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Biogeographical relationships and new regionalisation of high-altitude grasslands and woodlands of the central Pampean Ranges (Argentina), based on vascular plants and vertebrates

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Abstract. Evolutionary biogeography aims to provide a hierarchical system of biotic regionalisation for areas of the Earth that correspond to natural areas related by their common evolutionary history. In this context, the central Pampean Ranges of Argentina, formed by the mountain systems of Córdoba and San Luis, are immersed in the Chacoan dominion; however, higher-altitude environments of these mountains, namely highland grasslands and tabaquillo forests, have relationships with the Andean region and other Neotropical areas that are different from the Chacoan dominion, which would indicate that the current classification would not be natural. To clarify their biogeographic relationships, a track analysis of the distribution of the biota of vertebrates and vascular plants of the highland grasslands and tabaquillo forests of central Pampean Argentinian Ranges was conducted. The obtained distributional patterns suggest that the area under study has diverse geobiotic origins, both Andean and Neotropical, indicating that, in this area, an interaction of biota with different evolutionary origins occurs; so, its status as a biogeographic province is proposed, belonging to the South American transition zone.

Additional keywords: Comechingones province, highland grasslands, tabaquillo forests, panbiogeography.

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Introduction

Biogeography studies the distribution of taxa in time and space, analyses biotic evolution and the close relationship that organisms maintain with their ecological environment and provides a system of biotic regionalisation, with hierarchically ordered areas (Morrone 2004*a*; Escalante 2009). Biogeographic studies focused on regionalisation develop these schemes with the aim to build classification systems where the identified areas correspond to natural areas (Escalante 2009). Biological diversity is a spatial and temporal phenomenon where geographical barriers evolve in conjunction with the biota (Arana *et al.* 2011), resulting in taxa that are not randomly distributed, but have more or less recognisable boundaries that are repeated for several distantly related taxa (Escalante 2009; Arana *et al.* 2011). The naturalness of a biogeographic area would be given by a common geobiotic origin and, therefore, by the same evolutionary biotic history (Morrone 2001*a*). There have been several attempts of biogeographical regionalisation for Latin America and Argentina that have tried to achieve the purpose of delimiting and classifying natural areas. The Phytogeographic provinces delimited by Cabrera (1971), the ecoregions of Burkart *et al.* (1999) and the Neotropical and Andean regionalisation proposed by Morrone (2014*b*, 2015*b*) may be mentioned, among others. Because these studies differed in their methodology, classified areas also have differences in their categorisation, so that, in some cases, boundaries, names, or levels differ among the recognised areas. The regionalisations of Morrone (2014*b*, 2015*b*), in which both track and cladistic biogeographic analyses were used, came closer to a natural system of classification of areas, because the areas rest primarily on generalised tracks, representing patterns of spatial homology and indicating the presence of spatial–temporal integrated taxa in the same biotic component and, therefore, have a common evolutionary origin (Morrone 2004*a*).

In spite of these multiple biogeographic approaches, the regionalisation of the central Ranges of Argentina or eastern Pampean Ranges, which are composed of the mountain systems of Córdoba and San Luis, have not changed. They are included, in all classification systems, within the Chacoan area, indicating that their biota have close biogeographical relationships with the Neotropical region and, therefore, a common and a closer evolutionary origin with the tropical biota (Morrone 2000, 2001*b*, 2014*b*).

However, some authors have noted that the highest elevations of the central Pampean Ranges, occupied by environments of high-altitude grasslands and *Polylepis* forests (called 'tabaquillo forests'), may exhibit a closer relationship with areas of the Andean region rather than the Chacoan subregion (Arana *et al*. 2011, 2013; Chiapella and Demaio 2015). In support of this hypothesis, a study by Cabido *et al*. (1998) mentioned that the plant communities at >1850 m above sea level (ASL) in the mountains of Córdoba do not belong to the species of Chacoan distribution, but rather they correspond to a group of frequent taxa in Andean environments and high altitudes of the mountains of the north-western area of Argentina. In contrast, Kurtz (1904) divided the mountain vegetation into two zones, the first and lowest to a height of 1700 m, called 'Monte Serrano' area, and the highest zone, called sub-Andean area with tabaquillo forest formations and alpine grasslands. In the latter, Kurtz mentioned that the flora provide conspicuous relationships with the Andean–Magellanic vegetation.

From the ornithological point of view, Nores and Yzurieta (1983) indicated that from an altitude of 1500 m, coinciding with the beginning of the grasslands of 'Chaco Serrano' phytogeographical district in the mountains of Córdoba and San Luis, a system that is biologically isolated, clearly appears more closely related with the Andean–Patagonian dominion than the Chacoan dominion. In addition to these Andean relationships, according to biogeographic studies (Arana *et al*. 2011, 2013), these environments of high altitude also have links with the Montane Forests district of the biogeographical province of the Yungas, and they are representing biogeographic islands vicariantly fragmented by tectonic events or climate change, such as progressive aridification of South America. The floristic connection between the biota of the high-altitude grasslands of the Sierras of Córdoba and the Montane Forest district is

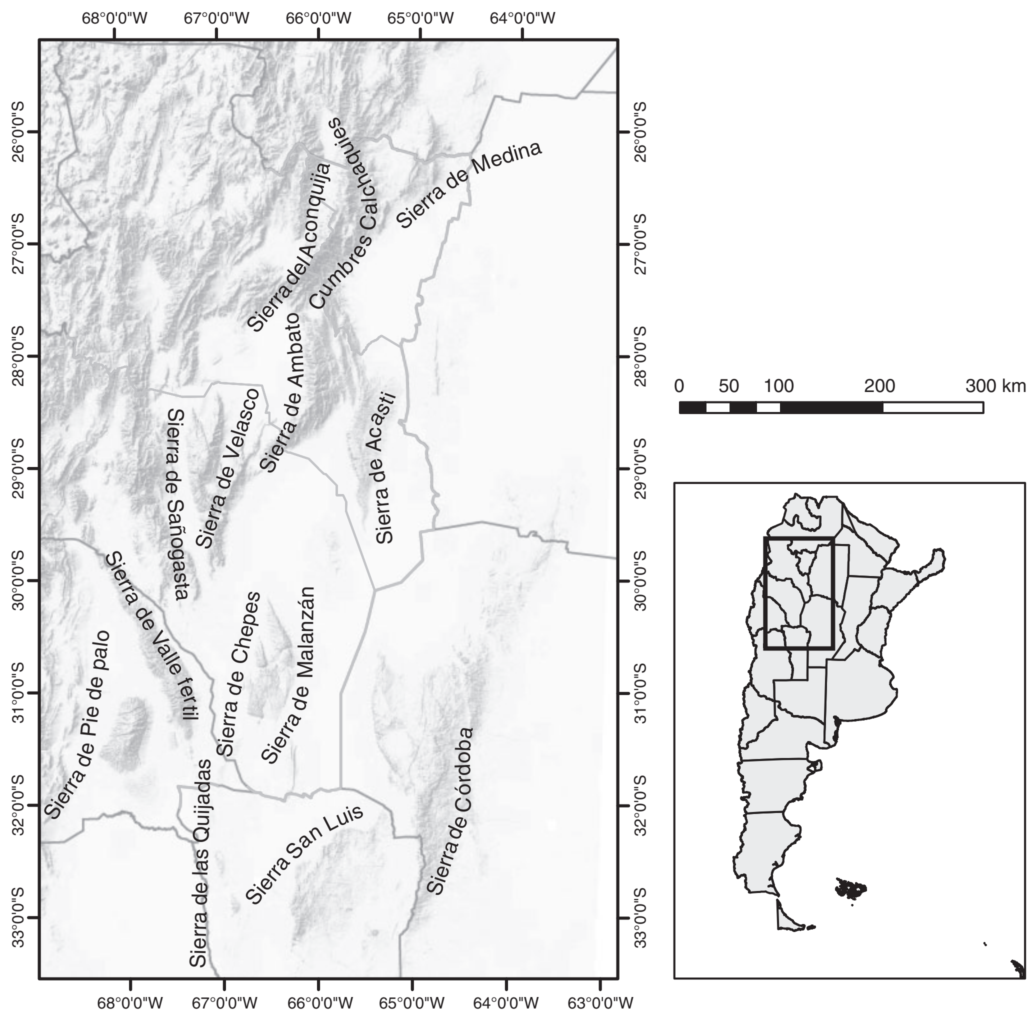

Fig. 1. Pampean Ranges geological province, located east of the Andes.

particularly evident if we consider ancient lineages of plants such as ferns and lycophytes (Arana *et al*. 2013). Considering that in the biota of high-altitude environments from the central Pampean Ranges of Argentina, there are species that could be integrating ancestral biotic components of both Andean–Patagonian and Yungean biotas, and, therefore, demonstrating a common evolutionary history of these three areas, the current classification of the high-altitude grasslands of central Pampean Ranges of Argentina belonging to the Chacoan province of the Neotropical region should be reviewed.

