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ORIGINAL ARTICLE

Influence of large South American rivers of the Plata Basin on distributional patterns of tropical snakes: a panbiogeographical analysis

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ABSTRACT

Aim The main drainages of the Plata Basin – the Paraná, Paraguay and Uruguay rivers – begin in tropical latitudes and run in a north–south direction into subtropical–temperate latitudes. Consequently, the biota of these rivers has tropical elements that contrast with temperate biomes through which the rivers run. We apply a panbiogeographical approach, to test whether the large rivers of the Plata Basin have a differential influence on distributional patterns of tropical snakes in subtropical and temperate latitudes of South America.

Location Subtropical and temperate sections of the major Plata Basin rivers, South America.

Methods We compared the individual tracks of 94 snake taxa. The track analysis consisted of: (1) plotting the localities of each taxon on maps, (2) connecting the localities of each taxon using a minimal geographical proximity determinant of the 'individual tracks', and (3) superimposing the individual tracks to determine generalized tracks. To detect tropical snakes that reach higher latitudes through the rivers we used the preferential direction of distribution concept. For each taxon we measured the angular deviations between the line of its individual track and the course of the rivers in a 100×100 km scaled grid. Average angular values $< 45°$ indicated a positive association with the rivers.

Results Thirty-five of 94 taxa showed distributions associated with the major rivers of the Plata Basin, including fauna from distinct biogeographical lineages, supported by the occurrence of five generalized tracks as follows: (1) the Paraguay–Middle Paraná, (2) the Paraguay–Paraná fluvial axis, Upper Paraná and Middle Paraná to Upper Delta, (3) the Lower Paraguay, Paraná and Uruguay rivers, excluding the sectors High Paraná and High Uruguay, (4) the Uruguay River and Upper Paraná, and (5) the High Paraná. The Atlantic species occurred with significantly higher frequency in the Uruguay River and High Paraná river sections, the Amazon species were found with significantly higher frequency in the Paraguay and Middle Paraná sections, and the species with a Pantanal distribution were found in all sections.

Main conclusions The observed distributional patterns may be explained by the interaction of ecological, geographical and historical factors. Previous authors have developed ecological (hydrological or environmental similarity) or dispersalist (effect of rivers as migration routes) explanations. The coincidence between generalized tracks and past geomorphological events that caused displacements and changed relationships between the Paraguay, Paraná and Uruguay river sections supports hypotheses involving the strong influence of historical factors in the present configuration of tropical snake distribution in temperate latitudes.

Keywords

Biogeographical corridor, Neotropical rivers, panbiogeography, Plata Basin, snakes, South America.

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INTRODUCTION

The Neotropical region is characterized by the presence of large hydrographic basins, such as the Amazon, Orinoco and Plata, which are considered areas of high diversity and endemism, and which play an important role in the distributional patterns and evolution of the Neotropical biota (Menalled & Adámoli, 1995; Haffer, 1997). The Amazon and Orinoco basins are located in intertropical regions and their main rivers run in a west–east direction, generally surrounded by tropical forests. In contrast, the main drainages of the Plata Basin – the Paraná, Paraguay and Uruguay rivers – begin in tropical latitudes and run in a north–south direction into subtropical–temperate latitudes (37° S) until they join the Río de la Plata (Menalled & Adámoli, 1995; Giraudo & Arzamendia, 2004). Consequently, the biota of these rivers has tropical elements that contrast with the xerophilous forests and temperate steppes (grassland and savannas) through which the rivers run (Nores *et al.*, 2005; Giraudo *et al.*, 2007). The effect of these Plata Basin rivers as biogeographical corridors of tropical biota towards temperate latitudes is a pattern described by numerous authors in relation to a number of diverse plant and animal groups, including aquatic (e.g. Bonetto, 1961; Bonetto & Drago, 1968; Ringuelet, 1975; José de Paggi, 1990; Morrone & Lopretto, 1994) and terrestrial (e. g. Rabinovich & Rapoport, 1975; Menalled & Adámoli, 1995; Giraudo, 2001; Giraudo & Arzamendia, 2004; Nores *et al.*, 2005) taxa, but it has not been quantified or analysed according to biogeographical methodologies (for exceptions see Menalled & Adámoli, 1995, and Nores *et al.*, 2005).

There is general agreement among a number of authors who have analysed the influence of the major rivers of the Plata Basin on the distributional pattern of tropical species in subtropical–temperate areas (Bonetto, 1961; Bonetto & Drago, 1968; Giraudo, 2001; Giraudo & Arzamendia, 2004). These authors suggest that the major rivers of the Plata Basin (Paraná, Paraguay and Uruguay) and, notably, different sections of the same river (e.g. Paraná) have a differential influence of floristic and faunal tropical elements derived from distinct biogeographical origins (e.g. tropical species of the Amazon or Atlantic biogeographical region *sensu* Stotz *et al.*, 1996). Following the discussions of the above-mentioned authors, the following hypotheses have been proposed: (1) the Lower Paraguay River and the Middle Paraná rivers sections (see Fig. 1 for river sections) show a strong influence of Amazonian tropical elements (i.e. species distributed mainly in the Amazonas basin); (2) the Uruguay River and the High Paraná river section show a strong influence of Atlantic–Paranaense tropical elements (i.e. species distributed in the Atlantic or Paranaense biogeographical province, eastern Brazil), and, furthermore, there is high affinity between their faunas; and (3) the Atlantic species present in the High and Upper Paraná sections do not reach the Middle Paraná section.

