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Direct analysis of vicariance in Neotropical mayflies (Ephemeroptera)

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Abstract: The distribution of aquatic insects has been poorly explored in quantitative analyses aiming at the historical reconstruction of area relationships in the Neotropics. Ephemeroptera is an ancient group, characterized by its low vagility, and of high richness and endemicity in this region. Systematic knowledge of the group has enormously increased in the last decades, achieving a sufficient background to explore biogeographical historical patterns. Our aim is to reconstruct area history in the Neotropics using the rationale of Barrier biogeography (Hovenkamp protocol). We present eleven mayfly phylogenies, representing groups that evolved independently at least from the Jurassic (i.e., not a one-taxon history). With these groups, we conducted independent biogeographical analyses (using Vicariance Inference Program), and extracted the events that repeated in two or more clades. We found fifty-eight TVEs (Traceable Vicariant Events), from which four were found at least twice, thus constituting SVEs (Supported Vicariant Events).

Key words: historical biogeography, South America, Neotropical, phylogeny, taxon history.

INTRODUCTION

Vicariance is one of the most frequently reported historical processes explaining large-scale biogeographical patterns since Croizat (1958) vigorously defended the concept. Much debate and many methods have dealt with the way in which area and organism distribution should be studied to identify vicariance (e.g., Hennig 1966, Brundin 1966, Rosen 1978, Nelson and Platnick 1981, Brooks 1990, Ronquist 1997, Hausdorf and Hennig 2003, Ebach and Williams 2016). Much of the problems of the methods rely on the way areas are delimited (Hovenkamp 1997, 2001, Hausdorf 2002, Ferrari 2018). *A priori* delimitation of areas from previously proposed classifications (geographical, geological, ecological, or biogeographical) is the most common procedure in DIVA (Ronquist 1997), S-DIVA (Yu et al. 2010), DEC (Dispersal-Extintion-Cladogenesis Model, Ree and Smith 2008), PAE (Morrone and Crisci 1995), and cladistic biogeography (Nelson and Platnick 1981). The simple and powerful proposal of Hovenkamp (1997, 2001) overcomes this problem, by focusing on the barrier separating two putative vicariant areas. Using a cladogram and the distribution of its terminals, Hovenkamp (1997) proposed a protocol to detect traceable vicariance events (TVEs), comparing the distribution of all sister taxa. Comparing the information from different taxa, supported vicariance events (SVEs) would ideally be found. This protocol was partially implemented by

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Arias (2010) and Arias et al. (2011), facilitating the analysis of complex datasets. Such implementation (VIP, Vicariance Inference Program, Arias 2010) deals with taxon history, thus we separately analyzed the different groups, to recover their shared patterns in a subsequent step as done by Domínguez et al. (2016).

The Neotropical region has been studied from an historical biogeographical perspective at many scales and based on different taxa. The Neotropical region, as defined by Morrone (2014a, b), includes most of tropical and subtropical South America, Central America, part of Mexico, and the Antilles. Mayflies are remarkable due to being an ancient group with poor dispersal capabilities (Edmunds 1972, Dos Santos et al. 2018), that might offer interesting information about the history of the Neotropics, as has been proved in other areas (Barber-James et al. 2008, Selvakumar et al. 2014, Gattolliat et al. 2015).

Different studies deal with mayfly historical biogeography at large scales, comparing biotas from different biogeographical regions: e.g. Nearctic, Neotropical, Andean-Patagonian (Edmunds 1972, Savage 1987, McCafferty 1998, Barber-James et al. 2008, Flowers and Ávila 2006, Flowers 2009). Mayfly studies focusing on Neotropical fauna have greatly increased in the last two decades (Shimano et al. 2013, Domínguez and Dos Santos 2014), and as a result, many phylogenies and new distributional data are now available to explore different biogeographical processes that have taken place in the area.

