Journal of Biogeography (J. Biogeogr.) (2015)

ORIGINAL ARTICLE

On the position of Uruguay in the South American biogeographical puzzle: insights from Ephemeroptera (Insecta)

Daniel A. Dos Santos, Daniel Emmerich, Carlos Molineri, Carolina Nieto and Eduardo Domínguez*

Instituto de Biodiversidad Neotropical (IBN), CONICET-UNT, Crisóstomo Álvarez 722, San Miguel de Tucumán, Tucumán 4000, Argentina

ABSTRACT

Aim To study the relationships between Uruguay and neighbouring geographical areas based on distributions of Ephemeroptera species (mayflies: an ancient order of aquatic insects). We wanted to evaluate whether Uruguay more closely represents (1) the southern limit of the tropical (Paranense and Amazonian) fauna or (2) the northern limit of the temperate (Pampean-Bonaerense) fauna.

Location South America with an emphasis on Uruguay.

Methods We compiled more than 5000 collection records of mayfly species throughout South America and evaluated these using current taxonomy and geographical validity. We used the Network Analysis Method (NAM) on these data to identify units of co-occurrence (UCs: mutually exclusive groups of co-distributed species, with each group connected through strong links of sympatry and disconnected from the others). We focused solely on those UCs that included Uruguay in their spatial ranges and used these to infer the vicinity relationships.

Results We recovered four UCs consisting of many species that link Uruguay with tropical areas of Brazil and NE Argentina. These groups followed a geographically nested pattern. The results contradict the previously held view that the Uruguayan fauna holds strong affinities to that of temperate grasslands that lie to the south in central oriental Argentina (i.e. the currently accepted concept of Pampas). A comparison of the genera known from Uruguay and Buenos Aires Province further reinforces the distinction between Uruguay and temperate areas to the south.

Main conclusions The hypothesis that Uruguay represents the southern limit of tropical affinities is strongly supported by mayfly distributions, indicating that a reappraisal of the Pampas as a cohesive biogeographical province is needed. We suggest that Uruguay and Buenos Aires should belong to different provinces, the former aligned with tropical provinces and the latter aligned with more temperate areas.

*Correspondence: Eduardo Domínguez, Instituto de Biodiversidad Neotropical (IBN), CONICET-UNT, Crisóstomo Álvarez 722, San Miguel de Tucumán, Tucumán 4000, Argentina.
E-mail: eduardo.mayfly@gmail.com

Keywords

Ephemeroptera, Neotropics, network analysis, Pampas, Paranense, regionalization

INTRODUCTION

The identification and description of geographical regions have long been the subject of attention from scientific disciplines concerned about earth-related phenomena (Montello, 2003). Biogeography applies the distribution of species to the task of delineating regions, and there is nothing to suggest that the interest in this subject is diminishing (e.g. Rueda *et al.*, 2013). Given the increasing knowledge of South American biodiversity (Domínguez & Dos Santos, 2014), it forms an appropriate basis for implementing new procedures and testing the validity of traditional regionalization schemes.

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/jbi.12623

Considering technological advances such as precisely georeferenced records and the computational capacity to analyse large amounts of data, we are at the point of an enormous changeover regarding the biogeographical map of South America. In this context, Uruguay provides a good example to illustrate the kind of changes that may arise using an approach that is independent from the Operative Geographic Units technique and strictly develops a study of the patterns based on point records.

At a continental scale, Uruguay is a relatively small landmass (176,220 km^2) surrounded by southern temperate grasslands, northern tropical formations, eastern maritime coastlines and a western zone area delimited by the large Uruguay and Paraná Rivers (i.e. Argentinean Mesopotamia). Physically, Uruguay is contiguous with Argentina to the south (the Río de la Plata, the world's widest river, acting as a separating barrier) and continuous with Brazil to the north. Pampean-Bonaerense streams to the south are characterized by loessic substrate, gentle slopes, high salinity and lack of riparian forests (Casset, 2013), whereas Uruguayan streams are characterized by granitic substrates, higher slopes, low salinity and a riparian forest that Cabrera & Willink (1973) assigned a Paranense affiliation. The prevailing physiognomy of the country has led to its inclusion within the widely accepted Pampean Province (Cabrera & Willink, 1973; Soriano, 1991; Morrone, 2001, 2002, 2006, 2014a,b; IBGE, 2004). The term 'Pampasia' was first used by Martin de Moussy (1860) in his classical *Description géographique et statistique de la Confédération Argentine*. This word comes from the Quechua and means plains or flatlands. The Pampas are composed of natural grasslands, mainly dominated by *Aristida, Stipa, Melica, Poa* and others (Emmerich, 2012), that cover extensive plains in the central region of Argentina, Uruguay and southern Brazil. This landscape has experienced frequent anthropic transformations for crops and pastures (Baldi *et al.*, 2006; Sell & Figueiró, 2011), promoting a peculiar anthrome (*sensu* Ellis & Ramankutty, 2008) characterized by the emergence of an anthropological phenomenon called 'the *gauchos*'. As a result, natural grasslands that have been subject to human transformations have defined our current concept of the Pampas.