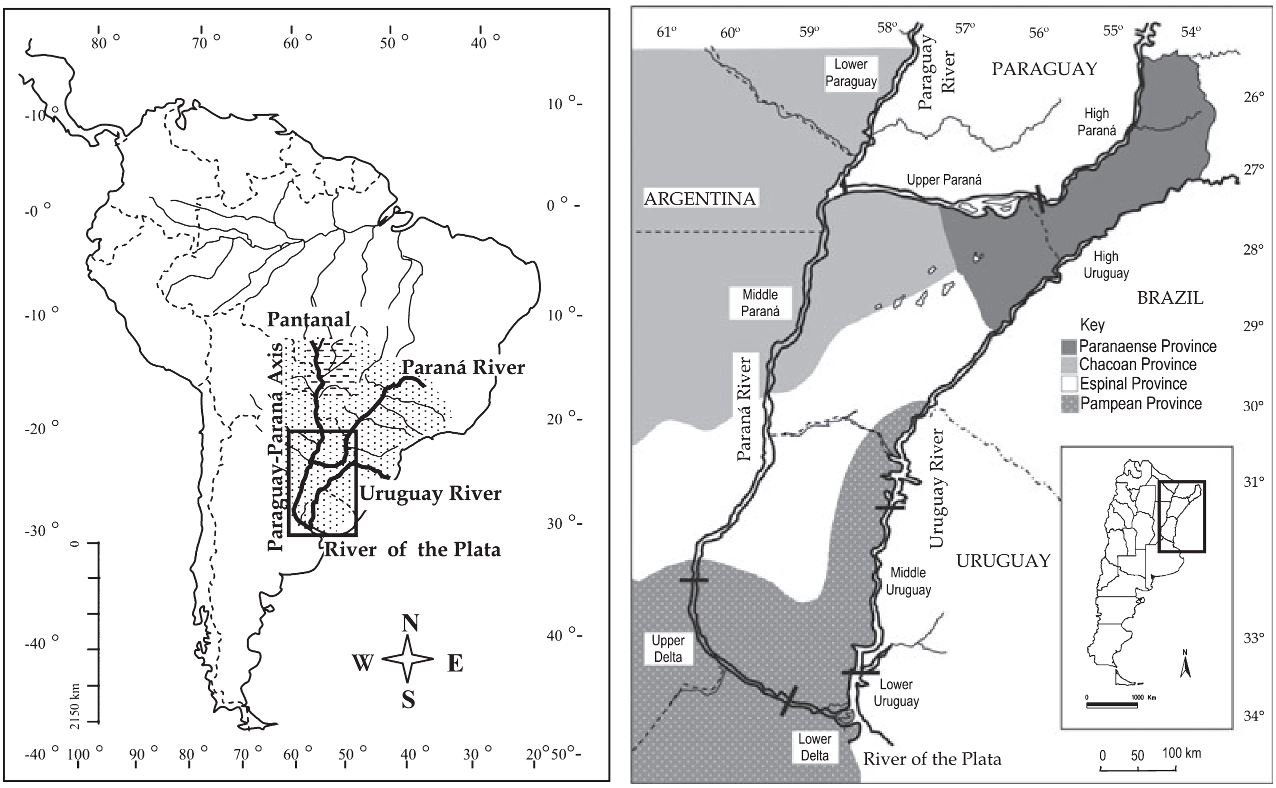

Figure 1 Location of the Plata Basin in South America (left) and of the subtropical–temperate region (right). The river sections considered and the phytogeographic provinces covering the study area are indicated.

In the last few decades, historical biogeography has developed several robust methods to test biogeographical hypotheses (Craw, 1989; Morrone & Crisci, 1995; Crisci *et al.*, 2000; Crisci, 2001; Szumik *et al.*, 2002). Panbiogeography, originally proposed by Croizat (1958, 1964) and subsequently discussed and used by several authors (Page, 1987; Craw, 1989; Morrone & Crisci, 1995; Morrone, 2001; Morrone & Márquez, 2001; Morrone & Gutiérrez, 2005), is a biogeographical approach that emphasizes the importance of the spatial or geographical dimension of biodiversity for understanding evolutionary patterns and processes (Croizat, 1958; Morrone & Lopretto, 1994; Craw *et al.*, 1999; Luna Vega *et al.*, 2000; Morrone & Gutiérrez, 2005).

Panbiogeographical analysis consists basically of plotting species' distribution records on maps and then connecting the localities with lines, termed individual tracks. The resulting summary line is termed a generalized track and indicates the pre-existence of an ancestral biota (Craw, 1989; Crisci *et al.*, 2000; Llorente *et al.*, 2000). The rivers are lineal elements inside the landscape; therefore, if tropical species reach temperate latitudes through the large rivers of the Plata Basin, it is likely that agreement will be found between individual and generalized tracks and the major river courses. Therefore, we decided to use the panbiogeographical approach to test the stated hypotheses concerning spatial homology between tropical snakes and the large rivers of the Plata Basin (see Morrone, 2001; Crisci, 2001; Morrone & Márquez, 2001; Morrone & Gutiérrez, 2005, for further discussion).

Our objective was to test, applying a panbiogeographical approach, whether the large South American rivers of the Plata Basin have a differential influence on tropical snakes with Amazonian or Atlantic biogeographical origin.

