ORIGINAL ARTICLE

Endemic tenebrionids (Coleoptera: Tenebrionidae) from the Patagonian steppe: a preliminary identification of areas of micro-endemism and richness hotspots

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Abstract

Based on data from sixteen museum collections we listed the endemic tenebrionids that inhabit the Patagonian steppe. Then, according to the geographical location of the species, we identified areas of micro-endemism and hotspots within this biogeographic province. Results showed 115 endemic tenebrionid species from the Patagonian steppe, 25 areas of micro-endemism and five hotspots. We used these outcomes to identify areas of importance for conservation. Based on the comparison with other biogeographic provinces, we suggest that the Patagonian steppe constitutes a center of high endemism for tenebrionids. We hypothesize that the isolation of the Patagonian steppe from other arid areas would cause the high occurrence of endemism. In addition, we suggest processes that could be responsible for the origin of the areas of micro-endemism and hotspots identified in this work.

Key words: Argentina, arid environments, biodiversity conservation, Chile, darkling beetles, high endemism, species richness.

INTRODUCTION

Tenebrionid beetles (Coleoptera: Tenebrionidae) are one of the most conspicuous insects to inhabit arid ecosystems (Cepeda-Pizarro *et al.* 2005; Cheli *et al.* 2010). Their ability to survive in arid conditions lies in the several morphological, physiological and ethological adaptations they present (Zachariassen 1996; Flores 1998; Cloudsley-Thompson 2001). Among these are nocturnal habits to avoid high temperatures, large body size to increase longevity and control of homeostasis, joined interlocking of the elytra along the suture and between the elytral epipleuron and the abdominal sternites and presence of a subelytral cavity that helps to control water loss through the spiracles. This subelytral cavity is developed as a consequence of the loss of wings found in flightless desert tenebrionids becoming apterous. Particularly, as the expression of apterism in tene-

brionids has serious implications for their dispersal capacity it is possible to find high endemism in arid environments of the world (Watt 1974; Flores 1998).

In southern South America, one of the most extensive arid environments is the Patagonian steppe, which is a biogeographic province that covers part of Southern Argentina and Chile (Cabrera & Willink 1980; Domínguez *et al.* 2006). The Patagonian steppe comprises 800 000 km^2 and is considered a critical or endangered area, where threats to biodiversity are overgrazing, oil exploitation and desertification (Paruelo *et al.* 2005). Regarding tenebrionid beetles that inhabit the Patagonian steppe, Kuschel (1969) established that this family is represented by a great number of endemic species mainly belonging to the tribes Nycteliini, Praociini and Scotobiini. Indeed, several investigations have focused on endemic tenebrionid species together with other insect taxa to delimit areas of endemism in the Patagonian steppe (Roig-Juñent & Flores 2001; Morrone *et al.* 2002; Domínguez *et al.* 2006). Others have considered its diversity and distributional patterns within local steppe areas (Sackmann & Flores 2009; Carrara *et al.* 2011a). Despite these studies, the total

number and identities of endemic tenebrionids that inhabit the entire Patagonian steppe were unknown until now.

Identifying areas of high endemism with their concentration of unique species is of prime interest for conservation (Riemann & Ezcurra 2007). These areas can be conceptually identified either because they have a high number of endemic species with restricted distributions (hereafter, areas of micro-endemism), or because they have high species richness (hereafter, hotspots). It has been suggested that environmental factors (e.g. geographic heterogeneity, area availability, climatic conditions) and historical factors promote the concentration of high endemism in an area (Rosenzweig 1995). Basically, it is thought that these factors have acted together through time by promoting speciation and preventing the expansion of distribution ranges of species (Huston 1994).

The objectives of this work, based on data from 180 years of prospection on the Patagonian steppe housed in several museums collections, are: (i) to present the first comprehensive list of endemic tenebrionid beetles that inhabit this area with their taxonomic arrangement; (ii) to identify areas of micro-endemism; and (iii) to identify hotspots. Although we emphasize that the list of species of endemic tenebrionids provided in this work is preliminary in nature and may increase in the future, we consider that this kind of research represents a good starting point for understanding the evolution of tenebrionid assemblages in the Patagonian steppe.

MATERIALS AND METHODS

Study area

The Patagonian steppe extends from 35° to 54°S to the east of the Andes mountain range (Fig. 1), with an average annual rainfall between 100 and 400 mm (Paruelo *et al*. 1998). Mean temperature varies from 13.4°C in the north to 5°C in Rio Grande (Tierra del Fuego) in the south (Cabrera 1971). The western and southern borders of the steppe are defined by a mean annual precipitation of 500 mm, whereas the northern and northwestern borders correspond to the boundary between Patagonian and Monte biogeographic provinces, approximately following the 13°C annual isotherm. From a floristic point of view, the Patagonian steppe is the southern extension of the Andean domain with 50% endemism in its flora (Haumman 1947). Examples of endemic genera of plants are *Pantacantha* (Solanaceae), *Benthamiella* (Solanaceae), *Duseniella* (Asteraceae), *Neobaclea* (Malvaceae), *Ameghinoa* (Asteraceae), *Xerodraba* (Brassicaceae) and *Lepidophyl-*

Figure 1 Spatial location of the Patagonian steppe within South America.

lum (Asteraceae). These genera are distinctive of the Patagonian steppe (Paruelo *et al*. 2005). For our analyses, the study area was based on the Patagonian steppe map provided by World Wildlife Fund (Olson *et al*. 2001). Because many endemic tenebrionids inhabit transitional or ecotonal zones between the Patagonian steppe and other biogeographic provinces such as High Andean, Monte, Valdivian Forest, Magellanic Forest (Roig 1998) and High Andean Deciduous Forest (Gajardo 1994), we added these transition zones to our study area (Fig. 2).

