

EPIGEAN TENEBRIONIDS (COLEOPTERA: TENEBRIONIDAE) FROM LEONES AND TOVA-TOVITA ISLANDS (CHUBUT, ARGENTINA) AND ITS COMPARISON WITH THE MAINLAND ASSEMBLAGE

GERMÁN H. CHELI^{1,2,*}, FERNANDO MARTÍNEZ^{1,2}, GUSTAVO PAZOS^{1,2}, DANIEL UDRIZAR SAUTHIER^{1,2}, FERNANDO CORONATO^{1,2} and GUSTAVO E. FLORES³

¹*Instituto Patagónico para el Estudio de los Ecosistemas Continentales (IPEEC), Centro Científico Tecnológico CENPAT-CONICET, Blvd. Brown 2915, 9120 Puerto Madryn, Chubut, Argentina*

²*Universidad Nacional de la Patagonia San Juan Bosco, Blvd. Brown 3051, 9120 Puerto Madryn, Chubut, Argentina*

³*Laboratorio de Entomología, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), Centro Científico Tecnológico CONICET Mendoza, Casilla de correo 507, 5500 Mendoza, Argentina*

*Corresponding author: e-mail: cheli@cenpat-conicet.gob.ar

Abstract.— The Parque Interjurisdiccional Marino Costero Patagonia Austral (PIMCPA) protects over 180 km of Patagonian Atlantic coastline of northern San Jorge gulf, including an archipelago that comprises more than 39 islands. In this work, we studied the darkling beetles (Coleoptera: Tenebrionidae) of the two largest islands in the PIMCPA archipelago: Leones and Tova-Tovita. Tenebrionids are reported for first time in these islands, in addition, we described their species assemblage. Likewise, a comparison between the islands and the mainland was also performed. The GLM, MDS, ANOSIM and PCA methods were employed. Islands share the same tenebrionid species assemblage but they differ from that displayed on the mainland. Considering both islands as a whole, the insular assemblage shows lower species richness and diversity than those seen in the mainland. We identified eight species in the islands which belong to eight genera and four tribes. We also found that six of these species were shared among islands. *Psectrascelis punctipennis* Kulzer was exclusively recorded from the Tova-Tovita, while *Platsthes kuscheli* Kulzer from the Leones island. The island assemblage is mainly composed of nocturnal or crepuscular species [including *Praocis (Hemipraocis) sellata bergi* Burmeister, *Patagonogenius quadricollis* (Fairmaire), *Emmallodera crenaticostata crenaticostata* Blanchard and *Scotobius akidioides akidioides* Waterhouse], while several diurnal species of *Nyctelia* Berthold are the most common and diverse darkling beetles among mainland fauna. Additionally, we discuss the effects of the mainland distance, paleoclimate, and the origin of insular assemblages. Finally, other insular implications of tenebrionid beetles are discussed.



Key words.— ‘Patagonia Austral’ National Park (PIMCPA), Pimeliinae, Tenebrioninae.

INTRODUCTION

Darkling beetles (Coleoptera: Tenebrionidae) are abundant and rich in number of species in northeastern Patagonia (Cheli *et al.* 2010). As in other arid regions, these organisms are an important faunal component and play a significant role in food webs as decomposers and herbivores (Flores 1998). Many tenebrionids are flightless and restricted to a small geographic distribution range, which makes them of particular interest for biogeographic and ecological studies (e.g., Flores and Pizarro Araya 2006, Fattorini 2009a, 2010, Kamiński 2015). In northeastern Patagonia, these beetles show great habitat fidelity (Carrara *et al.* 2011, Flores *et al.* 2011) and quick responses to habitat alterations (Cheli 2009, Cheli *et al.* 2010, Martínez 2013), thus they constitute good indicators of environmental changes in the region.

Islands fascinate ecologists because they are biologically simpler than mainland ecosystems, they are objectively defined as geographic isolates and the time of their geological formation is usually known (Fattorini 2009b, 2010). Therefore, islands are ideal for the study of biological patterns and also to address general problems of biological conservation (Fattorini 2009b, 2010, Pizarro-Araya *et al.* 2012). Nevertheless comparison of insect fauna between islands and mainland communities is unusual, since in most of the works, only island communities are described. Due to their abundance, species diversity, and low dispersal ability, insular tenebrionid beetles are an important insect group for studies on biological distributional patterns. In small islands, a unique and vulnerable tenebrionid species assemblage is usually hosted (Alfaro *et al.* 2009, Fattorini 2006, 2009a).

In northern San Jorge gulf, Chubut province, is located the Parque Interjurisdiccional Marino Costero Patagonia Austral (PIMCPA), the first National Argentinean Marine Park created to protect over 180 km of Patagonian Atlantic coastline and one archipelago with more than 39 islands (Crespo 2014). These islands are well known in terms of their marine fauna, but knowledge about their terrestrial biodiversity, especially insects, is scarce. Typically, small islands consist mainly of coastal ecosystems which may be under severe threats. These islands are becoming more and more attractive to tourists because of their increasing rarity. Thus, ecotourism, like other human activities, may cause a rapid degradation of natural insular habitats, leading to biodiversity loss (Fattorini 2009a, Pizarro-Araya *et al.* 2012).

This work is part of a multidisciplinary project whose overall objective is to contribute to the knowledge and conservation of the natural and historical heritage of the PIMCPA, generating information about terrestrial species of plants, mammals and arthropods

that inhabit Leones and Tova-Tovita islands, and to explore possible links between current biota and historical human settlements (Coronato 2016). The main aim of this work is to describe the community of darkling beetles (Tenebrionidae) in these two largest islands of the PIMCPA archipelago. In addition, we compared the tenebrionid species assemblages among these islands and the mainland.

