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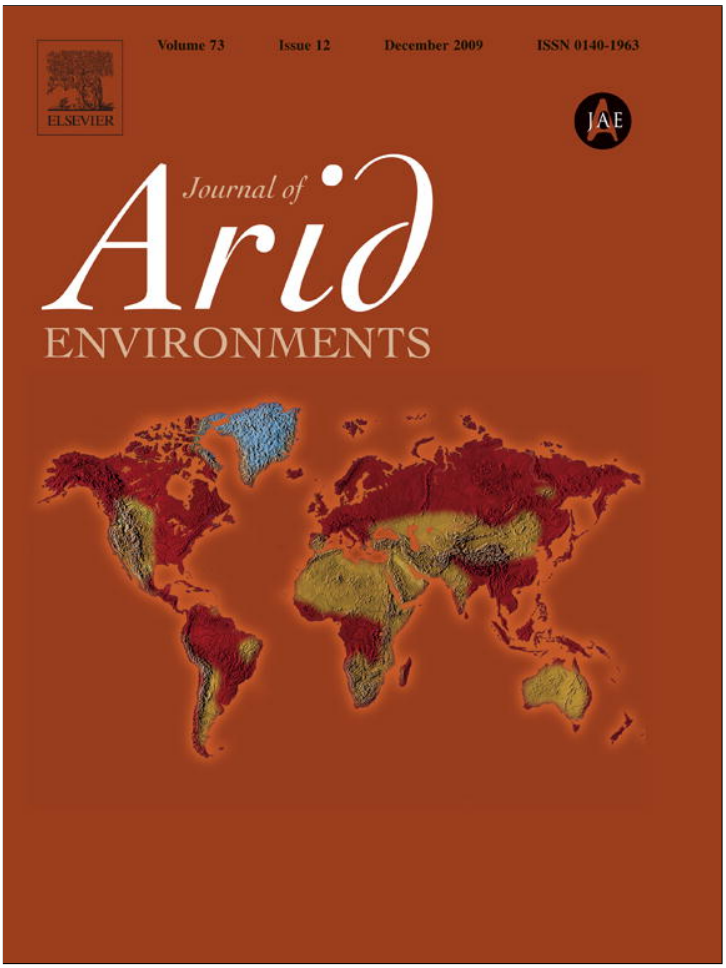

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Temporal and spatial patterns of tenebrionid beetle diversity in NW Patagonia, Argentina

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ABSTRACT

Spatial and temporal variation in abundance, richness and composition of Tenebrionidae beetle assemblages were described for north-western Patagonia. Beetles were collected using 450 pitfall traps arranged in 50 plots across an area of about 22,500 km^2 representative of the Subantarctic-Patagonian transition of Argentina. The study area included three different habitats: forest, scrub, and steppe. Beetles were trapped at five, eight day sampling periods in spring-summer between November 2004 and March 2006. A total of 30 species and 938 individuals were collected. Total abundance was higher in November and January than in March, and species richness did not change among samplings. Species richness was greater in the steppe than scrub. Assemblages differed between the northern and southern transects. There was little correlation between the measured environmental variables and species composition. Historical factors might explain the observed patterns, but other environmental variables such as soil characteristics may be more informative in explaining the present distribution of tenebrionid species.
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1. Introduction

Most species of arid and semi-arid environments live close to their limits of tolerance to one or more environmental variables. They usually show adaptations to extreme environmental conditions such as avoidance of those extremes, development of physiological and morphological characteristics that reduce water loss and thermal stress, and rapid response to availability of water and nutrients (Whitford, 2002). Among the insect fauna of arid and semi-arid environments, tenebrionid beetles are dominant in terms of biomass and abundance (Cepeda-Pizarro et al., 2005; Crawford and Seely, 1987). Tenebrionids exhibit a wide variety of morphological, physiological and behavioral adaptations to desert conditions (Cloudsley-Thompson, 2001). These adaptations are mostly influenced by temperature; however other factors such as vegetation type and soil topography may also affect their distribution and abundance (e.g. Ayal and Merkl, 1994; Botes et al., 2007; Krasnov and Ayal, 1995). Tenebrionid assemblages usually show spatial and temporal change in relation to variation in the environmental conditions (e.g. Ayal and Merkl, 1994; Botes et al., 2007; de los Santos et al., 2000; Krasnov and Ayal, 1995).

The Patagonian region of southern Argentina is temperate or cool-temperate and dominated by semi-desert steppe and scrubland (Paruelo et al., 1998a,b). As in other arid and semi-arid regions of the world, the beetle fauna of the Patagonian steppe is dominated by tenebrionids (Kuschel, 1969). Two studies carried out in the north-western Patagonian steppe near the cities of Bariloche and Maitén (Río Negro and Chubut provinces) showed that the Tenebrionidae has the highest species richness and abundance (Sackmann and Farji-Brener, 2006; Sackmann unpublished data). A review of the diversity of Tenebrionidae in Argentina indicated that a substantial proportion of the species inhabits xeric regions including Patagonia (Flores, 1998). However, this review also indicated that Patagonia is among the areas where sampling effort needs to increase (Flores, 1998). Knowledge of the species composition of tenebrionid assemblages within the region has been gained incidentally while studying other topics such as the influence of disturbances or habitat structure on beetle assemblages (Mazía et al., 2006; Sackmann and Farji-Brener, 2006; Sackmann et al., 2006). Despite the dominance of the Tenebrionidae in the beetle fauna, very little is known about their spatial and temporal patterns in the Patagonian steppe.