The aim of the present paper is to identify vicariant events in the Neotropics using different mayfly taxa (i.e., to reconstruct the history of the areas). To reach this objective, we selected eleven phylogenies representing groups that evolved independently from each other at least from the Jurassic (Ogden et al. 2009, Staniczek et al. 2011): Leptophlebiidae (*Farrodes* Peters 1971 and *Simothraulopsis* Demoulin 1966), Oligoneuriidae (*Oligoneuria* Pictet 1843), Baetidae (*Baetodes*-complex and *Callibaetis* Eaton 1881), Leptohyphidae (*Allenhyphes*-*Traverhyphes* group), Polymitarcyidae (Asthenopodinae, *Campsurus* Eaton 1868, *Tortopus* Needham and Murphy 1924 and *Tortopsis* Molineri 2010), and Caenidae (*Brasilocaenis* Puthz 1975).

MATERIALS AND METHODS

Publications referring to Neotropical mayfly phylogenies at the species level were selected. Character matrices were updated, including the following new species or new life stages described since their original publication: 1) *Baetodes* complex (Baetidae), 15 species from eight genera and *Baetodes* treated at the genus level (Nieto 2016, 1 species added here, see below); 2) *Callibaetis* (Baetidae), 37 species, including 28 species of the genus (Cruz et al. 2017); 3) *Brasilocaenis* and *Caenis* (Caenidae), 20 species (Lima et al. 2019); 4) *Simothraulopsis* (Leptophlebiidae), 14 terminals including 9 species of the genus (Nascimento et al. 2017); 5) *Farrodes* (Leptophlebiidae), with 23 species (Domínguez 1999, Domínguez and Zuñiga 2009); 6) *Allenhyphes*-*Traverhyphes* group (Leptohyphidae), 21 species (Molineri 2004) and 2 additional species included here; 7) *Oligoneuria* (Oligoneuriidae), 12 species (Salles et al. 2014), of which one was described later (Massariol and Cruz 2015) and was added here; 8) Asthenopodinae (Polymitarcyidae), 17 species (Molineri et al. 2015); 9) *Campsurus alfibilum* and *major* groups (Polymitarcyidae), 13 species (Molineri and Salles 2013); 10) *Tortopus* (Polymitarcyidae); and 11) *Tortopsis* (Polymitarcyidae) both from Molineri (2010), with 21 species (plus 2 species included here).

The present study deals with 197 species and 3554 geographic records in total. Table I summarizes the information regarding the studied datasets.

TABLE I
Data included in this study. 1 = number of species included in the original phylogeny, and number of species newly here incorporated (in brackets), 2 = total number of geographical records, 3 = number of TVEs found by VIP.

Taxon	species[1]	records[2]	TVEs found[3]	Reference
Farrodes	23	276	7	Domínguez 1999, Domínguez and Zúñiga 2009
Asthenopodinae	17	449	6	Molineri et al. 2015
Brasilocaenis	20	354	7	Lima et al. 2019
Oligoneuria	11(1)	74	4	Salles et al. 2013
Callibaetis	37	761	14	Cruz et al. 2017
Campsurus	13	110	2	Molineri and Salles 2013, 2017
Allenhyphes complex	21(2)	417	4	Molineri 2004
Baetodes complex	15(1)	620	5	Nieto 2016
Simothraulopsis	14	287	4	Nascimento et al. 2017
Tortopsis and *Tortopus*	21(2)	208	5	Molineri 2010
Total	197	3554	58	

PHYLOGENETIC SEARCHES

The phylogenetic matrices of each of the selected studies were edited to a format readable in TNT (Goloboff et al. 2008) (available at https://ibn.conicet.gov.ar/recursos/AABC_SMat1-2). Some of them were modified to include new species described after their publication (Table I): in the *Baetodes* complex *Moribaetis mimbresaurus* McCafferty (2007) was added, in the *Allenhyphes-Traverhyphes* group (Molineri, 2004), *Lumahyphes cocal* Boldrini et al. (2015), and *Traverhyphes (T.) frevo* Lima et al. (2011) were added, and in the *Tortopus-Tortopsis* matrix (Molineri, 2010), *Tortopsis canum* Gonçalves et al. (2011), and *Tortopus ipixuna* Molineri et al. (2012) were added. Finally, new information was added to the *Campsurus* matrix (Molineri and Salles 2013) regarding female adult and egg stages recently described (Molineri and Salles 2017) for *C. amapaensis* Molineri and Emmerich (2010). Following the settings and searches in each of the published phylogenies, all trees were obtained in TNT and saved in xml format using the "toxml" file provided in VIP (Arias 2010). When more than one shortest tree was recovered, strict consensus was used, except for *Tortopsis*, where a combinable component consensus was preferred. Clade support was calculated using 250 replicates of Jackknife with symmetric resampling (Goloboff et al. 2003) in TNT.