According to what has been mentioned above, and considering that the central Pampean Ranges of Argentina present numerous endemic species (Di Tada and Bucher 1996; Oggero and Arana 2012; Chiapella and Demaio 2015; Lescano *et al*. 2015), a track analysis of the biota of the high-altitude grasslands of the central Pampean Ranges of Argentina, including vertebrate and vascular-plant taxa, was conducted so as to establish their biogeographical relationships and verify that this area is a natural unit in the evolutionary biogeographic sense.

Materials and methods

Study area

The area of the high-altitude grasslands and tabaquillo forests develops as the highest-altitude vegetation unit of the Chaco Serrano district (Cabrera 1971) or western Chaco (Morrone 2014*b*) of the mountains of the provinces of Córdoba and San Luis (Fig. 1), which constitute the easternmost group of mountains of the Argentinean geological province, 'Sierras Pampeanas' (Ramos 1999). They range from 29°30′S to 33°15′S and from 64°20′W to 66°20′W, occurring mostly in Córdoba and San Luis Provinces, except for a small northern portion extending into the neighbouring province of Santiago del Estero, extending ~550 km from north-east to south-west and being ~110 km wide, with the highest point being represented by the Cerro Champaqui (2790 m). With an overall north-east–south-west orientation, the Sierras are older than the Andes; they rise above pampa plains of Quaternary origin (Baldo *et al*. 1996), comprising the following six main sections (from north to south): Sierras del Norte, Sierras Chicas-Las Peñas, Sierras Grandes-Sierra de Comechingones,

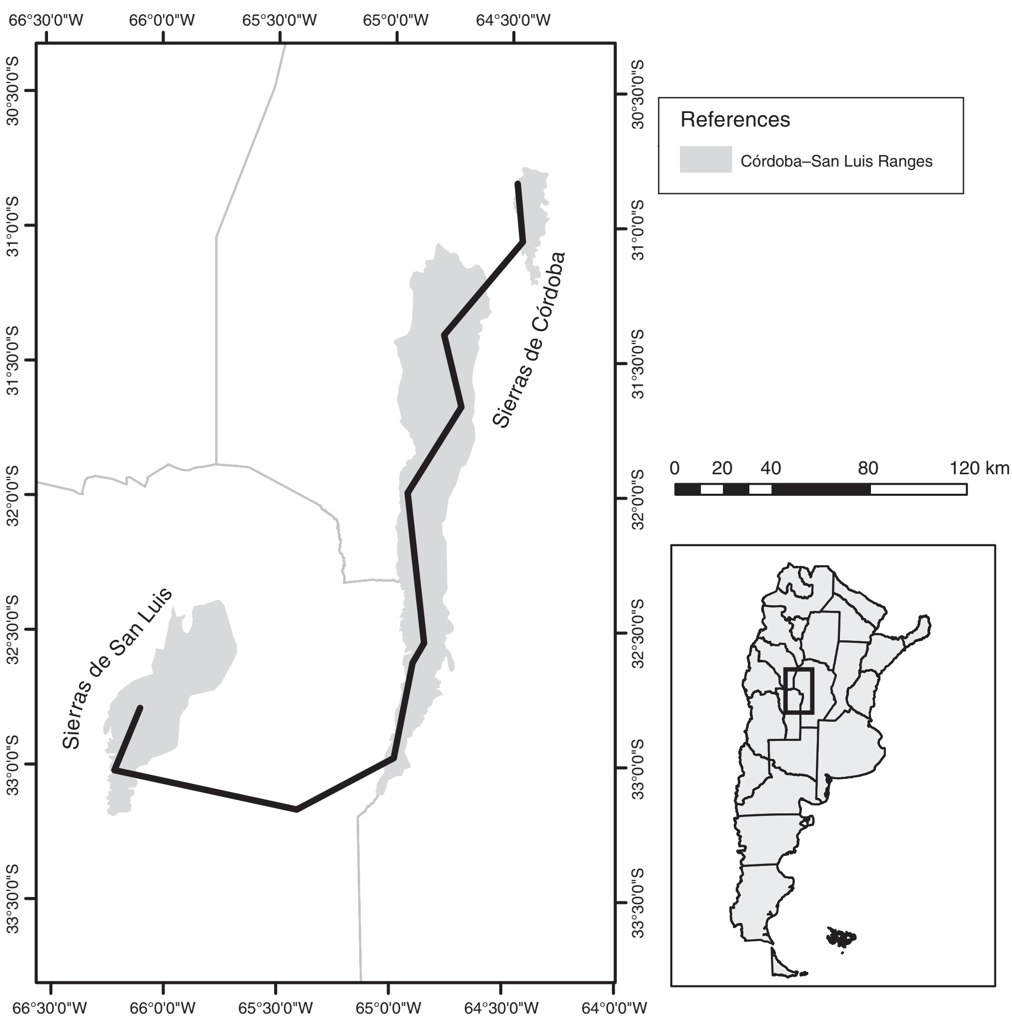

Fig. 2. Generalised track 1. Highland grassland and tabaquillo forests from the Pampean Ranges of Córdoba and San Luis.

Sierras de Pocho-Guasapampa, Sierra de San Luis and Sierra del Morro (Fig. 1; Carignano 1999). They consist of an igneous metamorphic basement composed mainly of schist and gneiss from higher Proterozoic to lower Paleozoic age, intruded in the Paleozoic by granitic batholiths (Suárez *et al.* 1992; Kraemer *et al.* 1995). The sedimentary cover is composed of isolated relict sandstones, shales and conglomerates of upper Paleozoic age and complex volcanic–sedimentary rocks from the lower Cretaceous. Continental clastic sedimentary rocks from the Paleogene, Neogene and Quaternary are well developed in the inter-mountain valleys (Martino *et al.* 1995).

The high-altitude grasslands stretch down the slopes, peaks and high plains exposed to the winds, descending from higher altitudes down to ~1000 m ASL. The grassland vegetation is characterised by Poaceae species belonging to the genera *Festuca* and *Nassella*, which are the most conspicuous and abundant plants and form the typical 'mountain grasslands'. To a higher altitude, on the so-called 'pampas de altitud', the variety of grasses and other plants increases, forming the so called pseudo-Andean meadows that alternate with rocky outcrops. The tabaquillo forests appear approximately from 1700 m ASL, reaching the highest altitudes as isolated 'islands' of small areas of protected slopes. They are composed mainly of 'tabaquillo' (*Polylepis australis* Bitter) and 'maiten' (*Maytenus boaria* Molina), accompanied by several species of ferns, lichens and epiphytes (Cabido and Acosta 1985; Oggero and Arana 2012).

Methods

To establish the biogeographic patterns of the biota of the highland grasslands, the distribution of 82 specific and subspecific taxa of vertebrates and vascular plants was obtained, selecting those that, according to the herbaria and field data and literature, inhabit only the areas that have grassland vegetation or tabaquillo forests. Taxa with a wider distribution in South America or cosmopolitans were not taken into account.

To determine the distribution of the selected taxa, a critical literature review was conducted (Partridge 1953; Nores and

