

# Vicariance events shaping Southern South American insect distributions

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The main goal of this study is to use multiple insect phylogenies along with geographical information to test known vicariance hypotheses for Southern South America. We analysed the phylogenies and geographical distributions of seven insect genera endemic to southern South America using Hovenkamp's (1997) protocol, which have been in part implemented in software (vicariance inference program). Using this software, we were able to hypothesize 55 traceable vicariance events; among these, we recognized four supported vicariance events (*i.e.* confirmed by more than a single sister group). The first supported vicariance event consisted of an East/West separation of the faunas in all analysed trees; the second supported vicariance event is a North/South separation of the fauna located East of the Andes; the third supported vicariance event was found in the southernmost fauna located East of the Andes, which separates allopatric Patagonian species in a North/South direction; and finally, the fourth supported vicariance event separates in a North/South direction clades of the Central Chilean fauna located West of the Andes. Our results suggest that these four supported vicariance events could be correlated with the uplifting of the Andes and the marine incursions that occurred during the Cenozoic that is the estimated age at which these events occurred. Finally, we discuss that current software implementation of Hovenkamp's ideas need to be expanded, particularly regarding the automated selection of traceable vicariance events.

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## Introduction

The particular distribution patterns exhibited by the flora and fauna of southern South America have led to many biogeographical studies; several authors have considered this region as different from the rest of South America (Jeannel 1962; Kuschel 1964; Brundin 1966; Crisci *et al.* 1991; Morrone 2015). Furthermore, many contributions have proposed a common origin and strong relationship of this region's biota with other of austral regions such as Australia, New Zealand and South Africa (Crisci *et al.* 1991; Roig-Juñent 2000; Ronquist & Sanmartin 2011). Additionally, there are numerous biogeographic studies focused on the endemic taxa of southern South America explaining present distributional patterns within this region

(Morrone *et al.* 1994; Roig-Juñent 1994, 2004; Domínguez *et al.* 2006; Donato 2006; Roig-Juñent *et al.* 2007).

Much of the recent work on biogeographical hypotheses explaining distributional patterns in southern South America is based on biogeographical methodologies that imply the replacement of the species cladogram by an area cladogram, where the terminal taxa are usually substituted by the area of endemism that they are known (or assumed) to occupy. In this study, we were interested in applying Hovenkamp's (1997) alternative approach, which instead of being centred on the search of the relationships among areas focuses on the recognition of barriers separating biotas and the proposition of the sequence of these vicariance events. Hovenkamp's (1997, 2001) methods have been

considered ostracized (Fattorini 2008); yet, the vicariance inference program (VIP) (Arias 2010; Arias *et al.* 2011) based on Hovenskamp's (1997, 2001) principles has renewed the interest on this method. This program hypothesizes vicariance events by recognizing allopatric sister pairs of taxa within the clades in a phylogeny; and does so directly from the distributional data (point data) of the analysed taxa (*i.e.* comparable to the direct method of Hovenskamp 2001). The VIP (Arias *et al.* 2011) has been used in studies dealing with the reconstruction of taxon history (*e.g.* Van der Merwe 2011; Ferretti *et al.* 2012; Gaetano & Rougier 2012; Latinne *et al.* 2012; Molineri & Salles 2013; Teixeira *et al.* 2013). Nevertheless, this is the first time that the VIP (Arias *et al.* 2011) is used to search for congruent vicariance events among multiple insect taxa in a large biogeographical region such as southern South America. All previous phylogenetic and biogeographic studies undertaken with the taxa included in this study (Flores & Pizarro-Araya 2006; Roig-Juñent *et al.* 2008; Vera *et al.* 2012) suggest that they were present before the Andean uplift. These studies also suggest that the Andes orogeny along with the subsequent climate changes provoked by this uplift affected the distribution of these genera. In these studies, three events are the most commonly used hypotheses to explain the pattern of distribution of the genera included in this study: the Andes orogeny, the progressive desertification of the eastern side of the Andean mountains and the formation of high-altitude grasslands and other montane habitats (Roig-Juñent & Flores 2001; Flores & Pizarro-Araya 2006; Domínguez *et al.* 2009). However, in this study we also expect to find other possible vicariance events, previously proposed for this area and this time frame.