BIOGEOGRAPHICAL ANALYSIS

Geographic records of all the treated species were included in separate files for each group (available at https://ibn.conicet.gov.ar/recursos/AABC_SMat1-2). Records from the species inside the focal area (Neotropical region, as delimited in the shapefile from Löwenberg Neto 2014) are exact points of occurrence obtained in the field, and copied directly from the material section of taxonomic papers, or from the labels in the vials. Each species record from our focal area was checked for accuracy of their taxonomic identification and geographical location. Doubtful data (i.e., outliers mostly due to erroneous identifications) were not included. For species outside of our focal area (e.g., Nearctic, Palearctic, Ethiopian or Oriental regions) only approximate locations were included (centroids of states, departments or counties). Most of them were extracted from the literature or regional faunistic lists.

The phylogenetic trees and geographical information of each group were studied independently in the VIP program (Arias 2010). A 1 x 1-degree grid was created, and for comparative purposes, 2º x 2º and 5º x 5º grids and different grid origins were also explored. The maximum fill option was not used, since it was considered risky to assume presence around the real data, especially with aquatic organisms, for which only observed records were analyzed. The default VIP reconstruction was used (OR reconstruction), this option was preferred because it considers all the input data (other type of VIP reconstructions delete terminals or partial distributions to find more "vicariance"). A maximum overlap of 10 % in the ranges of sister pairs (i.e., a small superposition of two sister groups is tolerated and they are still considered as allopatric) was allowed. A vegetation map was used to show the results (downloaded from https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MOD_NDVI_M).

Hovenkamp's (1997) protocol was implemented to search vicariant patterns supported by different groups. VIP analyzes this for each individual phylogeny, and the comparison between different phylogenies is not implemented in a computer program, having to be done by direct comparison of the resulting maps (Domínguez et al. 2016). All the maps showing the distribution of disjunct sister pairs were saved as "jpg" images, and compared to identify similar events (TVEs). Subsequently, these TVEs were ordered in the time-frame provided by the phylogenetic tree (some events appear later than others in the phylogenies). Events appearing two or more times in different phylogenies were marked as SVEs. It is worth remarking that vicariant sister clades shown in figures are separated by a white line, to be used as a visual reference (i.e., it does not imply a barrier). Finally, the historical order of the SVEs was searched. Any given barrier can appear in the same place more than once, thus, two similar TVE´s may be indicating different histories (i.e., they do not belong to the same time slice) (Hunn and Upchurch 2001). We attempted to reduce this methodological weakness by comparing the rank of the descendants (sister species, sister species groups, etc.) when different cladograms are compared, or by taking into consideration the position on the tree (when the same event appears more than once in the same cladogram).

RESULTS

Fifty-eight traceable vicariant events (TVEs) were recognized in all the analyzed datasets, of which most showed high (jackknife >50) support (Table I, Figs. S1-S10, available at https://ibn.conicet.gov.ar/recursos/AABC_SFigs), and four were found at least twice, thus constituting Supported Vicariant Events (SVE, Figs. 1-4).

The SVEs are roughly grouped in two sets: 1) one including continental South America (SVE1 and SVE2), and 2) another set involving North, Central and South America (SVE3 and SVE4).

SVE1 involves the separation of southeastern Venezuela and adjacent Brazil highlands from the tropical lowlands (Fig. 1a-c). SVE1 is supported by three TVEs: *Fittkauneuria* Pescador and Edmunds (1994) vs *Oligoneuria*, *Caenis tepuiensis* Molineri et al. (2011) vs *C. cuniana* Froehlich (1969) and *Spiritiops tepuiensis* Nieto and Derka (2012) vs *S. silvudus* Lugo-Ortiz and McCafferty (1998).