MATERIALS AND METHODS

Study area

We analysed the subtropical–temperate sections of the Plata Basin rivers, extending from 25°14′ S to 34°14′ S latitude in north-eastern Argentina and containing three major collectors: the Paraná, Uruguay and Paraguay rivers, which join to form the La Plata River (Fig. 1). These rivers show different geomorphological and hydrological characteristics over their courses (Soldano, 1947; Bonetto & Drago, 1968; Bonetto, 1986; Di Persia & Neiff, 1986; Paoli & Schreider, 2000), and these characteristics were used to determine five zones in the Paraná River (High Paraná, Upper Paraná, Middle Paraná, Upper Delta and Lower Delta), three zones in the Uruguay River (Upper Uruguay, Middle Uruguay and Lower Uruguay) and one in the Paraguay River (Lower Paraguay). In addition, the region encompasses four biogeographical provinces: Atlantic or Paranaense (dominated by subtropical deciduous forest); Chacoan (subtropical and temperate dry forest and savannas); 'Espinal' (savannas, grassland and dry shrublands); and Pampean (steppes) (Cabrera, 1994) (Fig. 1).

Data

We obtained 10,385 records of snakes by field sampling, by examination of 10 museum collections (CENAI: Centro Nacional de Investigaciones Iológicas, Buenos Aires, Argentina; CIES: Centro de Investigaciones Ecológicas Subtropicales, Parque Nacional Iguazú, Misiones, Argentina; CFA: Colección Félix de Azara, Corrientes, Argentina; FML: Instituto de Herpetología de la Fundación Miguel Lillo, Tucumán, Argentina; MFA: Museo provincial de Ciencias Naturales 'Florentino Ameghino', Santa Fe, Argentina; CUNAM: Universidad Nacional de Misiones, Posadas, Misiones. Argentina; MACN: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP: Colección del Museo de La Plata, Buenos Aires, Argentina; PNEP: Colección del Parque Nacional El Palmar, Entre Ríos, Argentina; UNNEC: Universidad Nacional del Nordeste, Corrientes, Argentina) and from the herpetological literature (see Appendix S1 in Supporting Information). Nomenclature follows Bérnils *et al.* (2007).

As in many biogeographical studies, the gaps in the distributional data (the Wallacean shortfall *sensu* Bini *et al.*, 2006) may be a methodological problem. We specifically undertook high-intensity sampling in the study area over 20 years, including poorly accessible or known localities, with the objective of complementing the museum collection materials in order to minimize biases in our data.

Analysis

The panbiogeographical or track analysis was based on a comparison of the individual tracks of 94 taxa belonging to 40 genera, representing 89% of the 106 known taxa of all families occurring in the study area (Giraudo, 2001). We excluded species of snake with few records in order to avoid the possibility of biases in the distributional pattern analyses. The track analysis consisted of: (1) plotting the localities of each taxon on maps, (2) connecting the localities of each taxon using a minimal geographical proximity determinant of the 'individual tracks', and (3) testing the hypothesis of biogeographical homology and the existence of a biota modelled by barriers or corridors using concurrent tracks to determine generalized tracks. Generalized tracks are equated to biogeographical homology or areas of endemism (Page, 1987; Craw, 1989; Morrone & Crisci, 1995; Craw *et al.*, 1999; Luna *et al.*, 2000; Morrone, 2001, 2004; Corona & Morrone, 2005).

Taxa distributions and individual and generalized tracks were mapped using a Geographical Information System (GIS) with SPRING 4.1 (Câmara *et al.*, 1996). To detect tropical snakes that reach higher latitudes through the rivers we used the preferential direction of distribution analysis (Rapoport, 1982; Menalled & Adámoli, 1995). We overlaid the individual tracks of 94 taxa on a 100 × 100 km scaled grid. In each grid unit we determined the prevailing angular deviation between the line of the individual track and the direction of the river section (Fig. 2). Discrete angles of 0°, 11.25°, 22.5°, 33.75°, 45°, 67.5° and 90° were used. Average angular values for each

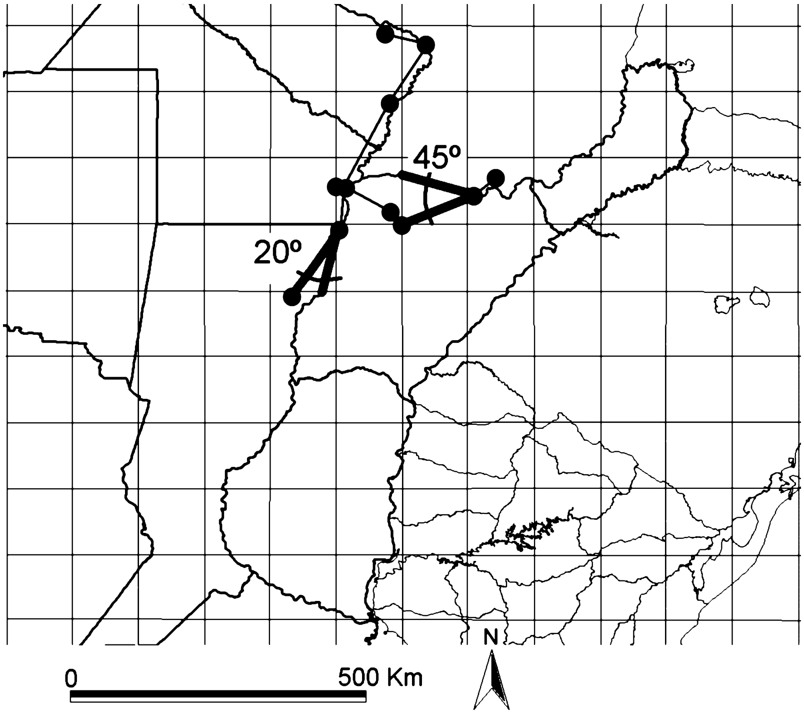

Figure 2 Individual track of *Clelia clelia*. The angular deviations (in degrees) between the line of the track and the course of the rivers in two cells of 1° × 1° are indicated.

taxon were calculated, and, following Rapoport (1982), we considered that values lower than 45° indicated a positive association with the river; mean angles of 45° (and with a uniform distribution of data) implied no association; and angles larger than 45° indicated a negative association. We performed a chi-square test to evaluate if values lower than 45° showed higher frequency.

