



Endemic epigean Tenebrionids (Coleoptera: Tenebrionidae) from the Andean Region: exploring the patagonian-diversification hypothesis

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Abstract

Tenebrionidae is a diverse insect family of Coleoptera that shows high levels of endemism in epigean species. For the Andean region, which is divided into three subregions: Central Chilean, Subantarctic and Patagonian, it has been hypothesized that epigean tenebrionids have diversified in the Patagonian subregion and subsequently, they dispersed to Subantarctic and Central Chilean subregions. In this work, based on information obtained from museum collections and scientific studies, we presented the first list of endemic epigean tenebrionids from the Andean region with their taxonomic arrangement and geographic distribution. Moreover, we used these data to explore the veracity of the Patagonian-diversification hypothesis. A total of 416 species grouped into six subfamilies, 17 tribes and 41 genera were identified as endemic to the Andean region. Considering the spatial distribution it was observed that subfamilies, tribes, genera and species were unequally distributed across subregions. Results did not support the Patagonian-diversification hypothesis; to the contrary, they were more concordant with processes of isolation among subregions that have promoted speciation by interrupting gene flow among populations, resulting in endemism because species can not expand their range sizes. Finally, we discuss the implications of our findings to be considered in biodiversity conservation, because endemic species, by their high extinction risk, are primary targets in conservation strategies.

Key words: Evolution, taxonomy, spatial distribution, Argentina, Chile, vicariance

Introduction

Tenebrionidae, one of the most diverse families of Coleoptera with about 20,000 described species (Matthews *et al.* 2010), has a cosmopolitan distribution with a great diversity in tropical and subtropical areas and in hot and cold deserts (Watt 1974; Matthews *et al.* 2010). According to the habitat preferences it is possible to recognize two main groups of tenebrionid beetles: 1) species associated with trees, and 2) species associated with soil or sand (Aalbu *et al.* 2002). Among the latter group several studies have reported the existence of a high level of endemism in different areas of the World (Watt 1974; Matthews *et al.* 2010; Carrara & Flores 2013; Cifuentes-Ruiz & Zaragoza-Caballero 2014). This high endemism has strong implications in tenebrionid subsistence, because species with restricted geographic distribution have a greater extinction risk than species with broad geographic distribution (Gaston & Fuller 2009). Indeed, because of this characteristic several endemic epigean species were considered as conservation targets in studies oriented to protect species diversity (see Carrara *et al.* 2011).

At a global level, the Andean region is one of the areas that particularly attract the attention of biogeographers and conservationists (Olson & Dinerstein 2002; Mittermeier *et al.* 2011). Geographically, it covers the south of Argentina and central and south of Chile (Fig. 1). According to available biogeographical classifications the Andean region is divided into three subregions: Central Chilean, Subantarctic and Patagonian (Morrone 2006, 2014, 2015). The Central Chilean subregion extends from 26° (Lowenberg-Neto 2014) to 37° south latitude in Chile (Morrone 2006, 2015). The Subantarctic subregion covers the southern Andes from 37° south latitude to Cape Horn in Argentina and Chile, and includes the Islands: Malvinas, Georgias del Sur, and Juan Fernandez (Morrone 2006, 2014, 2015). Finally, the Patagonian subregion extends at the east of the Andes from 35° south

latitude, mainly in Argentina, to Tierra del Fuego (54° south latitude) and includes part of Aysen and Magallanes in Chile (Escalante *et al.* 2009). Specifically, in the Andean region, several different studies have addressed the problem of taxonomy, biodiversity and conservation status of endemic epigeal tenebrionids. Unfortunately, they were conducted at local or ecoregional scales (Flores & Vidal 2000a, b; Flores & Roig-Juñent 2001; Flores 2004; Cepeda-Pizarro *et al.* 2005; Vergara *et al.* 2006; Cheli *et al.* 2010; Carrara *et al.* 2011; Flores *et al.* 2011; Pizarro-Araya *et al.* 2012; Flores & Pizarro-Araya 2012; Carrara & Flores 2013). Therefore the total number, identity and geographic distribution of tenebrionids remains unknown for the entire Andean region.

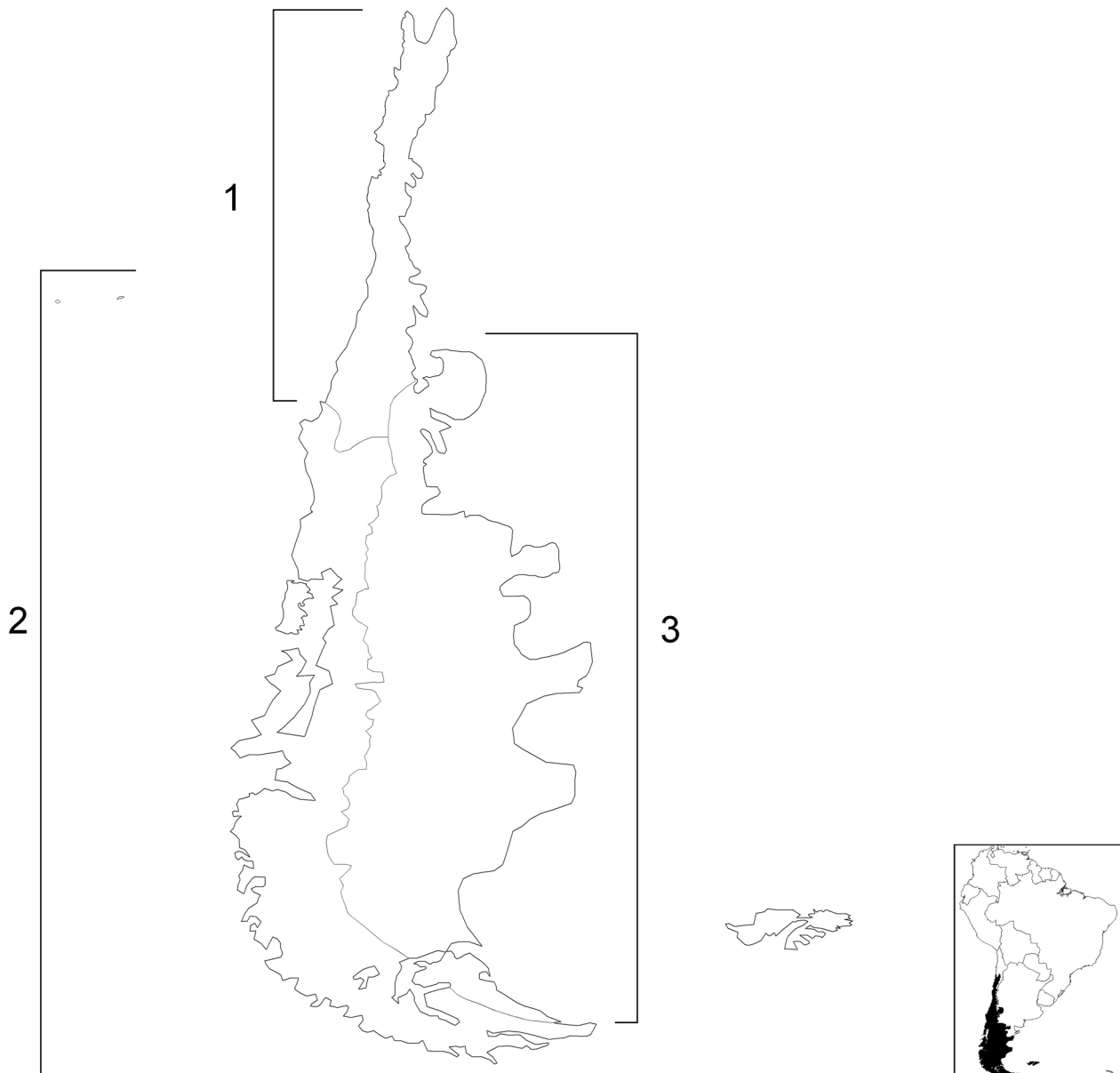


FIGURE 1. Spatial location of the Andean region. Horizontal bars indicate the geographic locations of the three subregions, where 1, is Central Chilean; 2, is Subantarctic and 3, is Patagonian (modified from Morrone 2006, 2015 and Lowenberg-Neto 2014).