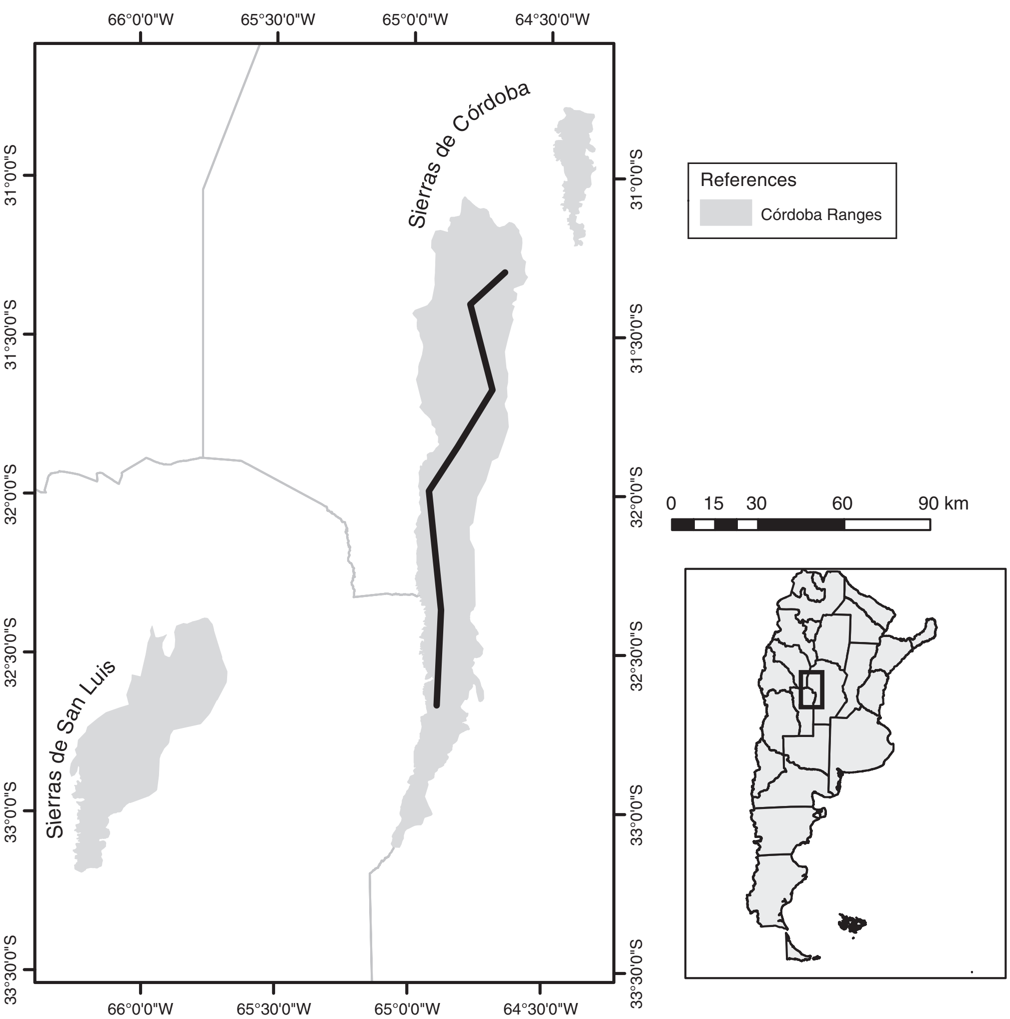

Fig. 3. Generalised track 2. Highland grasslands and tabaquillo forests from the Sierras Grandes, Comechingones of Córdoba.

Yzurieta 1979*a*, 1979*b*, 1983; Di Tada *et al*. 1980; Correa 1984; Cei 1986; Nores 1986; Bianco and Kraus 1996; Di Tada and Bucher 1996; Navas and Camperi 1999; Zuloaga and Morrone 1999; Steibel 2000; Navas and Bó 2001; Vischi *et al*. 2004; Márquez *et al*. 2005; Darrieu and Camperi 2006; Rúgolo de Agrasar 2006; Céspedez 2008; Fernández Pepi *et al*. 2008; Zuloaga *et al*. 2008; Bellis *et al*. 2009; Ferraro and Casagranda 2009; Gómez Romero and Grau 2009; Valetti *et al*. 2009; Narosky and Yzurieta 2010; Peterson and Giraldo-Cañas 2011; Arana and Øllgaard 2012; Bartoli *et al*. 2012; Gargiulo 2012; Katinas 2012; Oggero and Arana 2012; Arana *et al*. 2013; Cialdella *et al*. 2013; Ganem *et al*. 2013; Valetti *et al*. 2013; Sassone *et al*. 2014; Lescano *et al*. 2015; Chiapella and Demaio 2015).

The following databases were also consulted (last accessed June 2016): Instituto de Botánica Darwinion (www.darwin.edu.ar), Sistema de Información de Biodiversidad (www.sib.gov.ar), Ecoregistros (www.ecoregistros.org), Avibase – the world bird database (www.avibase.bsc-eoc.org), Flora Argentina (www.floraargentina.edu.ar), TROPICOS, (www.tropicos.org), GBIF (Global Biodiversity Information Facility, www.gbif.org), eBird Argentina (www.ebird.org), The Reptile Database (www.reptile-database.org), Argentavis (www.argentavis.org) and The plant list (www.ipni.org).

Because of differential efforts in the collection of specimens, these references may have geographical biases that result in generalisations and under-rated inferences of the areas of distribution (Escalante 2009). For this reason, some features of the environment occupied by the different taxa, such as habitat type and altitude above sea level, were also taken into account, so as to specify accurately their distribution.

Track analysis is based on three main concepts, namely, individual track, generalised track and node (Morrone 2009, 2015*a*, Escalante *et al*. 2016). The 1458 occurrences of the taxa studied were georeferenced and the software QGis 2.12.3-Lyon (GNU general public licence, see http://qgis.org/es/site/, accessed 25 March 2017) was used to build a database and generate maps containing all this information.

Species are represented by at least two occurrences. Once distribution points for each species were generated on a map, they

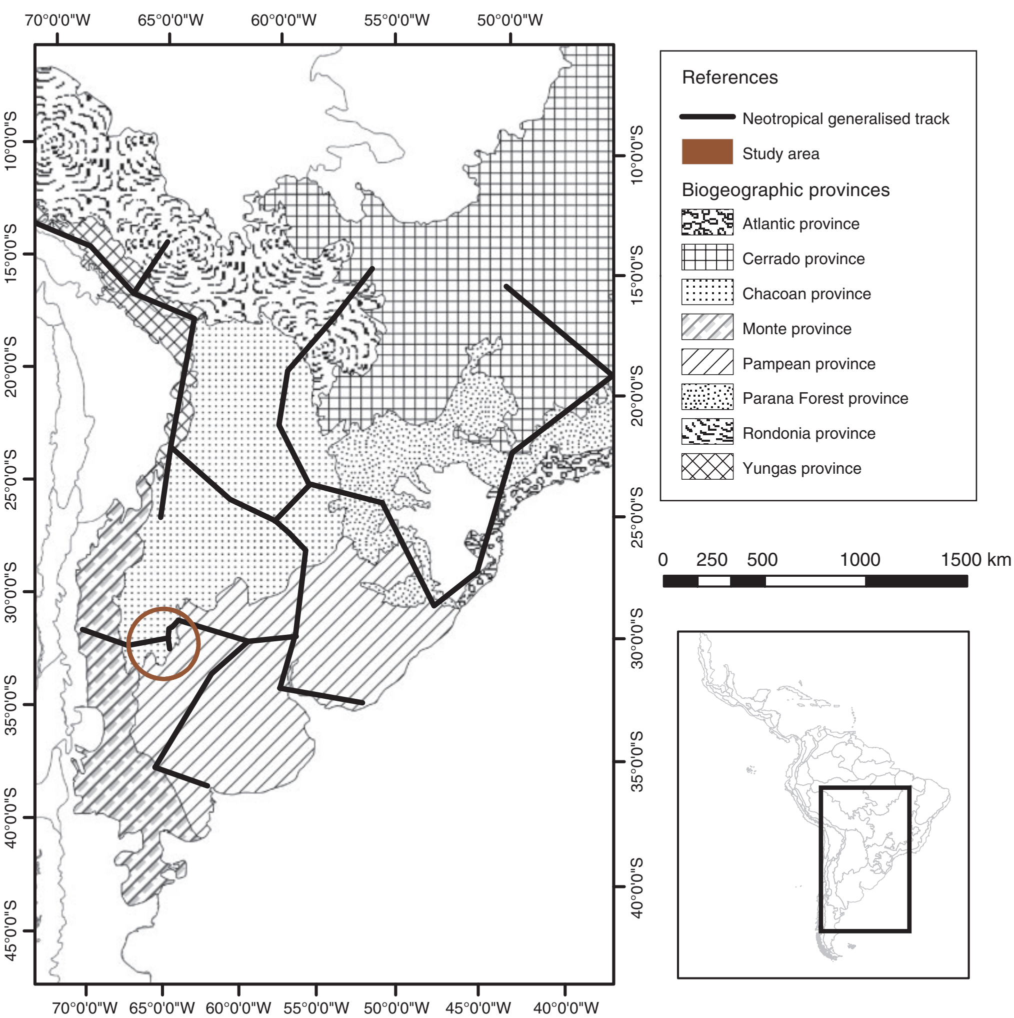

Fig. 4. Generalised track 3. Neotropical region, highland grasslands and tabaquillo forests.

were connected with a line representing the minimum distance between the points, known as the individual track. Individual tracks represent the spatial coordinates of a species or a group of related species in space. An individual track may be interpreted as a minimum-spanning tree, which, for n localities, contains n–1 connections. In the resulting graph, the sum of all the segments connecting the localities is minimal, following the criterion of geographic parsimony (Morrone 2004*a*, 2015*a*). The individual tracks were graphed using Google Earth.

When individual tracks from different taxa match, they reflect a generalised track, which allows to infer the existence of an ancestral biota widely distributed and fragmented by vicariance events, suggesting a shared history within a biota (Torres-Miranda and Luna-Vega 2006). The analysis and review of published contributions using track analysis made by Morrone (2015*a*) and Escalante *et al*. (2016) showed that the most popular method for identifying generalised tracks was the minimum spanning-tree method applied manually, and this was the method applied in the present work. According to Morrone (2014*a*, 2015*a*), the software packages draw individual tracks efficiently, but, unfortunately, they consider any overlap between parts of two or more of them as a generalised track. This results in a substantial modification of the original concept of a generalised track, which required a significant overlap of two or more individual tracks, not just parts of them.