The aim of this study was to describe the spatial and temporal variation in abundance, richness and species composition of tenebrionid beetle assemblages in north-western Patagonia, taking into account environmental factors to explain the observed patterns.

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2. Materials and methods

2.1. Study area

The study was conducted in north-western Patagonia in the Neuquén and Río Negro provinces of Argentina, between −39.8° and −41.4° S and −70.3° and −71.8° W in an area of approximately 28,000 km^2 (Fig. 1). Mean annual temperature is 8 °C, although temperature can fluctuate from a mean minimum of −2 °C in the coldest month, July, to a mean maximum of 23 °C in the warmest month, January. The Andean mountains act as a barrier to the westerly airflow at temperate latitudes, resulting in a pronounced eastward rain shadow. The humid winds from the Pacific blow up and over the Andean crests causing the most intense rainfalls on the western (Chilean) side of the Cordillera and a marked W-E gradient on the eastern (Argentinean) side. Mean annual precipitation along this gradient drastically declines from>3000 mm in the west to<500 mm only 100 km towards the east (Barros et al., 1983).

Major climatic, soil and biotic differences along the west-to-east gradient allow differentiate the three major habitat types: (1) evergreen forest, at sites with 2000–1600 mm of mean annual precipitation, (2) scrub, at sites with 2000–1200 mm of mean annual precipitation, and (3) xeric steppe, at sites with 800–400 mm of mean annual rainfall (Fig. 1, Dimitri, 1962). Most of the central portion of Patagonia receives less than 200 mm per year. Precipitation varies spatially as well as temporally. The winter distribution of precipitation results in an asynchrony between the wet and the growing season in Patagonia and a marked water deficit in spring and summer. Both the spatial and temporal patterns of climate variables influence ecosystem processes, mainly through their impact on water dynamics (e.g. relative abundance of plant functional types, Paruelo et al., 1998a).

Within the study area, five roads were followed, and 9–12 sites were selected along each road, resulting in a total of 50 sampling sites that covered the three main ecological units; forest ($n = 17$), scrub ($n = 9$) and steppe ($n = 24$) (Fig. 1). Forest has the highest values of precipitation and tree cover and the lowest values of