An increase of knowledge about endemic epigeal tenebrionids inhabiting the Andean region will contribute to the recognition of different processes that have influenced its evolution. In this regard, Kuschel (1969) hypothesized that epigeal tenebrionid fauna (as many other epigeal Coleoptera) has diversified in the Patagonian subregion (the Patagonian-diversification hypothesis), because of the transformation of temperate forests in open communities by the progressive cooling of this area. Afterwards, the ancestor of present day species gradually dispersed to Subantarctic and Central Chilean subregions probably during the Tertiary and Pleistocene (Kuschel

1969). This postulate agrees with the idea of Peña (1963) that considered the influence of the same processes in the evolution of the tenebrionid genus *Nyctelia* Latreille. From this hypothesis it is possible to derive three following predictions: 1) speciation rates should be highest in Patagonian subregion, because diversification process was restricted to this area, 2) maximum of taxonomic differentiation should occur in Patagonian subregion, because only this area is characterized by high speciation rates, 3) dispersal routes reconstructed for epigean tenebrionids should originate in Patagonian and terminates in Subantarctic and Central Chilean subregions, because the species that diversify in Patagonian were able to extend their ranges to the other subregions. In particular, the Patagonian-diversification hypothesis has never been explored. We consider that endemic epigean tenebrionids are a good study model to test the aforementioned predictions, mainly because of their ancient settlement in the region, which allows to evaluate diversification processes without the confounding influence of colonization and migration (Yoder & Nowak 2006; Shi *et al.* 2013).

The objectives of this work are: 1) to present the first comprehensive list of endemic epigean tenebrionids that inhabit the Andean region with their taxonomic arrangement and geographic distribution; 2) to test the predictions derived from the Patagonian-diversification hypothesis for epigean tenebrionids.

Materials and methods

Data source. In this study we defined endemic species as those with distribution ranges restricted to the Andean region. The final list of endemic epigean tenebrionids was built at both current species and subspecies levels. Hereafter, for simplicity in this work the term “species” will be used in reference to all tenebrionid taxa representing the species-group level (ICZN 1999). We followed the classification proposed by Bouchard *et al.* (2011) for assigning species and genera to tribes and subfamilies.

We obtained our data by studying the material 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; 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; 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.

For species identification we used keys and revisions from Kulzer (1955, 1958, 1962, 1963), Flores (1999, 2004), Flores & Vidal (2000a, 2001), Flores & Chani-Posse (2005) and Flores *et al.* (2011).

In addition, we obtained information from different scientific researches that addressed the study of taxonomy and ecology of epigean tenebrionids: Kaszab (1969, 1970), Freude (1960, 1987), Peña (1966, 1971, 1974a, b, 1980, 1991, 1995), Matthews (1998), Flores & Vidal (2000a), Pizarro-Araya & Jerez (2004), Vergara *et al.* (2006), Vidal & Flores (2007), Vidal & Guerrero (2007a, b), Guerrero *et al.* (2007), Flores & Pizarro-Araya (2012), Carrara & Flores (2013).

The specimens revised were assigned to each subregion according to their collection data and bibliographic information.

Data analysis. We constructed an incidence matrix where species, with their taxonomic arrangement, were represented in rows (i), subregions in columns (j) and the presence or absence of species in the subregions in each matrix cell (i.e. values 1 and 0, respectively). We estimated the observed species richness for each subregion by summing up the values in each column, and species geographic distribution by considering the presence values in each row of the matrix. Species with insufficient information about their geographic distribution were excluded from the incidence matrix.

To test the first prediction of the Patagonian-diversification hypothesis, we assessed for differences among species to genus ratio (S/G) among the three Andean subregions. We used S/G because is a variable that was recognized as positively related to speciation or diversification rates (Krug *et al.* 2008). However, as this variable is correlated with species richness (Gotelli & Graves 1996), it is necessary to make a correction for differences in

species abundances among sampling sites. To this end, we followed the methodology proposed by Arita (1997), who compared the observed S/G in local pools of species against the expected by randomly sampled species abundances from the regional pool of species. In our case, local pools of species are represented by the species that inhabit the Andean subregions, and the regional pool is represented by all species that inhabit the Andean region. Observations of S/G that significantly deviates from null expectations were interpreted as not influenced by species abundances. The analysis was performed with the software Ecosim (Gotelli & Entsminger 2010), by rarefying 1000 times the abundance of species by genus observed in the regional pool of endemic epigean tenebrionids to generate the number of expected genus (mean and 95% interval confidence) for the species abundances of each subregion.

To test the second prediction, we assessed for differences in species richness among the three Andean subregions. With the software BioGeoSim (Gotelli *et al.* 2013), we simulated the stochastic placement of species geographic distribution within a gridded domain that represents the three Andean subregions. Modelling settings were: cells with equiprobable opportunity to be colonized, species ranges spread through strict range cohesion and 1000 repetitions. We choose these settings because they represent the expected richness under a geometric constraint model (Rahbek *et al.* 2007), that was proposed as a possible explanation for richness patterns in endemic species (see Rahbek *et al.* 2007). From this null-model we generate the random expected species richness (mean and 95% interval confidence) for each subregion considering the distribution ranges of the regional pool of endemic epigean tenebrionids.

Finally, to test the third prediction of the Patagonian-diversification hypothesis we measured the likelihood of species dispersal from Patagonian to Central Chilean and Subantarctic subregions. To this end, we used the methodology proposed by Legendre & Legendre (1984; 1998), which identify in two adjacent areas (x_1 and x_2) the number of species that these regions have in common (a), the number of species only found in x_1 (b) and the number of species only found in x_2 (c), to estimate the coefficient of species dispersal direction (DD) from x_1 to x_2 :

$$DD(x_1 \rightarrow x_2) = \frac{a}{(a+b+c)} \frac{(b-c)}{(a+b+c)} \quad \text{eq. 1.}$$

High scores of DD are expected when a is high and $b > c$ (Legendre & Legendre 1984; 1998), values of $c > b$ gives negative sign to DD and support the hypothesis of dispersal from x_2 to x_1 . It should be noted that the first portion of DD is the Jaccard coefficient of similarity (Legendre & Legendre 1998).

