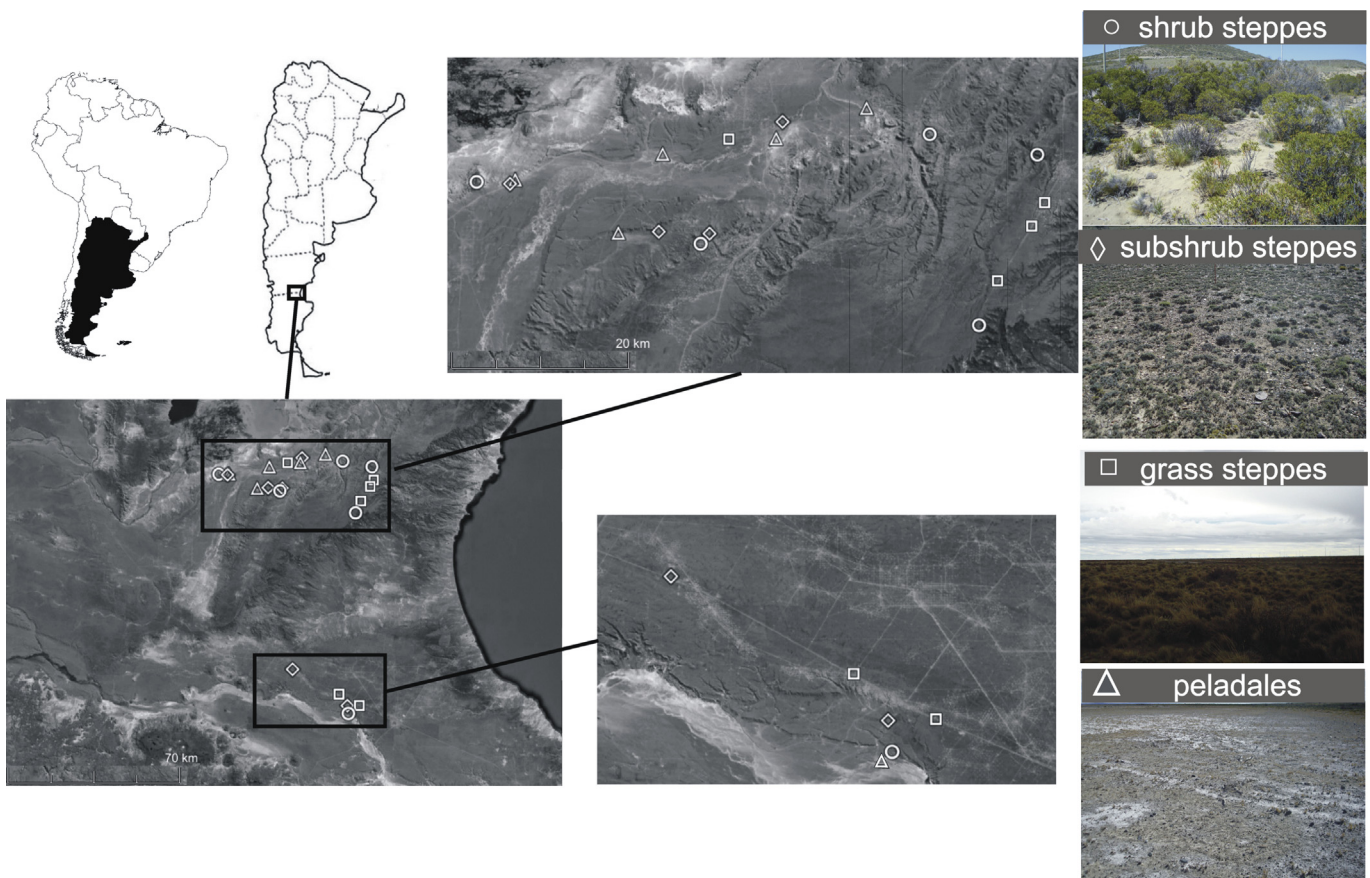
The Patagonian biogeographic province (Cabrera and Willink, 1980), located in the southern portion of South America, comprises vast xeric areas characterized by marked heterogeneity in climate, soil and vegetation at a range of spatial scales (Oesterheld et al., 1998). In fact, twelve physiognomic floristic units were defined (León et al., 1998) in this phytogeographic province (Cabrera, 1976), comprising shrub, subshrub, and grass steppes, with different plant cover and dominant life forms. Although Patagonian steppe covers a huge area (about 800,000 km<sup>2</sup> or 30% of the surface of Argentina), few studies have dealt with the diversity and composition of ants and beetles (e.g., Sackmann and Flores, 2009; Cheli et al., 2010; Pirk, 2014). Therefore, the knowledge of the ground-dwelling arthropod fauna in some areas of Patagonia is limited (Cuezzo, 1998; Flores, 1998; Claps et al., 2008), let alone their relation with vegetation structure (e.g., Mazia et al., 2006). Both ants and tenebrionids (darkling beetles) are among the predominant components of the terrestrial invertebrate fauna of Patagonia (Sackmann and Flores, 2009; Cheli et al., 2010). Knowledge of the local ant and beetle assemblages associated with vegetation types in Patagonia is valuable to any wildlife inventory of the area. This is useful in order to provide information to establish conservation priorities in response to human activities such as overgrazing and oil extraction, that tend to homogenize the landscape. Thus, the aims of this study are to describe ant and darkling beetle diversity and composition and to determine whether they differ among distinct vegetation types (grass, shrub and subshrub steppes and bare areas) of the Patagonian steppe.