The main aim of this contribution is to implement the protocol established by Hovenskamp (1997), to search for the existence of common vicariant events among these groups of insects as well as to hypothesize their temporal sequence and to compare our results with previous studies.

## Materials and methods

### Taxa analysed

We selected seven genera of insects, grouped in four monophyletic clades with sympatric distributions endemic to southern South America. These insects belong to the order Coleoptera (Carabidae and Tenebrionidae) and to the order Phasmatodea. These monophyletic groups are not closely related to each other. They are conspicuous insects, of large size and flightless (and hence with reduced dispersal power). These groups and the outgroups of each phylogeny comprise 87 species (Fig. 1A–D). We used the following phylogenies for each genus; for the carabid beetles *Baripus* Dejean: Roig-Juñent (1995), for the five tenebrionid beetle genera that account for two phylogenies:

(i) *Epipedonota* Solier + *Callyntra* Solier in Flores & Vidal (2000a) and Flores & Roig-Juñent (2001) (where *Callyntra* that was previously included within *Epipedonota* was revalidated by Flores & Vidal 2000b and hypothesized to be the sister group of *Epipedonota* by Flores 2000), and (ii) *Mitragenus* Solier + *Patagonogenius* Flores + *Auladera* Solier: Flores (1999). Finally, for the Phasmatodea genus *Agathemera* Stål: Vera *et al.* (2012).

All cladograms were rooted by their sister group (as selected by the original authors) as follows: *Baripus* (rooted by *Bembidiomorphum convexum* Champion), *Callyntra* + *Epipedonota* (rooted by *Nyctelia nodosa* Germar), *Auladera* + *Patagonogenius* + *Mitragenus* (rooted by *Scelidospecta lobata* (Burmeister)), and finally, *Agathemera* rooted by *Anisomorpha buprestoides* (Stoll).

### Databases

We obtained 1882 georeferenced distributional data points for all the collected specimens of each of the species in all genera from a database of Patagonian Insects (Proyecto Yamana), from the “Ecotono Laboratory” (CRUB, UNC) (Dr P. Sackmann); except for the genus *Agathemera* for which we used Domínguez *et al.* 2009, and the data for *Anisomorpha buprestoides* (Stoll), (3 records) were provided by Texas A&M University Insect Collection (Accessed through GBIF Data Portal, data.gbif.org 2012-05-22).

### Biogeographic analyses

The first step of Hovenskamp's (1997) protocol is to hypothesize a traceable vicariance event (TVE) or a node of which both descendants occupy mutually exclusive areas. We used the VIP (Arias 2010; Arias *et al.* 2011) to search for possible TVEs. The analyses with the VIP were performed using a grid of  $0.3 \times 0.3$  degrees, with the Von Neumann neighbourhood option, and we did not use the maximum fill option (the fill is the number of cells around the record to be counted as presences). Parameters for searches were set to 5 as cost of removal, allowing 25% of maximum overlap, and we did not use the partial removal option (this option sets a cost to the partial distribution removal). The search was performed allowing 500 iterations, keeping 10 reconstructions per iteration. Barriers were represented by mid-triangles.

The second step is the extraction of the historical information, specifying the temporal relation of each vicariance event to other vicariance events. This is achieved by noting the order in which the TVEs occur in all the analysed cladograms.