Specifically, for a complete analysis of dispersion processes, in our analysis we assessed for species dispersal routes as follow: from Patagonian to Subantarctic subregion, from Patagonian to Central Chilean subregion and from Subantarctic to Central Chilean subregion. It should be noted that dispersal analysis between Subantarctic and Central Chilean intent to elucidate the existence of an indirect dispersal route from Patagonian to Subantarctic subregion and then, from Subantarctic to Central Chilean subregion.

Results

A total of 416 species of epigean tenebrionids were identified as endemic to the Andean region (Table 1). These endemic species belong to six of the nine subfamilies currently assigned to Tenebrionidae (Bouchard *et al.* 2011): Diaperinae, Lagriinae, Phrenapatinae, Pimeliinae, Stenochinae and Tenebrioninae. The 416 species are grouped into 17 tribes: Nycteliini, Praociini, Adeliini, Amphidorini, Apocryphini, Cnodalonini, Elenophorini, Epitragini, Penetini, Phaleriini, Physogasterini, Scotobiini, Stenosini, Tenebrionini, Thinobatini, Trilobocarini and Ulomini, with the first two representing 57% of total species found. Among the 41 genera present in the Andean region, 18 are endemic: *Gondvanadelium* Matthews, *Penadelium* Matthews, *Valdivium* Matthews (Adeliini); *Heliofugus* Guérin-Méneville, *Myrmecodema* Gebien (Cnodalonini); *Aspidolobus* Redtenbacher (Epitragini); *Auladera* Solier, *Callyntra* Solier, *Gyriosomus* Guérin-Méneville (Nycteliini); *Asidelia* Fairmaire, *Gyrasida* Koch, *Neopraocis* Kulzer, *Patagonopraocis* Flores & Chani-Posse (Praociini); *Diastoleus* Solier (Scotobiini), *Hexagaonochilus* Solier (Stenosini); *Phanerops* Solier (Tenebrionini); *Peltolobus* Lacordaire (Trilobocarini) and *Oligocara* Solier (Ulomini). The most speciose genera are *Praocis* Eschscholtz, *Nyctelia*, *Heliofugus*, *Gyriosomus* and *Psectrascelis* Solier with more than 35 species endemic to the Andean region each one.

TABLE 1. Taxonomic position and distribution patterns of endemic species and subspecies from the Andean region. Capital letters between brackets represent subregions, where: *C* = Central Chilean, *S* = Subantarctic and *P* = Patagonian. Question marks indicates species probably endemic, but with not enough information about its geographic distribution.

Subfamily	Tribe	Genus	Species/Subspecies[Distribution]
Diaperinae	Phaleriini	<i>Phaleria</i>	<i>P. maculata</i> [C, S]
Lagriinae	Adeliini	<i>Gondvanadelium</i>	<i>G. gebieni</i> [S], <i>G. seirotranoides</i> [S]
		<i>Licinoma</i>	<i>L. penai</i> [C]
		<i>Penadelium</i>	<i>P. araucanum</i> [S]
		<i>Valdivium</i>	<i>V. aeneum</i> [C, S], <i>V. breve</i> [S], <i>V. chilense</i> [C], <i>V. dudichi</i> [S], <i>V. germaini</i> [S], <i>V. montemiliense</i> [C, S], <i>V. monticola</i> [C], <i>V. sulcatulum</i> [S]
Phrenapatinae	Penetini	<i>Archeophthora</i>	<i>A. penai</i> [S]
Pimeliinae	Elenophorini	<i>Psammetichus</i>	<i>P. cekalovici</i> [C], <i>P. crassicornis</i> [C], <i>P. pilipes</i> [C]
	Epitragini	<i>Aspidolobus</i>	<i>A. gayi</i> [C], <i>A. penai</i> [C], <i>A. piliger</i> [C]
	Nycteliini	<i>Auladera</i>	<i>A. andicola</i> [C], <i>A. atronitens</i> [C], <i>A. crenicosta</i> [C], <i>A. rugicollis</i> [C]
		<i>Callyntra</i>	<i>C. andina</i> [C], <i>C. cantillana</i> [C], <i>C. carbonaria</i> [C, S], <i>C. hibrida</i> [C], <i>C. inflata</i> [C, S], <i>C. laticollis</i> [C], <i>C. macrocosta</i> [C], <i>C. montana</i> [C], <i>C. multicosta</i> [C], <i>C. paulseni</i> [C], <i>C. penai</i> [C], <i>C. planiuscula</i> [C], <i>C. riverai</i> [C], <i>C. rossi</i> [S], <i>C. rugosa</i> [C], <i>C. servillei</i> [C], <i>C. subrugosa</i> [C], <i>C. unicosta</i> [C]
		<i>Epipedonota</i>	<i>E. elegantula</i> [P], <i>E. lata</i> [P], <i>E. nitida</i> [P], <i>E. subplana</i> [P], <i>E. tricostata</i> [P], <i>E. willinki</i> [P]
		<i>Gyriosomus</i>	<i>G. amabilis</i> [C], <i>G. angustus</i> [C], <i>G. atacamensis</i> [C], <i>G. barriai</i> [C], <i>G. batesi</i> [C], <i>G. bridgesi</i> [C], <i>G. chango</i> [C], <i>G. coriaceus</i> [C], <i>G. curtisi</i> [C], <i>G. elongatus</i> [C], <i>G. foveopunctatus foveopunctatus</i> [C], <i>G. foveopunctatus laevis</i> [C], <i>G. freyi</i> [C], <i>G. gebieni</i> [C], <i>G. granocostatus</i> [C], <i>G. granulipennis</i> [C], <i>G. hoppei</i> [C], <i>G. impressus</i> [C], <i>G. kingi</i> [C], <i>G. kulzeri</i> [C], <i>G. laevigatus</i> [C], <i>G. leechi</i> [C], <i>G. lucens</i> [C], <i>G. luczotii</i> [C], <i>G. marmoratus</i> [C], <i>G. melcheri</i> [C], <i>G. modestus</i> [C], <i>G. multigranulosus</i> [C], <i>G. parvus</i> [C], <i>G. paulseni</i> [C], <i>G. penai</i> [C], <i>G. penicilliger</i> [C], <i>G. planatus</i> [C], <i>G. planicollis</i> [C], <i>G. pumilus</i> [C], <i>G. reedi</i> [C], <i>G. subrugatus</i> [C], <i>G. whitei</i> [C]
		<i>Mitragenius</i>	<i>M. tristis</i> [S, P],
		<i>Nyctelia</i>	<i>N. alutacea</i> [P], <i>N. blairi</i> [P], <i>N. bremi</i> [P], <i>N. caudata</i> [P], <i>N. cicatriculata</i> [P], <i>N. confusa</i> [P], <i>N. consularis</i> [P], <i>N. corrugata</i> [P], <i>N. crassecostata</i> [P], <i>N. darwini</i> [P], <i>N. difficilis</i> [P], <i>N. discoidalis</i> [P], <i>N. fitzroyi</i> [P], <i>N. freyi</i> [P], <i>N. garciae</i> [P], <i>N. gebieni</i> [P], <i>N. geometrica</i> [P], <i>N. grandis</i> [P], <i>N. granulata</i> [P], <i>N. guerini</i> [P], <i>N. hayekae</i> [P], <i>N. kulzeri</i> [P], <i>N. laevis</i> [P], <i>N. laevis laevis</i> [P], <i>N. laevis rufipes</i> [P], <i>N. laticauda</i> [P], <i>N. latiplicata</i> [P], <i>N. multicristata</i> [P], <i>N. neglecta</i> [P], <i>N. nevadoensis</i> [P], <i>N. newporti</i> [P], <i>N. penai</i> [P], <i>N. planata</i> [P], <i>N. plicata</i> [P], <i>N. porcata</i> [P], <i>N. quadricarinata</i> [P], <i>N. quadriplicata</i> [P], <i>N. recteplicata</i> [P], <i>N. rotundipennis</i> [P], <i>N. sallei</i> [P], <i>N. solieri</i> [P], <i>N. stephensi</i> [P], <i>N. suturacava</i> [P], <i>N. torresi</i> [P], <i>N. undatipennis</i> [P], <i>N. unicostata</i> [P], <i>N. vulcanica</i> [C], <i>N. westwoodi</i> [P], <i>N. wittmeri</i> [P]