MATERIAL AND METHODS

Study area. The PIMCPA (Fig. 1) protects a broad coastal, marine and insular sector in the northern San Jorge gulf, stretching from Dos Bahías cape (44°55'46''S, 65°31'19''W) to a few kilometres south of Quintano island (45°14'46'' S, 66°42'01'' W) and including the adjacent marine zone up to 1.6 km from the coast (Crespo 2014). It comprises 104.812 hectares, extends along 180 km of coastline and includes numerous bays, coves and an archipelago with more than 39 islands. Overall, the area of PIMCPA has a semiarid and temperate climate, with an average annual temperature of 13°C and an annual rainfall of about 200 mm. The prevailing wind is from the west with an average speed of 22 km/h, although sustained eastern and southern winds occur during daylight hours in the months of high solar radiation (Frumento 2014).

Leones and Tova-Tovita islands. These islands are of volcanic origin, and consist of a pyroclastic basement of Jurassic age (Haller 2014) covered by agglomerates, sand, silt and shells from the coast and surrounding seabed. Nowadays, both islands have a similar exposed surface area (5 km² and 5.5 km² respectively) and are separated from the mainland by a sea channel about 25–30 m deep. But at the same time they differ in their distance to the mainland. Leones island is located approximately 1 km from the coast, whereas Tova-Tovita island is separated 6 km from the continent. Leones and Tova-Tovita islands became isolated from the mainland in the Pleistocene-Holocene transition, about 10–12,000 years BP (Ponce *et al.* 2011). The climate during the Late Pleistocene on this portion of Patagonia was semiarid and colder than today and the dominant vegetation physiognomies were herbaceous (mostly Poaceae) and shrub steppe of Patagonian elements such as Chenopodiaceae, Asteraceae (*Nassauvia* sp.) and Ephedraceae (*Ephedra* sp.) (Mancini *et al.* 2008).

The topography of Leones island (45°03'S, 65°36'W) (Fig. 1) consists of large rocky outcrops furrowed by extensive gullies that run from the top down to the lower terrain of the island. At higher altitudes (80 m) vegetation is represented by small herbs and grasses growing in cracks, while on the slopes grass-shrub steppe of *Poa ligularis*, *Pappostipa humilis* and

Lycium chilense establish on developed soils. In the lower topographic levels, sandy soils are well developed and support a shrubland of *Atriplex* sp. and *Senecio filaginoides*. The bottom of gullies is completely covered by a matrix of perennial grasses and annual herbs. Tova-Tovita island (45°06'S, 66°00'W) (Fig. 1) is actually a complex of two islands connected at low tide through a sand-gravel bridge. Thus, for our purposes we considered them as a single insular functional unit. The topography of Tova-Tovita island is simpler than that of Leones island, with its highest altitude (30 m) along the centre of the island. The soil is sandy and two well-defined vegetation communities dominate the entire area: a tall scrubland of *Suaeda divaricata* established on upper parts of the island and a shrub steppe of *Atriplex* sp. occupying lower areas.

Neither island was ever inhabited by Patagonian natives, but they were both occupied during the second half of XIX century by European sailors intent on exploiting their natural resources, like penguins, sea lions and guano (Vales *et al.* 2014, Coronato 2016). In the early XX century, a lighthouse and a small naval garrison were established at Leones island. These activities persisted until the 1970s. Meanwhile, in 1950s–60s, a small settlement devoted to algae and guano extraction was established in Tova-Tovita island (Crespo 2014), which lasted until the 1990s. Nowadays

both islands are uninhabited. Human presence had partially modified the natural environments of the islands through introduction of some herbaceous plants and mammals, such as rats, rabbits and armadillos (Udrizar Sauthier *et al.* pers. obs.).

Mainland. sampled mainland sites comprised those supra-littoral habitats most representative of the continental neighbouring areas of Leones and Tova-Tovita islands: 1) Wavy surfaces on Marifil Formation outcropping (dominant physiognomy: shrub-dwarf shrub steppe of *Chuquiraga avellanadae*, *Mulinum spinosum*, *Brachyclados caespitosus*, *Nardophyllum bryoides*, *Lycium* sp. and *Pappostipa humilis*); 2) Bottom of rocky gullies with sandy and deep soils in outcrops of the Marifil Formation (dominant physiognomy: low closed scrub of *Colliguaja integririma*) and 3) Soils covered by aeolian sands (dominant physiognomy: shrub-dwarf shrub steppe of *Chuquiraga avellanadae*, *Nardophyllum chiliotrichioides*, *Prosopis denudans*, *Colliguaja integririma*, *Berberis* sp., *Senecio filaginoides*, *Ephedra ochreata*, *Nassella tenuis*, *Pappostipa speciosa*, *Poa lanuginosa*).

Sampling. Three collection field trips were made to Leones and Tova-Tovita islands and to adjacent mainland areas (Dos Bahías cape and Puerto Visser; Fig. 1). Field trips were held during the late summers of 2012, 2013 and 2014. Darkling beetles were sampled using