The third step is to search for independently confirmed, non-contradictory TVEs that will be proposed as supported vicariance events (SVEs). To determine the degree of congruence among TVEs, we searched for similar

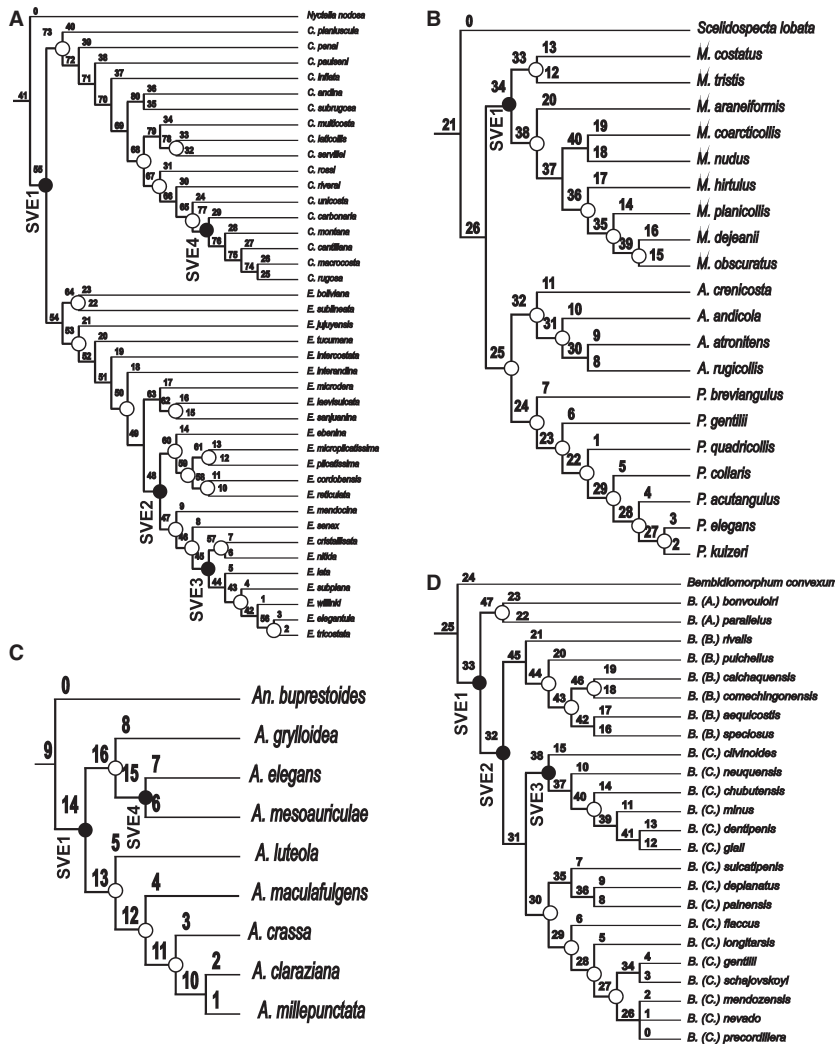


Fig. 1—(A) Cladograms of *Epipedonota* Solier + *Callyntra* Solier; (B) *Patagonogenius* Flores + *Auladera* Solier + *Mitragenius* Solier; (C) *Agathemera* Stål; (D) *Baripus* Dejean. Traceable vicariance events (TVEs) are marked as ○, and TVEs considered in supported vicariance events (SVEs) are marked as ●. C. = *Callyntra*; E. = *Epipedonota*; M. = *Mitragenius*; A. = *Auladera*; P. = *Patagonogenius*; An. = *Anisomorpha*; A. = *Agathemera*; (B.) = *Baripus*; (A. = *Arathymus*); (C.) = *Caridiophthalmus*.

vicariance events and for similarity in the areas occupied by the vicariant clades. Hovenkamp (1997) considered that for two TVE nodes to be grouped, it is not necessary for the area sets on each side of the nodes to be completely identical; however, an overlap between the area sets on both sides of the nodes must exist.