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TABLE 1. (Continued)

Subfamily	Tribe	Genus	Species/Subspecies[Distribution]
		<i>Patagonogenius</i>	<i>P. acutangulus</i> [P], <i>P. breviangulus</i> [P], <i>P. elegans</i> [P], <i>P. gentilii</i> [P], <i>P. kulzeri</i> [P], <i>P. quadricollis</i> [P]
		<i>Psectrascelis</i>	<i>P. aceitunoi</i> [C], <i>P. arenaria</i> [C], <i>P. atra</i> [P], <i>P. carrizalensis</i> [C], <i>P. cinerea</i> [C], <i>P. conjungens</i> [C], <i>P. costipennis</i> [C], <i>P. crassiventris</i> [C], <i>P. davidsi</i> [C], <i>P. difficilis</i> [C], <i>P. elguetai</i> [C], <i>P. elongata</i> [C], <i>P. freudei</i> [C], <i>P. gigas</i> [P], <i>P. grandis</i> [P], <i>P. hirta</i> [P], <i>P. kuscheli</i> [C], <i>P. latithorax</i> [P], <i>P. lucida</i> [P], <i>P. neuquenensis</i> [P], <i>P. penai</i> [C], <i>P. pilipes peninsularis</i> [C], <i>P. pilipes pilipes</i> [C], <i>P. pilipes specularis</i> [C], <i>P. pilosa</i> [C], <i>P. pudens</i> [C], <i>P. punctipennis</i> [P], <i>P. punctulata</i> [P], <i>P. rossoi</i> [C], <i>P. rotmanni</i> [C], <i>P. similis</i> [C], <i>P. soniae</i> [C], <i>P. strigosula</i> [C], <i>P. subcostata</i> [C], <i>P. subdepressa</i> [C], <i>P. sublaevicollis</i> [C], <i>P. sulcicollis</i> [P]
	Physogasterini	<i>Entomochilus</i>	<i>E. brendelli</i> [C], <i>E. ciliatus</i> [C], <i>E. franzi</i> [C], <i>E. freudei</i> [C], <i>E. grandis</i> [C], <i>E. hirtipes</i> [C], <i>E. illapelensis</i> [C], <i>E. laevipennis</i> [C], <i>E. minor</i> [C], <i>E. parvus</i> [C], <i>E. pilosus</i> [C], <i>E. quadratus</i> [C], <i>E. tomentosus</i> [C], <i>E. viali</i> [C]
		<i>Physogaster</i>	<i>P. ericius</i> [C], <i>P. globolus</i> [C], <i>P. kulzeri</i> [C], <i>P. penai</i> [C]
	Praociini	<i>Asidelia</i>	<i>A. contracta</i> [P]
		<i>Calymmophorus</i>	<i>C. peninsularis</i> [P]
		<i>Gyrasida</i>	<i>G. camilae</i> [C], <i>G. fernandoi</i> [C, S], <i>G. franciscae</i> [C], <i>G. lucianoii</i> [C], <i>G. propensa</i> [C], <i>G. tomasi</i> [C]
		<i>Neopraocis</i>	<i>N. reflexicollis</i> [P]
		<i>Patagonopraocis</i>	<i>P. magellanicum</i> [P], <i>P. minor</i> [P], <i>P. puncticollis</i> [P]
		<i>Platesthes</i>	<i>P. burmeisteri</i> [P], <i>P. depressa</i> [P], <i>P. granulipennis</i> [P], <i>P. hirtipes</i> [P], <i>P. humeralis</i> [P], <i>P. neuquensis</i> [P], <i>P. nigra</i> [P], <i>P. pilosa</i> [P], <i>P. silphoides</i> [P], <i>P. similis</i> [P], <i>P. unicosta</i> [P], <i>P. vidali</i> [C]
		<i>Praocis</i>	<i>P. adpersa</i> [C], <i>P. aenea</i> [C], <i>P. argentina</i> [P], <i>P. bicarinata</i> [P], <i>P. bicentenario</i> [C], <i>P. calderana</i> [C], <i>P. castanea</i> [C], <i>P. chevrolatii chevrolatii</i> [C], <i>P. chevrolatii nigra</i> [C], <i>P. chevrolatii subcostata</i> [C], <i>P. chilensis</i> [C], <i>P. costata</i> [C, S], <i>P. costatula</i> [C], <i>P. costipennis</i> [C], <i>P. cribrata</i> [C], <i>P. curta</i> [C], <i>P. curtisii</i> [C], <i>P. dentipes</i> [C], <i>P. depressicollis</i> [C], <i>P. ebenina</i> [C], <i>P. elliptica</i> [C], <i>P. flava</i> [C], <i>P. hirtella</i> [C], <i>P. hirtuosa</i> [C], <i>P. insularis</i> [C], <i>P. laevicollis</i> [C, S], <i>P. marginata</i> [C], <i>P. medvedevi</i> [C], <i>P. molinari</i> [P], <i>P. nitens</i> [C], <i>P. nuda</i> [C], <i>P. parva</i> [C], <i>P. pilula</i> [C], <i>P. pleuroptera</i> [C, S], <i>P. pubescens</i> [C], <i>P. quadrisulcata</i> [C], <i>P. reedi</i> [C], <i>P. rufilabris</i> [C], <i>P. rufipes</i> [C], <i>P. rugata</i> [C], <i>P. sanguinolenta</i> [C], <i>P. sellata bergi</i> [P], <i>P. sellata bruchi</i> [P], <i>P. sellata granulipennis</i> [P], <i>P. sellata peninsularis</i> [P], <i>P. sellata sellata</i> [P], <i>P. spinolai</i> [C], <i>P. striolicollis</i> [P], <i>P. subaenea</i> [C], <i>P. subreticulata</i> [C], <i>P. subsulcata</i> [C], <i>P. sulcata</i> [C], <i>P. tibialis</i> [C], <i>P. uretai</i> [P]
	Stenosini	<i>Discopleurus</i>	<i>D. baloghi</i> [C, S], <i>D. quadricollis</i> [C]
		<i>Grammicus</i>	<i>G. chilensis</i> [C], <i>G. latus latus</i> [C], <i>G. latus tenuicornis</i> [C], <i>G. mahunkai mahunkai</i> [C], <i>G. mahunkai robustus</i> [C]
		<i>Hexagonochilus</i>	<i>H. dilaticollis</i> [C], <i>H. tuberculatus</i> [C]