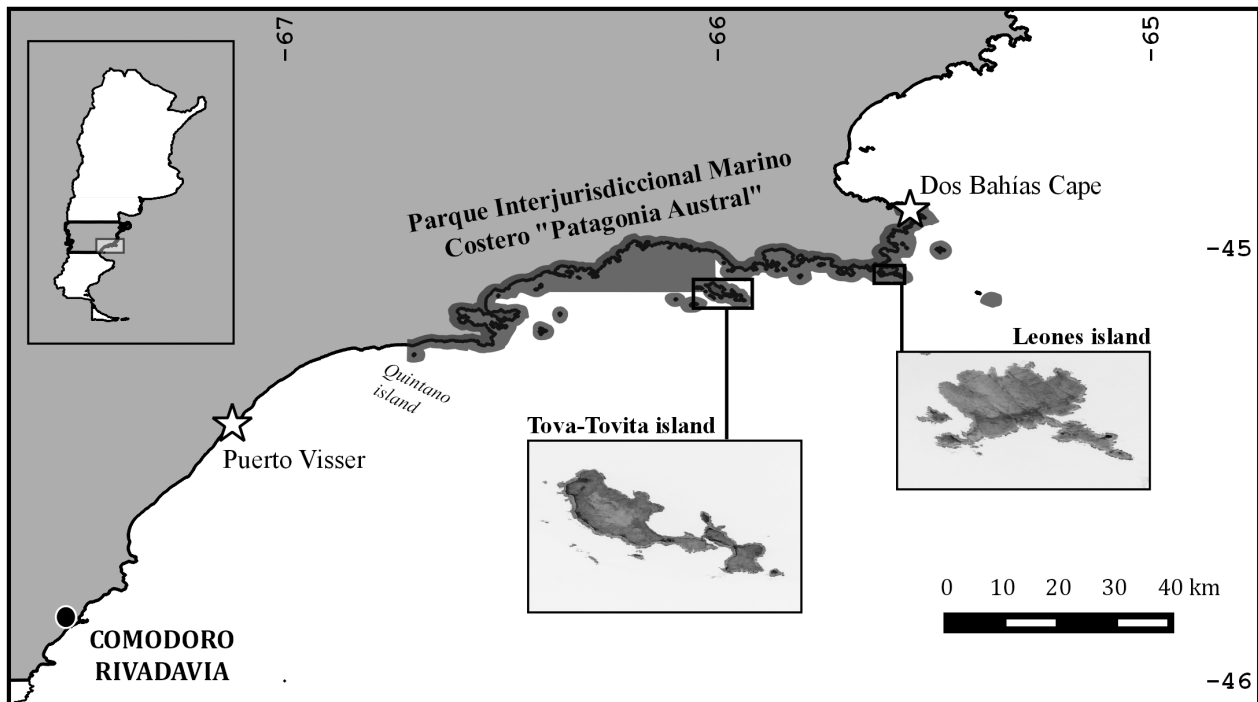


Figure 1. Geographical location of study area: PIMCPA, Leones and Tova-Tovita islands and adjacent mainland sites sampled (Puerto Visser and Cabo Dos Bahías).

two complementary methodological approaches at the same time: 1- *hand-collecting*: surveys in search for darkling beetles in representative habitats of the islands and adjacent mainland. Each survey consisted of a visual inspection by three observers scrutinizing the ground, shrubs, rocks or any other object on the ground that could offer shelter for tenebrionid species. Each survey comprised 20 min of searching, and all darkling beetles (live or dead) observed during this period of time were collected. From our previous experience, a 20-min qualitative sampling is enough to flatten the time-species curve for darkling beetles at each site (Carrara *et al.* 2011, Cheli pers. obs.). The area covered by each survey was approximately 0.5 ha and all sites were inspected by the same three observers. 2- *pitfall trapping*: tenebrionids were captured using pitfall traps 12 cm in diameter, containing 300 ml of 30% solution of ethylene glycol that operated for seven consecutive days (Cheli and Corley 2010). On each island and in the mainland we sampled with two groups of 10 pitfalls (arranged into two transects of five traps each). The traps were located at least 10 m from each other and both transects were separated by at least 20 m. Both hand-collection and pitfall trapping were performed in the dominant environmental units of the above-mentioned islands and mainland area. All collected tenebrionid specimens were deposited in the Entomological Collection of the IPEEC (CENPAT-CONICET). Tenebrionid beetles were identified at the species level on the basis of reviews and keys by Flores (1999, 2004), Flores *et al.* (2011), Kulzer (1955, 1958, 1963) and entomological material deposited in collection of IPEEC and IADIZA. We followed the classification proposed by Bouchard *et al.* (2011) to assign species and genera into subfamilies and tribes.

DATA ANALYSIS

Comparison of tenebrionid species richness and diversity between islands and mainland

Species richness and diversity indices traditionally used by ecologists have several limitations, e.g., they are highly sensitive to the sample number and size of surveyed area as well as they are frequently expressed in unintuitive units that do not allow comparisons (see Jost 2006, 2007, Colwell *et al.* 2012, Chao *et al.* 2014). Therefore, the observed number of species and the commonly used diversity indices frequently underestimate of the community parameters. To overcome many of these shortcomings, a more realistic and unbiased estimation of species richness and diversity were recently achieved through individual-based rarefaction curves constructed from richness and diversity indexes derivated from Hill numbers (Colwell *et al.* 2012,

Chao *et al.* 2014). In this regard, we performed rarefaction curves in order to compare the tenebrionid species richness and diversity between islands and mainland. We plotted individual-based rarefaction curves for both species richness (represented for the observed number of species at each site) and diversity (expressed as the exponential of the Shannon index) against the number of individuals, randomly selected, from the samples (Colwell *et al.* 2012). Likewise, we used 100 replicate bootstrap samples in order to estimate the 95% confidence intervals. Following Chao *et al.* (2014) rarefaction curves were also extrapolated by the maximum number of collected individuals (108 between island-island and 196 between islands-mainland).

Individual response to insularity

Based on Generalized Linear Models (GLMs) we compared between islands and mainland the overall darkling beetle abundance, the individual average abundances of each species, genus, tribe and subfamily. In each GLM model, the distribution of the response variables were modelled using either Poisson (link function: Log) or negative binomial (link function: logit) distribution (Crawley 2013). The statistical significance of each GLM was evaluated by comparing each of them against a null model lacking fixed effects through a Chi-square statistic calculated using the *anova* function in R (Crawley 2013).