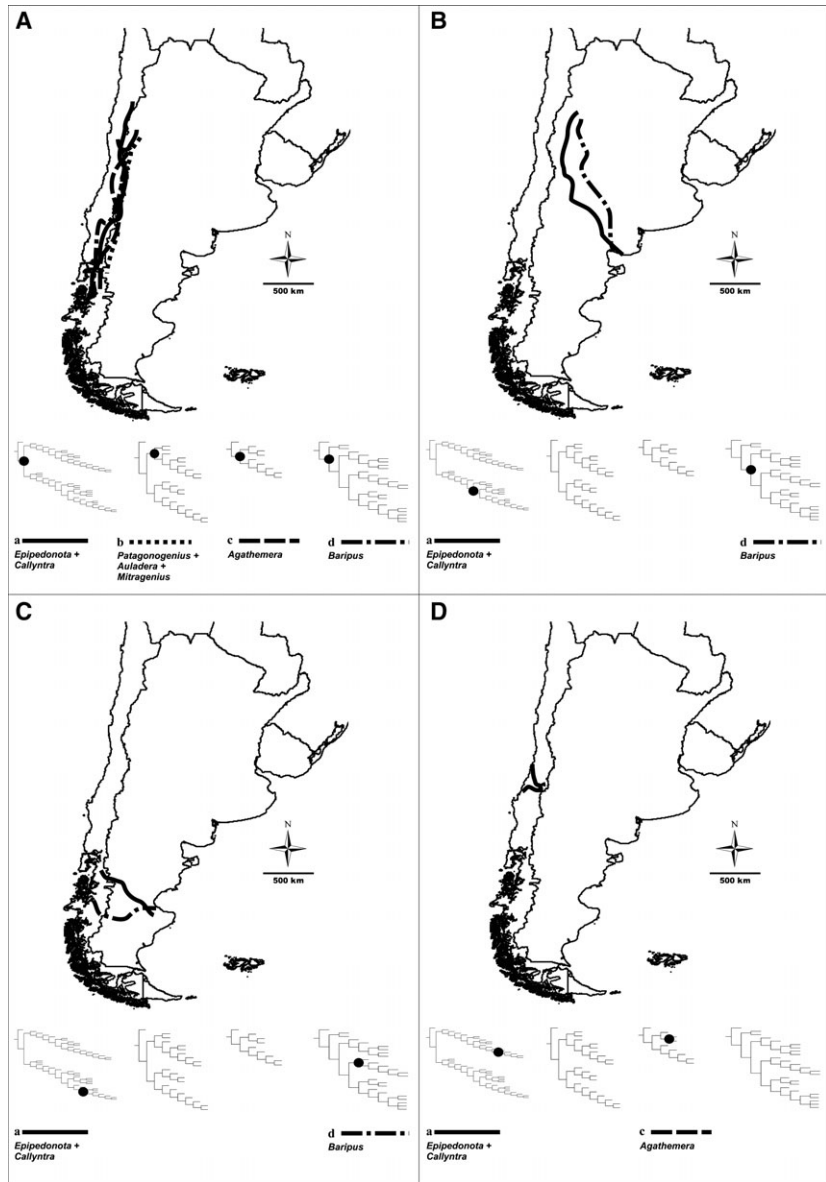
The last step is to order the supported vicariance events into a temporal sequence (Hovenkamp 1997): *on the basis of the relative ordering of the cladogram nodes, the SVEs can be ordered in directed pairs or series, corresponding to all the directed pairs or series extracted from the cladograms*. Based on the sequences of SVEs, these can then be arranged in a single sequence, which complies with all individual sequences (Hovenkamp 1997). Minimum convex polygons were used to summarize the TVEs within each SVE. Figure 3 was made with a map from Natural Earth, free vector and raster map data @naturalearthdata.com. Base map used for

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**Results**

The search for TVEs in each phylogeny performed with VIP resulted in 22 (*Epipedonota* + *Callyntra*), 15 (*Patagonogenius* + *Auladera* + *Mitragenius*), six (*Agathemera*) and 12 (*Baripus*) TVEs (Fig. 1; Supporting Information).