Data source

In this study we defined endemic species as those that had their distribution restricted to the Patagonian steppe. It should be noted that the species inhabiting transition zones were considered endemics if they exclusively occurred in steppe environments within these transitions. The final list of endemic tenebrionids was built at species and subspecies level. Hereafter, in this work, the term species will be used in reference to tenebrionid taxa for simplicity. For species identification we
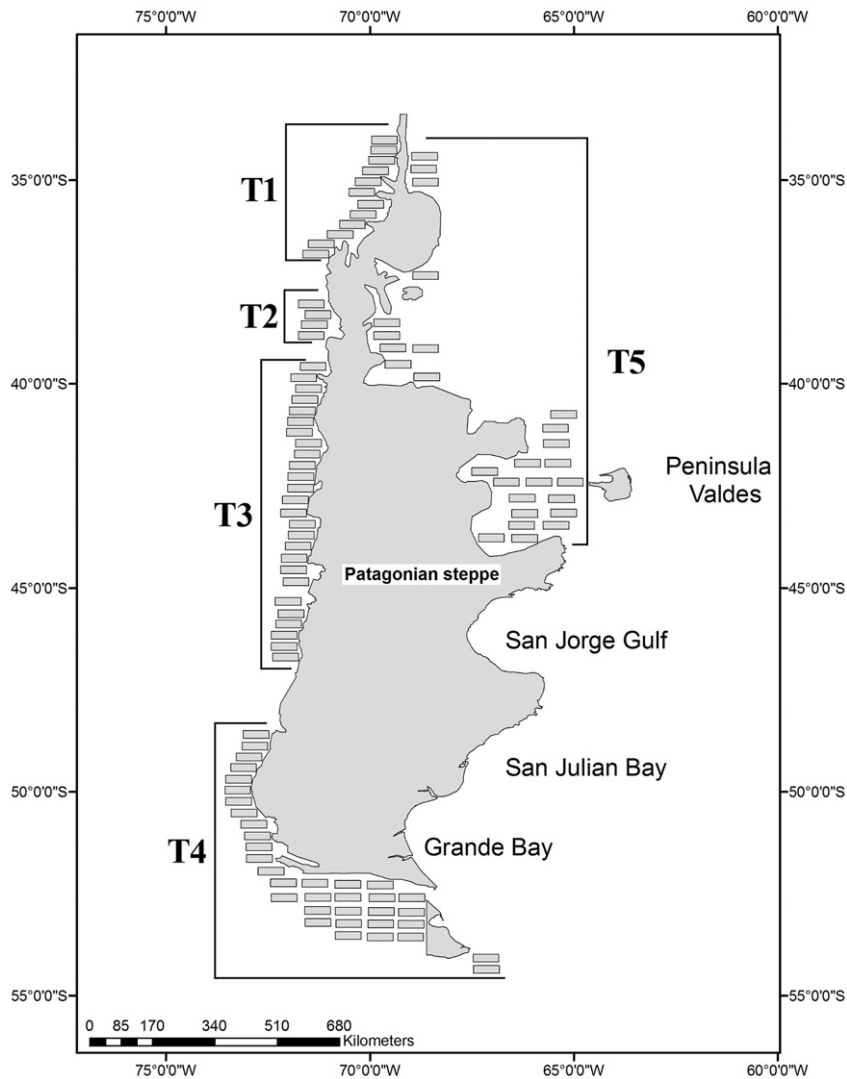
Figure 2 Patagonian steppe and its transition zones. Horizontal bars indicate the geographic locations of transition zones where T1 is the transition zone between Patagonian steppe and High Andean transition (Roig 1998), T2 is the transition zone between Patagonian steppe and High Andean Deciduous Forest (Gajardo 1994), T3 is the transition zone between Patagonian steppe and Valdivian Forest (Roig 1998), T4 is the transition zone between Patagonian steppe and Magellanic Forest (Roig 1998) and T5 is the transition zone between Patagonian steppe and Monte (Roig 1998).

used keys and revisions from Kulzer (1955, 1958, 1962, 1963), Flores (1999, 2004), Flores and Vidal (2001), Flores and Chani-Posse (2005) and Flores *et al*. (2011). We followed the classification proposed by Bouchard *et al*. (2011) for assigning species to tribes and subfamilies.

