Studies on Neotropical Fauna and Environment
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/nnfe20

Historical relationships among Argentinean biogeographic provinces based on mygalomorph spider distribution data (Araneae: Mygalomorphae)

Nelson Ferretti[a], Fernando Pérez-Miles[b] & Alda González[a]
[a] Centro de Estudios Parasitológicos y de Vectores CEPAVE (CCT-CONICET- La Plata), (UNLP), La Plata, Argentina
[b] Facultad de Ciencias, Sección Entomología, Montevideo, Uruguay
Published online: 13 May 2014.

Studies on Neotropical Fauna and Environment, 2014
http://dx.doi.org/10.1080/01650521.2014.903616

ORIGINAL ARTICLE

Historical relationships among Argentinean biogeographic provinces based on mygalomorph spider distribution data (Araneae: Mygalomorphae)

Nelson Ferretti[a]*, Fernando Pérez-Miles[b] & Alda González[a]

[a]*Centro de Estudios Parasitológicos y de Vectores CEPAVE (CCT–CONICET– La Plata), (UNLP), La Plata, Argentina;* [b]*Facultad de Ciencias, Sección Entomología, Montevideo, Uruguay*

(*Received 25 July 2013; accepted 10 March 2014*)

The present study used the previously defined biogeographic provinces from Argentina as the starting point for a parsimony analysis of endemicity and cluster analysis. The goal of the study was to use a dataset of distributional patterns of mygalomorph spiders from Argentina to evaluate the historical relationships of the biogeographic provinces. The analyses showed the following relationships: Yungas and Puna; Pampa and Chaco, Monte and Prepuna; Parana Forest and *Araucaria angustifolia* Forest; Central and Subandean Patagonia. Biogeographical regionalizations are useful as general reference models and their heuristic value should be explored by examining the geographical distribution of other taxa.

Keywords: Argentina; biogeography; Araneae; biogeographical regionalization

Introduction

South America has been subject to many biogeographical studies due to the particular distribution patterns of its flora and fauna, especially the austral region, which has been considered as different from the rest of South America (Monrós 1958; Jeannel 1967; Kuschel 1969). Consequently, the biota of Southern South America has always captivated the minds of those interested in biogeography. Several theories have been proposed to explain the origin of this region's biota and its relationship with other temperate areas such as Australia, New Zealand, and South Africa (Crisci et al. 1991). Biogeographic analyses based on the distribution of South American monophyletic groups represent, in turn, operative tests directed to corroborate or refute area relationship hypotheses.

Biotic components are sets of spatio-temporally integrated taxa that characterize a biogeographic area. They are historical entities, so their unity is the result of their common history, and identifying them is a key element in understanding evolution (Morrone 2006). Regionalization studies attempt to divide an area into regions by studying the distribution of its biotic components and applying an analytical method (Nori et al. 2011). Areas of endemism are the smallest units of biogeographical analysis and can be defined as groupings of organisms with restricted distributions caused by historical factors (Harold & Mooi 1994; Morrone 1994; Linder 2001). These areas may be especially important because they maintain unique taxa due to biodiversity production in the past and also prevent the extinction of species that were once widespread (Brooks et al. 1992). An important property of such areas is that they may be hierarchically organized, with endemic areas that share common histories grouped into biogeographic provinces, which in turn can be grouped to form biogeographic regions (Morrone 2006). Many biogeographic proposals that describe different regions, provinces, or domains in South America have been put forward (Cabrera 1971; Cabrera & Willink 1973; Ab'Saber 1977; Hueck 1978; Willink 1991; Morrone 2000, 2001a, 2006). Although based on the considerable experience of one or more specialists, most of these compilations are qualitative and/or based solely on the authors' common sense. Consequently, the validity of many of the areas proposed in these studies is difficult to reformulate and/or assess (Navarro et al. 2009).

Morrone (2001a, 2006) made the first effort towards a standard biogeographical classification in several levels of endemism for Latin America using many biological groups, and compiled a list of apparently endemic taxa, which includes some insect species. In this classification, Argentina is included in the Neotropical Region, the South American Transition Zone and the Andean Region and is divided into 11 biogeographic provinces coincident with main physiognomies of the biome: Yungas, Chaco, Pampa, Parana Forest and *Araucaria angustifolia* Forest

*Corresponding author. Email: nferretti@conicet.gov.ar

(Neotropical Region) from central to northeastern Argentina; Puna, Prepuna and Monte (South American Transition Zone) from northern to central western Argentina along the Andes mountain chain; and Magellanic Forest, Central Patagonia and Subandean Patagonia (Andean Region) from central western to southern Argentina.

Although Argentina has biogeographic relevance due to the inclusion of three different Regions (one of them a Transition Zone), few contributions analyze the historical relationships between the areas of endemism proposed for Argentina. The most relevant studies that covered fully or in part the Argentinean territory include the study of Roig-Juñent et al. (2006) of the historical relations of arid and semi-arid areas in South America based on arthropod distribution. Roig-Juñent et al. (2003) evaluated the relationships of areas of endemism of Argentina, mainly in the pre-Andean zone based on Coleoptera and Scorpiones. López et al. (2008) provided a geographic framework of Argentina based on the distribution patterns of freshwater fishes. Sigrist & de Carvalho (2009) examined the historical relationships among areas of endemism in the Neotropics (but considering mainly Amazonian areas). Ciprandi Pires & Marinoni (2010) evaluated the historical relationships among Neotropical endemic areas based on Diptera (*Sepedonea*) distribution data. Urtubey et al. (2010) analyzed the biotic evolution of the South American Transition Zone based on Asteraceae distributional patterns; finally, de Carvalho et al. (2013) estimated the area relationships in South America based on distributional records of lizards (*Tropidurus*).