Despite the similarities mentioned above, the area encompasses significant climatic and biophysical heterogeneity (Paruelo *et al.*, 2007; Vega *et al.*, 2009), non-uniform history (Ab'Saber, 1990; Donato *et al.*, 2003), unsuspected diversity (Fidelis, 2010; Guido & López Mársico, 2011) and contradictory affinities with neighbouring areas (Simó *et al.*, 2014). Grela (2004) demonstrated the influence of Paranense Forest in the Uruguayan dendroflora. Ringuelet (1961) considered that most of the Pampasia or Chacopampean flatlands had been occupied entirely by brasilic or tropical fauna, based on the Paranense nature (although impoverished) of the freshwater fauna (fishes and crustaceans). Ringuelet (1961:167) considered that this dominion was a transitional area and, ultimately, was distinguished by diminishing or negative characters. Cabrera & Willink (1973) split the Pampean Province into temperate (= Eastern + Western + Southern) and subtropical (= Uruguayense) districts, pointing out that species from the Paranense Province are typical elements in the composition of riparian forests of the latter district. It is therefore not surprising that some authors avoid referring to Uruguay and southern Brazil with the terminology of Pampean; yet they prefer to consider them as members of a distinct grassland entity called the Campos (e.g. Overbeck *et al.*, 2007). There is also some faunal evidence that supports a distinctive pattern for Uruguay with respect to southern Pampas. Nores *et al.* (2005) noted that Uruguay is the southern limit of many subtropical bird species. Collins *et al.* (2011) analysed the distributions of freshwater decapods in the La Plata basin, and grouped the Negro-Ibicui watershed with Upper Uruguay, Upper Paraná, Mata Atlántica and Alto Paraná, differentiating them from the cluster including Salado Sur – Río de La Plata basin. Emmerich (2012) and Dos Santos *et al.* (2015) concluded that the Uruguayan mayfly and caddisfly faunas, respectively, have close relationships with south-eastern Brazil and with Misiones Province in north-eastern Argentina. There are also strong palaeofaunal links (many mammal fossil taxa as well as other amniota groups) between Uruguay, Mesopotamian areas of Argentina and lower latitude Amazonian areas such as the Brazilian state of Acre (Cozzuol, 2006; Latrubesse *et al.*, 2007, 2010).

Nonetheless, the weight of biogeographical evidence may seem insufficient to transfer Uruguay (and southern Brazil) towards a dominion other than the one including austral Pampas. Although there is agreement that Uruguay represents an area differentiated from austral Pampas, the critical issue is to determine whether both are different districts of a common underlying province or if they actually belong to different provinces. To overlook the position of Uruguay in the biogeographical map of South America could lead to erroneous conclusions about the patterns of its biodiversity. Thus, for example, the dominant position ends up accommodating Uruguay with southern South America (e.g. the Austroamerican sub-kingdom in Rivas-Martinez *et al.*, 2011) or the Chacoan dominion (Morrone, 2000, 2014a,b; Löwenberg-Neto, 2014), whereas the alternative view leads to a closer affiliation of Uruguay with Paranense and Amazonian biota (e.g. south-east Neotropical region in Amorim & Pires, 1996). Given these conflicting views, the aim of this paper was to test the relationships of Uruguay and neighbouring areas based on Ephemeroptera and thereby evaluate the adequacy of the Pampas concept *sensu lato* based on Ephemeroptera point records.

MATERIALS AND METHODS

Data points

We analysed 5040 records from 561 South American Ephemeroptera species gathered from the repository of localities at the Aquatic Insects Database, administered by the Instituto de Biodiversidad Neotropical (IBN), CONICET-UNT, Argentina. The data set comprises data points scattered throughout South America. Some of these data are based on material determined by specialists and deposited in the collections of the IBN, Tucumán, Argentina; Fundación Miguel Lillo, Tucumán, Argentina and Universidad de la República, Uruguay. Additional sources include specialized literature and systematic works performed on material from other representative collections (Florida A & M Insect Collection, Tallahassee, FL, USA; Colecão Zoológica Norte Capixaba of the Universidade Federal do Espírito Santo, São Mateus, Brazil, etc.). Hjarding *et al.* (2014) stressed that there is an enormous difference in the degree of determination precision and taxonomic accuracy between specialist-determined material and massive databases uploaded without specialist supervision. Consequently, as suggested by Hjarding *et al.* (2014), most of the locality data was vetted against current taxonomy (Domínguez *et al.*, 2006; Domínguez & Dos Santos, 2014) and geographical validity prior to carrying out distributional analyses. This increased our confidence in the correct determination as well as in the precision of the point localities. We avoided the procedure of projecting point records onto pre-defined areas as a way to account for the distributions and conceal the uncertainty regarding true occurrence.