Data were obtained from fifteen collections: Argentina: Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), Mendoza; Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires; Museo de La Plata, Buenos Aires; Instituto Superior de Entomología "Dr. Abraham Willink", Fundación e Instituto Miguel Lillo, San Miguel de Tucumán; Instituto Patagónico de Ciencias Naturales, San Martín de los Andes, Neuquén (now deposited at IADIZA); Chile: Museo Nacional de Historia Natural, Santiago; Universidad Metropolitana de Ciencias de la Educación,

Santiago; Laboratorio de Entomología Ecológica, Universidad de La Serena, La Serena; Museo de Zoología, Universidad de Concepción, Concepción; Instituto de la Patagonia, Punta Arenas; USA: National Museum of Natural History, Smithsonian Institution, Washington DC; American Museum of Natural History, New York; Field Museum of Natural History, Chicago; France: Muséum National d'Histoire Naturelle, Paris; Switzerland: Natural History Museum, Basel.

Overall we revised 6178 specimens, which were identified according to their collection information and their geographical location considering latitude and longitude of the collection site (georeferencing). It should be noted that any specimen that was found more than once with the same collection information and georeference was considered a duplicate data point. These combined data points were entered into the database as a single record.

With this decision, aimed to avoid pseudoreplication, the number of records of species in the area decreased greatly (in total 1561 were valid records).

Geographic data

To identify areas of micro-endemism and hotspots, we constructed a gridded map of the Patagonian steppe. We divided this biogeographic province into 136 cells of $1° \times 1°$ (i.e. approximately $100\,km \times 100\,km$), using geographic information system (GIS) with DIVA-GIS software (Hijmans *et al.* 2005). Georeferenced records were assigned to each of the geographic cells. To make our results comparable, we considered a cell size of $10\,000\,km^2$ as this resolution was used in another study that identified areas of endemism in the Patagonian steppe considering multiple insect distributions (Domínguez *et al.* 2006). As cells with no records were eliminated, our analyses were conducted with 99 valid cells.

From the records assigned to each cell, we constructed two matrices: an incidence matrix and a quantitative matrix. Both matrices were represented by species in rows (i) and geographical cells in columns (j), but differed in the elements (i, j) that each one contained. The incidence matrix considered presence or absence of species in each matrix cell (i.e. values 1 and 0, respectively), whereas the quantitative matrix considered the number of specimens recorded per species per geographic cell. We estimated the collection effort and observed species richness (o_j) for each geographic cell by summing the values in each column of the quantitative and incidence matrices, respectively.

Mapping endemicity and defining areas of micro-endemism

We calculated the level of endemism (endemicity (E)) in each cell (Riemann & Ezcurra 2007). Specifically, E is a measure that only provides an estimation of geographical distribution of rarity (Kerr 1997). To do this, we gave each species a weight factor (w) inversely proportional to the area occupied by the species (Riemann & Ezcurra 2007). The area occupied by each species was calculated by summing the values in each row of the incidence matrix. The weight factor for species i was calculated as $w_i = 1/area(i)$, and was used to weight the species richness count for each cell. That is, according to Equation 1:

$$E_j = \sum_i^s a_{ij} w_i \tag{1}$$

where a_{ij} corresponds to values of presence–absence of species in a cell. Thus, within the endemic tenebrionids

of the Patagonian steppe, cells with a high proportion of geographically restricted taxa will have higher endemism scores than cells containing principally wide-ranging species (Riemann & Ezcurra 2007).

Then, we partitioned the obtained values of E per cell into quartiles, and considered each cell with values of E falling within the fourth quartile as an individual area of micro-endemism. Statistical analyses were performed using the "stat" package of R statistical software (R Development Core Team 2010).

Identification of hotspots

We statistically tested whether the variation in species richness per cell can be attributed to random variation (i.e. the null hypothesis), or to some other non-random cause (i.e. hotspots). For this, we followed the methodology used by Riemann and Ezcurra (2007). First, because area availability can positively influence the number of species (Rosenzweig 1995), we standardized the observed species richness by surface area (i.e. land area) in each cell using Preston's power function model ($s = cA^z$, where s is the number of species present in an area of size A, and z and c are fitted constants; see Preston 1962). The constant c represents a coefficient of proportionality that is interpreted as the species richness standardized by area, and the constant z is the exponent that is interpreted as the turnover of species among areas (Preston 1962; Rosenzweig 1995). The power function's z-value was estimated following Garcillán *et al.* (2003) by resampling our geographic cell at different scales and fitting the constants by log–log regression. It should be noted that to avoid bias in the estimation of z, we considered in those cells that fell into transitions zones arbitrarily only the 50% of the calculated surface area. We did this because we did not have the appropriate data to discriminate how much of the total surface area corresponded to Patagonian steppe or other biogeographic provinces in those cells. A value of z of 1.02 was obtained, which indicates a high turnover in species across cells (Rosenzweig 1995). With this method we brought observed species richness to a comparable and standard cell size (for details see Garcillán *et al.* 2003).