When two or more generalised tracks overlap in an area, a node is identified. It is considered a complex area, where different ancestral biotic and geological fragments inter-relate in space–time as a consequence of terrane collision, docking or suturing (Morrone and Crisci 1995; Morrone 2004*a*; Miguel-Talonia and Escalante 2013).

The tracks and panbiogeographic nodes were graphed on the modified shapefiles based on Olson *et al*. (2001) and Morrone's biogeographic scheme (Löwenberg-Neto 2014, 2015).

Results

Generalised tracks

From the results of the analysis of individual tracks, different spatial-distribution patterns were detected and seven generalised tracks (Figs 2–9) were obtained. Representative taxa of each generalised track are indicated in Table 1. Two of these seven

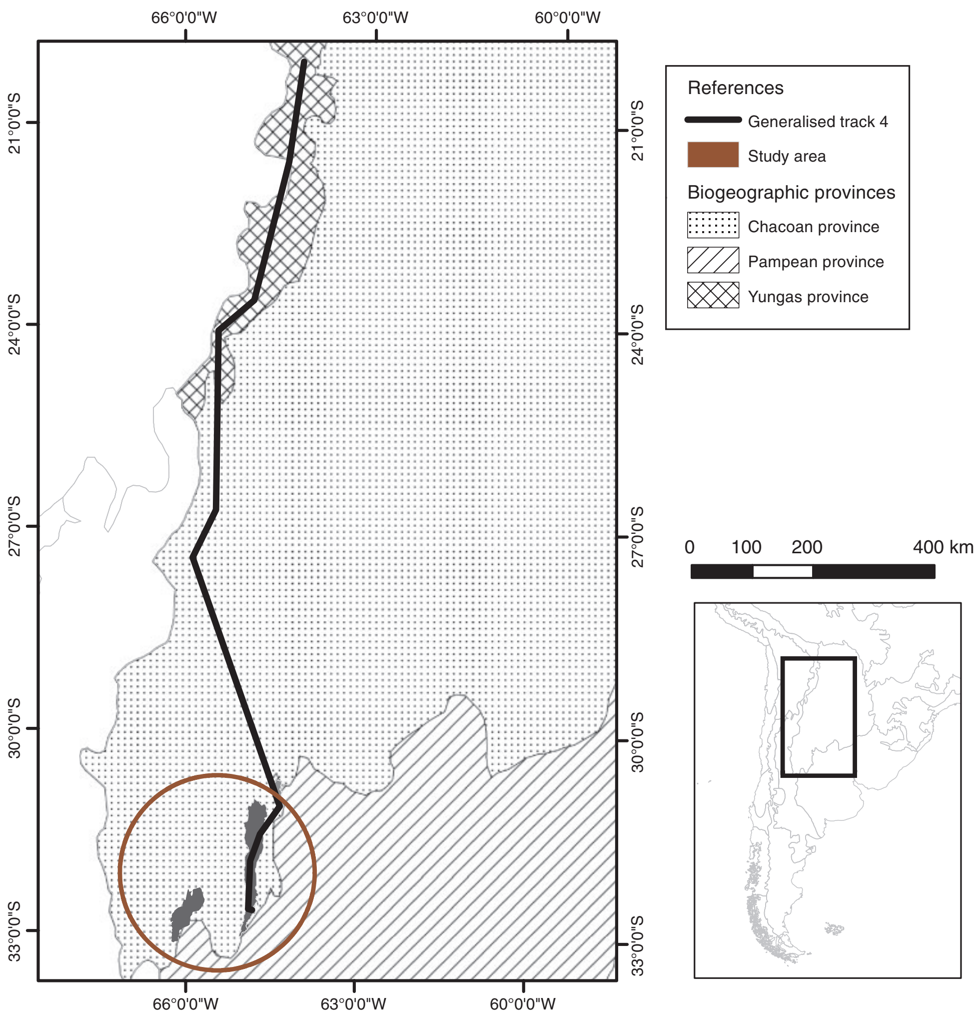

Fig. 5. Generalised track 4. Yungas province, highland grasslands and tabaquillo forests.

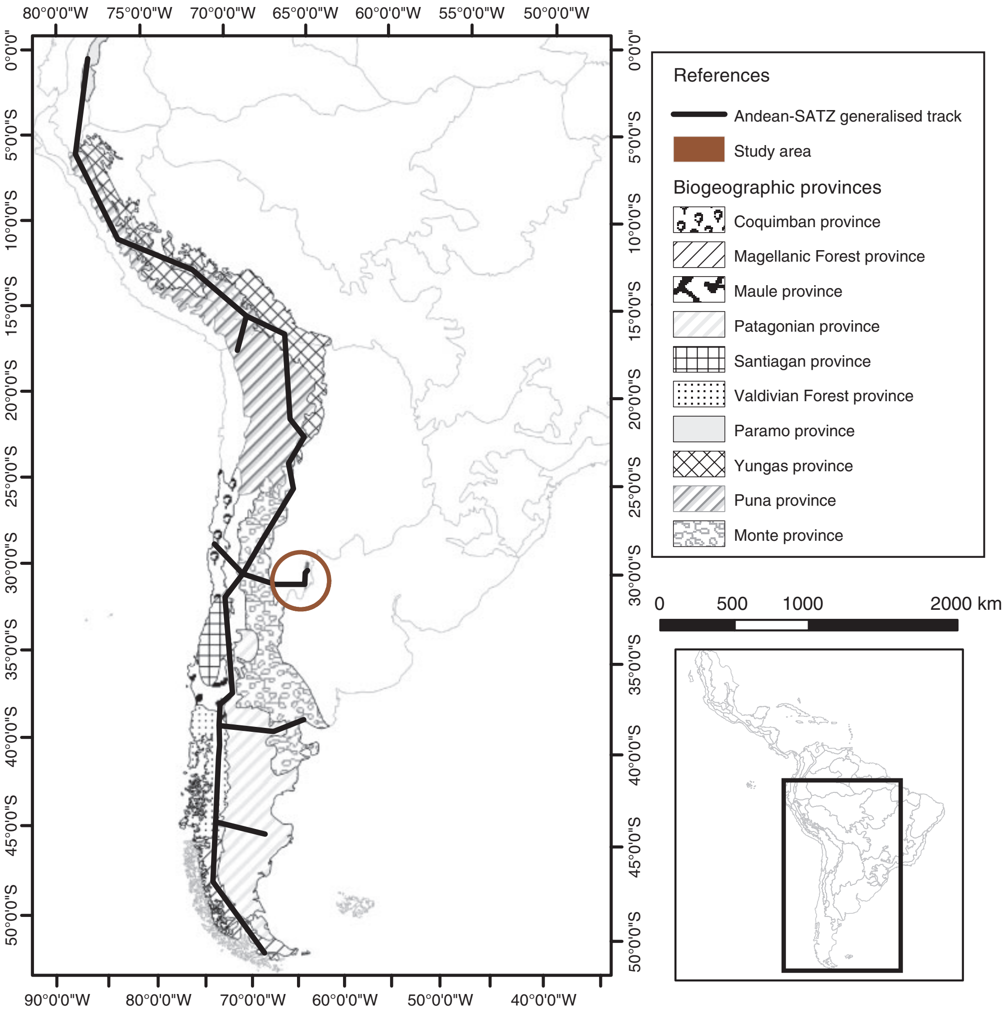

Fig. 6. Generalised track 5. Andean region and South American transition zone, highland grasslands and tabaquillo forests.

generalised tracks were considered restricted only to highland grasslands and forests of tabaquillo from the central Pampean Ranges of Argentina, and allowed us to recognise an endemic area. One of these generalised tracks stretches along the mountains of San Luis, Sierras Grandes–Comechingones and Sierras Chicas (Fig. 2), whereas the other is located just in the highland grassland and tabaquillo forests of Córdoba Ranges (Fig. 3).

The third generalised track obtained links the area of highland grasslands and tabaquillo forests with the biogeographic provinces of the Neotropical region, such as the Yungas and Rondonia of the Brazilian subregion, and the provinces of Chaco, Cerrado, Pampean and Parana Forest, from the Chacoan subregion. This third generalised track also connects the highland grasslands and tabaquillo forests of the mountains of Córdoba and San Luis with the Monte biogeographical province belonging to the South American transition zone (Fig. 4).

The fourth generalised track could be considered included in the one mentioned above, because it binds only the highland grassland of the central Pampean Ranges of Argentina with the biogeographic province of the Yungas (Fig. 5). It is important to add that this generalised track also links the study area with other highland grasslands of the Pampean Ranges such as Calchaquíes Ranges, the mountains of Aconquija and the mountains of Acasti, currently classified as belonging to the biogeographic province of Chaco (Morrone 2014*b*).