Joint variation of the tenebrionid species community

Changes in species abundance and composition of the darkling beetle community among Leones, Tova-Tovita islands and the mainland were analysed using non-metric multidimensional scaling (MDS), an ordination of a matrix of similarity between beetle species abundance at each sampling site based on the Bray-Curtis similarity (Borcard *et al.* 2011, Oksanen 2015). To test for statistical differences in the community structure detected by MDS, we performed a non-parametric one-way analysis of similarity (ANOSIM), which is a permutation procedure applied to (rank) similarity matrices. The R statistic values generated by ANOSIM are a relative measure of separation of *a priori* defined groups ($R \sim 0$ -> no difference among groups; $R \sim 1$ -> all samples within groups are more similar to each other than to any sample from different groups) (Borcard *et al.* 2011, Oksanen 2015). Finally, we carried out a Principal Component Analysis (PCA) to identify which species of darkling beetles are primarily responsible for changes observed in community structure (Borcard *et al.* 2011). The Broken stick criterion was

adopted to test for statistical differences in community structure accounted for PCA ordination axes (Borcard *et al.* 2011).

All analyses were performed using 'Boot', 'AER', 'Mass' 'Vegan', 'Stats' and 'iNEXT' libraries for R package (Hsieh *et al.* 2013, Oksanen *et al.* 2015, R Core Team 2015).

RESULTS

A total of 274 tenebrionid specimens were collected (196 from islands + 78 from mainland), belonging to 15 species arranged in 11 genera and 5 tribes (Table I). Fourteen species were identified living in the mainland, with *Nyctelia undatipennis* Curtis (28%), *Mitragenus araneiformis* Curtis (22%) and *Emmallodera crenaticostata crenaticostata* Blanchard (10%) being the most abundant (Fig. 2). On the other hand, eight species were reported as occurring on the islands, of which *Praocis (Hemipraocis) sellata bergi* Kulzer (34%), *Patagonogenius quadricollis* (Fairmaire) (26%), *Emmallodera crenaticostata crenaticostata* (15%), and *Mitragenus*

araneiformis (13%) were the most abundant, making up 87% of the total capture (Fig. 2). All these species are for the first time reported as inhabiting islands (Table I). Also six genera/subgenera are reported for the first time as occurring on islands: *Patagonogenius* Flores, *Mitragenus* Solier, *Praocis (Hemipraocis)* Flores and Pizarro-Araya, *Hylithus* Guérin-Méneville, *Emmallodera* Blanchard and *Platesthes* Waterhouse (for the last two there are species inhabiting a large island: Tierra del Fuego [Kulzer 1955, Flores 2004]). *Psectrascelis* Solier and *Scotobius* Germar were reported for islands in Alfaro *et al.* (2009) as well as the following subgenera of *Praocis* Eschscholtz: *Orthogonoderes* Gay and Solier (Kulzer 1958), *Praocis* Eschscholtz, *Mesopraocis* Flores and Pizarro-Araya, and *Postpraocis* Flores and Pizarro-Araya (Alfaro *et al.* 2009).

Rarefaction curves for both tenebrionid species richness and diversity is flattened to the right, confirming that island and mainland inventories were relatively complete (Fig. 3). The islands shows similar tenebrionid species richness and diversity (Figs. 3a and 3b). However, if both islands are combined, they display lower species richness and diversity than that observed

Table I. Tenebrionid species present in Leones and Tova-Tovita islands and in adjacent mainland areas (Dos Bahías cape and Puerto Visser).

Subfamily/ Tribe	Species	Mainland		Islands	
		Dos Bahías cape	Puerto Visser	Leones	Tova-Tovita
Pimeliinae					
Nycteliini	<i>Epipedonota cristallisata</i> (Waterhouse)	0	4	0	0
Nycteliini	<i>Mitragenus araneiformis</i> Curtis	1	16	21	4
Nycteliini	<i>Nyctelia fitzroyi</i> Waterhouse	0	1	0	0
Nycteliini	<i>Nyctelia freyi</i> Kulzer	0	3	0	0
Nycteliini	<i>Nyctelia latiplicata</i> Kulzer	0	4	0	0
Nycteliini	<i>Nyctelia undatipennis</i> Curtis	11	11	0	0
Nycteliini	<i>Patagonogenius quadricollis</i> (Fairmaire)	0	1	22	30
Nycteliini	<i>Psectrascelis punctipennis</i> Kulzer	6	0	0	3
Praociini	<i>Praocis (Hemipraocis) sellata bergi</i> Kulzer	3	1	28	38
Praociini	<i>Platesthes kuscheli</i> Kulzer	2	0	1	0
Edrotini	<i>Hylithus tentyroides</i> Lacordaire	0	0	1	1
Trilobocarini	<i>Salax lacordairei</i> Guérin-Méneville	2	0	0	0
Tenebrioninae					
Scotobiini	<i>Emmallodera crenaticostata crenaticostata</i> Blanchard	1	7	13	16
Scotobiini	<i>Emmallodera obesa punctipennis</i> Kaszab	0	3	0	0
Scotobiini	<i>Scotobius akidioides akidioides</i> Waterhouse	0	1	2	16
		26	52	88	108
	Total	78		196	
		274			