Distributional analyses

We employed dot maps to infer the sympatry network of studied species. The SYNET package (Dos Santos, 2011) for R (http://www.cran-r.project) was used to analyse the sympatry network under the Network Analysis Method (NAM) approach (Dos Santos *et al.*, 2008, 2012). The NAM estimates the coefficient of spatial association between point sets by measuring the degree of proximity (through the profiles of nearest neighbour distances) and interpenetration (through changes in the length of minimum spanning trees) between the respective dot clouds. Once the weighted network is constructed, meaningful links are filtered via a thresholding operation (Dos Santos *et al.*, 2015). In the final sympatry network, a pair of species can be directly connected (1) or not (0). Intermediary species provide links between pairs of species otherwise disconnected from each other. The iterative removal of intermediary species (guided by the betweenness score) leads to a disaggregation of the sympatry network into components successively smaller in size. By removing intermediary species, NAM aims to segregate groups of species with the following duality: (1) intragroup cohesive connection and (2) intergroup disconnection. Groups deemed as cohesive ones (i.e. internally sustained by many strong links of sympatry) are selected. They are called units of co-occurrence (UCs) and correspond ultimately to distinct sets of co-distributed species that confer uniqueness to the area where they are expressed.

We focused on the UCs that express or occur in Uruguay, and inferred the faunal vicinity relationships of this country by recognizing their distributional nature. For that purpose, we used colorimetric maps (Dos Santos *et al.*, 2015) and minimum spanning trees (MST) to show the geographical context or 'spatial backdrop' concerning the UCs. The MST shows the localities joined by arcs via a geometric network of minimal cost (measured in terms of geographical distance). The colorimetric maps reveal the proximity of any place in the continuous space to the species dot sets under study. To generate these maps, we established a rectangular lattice of points over the study region and then measured the geographical distance between these imaginary sampling points and the dot clouds of included species. Colorimetric maps help to extract the main geographical features of a given group in a continuous spatial scenario. They also assist in recognizing noise from the distributional core associated with each spatial expression. Some of the individual MSTs found for species of each UC were also included to exemplify, through specific distributions, the overall pattern depicted by the UC itself.

RESULTS

Analysis of the entire data set from continental South America resulted in 29 UCs. It is notable that none of the 29 UCs recovered in our analysis fit the pattern of a Pampean Province as has been traditionally delimited (Buenos Aires + Uruguay + SE Brazil). Here, we focus on the four UCs that were informative for the present study (Fig. 1). UC1 contained 38 species, representing 16 genera from five families (Figs 1 & 2a, Table 1). The distributional core identified in the colorimetric map is centred in north-eastern Argentina (Misiones Province) and southern Brazil, and is strongly connected with Uruguay, reflecting the robust relationship among them. The collection localities of the species belonging to UC1 are almost evenly distributed in Uruguay (albeit more densely along a north–south strip near its eastern border). A few records are found in Paraguay and northern Argentina, with the westernmost records in the southern Andean Yungas. The scarce records extending into Buenos Aires are mainly recorded from the Paraná-La Plata system. UC2 included 19 species in 12 genera from 4 families (Figs 1 & 2b, Table 1), relating mainly to an important portion of the Atlantic Forest (south-eastern Brazil), north-western Argentina (Misiones Province) and northern Uruguay. Although the core of this UC only involved northern Uruguay, it still showed closer affinity with south-eastern Brazil – Misiones Province than to Buenos Aires Pampas. UC3 included 28 species in 16 genera from 4 families (Figs 1 & 3a, Table 1). This group of connected species spanned a broader area along the Atlantic coast. Together the three mentioned UCs seemed to follow a nested pattern. UC4 comprised nine species in six genera from four families (Figs 1 & 3b, Table 1). UC4, despite including Uruguay – north-eastern Argentina (Misiones Province) relationship, depicted an overall pattern totally different from UC1-3. In this case, the network of co-distributed species extended into eastern Paraguay and western Amazonia (northern Bolivia, eastern

Brazil and southern Colombia). This UC would support a linkage between the Uruguayan and Amazonian fauna.

If we consider the generic taxonomic list of Ephemeroptera recorded in Uruguay and Buenos Aires (Table 2), a clear distinction also emerges between both areas. While Uruguay contains 31 genera from seven families, Buenos Aires contains only six genera from three families. Furthermore, two of these six genera are restricted to Ventania, a particular isolated orographic system within the Pampas (Posadas *et al.*, 2011).