The fifth generalised track (Fig. 6) relates the highland grassland of Córdoba and San Luis with steppe environments of Patagonia and the Andes, ranging from southern Argentina, central Chile, Bolivia and Peru, to the Ecuadorian Andes. This generalised track links the biogeographic provinces of the Andean region, such as Patagonian, Magellanic Forest, Valdivian Forest, Maule, Santiagan and Coquimban, with provinces of the South American transition zone, such as Monte, Puna and Paramo. In addition, because of the type of environment where these taxa are found, this biotic component would also link the study area with highland grassland areas currently included in the biogeographic province of the Yungas.

Within the last generalised track, two minor biotic components can be included. One represents mostly the part of the Andean

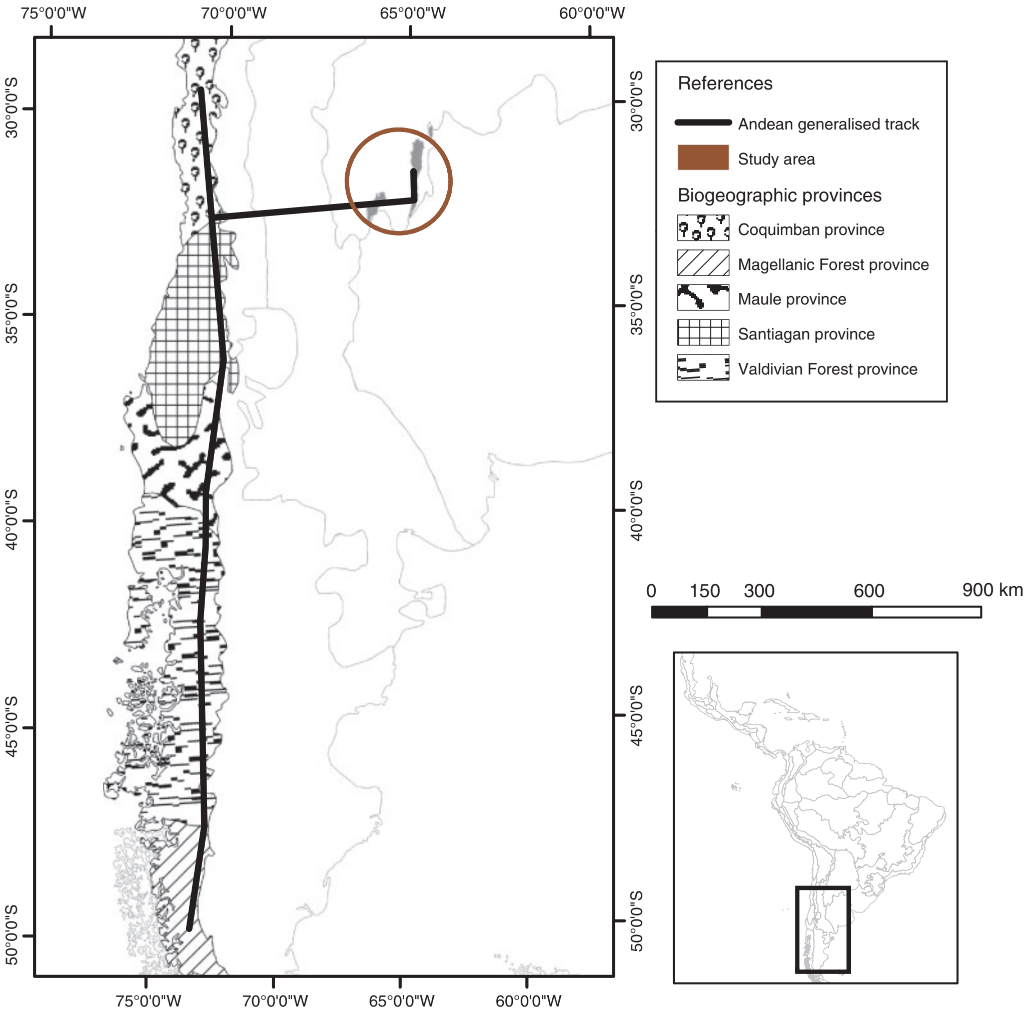

Fig. 7. Generalised track 6. Andean region, highland grasslands and tabaquillo forests.

region (Fig. 7) occupying the biogeographic provinces of Magellanic Forest, Valdivian Forest, Maule, Santiagan and Coquimban, and the other represents the portion corresponding to the South American transition zone (Fig. 8), relating the area of highland grassland and tabaquillo forests with the provinces of Monte and Puna.

Furthermore, the second component of the fifth generalised track, because of the type of environments that the taxa inhabit, also relates all the above-mentioned areas with areas of highland grassland of the province of the Yungas and other high-altitude environments belonging to some of the Pampean Ranges of Argentina, such as, for example, the mountains of Ambato and Aconquija, and Calchaquíes Ranges, currently classified as part of the biogeographical province of Chaco (Morrone 2014*b*).

Nodes

Owing to the confluence of multiple generalised tracks in the area of highland grasslands and tabaquillo forests of central Pampean Ranges of Argentina, several nodes, with different hierarchical levels, are present. This could be interpreted as an evidence of the complex biotic origin of the area.

A node is formed by the intersection of biotic components of the province of the Yungas (Generalised track 4), the Andean region (Generalised track 6) and the South American transition zone (Generalised track 7). As seen in Fig. 9, Generalised tracks 4 and 7 also form two nodes outside the area of highland grasslands of the central Pampean Ranges. One of them is located in the sub-Andean Ranges in the Yungas biogeographic province and the other in the Calchaquíes Ranges.

With regard to the biotic components of (i) Andean type, (ii) South American transition zone (Generalised track 5) and (iii) Neotropical region (Generalised track 3), their intersection in the area of highland grasslands and tabaquillo forests of the central Pampean Ranges of Argentina forms another node (Fig. 10). Because these two biotic components were considered as the biggest generalised tracks within which minor biotic components are nested, as has been described above, this second node includes the first, and, therefore, it is here considered of a higher hierarchical level.

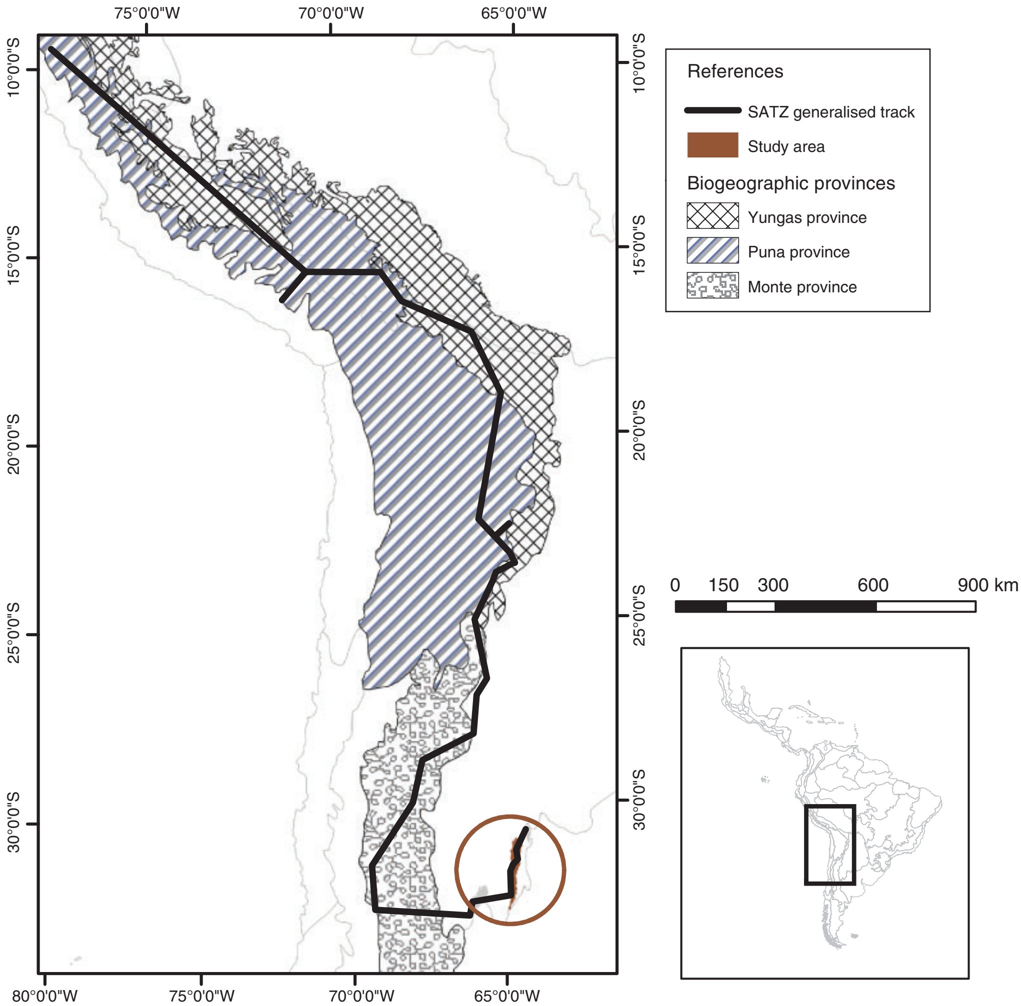

Fig. 8. Generalised track 7. South American transition zone (SATZ), highland grasslands and tabaquillo forests.