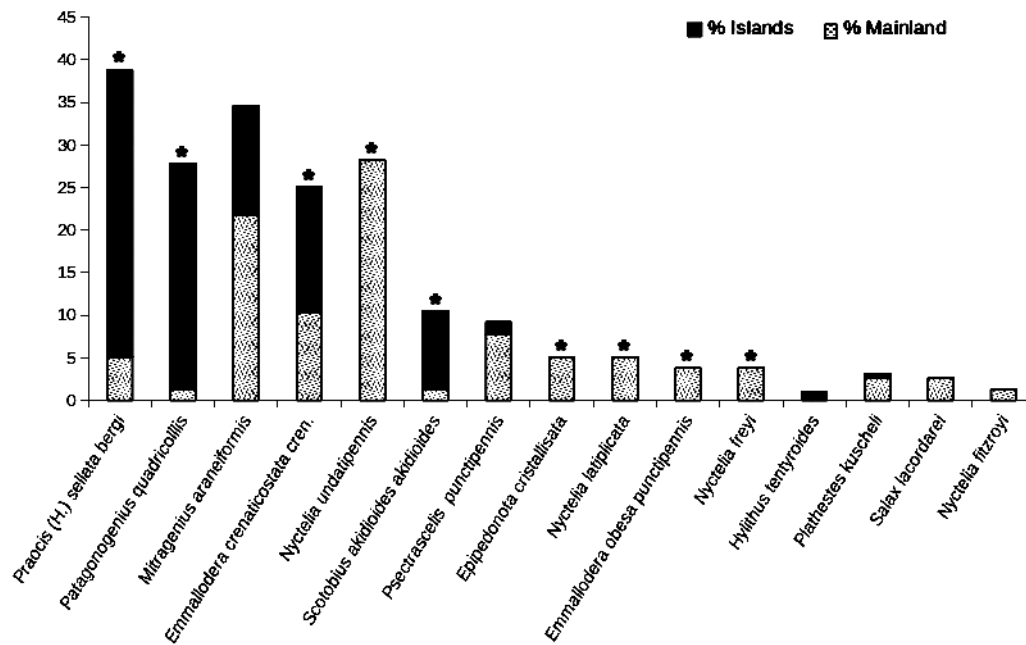


Figure 2. Relative abundances of tenebrionid species (%) collected in islands and mainland. * indicate statistically significant differences.

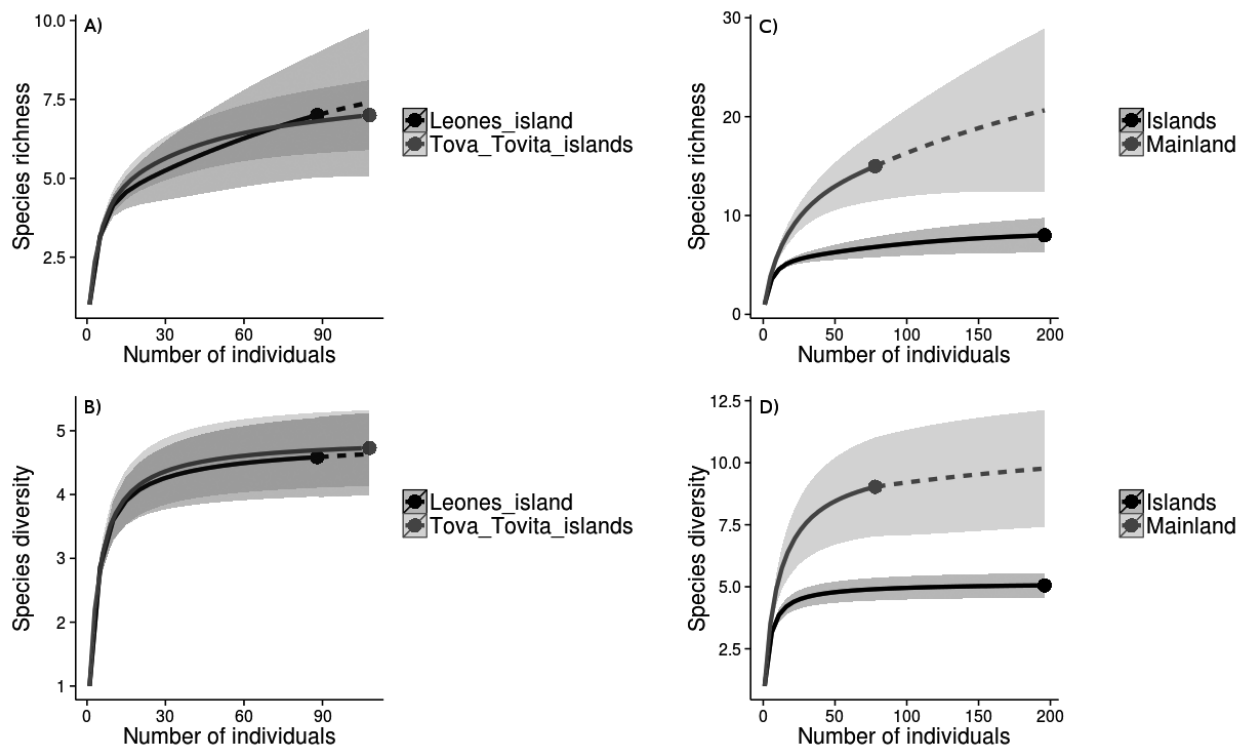


Figure 3. Individual-based rarefaction curves of tenebrionid species richness and diversity. A and B represent comparison between islands, C and D refer to mainland-island comparison. Dashed lines refer to the extrapolation part of each curve up to 108 individuals (between islands) and 196 (between mainland and islands). The 95% confidence intervals are shown as gray-shaded regions.

in the mainland (Figs. 3c and 3d). At the same time, overall darkling beetle abundance was larger in islands than in mainland (Table II).

MDS and ANOSIM analyses demonstrated that both islands share the same tenebrionid species assemblage (Fig. 4; ANOSIM: $R = 0.001$, $p = 0.543$), which, at the same time, was different from that of the mainland (Fig. 4; ANOSIM: $R = 0.836$, $p = 0.003$). The first PCA axis explained a significant portion of the variability between tenebrionid species composition and abundances (Fig. 5). Thus, it showed that the island assemblage differs from those of the mainland by more than 40% (Figs. 5 and 6). Positive values of this axis exhibited that island tenebrionid assemblage was correlated with higher abundances of *Praocis (Hemipraocis) sellata bergi*, *Patagonogenius quadricollis*, *Emmallodera crenaticostata crenaticostata* and *Scotobius akidioides akidioides* Waterhouse (Fig. 6). GLMs at individual species level supported this pattern, since all these species significantly increased their abundances on islands (Table II, Fig. 2).