.....continued on the next page

TABLE 1. (Continued)

Subfamily	Tribe	Genus	Species/Subspecies[Distribution]
	Thinobatini	<i>Thinobatis</i>	<i>T. arenaria</i> [C], <i>T. brevicolis</i> [C], <i>T. calderana</i> [C], <i>T. confusa</i> [C], <i>T. ferruginea</i> [C], <i>T. intermedia</i> [S], <i>T. melcheri</i> [C], <i>T. punctata</i> [C], <i>T. rotundicollis</i> [C], <i>T. rufipes penai</i> [S], <i>T. rufipes rufipes</i> [C], <i>T. simplex</i> [C]
	Trilobocarini	<i>Peltolobus</i>	<i>P. ardoini</i> [P], <i>P. desertorum</i> [P], <i>P. patagonicus</i> [P], <i>P. waterhousei</i> [C]
		<i>Trilobocara</i>	<i>T. ciliata</i> [C]
	Cnodalonini	<i>Heliofugus</i>	<i>H. aconcaguensis</i> [C], <i>H. arenosus</i> [C, S], <i>H. barrosi barrosi</i> [C], <i>H. barrosi chillanensis</i> [C], <i>H. biobioensis?</i> , <i>H. bremeri</i> [C], <i>H. collaris</i> [C], <i>H. coquimboensis</i> [C], <i>H. cribriceps</i> [S], <i>H. cryptocephalus cryptocephalus</i> [C], <i>H. cryptocephalus curicoensis</i> [C], <i>H. fairmairei</i> [C], <i>H. germani</i> [C, S], <i>H. impressus cribriceps</i> [C], <i>H. impressus impressus</i> [S], <i>H. impressus punctatus</i> [C, S], <i>H. kuscheli</i> [C], <i>H. laticollis</i> [C], <i>H. laticollis colchahuensis</i> [C], <i>H. leechi leechi</i> [C], <i>H. leechi maulensis</i> [C], <i>H. neuqueni</i> [S], <i>H.</i> <i>penai ohigginsii</i> [C], <i>H. penai penai</i> [C], <i>H. proximoides</i> [C], <i>H.</i> <i>proximus proximus</i> [C], <i>H. proximus punctatosulcatus</i> [C], <i>H.</i> <i>quillotaensis</i> [C], <i>H. rossi grandepunctatus</i> [S], <i>H. rossi rossi</i> [S], <i>H. rossi valdiviensis</i> [S], <i>H. sulcatulus</i> [C], <i>H. sulcipennis</i> <i>brevipennis</i> [C], <i>H. sulcipennis sulcipennis</i> [C], <i>H.</i> <i>tenuipunctatus</i> [C], <i>H. valenciai</i> [C], <i>H. ventriosus</i> <i>nancaguensis</i> [C], <i>H. ventriosus ventriosus</i> [C], <i>H. zicsii</i> [C]
		<i>Myrmecodema</i>	<i>M. elegantula</i> [C], <i>M. freudei</i> [C], <i>M. kochi?</i> , <i>M. maritima</i> [C], <i>M. michelbacheri</i> [C], <i>M. nycterinoides</i> [C]
Tenebrioninae	Amphidorini	<i>Nycterinus</i>	<i>N. abdominalis</i> [C, S], <i>N. andinus</i> [C], <i>N. angusticollis</i> [C], <i>N. barriai</i> [C], <i>N. chango</i> [C], <i>N. coquimbensis</i> [C], <i>N. diaguita</i> [C], <i>N. genei</i> [C], <i>N. kaszabi</i> [C], <i>N. kulzeri</i> [C], <i>N. laevigatus</i> [C], <i>N. mannerheimi</i> [C], <i>N. opacus</i> [C], <i>N. quadricollis</i> [C], <i>N. rossi</i> [C], <i>N. rugiceps australis</i> [C], <i>N. rugiceps costulatus</i> [C], <i>N. rugiceps rugiceps</i> [C], <i>N. substriatus</i> [C], <i>N. thoracicus</i> [C]
	Apocryphini	<i>Apocrypha</i>	<i>A. baloghi</i> [C], <i>A. elegans</i> [C], <i>A. globosa</i> [C], <i>A. mahunkai</i> [C], <i>A. ovipennis</i> [C], <i>A. solieri</i> [C]
	Scotobiini	<i>Diastoleus</i>	<i>D. bicarinatus</i> [C], <i>D. collaris</i> [C], <i>D. girardi</i> [C]
		<i>Emmallodera</i>	<i>E. atronitens</i> [P], <i>E. coriacea</i> [P], <i>E. crenatocostata crenatocostata</i> [P], <i>E. inflatithorax</i> [P], <i>E. marginipennis</i> [P], <i>E. multipunctata curvidens</i> [P], <i>E. multipunctata multipunctata</i> [P], <i>E. nitens</i> [P], <i>E. obesa costata</i> [P], <i>E. obesa obesa</i> [P], <i>E. obesa punctipennis</i> [P], <i>E. ovata</i> [P], <i>E. rugosa</i> [P]
		<i>Leptynoderes</i>	<i>L. tuberculata</i> [P]
		<i>Scotobius</i>	<i>S. akidioides akidioides</i> [P], <i>S. akidioides bicostatus</i> [P], <i>S. alaticollis</i> [P], <i>S. ardoini</i> [P], <i>S. asperatus</i> [C], <i>S. brevipes brevipes</i> [C], <i>S. brevipes chicoanus</i> [C], <i>S. bullatus</i> [C], <i>S. caraboides</i> [P], <i>S. crenicollis</i> [C], <i>S. emarginicollis</i> [C], <i>S. gayi</i> [C], <i>S. inauditus</i> [C], <i>S. kirby</i> [C], <i>S. obscurus</i> [S, P], <i>S. punctithorax</i> [P], <i>S. rugicollis</i> [C], <i>S. rugosulus</i> [C]
	Tenebrionini	<i>Phanerops</i>	<i>P. elongata</i> [S], <i>P. unicolor</i> [C]
	Ulolomini	<i>Oligocara</i>	<i>O. cantillana</i> [C], <i>O. galvezi</i> [C, S], <i>O. intermedia</i> [C], <i>O. minor</i> [C], <i>O. moronii</i> [C], <i>O. nitidum</i> [C, S], <i>O. silvabudgei</i> [C]

Speciation rates in the Andean subregions showed a dichotomous outcome with Central Chilean ($S/G = 9.44$) and Patagonian ($S/G = 8.13$) having practically four times greater observed values of S/G than of that of Subantarctic subregion ($S/G = 2.25$). In addition, when corrected by species richness the observed S/G values in the former two subregions were significantly higher than random expectation, while S/G in the Subantarctic did not deviate of expected by chance (Fig. 2). These results indicate that S/G in Central Chilean and Patagonian subregions can be explained by forces different to that of the number of species.

Observed species richness among subregions showed a great variation, being Central Chilean the area with highest species abundance ($n = 274$), followed by Patagonian with less than half of species ($n = 122$) and finally, by the Subantarctic with practically eight times fewer species than the first subregion ($n = 36$). When we assessed by random expectations in species richness among Andean subregions, we found that Central Chilean has higher richness than expected, while richness in Patagonian did not differ of random expectations and Subantarctic has lower species richness than expected by chance (Fig. 3). These outcomes suggest that the stochastic placement of species distribution ranges were not enough explanation for the highest and lowest species richness found in Central Chilean and Subantarctic subregions respectively.