In addition to this node within the study area, the Generalised tracks 5 and 3 also form two other nodes, one located in the Quijadas Ranges (biogeographic province of Chaco) and another one in the biogeographic province of Monte (Fig. 10).

Discussion

Generalised tracks can be used to recognise natural areas in terms of their biota because they result from more or less consistent overlapping distributions of two or more endemic taxa. Thus, the defined areas can be also named as areas of endemism (Escalante 2009), which, in turn, can be ordered hierarchically in a biogeographic classification system (Morrone 2004*a*). In this case, minor generalised tracks found only in highland grasslands and tabaquillo forests (Figs 2, 3) would belong in an endemic area included in the central Pampean Ranges of Argentina; so, it is possible to assume the existence of geographical barriers and a certain degree of isolation for environments in these altitudes, ranging from 1000 to ~2800 m ASL.

This geographic isolation could be related with the effects of reactivation of older faults that led to a new uplift of the central Pampean Ranges, which is a result of the geological evolution of the last orogenic event that affected the structure of these mountains and that was described as Andean orogenesis. This Andean cycle had its effects on the Pampean Ranges of Córdoba and San Luis from the Eocene, determining that the current structure of the mountains started *c.* 12–10 million years ago and had already been formed in the lower Miocene–Pliocene limit, 5.3 million years ago (Jordan and Allmendinger 1986; Jordan *et al*. 1989; Baldo *et al*. 1996; Sagrispanti *et al*. 2012; Martino *et al*. 2016). The obtained results allow us to define this area as a natural unit in the evolutionary biogeographic sense, and with an identity of its own, given by the existence of an endemic biota. The generalised track of reduced extension (Fig. 3) allows the delimitation of an area of a lower category nested within the Pampean Ranges of Córdoba and San Luis, and restricted only to highland grasslands of the Pampean Ranges of Córdoba.

Also, generalised tracks can also represent ancestral biotic components that do not necessarily correspond to an area of endemism; rather, this could indicate that two or more taxa are integrated in space and time (spatial–temporal) in the same biota that could be fragmented by tectonic or geological events (Craw 1988). In this way, they can be used to demonstrate

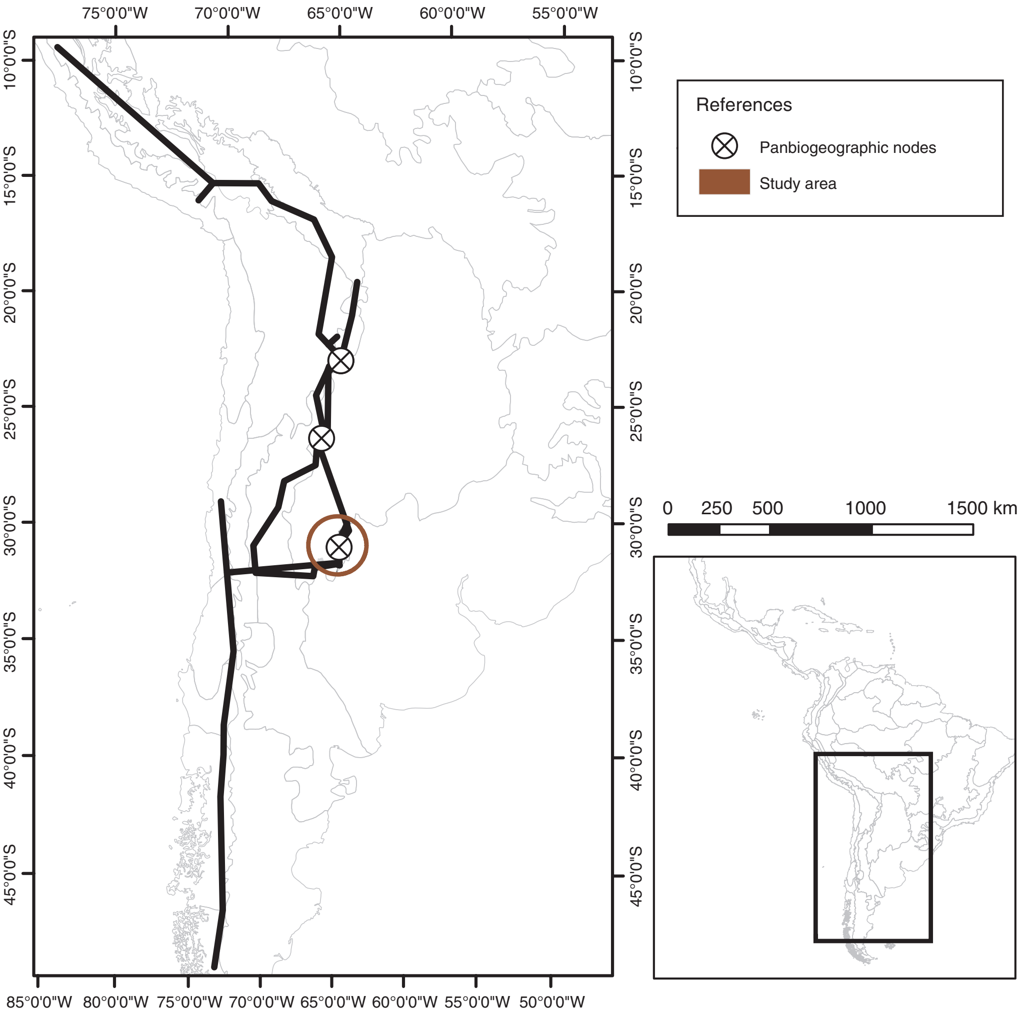

Fig. 9. Nodes conformed by Generalised tracks 4, 6 and 7.

biogeographical relationships among different areas of endemism. In this sense, the connections resulting from the multiple intersecting generalised tracks forming several nodes for the study area show a complex geobiotic origin. According to the spatial scale of the areas occupied by generalised tracks and the nesting effect that they present, it is possible to establish a nodal hierarchy reflecting evolutionary events that led to the mixture of biotic components of different times (Miguel-Talonia and Escalante 2013).

The main node linking older components, at a biogeographic region level, is the result of the intersection between the Neotropical and Andean tracks (Fig. 10). The relationship of the highland grasslands of the central Pampean Ranges with areas of the Neotropical region is in accordance with the traditional classification of these environments as belonging to the biogeographic province of Chaco, Chacoan subregion, Neotropical region; however, generalised tracks of Andean type (Generalised tracks 5 and 6) demonstrated the relationships of the highland grasslands of the central Pampean Ranges with areas of environments of Andean–Patagonian type, as has been indicated by the many observations made previously by different authors (Kurtz 1904; Nores and Yzurieta 1983; Cabido *et al.* 1998; Arana *et al.* 2013).

This could be evidence that in the highland grasslands of the central Pampean Ranges of Argentina, an interaction between biotas with different evolutionary histories occurs. This interaction would be the result of historical–ecological changes that allowed the confluence, exchange and hybridisation of biotas from different origin (Escalante 2009). In this particular case, the confluence would be between a biota with an essentially Neotropical distribution, with evolutionary historical affinities related to areas of East Gondwanan paleo continent, and a biota from biogeographic Andean region, which is more related to the areas of West Gondwanan paleo continent (Morrone 2004*b*). This can be observed in the area designated by Morrone (2004*a*) as South American transition zone, which is recognised by the concentration of multiple nodes between Andean and Neotropical generalised tracks. This area corresponds to the boundary between these two regions, Andean and Neotropical, ranging along the arid diagonal of South America, from the Venezuelan Andes to the biogeographic province of Monte in western central Argentina.