The analyses at individual supraspecific level reported the same pattern for the genera *Emmallodera* and *Praocis*, for the tribe Scotobiini and for the subfamilies Pimeliinae and Tenebrioninae (Table II). On the other hand, negative values of first PCA axis also displayed that *Nyctelia undatipennis*, *Mitrageenius araneiformis*, *Epipedonota cristallisata* (Waterhouse), *Nyctelia latiplicata* Kulzer, *Nyctelia freyi* Kulzer, and *Emmallodera obesa punctipennis* Kaszab are the dominant species in mainland (Fig. 6). With the exception of *M. araneiformis*, this pattern was confirmed by GLMs on individual abundances of these species and by the genus *Nyctelia* Berthold which the abundances increased in mainland (Table II, Fig. 2). GLMs based on individual analyses of *M. araneiformis*, *Psectrascelis punctipennis* Kulzer, *Platsthes kuscheli* Kulzer, *Hylithus tentyroides* Lacordaire, *Salax lacordairei* Guérin-Méneville and the tribes Nycteliini and Trilobocarini showed non significant differences in their abundances between mainland and islands (Table II, Fig. 2).

Table II. Comparison of tenebrionid species, genus, tribes and subfamilies abundances between mainland and island using GLM. Chi-square statistic and its p value (d.f. = 2) for the change in deviance in relation to the null model are presented. Mean value and standard error (between brackets) are indicated for each taxa at mainland and islands. It was not possible to build a GLM for *Nyctelia fitzroyi* Waterhouse because only a single specimen was collected. # – Distribution model of the response variable used in GLMs: & – Poisson, * – Negative Binomial.

Variable [#]	Mainland	Islands	Chi-square	p-value
Total abundance*	39 (18.4)	98 (14.1)	16.4409	0.0003
<i>Epipedonota cristallisata</i> (Waterhouse) ^{&}	2 (2.8)	0 (0)	7.9767	0.0185
<i>Mitrageenius araneiformis</i> Curtis*	8.5 (10.6)	12.5 (12)	0.7684	0.681
<i>Nyctelia freyi</i> Kulzer ^{&}	1.5 (2.1)	0 (0)	6.368	0.0414
<i>Nyctelia latiplicata</i> Kulzer ^{&}	2 (2.8)	0 (0)	7.9767	0.0185
<i>Nyctelia undatipennis</i> Curtis ^{&}	11 (0)	0 (0)	>29.8237	3.341E-08
<i>Patagonogenius quadricollis</i> (Fairmaire) ^{&}	0.5 (0.7)	26 (5.7)	>26.7391	1.562E-15
<i>Psectrascelis punctipennis</i> Kulzer ^{&}	3 (4.2)	1.5 (2.1)	2.325	0.3127
<i>Praocis (Hemipraocis) sellata bergi</i> Kulzer ^{&}	2 (1.4)	33 (7.1)	>29.6055	3.726E-16
<i>Platsthes kuscheli</i> Kulzer ^{&}	1 (1.4)	0.5 (0.7)	1.16	0.5599
<i>Hylithus tentyroides</i> Lacordaire ^{&}	0 (0)	1 (0)	4.6891	0.0959
<i>Salax lacordairei</i> Guérin-Méneville ^{&}	1 (1.4)	0 (0)	4.6883	0.0959
<i>Emmallodera crenaticostata crenaticostata</i> Blanchard ^{&}	4 (4.2)	14.5 (2.1)	15.7841	0.0004
<i>Emmallodera obesa punctipennis</i> Kaszab ^{&}	1.5 (2.1)	0 (0)	6.368	0.0414
<i>Scotobius akidioides akidioides</i> Waterhouse ^{&}	0.5 (0.7)	9 (9.9)	21.9705	0.00002
<i>Nyctelia Berthold</i> ^{&}	15 (5.7)	0 (0)	>27.3937	1.126E-10
<i>Emmallodera</i> Blanchard ^{&}	5.5 (6.4)	14.5 (2.1)	11.1688	0.0038
Nycteliini Solier ^{&}	29 (15.6)	40 (4.2)	5.6086	0.0606
Praociini Eschscholtz ^{&}	3 (2.8)	33.5 (6.4)	>27.455	1.092E-14
Trilobocarini Lacordaire ^{&}	1 (1.4)	0 (0)	4.6883	0.0959
Scotobiini Solier*	6 (7.1)	23.5 (12)	6.6149	0.0366
Pimeliinae Latreille ^{&}	33 (11.3)	74.5 (2.1)	>27.6804	9.756E-09
Tenebrioninae Latreille*	6 (7.1)	23.5 (12)	6.6149	0.0366

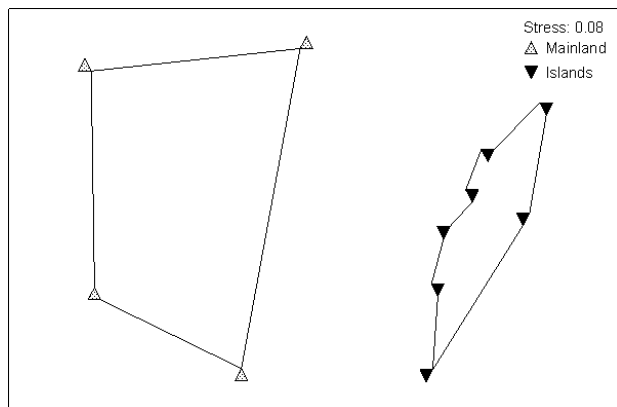


Figure 4. Bidimensional MDS ordination diagram showing the dissimilarity between tenebrionid species assemblages from islands and mainland.