We analysed the continental patterns of distribution of the tropical taxa that reach higher latitudes through the rivers, constructing continental distributional maps based on the literature (Fig. 3). We then compared the patterns with the phytogeographic and zoogeographic regions of South America proposed by Cabrera & Willink (1980) and Stotz *et al.* (1996). We determined six continental distributional patterns (Fig. 3) as follows.

1. Wide tropical distribution (WTR) – taxa with a broad Neotropical distribution that occur in several biogeographical tropical regions reaching northern South America and sometimes Central America.

2. Amazonian distribution (AM, Fig. 3a) – taxa distributed mainly throughout the Amazon and Orinoco basins.

3. Pantanal distribution (PA, Fig. 3b) – taxa distributed mainly in the Pantanal from the headwaters of the Paraguay River in the boundary region of Bolivia, Brazil and Paraguay to north-east of Argentina throughout the Paraguay–Middle Paraná fluvial axis floodplains, covering complex wetland systems, gallery forests, palms and flooded savannas.

4. Cerrado distribution (CE, Fig. 3c) – a complex of semiarid habitats (savannas, palm and semi-xerophytic forests), and humid gallery forests of rivers and streams, occurring from central Brazil to eastern Bolivia and north-eastern Paraguay.

5. Atlantic distribution (AT, see map 1 in Stotz *et al.*, 1996; and Fig. 3d) – the humid coastal and interior forest region of eastern Brazil, eastern Paraguay and north-eastern Argentina, including the Atlantic and Paranaense provinces (Cabrera & Willink, 1980).

6. Amazonian South–Central South American distribution (AMS–CSA, see map 1 in Stotz *et al.*, 1996) – occupying the southern section of the Amazon River through central South America, including the 'Caatinga' (north-eastern Brazil) and 'Cerrado' (central Brazil), to the 'Chaco' (eastern Bolivia, western Paraguay and northern Argentina).

A contingency matrix with the frequency of taxa of each distributional pattern and the river sections compared was completed along with a G^2 test using a significance level of 5%. The residuals were analysed to measure the positive or negative association with the various river sections.

RESULTS

Thirty-five of 94 taxa showed distributions associated with major rivers (see Appendices S2–S4). The 35 taxa represent 23 genera and five (Anomalepididae, Boidae, Colubridae, Elapidae and Viperidae) of the seven families of snakes in the study area. These species showed angular deviation values between 0° and 90°, although values smaller than 45° occurred most frequently ($\chi^2 = 11.83$; $P = 0.0084$) (Table 1). The range between 0° and 11.25° represented the most taxa, followed by the range of deviation of 11.25°–22.5°.

A comparison among individual tracks (see Appendixes S2–S4) revealed the existence of at least five generalized tracks (Fig. 4).