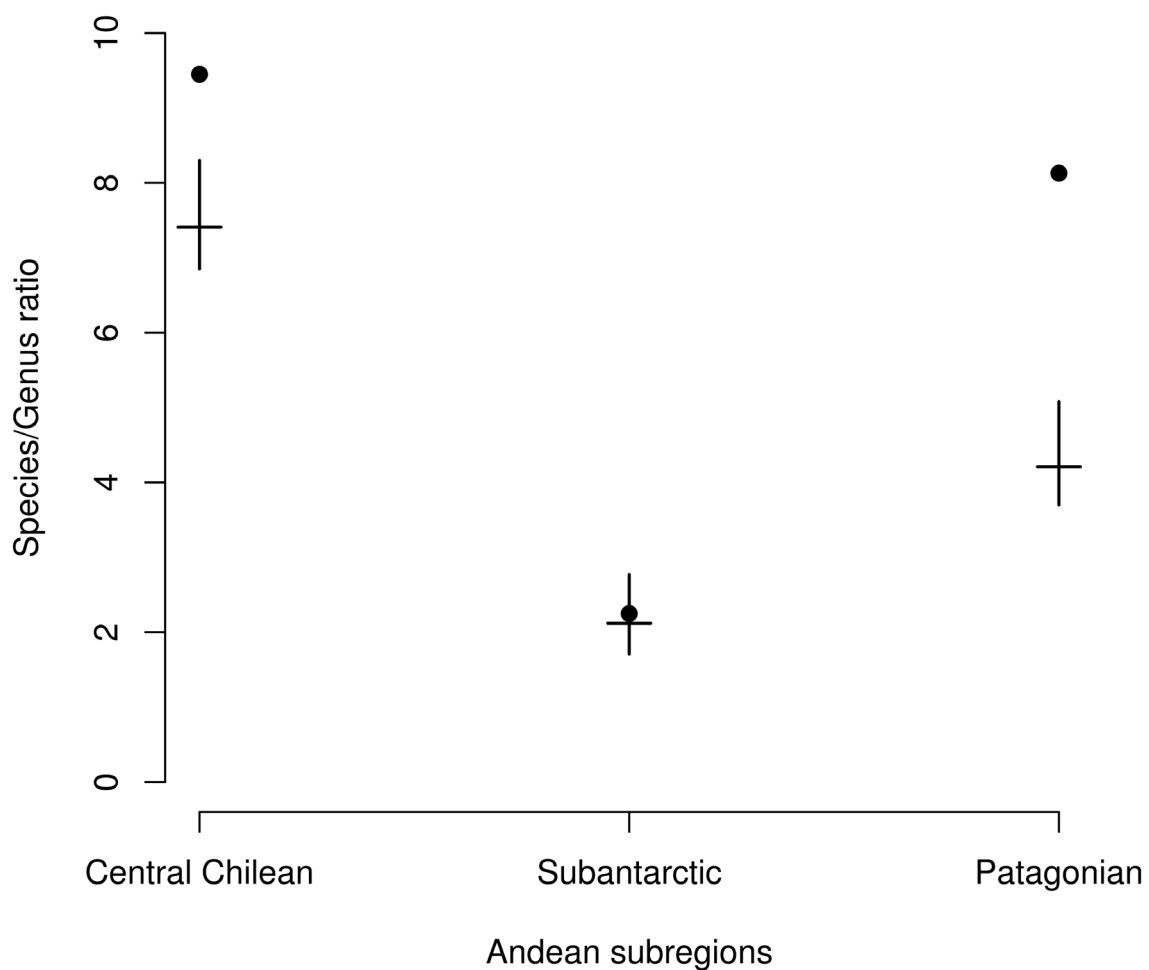


FIGURE 2. Observed and expected endemic epigeal tenebrionids species/genus ratios (S/G) on Andean subregions. Black points represent observed S/G , and bars indicate the expected S/G (horizontal), and the 95% confidence interval (vertical).

The analysis of species dispersal showed practically the absence of direct and indirect dispersal routes from Patagonian to other subregions (Table 2). Clearly, value of DD that measures dispersion from Patagonian to Subantarctic was more influenced by the differences in the number of exclusive species that these subregions have (120 for Patagonian and 34 for Subantarctic) than for the number of species that they share (of a total of 156 species only 2 inhabit both subregions). We observed the absence of dispersal routes from Patagonian to Central Chilean because these subregions did not share any species. Finally, from Subantarctic to Central Chilean we found

the highest score of DD among all dispersal routes (although still very close to zero; see Table 2). This score was strongly influenced by the differences in the number of exclusive species that these subregions harbour (259 for Central Chilean and 20 for Subantarctic) and by having the greatest number of species shared between two subregions (of a total of 295 species 16 inhabit both subregions). It should be noted that as we assessed for dispersal from Subantarctic to Central Chilean, the resulting coefficient of dispersion was negative, indicating that if dispersal has occurred it was directed from Central Chilean to Subantarctic.