Since the availability of distinct plant associations makes a non-uniform distribution of resources and abiotic conditions, and ant and tenebrionid species have a variety of ecological requirements, we expected different vegetation types to harbor distinct ant and tenebrionid assemblages.

## 2. Methods

### 2.1. Study area

This study was conducted in the San Jorge Gulf area (South-eastern Patagonia, Argentina), a distinct vegetation district within the Patagonia phytogeographic province (Cabrera, 1976) (Fig. 1). The climate is meso-thermal dry with an average precipitation of 245 mm and a mean annual temperature of 13 °C (Rueter and Bertolami, 2010). Given the Mediterranean precipitation regime and strong westerly winds, the extended water deficit and heat concentration occurs in January (Paruelo et al., 1991). The soils have sandy-clayish characteristics, with little vertical development, and low organic matter and moisture content (Andreis et al., 1975). The dominant vegetation in the area includes typical herbs and shrubs of the Patagonian steppe (e. g. *Retanilla patagonica*, *Colliguaja integerrima*, *Adesmia campestris*, *Anarthrophyllum rigidum*, *Ephedra frustillata*, *Stipa humilis*, *Poa ligularis*, *Poa ligularis*, *Stipa patagonica*, *Festuca pallescens*, *Festuca argentina*; Cabrera, 1976; Paruelo et al., 1991). However, there are five well-defined plant communities: shrub steppes, subshrub steppes, grass steppes, bare areas or “peladales”, and wetland meadows or “mallines” (Fig. 1). Although wetland meadows are floristically important, they were excluded



**Fig. 1.** Map of the sampling area in the San Jorge Gulf, South-eastern Patagonia, Argentina, showing the sampling units among the four vegetation types: shrub steppes (○), subshrub steppes (◇), grass steppes (□), and *peladales* (△). Upper inset shows Valle Hermoso area while lower inset is Koluel Kaike.

from this study because their flooded soils are not suitable for terrestrial insects. Physiognomic–floristical descriptions of the regional vegetation (León et al., 1998; Elissalde et al., 2002) characterized these plant communities as follows: **shrub steppes** are floristically homogeneous, with around 65% plant cover, and shrubs higher than 1 m (e.g., *Colliguaja integerrima*, *Retanilla patagonica*) dominate; **subshrub steppes** present a dominant stratum of subshrubby forms with chamaephytes (e.g., *Nassauvia ulicina*, *N. glomerulosa*, *Chuquiraga aurea*, *Azorella caespitosa*), with 20–40% plant cover, while the herbaceous layer is poorly defined and limited in cover; **grass steppes** have a dominant herbaceous stratum, composed mainly of tall tussock-grasses 25–40 cm high (e.g., *Festuca argentina*, *F. pallidissima*, *Pappostipa humilis*), with 80% cover, and often present scattered shrubs and subshrubs; **“peladales”** have low total vegetation cover (<10%), and some subshrubs and cushion plants (e.g., *Chuquiraga aurea*, *N. ulicina*, *Frankenia patagonica*). We sampled these four main vegetation types between the areas of Valle Hermoso (Chubut, –68.3 W; –45.73 S) and Koluel Kaike (Santa Cruz, –68.21 W; –46.71 S; 133 km maximum distance between sites) (Fig. 1).