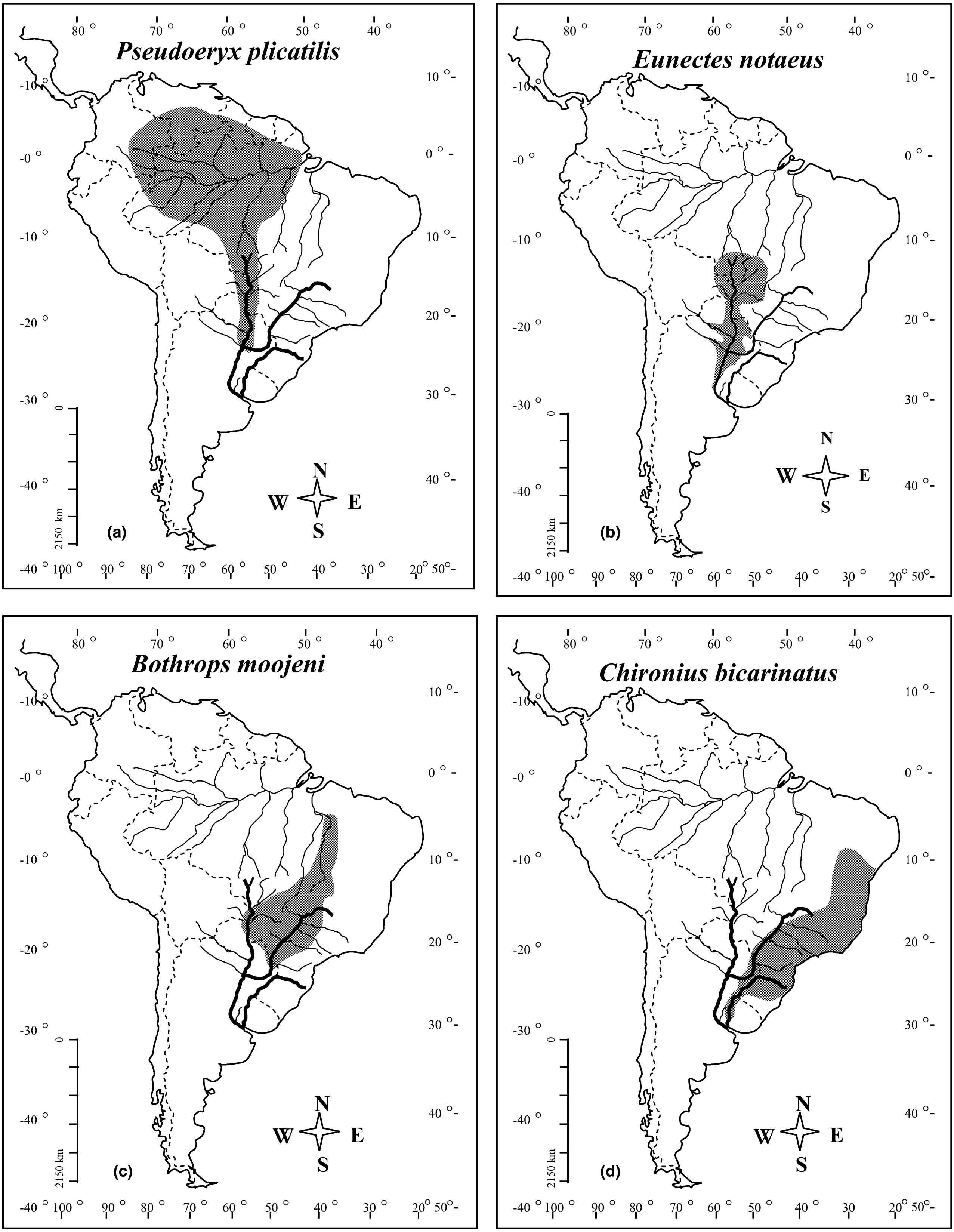

Figure 3 Continental distributional patterns of (a) *Pseudoeryx plicatilis* with Amazonian distribution; (b) *Eunectes notaeus* with Pantanal distribution; (c) *Bothrops moojeni* with Cerrado distribution; and (d) *Chironius bicarinatus* with Atlantic distribution.

Table 1 Tropical snake taxa that reach higher latitudes through the large rivers of the Plata Basin.

Taxa	GDP	Habitat	AAD	Taxa	GDP	Habitat	AAD
Liotyphlops ternetzii	AMS–CSA	Ge	10°	*Liophis frenatus*	AT	Aq	22°
Epicrates cenchria crassus	AT	Fo	0°	*Liophis jaegeri coralliventris*	PA	Ge	21°
Eunectes notaeus	PA	Aq	16°	*Liophis meridionalis*	AMS–CSA	Gr	16°
Atractus snethlageae	AM	Fo	0°	*Liophis semiaureus*	PA	Aq	24°
Atractus taeniatus	AT	Fo	23°	*Liophis reginae*	WTR	Aq	28°
Clelia clelia	WTR	Fo	18°	*Mastigodryas bifossatus*	WTR	Ge	33°
Clelia quimi	AT	Fo	0°	*Oxyrhopus guibei*	AT	Fo	18°
Chironius bicarinatus	AT	Fo	23°	*Philodryas mattogrossensis*	PA	Fo	38°
Dipsas indica bucephala	AT	Fo	40°	*Philodryas olfersii latirostris*	AMS–CSA	Fo	30°
Erythrolamprus aesculapii venustissimus	AT	Fo	16°	*Philodryas olfersii olfersii*	AT	Fo	24°
Helicops infrataeniatus	AT	Aq	20°	*Pseudoeryx plicatilis*	AM	Aq	0°
Helicops leopardinus	PA	Aq	21°	*Sibynomorphus mikanii*	CE	Ge	30°
Hydrodynastes gigas	PA	Aq	28°	*Spilotes pullatus anomalepis*	AT	Fo	29°
Hydrops caesurus	AM	Aq	36°	*Thamnodynastes hypoconia*	AMS–CSA	Ge	15°
Imantodes cenchoa	TRA	Fo	13°	*Thamnodynastes strigatus*	AT	Aq	24°
Leptophis ahaetulla marginatus	PA	Fo	19°	*Micrurus altirostris*	AT	Fo	28°
Liophis almadensis	AMS–CSA	Ge	41°	*Bothrops moojeni*	CE	Fo	23°
Liophis flavifrenatus	AT	Gr	15°				

GDP, general distributional pattern of each taxon; AAD, averages of the angular deviations (in degrees) between the line of the individual track and the course of the rivers. AM, Amazonian distribution; AMS–CSA, Amazonian South–Central South America distribution; AT, Atlantic distribution; CE, Cerrado; PA, Pantanal distribution; WTR, Wide tropical distribution; Habitat: Aq, aquatic; Fo, forest; Ge, generalist; Gr, grassland.