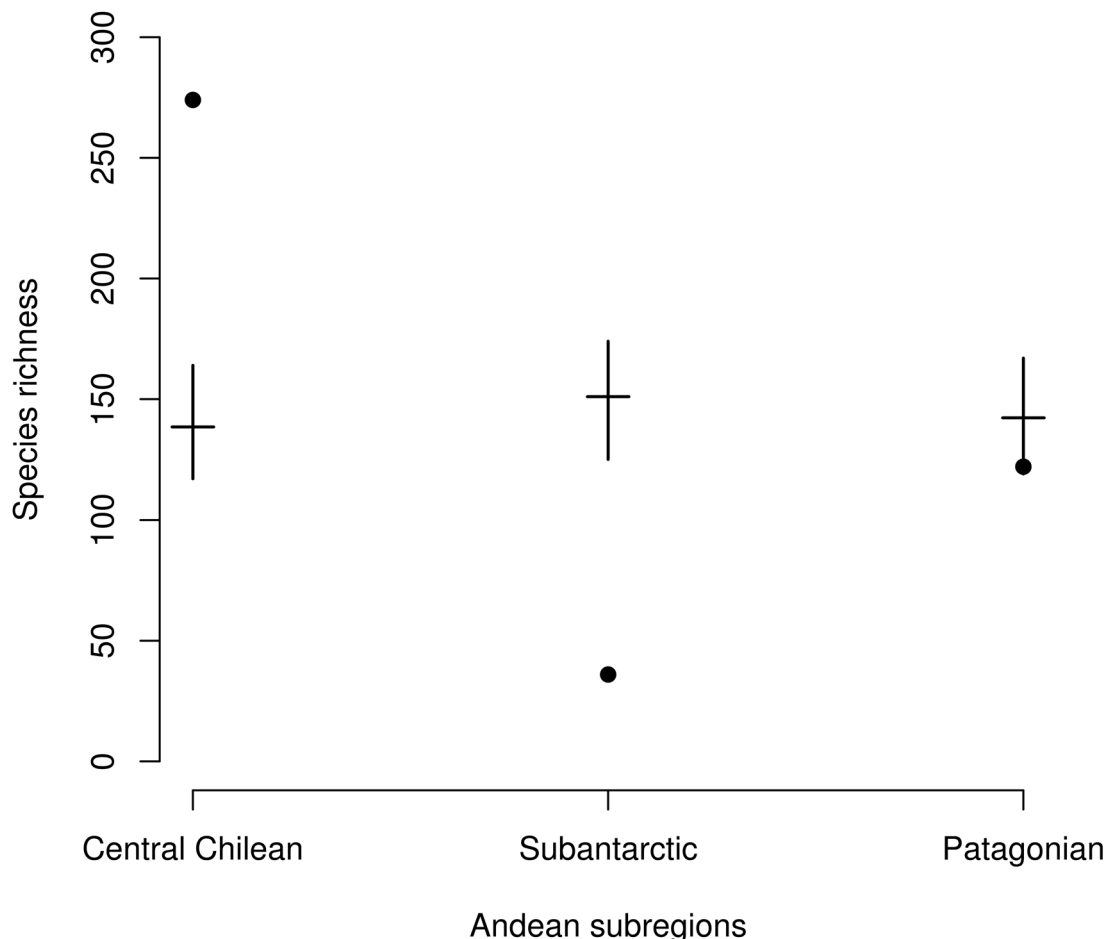


FIGURE 3. Observed and expected endemic epigean tenebrionids species richness on Andean subregions. Black points represent observed species richness, and bars indicate the expected species richness (horizontal) and the 95% confidence interval (vertical).

TABLE 2. Dispersal routes analyses between subregions. Where $x_1 \Rightarrow x_2$ indicate the expected direction of dispersal between subregions; a is the number of species shared by two subregions; b , is the number of species only found in subregions x_1 ; c , the number of species only found in subregion x_2 , and DD is the dispersal direction statistic.

$x_1 \Rightarrow x_2$	a	b	c	DD
Patagonian \Rightarrow Subantarctic	2	120	34	0,01
Patagonian \Rightarrow Central Chilean	0	122	274	0
Subantarctic \Rightarrow Central Chilean	16	20	258	-0,04

Discussion

The finding of 416 species of epigean tenebrionids endemic to the Andean region constitutes one of the first attempts, together with that of Löbl *et al.* (2008) who identified epigean and arboreal tenebrionids endemic from the Palearctic, to recognize the total number of these species restricted to an entire biogeographic region (*sensu* Morrone 2009, 2015). Considering both the taxonomic arrangement and the spatial distribution of endemic epigean tenebrionids, it was observed that subfamilies, tribes and genera are unequally distributed across subregions. For example, Nycteliini and Praociini (Pimeliinae) and Scotobiini (Tenebrioninae) were the unique tribes that occurred in the three subregions. It should be noted that these tribes are distributed mainly in arid environments of South America (Kuschel 1969; Flores 1997; Matthews *et al.* 2010; Flores *et al.* 2011; Silvestro *et al.* 2015). Other tribes of Pimeliinae distributed in arid environments of South America (Matthews *et al.* 2010) are present in Central Chilean (Physogasterini), in Central Chilean and Subantarctic (Thinobatini) and in Central Chilean and Patagonian (Trilobocarini). Within Andean region, tribes with distribution in arid environments that extend outside of South America only occur in Central Chilean or/and Subantarctic subregions but not in Patagonian: for example Apocryphini (Tenebrioninae) occurs in Central Chilean, California and Mediterranean area (Doyen & Kitayama 1980; Matthews *et al.* 2010); Elenophorini (Pimeliinae) inhabits xeric habitats in Central Chilean, Monte and Chaco (Argentina) and western Mediterranean area (Roig-Juñent *et al.* 2001; Matthews *et al.* 2010), Epitragini (Pimeliinae) inhabits in Central Chilean and in arid or semi-arid environments of North and South America (Peña 1966; Freude 1967, 1968) and Amphidorini (Tenebrioninae) which occurs in Central Chilean, Subantarctic and in arid and semi-arid environments of North America (Matthews *et al.* 2010). The tribes with pantropical distribution (Cnodalonini: Stenochinae, Stenosini: Pimeliinae, Tenebrionini and Ulomini: Tenebrioninae (Matthews *et al.* 2010), austral distribution (Adeliini: Lagriinae; Matthews 1998) as well as the widely distributed Phaleriini (Diaperinae) (Triplehorn & Watrous 1979), are also represented in Central Chilean and Subantarctic.

Regarding the genera, 12 of the 18 endemic to the Andean region are restricted to one subregion and six are shared by two subregions. For example the following are restricted to Central Chilean: *Aspidolobus*, *Auladera*, *Diastoleus*, *Gyriosomus*, *Hexagonochilus*, *Myrmecodema* and *Oligocara*; to Subantarctic: *Gondvanadelium* and *Panadelium* and to Patagonian: *Asidelia*, *Neopraocis* and *Patagonopraocis*. From the remaining 6 endemic genera, 5 are shared between Central Chilean and Subantarctic subregions: *Callyntra*, *Gyrasida*, *Heliofugus*, *Phamerops* and *Valdivium* and one, *Peltolobus*, between Central Chilean and Patagonian subregions. The 24 non endemic genera also show a differential distribution among subregions. Seven genera are distributed in Central Chilean and other World regions: *Apocrypha* Eschscholtz (Tenebrioninae) occur also in California (Doyen & Kitayama 1980); *Licinoma* Matthews is distributed also in Australia (Matthews 1998), and *Entomochilus* Solier, *Grammicus* Waterhouse, *Physogaster* Guérin-Méneville, *Psammetichus* Latreille and *Trilobocara* Solier are distributed in the South American transition zone (Bruch 1915; Kaszab 1969; Peña 1973, 1980, 1995); one genus, *Archeophthora* Kaszab is distributed in the Subantarctic subregion and also in Tasmania (Kaszab 1978), four genera are distributed in Patagonian and in the South American transition zone: *Calymmophorus* Solier, *Emmallodera* Blanchard, *Epipedonota* Solier and *Patagonogenius* Flores (Flores 1999; Flores & Vidal 2001; Flores *et al.* 2011; Silvestro & Flores 2012), and one genus, *Leptynoderes* Solier is distributed in Patagonian, the South American transition zone and in the Neotropical region (Kulzer, 1955). Four genera are shared by two subregions, Central Chilean and Subantarctic: *Discopleurus* Lacordaire, *Nycterinus* Eschscholtz, and *Thinobatis* Eschscholtz which are distributed also in the South American transition zone (Peña 1971, 1974a; Aalbu & Andrews 1996) and *Phaleria* Latreille is distributed in Central Chilean and Subantarctic and in coastal environments of the World (except Australia and the Polar areas; Triplehorn & Watrous 1979); one genus is shared between Subantarctic and Patagonian subregions: *Mitragenius* Solier which is distributed also in the south American transition zone and in the Neotropical region (Flores 1999). Three genera are shared by Central Chilean and Patagonian subregions: *Platesthes* Waterhouse which is distributed also in the South American transition zone (Flores 2004), and *Nyctelia* and *Psectrascelis* that are distributed in the South American transition zone and in the Neotropical region (Flores 1997). Two genera share their distribution ranges in the three subregions: *Scotobius* Germar and *Praocis* which are distributed in the South American transition zone and in the Neotropical region (Silvestro *et al.* 2012; Flores & Pizarro-Araya 2014). These findings suggest that processes of diversification and extinction have modelled the endemic biota among subregions because in the Central Chilean and Subantarctic, endemic epigean tenebrionids belong to a diverse number of subfamilies, tribes and genera; whilst, those of the Patagonian belong to a low number of subfamilies and tribes but a relatively high number of genera.

