

# Evolutionary biogeography of South American weevils of the tribe Naupactini (Coleoptera: Curculionidae)

M. Guadalupe del Río<sup>1,2\*</sup>, Juan J. Morrone<sup>3</sup> and Analia A. Lanteri<sup>1,2</sup>

<sup>1</sup>División Entomología, Facultad de Ciencias Naturales y Museo, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque, 1900 La Plata, Argentina, <sup>2</sup>CONICET-Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina, <sup>3</sup>Departamento de Biología Evolutiva, Facultad de Ciencias, Museo de Zoología 'Alfonso L. Herrera', Universidad Nacional Autónoma de México (UNAM), 04510 Mexico City, Mexico

## ABSTRACT

**Aim** Naupactini are highly diverse weevils, widespread in the Neotropical region. Their evolution may have been driven by geological and environmental changes. Our main goals were to explain the biotic diversification of this tribe in South America and to test previous hypotheses on the relationships between distribution areas.

**Location** Neotropical South America.

**Methods** We compiled geographical records for 165 species of South American Naupactini. We then applied a track analysis and a parsimony analysis of paralogy-free subtrees to obtain generalized tracks and a general area cladogram, respectively.

**Results** We retrieved 11 generalized tracks that coincided broadly with biogeographical areas of Neotropical South America: Northern Venezuelan, Galápagos Islands, Ecuadorian, Yungas, Cerrado, Caatinga, Puna+Pacific coastal deserts, Chacoan, Atlantic+Parana forests, Monte and Pampean. The single general area cladogram obtained showed the following topology: ((Northern Venezuelan–Ecuadorian) (Galápagos Islands–Puna+Pacific coastal deserts) (Yungas (Cerrado (Monte (Pampean (Chacoan–Atlantic+Parana forests)))))).

**Main conclusions** The general patterns identified agree with biogeographical provinces of modern regionalizations, assumed to have been caused by vicariance. These biogeographical units form two main components, one from north-western South America and the other from south-eastern South America, separated by the barrier of the Andean cordillera. The absence of other discernible geological barriers and the influence of the Plio-Pleistocene cycles make it difficult to elucidate the historical relationships between most forest areas and nearby open areas of South America. These observations indicate that the taxa under consideration underwent dispersal at different times, contributing to complex biogeographical patterns.

## Keywords

Area relationships, general area cladogram, historical biogeography, Neotropical region, South America, tracks, weevils.

\*Correspondence: M. Guadalupe del Río, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque, 1900 La Plata, Argentina.  
E-mail: gdelrio@fcnym.unlp.edu.ar

## INTRODUCTION

Biogeographical analyses integrating both forest and open biomes of South America are uncommon (e.g. Costa, 2003; Sigris & Carvalho, 2009; Pires & Marinoni, 2010; Morrone, 2014a), even though South American forests support high levels of biodiversity and suffer the most severe deforestation in the world (Laurence, 1999). We have undertaken a

preliminary evolutionary biogeographical analysis of South America based on records of a group of broad-nosed weevils, the tribe Naupactini (Coleoptera: Curculionidae), which includes more than 600 species and 65 Neotropical genera (O'Brien & Wibmer, 1982; Wibmer & O'Brien, 1986). Its highest species richness is found in South America, followed by Mexico and Central America, but the fauna of these areas is still poorly known (Rosas-Echeverría *et al.*, 2011).

Naupactini are highly diverse in forests and xeric woodlands, and, to a lesser extent, in grasslands, being mainly associated with angiosperms, especially Fabaceae (Lanteri *et al.*, 2002, 2013a). Adults feed on the green parts of the plants, and larvae on the roots. Some have become agricultural pests, particularly in countries of Africa, Europe, Asia and Australasia, where they have been introduced along with different crops (Lanteri *et al.*, 2013b).

Our main objective was to propose a biogeographical scenario for the Naupactini, contributing to our understanding of their diversification in South America, and to generate hypotheses for their distribution and evolution. To achieve this goal, we undertook track and cladistic biogeographical analyses (Morrone, 2009). Track analysis emphasizes the importance of the spatial or geographical dimension of biodiversity for understanding evolutionary patterns and processes (Craw *et al.*, 1999). Cladistic biogeographical analysis assumes a correspondence between phylogenetic relationships and area relationships, and the resulting general area cladograms represent hypotheses on the biogeographical history of the taxa analysed (Parenti & Ebach, 2009).