The comparison of these TVEs yielded four SVEs (Figs 1–3): the first SVE (SVE1, Figs 1, 2A and 3) consists of an East/West separation of the fauna in all analysed trees, which coincides with the southern Andean Mountain range. In (*Epipedonota* + *Callyntra*), it was hypothesized at node 55; in *Patagonogenius* + *Mitragenius* + *Auladera* at



**Fig. 2** —(A) TVEs considered in SVE1; (B) TVEs considered in SVE2; (C) TVEs considered in SVE3; (D) TVEs considered in SVE4. TVE = traceable vicariance events; SVE = supported vicariance event.

node 34, which groups *Mitragenius tristis* Kulzer + *M. costatus* Kulzer; at node 14 in *Agathemera*, which separates all Chilean species from Argentinean (except for *A. millepunctata* Redtenbacher and *A. maculafulgens* Camousseight which are distributed in both countries); and in the genus *Baripus*, this event was hypothesized at node 33, which separates the subgenera *B. (Arathymus)* Guerin-Meneville and *B. (Cardiophthalmus)* Curtis.

The second SVE (SVE2, Figs 1, 2B and 3) is a North/South diagonal separation of the fauna located at the East of the Andes. This barrier is roughly located at the line that connects the Atlantic southern coast at 41° S at Buenos Aires province with the Andes at 28° S in the northern part of San Juan province, separating the austral (Patago-

nian) region of southern South America from its most Meridional or northern or neotropical region. It was hypothesized in *Epipedonota + Callyntra* at node 48 and at node 32 in *Baripus*.

The third SVE (SVE3, Figs 1, 2C and 3) was hypothesized in the southernmost fauna located East of the Andes, which separates in a North/South direction clades of allopatric Patagonian species from the Atlantic coast at 46° S to the Andes at 43° S. SVE 3 was hypothesized and in *Epipedonota + Callyntra* at node 45, and in *Baripus* at node 38.

Finally, the fourth SVE (SVE4, Figs 1, 2D and 3) separates in a North/South direction the Chilean fauna located West of the Andes, from the Pacific coast to the Andes at



**Fig. 3** Minimum convex polygons summarizing TVEs considered in SVE1-4. TVE = traceable vicariance events; SVE = supported vicariance event.

34°–36° S. This SVE separates groups of allopatric species that occupy the Chilean central valley region. This SVE was hypothesized at node 77 in *Epipedonota* + *Callyntra* and in *Agathemera* at node 15.

### Discussion

The VIP allows the visualization of the barriers separating clades or individual taxa with allopatric distributions, and the localization of the events in the cladograms. The individual TVEs can be spatially compared following Hovenvkamp (2001) to hypothesize whether they are signalling the same vicariance event and their chronological order.

The first vicariance event or SVE1 appears in all four of the analysed cladograms and it is therefore the best supported. The TVEs supporting this SVE are located at the

base of the four cladograms (Figs 1 and 2A). This SVE can be clearly related to the Andean mountain ridge, which according to the Flores & Roig-Juñent (2001) split the ancestral stock of *Callyntra* and *Epipedonota* species (Figs 1A and 2A). In *Mitragenius*, *Patagonogenius* and *Auladera* (Figs 1B and 2A), SVE1 splits the Chilean *M. costatus* and *M. tristis* from the remaining *Mitragenius* distributed in Argentina. This pattern could resemble that of *Callyntra* and *Epipedonota*, because once these lineages separated each on one side of the mountain range, they never came into contact again (Roig-Juñent & Flores 2001), contrary to what has been proposed for the genus *Agathemera*. This genus of Phasmatodea, according to the analysis of Vera *et al.* (2012), supported the hypothesis of the vicariance effect of the Andes range on the diversification of the

species, acting on both slopes since the first bifurcation of the lineages (Figs 1C and 2A). Vera *et al.* (2012) proposed that both lineages at each side of the Andes Mountain ridge appear to have evolved from a common ancestor present at each respective side. Vera *et al.* (2012) also proposed that *A. crassa* (Blanchard) would have originated from an ancestor on the eastern side and dispersed to the western slopes of central Chile, arguing that this scenario for *A. crassa* is reasonable, as the Andes range is not an insurmountable barrier for *Agathemera*.