Table 1. Endemic taxa *v.* generalised tracks

Taxon or species	Generalised track						
	1	2	3	4	5	6	7
Lissamphibia							
Pleurodema cordobae		X					
Pleurodema kriegi		X					
Odontophrynus achalensis		X					
Melanophryniscus estebani	X						
Rhinella achalensis	X						
Lepidosauria							
Ophiodes vertebralis			X				
Aspronema dorsivittatum			X				
Pantodactylus schreibersii schreibersii			X				
Pristydactilus achalensis		X					
Anops kingii			X				
Liophis anomalus			X				
Aves							
Theristicus caudatus			X				
Vultur gryphus					X		
Geranoaetus polyosoma					X		
Bolborhynchus aymara							X
Aeronautes andecolus					X		
Colaptes campestris			X				
Cinclodes comechingonus	X						
Cinclodes olrogi	X						
Cinclodes atacamensis schocolatinus	X						
Geositta rufipennis ottowi	X						
Leptasthenura fuliginiceps paranensis							X
Asthenes modesta cordobae		X					
Asthenes sclateri							X
Tarphonomus certhioides			X				
Tachycineta leucorrhoa			X				
Catamenia inornata cordobensis		X					
Poospiza hypochondria							X
Phrygilus alaudinus							X
Phrygilus plebejus naroskyi		X					
Phrygilus unicolor cyaneus		X					
Agriornis montana fumosus		X					
Anairetes parulus					X		
Muscisaxicola rufivertex achalensis		X					
Molothrus rufoaxillaris			X				
Sturnella loica						X	
Lycopodiidae							
Isoëtes hieronymii		X					
Selaginella microphylla			X				
Polypodiidae							
Amauropelta achalensis				X			
Magnoliidae							
Alternanthera pumila		X					
Berberis hieronymi		X					
Escallonia cordobensis	X						
Apurimacia dolichocarpa		X					
Lathyrus magellanicus var. *magellanicus*						X	
Achyrocline alata			X				
Grindelia globulariifolia		X					
Hypochaeris caespitosa	X						
Hieracium cordobense	X						
Lucilia acutifolia			X				
Noticastrum argenteum							X
Ophryosporus axilliflorus				X			
Perezia multiflora ssp. *multiflora*							X
Proustia cuneifolia var. *mendocina*							X
Senecio retanensis	X						
Senecio achalensis		X					
Siegesbeckia serrata				X			
Stevia achalensis				X			
Hysterionica dianthifolia var. *danthifolia*		X					
Polylepis australis							X
Maytenus boria						X	

(*continued next page*)

Table 1. (*continued*)

Taxon or species	Generalised track 1	2	3	4	5	6	7
Hypericum connatum			X				
Aa achalensis	X						
Puya spathacea							X
Tillandsia argentina				X			
Jarava plumosa			X				
Nassella stuckertii		X					
Nassella nidulans	X						
Nassella niduloides							X
Nassella hunzikeri	X						
Nassella pseudopampagrandensis							X
Nothoscordum achalense		X					
Koeleria kurtzii					X		
Agrostis imberbis						X	
Poa ligularis var. *resinulosa*						X	
Poa stuckertii	X						
Muhlenbergia torreyi							X
Muhlenbergia peruviana							X
Bouteloua simplex							X
Deyeuxia hieronymi							X
Festuca hieronymi							X
Festuca dissitiflora							X
Zephyranthes longistyla		X					

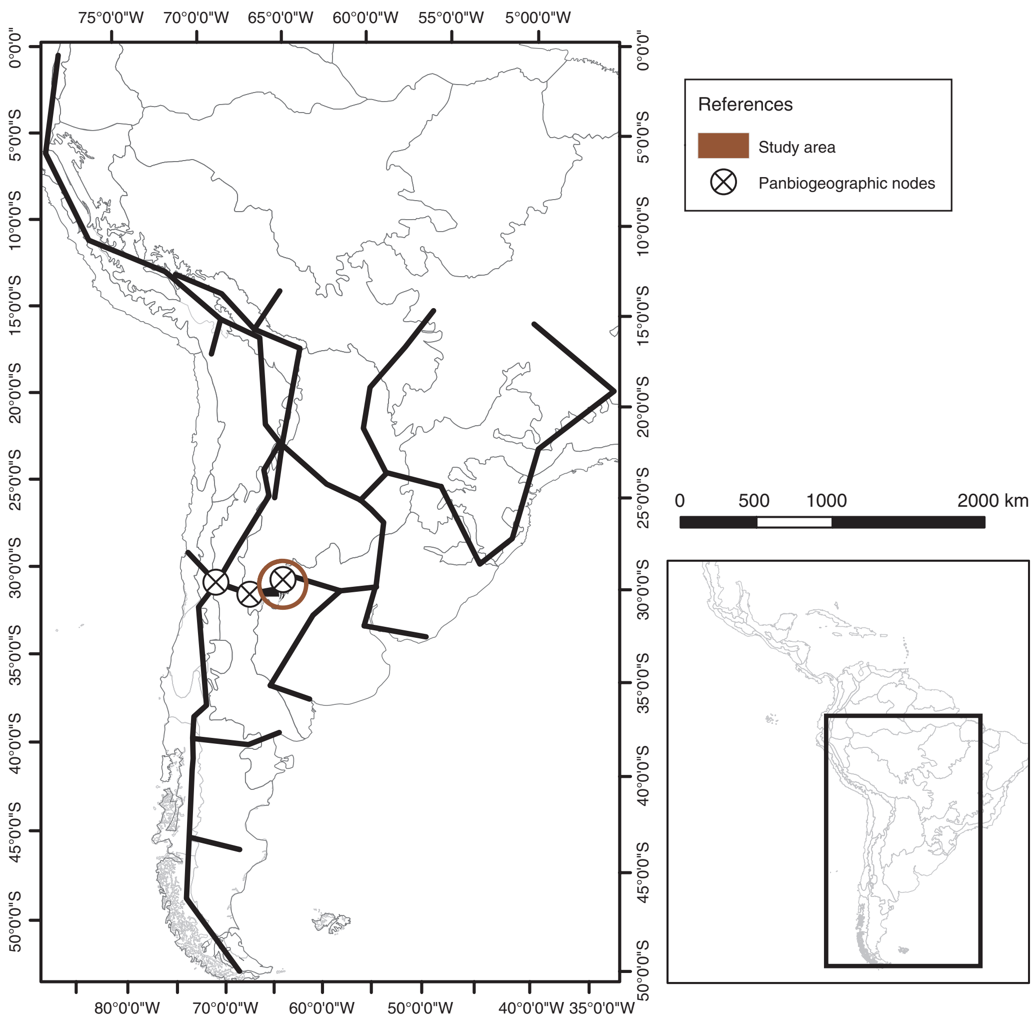

Fig. 10. Nodes conformed by Generalised tracks 3 and 5.

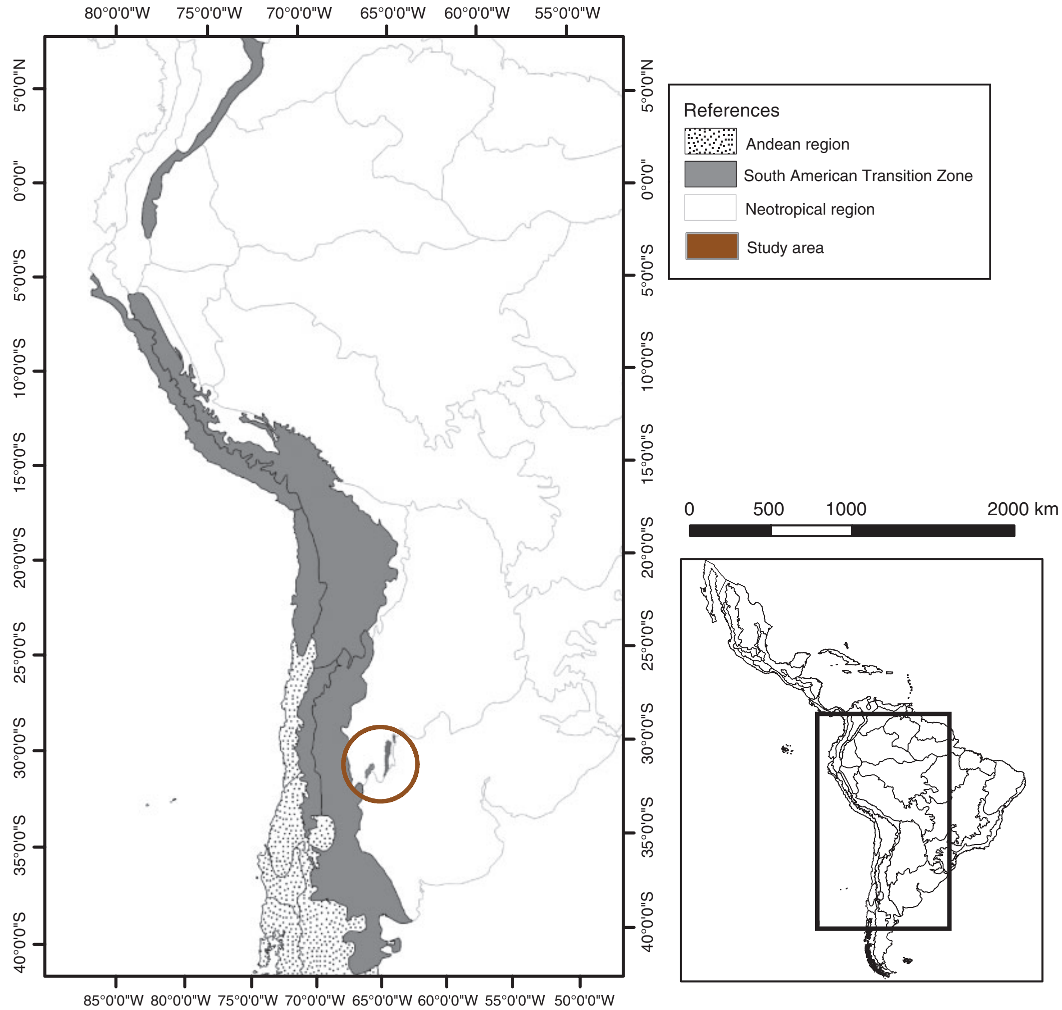

Fig. 11. Comechingones province included in the South American transition zone.