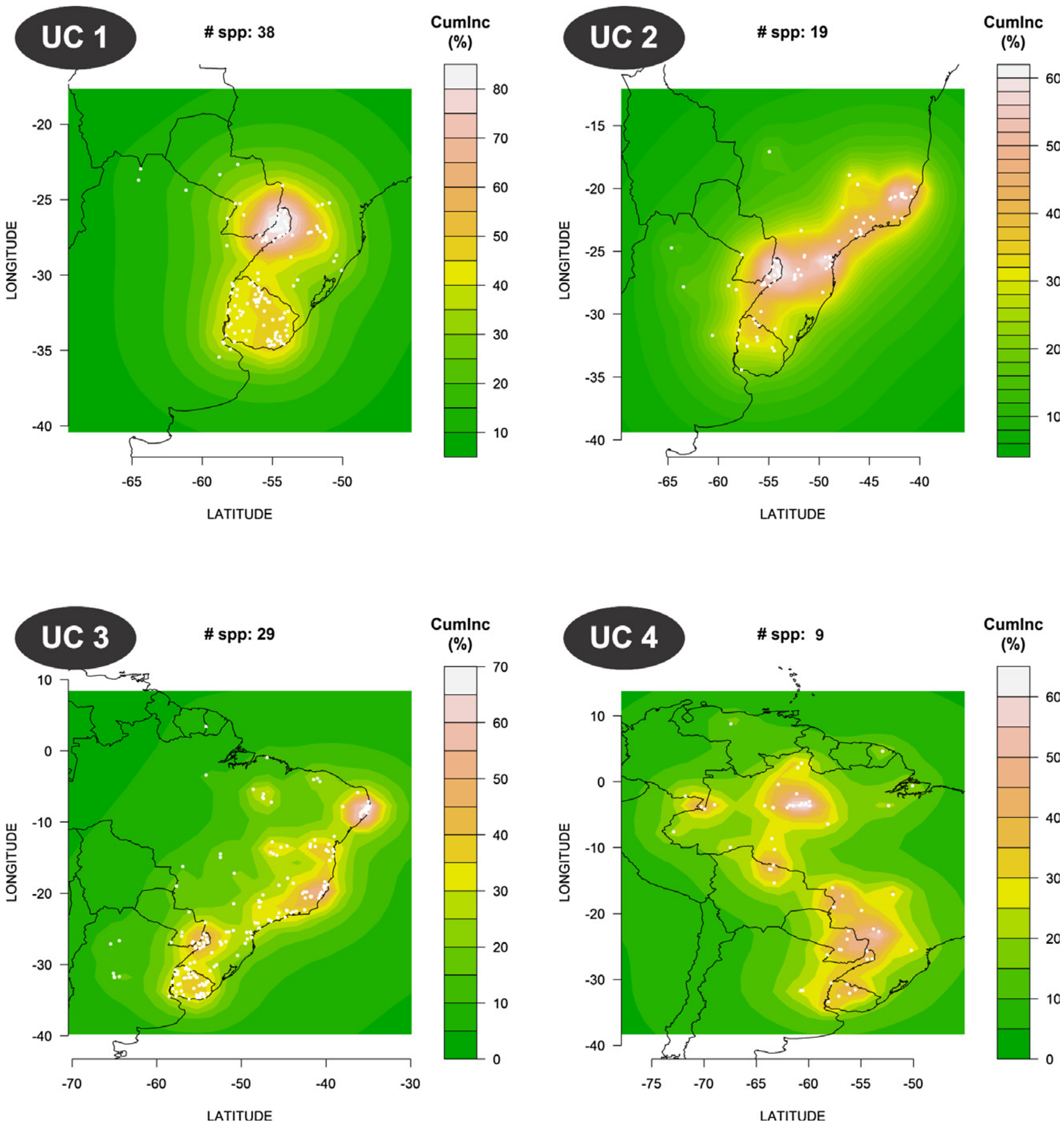

Figure 1 Colorimetric maps obtained after processing the sympatry network between mayfly species. The four units of co-occurrence (UCs) included here concern to the species shared by Uruguay and the rest of South America. White dots represent the actual localities associated with the pooled set of records for the group under consideration. #spp: total number of species belonging to the selected branch of the cleavogram (group of connected species). CumInc: cumulative incidence of taxa (expressed as a percentage of the theoretical maximum) derived from their geographical proximity to hypothetical sampling points scattered throughout the study area. See text for explanation of incidence value represented in the accompanying colour scale bar.