## 2.2. Sampling and sample processing

We sampled ants and tenebrionids in spring (11 and 19 October 2012) and summer (9 and 18 January 2013) when their activity is

maximum (Ruggiero et al., 2009). We used pitfall traps (diameter, 9 cm; depth, 12 cm), grouped into sampling units, which consisted of five traps forming a 100 m<sup>2</sup> square (one at each corner and one at the center). In total, we placed 24 sampling units (six replicates by four vegetation types), at least 1 km apart. Sampling units of different vegetation types were interspersed in order to avoid spatial pseudo-replication (Fig. 1). Traps were buried at ground level and filled with diluted propylene glycol (40% propylene glycol and water) and a drop of detergent. All traps were opened for 3 days during October (except for those in 6 sites near Koluel Kaike which were opened for 5 days) and 5 days during January. When we collected the traps, we pooled the contents from the five traps of each sampling unit into a single vial filled with 80% ethanol.

Ants and tenebrionids were identified to species/morphospecies at the lab using available keys for taxonomic identification (Kulzer, 1963; Kusnezov, 1978; Aalbu and Andrews, 1996; Flores, 1999; Flores and Vidal, 2001; Flores et al., 2011), as well as reference collections from the Laboratorio Ecotono (INIBIOMA, Bariloche, Argentina) and IADIZA (CCT CONICET-Mendoza, Argentina). Taxonomic identifications were checked by expert taxonomists. Voucher specimens were deposited in these two collections.

## 2.3. Statistical analyses

First, we used species accumulation curves and species richness

**Table 1**

Ant and tenebrionid species collected in each vegetation type. For each species we indicate the abundance (total number of individuals, # ind), and for ants we also include the incidence (number of traps with the species “X”/number total of traps, %inc). Asterisks indicate two new undescribed species different from the undescribed *Discopleurus* sp. 1 mentioned in Sackmann and Flores (2009).

Family	Subfamily	Tribe	Species	Grass steppes		Subshrub steppes		Shrub steppes		Peladales			
				#ind	%inc	#ind	%inc	#ind	%inc	#ind	%inc		
Formicidae	Dolichoderinae	Leptomyrmecini	<i>Dorymyrmex antarticus</i>	112	66.7	136	66.7	559	83.3	3440	83.3		
			<i>Dorymyrmex flavescens</i>	2	16.7	141	83.3	16	33.3	1	16.7		
			<i>Dorymyrmex minutus</i>	8	50.0	8	50.0	7	50.0	1	16.7		
			<i>Dorymyrmex richteri</i>	0	0.0	61	33.3	5	16.7	0	0.0		
	Formicinae	Camponotini	<i>Camponotus distinguendus</i>	2	16.7	12	16.7	0	0.0	0	0.0		
			Melophorini	<i>Lasiophanes valdiviensis</i>	7	33.3	0	0.0	0	0.0	0	0.0	
		Plagiolepidii	<i>Brachymyrmex</i> sp.	5	33.3	17	66.7	20	66.7	0	0.0		
			Pogonomyrmecini	<i>Pogonomyrmex brevibarbis</i>	12	33.3	4	33.3	1	16.7	110	83.3	
		Myrmicinae	Solenopsidini	<i>Pogonomyrmex carbonarius</i>	13	16.7	0	0.0	0	0.0	0	0.0	
	<i>Pogonomyrmex</i> sp. Nova			9	16.7	8	50.0	2	16.7	42	33.3		
	<i>Solenopsis</i> sp. 1			34	33.3	8	33.3	9	33.3	0	0.0		
	<i>Solenopsis</i> sp. 2			0	0.0	15	16.7	0	0.0	0	0.0		
			<i>Solenopsis</i> sp. 3	0	0.0	1	16.7	0	0.0	0	0.0		
<b>Total number of species</b>			<b>13</b>		<b>11</b>		<b>8</b>		<b>5</b>				
Tenebrionidae	Pimeliinae	Cossyphodiini	<i>Cossyphodini</i> sp.	1		0		0		0			
			Epitragini	<i>Nyctopetus neuquensis</i>	0		1		0		0		
			Nycteliini	<i>Epipedonota cristallisata</i>	5		0		0		0		
				<i>Epipedonota lata</i>	8		1		3		0		
				<i>Mitragenius araneiformis</i>	2		0		0		0		
				<i>Nyctelia blairi</i>	2		1		0		0		
				<i>Nyctelia darwini</i>	11		23		0		0		
				<i>Nyctelia fitzroyi</i>	25		3		13		0		
				<i>Nyctelia freyi</i>	6		0		0		0		
				<i>Nyctelia latiplicata</i>	46		7		2		1		
				<i>Nyctelia stephensi</i>	2		0		0		0		
				<i>Nyctelia vidalae</i>	1		0		0		1		
				<i>Nyctelia westwoodi</i>	0		1		0		0		
				<i>Patagonogenius quadricollis</i>	0		0		0		1		
				<i>Psectrascelis sulcicollis</i>	1		1		0		0		
				Praociini	<i>Praocis sellata bergi</i>	1		0		1		0	
				Stenosini	<i>Discopleurus</i> sp. 2*	0		1		0		1	
			<i>Discopleurus</i> sp. 3*		0		0		1		0		
				Trilobocarini	<i>Salax lacordairei</i>	0		0		0		8	
		Tenebrioninae	Scotobiini	<i>Emmalodera crenaticostata crenaticostata</i>	0		0		3		1		
				<i>Scotobius akidioides</i>	0		0		5		0		
	<b>Total number of species</b>			<b>21</b>		<b>13</b>		<b>9</b>		<b>7</b>		<b>6</b>	