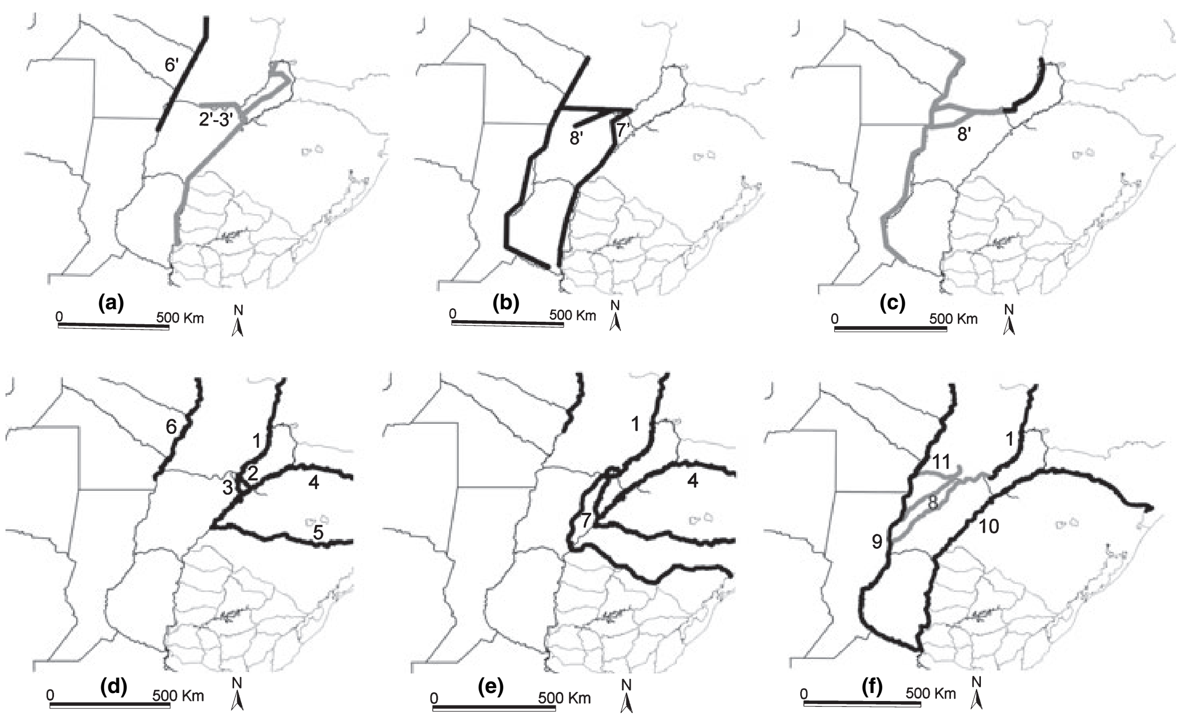

Figure 4 Generalized tracks obtained (panels a–c) and palaeochannels of the rivers (panels d–f). (a) Generalized tracks 1 (black) and 4 (grey), (b) generalized track 3, and (c) generalized tracks 2 (grey) and 5 (black). (d) Connection of the High Paraná (1) through Garupá–Tunas (2) and Pindapoy–Chimiray (3) streams to High Uruguay (4) draining to the sea by the Ibicuy River (5); the Paraguay River (6) was a tributary of the Amazon Basin. (e) Connection of the High Paraná (1) through Aguapey and Miriñay (7) streams to the Uruguay River towards the sea in the south-east of Brazil. (f) Connection of the High Paraná (1), for the Iberá–Carambola–río Corriente and Santa Lucía (8) basins, draining in the Middle Paraná–Paraguay fluvial axis (9). The High Paraná (1) reaches the Yabebiry River (11), where it takes the present Upper Paraná channel. The Uruguay River (10) is in its present position. Notice the coincidence between sections of the generalized tracks and some palaeochannels of rivers (2'–3' above with 2–3 below, 6' with 6, 7' with 7, 8' with 8).

Table 2 Contingency matrix with frequency of general distributional patterns of the snake species and sections of rivers studied; values within parentheses are adjusted residuals of the G^2 test ($G^2 = 38.20$, $P < 0.0001$) showing positive or negative association with different sections of the rivers.

Section of rivers	AM	AT	CE	PA	AMS–CSA	WTR	Total
Paraguay–Middle Paraná	3 (2.86)	0 (−3.06)	0 (−0.92)	2 (0.00)	3 (1.68)	2 (1.01)	10 (1.58)
Uruguay and High Paraná	0 (−1.48)	11 (3.80)	2 (1.78)	0 (−2.42)	0 (−1.97)	1 (−0.65)	14 (−0.93)
All river sections	0 (−1.23)	3 (−1.04)	0 (−0.99)	5 (2.55)	2 (0.45)	1 (−0.29)	11 (−0.55)
Total	3 (0.16)	14 (−0.29)	2 (−0.12)	7 (0.13)	5 (0.15)	4 (0.06)	35 (0.09)

AM, Amazonian distribution; AT, Atlantic distribution; CE, Cerrado; PA, Pantanal distribution; AMS–CSA, Amazonian South–Central South America distribution; WTR, Wide tropical distribution.

Generalized track 1 (Fig. 4a): based on *Atractus snethlageae*, *Hydrops caesurus* and *Pseudoeryx plicatilis*, all species with Amazonian distributions, reaching the Lower Paraguay and the northern region of Middle Paraná.

Generalized track 2 (Fig. 4c): based on *Clelia clelia*, *Helicops leopardinus*, *Liophis almadensis*, *Liophis meridionalis*, *Imantodes cenchoa*, *Mastigodryas bifossatus*, *Oxyrhopus guibei*, *Philodryas mattogrossensis* and *Philodryas olfersii latirostris*, comprising an Upper Paraná and Paraguay–Middle Paraná fluvial axis to the Upper Delta.

Generalized track 3 (Fig. 4b): determined by *Eunectes notaeus*, *Hydrodynastes gigas*, *Imantodes cenchoa*, *Leptophis ahaetulla marginatus*, *Liophis jaegeri coralliventris*, *Liophis semiaureus*, *Liotyphlops ternetzii*, *Micrurus altirostris*, *Thamnodynastes hypoconia* and *T. strigatus*, consisting of the Lower Paraguay, Paraná, and Uruguay rivers, excluding the High Paraná and High Uruguay sectors.

Generalized track 4 (Fig. 4a): determined by *Atractus taeniatus*, *Chironius bicarinatus*, *Helicops infrataeniatus*, *Liophis flavifrenatus*, *Liophis reginae*, *Philodryas olfersii olfersii* and *Spilotes pullatus anomalepis*, occurring in the Uruguay River, Upper Paraná and the province of Misiones.

Generalized track 5 (Fig. 4c): determined by *Epicrates cenchria crassus*, *Erythrolamprus aesculapii*, *Dipsas indica bucephala*, *Liophis frenatus*, *Sibynomorphus mikani* and *Bothrops moojeni*, comprising the High Paraná in Misiones Province.