Mygalomorph spiders are well-suited models for biogeographical analysis (Ferretti et al. 2012a, 2012b). These spiders are distributed worldwide, but they are especially abundant in tropical regions and temperate austral regions of South America, southern Africa and Australasia (Raven 1985; Platnick 2013). They are long-lived and univoltine, and show high local endemicity. Moreover, mygalomorphs possess life-history traits that markedly differ from other spiders. For example, some species live for 15–30 years and require 5–6 years to reach reproductive maturity (Main 1978). They are habitat specialists and females and juveniles are sedentary (Main 1978; Coyle & Icenogle 1994). These life-history traits promote geographic isolation through fragmentation over space and time, resulting in a large number of taxa that have small geographical distributions (Bond et al. 2006). Biogeographically, they are informative because mygalomorphs are animals with poor vagility, limited dispersal mechanisms and sedentary habits (Griswold 1985; Raven 2010). These biological characteristics of the Mygalomorphae make them a promising group for biogeographical studies. Unfortunately, to date, there have been few formal contributions to the biogeography of mygalomorph spiders. Bond et al. (2006) used an ecological biogeographical approach to evaluate population extinction while other studies focused on molecular biogeography inferred from the phylogeny of a single species from the Nearctic region (Hendrixson & Bond 2007; Starrett & Hedin 2007). Some works deal with cladistic biogeography of Brazilian species, mainly of the Theraphosidae (Bertani 2001, 2012; Guadanucci 2011). Recently, Ferretti et al. (2012a) used a panbiogeographical approach that involved all mygalomorph species from the peripampasic orogenic arc in southern South America, and Ferretti et al. (2012b) evaluated the historical biogeography of a Neotropical tarantula according to an event-based method and spatial analysis of vicariance.

The objective of this study is to test previous hypotheses of historical relationships among areas proposed for the Argentinean territory (southern South America) (Morrone 2001a, 2006) by using parsimony analysis of endemicity (PAE) and a cluster analysis based on the distributional records of the Mygalomorphae spiders.

Materials and methods

Areas

The units of the analysis were the 11 biogeographic provinces of Argentina (Figure 1), which have been identified by analyzing distributional patterns of several plant and animal taxa (Morrone 2001a, 2006): Yungas, Chaco, Pampa, Parana Forest, *Araucaria angustifolia* Forest, Puna, Prepuna, Monte, Magellanic Forest, Central Patagonia and Subandean Patagonia.

Species and records

All analyses employed the distributional dataset based on an exhaustive survey of the literature and the most representative Argentinean collections for Mygalomorphae, accessed to review specimen records and identifications. The accessed museums were: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Ar), Buenos Aires and Museo de La Plata (MLP), La Plata. We obtained 772 records of mygalomorph spiders belonging to 55 species (Table 1) present in Argentina. Species represented the families Dipluridae Simon 1889, Hexathelidae Simon 1892, Idiopidae Simon 1889, Migidae Simon 1889, Mecicobothriidae Holmberg 1882, Microstigmatidae Roewer 1942, Nemesiidae Simon 1889 and

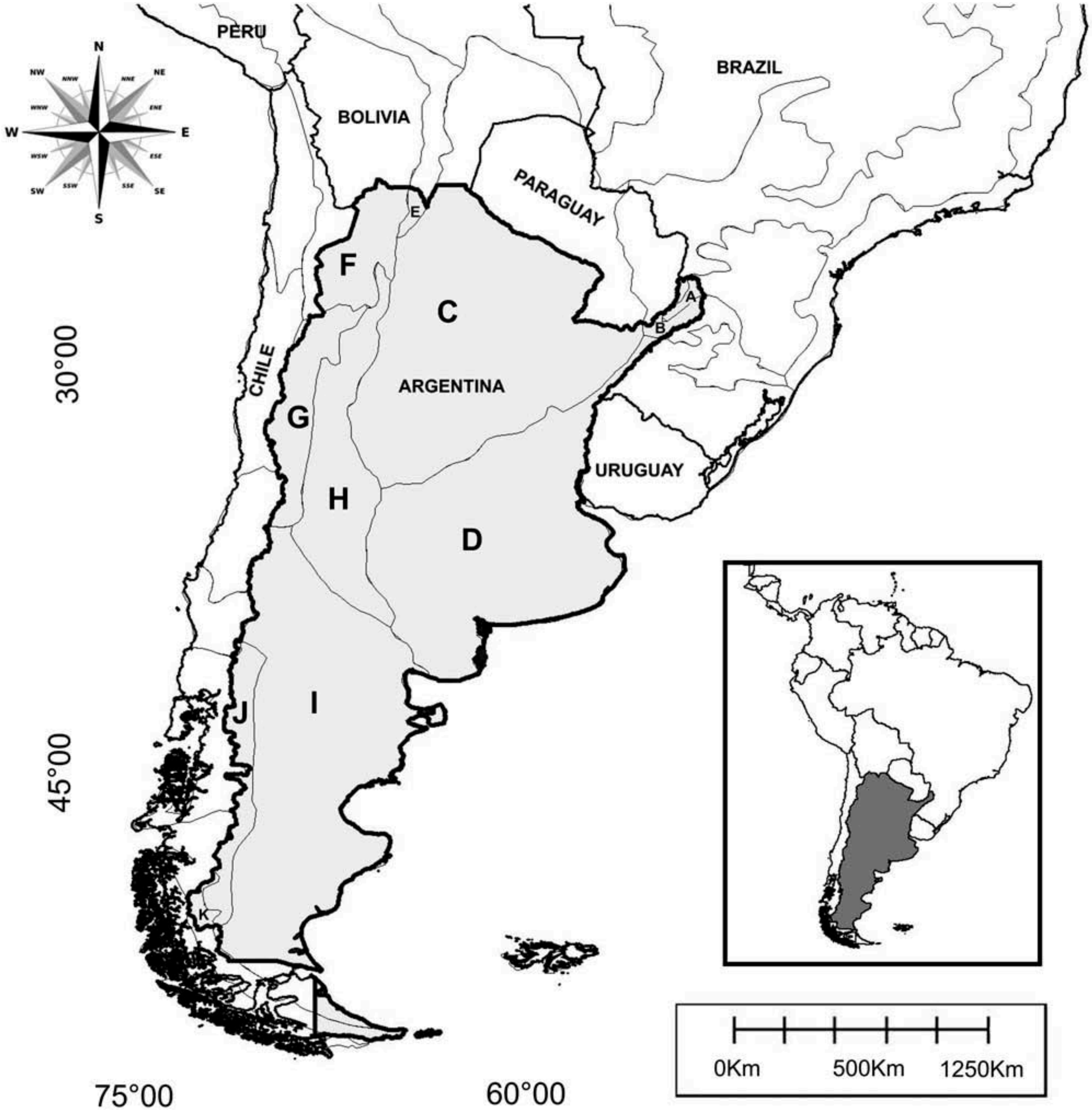

Figure 1. Southern South America, Argentina. Biogeographic provinces analyzed with PAE and multivariate analysis. (A) *Araucaria angustifolia* Forest; (B) Parana Forest; (C) Chaco; (D) Pampa; (E) Yungas; (F) Puna; (G) Prepuna; (H) Monte; (I) Central Patagonia; (J) Subandean Patagonia; (K) Magellanic Forest.