Second, species richness corrected by area (S_A) was regressed against a set of predictor variables: collection effort (CE), longitude (LON), latitude (LAT), mean temperature (MT), mean precipitation (MP) and altitude range (ALT) of each geographic cell. ALT was estimated as the maximum minus minimum altitude of each cell; i.e. a measure of geographic heterogeneity. CE, LON, LAT, MT, MP and ALT were used as in Mourelle and Ezcurra (1996). Climatic data were extracted from the mean monthly climate database published by Hijmans *et al.* (2005), which was compiled at $1\,km \times 1\,km$

latitude–longitude resolution from 1961 to 1990. Appendix S1 provides a table with values for each cell of observed species richness, predictor variables and species richness corrected by area.

As species richness is frequency counts, the regression errors follow a Poisson distribution; thus, we performed multiple regression analysis with general linear models on our data. The selection of variables was conducted using stepwise procedure (backward) with the "stat" package of R statistical software (R Development Core Team 2010).

Finally, considering the best fitted model, we estimated the expected richness by cell to identify hotspots. As a property of random frequency counts (Poisson distribution) is that the mean equals the variance, we calculated the Pearson residuals, that is, the difference between observed (o_i) and expected richness (e_i) values $\left(r_i = (o_i - e_i)/\sqrt{e_i}\right)$, to test whether observed species richness is higher than estimated species richness by random variation alone. Because e_i is the expected richness, it follows that $\sqrt{e_i}$ is the standard deviation (Riemann & Ezcurra 2007). Thus, under the null hypothesis of random variation of the model residuals, the values of the Pearson residuals should behave as normalized deviates and their probability of occurrence can be calculated from the normal distribution. We identified as hotspots those cells whose residuals departed significantly ($P < 0.05$) from the normal distribution, indicating that the species richness observed in that cell is not explained by the regression model, and that other causes are also intervening in the concentration of endemic species there (Mourelle & Ezcurra 1996).

RESULTS

A total of 115 species of tenebrionid beetles were identified as endemic to the Patagonian steppe (Table 1). These endemic species belong to only two of the nine subfamilies assigned to Tenebrionidae (Bouchard *et al.* 2011): Tenebrioninae and Pimeliinae. The 115 species are grouped into five tribes: Scotobiini (Tenebrioninae), Nycteliini, Praociini, Cossyphodini and Trilobocarini (Pimeliinae), with the first three representing 98% of total species found. Among the genera considered, three genera of Praociini are endemic to the Patagonian steppe: *Asidelia* Fairmaire, *Neopraocis* Solier and *Patagonopraocis* Flores and Chani-Posse. Other genera with more than 50% of species endemic to this biogeographic province are *Emmallodera* Blanchard (Scotobiini), *Nyctelia* Latreille, *Patagonogenius* Flores (Nycteliini), *Platesthes* Waterhouse (Praociini) and *Pel-*

tolobus Lacordaire (Trilobocarini). It should be noted that all endemic tenebrionids are flightless, suggesting that dispersal capabilities (i.e. ability to fly) can influence endemicity patterns in these organisms.

After mapping E per cell (Fig. 3) and defining cells with high endemicity it was possible to recognize 25 areas of micro-endemism (Fig. 4). Fifteen of these areas are located along the Andes to the west; seven are situated along the east coastal line and three are in the central part of the Patagonian steppe. Considering the western areas, it is possible to observe that they are located in the central-west and in the south-west part of the Patagonian steppe. In the central-west there are six in the north (areas 1–6 in Fig. 4), two in the center (areas 7 and 9) and three in the south of this area (11, 12 and 15); in the south-west there are four areas (19, 20, 22 and 23). Considering the eastern areas, one is specifically located in Peninsula Valdés (area 8), three in San Jorge Gulf (areas 16–18), one in San Julian Bay (area 21) and two in Grande Bay (areas 24 and 25). Finally, the three remaining areas are located in the center of the Patagonian steppe (areas 10, 13 and 14).

The best fitted model that explained endemic species richness corrected by area included collection effort, latitude, longitude and precipitation as predictor variables. The final model is given by Equation 2:

$$S_A = \exp(-18.72 + 0.61CE + 0.04LAT \\ - 0.31LON - 0.001MP) \tag{2}$$

with a high explained deviance (73.62%). Additional model fit information is provided in Appendix S2. This model suggests that collecting effort positively influenced the presence of endemic taxa in a cell. In addition, it implies that there is an effect of geographic position on the distribution of species richness and that precipitation inversely affected the spatial occurrence of endemic tenebrionids. To test whether richness patterns are only the result of collection effort (*CE*; Mourelle & Ezcurra 1996) and/or the random placement of species in a bounded domain (*LAT* and *LON*; Colwell & Hurtt 1994), we performed a new regression analysis of endemic species richness (controlling by the effects of *CE*, *LAT* and *LON* with partial regression analysis, Legendre & Legendre 1998) and *MP* to recognize the significance of the environment on richness patterns. We found that precipitation remained as a significant and inversely related variable that influences endemic richness distribution. Based on the analysis of Pearson residuals (Appendix S3), it was possible to identify five hotspots of endemic tenebrionids. Moreover, of these hotspots three are overlapped with areas of

Table 1 Taxonomic position of species and subspecies endemic to the Patagonian steppe