The Neotropical biota with Chacoan origin and that is related to arid environment could have evolved with possibilities of extending over the arid diagonal of South America. So much so that biogeographic affinities of the Prepuna district, currently belonging to the province of Monte (Morrone and Ezcurra 2016), but with phytogeographic provincial status according to Cabrera (1971), made Cabrera describe it as belonging to the Chacoan dominion, whereas Morrone (2000) incorporated it into the province of Monte. Given the recognition of this hybrid zone, different nodes obtained outside the study area as a result of the intersection of these major generalised tracks (Fig. 10) are interpreted here as Andean and Neotropical biotic components that extend beyond the limits allotted to these two regions.

The generalised track linking the endemic area of the highland grasslands of Pampean Ranges, which has been analysed here, with Puna and Monte of the South American transition zone (Fig. 8), supports the inclusion of highland grasslands and tabaquillo forests of the central Pampean Ranges of Argentina as belonging to this hybrid zone of transitional character (Morrone 2004*b*). Thus, the node formed by the intersection of the generalised Andean track, the South American transition zone generalised track and the Yunguean generalised track (Fig. 9) could be the result of the influence of Andean elements in the South American transition zone, interacting with its endemic biota, and with an already established Neotropical biota.

In addition, the type of environments occupied by the taxa of the Yunguean ancestral biotic component (Generalized track 4) could indicate that the biogeographical relationships between the area of highland grasslands and tabaquillo forests of central Pampean Ranges of Argentina and the biogeographic province of Yungas, would happen especially with the Montane Forest district. Arana *et al*. (2011, 2013), in a track and cladistic analyses conducted using the biota of ferns and lycophytes of the central Pampean Ranges of Argentina, also proposed the relationships between the studied area and the sub-Andean mountains, where these Yunguean environments develop.

The establishment and survival of this ancestral biotic component of fern and lycophyte flora, supported with other different taxa, associated with a wetter climate in the study area, would have been favoured by the uplifting of central Pampean Ranges, which, given their environmental heterogeneity, would allow the development of different microclimates (Moran 1995).

Conclusions

The results obtained here indicated that the area of highland grasslands and tabaquillo forests of central Pampean Ranges of Argentina corresponds to a natural unit with a unique identity, given the existence of an endemic biota of diverse lineages. Besides, this area has biogeographic relationships with the Neotropical region as well as with the Andean region, and, therefore, it is possible to assign a hybrid evolutionary origin to it, with numerous nodes. Added to this, the data showed biogeographical relationships with the South American transition zone.

Considering that regionalisation schemes aim to define natural units, which would be given by areas with the same geobiotic and evolutionary history (Morrone 2001*a*; Escalante 2009), it is here proposed to categorise the endemism area of highland grassland and tabaquillo forests of the central Pampean Ranges of central Argentina as a biogeographic province belonging to the South American transition zone (Fig. 11). We propose the area as a new province and not as a district within another province of the South American transition zone because we could not establish relationships between the studied area and any specific province of the transition zone. The obtained generalised tracks connect, in the same way, the biota of the area of highland grasslands and tabaquillo forests of the central Pampean Ranges of central Argentina with those of the Monte and Puna biogeographical provinces (Figs 6, 8). Further studies are necessary to establish with which biogeographic province of the South American transition zone the highland grasslands and tabaquillo forests of de central Pampean Ranges of central Argentina are more closely related to, or even to establish the relationships of other areas of highland grasslands in Pampean Ranges (such as Calchaquíes Ranges, the mountains of Aconquija and the mountains of Acasti, Sierra Aguilar, Alfarcito east of Guayatayoc, and along Río Grande de San Juan in the extreme north-eastern Jujuy) with the proposed province.

Area taxonomy

Comechingones province

- Alpine grasslands of Subandean zone Kurtz 1904: 273.
- Tabaquillo forests of Subandean zone Kurtz 1904: 281.
- High-altitude grasslands and woodlands Luti *et al*. 1979: 342.

Diagnosis

Altitude grasslands with predominance of genera *Festuca* and *Nassella* and woodlands with predominance of *Polylepis australis* ('tabaquillo') and *Maytenus boaria* ('maitén') in mountainous regions of central Argentina, between 29° and 33°S, in Córdoba and San Luis provinces, at an altitude above 1000 m.

Endemic taxa: LYCOPODIIDAE. Isoëtaceae: *Isoëtes hieronymii* (Arana *et al*. 2013). MAGNOLIIDAE. Amaranthaceae: *Alternanthera pumila* (Chiapella and Demaio 2015); Amaryllidaceae: *Nothoscordum achalense* (Sassone *et al*. 2014; Chiapella and Demaio 2015); *Zephyranthes longistyla* (Ravenna 2005; Chiapella and Demaio 2015); Asteraceae: *Grindelia globulariifolia* (Chiapella and Demaio 2015), *Hieracium cordobense* (Oggero and Arana 2012; Chiapella and Demaio 2015), *Hypochaeris caespitosa* (Oggero and Arana 2012; Chiapella and Demaio 2015), *Hysterionica dianthifolia* var. *dianthifolia* (Chiapella and Demaio 2015), *Senecio retanensis* (Cabido and Acosta 1985; Zuloaga and Morrone 1999; Chiapella and Demaio 2015); Berberidaceae: *Berberis hieronymi* (Orsi 1976); Escalloniaceae: *Escallonia cordobensis* (Cabido and Acosta 1985; Zuloaga and Morrone 1999; Chiapella and Demaio 2015); Fabaceae: *Apurimacia dolichocarpa* (Chiapella and Demaio 2015); Orchidaceae: *Aa achalensis* (Vischi *et al*. 2004); Poaceae: *Nassella hunzikeri* (Oggero and Arana 2012; Cialdella *et al*. 2013; Chiapella and Demaio 2015), *Nassella nidulans* (Oggero and Arana 2012; Cialdella *et al*. 2013; Chiapella and Demaio 2015), *Nassella stuckertii* (Oggero and Arana 2012; Cialdella *et al*. 2013; Chiapella and Demaio 2015), *Poa stuckertii* (Oggero and Arana 2012; Chiapella and Demaio 2015). VERTEBRATA. Bufonidae: *Rhinella achalensis* (Di Tada and Bucher 1996; Céspedez 2008; Lescano *et al*. 2015), *Melanophryniscus estebani* (Di Tada and Bucher 1996; Céspedez 2008; Lescano *et al*. 2015); Cycloramphidae: *Odontophrynus achalensis* (Di Tada and Bucher 1996; Céspedez 2008; Lescano *et al*. 2015); Leiuperidae: *Pleurodema cordobae* (Valetti *et al*. 2009, 2013), *Pleurodema kriegi* (Di Tada and Bucher 1996; Céspedez 2008; Ferraro and Casagranda 2009; Lescano *et al*. 2015); Leiosauridae: *Pristydactilus achalensis* (Cei 1986; Di Tada and Bucher 1996; Céspedez 2008); Furnariidae: *Asthenes modesta cordobae* (Nores 1986), *Cinclodes atacamensis schocolatinus* (Partridge 1953, Nores and Yzurieta 1983), *Cinclodes comechingonus* (Navas and Camperi 1999), *Cinclodes oustaleti olrogi* (Nores and Yzurieta 1979*b*), *Geositta rufipennis ottowi* (Darrieu and Camperi 2006), *Muscisaxicola rufivertex achalensis* (Nores and Yzurieta 1983); Thraupidae: *Catamenia inornata cordobensis* (Nores and Yzurieta 1983), *Phrygilus plebejus naroskyi* (Nores and Yzurieta 1983), *Phrygilus unicolor cyaneus* (Nores and Yzurieta 1983); Tyrannidae: *Agriornis montana fumosus* (Nores and Yzurieta 1983).

Etymology

The name of this biogeographic province is in honour of the native people that belong to two ethnic groups that inhabited the Pampean Ranges of Córdoba and San Luis, namely the Hênîa and Kâmîare people, whom the Spaniard conquerors collectively designated as Comechingones.

Regarding the previous names given to the area, we propose a new one because the previous names given by Kurtz could produce a misinterpretation of the area; alpine is a direct reference to the Alps, an extensive mountain-range system that lies entirely in Europe; and Subandean is a subprovince of the Patagonian province of the Andean region. The name given by Luti *et al*. (1979) is unsuitable, imprecise and vague, because there are many high-altitude grasslands that belong to different biogeographic units.

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