Theraphosidae Thorell 1869. For species with wide distributions occurring in other countries, we only consider the presence data in the study area. The species *Acanthogonatus birabeni* Goloboff 1995, *A. pissii* (Simon 1889), *A. parana* Goloboff 1995, *Chaco patagonica* Goloboff 1995, *C. sanjuanina* Goloboff 1995, *C. tecka* Goloboff 1995, *Diplura argentina* (Canals 1931), *D. parallela* (Mello-Leitão, 1923) and *Neocteniza spinosa* Goloboff 1987 are known only for their type locality. Because this type of data does not contribute to the score of the PAE, they were excluded from the analyses.

Biogeographic analyses

PAE (Rosen 1988; Rosen & Smith 1988) is a historical biogeography method using presence/absence data to recover natural distribution patterns of organisms (Morrone & Crisci 1995; Crisci et al. 2000). PAE was

Table 1. List of Mygalomorphae species from Argentina used in the biogeographical analysis and the biogeographic provinces with occurrences.

Species	Biogeographic provinces
Acanthogonatus centralis (Goloboff 1995)	Chaco – Monte – Pampa
Acanthogonatus confusus (Goloboff 1995)	Subandean Patagonia
Acanthogonatus fuegianus (Simon 1902)	Central Patagonia – Subandean Patagonia – Pampa
Acanthogonatus notatus (Mello-Leitão 1940)	Central Patagonia – Subandean Patagonia
Acanthogonatus patagonicus (Simon 1905)	Central Patagonia – Subandean Patagonia
Acanthoscurria chacoana (Brèthes 1909)	Chaco
Acanthoscurria cordubensis (Thorell 1894)	Chaco – Monte – Yungas
Acanthoscurria sternalis (Pocock 1903)	Chaco – Monte – Puna – Yungas
Acanthoscurria suina (Pocock 1903)	*Araucaria angustifolia* Forest – Chaco – Pampa – Parana Forest
Calathotarsus simoni (Schiapelli & Gerschman 1975)	Pampa
Catumiri argentinense (Mello-Leitão 1941)	Chaco – Monte – Pampa
Chaco obscura (Tullgren 1905)	Chaco – Yungas
Chaco tucumana (Goloboff 1995)	Chaco – Puna
Chilehexops misionensis (Goloboff 1989)	Parana Forest
Cyriocosmus versicolor (Simon 1897)	Chaco
Diplothelopsis bonariensis (Mello-Leitão 1938)	Central Patagonia – Chaco – Monte – Pampa – Subandean Patagonia
Diplothelopsis ornata (Tullgren 1905)	Chaco – Monte – Pampa – Subandean Patagonia
Diplura paraguayensis (Gerschman & Schiapelli 1940)	*Araucaria angustifolia* Forest – Pampa – Parana Forest
Euathlus truculentus (Koch 1875)	Central Patagonia – Chaco – Prepuna – Puna – Subandean Patagonia
Eupalaestrus campestratus (Simon 1891)	*Araucaria angustifolia* Forest – Parana Forest
Eupalaestrus weijenberghi (Thorell 1894)	Chaco – Pampa – Parana Forest
Grammostola anthracina (Koch 1842)	Chaco – Pampa
Grammostola burzaquensis (Ibarra-Grasso 1946)	Pampa
Grammostola chalcothrix (Chamberlin 1917)	Chaco – Monte
Grammostola doeringi (Holmberg 1881)	Central Patagonia – Monte – Pampa
Grammostola grossa (Ausserer 1871)	Chaco – Pampa – Parana Forest
Grammostola inermis (Mello-Leitão 1941)	Central Patagonia – Chaco – Monte
Grammostola pulchripes (Simon 1891)	Chaco – Pampa – Yungas
Grammostola vachoni (Schiapelli & Gerschman 1961)	Central Patagonia – Chaco – Monte – Pampa
Homoeomma uruguayense (Mello-Leitão 1946)	Pampa
Homoeomma elegans (Gerschman & Schiapelli 1958)	Parana Forest
Idiops clarus (Mello-Leitão 1946)	*Araucaria angustifolia* Forest – Chaco – Pampa
Idiops hirsutipedis (Mello-Leitão 1941)	Chaco – Parana Forest
Ischnothele annulata (Tullgren 1905)	Chaco
Lycinus longipes (Thorell 1894)	Central Patagonia – Chaco – Monte –Prepuna
Mecicobothrium thorelli (Holmberg 1882)	Pampa
Melloleitaoina crassifemur (Gerschman & Schiapelli 1960)	Chaco – Monte – Yungas
Neocteniza australis (Goloboff 1987)	Chaco – Pampa – Parana Forest
Neocteniza chancani (Goloboff & Platnick 1992)	Chaco
Neocteniza minima (Goloboff 1987)	Chaco
Neocteniza toba (Goloboff 1987)	Chaco – Yungas
Paraphysa scrofa (Molina 1788)	Central Patagonia – Prepuna – Puna – Subandean Patagonia
Plesiopelma longisternale (Schiapelli & Gerschman 1942)	Chaco – Monte – Pampa – Parana Forest
Pycnothele modesta (Schiapelli & Gerschman 1942)	Chaco – Pampa
Rachias timbo (Goloboff 1995)	*Araucaria angustifolia* Forest – Parana Forest
Scotinoecus fasciatus (Tullgren 1901)	Central Patagonia
Stenoterommata crassistyla (Goloboff 1995)	Pampa
Stenoterommata iguazu (Goloboff 1995)	*Araucaria angustifolia* Forest – Parana Forest
Stenoterommata palmar (Goloboff 1995)	Chaco – Pampa
Stenoterommata platensis (Holmberg 1881)	*Araucaria angustifolia* Forest – Pampa – Parana Forest
Stenoterommata quena (Goloboff 1995)	Chaco
Stenoterommata tenuistyla (Goloboff 1995)	Pampa
Stenoterommata uruguai (Goloboff 1995)	*Araucaria angustifolia* Forest – Parana Forest
Vitalius paranaensis (Bertani 2001)	*Araucaria angustifolia* Forest – Parana Forest
Xenonemesia platensis (Goloboff 1989)	Pampa

implemented to identify patterns of area relationships in Argentina. We adopted the protocols proposed by Morrone (1994), employing the biogeographic provinces for Argentina defined by Morrone (2001a, 2006) as operational geographic units. For this purpose, we analyzed the binary matrix with TNT 1.1

package (Goloboff et al. 2003), using a traditional heuristic search using collapsing rule "tbr" (tree bisection reconnection) (Goloboff et al. 2008).