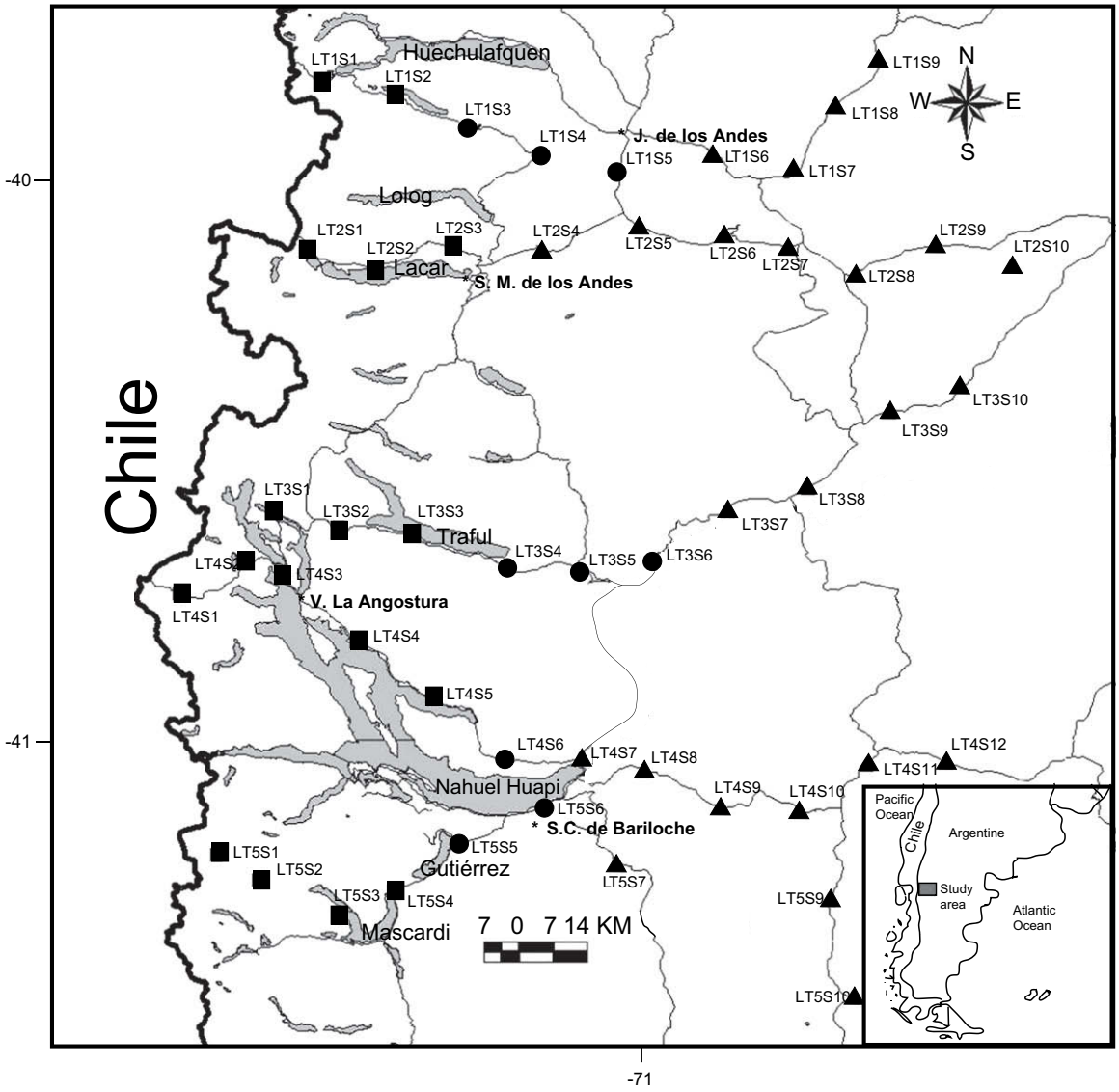

Fig. 1. Map of the studied area indicating the location of the five transects and sampling plots. The labels beside the symbols (squares = forest, circles = scrub and triangles = steppe) indicate transect number (T1, T2, T3, T4 or T5) and identification of the sampling plot within that transect (S1, …, Sn).

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Table 1
Mean values (± 1 SE) of environmental variables within three habitats included in BIOENV analysis (see Methods). Results of one-way ANOVAs are shown. Fisher LSD Test was used for a posterior comparisons; different letters in different habitats within a row indicates significant differences at $p < 0.05$.

Variable	Forest ($n = 17$)	Scrub ($n = 9$)	Steppe ($n = 24$)	$F_{(2, 47)}$	p
Mean annual precipitation	2111.8 ± 85.0 a	1100.0 ± 116.9 b	512.5 ± 71.6 c	103.9	**<0.0001**
Minimum daily T (°C)	8.5 ± 1.3 a	7.4 ± 0.9 b	7.1 ± 1.7 b	4.67	**0.014**
Maximum daily T (°C)	20.5 ± 1.5 a	34.8 ± 2.1 b	41.8 ± 1.3 c	55.6	**<0.0001**
Mean T (°C)	13.6 ± 0.6 a	17.5 ± 0.8 b	21.3 ± 0.5 c	44.87	**<0.001**
Daily temperature range (°C)	12.0 ± 1.5 a	27.4 ± 2.1 b	34.6 ± 1.3 c	63.78	**<0.001**
Minimum daily RH	73.3 ± 1.7 a	56.8 ± 2.4 b	47.6 ± 1.5 c	60.37	**<0.001**
Maximum daily RH	87.3 ± 8.6 a	82.5 ± 3.8 a	79.3 ± 6.2 b	6.7	**0.003**
Mean RH	73.3 ± 1.7 a	56.8 ± 2.4 b	47.6 ± 1.5 c	60.37	**<0.001**
Tree cover (%)	70.8 ± 2.7 a	28.8 ± 3.8 b	0 c	196	**<0.0001**
Shrub cover (%)	48.3 ± 7.5 a	43.2 ± 6.5 a	24.2 ± 2.5 b	6.8	**<0.002**
Herb cover (%)	18.4 ± 4 a	56.7 ± 6.8 b	40.1 ± 3.7 c	14.5	**<0.0001**
Leaf litter cover (%)	80.6 ± 4.5 a	38.2 ± 6.2 b	14.4 ± 3.8 c	61.44	**<0.001**
Number of fecal pats	1.52 ± 0.5	4.9 ± 1.8	4.0 ± 0.8	3.1	0.06
Stones (categories)	0.29 ± 0.3 a	1.33 ± 0.42 b	2 ± 0.2 b	9.01	**0.0005**

temperature, herb cover and herb richness (Table 1). Scrub has the highest values of herb cover and herb richness and intermediate averages for the other variables. Xeric steppe has the highest values of temperature, and the lowest values of precipitation and tree cover. Along each transect, sampling sites were separated by an average of 15 km, and all were georeferenced. Altitude averaged 880 ± 16 (SE) (range: 600–1000) m above sea level.

2.2. Beetle sampling

At each site one 10 × 10 m plot was established, which was in turn subdivided into four quadrants. On each plot, nine pitfall traps were placed in a 10 × 10 m area, with 5-m spacing between them. Traps were opened for 8 days in November 2004, January and March 2005, and January and March 2006 (i.e. 40 days in total and 450 traps per day) covering the main activity period of beetles in north-western Patagonia, which occurs between late spring and the end of the summer (Mazía et al., 2006; Sackmann et al., 2008, Sackmann pers. obs.). We did not carry out the spring sampling in November 2005 because it was too cold and rainy and many sites were covered with snow.

Traps were plastic cups of 9 cm diameter, 12 cm depth, partly filled with water, propylene glycol and detergent. To minimize ground disturbance while inserting and removing the contents of traps during subsequent sampling periods, two traps were nested one inside the other at each site, and sunk into the ground with their rims touching, and the mouth of the trap level with the soil surface. In this way, only the inner container was removed to collect the contents of the cups in each sampling period. The contents from the nine traps at each plot were pooled into one sample and taken to the laboratory in ethyl alcohol 80%. Beetle specimens were then separated and all tenebrionids were identified and counted. We used keys and reviews by Aalbu and Andrews (1996), Flores (1999, 2004), Kulzer (1955, 1958, 1963), Steiner (1980) and comparisons with material deposited in the IADIZA collection to identify the samples. We followed Bouchard et al. (2005) to assign species into subfamilies and tribes.