## MATERIALS AND METHODS

### Taxa and geographical records

We compiled distribution data for about 12,000 specimens belonging to 165 species and 32 genera of Naupactini weevils: *Acyphus* (1 species), *Alceis* (1), *Amitrus* (3), *Amphideritus* (5), *Aramigus* (2), *Asymmathetes* (2), *Atrichonotus* (6), *Brachystylodes* (2), *Briarius* (1), *Cyphopsis* (1), *Cyrtomon* (5), *Enoplopactus* (4), *Ericydeus* (4), *Eurymetopus* (6), *Galapaganus* (8), *Hadropus* (1), *Hoplopactus* (1), *Leschenius* (1), *Litostylodes* (1), *Litostylus* (1), *Macrostylus* (6), *Naupactus* (65), *Pantomorus* (15), *Parapantomorus* (2), *Platyomus* (9), *Priocyphus* (1), *Symmathetes* (1), *Teratopactus* (6), *Thoracocyphus* (1), *Trichocyphus* (1), *Trichonaupactus* (1) and *Wagneriella* (1). For the scientific names we followed Wibmer & O'Brien (1986), Bordón (1991, 1997) and Alonso-Zarazaga & Lyl (1999). Most of the geographical records were derived from taxonomic contributions and studies on potential geographical distributions of parthenogenetic species published by the authors of this paper (Lanteri, 1982, 1984, 1985, 1989, 1990a,b,c, 1992, 1995a, 2004; Lanteri & Loíacono, 1990; Lanteri & O'Brien, 1990; Bordón, 1991, 1997; Lanteri *et al.*, 1991, 2013b; Morrone & Lanteri, 1991; Lanteri & Diaz, 1994; Lanteri & Marvaldi, 1995; Lanteri & del Río, 2003, 2005, 2006a,b; del Río *et al.*, 2006, 2012; del Río & Lanteri, 2011; Guzmán *et al.*, 2012). We added other geographical records from specimens collected and/or examined subsequent to previous publications and deposited in different entomological collections (for information on voucher specimens see [http://www.museo.fcnym.unlp.edu.ar/uploads/docs/georreferencias\\_naupactini.pdf](http://www.museo.fcnym.unlp.edu.ar/uploads/docs/georreferencias_naupactini.pdf)). The specimens used for the analyses were georeferenced using gazetteers available at <http://www.diva-gis.org>. Geographical coordinates were

expressed in decimal degrees. The file containing this information is available at the web site mentioned above. Specimens of uncertain identity or provenance were excluded from the analysis. Species from Amazonia and northern South America were under-represented in the analyses because of the lack of collections and modern taxonomic revisions.

### Biogeographical methods

#### Track analysis

Localities for each species were plotted on maps using DIVA-GIS 7.5 (Hijmans *et al.*, 2012) and then connected by their geographical proximity, applying the minimum spanning tree method manually to draw individual tracks (Craw *et al.*, 1999; Morrone, 2009). Generalized tracks were obtained by superimposing the individual tracks manually and then characterized following Morrone's (2014b) biogeographical regionalization. We considered a species to support a given generalized track even if a small fraction of the corresponding points fell outside the area defined by that track.

#### Cladistic biogeographical analysis

We considered 10 areas of South America (Fig. 1) that were previously identified based on track analysis (Fig. 2). These areas corresponded to the biogeographical units resulting from the regionalization of the Neotropical region proposed by Morrone (2014b). Some of them were consistent with biogeographical provinces (Galápagos Islands, Cerrado, Yungas, Monte, Chacoan and Pampean) and others extended over two or three provinces of Morrone's scheme (Ecuadorian, Northern Venezuelan, Atlantic+Parana forests and Puna+Pacific coastal deserts). Ecuadorian includes Western Ecuador, Cauca and Paramo provinces; Northern Venezuelan includes the Guajira and Venezuelan provinces; Atlantic+Parana forests includes these two provinces plus the *Araucaria* forest province; and Puna+Pacific coastal deserts includes Atacama, Desert and Puna provinces. Although the track analysis allowed us to identify the Caatinga, this area was not represented in the general area cladogram because there was no phylogenetic information on the Naupactini from this biogeographical unit.

Assessment of the taxonomic distributions over a certain area or areas was carried out using DIVA-GIS 7.5 (Hijmans *et al.*, 2012) with the shapefile generated by Lowenberg-Neto (2014). A parsimony analysis of paralogy-free subtrees was used to construct a general area cladogram(s) (Nelson & Ladiges, 1996; Morrone, 2014a). A cladistic biogeographical analysis comprises three basic steps: (1) construction of taxon–area cladograms based on selected taxon cladograms; (2) resolution of problems as a result of widespread taxa, redundant distributions and missing areas; and (3) construction of a general area cladogram (Morrone, 2009; Parenti & Ebach, 2009).



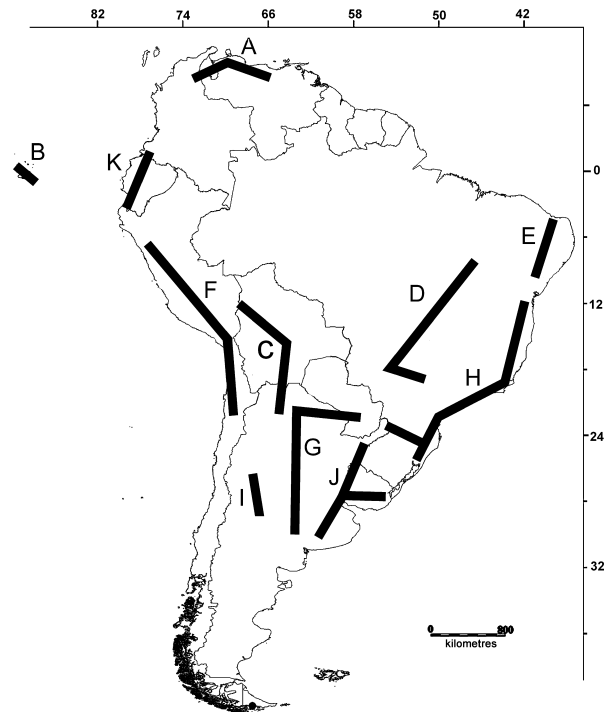
**Figure 1** A map of South America showing the areas considered in biogeographical analyses of weevils of the tribe Naupactini. (A) Northern Venezuelan, (B) Galápagos Islands, (C) Yungas, (D) Cerrado, (E) Caatinga, (F) Puna+Pacific coastal deserts, (G) Chaco, (H) Atlantic+Parana forests, (I) Monte, (J) Pampean and (K) Ecuadorian.