Multivariate methods can be used as an alternative to PAE for classifying biotas. Assemblages can be identified subjectively by assessing how far the biota in one area corresponds to that in another, and thereby grouping areas accordingly. Some assemblages are closer in taxonomic composition, which can be expressed statistically in terms of cluster hierarchies or relative biotic distances. The resulting patterns are expressed in numerous ways, cluster diagrams being the most common (Rosen 1988; López et al. 2008; Nori et al. 2011). In order to perform the cluster analysis, we used the Jaccard association index to construct the similarity matrix (Hubalek 1982; Murguía & Villaseñor 2003; López et al. 2008) and UPGMA (unweighted pair-group method using arithmetic averages) was applied to obtain the clustering graph (dendrogram). Cluster analysis was performed using the program Past (Hammer et al. 2009). We also computed the co-phenetic coefficient (Sokal & Rohlf 1962) to evaluate the degree of distortion of the analysis.

Results

The PAE resulted in 15 trees of length 89, consistency index of 0.618 and retention index of 0.558; the strict consensus of them had a length of 92 (Figures 2, 3). This cladogram shows a basal polytomy with three biogeographic provinces with remarkably different physiognomic characteristics: Yungas, Puna and Magellanic Forest. All remaining areas formed three distinct components. The first component comprised Central Patagonia and Subandean Patagonia (from Andean Region) defined by the species *Acanthogonatus notatus* and *A. patagonicus*. The second component comprised the Atlantic Forest areas (Parana Forest and *Araucaria angustifolia* Forest) from the Neotropical Region supported by the species *Eupalaestrus campestratus* and *Rachias timbo*. The third component comprised four areas belonging to Neotropical and the South American Transition zone, within which Pampa is nested and closely related to Chaco supported by the species *Grammostola anthracina, G. pulchripes, Pycnothele modesta* and *Stenoterommata palmar*. Note that in this component, Chaco and Pampa grouped with Monte (defined by the species *Acanthogonatus centralis* and *Grammostola chalcothrix*) and Prepuna, both from the South American Transition Zone.

The dendrogram (Figure 4) derived from the application of the Jaccard index presented three groups at a similarity level of approximately 0.12. Magellanic Forest was unresolved and joined the other clusters at the lowest level of similarity. Cluster C1 grouped Yungas and Puna. Cluster C2 included the biogeographic provinces of Parana Forest and *Araucaria angustifolia* Forest. Cluster C3

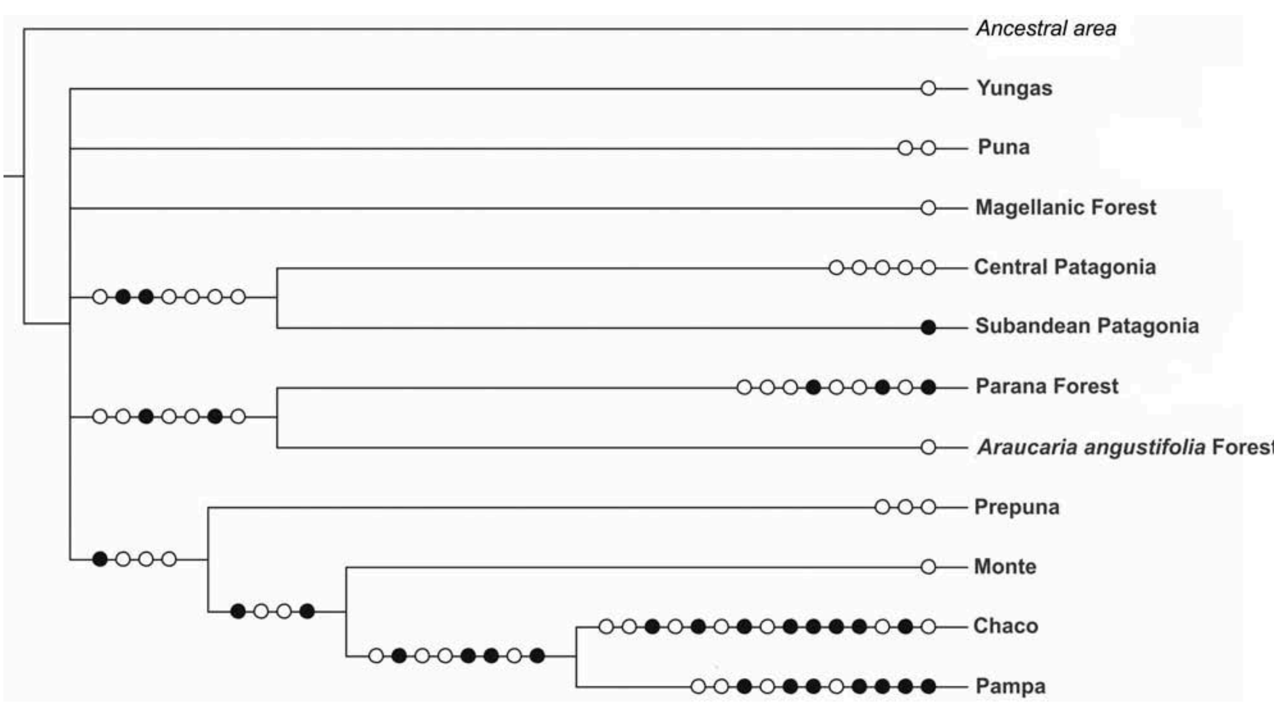

Figure 2. Consensus of the cladogram generated by parsimony analysis of endemicity based on the distribution of Mygalomorphae spiders from Argentina.