Subfamily	Tribe	Genus/Subgenus	Species/Subspecies
Tenebrioninae 19†	Scotobiini 18	*Emmallodera* 12	*E. atronitens, E. coriacea, E. crenaticostata crenaticostata, E. inflatithorax, E. marginipennis, E. multipunctata multipunctata, E. multipunctata curvidens, E. nitens, E. obesa costata, E. obesa obesa, E. obesa punctipennis, E. ovata*
		Leptynoderes 1	*L. tuberculata*
		Scotobius 6	*S. akidioides akidioides, S. akidioides bicostatus, S. alaticollis, S. caraboides, S. obscurus, S. punctithorax*
Pimeliinae 96	Cossyphodini 1	Undetermined genus (Sackmann & Flores 2009)	Undetermined species
	Nycteliini 63	*Epipedonota* 6	*E. tricostata, E. elegantula, E. willinki, E. lata, E. subplana, E. nitida*
		Mitragenius 1	*M. tristis*
		Nyctelia 45	*N. blairi, N. bremi, N. caudata, N. cicatricula, N. confusa, N. consularis, N. corrugata, N. crassecostata, N. darwini, N. difficilis, N. discoidalis, N. fitzroyi, N. freyi, N. garciae, N. gebieni, N. geometrica, N. grandis, N. granulata, N. guerini, N. hayekae, N. kulzeri, N. laevis laevis, N. laevis rufipes, N. laticauda, N. latiplicata, N. multicristata, N. neglecta, N. nevadoensis, N. newporti, N. penai, N. planata, N. plicata, N. porcata, N. quadricarinata, N. quadriplicata, N. rotundipennis, N. sallaei, N. solieri, N. stephensi, N. suturacava, N. torresi, N. undatipennis, N. unicostata, N. westwoodi, N. wittmeri*
		Patagonogenius 6	*P. acutangulus, P. breviangulus, P. elegans, P. gentilii, P. kulzeri, P. quadricollis*
		Psectrascelis 5	*P. atra, P. hirta, P. maximus, P. punctipennis, P. punctulata*
	Praociini 29	*Asidelia* 1	*A. contracta*
		Calymmophorus 1	*C. peninsularis*
		Neopraocis 1	*N. reflexicollis*
		Patagonopraocis 3	*P. magellanicum, P. minor, P. puncticollis*
		Platesthes 12	*P. burmeisteri, P. depressa, P. granulipennis, P. hirtipes, P. humeralis, P. kuscheli, P. neuquensis, P. nigra, P. pilosa, P. silphoides, P. similis, P. unicosta*
		Praocis (Hemipraocis) 7	*P. sellata bergi, P. sellata bruchi, P. sellata granulipennis, P. sellata peninsularis, P. sellata sellata, P. striolicollis, P. sp.*
		Praocis (Filotarsus) 1	*P. uretai*
		Praocis (Praonoda) 2	*P. bicarinata, P. molinari*
		Praocis (Orthogonoderes) 1	*P. argentina*
	Trilobocarini 3	*Peltolobus* 3	*P. ardoini, P. desertorum, P. patagonicus*

†Numbers indicate the number of species by taxonomic category.

micro-endemism of San Jorge Gulf, one with area of micro-endemism of San Julian Bay and the last is located in Peninsula Valdés next to an area of micro-endemism (Fig. 5). Contrary to the results of areas of micro-endemism, no hotspots were recognized in the west of the Patagonian steppe.

DISCUSSION

Endemic tenebrionids from the Patagonian steppe

The finding of 115 tenebrionid species endemic to the Patagonian steppe suggests that this biogeographic
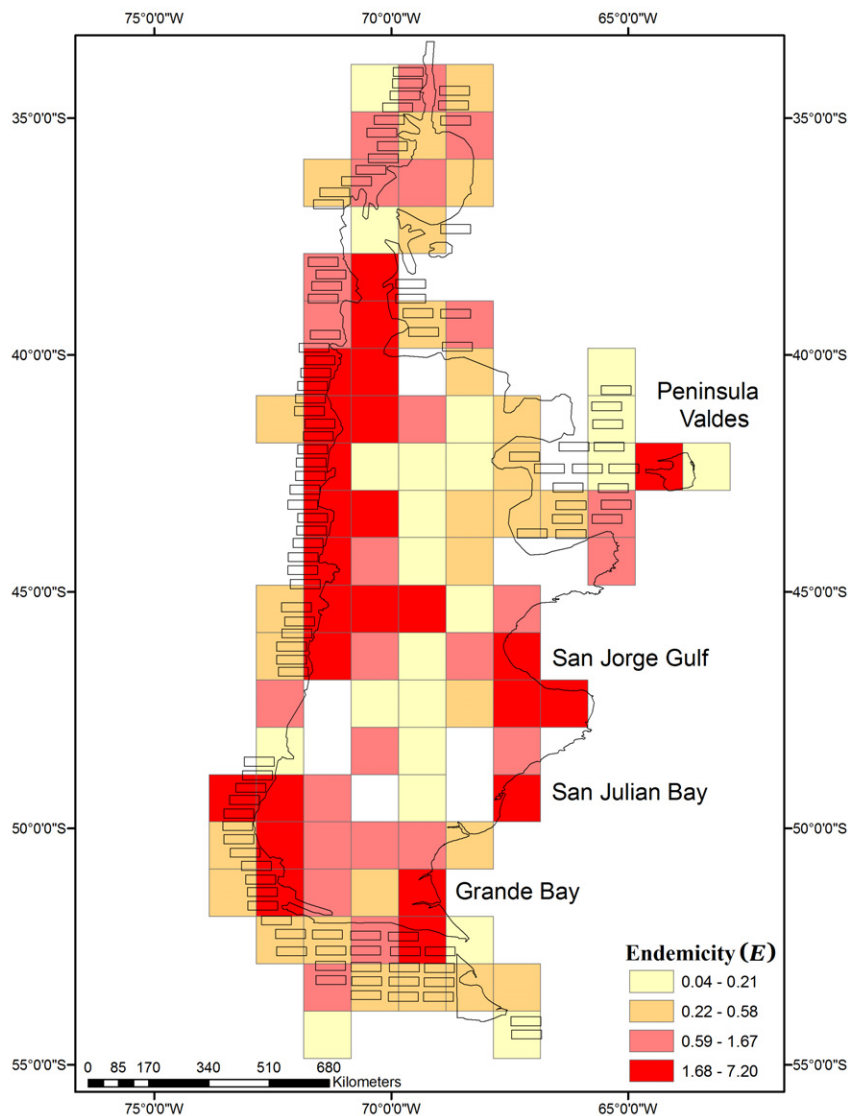
Figure 3 Endemicity (*E*) of tenebrionid beetles across the Patagonian steppe.