The correlation of SVE1 with the uplift of the Andes allowed us to estimate the chronological order of the remaining SVEs. Nevertheless, to properly estimate what other known vicariance event can be inferred from the remaining SVEs, it is important to estimate a reasonable temporal frame in which the Andes mountain ridge began to act as an effective barrier. Although the uplift of the Andes began in the Inca Phase in the Late Eocene, the entire process occurred in several phases (Ortiz-Jaureguizar & Cladera 2006). Extant evidence shows that the initial uplifting phases of the Andes did not constitute a barrier, since the vertebrate fauna of Patagonia was in contact with that of central Chile and was very similar (Flynn *et al.* 2003; and references therein). Later, in mid-Miocene and Pliocene–Pleistocene uplifting phases were the most important in the formation of the current landscape. The phase in which the Andes reached the necessary height to constitute a barrier (approximately 3000 m.a.s.l.) occurred during mid-Miocene (11–15 Myr ago) and is known as the Quechua phase (Ortiz-Jaureguizar & Cladera 2006). Therefore, it is feasible to estimate this time frame for SVE1 with the remaining three SVEs occurring subsequently [single sequence of events complying with all individual sequences, as described by Hovenkamp (1997) in Fig. 3].

SVE2 and SVE3, which occurred after SVE1, cannot be correlated to any geological structure that could be considered a barrier as currently observed; nevertheless, paleogeographical studies have detected the occurrence of series marine incursions at the East of the Andes (Del Rio 2000). In this regard, the late Neogene was a time of very active diastrophism, as well as a time of increased frequency of relative global sea-level changes (Haq *et al.* 1987). Both phenomena appear to be tightly connected to each other and tied to the complex causes of the wide swings and cyclicity of the Late Neogene climates (Iglesias *et al.* 2011; and references therein). Marine incursions or epicontinental seas occurred for South America during the Miocene (Donato 2006). The largest marine incursion occurred after the Quechua phase, the Chasiquense (11–9 Myr ago), covering most of Argentina, in northern Patagonia and the Chaco–Pampean plains up to the sub-

Andean hills and north-western Pampean hills. This incursion was followed by the incursion known as the Paraná formation (9.11 and 9.55 Myr ago), which was cyclic during the Miocene (Pascual & Bondesio 1982). Therefore, these latter marine incursions could be related with SVE2 and SVE3, yet more evidences are needed to support this hypothesis.

With respect to SVE4, it was not possible to correlate any vicariance event after the Quechua phase in this region of Chile. It has been proposed that the Central valley of Chile (between 28° S and 33° S) suffered a fragmentation because of the segmentation of the Nazca plate (Uliana & Biddle 1988); but although this process accompanied the uplift of the Andes and occurred after SVE1, it took place north of the TVE proposed in our analysis.

Finally, we would like to mention that although the VIP software allowed us to hypothesize TVEs, the third step in Hovenkamp's protocol (the search for independently confirmed, non-contradictory TVEs to be proposed as SVEs) has not yet been implemented in VIP, or in any other software. For this contribution, we deal with this issue evaluating each TVEs qualitatively (*i.e.* following Hovenkamp's protocol). The automation of this step would be most welcomed. Such implementation, in addition to the use of explicit congruence criteria to conflate TVEs barriers into likely SVEs, would make these analyses unambiguously repeatable, thus enabling the complete use of Hovenkamp's protocol computationally. In spite of this limitation, the VIP allowed us to complete the analysis of these four phylogenies in search of vicariant events that affected the distribution patterns of these Southern South American insects, which support previous biogeographical studies for the region.

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### Supporting Information

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

**Data S1.** Fifty-five TVEs for the four analysed phylogenies, obtained with the VIP.