Ten taxon cladograms (Lanteri & Morrone, 1991, 1995; Lanteri, 1992, 1995a,b; Normark & Lanteri, 1998; del Río *et al.*, 2006; del Río, unpublished data; Lanteri *et al.*, 2010) including about 100 species of Naupactini were used to obtain taxon–area cladograms. The paralogy-free subtrees were constructed manually from the taxon–area cladograms by eliminating areas duplicated or redundant in the descendants of each node after applying the transparent method (Ebach *et al.*, 2005) and then checked with LISBETH (Zaragüeta-Bagils *et al.*, 2012). The components retrieved from the paralogy-free subtrees were used to generate a data matrix of areas by components (see Appendix S1). This data matrix was analysed under maximum parsimony with TNT (Goloboff *et al.*, 2008) using equal weights, 100 replications, tree bisection–reconnection (TBR) and holding 10 trees per replication, to obtain a general area cladogram.

## RESULTS

### Track analysis

The overlap of the 165 individual tracks (see Appendix S2) produced 11 generalized tracks (Table 1, Fig. 2). They were



**Figure 2** Eleven generalized tracks obtained from 165 individual tracks of Naupactini species in a study of the evolutionary biogeography of South American weevils of the tribe Naupactini: (A) Northern Venezuelan, (B) Galápagos Islands, (C) Yungas, (D) Cerrado, (E) Caatinga, (F) Puna+Pacific coastal deserts, (G) Chacoan, (H) Atlantic+Parana forests, (I) Monte, (J) Pampean and (K) Ecuadorian.

partially coincident with biogeographical provinces of the Neotropical region, especially from the Chacoan and Parana dominions and the South American transition zone. No tracks could be recovered from Amazonia and other smaller biogeographical units, probably because of the low number of geographical records available. The biogeographical units corresponding to each track are briefly characterized below according to Cabrera & Willink (1973), Morrone (2006, 2014b) and Roig-Juñent *et al.* (2006).

*Northern Venezuelan track:* extends along the coastal cordilleras of Venezuela and is dominated by cloud forests. It is supported by 11 species (see Appendix S2: Figs S30a, S32d, S33d, S34c, S35c, S36a, S37a, S38a, S39a, S40a, S41a).

*Galápagos Islands track:* in the Galápagos archipelago, located in the Pacific Ocean about 1000 km off Ecuador, with habitats ranging from xeric coastal areas to more humid Scalesia forests and fern zones in the highest islands. This track is supported by five species endemic to the archipelago (see Appendix S2: Figs S36c, S38b,c, S39b, S40b).

*Yungas track:* extends through Bolivia and north-western Argentina, along the cloud forest and seasonal dry montane forest of the Yungas. It is supported by 11 species (see Appendix S2: Figs S1b, S2b, S3d, S5c, S7a, S12a, S13a, S15b, S19a, S25a, S30c).

**Table 1** The species supporting each of 11 generalized tracks obtained in a study of the evolutionary biogeography of South American weevils of the tribe Naupactini, and the biogeographical provinces where those tracks were located.