estimators to assess sampling completeness (Colwell and Coddington, 1994). Then, we used Constrained Analysis of Principal Coordinates (CAP) to evaluate whether ant and tenebrionid assemblages differed among vegetation types. CAP is an ordination method similar to Redundancy Analysis (RDA), which allows the use non-Euclidean dissimilarity indices (Oksanen et al., 2007). For ants we used the Jaccard Index to obtain the distance matrix on presence/absence data because a high abundance in colonial organisms may reflect the closeness to a nest rather than the actual abundance (Agosti et al., 2000). For darkling beetles we used abundance, and we obtained the distance matrix with the Bray-Curtis index, which is not as sensitive to excess of zeros as Euclidean distance is (Legendre and Legendre, 1998). We tested for significance using permutation tests, implemented in the *capscale* function of the Vegan package (Oksanen et al., 2007) for the R-environment (R Development Core Team, 2012).

We calculated abundance of individuals of each species per sampling unit using the total number of individuals caught during both sampling periods. However, as some traps were opened for a different time span in October, we ran the same analyses with all the samples and then re-ran the analyses excluding the six sites that were sampled differently (which were also those sites located in Koluel Kaike, Fig. 1). As both analyses showed similar results (Appendix A), we worked with the full data set.

### 3. Results

We found 13 species of ants (4828 individuals, 6 genera, 6 tribes and 3 subfamilies) and 21 species of tenebrionids (191 individuals, 12 genera, 7 tribes and 2 subfamilies) (Table 1). Both groups were widespread in the area: 100% and 83.3% of the sampling units had ants and tenebrionids, respectively. Although accumulation curves did not reach an asymptote for any group (Appendix B), species estimations were similar to our results (for ants: Jaccard 1 = 15.9, Bootstrap = 14.8 species; for tenebrionids: Jaccard 1 = 27.6, Bootstrap = 24.5 species).

Both ant and tenebrionid communities differed with vegetation type according to the CAP analyses. For ants, vegetation type accounted for a 21% of the variation in community composition ( $P = 0.02$ ), and the most distinct assemblages were those present in subshrub steppes and *peladales*, characterized by *Dorymyrmex flavescens* Mayr and *Pogonomyrmex brevisbarbis* Emery, respectively (Fig. 2). In contrast, ant assemblages from grass steppes and shrub steppes were more similar (Fig. 2). For tenebrionids, vegetation type accounted for 31% of the variation ( $P = 0.005$ ), and the assemblages present in all vegetation types were distinct (Fig. 3). Shrub steppes were not characterized by any tenebrionid species (Fig. 3), while the grass steppes were characterized by three species (*Nyctelia latiplicata* Kulzer, *N. fitzroyi* Waterhouse and *N. freyi*