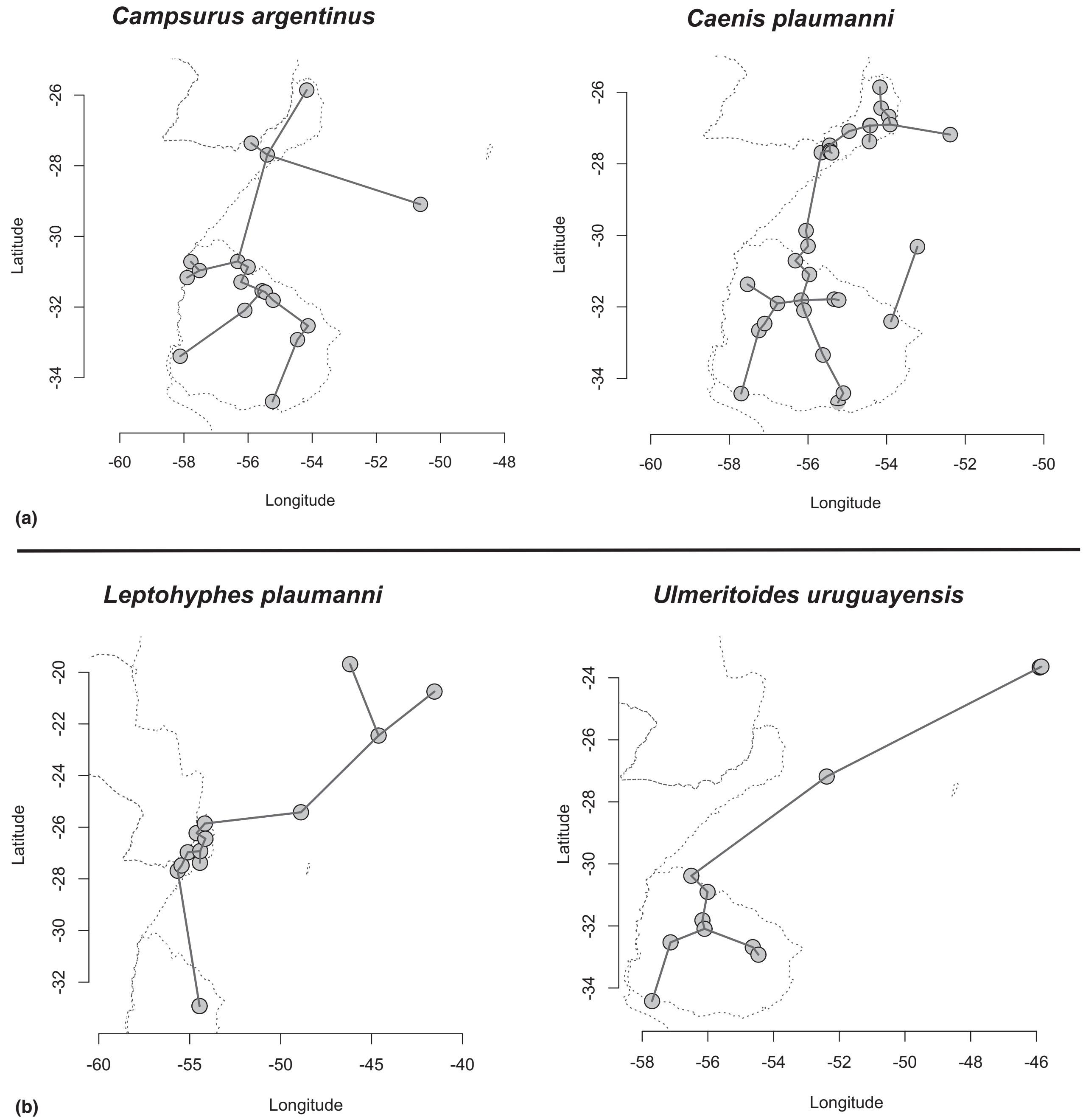

Figure 2 Individual minimum spanning trees exemplifying overall patterns through some of the specific distributions. (a) UC1, *Campsurus argentinus* and *Caenis plaumanni*. (b) UC2, *Leptohyphes plaumanni* and *Ulmeritoides uruguayensis*.

DISCUSSION AND CONCLUSION

What appears to be a homogeneous 'Pampean' grassland covering the flatlands of Buenos Aires, Uruguay and southern Brazil, is the result of a much more complex biogeographical history. One contributing factor may have been the Paranean Sea, which consisted of successive Atlantic marine transgressions that occurred in the Middle and Late Miocene (Marshall & Lundberg, 1996; Pascual *et al.*, 1996; Donato *et al.*, 2003; Ortiz-Jaureguizar & Cladera, 2006) and was one of the most important historical events that affected the distributional patterns in the studied area. It covered most of what is presently known as the Chaco-Pampean plains (Uliana & Biddle, 1988; Hernández *et al.*, 2005), completely separating the 'Guaranian' land mass (north-eastern Argentina, eastern Paraguay and southern Brazil and most of Uruguay) from the Andean-Patagonian region. The Buenos Aires continental fauna was depopulated, while the Uruguayan biotic assemblage maintained its physical connection with its subtropical neighbours. In this way, while the fauna of Buenos

Table 1 Species composition of units of co-occurrence (UCs) recovered through Network Analysis Method applied to the South American Ephemeroptera data set. Species in bold were recorded from Uruguay.