Results of predictions tests did not supported the Patagonian-diversification hypothesis because speciation rates were highest in both Patagonian and Central Chilean, maximum species differentiation occurred only in Central Chilean and there were no evidences of dispersal routes from Patagonian to other subregions. By the contrary, prediction results are more concordant with process of isolation that have promoted speciation by interrupting gene flow among populations and originating endemism because species can not expand their range sizes (Carrara & Flores 2013). Accordingly, different authors that have addressed studies on insect distribution patterns in the Andean region suggested that orogenic and climatic events have been factors that isolated the biota within this area. For example, Roig-Juñent & Flores (2001), Flores & Pizarro-Araya (2006), and Donato (2006), recognized that the Andean uplift was the main vicariant event that isolated both Central Chile and Subantarctic subregions from the Patagonian subregion, and Villagran *et al.* (2004) recognized that the progressive aridization of Central Chilean was the climatic event that isolated this region from the Subantarctic subregion. In agreement with these authors, we consider that these events probably have influenced processes of speciation and dispersion, and promoted maximum of species differentiation in the endemic fauna of epigeal tenebrionids within the Andean region.

In this regard, it is possible to observe that high speciation rates are strongly related with subregions that experience xeric climatic conditions (Schmida 1985). That is, Central Chilean and Patagonian, which are characterized by having relatively large desert areas (Escalante *et al.* 2009; Carrara & Flores 2013), showed that a 78% and 100% respectively of total species belong to tribes that are distributed mainly in arid or semi-arid environments of the World; while in Subantarctic, that is characterized by large humid areas (Escalante *et al.* 2009), only the 38% of total species belong to tribes distributed mainly in arid or semi-arid environments. It is suggested that deserts stimulate rapid diversification (Stebbins 1952; Raven & Axelrod 1972) because organisms shift their dispersal strategies (Schmida 1985). This fact apparently can be the case of many epigeal tenebrionids from the Andean region that have low vagility because they evolved to the flightless condition to survive in arid environments (Carrara & Flores 2013). Specifically, this low vagility may prompt speciation by reducing migration between populations (Kergoat *et al.* 2014).

The maximum of species differentiation in Central Chilean is probably linked to the existence of favourable conditions in this subregion that enabled the species to reduce their extinction risk, and therefore, accumulate species on time (Huston 1994). Two distinctive characteristics of this subregion can be related to low extinction rates in endemic epigeal tenebrionids: its floristic diversity and the antiquity of its xeric environments. Specifically, Central Chilean is a heterogeneous phylogeographic mosaic, determined by the action of a changing topographic relief that condition sun radiation, moisture and soil types (Armesto *et al.* 2007), where converge dry xerophytic vegetation with humid Neotropical and Austral elements (Villagran *et al.* 2004). Instead, the Subantarctic is a subregion dominated by humid Austral, Neotropical and Holarctic vegetation (Van der Hammen & Cleef, 1983) with absence of arid elements, and the Patagonian is an arid subregion dominated by High Andean xerophytic vegetation with absence of humid elements (Paruelo *et al.* 2005). It is widely recognized that more heterogeneous environments promoted a wide spectrum of habitats and resources that diminishes species extinction by competence, allowing the coexistence of a high diversity of species (Huston 1994). As a direct evidence of this, in Central Chilean inhabit endemic tenebrionids belonging to tribes distributed in arid environments of the World and species belonging to tribes distributed in Neotropical, Austral and Pantropical regions of the globe. By the other hand, in Subantarctic subregion most of tenebrionid species belong to tribes with wide, Pantropical or Austral distribution, while in Patagonian, as we showed above, only inhabit species belonging to tribes distributed mainly in arid or semi-arid environments. In relation to the antiquity of its xeric environments, in Central Chilean existed arid lands from the Late Triassic–Early Jurassic (Clarke 2006), implying that these environments were available to tenebrionid colonization and evolution since long time ago. In this regard, it is recognized that stable and predictable environments diminishes stochastic extinctions, allowing the accumulation of a high number of species (Huston 1994). In the other arid subregion, Patagonian, arid lands are relatively recent, from Middle to Late Miocene (Barreda & Palazzesi 2007); thus, in this subregion the time for species accumulation was lower than of Central Chilean.

The absence of endemic epigeal tenebrionids dispersal routes among subregions denote the existence of barriers that avoid that species can expand their distribution ranges. Within the Andean region, the major dispersal barrier that produced vicariance in several coleopterans was the uplift of the Andean mountain range (Roig-Juñent & Flores 2001; Flores & Pizarro-Araya 2006). The greatest phase of the Andean uplift occurred during the Middle

Miocene generating a geographical barrier of approximately 3000 meters of altitude (Roig-Juñent & Flores 2001) in the central part of the Andean region that affected the distribution of tenebrionid biota in Central Chilean and Patagonian subregions (Flores & Vidal 2000b; Flores & Roig-Juñent 2001). However, to the south, between the Subantarctic and Patagonian subregions, the Andean mountain diminishes notoriously its altitude, ceasing to be a geographical barrier for some groups of coleopterans (Roig-Juñent *et al.* 2004). But, this is not seen to be the case for endemic epigean tenebrionids that inhabit these subregions because only a scarce number of species are shared between them. Thus, other factor different of the geographical barrier caused the vicariance in these species. We consider that the differential climatic conditions of Subantarctic and Patagonian subregions acted as a barrier for species dispersal. Taking into account that in Subantarctic subregion preponderate species adapted to humid environments and that in Patagonian only inhabit species adapted to arid environments (Carrara & Flores 2013), it is probable that climate is the factor that limits to species expand their distribution.

Finally, we sustain that the full list of endemic epigean tenebrionids provided in this work has strong implications to be considered in biodiversity conservation because endemic species, by their high extinction risk, are primary target in conservation strategies (Myers 2003). As it is very uncommon to have data of species confined to a particular biogeographic regions, especially in hyperdiverse taxa (Jimenez-Valverde & Hortal 2004), this information should be included to set priority areas. Fortunately, Central Chilean and Subantarctic subregions are part of the global hotspots of biodiversity “Chilean winter rainfall-Valdivian forest” setting with priority to conserve by Conservation International (CI); while, the Patagonian subregion is part of the initiative “Global 200” setting with priority to conserve by the World Wildlife Fund for Nature (WWF). Thus, we strongly suggest that data on tenebrionids identities and distribution must be included to reinforce those areas that already are considered as a target for biodiversity conservation. In addition, as evolution of endemic epigean tenebrionids appear strongly influenced by climatic events, we consider that more research at long-term should be advocated to understand how their distribution ranges can vary under the probable global climate change.

Acknowledgements

We acknowledge Florencia Fernández Campón (IADIZA, Mendoza, Argentina) for critical reading of the manuscript and two reviewers (Marcin J. Kamiński and Warren E. Steiner) for suggestions for improving this paper. This study was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina), and by grants PIP 112-201101-00987 (CONICET, Argentina) and PICT 2013-3128 (ANPCYT).

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