Generalized track	Biogeographical province	Species supporting each track
Northern Venezuelan	Guajira and Venezuelan	<i>Ericydeus nigropunctatus</i> , <i>Hoplopactus pavidus</i> , <i>Macrostylus pittieri</i> , <i>M. uliani</i> , <i>M. avilensis</i> , <i>M. litoralis</i> , <i>Naupactus litoris</i> , <i>N. annae</i> , <i>N. llanensis</i> , <i>N. vilmae</i> , <i>N. venezolanus</i>
Galápagos Islands	Galápagos Islands	<i>Galapaganus collaris</i> , <i>G. darwini</i> , <i>G. vandykei</i> , <i>G. galapagoensis</i> , <i>G. ashlocki</i>
Yungas	Yungas	<i>Brachystylodes pilosus</i> , <i>B. rotundatus</i> , <i>Ericydeus argentinensis</i> , <i>Naupactus ambitiosus</i> , <i>N. argentinensis</i> , <i>N. bridgesi</i> , <i>N. denudatus</i> , <i>N. hirsutus</i> , <i>Pantomorus minutus</i> , <i>P. similis</i> , <i>Parapantomorus quatuordecimpunctatus</i>
Cerrado	Cerrado	<i>Naupactus albopunctatus</i> , <i>N. ambiguus</i> , <i>Pantomorus setarius</i> , <i>P. carinirostris</i> , <i>Teratopactus elegans</i> , <i>T. capucinus</i> , <i>T. tuberculatus</i> , <i>Thoracocyphus denticollis</i>
Caatinga	Caatinga	<i>Cyphopsis clathrata</i> , <i>Pantomorus bondari</i> , <i>P. glaucus</i>
Puna+Pacific coastal deserts	Puna, Atacama and Desert	<i>Amitrus mundus</i> , <i>A. alutaceus</i> , <i>A. nitens</i> , <i>Amphideritus puberulus</i> , <i>A. tomentosus</i> , <i>A. leporinus</i> , <i>A. chilensis</i> , <i>Galapaganus squamosus</i> , <i>Trichocyphus formosus</i>
Chacoan	Chaco	<i>Acyphus renggeri</i> , <i>Atrichonotus convexifrons</i> , <i>Cyrtomon ovalipennis</i> , <i>Enoplopactus ortizi</i> , <i>E. brunneomaculatus</i> , <i>Naupactus cyphoides</i> , <i>N. sulphurifer</i> , <i>N. bruchi</i> , <i>N. argentatus</i> , <i>N. peregrinus</i> , <i>Pantomorus obrieni</i> , <i>P. humilis</i> , <i>P. setulosus</i> , <i>Wagneriella lineata</i>
Atlantic+Parana forests	Atlantic, Parana and Araucaria forests	<i>Alceis longimanus</i> , <i>Briarius augustus</i> , <i>Cyrtomon gibber</i> , <i>C. luridus</i> , <i>Eurymetopus bucki</i> , <i>Hadropus albiceris</i> , <i>Macrostylus ocellatus</i> , <i>M. micaceus</i> , <i>Naupactus ancora</i> , <i>N. suturalis</i> , <i>N. transversus</i> , <i>N. serenus</i> , <i>N. polliger</i> , <i>N. condecoratus</i> , <i>N. rivulosus</i> , <i>N. versatilis</i> , <i>N. decorus</i> , <i>N. delicatulus</i> , <i>N. bipes</i> , <i>N. bellus</i> , <i>N. curvilineus</i> , <i>N. dapsilis</i> , <i>N. navicularis</i> , <i>N. latifrons</i> , <i>N. curtus</i> , <i>N. dissimilis</i> , <i>N. ochreonotatus</i> , <i>Platyomus besckei</i> , <i>P. piscatorius</i> , <i>P. periepidus</i> , <i>P. nodipennis</i> , <i>Symmalthetes kollari</i> , <i>Teratopactus gibbicollis</i> , <i>T. vittatus</i>
Monte Pampean	Monte Pampa	<i>Enoplopactus lizeri</i> , <i>Naupactus rugosus</i> , <i>Pantomorus luteipes</i>
Ecuadorian	Western Ecuador, Cauca and Paramo	<i>Atrichonotus marginatus</i> , <i>A. sordidus</i> , <i>A. obscurus</i> , <i>Cyrtomon glaucus</i> , <i>Eurymetopus unicolor</i> , <i>E. globosus</i> , <i>Naupactus chordinus</i> , <i>N. dissimulator</i> , <i>N. minor</i> , <i>Platyomus mollis</i> , <i>Trichonaupactus densius</i>
		<i>Asymmalthetes pascoei</i> , <i>A. episternalis</i> , <i>Galapaganus femoratus</i> , <i>G. howdenae</i> , <i>Leschenius vulcanorum</i>

*Cerrado track*: extends along the savannas of the central-eastern plateau of Brazil, in the states of Tocantins, Goias, eastern Minas Gerais, Mato Grosso and Mato Grosso do Sul. It is supported by eight species (see Appendix S2: Figs S2c, S3c, S4a, S5a, S6a, S10a, S16a, S21a).

*Caatinga track*: extends along the seasonal xeric woodlands and shrublands of north-eastern Brazil, in the states of Ceará, Natal, Paraíba and Pernambuco. It is supported by three species (see Appendix S2: Figs S1a, S3b, S20a).

*Puna and Pacific coastal deserts track*: extends along the coastal deserts of Peru and Chile (Atacama) and high plains of Bolivia and Peru up to about 4000 m, characterized as shrubland steppes. It is supported by nine species (see Appendix S2: Figs S22a, S36d, S37b–d, S38e, S39d, S40d,e).

*Chacoan track*: extends from Paraguay to north-central Argentina, along the xerophyllous deciduous woodlands of Chaco southwards through the Pampas to the border of the southern Pampean sierras. It is supported by 14 species (see Appendix S2: Figs S4b,c, S9a, S14b, S16b, S21b,c, S25b, S28b, S29b, S39f, S40f, S42b, 44b).

*Atlantic+Parana forests track*: extends along the coastal pluvial forests of eastern Brazil from the states of Bahia in the north to Santa Catarina in the south and then turning westwards to Misiones province in Argentina, crossing the Araucaria forest province. It is supported by 34 species (see Appendix S2: Figs S1d, S4e, S5b, S7b,d, S9b, S10c, S12b,

S13b, S15a, S19b, S20b, S21d,e, S22c, 25e, S26b,c, S27a,b, S28a, S29a, S31b, S32b, S33b, S34a, S37e, S40 g, S41b,c, S43a, S44a, S45a,c).

*Monte track*: extends in central-western Argentina, near mountain areas of Mendoza and San Luis provinces, characterized by shrub–steppe dominated by Zygophyllaceae. It is supported by three species (see Appendix S2: Figs S5d, S12c, S29c).

*Pampean track*: extends through central grasslands of Buenos Aires province in Argentina, along the Uruguay river northwards to Corrientes province, and eastwards to Uruguay. It is supported by 11 species (see Appendix S2: Figs S1c, S9c, S11c, S19c, S25c, S28c, S32c, S41d, S43c, S44a, S45b).