2.3. Environmental variables

At each plot a set of environmental variables was measured. We used a HOBBO H8 logger (Onset Computer Corporation, www.onsetcomp.com) to estimate mean temperature, maximum and minimum daily temperature, daily temperature range, mean relative humidity, maximum and minimum daily relative humidity. We also estimated tree, shrub and herb cover (%), litter cover (%), bare soil (%), and the number of cattle fecal pats (Table 1; see details in Fergnani et al., 2008). Vegetation cover gives a good measure of plant biomass, i.e. an indication of the capacity of vegetation to accumulate organic material that can be used as food and shelter for animals (e.g. Mueller-Dombois and Ellenberg 1974). Given that plant biomass correlates strongly and positively with net primary productivity (e.g. Evans et al., 2005 and other references therein) we consider that vegetation cover is a good productivity estimator. We also recorded the most frequent size of the stones observed on the ground surface. We categorized each site as: 0 = no stones, 2 = small stones, 3 = medium size stones, 4 = large size stones, 5 = rocks. Each category comprises stones included in smaller size categories. Mean annual precipitation was estimated by interpolation from a regional isoline map (Barros et al., 1983).

2.4. Data analysis

Forest sites were not included in the analyses because only one species was captured in that habitat (see Results). To evaluate sampling completeness (e.g. proportion of species captured from a possible total if sampling effort had been infinite), we estimated the expected richness for the whole assemblage through extrapolation based on all obtained samples ($N = 33$), which included all scrub and steppe sampling sites (Colwell and Coddington, 1994). We used the Chao 1 estimator because it showed the lowest deviations from the observed species accumulation curve (analyses not shown, see Palmer, 1990; Sackmann et al., 2006). As another measure of sampling completeness we computed sample-based rare species accumulation curves for the whole data set. We considered the number of *singletons* (i.e. species with only one individual), *doubletons* (i.e. species for which only two individuals were captured), *uniques* (i.e. species occurring in only one sample) and *duplicates* (i.e. species occurring in only two samples) in the pooled 33 samples as different expressions of rarity.

To eliminate variation in species richness due to differences in sample size (e.g. number of beetles captured on each plot), rarefaction was used to estimate tenebrionid species richness in different sampling periods and habitats (Gotelli and Colwell, 2001). We rescaled rarefaction curves to the number of individuals captured and visually compared different curves (e.g. expected beetle richness in scrub and steppe) at the highest value shared among curves.

Variation in beetle abundance was analyzed with repeated measures ANOVA, with "habitat" being a fixed factor (2 levels: scrub, steppe) and "time" the repeated measures factor (five sampling periods). Data were transformed [$\log(x + 1)$] to meet the assumption of equal variances. The Tukey test was used for *a posteriori* comparisons.

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Spatial autocorrelograms were constructed using Moran's I coefficients to examine whether the distribution of abundance and rarefied species richness were random ($p > 0.05$), clustered ($p < 0.05$, Moran's I values between 0 and +1) or dispersed ($p < 0.05$, Moran's I values from 0 to −1 values) (SAM v3.0, Rangel et al., 2006).

Multivariate community analyses were undertaken using PRIMER v5.0 (Clarke and Warwick, 2001) to assess changes in assemblage composition (i.e. identity and relative abundance of species). We used analysis of similarity (ANOSIM) with the Bray–Curtis similarity index to determine whether there were differences between sampling periods and habitats, in the composition of the assemblages. ANOSIM produces an R statistic that is an absolute measure of distance between groups. A large positive R (up to 1) implies dissimilarity between groups. To display the relationships between different plots, we used non-metric multidimensional scaling (NMDS) with the Bray–Curtis similarity coefficient. One-way ANOSIM was performed to analyze variation in species composition among the five sampling periods. A preliminary analysis showed that January and March assemblages of different years were similar ($R < 0.005$). We then pooled data for these two dates and performed subsequent analyses considering three temporal levels: November, January and March. Two-way crossed ANOSIM was applied to analyze spatial variation in species composition, in relation to habitat (scrub or steppe) and transect number (Transects 1–5, transects with larger number are further south, see Fig. 1). The inclusion of the "transect" factor intended to capture the latitudinal variation in species composition.

We used the SIMPER ("similarity percentages") routine of PRIMER-E to determine the contribution of the species to the average dissimilarity (i.e. Bray-Curtis dissimilarity) between groups (e.g. assemblages of the north vs. assemblages of the south, or scrub and steppe assemblages).

The BIOENV routine of PRIMER-E was used to examine relationships between environment (biotic and abiotic variables) and beetle assemblages. The premise adopted here is that if the set of environmental variables responsible for structuring the community were known, then the samples having rather similar values for these variables would be expected to have rather similar species composition, and an ordination based on this environmental information would group sites in the same way as for the species plot (Clarke and Warwick, 2001). We performed all the analyses on the untransformed and square root transformed species data. Because there were no differences in the test outputs, we show results for untransformed data.

Isoline maps were constructed to model the spatial patterning of environmental variables that best explain spatial distribution of species. Only scrub and steppe sites were included in the maps. Contour lines were obtained by the application of a geostatistical technique ('kriging'; Matheron, 1963) that uses an estimation of the semivariance of the data to perform interpolations.