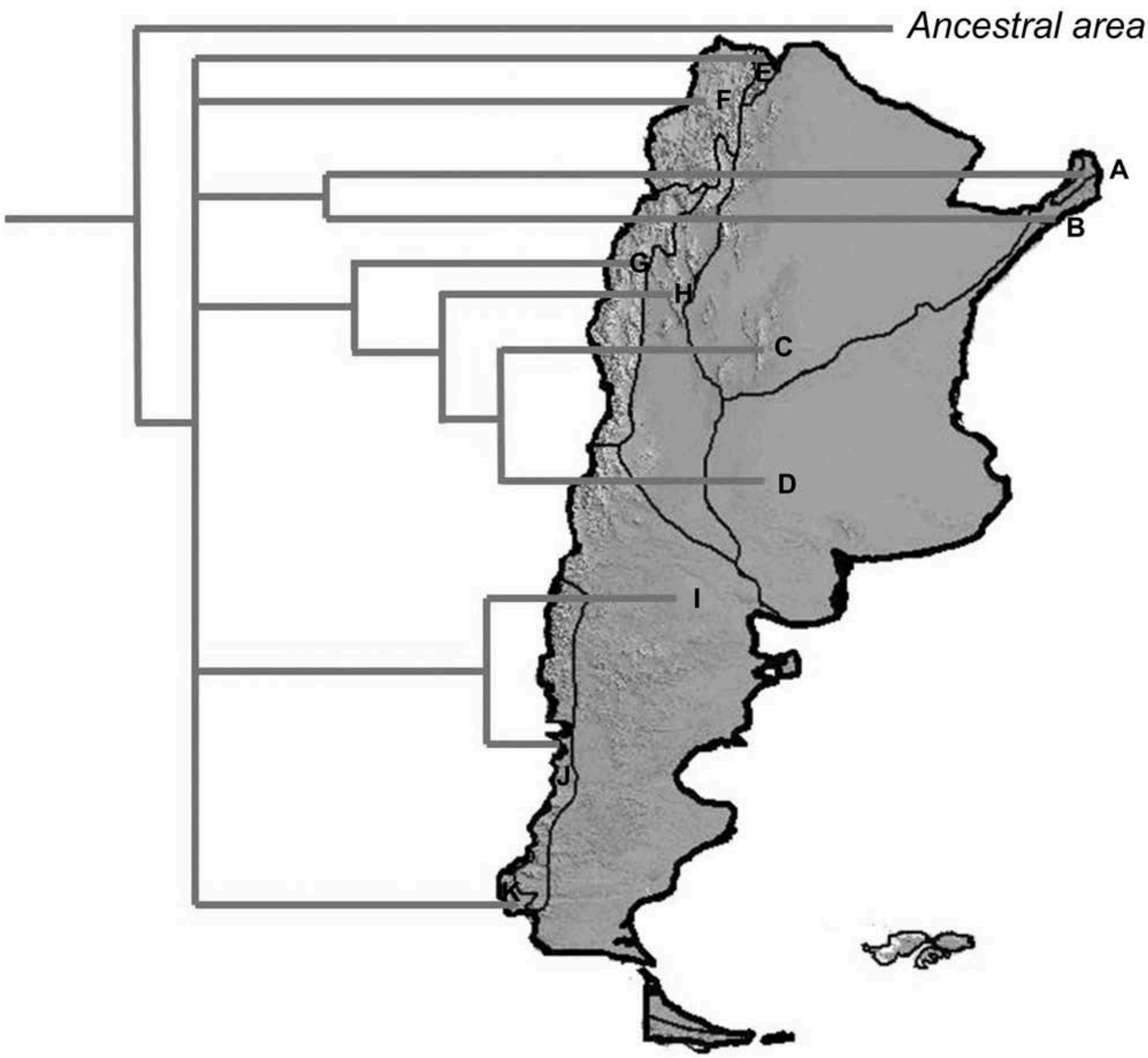

Figure 3. Schematic area relationships of Argentinean biogeographic provinces resulting from PAE based on the distribution of Mygalomorphae spiders. (A) *Araucaria angustifolia* Forest; (B) Parana Forest; (C) Chaco; (D) Pampa; (E) Yungas; (F) Puna; (G) Prepuna; (H) Monte; (I) Central Patagonia; (J) Subandean Patagonia; (K) Magellanic Forest.

appeared to be related to C2 and included Chaco, Pampa, Monte, Prepuna, Central Patagonia and Subandean Patagonia. Inside this cluster, Central Patagonia and Subandean Patagonia joined at the maximum level of similarity (0.50 of similarity). Then Pampa and Chaco joined at a similarity level of 0.40. Finally, Monte and Prepuna grouped at a level of approximately 0.30.

Discussion

The historical relationships obtained in this study in part adjusted to the scheme proposed by Morrone (2001a, 2006) for Argentina. Magellanic Forest, Yungas and Puna were unresolved in PAE. Moreover, from the cluster analysis this biogeographic province joined the other clusters at the lowest level of similarity. This could be explained by the presence of only one mygalomorph species reported for Magellanic Forest, *Scotinoecus fasciatus* (Hexathelidae). Also, Yungas and Puna joined at low similarity from the rest of the provinces (Chaco, Pampa, Monte, Prepuna, Central Patagonia, Subandean Patagonia, *Araucaria angustifolia* Forest and Parana Forest). This relationship of the Andean province of Yungas and Puna from the South