*Ecuadorian track*: extends in western Ecuador, along the slopes of the western cordillera from the Cauca valley up to the paramos, at about 4500 m. It is supported by five species (see Appendix S2: Figs S38d, S39c, S40c, S44d, S45e).

Based on the generalized tracks obtained, we recognized the following generic distribution patterns.

#### *Widespread genera with species supporting several tracks*

*Naupactus*, the most diverse genus of Naupactini, is distributed mainly in forest areas, from southern Mexico to Argentina (Rosas-Echeverría *et al.*, 2011); it contributes to seven generalized tracks. The closely related genus *Pantomorus*,

with flightless species adapted to open vegetated areas, mainly grasslands, steppes and savannas, supports five tracks.

#### Endemic genera with species supporting a single track

*Trichocyphus* and *Amitrus* (Lanteri, 1989) support the Puna track; *Leschenius* and *Asymmathetes* are endemic to paramos in Ecuador and Colombia (del Río *et al.*, 2012); and *Brachystylodes* supports the Yungas track.

#### Genera with species contributing to two to three tracks in neighbouring areas

*Hadropus*, with the single species *Hadropus albiceris*, is widespread in the Atlantic forest and Cerrado (del Río & Lanteri, 2011), as is *Teratopactus* (del Río *et al.*, 2006). *Cyrtomon* is distributed in the Atlantic+Parana forests and Chaco, reaching the pampas through the gallery forests along the Parana and La Plata rivers (Lanteri, 1990a). *Enoplopactus* occurs in Monte, where its species are mainly associated with *Larrea* shrubs, and also in Chaco (Lanteri, 1990b). *Wagneriella* and *Priocyphus* (Lanteri, 1982, 1990c) are distributed in a narrow arc called Espinal, a xerophyllous forest dominated by *Prosopis* spp. (Cabrera & Willink, 1973).

Some species found throughout the pampas and neighbouring areas show complex distribution patterns and do not support any track, e.g. *Naupactus cervinus*, *Naupactus leucoloma*, *Pantomorus ruizi*, *Atrichonotus taeniatus* and *Aramigus tessellatus*. Most of them are parthenogenetic and have become widespread mainly because of their association with crops in several countries (Lanteri & Normark, 1995; Guzmán *et al.*, 2012; Lanteri *et al.*, 2013b).

#### Cladistic biogeographical analysis

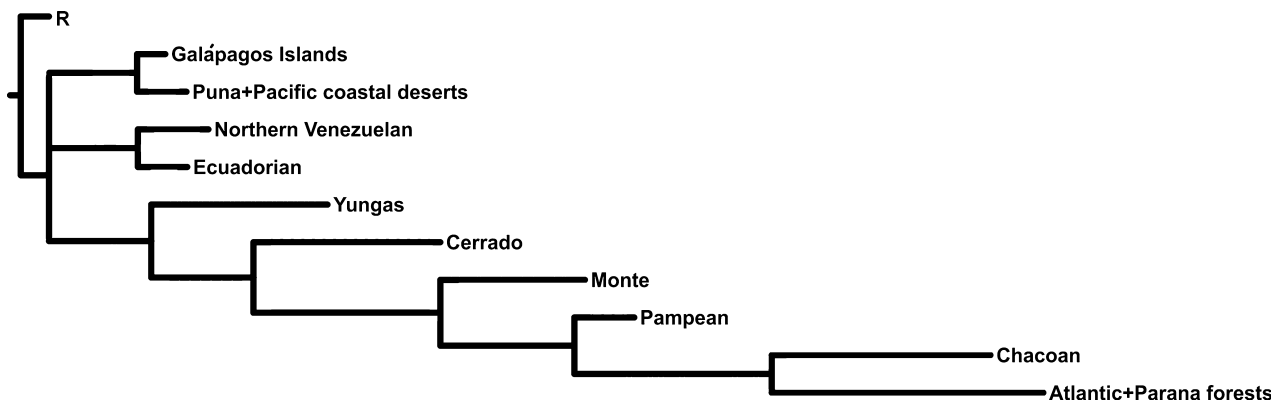
The 10 taxon–area cladograms resulted in 44 paralogy-free subtrees, from which 122 components were extracted (see Appendix S3). Analysis of the data matrix of areas by components (see Appendix S1) produced a single

general area cladogram (Fig. 3) with the following relationships among areas: ((Northern Venezuelan–Ecuadorian) (Galápagos Islands–Puna+Pacific coastal deserts) (Yungas (Cerrado (Monte (Pampean (Chacoan–Atlantic+Parana forests)))))). The first split is a trichotomy that separates Northern Venezuelan–Ecuadorian, Galápagos Islands–Puna+Pacific coastal deserts and the remaining areas (east of the Andes).