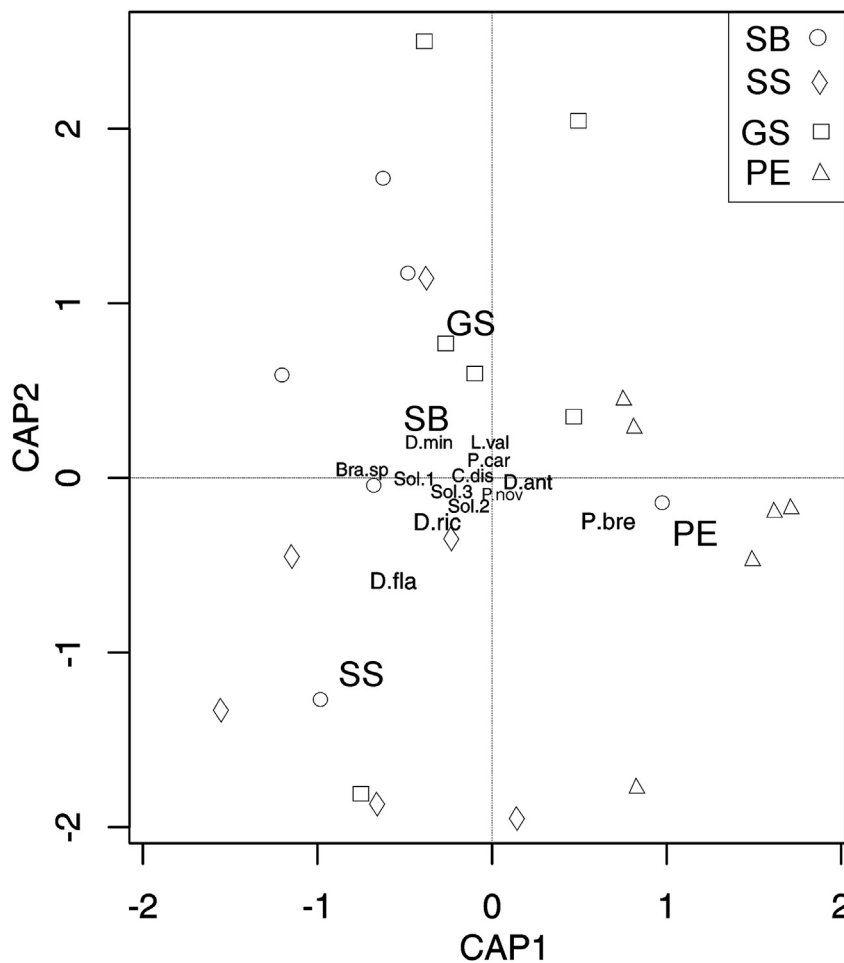
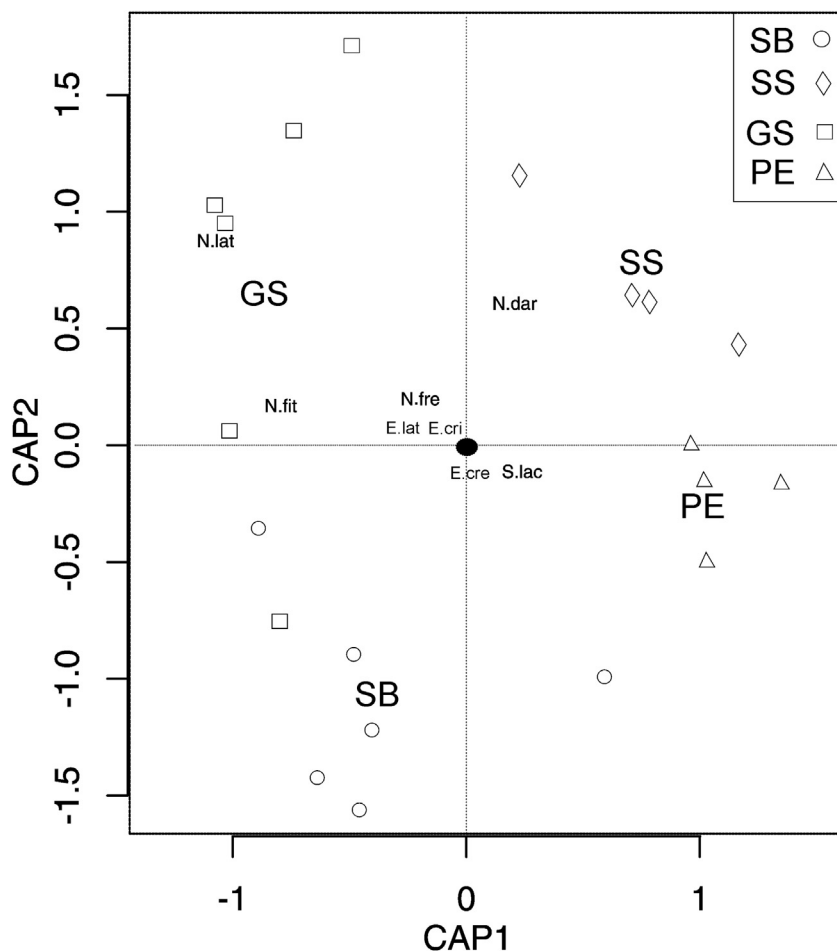