3. Results

A total of 30 tenebrionid beetle species and 938 individuals comprising four subfamilies and nine tribes was collected (Appendix 1). This represents 91% of the expected species richness for the study area according to Chao 1 index estimation of 33 species. The small difference between the observed and the expected richness is explained by the decrease in all kinds of rare species with increased sampling effort (i.e. number of collected individuals, Fig. 2). Only one species, *Heliofugus* sp., was collected in the forest. The other 29 species were collected only in the scrub (1 sp.) or steppe (15 spp.) or in both habitats (13 spp.; see Appendix 1).

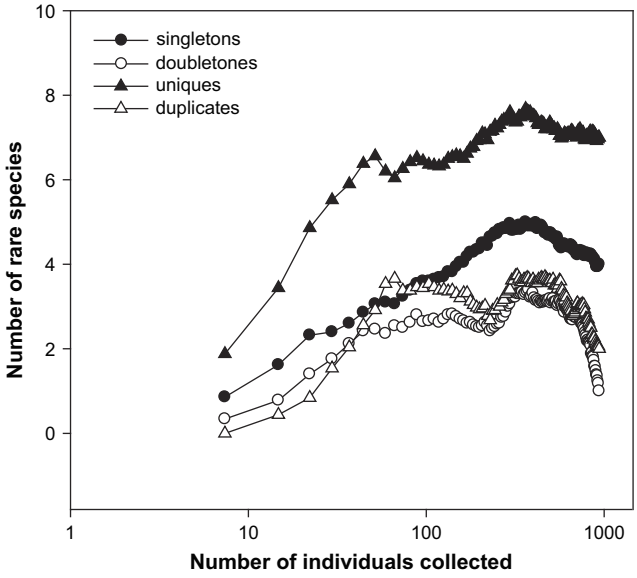

Fig. 2. Sampled-based accumulation curves of rare species rescaled to individuals used to estimate completeness of the species richness sampling. *Singletons* and *doubletons* are species for which only one or two individuals were captured respectively. *Uniques* and *duplicates* are species that appeared in only one or two samples respectively (irrespectively of the number of individuals collected).

3.1. Temporal and spatial variation in beetle abundance

Total abundance of beetles varied between sampling events ($F_{\text{time}\ (4,\ 116)} = 32$, $p < 0.001$; Fig. 3). Abundance was similar in November and January and higher than in March. In turn, differences between years in the same periods were not detected (Fig. 3). Total abundance of beetles did not differ between scrub (25.2 ± 26) and steppe (28 ± 17.1) sites ($p = 0.37$). This abundance was consistent over time ($p < 0.88$; Fig. 3). Accordingly, values of abundance were randomly distributed across the sampled area (p for Moran's I between 0.3 and 0.8).

3.2. Temporal and spatial variation in rarefied species richness

Rarefied species richness did not differ between sampling events when it was compared at a common number of individuals

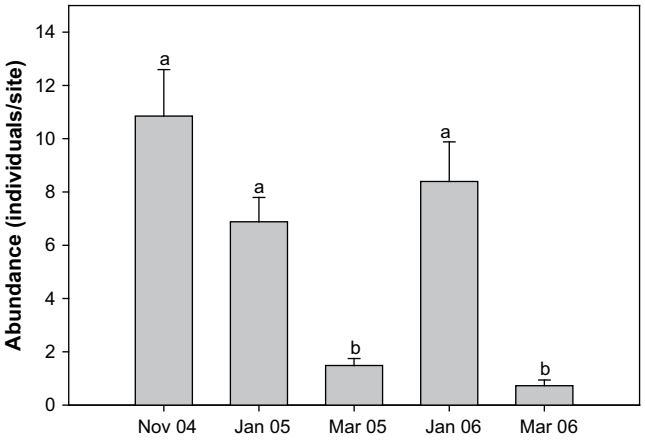

Fig. 3. Temporal abundance variation in all scrub and steppe sampling plots ($n = 35$). Means and standard deviation are shown. Different letters above the bars indicate significantly different means according to the post hoc Tukey Test ($\alpha = 0.05$).

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collected (Fig. 4a). For 40 collected individuals, the number of species ranged between 11 in March 2006 and 14 in March 2005. If we compare the accumulation curves at a higher number of individuals (*ca.* 175 individuals) the number of species in January 2005 is slightly lower (*ca.* 15 spp.) than in November 2004 and January 2006 (*ca.* 18 spp.), indicating that small differences in species richness between years in the same period may exist (Fig. 4a).

The steppe habitat supported a greater number of species than the scrub. For 210 collected individuals, species richness in the steppe was 60% higher than in the scrub (Fig. 4b). Rarefied species richness showed a random spatial distribution and was not autocorrelated at any spatial scale (p for Moran's I between 0.05 and 0.9).