UC1 Paranense (NE Argentina + Uruguay)	UC2 Atlantic Forest (SE Brazil + NE Argentina + N Uruguay)	UC3 Tropical Eastern SA (Uruguay + NE Argentina + E Brazil)	UC4 Tropical Central SA (Uruguay + NE Argentina + E Paraguay + W Amazonia)
Americabaetis maxifolium	*Americabaetis tithion*	***Americabaetis labiosus***	*Apobaetis signifer*
Americabaetis mecistognathus	*Asthenopus guarani*	***Aturbina beatrixae***	*Asthenopus angelae*
Asthenopodes picteti	***Asthenopodes traverae***	*Baetodes santatereza*	***Priasthenopus gilliesi***
Baetodes uruguai	*Baetodes sancticatarinae*	***Callibaetis guttatus***	*Campsurus albifilum*
Caenis burmeisteri	*Callibaetis gregarius*	*Callibaetis pollens*	*Campsurus lucidus*
Caenis plaumanni	*Callibaetis radiatus*	*Camelobaetidius francischettii*	***Campsurus violaceus***
Caenis pseudamica	*Campsurus ulmeri*	*Camelobaetidius lassance*	*Macunahyphes australis*
Caenis tenella	*Leptohyphes cornutus*	*Camelobaetidius tuberosus*	*Tomedontus primus*
Caenis uruzu	***Leptohyphes plaumanni***	***Campsurus duplicatus***	***Ulmeritoides misionensis***
Callibaetis fasciatus	*Massartella alegrettae*	*Campsurus latipennis*	
Callibaetis zonalis	*Massartella brieni*	***Campsurus vulturorum***	
Camelobaetidius phaedrus	*Rivudiva minantenna*	***Cloeodes hydation***	
Camelobaetidius serapis	*Thraulodes alapictus*	*Cloeodes irvingi*	
Camelobaetidius yacutinga	*Thraulodes pinhoi*	*Cryptonympha dasilvai*	
Campsurus argentinus	*Tricorythodes bullus*	*Fittkaulus cururuensis*	
Campsurus assimilis	***Tricorythodes santarita***	*Hermanella froehlichi*	
Campsurus major	*Tricorythopsis gibbus*	*Hermanella maculipennis*	
Farrodes iguazuanus	*Tricorythopsis undulatus*	*Hydrosmilodon plagatus*	
Hermanella grandis	***Ulmeritoides uruguayensis***	***Needhamella ehrhardti***	
Hermanella guttata		***Paracloeodes charrua***	
Hermanella thelma		*Paracloeodes eurybranchus*	
Homothraulus misionensis		*Terpides sooretamae*	
Miroculis misionensis		***Traverhyphes edmundsi***	
Paracloeodes ibicui		***Traverhyphes indicator***	
Paracloeodes leptobranchus		*Traverhyphes pirai*	
Thraulodes bomplandi		*Traverhyphes yuati*	
Thraulodes flinti		***Tricorythopsis minimus***	
Thraulodes paysandensis		*Tricorythopsis spongicola*	
Thraulodes ulmeri			
Traverella bradleyi			
Traverella valdemari			
Tricorythodes arequita			
Tricorythodes barbus			
Tricorythopsis yacutinga			
Ulmeritoides haarupi			
Ulmeritoides patagiatus			
Ulmeritoides spinulipenis			
Ulmeritus carbonelli			

Aires apparently represents an impoverished fauna with respect to Uruguay, it actually shows a different faunal assemblage, composed of taxa of widespread distribution.

Our results clearly support the strong relationship of Uruguay with south-eastern Brazil and the north-eastern Argentinean province of Misiones, as represented in UC1. In a nested sequence, the co-distribution patterns extended north-eastward gradually, as shown in UC2 and UC3. An alternative pattern in our data was that of UC4 which related Uruguay and Misiones Province with the western periphery of the Amazon basin. We did not find a pattern of Ephemeroptera distribution supporting a close relationship between Uruguay and the Buenos Aires Pampas. Emmerich (2012) noted that all the evidence from Ephemeroptera supports a strong relationship of Uruguay with the Paranense area. This was supported by our own data for UC3, with the relationships of Uruguay – Misiones to the Atlantic Forest and to a lesser extent with Amazonia, coinciding with the emerged land masses during the Middle Miocene – Late Miocene marine transgression. Even older, embedded patterns probably contribute to the complexity of the Uruguay relationships. Certain palaeo-elements are consistent with the pattern displayed by UC4, showing the former relationships between Uruguay and other South American areas located in the tropical belt. An important example is the fauna of Acre (Cozzuol, 2006; Latrubesse *et al.*, 2007, 2010). In mammals, 20 genera and 10 species recorded from Acre are also present in the Argentinean Mesopotamia and Uruguay. This