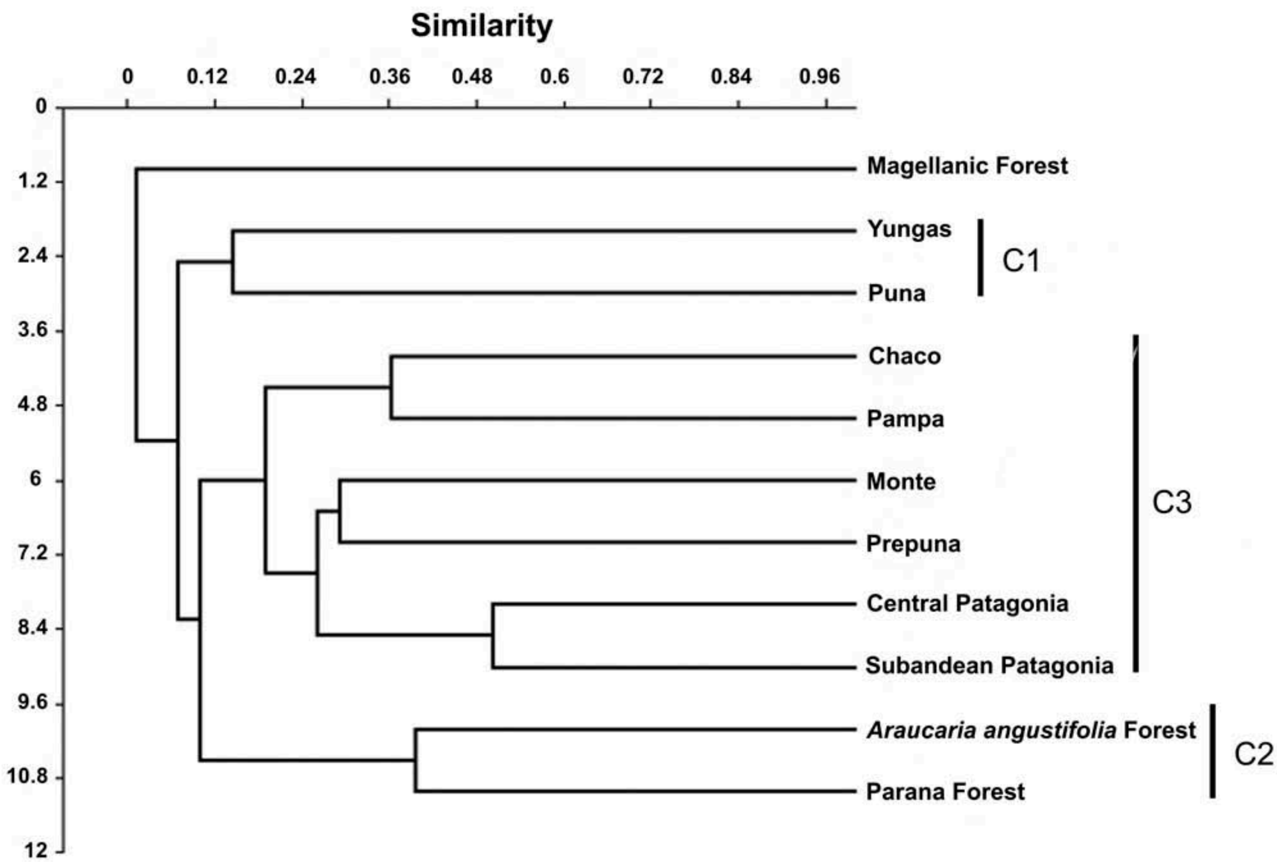

Figure 4. Cluster analysis of the biogeographic provinces from Argentina (UPGMA: unweighted pair-grouped method using arithmetic averages) resulting from the Jaccard matrix of 11 biogeographic provinces by 55 species. Cophenetic correlation value = 0.86. C1, C2 and C3: main groups detected by the analysis.

American Transition Zone has been recovered for lizards (*Tropidurus*) by de Carvalho et al. (2013).

From PAE and cluster analysis we obtained a group formed by the biogeographic provinces of Pampa and Chaco (Chacoan Subregion), Monte and Prepuna (both from the South American Transition Zone), and a closely related Pampa and Chaco. This relationship is based on the species *Grammostola anthracina, G. pulchripes* (both from Theraphosidae), *Pycnothele modesta* and *Stenoterommata palmar* from Nemesiidae. Numerous authors have considered the biogeographic province of Pampa as a complex from biotic components that originated from Monte and Chaco, and to a lesser extent from the Atlantic and Parana Forests (Porzecanski & Cracraft 2005; Morrone 2001a, 2006; Ciprandi Pires & Marinoni 2010). However, Morrone (1993, 2001a, 2006) proposed a close relationship between Pampa and Chaco. The historical relationship obtained from Prepuna and Monte (both from the South American Transition Zone) with Chaco and Pampa did not fit to the scheme of Morrone (2001a, 2006), but partially adjusted to the phytogeographic scenario from Cabrera & Willink (1973) for Argentina. Also, there is a sequential biotic impoverishment from the biogeographic province of Chaco through Pampa, with Monte being an intermediate province between both (Ringuelet 1956; Cabrera 1971, 1976; Ribichich 2002). The relationship between Chaco and Monte has been observed in arthropods by Roig-Juñent et al. (2003).

The separation of the high altitude biotas must have been due to the subsequent phases of the uplift of the Andes (Roig-Juñent et al. 2006). Between 14 and 11 Ma in the middle Miocene, the uplift of the Andes attained the Quechua phase, and the Andes reached altitudes of 2000 to 3000 m which generated the formation of high altitude environments such as the Puna (Roig-Juñent et al. 2006). Likewise, it resulted in the development of dry climates along the west coast of South America and on the east side of the Andes the development of xeric scrubs steppes such as the Monte in Argentina (Axelrod et al. 1991). At this time, 9.55–9.11 Ma, one of the greatest marine transgressions occurred (Pascual et al. 1996); it covered a large portion of the northern area of Patagonia and the Chaco plain and Pampean region, reaching the northern portion of the sub-Andean mountains and Northwestern Pampean mountains in Argentina. This probably isolated the areas of the Monte, together with the Chaco of the Patagonian areas (Pascual & Bondesio 1982). These two biotas, the Patagonian and the Chacoan, evolved under different climatic conditions, in accordance with their latitudinal location (Pascual et al. 1996). Porzecanski & Cracraft (2005) highlighted the physiognomic heterogeneity presented by the Pampa (which carries a mosaic of physiognomies of Monte, Chaco, and Atlantic Forest) and proposed the structural diversity of this area as a possible factor responsible for guaranteeing "hospitality" to dispersal of organisms coming from adjacent provinces.

Roig-Juñent & Debandi (2004) found that Pampa could be more closely related to Patagonia based on carabid beetles, a relation not observed in the present study. Roig-Juñent et al. (2003, 2006) observed a relation between the provinces of Chaco and Monte, based on the distributional patterns of arthropods, but unlike in the present study, the arthropod fauna of these provinces were more related to the biota of the Pre-Andean and Patagonic.

Another identified group through PAE and cluster analysis was formed by Parana Forest and *Araucaria angustifolia* Forest. This relationship has been proposed by many authors based on insect distributional data (Morrone 2001a, 2006; Nihei & de Carvalho 2007; Ciprandi Pires & Marinoni 2010). Atlantic Forest has been recently regarded as a biogeographical unit by Sigrist & de Carvalho (2009) who investigated area relationships. However, several studies of the monophyly of Atlantic Forest (one of the most biodiverse regions in South America) indicate that the area is hybrid (non monophyletic) (Cracraft & Prum 1988; Costa 2003; Nihei & de Carvalho 2007; de Carvalho et al. 2013; Morrone 2013). Moreover, paleontological, paleoclimatological and geological evidence of Tertiary show that a temperate climate prevailed in southern South America. This climate probably allowed the development of a continuous rainforest even more southerly extended than at present (Kuschel 1969; Maury et al. 1996; Morrone 2006). Consequently, during the Oligocene and Miocene, southern South America showed cooling and intense aridification, and then the cloud forest suffered fragmentation along with the climatic changes produced from the Andean uplift and the expansion of the Chacoan biota (Kuschel 1969; Ron 2000).

Finally, we obtained a close relationship between Central Patagonia and Subandean Patagonia, both from the Andean Region. These two provinces belong to the Patagonian Subregion that extends in southern Argentina from central Mendoza, widening through Neuquén, Río Negro, Chubut, and Santa Cruz, to northern Tierra del Fuego (Morrone 2001b). The relation of these two provinces was also observed in insects, plants and birds (Morrone 2001a, 2006).

Biogeographical regionalizations are useful as general reference models (Ribichich 2002; Morrone 2013) and their heuristic value should be explored by examining the geographical distribution of other plant and animal taxa.