province constitutes a center of high endemicity for this family of beetles. This idea is supported by the comparison of our results with data on tenebrionid species endemic to other arid biogeographic provinces of southern South America (Cabrera & Willink 1980). That is, for the Monte, 53 endemic tenebrionids were recognized and 46 for Chaco (Roig-Juñent *et al*. 2001). These findings can not be explained by differences in the areal sizes of these biogeographic provinces. While the Monte areal size is similar to that of the Patagonian steppe, the areal size of Chaco is almost the double of the steppe. In addition, the existence of endemic genera and other genera with more than 50% of species endemic to the Patagonian steppe highlights the importance of the evolutionary processes that occurred in this biogeographic province. Considering the species list, it was possible to

recognize that 98% of species belong to the tribes Scotobiini, Nycteliini and Praociini. This result coincides with that of Kuschel (1969), who identified these tribes as the most representative of the Patagonian steppe, and with those of Sackmann and Flores (2009) and Carrara *et al*. (2011a) who found the dominance of species of these three tribes for small-scale studies within the steppe.

The high occurrence of endemic tenebrionids in the Patagonian steppe compared with other close arid biogeographic provinces suggests a role of its environmental history as the primary cause. Taking into account that the Patagonian steppe is the southernmost desert in the world, it is possible to relate the presence of endemic species to a process of isolation by vicariance (Roig-Juñent *et al*. 2008). Specifically, isolation was considered a process that promotes speciation by interrupting gene
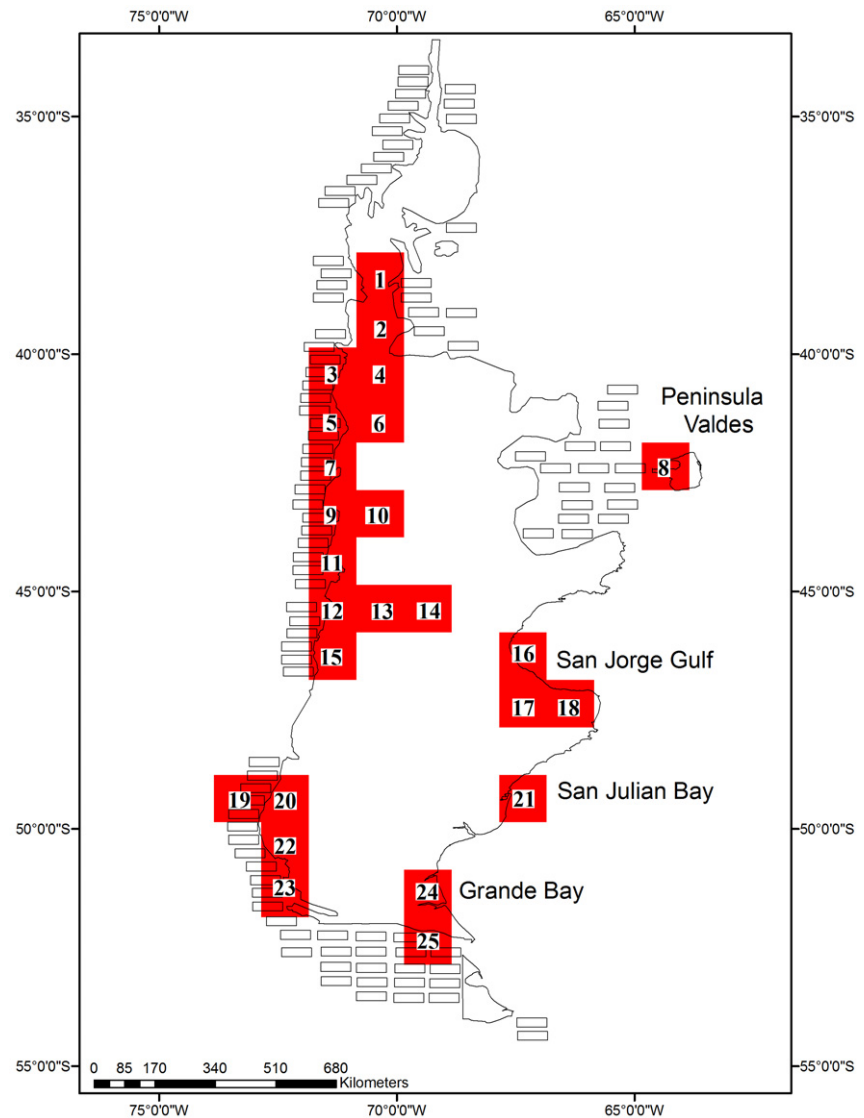
Figure 4 Spatial distribution of areas of micro-endemism in the Patagonian steppe, where numbers represent the 25 areas of micro-endemism identified.