Fig. 2. First and second axes of CAP analysis for the ant community. Species are abbreviated by the first letter of the genus and the first three letters of the species name (see Table 1), vegetation type centroids (black letters) and sampling sites positions (symbols) are abbreviated as in the legend (SB = shrub steppes, SS = subshrub steppes, GS = grass steppes, PE = *peladales*).





**Fig. 3.** First and second axes of CAP analysis for the tenebrionid community. Species are abbreviated by the first letter of the genus and the first three letters of the species name (see Table 1), vegetation type centroids (black letters) and sampling sites positions (symbols) are abbreviated as in the legend (SB = shrub steppes, SS = subshrub steppes, GS = grass steppes, PE = *peladales*). Twelve species were in the center of the biplot (black dot): *Cossyphodini* sp., *Discopleurus* sp. 2, *Discopleurus* sp. 3, *Nyctopetus neuquensis*, *Mitragenus araneiformis*, *Nyctelia blairi*, *N. stephensi*, *N. vidalae*, *N. westwoodi*, *Patagonogenius quadricollis*, *Psectrascelis sulcicollis*, *Scotobius akidioides*.

Kulzer), and the subshrub steppes and *peladales* by one species each (*N. darwini* Waterhouse and *Salax lacordairei* Guérin-Méneville, respectively).

#### 4. Discussion

Vegetation patchiness in an environment reflects the spatially heterogeneity of biotic and abiotic resources, which then affect the distribution of animals, including invertebrates (e.g., Seymour and Dean, 1999; Mazia et al., 2006). Here we found differences in composition of ants and tenebrionids among vegetation types in the Patagonian steppe, with some characteristic species in most of them, implying that these taxa perceive them as different in suitability. These results indicate the importance of not considering this system as simple and structurally homogeneous. Also, as arid environments are subjected to different human activities which affect vegetation cover (e.g., overgrazing, oil exploitation) and tend to homogenize the landscape (Pruel et al., 2005; Bainbridge, 2007), it would be necessary to protect all the vegetation types in order to preserve the greatest number of ant and tenebrionid species in the Patagonian steppe.

Species richness of both taxa was slightly lower than in other areas of the Patagonian steppe. For example, 26 ant species were reported on the northwestern edge of Patagonia (Fergnani et al., 2010). As for darkling beetles the two subfamilies in our results

(Pimeliinae and Tenebrioninae) agree with those found by Sackmann and Flores (2009) and Carrara et al. (2011), but they reported more tribes and species (8 tribes, and 30 and 25 species, respectively). All previous studies were performed at lower latitudes (–39 to –42 S, Fergnani, et al., 2010; –39.8 to –41.5 S, Sackmann and Flores, 2009; –42.1 to –42.9 S, Carrara et al., 2011; –45.7 to –46.7 S this work), so the lower number of species found here could be due to a latitudinal gradient of decreasing diversity towards higher latitudes (Hillebrand, 2004). As for species composition, our study only shares some species with previous studies, particularly for darkling beetles. All studies were performed in different districts of the same phytogeographic province, highlighting that the intrinsic characteristics of each district (e.g., temperature, vegetation species, soils) can affect the presence of particular species of ants and tenebrionids. Also, tenebrionid species turnover among different areas of Patagonian steppe could be related to the high degree of endemism reported for this group in the area (Carrara and Flores, 2013).