3.3. Temporal and spatial variation in beetle assemblages

The species composition of the assemblages varied very little between sampling events (Global $R = 0.05$, $p < 0.001$). In contrast, species composition varied markedly between scrub and steppe (Global $R = 0.61$, $p = 0.03$; Fig. 5) and between transects (Global $R = 0.34$, $p = 0.001$). The species that contributed most to the differences between habitats were *Nyctelia rotundipennis* Fairmaire and *N. crassecostata* Fairmaire, which were more abundant in the scrub than in the steppe, and *N. suturacava* Fairmaire, that was only collected in the steppe. The assemblage at transects 1 and 2 (designated 'north') differed from that at transects 3, 4 and 5 (designated 'south'; Table 2). *N. rotundipennis* was only captured in the south, whereas *N. crassecostata* was only captured in the north. Also, other less abundant species were collected only from the north or south transects (e.g. *N. quadricarinata* Fairmaire and *Praocis molinari* Kulzer were found only in the north and *N. porcata* Burmeister in the south). In addition, *N. suturacava* and *Epipedonota nitida* (Philippi & Philippi) were more abundant in the northern part of the sampled area. While *E. nitida* showed a broader distribution reaching the southern part of the sampled area, *N. suturacava* was only captured at one site in the south (i.e. transect 3, site 9; see Appendix 1 and Fig. 1).

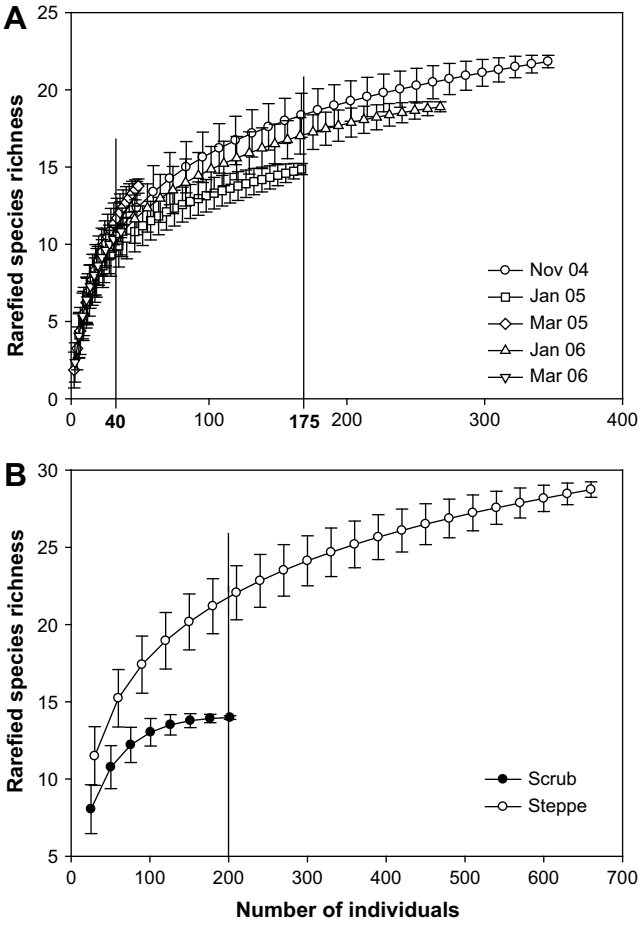

Fig. 4. Sample-based rarefaction curves rescaled to individuals used to compare species richness at (A) different sampling periods, (B) different habitats. Bars show the standard deviation of the mean after 50 re-samplings. Vertical lines show the common number of individuals captured at which the curves should be compared.

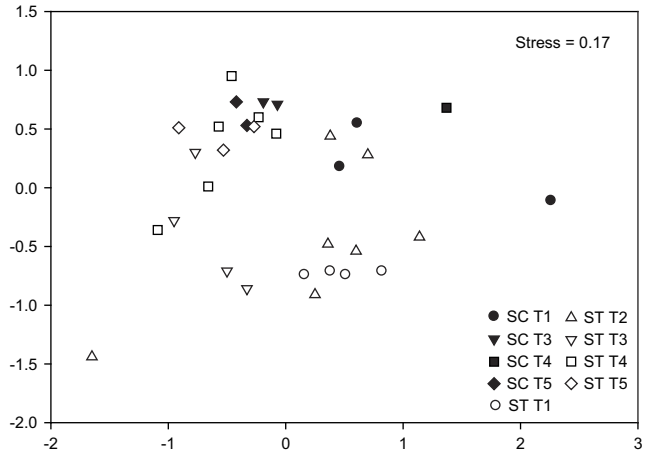

Fig. 5. Spatial variation in species composition. MDS based on species composition at each sampling plot. Black symbols indicate scrub (SC) samples and white symbols indicate steppe (ST) samples. The different transects are also indicated (T1-T5). T1 has the most northernmost location and T5 the most southernmost location, see Fig. 1 for details.

We found a low correlation between spatial ordination of sites based on species composition and ordination of sites based on environmental variables. Minimum daily temperature, daily temperature range, maximum daily relative humidity and stone size explained 30% of the variation in species composition. Individually, each variable explained between 11 and 18% of the variation (Fig. 6).

4. Discussion

Tenebrionid beetle assemblages of north-western Patagonia show spatial variations in their structure. Species richness and composition differed between the scrub and steppe habitats, and two distinct assemblages occurred in the north and south of the study area. The measured environmental variables were poorly related to the spatial ordination of species and temporal variations were only apparent for total species abundance.

Table 2
Analysis of similarity (Two-way crossed ANOSIM, factors: habitat (scrub, steppe) and transects (T1, T2, T3, T4 and T5)). Only the transect results are shown (see results for Habitat results). The difference was averaged across habitats. Rs (which are shown in the upper diagonal) reflect the degree of separation of the assemblages based in their species composition: if R is close to one, the compared assemblages are dissimilar. P values are shown down of the table diagonal, significant p are shown in bold.