Atlantic species occurred with higher frequency in the Uruguay River and the High Paraná river section ($G^2 = 38.20$, $P < 0.0001$, Table 2), Amazonian species were found with higher frequency in the Paraguay–Middle Paraná fluvial axis (Lower Paraguay and Middle Paraná sections), and species with a Pantanal distribution were found in all river sections (Table 2).

DISCUSSION

The major rivers of the Plata Basin in Argentina act as corridors or areas of relictual distributions for 35 tropical snake species (37% of total of analysed snakes), including faunas from distinct biogeographical lineages, as indicated by the high occurrence of generalized tracks (5), representing complex areas.

The existence of a relatively mesic microclimate on the riverbanks and the development of riparian humid forests and numerous wetlands facilitate the survival of tropical floristic and faunistic species in temperate latitudes of the large rivers in the Plata Basin (Cabrera, 1994; Forman, 1995; Menalled & Adámoli, 1995). Indeed, the majority of the 35 taxa exhibiting distributional associations with the major rivers analysed inhabit forest (17 species, 49%), followed by semi-aquatic (10, 29%). A minor proportion are generalists (6, 17%) and grassland snakes (2, 6%). The forest and semi-aquatic species are over-represented in relation to the total pool of 94 analysed taxa ($\chi^2 = 29.27$, d.f. = 3, $P < 0.0001$), whereas the forest species represent 30% (28 taxa) and the semi-aquatic species 13% (12 taxa). The generalist (44 species, 47%) and grassland (10 species, 11%) snakes are under-represented in relation to the total pool of snakes.

It is well known that riparian forests regulate light and temperature regimes and provide nourishment to the terrestrial biota (Naiman *et al.*, 1993; Chen *et al.*, 1999). The semi-aquatic species are probably favoured by their water dispersal ability (Mouw & Alaback, 2003). The mesic river microclimate maintains higher temperatures with respect to the surrounding uplands, especially during cold days, favouring the possibilities for thermoregulation by tropical snakes in subtropical–temperate latitudes. For example, the water temperature in the Middle Paraná river varies between 7°C and 30°C, although the air temperature reaches values below zero in winter (Drago, 2007). The large rivers analysed are characterized by well-developed, geomorphologically complex floodplains, long periods of seasonal flooding, a diverse vegetative community and moist soils. The rivers have a strong effect on habitat formation and stability, on the attributes of riparian vegetation, on local geomorphology and microclimate, and on the diversity of ecological functions (Salo *et al.*, 1986; Naiman *et al.*, 1993).

No identifiable phylogenetic pattern was detected in the 35 species. Rather, a wide variety of families (Anomalepididae, Boidae, Colubridae, Elapidae and Viperidae) and tribes (e.g. Colubrini, Xenodontini, Dipsadini, Tachymenini, Pseudoboini) of independent lineages are represented.

The Paraguay–Middle Paraná, High Paraná and Uruguay river sections have different functions as corridors or relictual areas for Amazonian and Atlantic tropical species. This pattern has been noted for several aquatic (Bonetto, 1961; Ringuelet, 1961, 1975; Bonetto & Drago, 1968; José de Paggi, 1990; Morrone & Lopretto, 1994) and terrestrial (Rabinovich &

Rapoport, 1975; Menalled & Adámoli, 1995; Giraudo, 2004; Giraudo & Arzamendia, 2004; Oakley *et al.*, 2005) organisms.

The homologous patterns of distributions of snakes (generalized tracks) are probably a result of the complex interaction between ecological, geographical and historical factors. Generalized track 1 supports the hypothesis that the Lower Paraguay and the Middle Paraná rivers (north section) have a strong influence of tropical Amazonian elements. This generalized track coincides with distributional patterns proposed by Bonetto (1961), Bonetto & Drago (1968), Rabinovich & Rapoport (1975), José de Paggi (1990), Morrone & Lopretto (1994), Giraudo (2004), Oakley *et al.* (2005) and Giraudo *et al.* (2007) for various aquatic and terrestrial biotic groups. Furthermore, the generalized track is also demonstrated in the Heteroptera in the Amazonian region, as described by Morrone *et al.* (2004). The Lower Paraguay and northern Middle Paraná sections share some ecological and hydrological similarities with the Amazonian plain river ecosystems, namely wide floodplains, low transparencies, high suspended solid loads, numerous islands and wetlands, and seasonally flooded humid forests.

From a geographical point of view, the headwaters of the major tributaries of the Paraguay River are close to the headwaters of southern tributaries of the Amazon, and in times of increased rainfall a hydrographic communication appears between the basins (Bonetto, 1986; Paoli *et al.*, 2000; Iriondo & Paira, 2007). A historical explanation of this pattern can be provided in the form of the hypothesis of Castellanos (1965), followed by Bonetto (1986) and Paoli *et al.* (2000), who postulated that the River Paraguay was formerly a tributary of the Amazon, separating from the Amazon Basin when tectonic Andean movements (at the beginning of the Pleistocene) produced the fracture zone where the Paraguay and Middle Paraná rivers currently flow, and changing its drainage towards the Plata Basin. This historical connection between the Paraguay–Middle Paraná and the Amazon rivers could be the reason for the high frequency of Amazonian species in these sections compared with other sections of river included in the analysis.