Acknowledgments

We are grateful to CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas). We also thank the Universidad Nacional de La Plata for financial support (UNLP N611 to Alda González). We would like to thank C. Scioscia, M. Ramírez, C. Grismado and L. Pereira for their help during the scientific stage at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" and Museo de La Plata, Argentina.

References

Ab'Saber AN. 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação. Geomorfología. 52(1):1–22.

Axelrod DI, Arroyo MTK, Raven PH. 1991. Historical development of temperate vegetation in the Americas. Rev Chil Hist Nat. 64(3):413–446.

Bertani R. 2001. Revision, cladistic analysis, and zoogeography of *Vitalius, Nhandu*, and *Proshapalopus*; with notes on other theraphosine genera (Araneae, Theraphosidae). Arquivos de Zoologia do Estado de São Paulo. 36(3):265–356.

Bertani R. 2012. Revision, cladistic analysis and biogeography of *Typhochlaena* C. L. Koch, 1850, *Pachistopelma* Pocock, 1901 and *Iridopelma* Pocock, 1901 (Araneae, Theraphosidae, Aviculariinae). Zookeys. 230(2012):1–94.

Bond JE, Beamer DA, Lamb T, Hedin M. 2006. Combining genetic and geospatial analyses to infer population extinction in mygalomorph spiders endemic to the Los Angeles region. Anim Conserv. 9(2):145–157.

Brooks DR, Mayden RL, Mclennan D. 1992. Phylogeny and biodiversity: conserving our evolutionary legacy. Trends Ecol Evol. 7(2):55–59.

Cabrera AL. 1971. Fitogeografía de la Republica Argentina. Bol Soc Argent Bot. 14(1–2):1–42.

Cabrera AL. 1976. Regiones fitogeográficas argentinas. In: Kugler WF, editor. Enciclopedia Argentina de Agricultura y Jardineria II. Buenos Aires (Argentina): ACME. p. 1–85.

Cabrera AL, Willink A. 1973. Biogeografía de América Latina. Monografía 13. Washington (DC): Serie de Biología, OEA.

Ciprandi Pires A, Marinoni L. 2010. Historical relationships among Neotropical endemic areas based on *Sepedonea* (Diptera: Sciomyzidae) phylogenetic and distribution data. Zoologia. 27(5):681–690.

Costa LP. 2003. The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. J Biogeogr. 30(1):71–86.

Coyle FA, Icenogle WR. 1994. Natural history of the California trapdoor spider genus *Aliatypus* (Araneae, Antrodiaetidae). J Arachnol. 22(3):225–255.

Cracraft J, Prum RO. 1988. Patterns and processes of diversification: speciation and historical congruence in Neotropical birds. Evolution. 42(3):603–620.

Crisci JV, Cigliano MM, Morrone JJ, Roig-Juñent S. 1991. Historical biogeography of southern South America. Syst Zool. 40(2):152–171.

Crisci JV, Katinas L, Posadas P. 2000. Introducción a la teoría y práctica de la Biogeografía Histórica. Buenos Aires (Argentina): Sociedad Argentina de Botanica.

de Carvalho ALG, de Britto MR, Fernandes DS. 2013. Biogeography of the lizard genus *Tropidurus* Wied-Neuwied, 1825 (Squamata, Tropiduridae): Distribution, endemism, and area relationships in South America. PLoS ONE. 8(3):1–14.

Ferretti N, González A, Pérez-Miles F. 2012a. Historical biogeography of mygalomorph spiders from the peripampasic orogenic arc based on track analysis and PAE as a panbiogeographical tool. Syst Biodivers. 10(2):179–193.

Ferretti N, González A, Pérez-Miles F. 2012b. Historical biogeography of the genus *Cyriocosmus* (Araneae: Theraphosidae) in the neotropics according to an event-based method and spatial analysis of vicariance. Zool Stud. 51(4):526–535.

Goloboff P, Farris J, Nixon K. 2008. TNT, a free program for phylogenetic analysis. Cladistics. 24(5):774–786.

Goloboff P, Nixon K, Farris J. 2003. TNT, Tree analysis using New Technology. Tucumán (Argentina): Published by the authors.

Griswold CE. 1985. A revision of African spiders of the family Microstigmatidae (Araneae: Mygalomorphae). Ann Natal Mus. 27(1):1–37.

Guadanucci JPL. 2011. Cladistic analysis and biogeography of the genus *Oligoxystre* Vellard 1924 (Araneae: Mygalomorphae: Theraphosidae). J Arachnol. 39(2):320–326.

Hammer O, Harper DAT, Ryan PD. 2009. PAST: Paleontological Statistics, version 1.89 [Internet]; [cited 2013 March 15]. Available from: http://folk.uio.no/ohammer/past

Harold AS, Mooi RD. 1994. Areas of endemism: definition and recognition criteria. Syst Biol. 43(2):261–266.

Hendrixson BE, Bond JE. 2007. Molecular phylogeny and biogeography of an ancient Holarctic lineage of mygalomorph spiders (Araneae: Antrodiaetidae: *Antrodiaetus*). Mol Phylogenet Evol. 42(3):738–755.

Hubalek Z. 1982. Coefficients of association and similarity, based on binary (presence–absence) data: an evaluation. Biol Rev. 57 (4):669–689.

Hueck K. 1978. Los bosques de Sudamérica. Ecología, composición e importancia económica. Eschborn (Germany): Sociedad Alemana de Cooperacion Tecnica Ltda (GTZ).

Jeannel R. 1967. Biogeographie de l'Amerique Australe. In: Delamare-Deboutteville CD, Rapoport E, editors. Biologie de l'Amerique Australe, Volume 3. Paris: CNRS et CNICT. p. 401–460.

Kuschel G. 1969. Biogeography and ecology of South American Coleoptera. In: Fittkau EJ, Illies J, Klinge H, Schwabe GH, Sioli H, editors. Biogeography and ecology in South America. La Haya: Junk. p. 709–722.

Linder HP. 2001. On areas of endemism, with an example from the African Restionaceae. Syst Biol. 50(6):892–911.

López HL, Menni RC, Donato M, Miquelarena AM. 2008. Biogeographical revision of Argentina (Andean and Neotropical regions): an analysis using freshwater fishes. J Biogeogr. 35(9):1564–1579.

Main BY. 1978. Biology of the arid-adapted Australian trapdoor spider *Anidiops villosus* (rainbow). Bull Br Arachnol Soc. 4(4):161–175.

Maury EA, Pinto-da-Rocha R, Morrone JJ. 1996. Distribution of *Acropsopilio chilensis* Silvestri 1904 in Southern South America (Opiliones, Palpatores, Caddidae). Biogeographica. 72(3):127–132.