	T1	T2	T3	T4	T5
T1		−0.12	0.72	0.86	0.9
T2	0.77		0.36	0.42	0.34
T3	**0.003**	**0.018**		0.1	0.17
T4	**0.001**	**0.018**	0.235		−0.22
T5	**0.003**	**0.042**	0.2	0.86	

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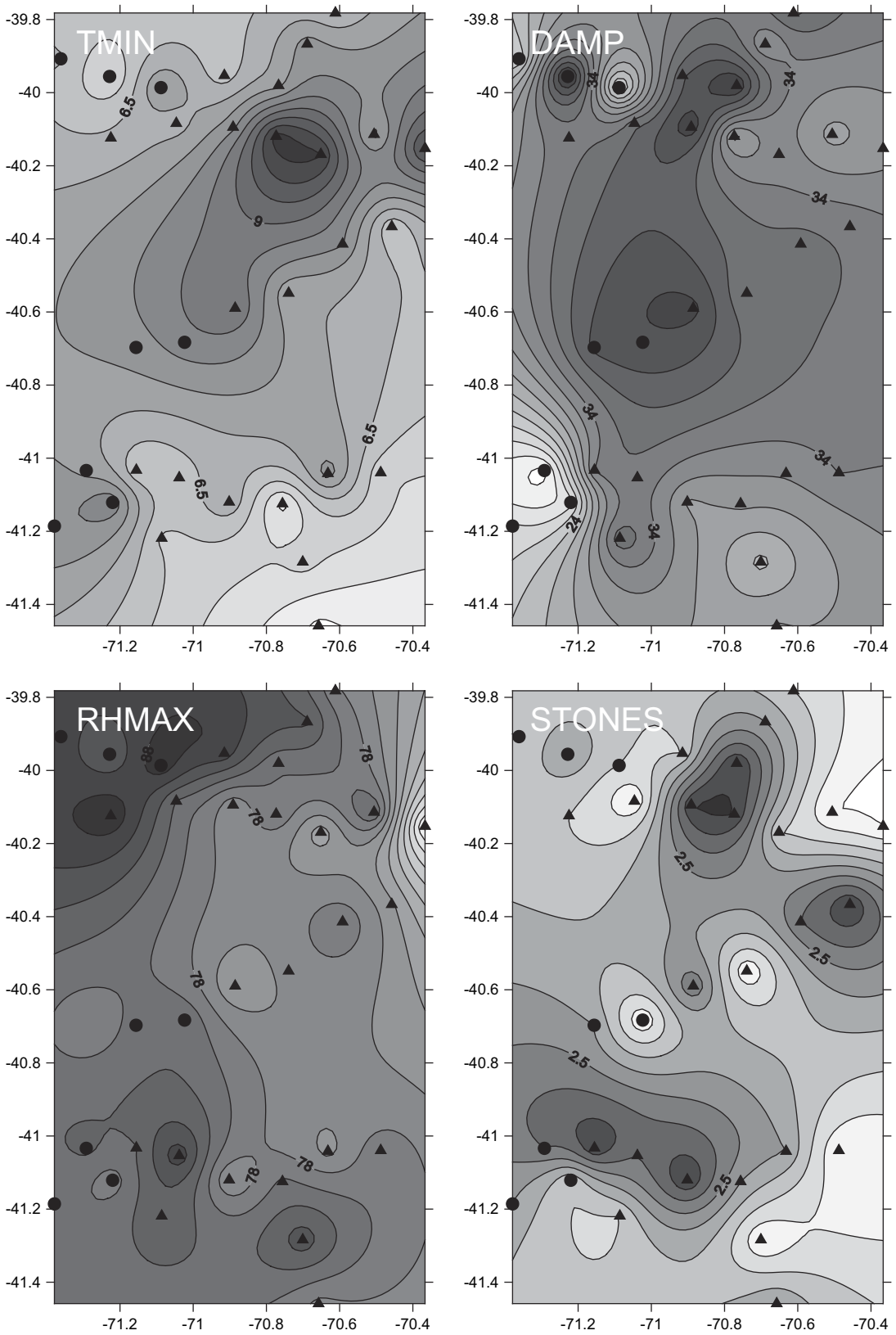

Fig. 6. Mapping of the spatial pattern of the variables that best matched the spatial variation in species composition. Only the area covered by scrub and steppe sites is shown (consult Fig. 1 to see how sampling points match the area shown). TMIN = Minimum daily temperature, DAMP = Daily temperature range, RHMAX = Maximum daily relative humidity, STONES = most frequent size of stones expressed as categories (see Methods for details). Sampling sites are indicated as squares (forest), circles (scrub) and triangles (steppe).