DISCUSSION

This study reveals for the first time the presence of tenebrionid beetles on islands of the Parque Interjurisdiccional Marino Costero Patagonia Austral (PIMCPA), and affords the first record of insular tenebrionids in Atlantic coast of Patagonia. We also showed that Leones and Tova-Tovita islands share a common tenebrionid species assemblage that differs from that of the neighbouring mainland. Because of the presence of other vegetated islands in the PIMCPA, it is expected that they can also harbour tenebrionid populations. It is an interesting fact that the two most abundant tenebrionid species on the islands (*Praocis sellata bergi* and *Patagonogenius quadricollis*) have low abundances in the mainland, not exceeding 5%. At the same time, particularly remarkable is the absence of diurnal tenebrionids on these islands, especially species of *Nyctelia* and *Epipedonota* Solier which qualitatively and quantitatively dominate the

mainland tenebrionid assemblage (Figs. 2 and 6). These absences could explain the lower richness and diversity of tenebrionid recorded on the islands respect to the mainland.

In terms of tenebrionid species richness, 13 of the 15 total captured species belong to the tribes Nycteliini, Praociini and Scotobiini. These finding is in agreement with Kuschel (1969) who stated that the species belonging to these tribes are dominant among tenebrionid beetles inhabiting the Patagonian steppe. Other recent studies dealing with tenebrionids in the Patagonian steppe have also identified species of these tribes as dominant (Sackman and Flores 2009, Cheli *et al.* 2010, Carrara *et al.* 2011). According to this pattern the insular tenebrionid species assemblage included four species belonging to the tribes Nycteliini (*Patagonogenius quadricollis* and *Mitragenius araneiformis*), Praociini (*Praocis (Hemipraocis) sellata bergi*), and Scotobiini (*Emmallodera crenaticostata crenaticostata*), making up 87% of the total captured individuals (Fig. 2).

In our samples, *Hylithus tentyroides* Lacordaire is recorded in both islands, however, it is not present in the mainland. This beetle is omnivorous, since this species has been reported as phytophagous (Flores and Debandi 2004) and feeding on decomposing mammal carcasses (Aballay *et al.* 2016, this volume). This broad food spectrum increases the chances of survival of this species in environments with little organic matter such as islands. At the same time, the presence of *H. tentyroides* on islands is probably related with the human activities performed on both islands in the past. This beetle shows a highly adaptable behaviour, it has been observed in northeastern Patagonia (Cheli 2009). This behaviour increases its abundance using new environmental resources generated by human activities (e.g. man-made shelters, pieces of wood/concrete, unused containers or garbage, dumps near human towns and ovine feces (see Cheli 2009; Cheli and Flores, unpublished data). In this study we only found

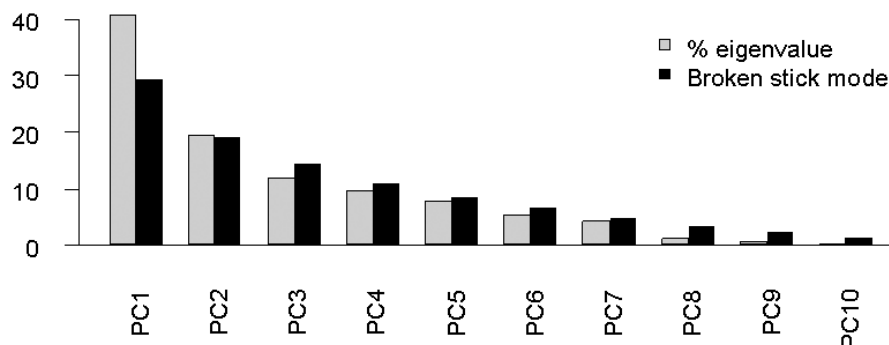


Figure 5. Significance of first ten PCA's ordination axes using the Broken stick criteria.

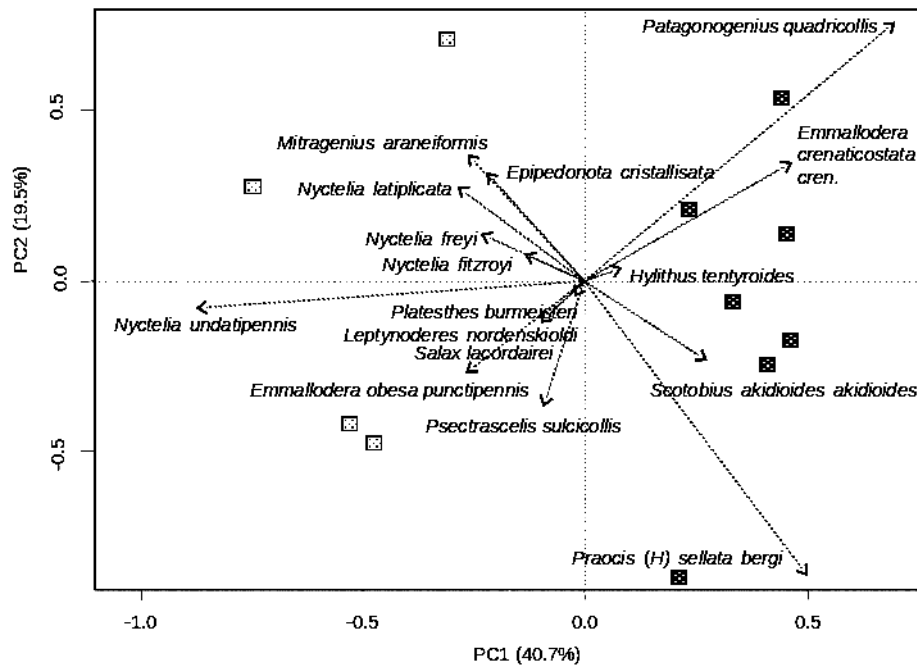


Figure 6. PCA ordination diagram showing the tenebrionid species composition and their abundances in islands and mainland. White dotted triangles refer to mainland sites while dark ones indicate those from islands.