Monrós F. 1958. Consideraciones sobre la fauna del Sur de Chile y revisión de las tribus Stenomelini (Coleoptera, Chrysomelidae). Acta Zool Lilloana. 15:143–153.

Morrone JJ. 1993. Beyond binary oppositions. Cladistics. 9 (4):437–438.

Morrone JJ. 1994. On the identification of areas of endemism. Syst Biol. 43(3):438–441.

Morrone JJ. 2000. El tiempo de Darwin y el espacio de Croizat: Rupturas epistémicas en los estudios evolutivos. Ciencia. 51-(2):39–46.

Morrone JJ. 2001a. Biogeografía de América Latina y el Caribe. Zaragoza (España): M&T Manuales & Tesis SEA.

Morrone JJ. 2001b. Review of the biogeographic provinces of the Patagonian Subregion. Rev Soc Entomol Argent. 60(1–4):1–8.

Morrone JJ. 2006. Biogeographic areas and transition zones of Latin America and the Caribbean islands based on panbiogeographic and cladistic analyses of the entomofauna. Annu Rev Entomol. 51:467–494.

Morrone JJ. 2013. Cladistic biogeography of the Neotropical Region: identifying the main events in the diversification of the terrestrial biota. Cladistics. 30(2):202–214. doi:10.1111/cla.12039.

Morrone JJ, Crisci JV. 1995. Historical biogeography: Introduction to methods. Annu Rev Ecol Syst. 26:373–401.

Murguía M, Villaseñor JL. 2003. Estimating the effect of the similarity coefficient and the cluster algorithm on biogeographic classifications. Ann Bot Fenn. 40(6):415–421.

Navarro FR, Cuezzo F, Goloboff P, Szumik C, Lizarralde de Grosso M, Quintana G. 2009. Can insect data be used to infer areas of endemism? An example from the Yungas of Argentina. Rev Chil Hist Nat. 82(4):507–522.

Nihei SS, de Carvalho CJB. 2007. Systematics and biogeography of *Polietina* Schnabl & Dziedzicki (Diptera: Muscidae): Neotropical area relationships and Amazonia as a composite area. Syst Entomol. 32(3):477–501.

Nori J, Diaz Gomez JM, Leynaud GC. 2011. Biogeographic regions of Central Argentina based on snake distribution: evaluating two different methodological approaches. J Nat Hist. 45(17–18):1005–1020.

Pascual R, Bondesio P. 1982. Un roedor Cadiatheriinae (Hydrochoeridae) de la edad Huayqueriense (Mioceno tardío) de la Pampa. Sumario de los Ambientes terrestres en la Argentina durante el Mioceno. Ameghiniana. 19(1–2):19–35.

Pascual R, Ortiz-Jaureguizar E, Prado JL. 1996. Land mammals: paradigm of Cenozoic South American geobiotic evolution. In: Arratia G, editor. Contribution of Southern South America to Vertebrate Paleontology. München (Germany): Münchner Geowissenschaftliche Abhandlungen; p. 265–319.

Platnick NI. 2013. The world spider catalog, version 13.5 [Internet]. New York (NY): American Museum of Natural History; [cited 2013 May 2]. Available from: http://research.amnh.org/iz/spiders/catalog. doi:10.5531/db.iz.0001

Porzecanski AL, Cracraft J. 2005. Cladistic analysis of distributions and endemism (CADE): using raw distributions of birds to unravel the biogeography of the South American aridlands. J Biogeogr. 32(2):261–275.

Raven RJ. 1985. The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. B Am Mus Nat Hist. 182(1985):1–180.

Raven RJ. 2010. A review of the Mygalomorphae: biology, morphology and systematics. Book of Abstracts of the 18th International Congress of Arachnology; 2010 Jul 11–17; Siedle, Poland.

Ribichich AM. 2002. El modelo clásico de la filogeografía de Argentina: un análisis crítico. Interciencia. 27(12):669–675.

Ringuelet RA. 1956. Panorama zoogeográfico de la provincia de Buenos Aires. Notas Mus La Plata. 18:1–15.

Roig-Juñent S, Debandi G. 2004. Prioridades de conservación aplicando información filogenética y endemicidad: un ejemplo basado en Carabidae (Coleoptera) de América del Sur austral. Rev Chil Hist Nat. 77(4):695–709.

Roig-Juñent S, Domínguez MC, Flores GE, Mattoni C. 2006. Biogeographic history of South American arid lands: a view from its arthropods using TASS analysis. J Arid Environ. 66(2006):404–420.

Roig-Juñent S, Flores G, Mattoni C. 2003. Consideraciones biogeográficas de la Precordillera (Argentina), con base en artropodos epigeos. In: Morrone JJ, Llorente–Bousquets J, editors. Una perspectiva latinoamericana de la Biogeografia. Mexico DF: Las Prensas de Ciencias, Facultad de Ciencias, UNAM; p. 275–288.

Ron SR. 2000. Biogeographic area relationships of lowland Neotropical rainforest based on raw distributions of vertebrates groups. Biol J Linn Soc. 71(3):379–402.

Rosen BR. 1988. From fossils to earth history: applied historical biogeography. In: Myers AA, Giller PS, editors. Analytical biogeography – An integrated approach to the study of animal and plant distributions. London: Madras, Chapman and Hall; p. 437–481.

Rosen BR, Smith AB. 1988. Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from late Cretaceous to Recent, using a new method. In: Audley-Charles MG, Hallam A, editors. Gondwana and Tethys. London: Geological Society of London. Special publication no. 37; p. 275–306.

Sigrist MS, de Carvalho CJB. 2009. Historical relationships among areas of endemism in the tropical South America using Brooks Parsimony Analysis (BPA). Biota Neotrop. 9(4):1–12.

Sokal RR, Rohlf FJ. 1962. The comparison of dendrograms by objectives methods. Taxon. 11(1):33–40.

Starrett J, Hedin M. 2007. Multilocus genealogies reveal multiple cryptic species and biogeographic complexity in the California turret spider *Antrodiaetus riversi* (Mygalomorphae, Antrodieatidae). Mol Ecol. 16(2006):583–604.

Urtubey E, Stuessy TF, Tremetsberger K, Morrone JJ. 2010. The South American biogeographic transition zone: an analysis from Asteraceae. Taxon. 59(2):505–509.

Willink A. 1991. Contribución a la zoogeografía de los insectos Argentinos. Bol Acad Nac Cienc, Córdoba. 59(3–4):125–147.