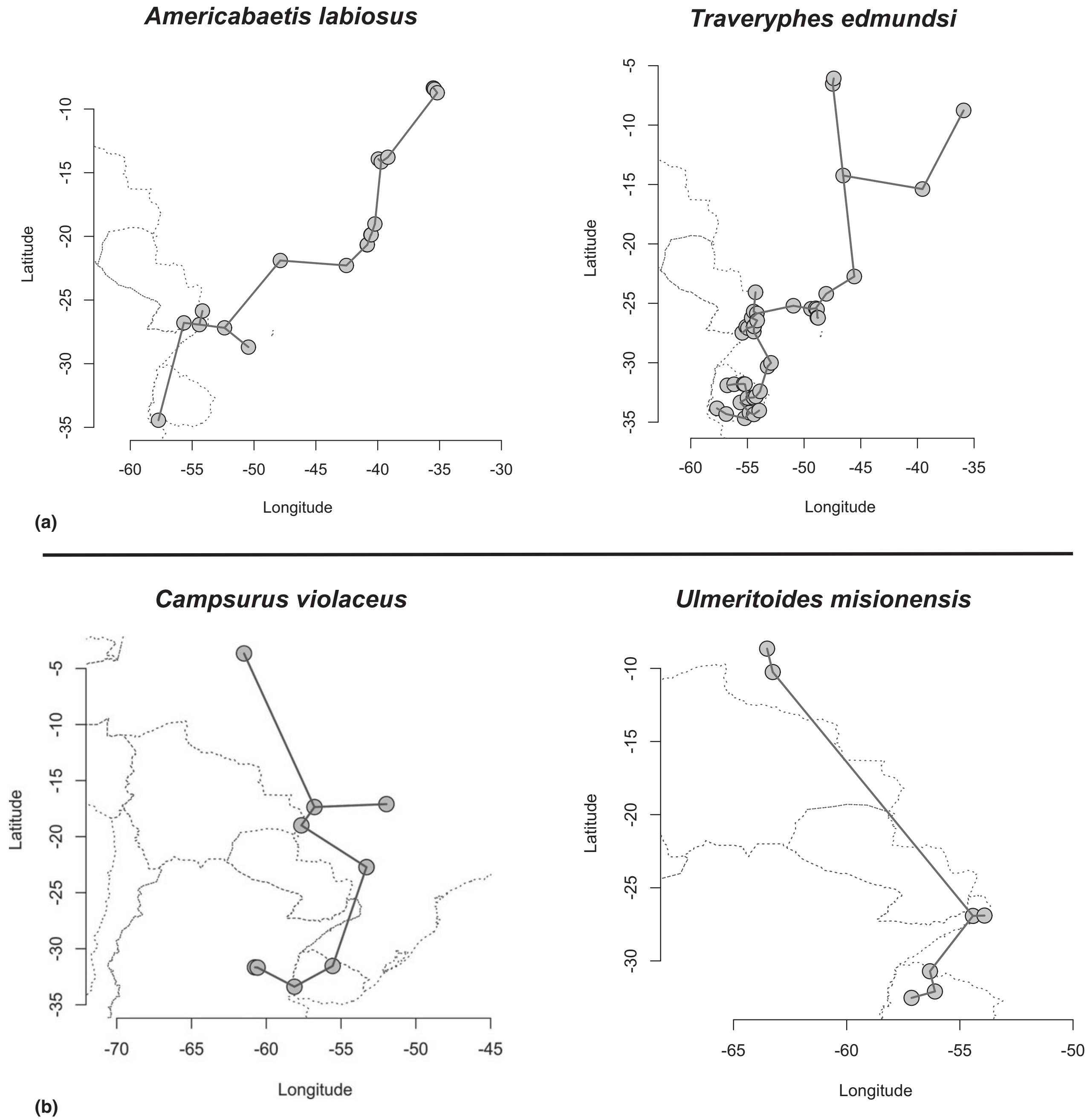

Figure 3 Individual minimum spanning trees exemplifying overall patterns through some of the specific distributions. (a) UC3, *Americabaetis labiosus* and *Traveryphes edmundsi*. (b) UC4, *Campsurus violaceus* and *Ulmeritoides misionensis*.

faunal evidence suggests an environmental correlation as well as a physical continuity of environments from the Brazilian massif to which Uruguay belongs. Another contributing factor to the observed biological differentiation between the Uruguayan and Bonaerense areas concerns the nature of the available habitats that are very different between the two regions.

Several elements that could, at first glance, support the Pampean Province are in fact corresponding to the Peripampasic Arc (Crisci *et al.*, 2001; Ferretti *et al.*, 2012). Frenguelli (1950) proposed this name for the Orogenic Arc constituted by extra-Andean hills from north-western and central Argentina (Subandean and Pampean ranges), Mahuidas, Tandilia and Ventania. A close inspection of the Peripampasic Arc led us to the conclusion that this ancient mountainous landscape, which exceeds the conventional limits of the Pampean Province and has different features of the grassy steppe, can hardly be used to justify the merging of Buenos Aires, Uruguay and Southern Brazil, into a single Pampean Province.

Table 2 List of Ephemeropteran taxa present in Uruguay and/or Buenos Aires.

Family	Genera	Uruguay	Buenos Aires
Baetidae	*Americabaetis*	X	X
	Apobaetis	X	
	Aturbina	X	
	Baetodes	X	
	Callibaetis	X	X
	Camelobaetidius	X	
	Cloeodes	X	X*
	Fallceon	X	
	Paracloeodes	X	X*
	Rivudiva	X	
	Varipes	X	
	Zelusia	X	
Caenidae	*Caenis*	X	X
Ephemeridae	*Hexagenia*	X	
Leptohyphidae	*Leptohyphes*	X	
	Traverhyphes	X	
	Tricorythodes	X	
	Tricorythopsis	X	
Leptophlebiidae	*Farrodes*	X	
	Hagenulopsis	X	
	Hermanella	X	
	Homothraulus	X	
	Miroculis	X	
	Needhamella	X	
	Thraulodes	X	
	Ulmeritoides	X	
	Ulmeritus	X	
Oligoneuriidae	*Spaniophlebia*	X	
Polymitarcyidae	*Asthenopodes*	X	
	Campsurus	X	X
	Priasthenopus	X	

*Restricted to Ventania. Note the unbalance between both faunas.