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4.1. Temporal changes in abundance

Total abundance of individuals showed changes within the main activity period of the family. Late summer samplings (i.e. March) yielded fewer individuals than samplings carried out in late spring or mid-summer. Habitat productivity usually explains the variation of ectotherm abundance, such as ants (Kaspari et al., 2000), other arthropods (Perner et al., 2005) and lizards (Buckley et al., 2008). In particular, total abundance of the tenebrionid community in the Negev desert peaks in spring when environmental conditions are most variable (Krasnov and Shenbrot, 1997). These authors stated that tenebrionid species respond to factors related to the level of primary production, reflecting a complex web of relationships between structure of animal communities and productivity. In north-western Patagonia, the Normalized Difference Vegetation Index (*NDVI*) or "greenness index", which is a reasonable predictor of primary productivity, peaks between November and January (Paruelo et al., 1998b; Flombaum and Sala, 2009), suggesting that tenebrionid beetles in north-western Patagonia are sensitive to changes in habitat productivity. Also, it has been shown that in arid and semi-arid environments shrub cover favors beetle abundance as shrubs provide important resources of food, thermal refuges, and protection against predators for beetles (e.g. Kitzberger et al., 2000; Mazía et al., 2006; Stapp, 1997). However, because the ecology of adult and larval tenebrionids is largely unknown (Flores, 1998), it is difficult to asses the mechanisms behind the coincidence of increased pitfall catches and high habitat productivity i.e. increased beetle activity or increased adult emergence mediated by increased food supply.

4.2. Differences in species richness and composition between the scrub and steppe habitats

We captured more species in the steppe than in the scrub, and species composition differed among the two habitats. The Pimelinae subfamily (e.g. Tribes Nycteliini and Praocini) has its origin and in the central region of southern South America, and its species are always restricted to arid lands (Kuschel, 1964). However, dispersion events are likely to occur because some species are capable of using different micro-habitats within different environments, and species can enlarge their distributional ranges occupying new habitats (e.g. scrub in the Patagonian-Subantarctic biogeographical transition, Mazía et al., 2006; Roig-Juñent et al., 2007; Roig-Juñent and Domínguez, 2001; Sackmann and Farji-Brener, 2006). An example of this are *N. rotundipennis*, *Emmallodera obesa costata* Kulzer, *Nyctopetus argentinus* Freude and *Scotobius alaticollis* Kulzer that have become common insects in scrublands and open and dry forests (Mazía et al., 2006; Sackmann and Farji-Brener, 2006; Sackmann et al., 2008). A similar pattern has been described for the Cape floristic region, where the eastward decline in species richness of tenebrionid assemblages reflects movement away from the southern end of the south-west African centre of tenebrionid endemism and diversity (Botes et al., 2007).

Environmental disturbances may also be factors explaining the observed pattern. The ecotone between the Patagonian steppe and the Subantarctic forests (i.e. scrub) has been subjected to disturbances such as fire and grazing by cattle in the last century (Schlichter and Laclau, 1998). These disturbances reduce habitat complexity by, for example, increasing the amount of bare soil making the disturbed habitat more steppe-like. These changes favor steppe-dwelling species which can extend their distribution towards the modified habitat (Farji-Brener et al., 2002; Sackmann and Farji-Brener, 2006).

4.3. Latitudinal changes in species composition

We found a marked latitudinal species replacement. The two northern transects differed in composition from the three southern transects (Appendix 1 and Fig. 1). We expected to find an environmental gradient effect on beetle assemblages (de los Santos et al., 2006; Koivula et al., 1999; Mazía et al., 2006; Sinclair and Chown, 2005; Stapp, 1997), but there was little correlation between the measured environmental variables and the spatial ordination of species. Temperature variables such as mean monthly range and annual mean are thought to be positively related to abundance and density of tenebrionid beetles (Botes et al., 2007; de los Santos et al., 2002; de los Santos et al., 2006; Koivula et al., 1999; Mazía et al., 2006; Sinclair and Chown, 2005; Stapp, 1997). Similarly, humidity is involved in water balance and larval development, which in turn can affect tenebrionid communities (de los Santos et al., 2002; de los Santos et al., 2006; Krasnov et al., 1996). However, the environmental variables in our study did not show a clear latitudinal variation, which might explain the lack of correlation between species composition and the environmental gradient. Other variables such as soil texture, water holding capacity and soil temperature may prove to be factors explaining the observed latitudinal replacement of species.

A possible explanation for the distributional pattern of species may be related to their origin. Species could have had an allopatric origin and then dispersed due to environmental changes, or species could have coexisted due to niche differentiation within a shared area. It is outside the goals of this paper to speculate on these, but because the latitudinal environmental gradient is poorly-defined, we suspect an allopatric origin. Moreover, previous studies on *Nyctelia* and *Cnemalobus* (Carabidae), common genera from arid north-western Patagonia, have shown that these genera initially had an allopatric distribution but that sympatry could have resulted from secondary dispersal. Secondary dispersal could occur when a change in climate induces an expansion of the species' distribution area resulting in a larger distribution range (Flores and Carrara, 2006; Roig-Juñent et al., 2007). This hypothesis can explain the distribution of the *Nyctelia* species on our study. Dominant species such as *N. rotundipennis* and *N. crassecostata* are spatially segregated and sympatry is rare among the eight species collected in this study. No more than three species were captured together, and one was always more abundant than the others (see Appendix 1).

In conclusion, the environmental data considered in the present study did not explain the observed pattern of tenebrionid species in north-western Patagonia. Although historical factors may in part be responsible for the observed species patterns, other environmental variables such as soil characteristics may be more informative, and might improve our understanding of the distribution of tenebrionid species in this area, which represents an one of the richest areas of endemism in the Patagonian steppe (Domínguez et al., 2006).

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Appendix Supplementary information

Supplementary information associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2009.05.007

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