The high frequency of Atlantic species in the High Paraná and Uruguay River and generalized track 4 taxa support other findings by Bonetto (1961), Ringuelet (1961), Morrone & Lopretto (1994), Menalled & Adámoli (1995), Bonetto & Hurtado (1998) and Capllonch *et al.* (2005). The nascent and main tributaries of the Paraná and Uruguay rivers are located geographically in the Serra Geral and Serra do Mar in the Atlantic forest ecoregion (Soldano, 1947; Bonetto, 1986; Di Persia & Neiff, 1986; Paoli *et al.*, 2000). The High Paraná and High Uruguay flow through basaltic outcrops surrounded by hills, with narrow flood valleys, high transparencies, and low suspended solid loads, showing a greater ecological similarity with habitats of Serra do Mar and Serra Geral (Di Persia & Neiff, 1986).

The Atlantic species present in the High and Upper Paraná sections do not reach the Middle Paraná section. Generalized tracks 4 and 5 support this hypothesis, showing that 11 Atlantic species are distributed in the High Paraná and Uruguay River. Although some taxa reach the Lower Uruguay section (e.g. *Atractus taeniatus* and *Chironius bicarinatus*, Appendix S2d–g), their distribution in the Paraná River does not extend to the Middle Paraná. These tracks coincide with the generalized track of the Paranaense sub-region indicated for crustaceans by Morrone & Lopretto (1994, 2001) and for Heteroptera by Morrone *et al.* (2004). Generalized track 5 taxa occupy the High Paraná. This track is unusual in its faunal composition – with regional endemisms or species with distributions restricted to within this river section, including vascular plants, aquatic invertebrates, reptiles and birds (Bonetto, 1961; Giraudo, 2004).

In spite of the hydrogeographical connection between the High Paraná and the Middle Paraná, a link that facilitates the expansion of species, many taxa do not reach southern latitudes through this fluvial corridor. Historically, the High Paraná was isolated for long periods from the Middle Paraná (Castellanos, 1965; Orfeo, 2005). The High Paraná has changed its course several times in the last million years (Castellanos, 1965; Iriondo, 1996, 2004; Paoli *et al.*, 2000; Aceñolaza, 2004; Orfeo, 2005; Fig. 4). Initially, the High Paraná was connected to the Uruguay River, flowing through the Garupá–Tunas, Pindapoy–Chimiray streams towards the High Uruguay and draining to the sea in the Laguna do Patos (Brazil), whereas the Paraguay River was a tributary of the Amazon Basin (Fig. 4d). Subsequently, the High Paraná changed its course, reaching the Uruguay River in the present-day Aguapey and Miriñay rivers (Fig. 4e). The Paraguay–Paraná and Uruguay faults were created as a consequence of the tensions generated by the Andean tectonic movements (Castellanos, 1965; Iriondo, 2004; Orfeo, 2005). Following this, the High Paraná flowed through the Iberá–Corrientes River basin, and subsequently through the Carambola and Santa Lucía basins, draining into the Paraguay–Paraná fluvial axis (Fig. 4f). Comparing the panels in Fig. 4 (a, b, c with d, e, f), a geographical concurrence between sectors of generalized tracks 1, 2, 3 and 4 and the previously described palaeochannels of the rivers is evident. The tectonic fracture of the Lower Uruguay captured the High Uruguay, changing its direction towards its present location. Recently, in the Holocene, the High Paraná reached its present position, draining through the Upper Paraná to the Paraguay–Middle Paraná fluvial axis (Castellanos, 1965; Fig. 4f).

Previous authors (Bonetto, 1961; Ringuelet, 1961, 1975; Bonetto & Drago, 1968; José de Paggi, 1990) developed ecological (hydrological or environmental similarity) or dispersalist (effect of rivers as migration routes of fauna) explanations, without taking historical factors into account. Agreement between congruent distributional patterns (generalized tracks) and past geomorphological events, which motivated displacements and changed the relationships between the Paraguay, Paraná and Uruguay rivers, allows the formation of hypotheses about historical factors that affected actual configurations of snake distributions, when hydrological or ecological similarity alone could not explain their distributional patterns.

We conclude that the differential function of the Paraguay–Middle Paraná fluvial axis, High Paraná and Uruguay River as biogeographical corridor areas for species of snakes of different tropical biogeographical lineages is best explained as the result of the interaction between ecological, geographical and historical factors, but historical factors have probably been decisive in the creation of the present patterns of distribution of tropical snakes in temperate latitudes.

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SUPPORTING INFORMATION

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

Appendix S1 Literature used to obtain localities of snakes.
Appendix S2 Individual tracks of *Oxyrhopus guibei*, *Thamnodynastes hypoconia*, *Helicops leopardinus*, *Erythrolamprus aesculapii venustissimus*, *Clelia Clelia*, *Atractus taeniatus*, *Liophis meridionalis*, *Spilotes pullatus anomalepis*, *Philodryas mattogrossensis*, *Liophis frenatus*, *Pseudoeryx plicatilis*, *Chironius bicarinatus*, *Philodryas olfersii latirostris* and *Philodryas olfersii olfersii*.
Appendix S3 Individual tracks of *Liotyphlops ternetzii*, *Atractus snethlageae*, *Clelia quimi*, *Imantodes cenchoa*, *Liophis almadensis*, *Helicops infrataeniatus*, *Hydrodynastes gigas*, *Mastigodryas bifossatus*, *Eunectes notaeus* and *Dipsas indica bucephala*.
Appendix S4 Individual tracks of *Leptophis ahaetulla marginatus*, *Thamnodynastes strigatus*, *Liophis reginae*, *Micrurus altirostris*, *Hydrops caesurus*, *Liophis flavifrenatus*, *Sibynomorphus mikanii*, *Liophis semiaureus*, *Bothrops moojeni*, *Liophis jaegeri coralliventris* and *Epicrates cenchria crassus*.

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