#### DISCUSSION

The 11 generalized tracks we obtained are coincident or partially coincident with tracks based on several animal and plant taxa (Table 2). For example, the Northern Venezuelan track is coincident with a track based on plant species of the genus *Piper* (Piperaceae); the Galápagos Islands track with the Eastern Pacific track based on several plants and animals endemic to this archipelago; the Yungas track with a track based on species of *Bombus* (Hymenoptera); the Cerrado track with a track based on plant species of Sapindaceae; the Caatinga track with a track based on species of *Sepedonea* (Diptera) and another on species of Sapindaceae; the Puna+Pacific coastal deserts track with several tracks based on vascular plants (e.g. Fabaceae, Sapindaceae and Asteraceae); the Chacoan track with a track based on Asteraceae; the Atlantic+Parana forests track with several tracks based on groups of insects (Coleoptera, Diptera and Hymenoptera) and vascular plants (Piperaceae and Sapindaceae); the Monte track with a homonymous track based on epigeous arthropods; the Pampean track with several tracks based on heteropteran insects, snakes and amphipods; and the Ecuadorian track with several tracks based on families of vascular plants (e.g. Cactaceae, Fabaceae and Onagraceae) and insects (Coleoptera and Hymenoptera).

The Atlantic+Parana forests track is supported best by the Naupactini (34 species) as well as by other animal and plant groups. The remaining tracks are expected to be extended and better supported by species when more taxonomic and geographical information become available, e.g. the Galápagos Islands track is probably connected with the Ecu-



**Figure 3** The general area cladogram obtained from a cladistic biogeographical analysis based on paralogy-free trees in a study of the evolutionary biogeography of South American weevils of the tribe Naupactini.

**Table 2** A comparison of 11 generalized tracks generated in this study of the evolutionary biogeography of South American weevils of the tribe Naupactini, with generalized tracks recovered for other plant and animal taxa.

Generalized tracks	Similar tracks for other taxa	References
Northern Venezuelan	Track 15 – <i>Piper</i> (Piperaceae)	Quijano-Abril <i>et al.</i> (2006)
Galápagos Islands	Eastern Pacific track	Grehan (2001)
Yungas	Track 6 – <i>Bombus</i> (Hymenoptera)	Abrahamovich <i>et al.</i> (2004)
Cerrado	Track 4 (in part) – Sapindaceae	Coulleri & Ferrucci (2012)
Caatinga	Track F – <i>Sepedonea</i> (Diptera)	Ciprandi-Pires <i>et al.</i> (2008)
	Track 4 (in part) – Sapindaceae	Coulleri & Ferrucci (2012)
Puna+Pacific coastal deserts	Track 1 (in part) – vascular plants	Posadas <i>et al.</i> (1997)
	Track 2 – <i>Adesmia</i> (Fabaceae)	Mihoč <i>et al.</i> (2006)
	Track 1 – Asteraceae	Urtubey <i>et al.</i> (2010)
	Track 2 – Sapindaceae	Coulleri & Ferrucci (2012)
Chacoan	Track 3 (in part) – Asteraceae	Urtubey <i>et al.</i> (2010)
Atlantic+Parana forests	Tracks f and g – <i>Cyrtoneurina</i> (Diptera)	Barros Carvalho <i>et al.</i> (2003)
	Track 7 – <i>Bombus</i> (Hymenoptera)	Abrahamovich <i>et al.</i> (2004)
	Track 25 – <i>Piper</i> (Piperaceae)	Quijano-Abril <i>et al.</i> (2006)
	Track b – Curculionidae (Coleoptera)	Romo & Morrone (2011)
	Tracks 5 and 6 – Sapindaceae	Coulleri & Ferrucci (2012)
Monte	Monte track (in part) – epigeous arthropods	Roig-Juñent <i>et al.</i> (2003)
Pampean	Track 4 (in part) – aquatic Heteroptera	Morrone <i>et al.</i> (2004)
	Track 3 (in part) – tropical snakes	Arzamendia & Giraud (2009)
	Track 4 (in part) – <i>Hyaella</i> (Amphipoda)	de los Ríos-Escalante <i>et al.</i> (2012)
Ecuadorian	Track 1 (in part) – Fabaceae, Onagraceae	Posadas <i>et al.</i> (1997)
	Track 5 – <i>Bombus</i> (Hymenoptera)	Abrahamovich <i>et al.</i> (2004)
	Track B – Staphylinidae (Coleoptera)	Asiain <i>et al.</i> (2010)
	Tracks II and III – Cactaceae	Loaiza & Morrone (2011)

adorian track, as suggested by previous phylogenetic studies on the Naupactini genus *Galapaganus* (Lanteri, 1992, 2004; Sequeira *et al.*, 2000, 2008).

The results of our track analysis help support several provinces recognized in Morrone's (2014b) regionalization, e.g. Galápagos Islands, Cerrado, Yungas, Monte, Chacoan and Pampean. They also suggest a connection among provinces, e.g. the Puna with Desert and Atacama provinces; Atlantic with the Parana forests; and Western Ecuador and Cauca with the Paramo province.

The general area cladogram resulting from our cladistic biogeographical analysis (Fig. 3) shows a north-western–south-eastern sequence, consistent with that obtained by Morrone (2014a) for the whole Neotropical region based on animal and plant taxa. According to Morrone (2014a), the Neotropical region constitutes a monophyletic unit, with a first split separating the Antilles and a second split dividing the continental areas into a north-western and a south-eastern component (Morrone, 2014a).

Near the root of the cladogram there is a trichotomy formed by Galápagos Islands–Puna+Pacific coastal deserts, Northern Venezuelan–Ecuadorian and the remaining areas east of the Andes. The first two groups belong to either the Pacific dominion or the South American transition zone.