Even though both ants and tenebrionids were associated with specific vegetation types, they responded differently to vegetation heterogeneity. While ant composition differed only between two vegetation types (*peladales* and subshrub steppes), tenebrionid assemblages were distinct in all vegetation types. Ants represented the 96% of total captures, however their individuals only belonged to 6 genera, and sampled species are generalists (e.g., *Dorymyrmex*

Mayr spp., *Solenopsis* Westwood spp.) or granivores (e.g., *Pogonomyrmex* Mayr spp.) and nest in bare soil (Kusnezov, 1978; Gi Pirk pers. obs.). Although shrub and grass steppes are physiognomically different (>1 m high shrubs dominate shrublands, while tussock grasses prevail in grass steppes), both have the highest plant cover (>65% in shrublands and >80% in grass steppes), which makes them less exposed to harsh environmental conditions. We did not find ant species with particular requirements associated to shrublands and grass steppes, perhaps due to this high vegetation cover, which could buffer extreme local conditions such as soil insolation and fluctuations in temperature and humidity. In contrast, *peladales* and subshrub steppes had distinctive ant assemblages associated, with species that are probably stress tolerant and pre-adapted to harsh conditions. For example, *Pogonomyrmex breviparbis* Emery, which was abundant in *peladales*, is particularly adapted to droughts and could nest in either in rocky or fine soil, and is tolerant to mechanical qualities of the substrate (Kusnezov, 1978). Finally, it is noteworthy that *Dorymyrmex antarcticus* Forel accounts for over 70% of individuals collected. In arid environments of Argentina, numerically dominant ants usually belong to *Dorymyrmex* genus, and in particular, *D. antarcticus* is usually the most representative species in southeastern Patagonia (Kusnezov, 1960). Also, the fact that it was very abundant in all vegetation types is probably due to its generalist foraging habits (Kusnezov, 1952).

Regarding tenebrionids, the particular assemblages associated with each vegetation type could be related to the highest species richness of this group (twice the number of tenebrionid genera as ant genera), and because of the higher proportion of “rare” species (i.e., those with very few individuals). Thus, tenebrionid assemblages probably comprise species with a variety of habitat and food requirements, resulting in distinct groups for each vegetation type. Although there is little information on darkling beetles, their feeding habits are diverse, consisting mainly of plant substances, dead animals, fungi, moss, lichens, seeds, fruits and leaves (Matthews et al., 2010). Also, they occupy a wide range of microhabitats, such as soil surface, under tree barks or litter, inside ant nests (Flores, 1998). For example, the diurnal genus *Nyctelia* Berthold (*Nycteliini*) appears dominant in number of species and specimens in the four vegetation types but with few specimens in “*peladales*”, with scarce vegetation cover, probably due to the fact that they are phytophagous (Flores and Debandi, 2004). Conversely, *Discopleurus* sp. 2 was present in this vegetation type where *Pogonomyrmex breviparbis* prevails, and it was later found inside *P. breviparbis* nest in a nearby location (42 specimens in one nest; GE Flores, pers. obs., F Cuzzo ant det.). This shows how the influence of vegetation on one species (*P. breviparbis*, adapted to harsh conditions; Kusnezov, 1978) may indirectly influence the distribution of an associated species (the myrmecophilic *Discopleurus* sp. 2). All in all, the higher species richness of tenebrionids when compared with ants may explain *per se* a great diversity of habitat use and consequently the marked differences in the composition between different vegetation types.

The results of this study contribute to valuable biogeographical information, since they extend the known distribution of a new species of the tribe Cossyphodini (Tenebrionidae: Pimeliinae), which is the same undescribed species reported in Sackmann and Flores (2009) by about 800 km south. This new species is considered a Gondwanan relict (Matthews et al., 2010). Also two new species of *Discopleurus* Lacordaire, a Neotropical genus comprising six known species, with one inhabiting northern Argentina, were captured. This genus belongs to the tribe Stenosini that exhibits a worldwide pantropical distribution and some genera have been reported in myrmecophily (Aalbu and Andrews, 1996; Matthews et al., 2010). The records of these two new species are the southernmost ones for the genus and for the tribe. These reports

evidence the relevance of studies of this type, which provide important information on the taxonomy and geographical distribution of some insect families as Tenebrionidae.

Finally, this work is the first to describe ant and tenebrionid beetle assemblages in relation to vegetation in the San Jorge Gulf district, Patagonia, and shows that both taxa responded differently to vegetation types. Thus, the environmental fluctuations and human disturbances that affect vegetation structure would lead to changes in the arthropod community affecting the variety of ecological processes in which they are involved. This highlights the importance of considering vegetation heterogeneity for developing management plans to conserve biological diversity and ecological functions in arid environments.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2016.12.002>.

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