H. tentyroides near the insular ruins of the human settlement, suggesting that it is likely that this species was inadvertently introduced into the islands by the ancient settlement. Furthermore, this species can significantly increase its chances of survival on the islands by exploiting the artificial shelters offered by the remains of past human activities.

Most common tenebrionid genera that currently live on mainland Patagonia and Pampas have been present there for over 12,000 years (Ramírez *et al.* 2016, this volume). Because all tenebrionid species found on Leones and Tova-Tovita islands were able to survive the Late Pleistocene paleoclimate in the region, we believe that the current island assemblages likely originated from a relict tenebrionid community present on the islands at the moment of their separation from the mainland. The insular distribution patterns of tenebrionids in several archipelagos of the Mediterranean Sea are also explained by relict models (see Fattorini 2009a, 2010). This suggests that the history of the PIMCPA islands have played and even today continue to play an important role in shaping insect distributions.

It has been argued that distance to mainland is a key feature to explain distributional patterns of animals on islands (Fattorini 2010). Our results show that distances of at least 1 km are enough to alter the composition and abundance of tenebrionids, giving rise to different species assemblages. This agrees

with Fattorini (2009a, 2010), who pointed out that even relatively short distances preclude tenebrionids from colonizing islands from the mainland. The Tova-Tovita complex is approximately 6 times farther from the continent than Leones island, and even so they share the same tenebrionid species assemblage. Therefore, a variation of 1 or 6 km in distance to mainland would not be a factor affecting tenebrionid species assemblages on these islands. Our results agree with Fattorini (2010), who found no evidence for a correlation between island distance to mainland and tenebrionid species assemblages. We believe that the structure of the tenebrionid community on Leones and Tova-Tovita islands is mainly affected by the fact of being separated from the mainland rather than by the distance from it. Thus, we consider unlikely that the present immigration could be a major factor shaping the island tenebrionid assemblage in the PIMCPA. In fact, the great similarity in darkling beetle composition and species abundances between Leones and Tova-Tovita islands suggests that their environmental requirements or predation pressure may have been major players shaping this present community. These factors could also explain the absence of diurnal tenebrionid species on these islands. This idea is in accordance with Fattorini (2009a), who postulated that some islands of the Tuscan archipelago were largely colonized by several animal groups during the Pleistocene sea regressions, followed by extinctions as a result of area reduction

and habitat loss. Thus, it is likely that either habitat modification over the last 10,000 years or predation pressures may have led the diurnal tenebrionids from the PIMCPA islands to extinction.

In this sense, the framework project of this study has also recorded for the first time the presence of wild populations of Norway rats (*Rattus norvegicus* Berkenhout), rabbits (*Oryctolagus cuniculus* Linnaeus), pichis (*Zaedyus pichi* Desmarest) and large hairy armadillos (*Chaetophractus villosus* Desmarest) in Leones and Tova-Tovita islands (Udrizar Sauthier pers. obs.). The presence of these mammals is man-made, implying a potential conflict with the conservation of the entomofauna due to predation (Superina *et al.* 2009) or habitat modification (Pizarro-Araya *et al.* 2012). Therefore, we suggest monitoring programs to assess the activities of these mammals.

In a recent study conducted on three Pacific islands of coastal Chile, only a single endemic tenebrionid species was reported (Alfaro *et al.* 2009). Conversely, in our study we did not find any tenebrionid species endemic to Leones or Tova-Tovita islands. In agreement with Fattorini (2006, 2009a), the absence of endemic tenebrionid species on these islands may be due to their quite recent formation, which probably means that there has not been enough time for extensive speciation to occur. Nevertheless, we observed some morphological differences between individuals of the same species from mainland and islands that could suggest an incipient differentiation into subspecies or microgeographic races. For example, insular specimens of *Emmallodera crenaticostata crenaticostata* and *Mitrageni* *araneiformis* are bigger than those from the mainland. These populations could be all reproductively compatible, but differ in size and ecological requirements as well as in temperature and substrate preferences (Doyen and Slobodchikoff 1984). There are some precedents in other tenebrionid species of South American islands that support this idea. Benítez *et al.* (2014) found morphological variations among individuals of *Praocis (Praocis) spinolai* Gay and Solier from island populations in Los Choros archipelago (transitional coastal desert, Chile). These authors claim that this morphological patterns are due to the isolation of the populations and to environmental effects mediated by higher arid pressures on islands than in the continent, where there is a more stable and humid environment. These authors also suggest that the pattern of variation found indicates an evolutionary trend among the populations examined (Benítez *et al.* 2014).

From a methodological point of view, multivariate analyses were more effective than univariate methods. For example, the positive correlation between the abundance of *M. araneiformis* with mainland environments may have been unnoticed, if we only used

univariate methods. If we considered simultaneously several variables, the data structure is more stable giving to multivariate analyses a greater predictive ability (Varona *et al.* 1999) and more accuracy of predicted values over univariate methods (McGarigal *et al.* 2000).

Finally, this work enhances the value of the PIMCPA archipelago off the Patagonian coast, highlighting the importance of entomofauna on these islands. Due to their high abundance and sensitivity to environmental changes in arid northern Patagonia (Cheli 2009, Martínez 2013), tenebrionid beetles constitute useful tools to perform zoning, monitoring and other conservation actions in the PIMCPA. Fattorini (2009a) suggested that the relict distribution of insular tenebrionids should be a matter of concern for conservation biologists, because local species extinction is not compensated by immigration from adjacent mainland areas. Therefore, insular tenebrionids may be more vulnerable to extinction (Pizarro-Araya *et al.* 2012). Deepening the study of the insect of these islands and the rest of the PIMCPA will increase the chances of biodiversity conservation success at a regional scale in arid Patagonia.

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