The Northern Venezuelan area (Guajira and Venezuelan provinces) shares some floristic elements with the valleys of Ecuador, and it also shows floristic similarities with the Mexican–Central American biota (Lopez *et al.*, 2006). Unfortunately, geographical and cladistic information on

Naupactini from northern South America is insufficient to draw final conclusions about the relationships of these areas.

The relationship between the Galápagos Islands and the Pacific coastal deserts has been justified by cladistic analysis of the weevil genus *Galapaganus* (Lanteri, 1992). The flightless species of the *darwini* group of *Galapaganus* inhabit both areas and probably arrived at the Galápagos archipelago via the Humboldt Current. The diversification of this group on the islands would have started about 11 Ma ( $10.7 \pm 12.1$  Ma, late Miocene; Sequeira *et al.*, 2000). Although this time span may exceed the geological estimates of the extant emerged islands, the discordance has been justified with geological evidence of older, drowned islands as potential colonization platforms for *Galapaganus* ancestors (Sequeira *et al.*, 2000, 2008). The relationship between Puna and Paramo (here part of the Ecuadorian province), as well as that between these areas and the Pacific coastal deserts, is supported by several groups of animals and plants (Posadas *et al.*, 1997; Katinas *et al.*, 1999; Urtubey *et al.*, 2010). In our cladogram, these areas do not constitute a monophyletic unit because the genera endemic to Puna (e.g. *Amitrus* and *Trichocyphus*) are absent in Paramo, and the genera endemic to Paramo (e.g. *Leschenius* and *Amphideritus*) are absent in Puna. Pleistocene glacial cycles would have increased the opportunities for organisms isolated at higher elevations in Puna and Paramo to spread downwards and/or migrate between different mountain areas along with the vegetation zones they inhabited, favouring their diversification (Simpson-Vuilleumier, 1971; van der Hammen, 1974). These

cycles would also explain why the Puna+Pacific coastal desert track (Puna, Atacama and Desert provinces) extends over areas at different elevations as well as the Ecuadorian generalized track (Western Ecuador, Cauca valley and Paramo provinces). On the other hand, it is worth mentioning that the Naupactini inhabiting deserts and highlands show similar adaptations to these environments: their integument is highly sclerotized and usually black, lacking vestiture of iridescent scales but usually covered with fine pilosity, and with reduced or absent hind wings, a feature associated with flightlessness.

Our general area cladogram recovers a clade with the following sequence: (Yungas (Cerrado (Monte (Pampean (Chacoan–Atlantic+Parana forests))))). According to Prado (1995), cloud forests and seasonal dry montane forests of the Yungas, or at least their southern portion called Tucumane–Bolivian Yungas (Ibisch *et al.*, 2003), are linked to nearby south-eastern areas. In fact, several woody plants that occur in the piedmont areas of the sub-Andean sierras of the Yungas are occasionally found in drier south-eastern areas of the Chaco (Prado, 1995), with the limits of the two neighbouring areas being difficult to define. This is probably because the Yungas expanded eastwards during the humid climatic cycles of the Pleistocene (Simpson-Vuilleumier, 1971; Ab'Saber, 1977). In our area cladogram, the Yungas starts a paraphyletic sequence mainly formed by eastern drier areas (Cerrado, Monte, Pampean and Chacoan), except for the Atlantic+Parana forests. This is not consistent with the traditional geographical regionalization of Cabrera & Willink (1973), where the Yungas is part of the Amazonian dominion, the same as the Cerrado and Atlantic+Parana forests, and the remaining areas belong to the Chacoan dominion. Unfortunately, geographical information for Naupactini from Amazonia is insufficient to draw conclusions about the biogeographical relationships of this complex area (Bush, 1994; Nihei & Carvalho, 2007; Morrone, 2014a).

The Cerrado is the largest savanna in South America (Ab'Saber, 1977) and occupies a central position in relation to other large South American biomes (Cardoso da Silva & Bates, 2002). In our general area cladogram, the Cerrado is the sister group to the Monte, Pampean, Chacoan and Atlantic+Parana forests. Gomes de Carvalho *et al.* (2013) suggested that the uplift of the Brazilian Central Plateau in the late Pliocene–early Pleistocene may have caused the isolation and differentiation of this area and may have split a former Amazonian plus Atlantic+Parana forests biogeographical unit (Costa, 2003; Nihei & Carvalho, 2007; Sigrist & Carvalho, 2009; Pires & Marinoni, 2010). Silva (1996) and Costa (2003) assumed that the Cerrado gallery forests harbour many Atlantic and Amazon species.

Prado & Gibbs (1993) hypothesized the existence of a once extensive dry seasonal woodland formation extending from the Caatinga in north-eastern Brazil to the Chaco in Bolivia, Paraguay and Argentina. Our general area cladogram does not support a sister relationship between Cerrado+Chaco; indeed, very few Naupactini are common to Cerrado+Chaco,

or Cerrado+Caatinga, and none to Caatinga+Chaco, even though some species from these areas show similar adaptations to dry environments.