flow among populations and originating endemism in those species that can not expand their range sizes (Rosenzweig 1995; Gillespie & Roderick 2002). The isolation of the Patagonian steppe is related to two connected events: first, the uplift of the southern Andes that accentuated dry conditions (Roig-Juñent *et al.* 2008); second, a strong temperature decrease caused by the separation of Antarctica from both Australia and South America, which originated cooler conditions by the action of cold marine currents (Barreda & Palazzesi 2007). Particularly, this decrease in temperature during the late Miocene (estimated at 10–5 million years before present, Barreda & Palazzesi 2007), transformed this biogeographic province into a cold desert that differs from the temperate desert that borders the Patagonian steppe on its northwestern boundary, the Monte

(Cabrera & Willink 1980). Indeed, it has been demonstrated that several insect groups from the Patagonian steppe are related to those in dry, cold and high-altitude environments more than to those in temperate deserts (Roig-Juñent *et al.* 2003). Based on this evidence and considering the low dispersion capabilities of the endemic tenebrionids listed, it is feasible to suggest that the period of isolation of the Patagonian steppe allowed processes of speciation and that the conjunction of cold and dry conditions form a strong climatic barrier to these apterous beetles.

The distribution pattern of endemic tenebrionids within the Patagonian steppe was inversely related to current precipitation. This result was consistent with that of Carrara *et al.* (2011b) who found a negative relationship between water availability (measured as
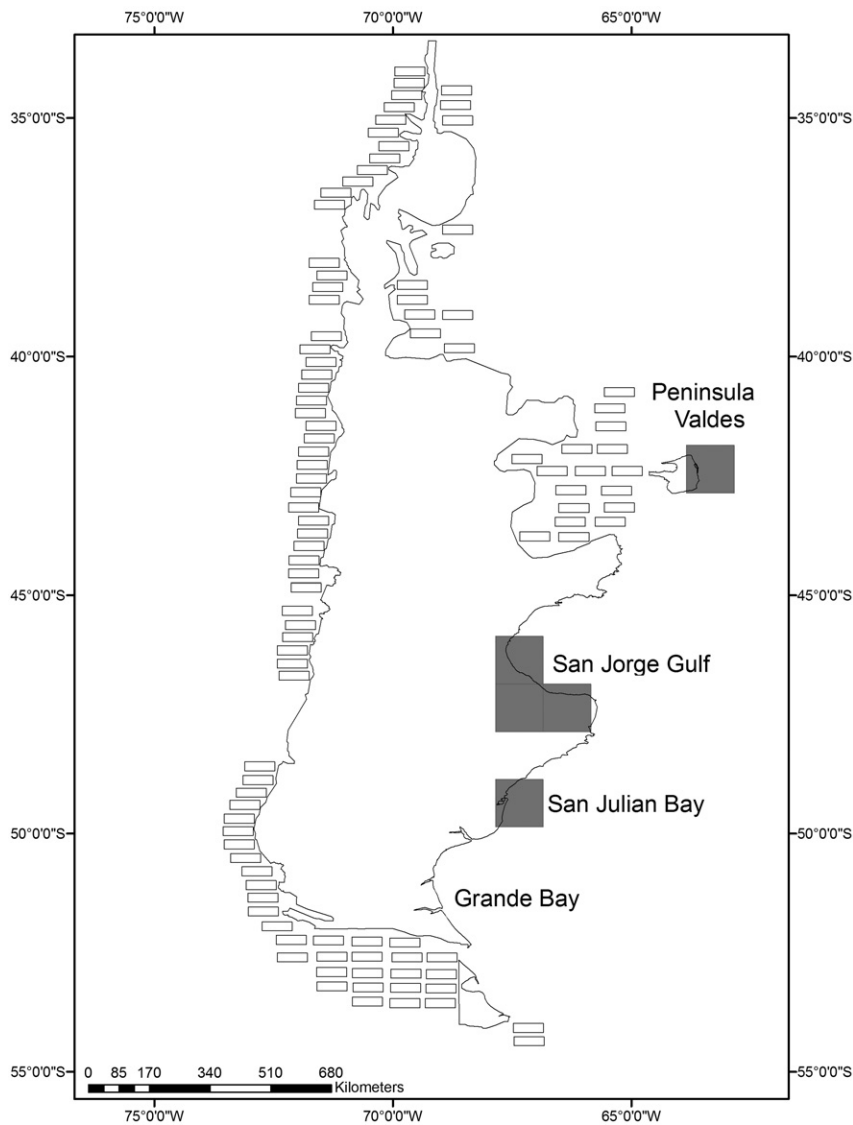
Figure 5 Cells identified as hotspots.