We reviewed the Ephemeroptera data used in recent publications that conclude an affinity between Bonaerense Pampas with Uruguay (Morrone, 2014a,b). All of the records were taken from Domínguez (1998). Some species were selected as 'endemics' from the list of species recorded or described from Argentina and neighbouring countries to support each proposed biogeographical province. The species supporting the Pampean Province (central eastern Argentina between 30° and 39° S, Uruguay and southern portion of the Brazilian state of Rio Grande do Sul, Morrone, 2000, 2006, 2014a) were: *Baetis alcyoneus*, *B. coveloe*, *B. inops*, *B. yaro*, *Cloeodes aymara*, *Homothraulus larensis*, *Asthenopus gilliesi* and *Tricorythodes arequita*. Of these taxa, it is necessary to note that: (1) the genus *Baetis* is no longer considered to be present in South America (Lugo-Ortiz & McCafferty, 1999); (2) the present valid names are: *Camelobaetidius alcyoneus*, *Rivudiva coveloae*, *Fallceon inops* (currently *nomen dubium*, McCafferty, 2000), *Fallceon yaro* and *Priasthenopus gilliesi*; (3) *H. larensis* is recorded from Buenos Aires, *C. alcyoneus* from Venezuela and *F. inops* from Paraguay, with the remaining species only registered from Uruguay (except *T. arequita* which is also known from north-eastern Argentina and southern Brazil, Domínguez *et al.*, 2006; Emmerich, 2012). The known distributions mentioned in the last point do not provide support for grouping Buenos Aires and Uruguay. It is also important to note that in Domínguez (1998), the original source of Morrone (2000), 10 other species are reported that could be considered supporting elements of the Uruguay's Paranense affinity, with records from 'Misiones, Brazil and Uruguay', 'Misiones and Uruguay' or 'Brazil and Uruguay'.

Morrone (2014a) provides a list of supporting endemics for the Pampean province, including plants, terrestrial vertebrates and arthropods. However, it is important to note that the majority of such species, upon closer inspection, are not restricted and evenly distributed over the total area of the Pampean province. For example, some species are restricted to Buenos Aires (e.g. *Aphilodon spegazzini*, *Apogeophilus bonariensis*, *Schendilops pampeanus)*, or to Uruguay (e.g. *Ctenomys pearsoni*, *Borellia alejomesai*), or are widely distributed (e.g. *Epilobium hirtigerum*, also in Australasia; *Brachistosternus pentheri*, central and northern Argentina; *Calomys musculinus*, Bolivia, Paraguay and Argentina; *Carduelis chloris*, world-wide – introduced in Argentina). On the other hand, the list includes species that are in agreement with the mayfly patterns reported here. For instance, *Leopardus braccatus, Leiotettix politus*, Notiokasiini among others support the Paranense affinity of Uruguay.

Although Uruguay has traditionally been considered a part of the Pampean Province, the influence of Paranense elements cannot be ignored (Haretche *et al.*, 2012). Chebataroff (1942, 1960), Castellanos & Pérez Moreau (1944), Ringuelet (1961), Prado (2000), Grela (2004), Guido & López Mársico (2011) and Emmerich (2012), among others, disagreed with the uniform denomination of Uruguay as part of the Pampean province. Ab'Saber (1990) also separated Buenos Aires from Uruguay based on the conclusion that they belong to different phyto-morphoclimatic dominions in the Last Glacial Maximum (18,000 to 13,000 years ago). Our results also indicate that Uruguay presents an Ephemeroptera fauna radically different from the rest of the austral portion of the Pampas. Furthermore, the emerging distributional patterns that include Uruguay are also incidental to areas of Paranense influence. For this reason, we hypothesize that Uruguay represents a different biogeographical province belonging to the Parana dominion (*sensu* Morrone, 2014a).

ACKNOWLEDGEMENTS

This research was supported by the grants PIP CONICET 0330 and PICTs ANPCyT 2012-1067 and 2012-1910. We thank M.G. Cuezzo for her comments on an early version of the manuscript. We are grateful to our colleagues R. Wills Flowers, C. Anderson and M. Monaghan for revising the English text. M. Ebach, J.J. Morrone and an anonymous referee made helpful comments. The authors are grateful to CONICET for continued support.

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BIOSKETCH

The authors belong to the Instituto de Biodiversidad Neotropical, from the Argentine National Council of Scientific Research (CONICET) and National University of Tucumán, Argentina. The team has been working on systematics, biology and biogeography of Neotropical Ephemeroptera for more than 35 years. Other interests of the institute include freshwater bioindication, aquatic macroinvertebrate systematics, bioinformatics, theoretical and applied limnology.

Editor: Malte Ebach