Traditional biogeographical regionalizations (e.g. Cabrera & Willink, 1973) have assumed a strong connection among Monte, Chaco and Pampa, and suggest that there is a progressive lack of trees from Chaco (xeric woodland) to Pampa (grasslands). Recent analyses have indicated the presence of several species endemic to Monte and its importance as a monophyletic biogeographical unit (Roig-Juñent *et al.*, 2006). Most Naupactini occurring in Monte are associated with *Larrea* shrubs (Zygophyllaceae) and they are either endemic to this area or they have their closest relatives in Chaco, e.g. *Enoplopactus*. In the most recent biogeographical regionalization, Morrone (2014b) placed Monte within the South American Transition Zone because of its conflicting relationships with other areas (Morrone, 2014b). The Chaco–Pampa area is well delimited by an arch formed by the Andean Piedmont and sub-Andean sierras and the Pampean sierras (Crisci *et al.*, 2001; Speranza *et al.*, 2007), and several plant and animal species inhabit these two areas. However, in our analysis these provinces do not form a monophyletic unit, although they are in a paraphyletic sequence.

The Pampean plains constitute a depressed area affected by Cenozoic marine incursions into Buenos Aires province and refilled by Quaternary continental sediments (Ringuélet, 1956); consequently, the pampas harbours very few endemics and several taxa that are recent colonizers also occurring in neighbouring areas, mainly Chaco, Atlantic+Parana forests and Patagonia (Ringuélet, 1961), e.g. the *Aramigus tessellatus* complex (Normark & Lanteri, 1998). Most of the Pampean Naupactini are flightless species adapted to environments of open communities that have certainly succeeded in extending their ranges southwards, towards more temperate areas. The margins of La Plata River are clearly subtropical (Ringuélet, 1961), as this area is inhabited by species also occurring in the Parana forest, which could expand southwards along the gallery forests of the Parana and Uruguay rivers (Menalled & Adámoli, 1995; Nores *et al.*, 2005; Arzamendia & Giraud, 2009). Their effect as biogeographical corridors is a pattern previously described for several groups of aquatic (e.g. Bonetto & Drago, 1968; Ringuélet, 1975; Morrone & Lopretto, 1994) and terrestrial organisms (e.g. Rabinovich & Rapoport, 1975; Menalled & Adámoli, 1995; Nores *et al.*, 2005), and it is also true for the Naupactini. The gallery forests flanking the Parana River, crossing the Chaco–Pampa, explain the close relationships of these provinces with the Atlantic+Parana forests.

A comparative analysis of open and forest biomes through geological time, especially from middle–late Pleistocene to present, is essential for interpreting the relationships among biogeographical areas in South America (Tonni *et al.*, 1999). Climatic alterations of glacial and interglacial epochs dramatically modified the distribution, composition and biomass of plant and animal communities in South America, as in other regions of the world (Simpson-Vuilleumier, 1971; van der Hammen, 1974). As the climate became colder and drier, open

areas expanded, and organisms adapted to these environments spread and increased their biomass; in turn, rain forests expanded when the climate was warmer and more humid during the shorter interglacial periods (Behling & Negrelle, 2001).

The absence of discernible geological barriers and the influence of the Plio-Pleistocene cycles make it difficult to draw a definite conclusion about the historical relationships among most forest areas and nearby open areas of South America. In this context, the discordant results among analyses of area relationships have led some authors to conclude that the current distribution of the Neotropical terrestrial biota cannot be explained consistently by a single hypothesis (Bush, 1994; Bates *et al.*, 1998; Marks *et al.*, 2002; Costa, 2003; Nihei & Carvalho, 2007). Our track and cladistic biogeographical analyses have allowed us to identify general patterns that may reasonably be assumed to have been caused by vicariance. These biotic patterns are useful for proposing natural biogeographical regionalizations and allow testing of previous biogeographical schemes. Furthermore, our analyses highlight the relevance of dispersal in shaping complex biogeographical patterns, by suggesting that subsets of the taxa under consideration underwent dispersal at different times. To identify these cenocrons (sets of taxa that share the same biogeographical history, constituting identifiable subsets within a biota by their common origin and evolutionary history; Morrone, 2009) clearly, we need dated molecular phylogenetic hypotheses (where the minimal ages of the clades are estimated), information on the geographical distribution of the related taxa and a geotectonic database. A general theory of a geobiotic scenario can be formulated only after the required information has been gathered (Morrone, 2009). Until then, analyses such as those presented here must be regarded as preliminary.

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## SUPPORTING INFORMATION

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

**Appendix S1** Data matrix of 10 areas by 122 components used in the cladistic biogeographical analysis.

**Appendix S2** Individual tracks of the 165 Naupactini species used in the track analysis.

**Appendix S3** Taxon–area cladograms and the paralogy-free subtrees derived from them.

## DATA ACCESSIBILITY

The list of the species used in the track analysis, with information on the locations, geographical coordinates, literature references and collection information, is available as a PDF file at [http://www.museo.fcnym.unlp.edu.ar/uploads/docs/georreferencias\\_naupactini.pdf](http://www.museo.fcnym.unlp.edu.ar/uploads/docs/georreferencias_naupactini.pdf).

## BIOSKETCH

**M. Guadalupe del Río** is an assistant researcher at the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina. Her main interests are the phylogenetics and systematics of weevils.

**Analia A. Lanteri** is a principal researcher at the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Professor of Taxonomy at the Facultad de Ciencias Naturales y Museo (UNLP), Argentina. Her main interests are the phylogenetics and systematics of weevils.

**Juan J. Morrone** is a Professor of Biogeography, Systematics and Comparative Biology at the Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), Mexico. His main interests are evolutionary biogeography and phylogenetic systematics.

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