actual evapotranspiration) and species richness for tenebrionids highly adapted to xeric conditions in southern South America. In agreement with these authors, we consider that changes in precipitation dynamics through geological time in the Patagonian steppe have led to processes of speciation and extinction that generated current patterns of endemic richness. Particularly, we postulate that endemic tenebrionids were under selection pressure by a sequential decline in precipitation levels as a consequence of the Andes uplift (Ortíz-Jaureguizar & Cladera 2006). This pressure resulted in developmental adaptations to survive increasingly in arid environments and extinction processes in species that can not adapt to aridity (Carrara *et al*. 2011b). In addition, because decreased precipitation also caused

habitat fragmentation that led to speciation processes (Roig-Juñent *et al*. 2007, 2008), currently it is likely that high endemic richness will be found in areas with low precipitation levels.

Areas of micro-endemism and hotspots

The 25 areas of micro-endemism mostly overlap with the areas of endemism of multiple groups of insects proposed by Domínguez *et al*. (2006). For example, our areas 1–6 are congruent with the Western Patagonian, areas 7 and 9–10 coincide with the Northern Subandean, areas 11–13 and 15 are compatible with the Chubutian and areas 19–20 and 22–25 agrees with the Santacrucian of Domínguez *et al*. (2006). The remaining areas have no match with other areas of endemism

defined for insects; however, it should be noted that areas 14, 16–18 and 21 are congruent with an area of endemism defined for plants (Roig 1998; Cosacov *et al.* 2010). Area 8 stands as a special case because Peninsula Valdés is like an island (separated from the mainland of the Patagonian steppe by the Monte, Fig. 2). Moreover, the formation of the isthmus generated isolation between the populations of species living inside and outside the peninsula (Carrara *et al.* 2011a), which originated its own fauna of tenebrionids beetles (Carrara *et al.* 2011a; Flores *et al.* 2011).

When analyzing hotspots, it is evident that all of them occur in coastal environments. This finding is consistent with the idea that coastlines constitute corridors for species distribution (Riemann & Ezcurra 2007). Evidence supporting this finding is the study on epigean tenebrionids that inhabit Peninsula Valdés, which reports that all 25 species occurring at the Peninsula are found in coastal environments but only 17 species are found in the center (Carrara *et al.* 2011a). It is possible that these sandy environments provide favorable environmental conditions for the development of tenebrionids since the type of substrate may influence oviposition (Tschinkel & Doyen 1980; Flores *et al.* 2011).

It is difficult to recognize the factors that have originated areas of micro-endemism or hotspots because of the absence of direct evidence. However, based on studies that have addressed the causes behind the high occurrence of other endemic organisms in the Patagonian steppe, we hypothesized that the effects of quaternary glaciations, past sea-level fluctuations and geographic barriers that led to vicariant events may have caused not only the isolation of populations, which promoted speciation, but also the inability of species to expand their distribution ranges (Roig 1998; Flores 2004; Rabassa 2008; Cosacov *et al.* 2010).

Study caveats

We are aware of the caveats in this study, e.g. the use of museum records that represent historical patterns and not necessarily current presence of species, the existence of some false absences, and the use of oversimplifications (the species richness – area correction; for details see Riemann & Ezcurra 2007). Nevertheless, we consider that our work is a first step that gives important information not only on the total number of endemic tenebrionid species from to the Patagonian steppe but also constitutes supporting information to be considered in the conservation of the area's biodiversity. We strongly believe that this work can be improved by implementing predicted individual species distribution models as primary data to identify areas of micro-endemism and hotspots. It was not possible to develop reliable individual species models in this work because geographical information for species is scarce.

Implications for conservation

We consider that our findings have important consequences for the setting of conservation priorities. Taking into account that tenebrionid species with limited distributions allow greater likelihood of extinction (Alfaro *et al.* 2009), the areas of micro-endemism represent sites of higher significance to conservation than those identified as hotspots. Nonetheless, some cells shared the hotspots and micro-endemism conditions in our study, making it difficult to determine their rank in terms of conservation. In addition, these cells are located in places that are affected by the major threats to biodiversity in the Patagonian steppe: tourism, overgrazing and oil exploitation (Paruelo *et al.* 2005). Thus, to our knowledge, the 25 areas identified here should be considered of importance for conservation purposes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Table with values of observed richness, predictor variables and species richness corrected by area in each cell.

Appendix S2 Table showing general linear model regression analysis results.

Appendix S3 Table showing Pearson residual analysis results.