SVE2 (Fig. 2a-g) separates southern Atlantic-Paranaense and eastern Pampa (excluding the Argentine portion) from northern tropical areas (Amazonas and/or central and northern Atlantic forest). The barrier is located around latitude 22-23°S. This SVE2 is the most frequent, and is supported by seven TVEs, in the following sister clades: *Asthenopodes chumuco* Molineri et al. (2015) vs *A. traverae* Molineri et al. (2015) + *A. picteti* Hubbard (1975), *Campsurus amapaensis* vs *C. major* Needham and Murphy (1924) + *C. argentinus* Esben–Petersen (1912), *Homothraulus*

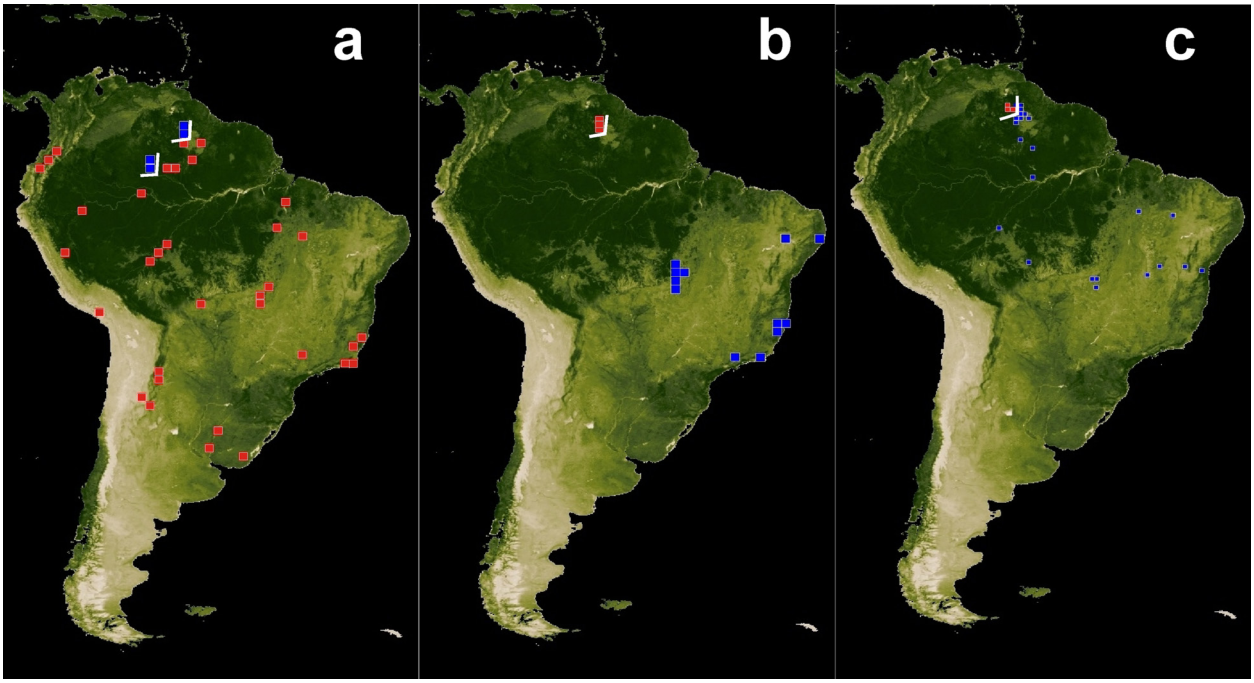

Figure 1 - SVE1 (Supported Vicariant Event 1): **(a)** *Fittkauneuria* (blue) and *Oligoneuria* (red); **(b)** *Caenis tepuinensis* (red) and *Caenis cuniana* (blue); **(c)** *Spiritiops tepuinensis* (red) *and S. silvudus* (blue). White lines are for visual reference (they are located in the same place in all the maps).

vs *Simothraulopsis*, *Callibaetis* (three times) and *Caenis gaucha* Lima et al. (2015) vs *C. chamie* Alba-Tercedor and Mosquera (1999).

SVE3 (Fig. 3a-d) involves the separation of North and South America. The limit includes the Panama isthmus, but the separation area of the sister pairs is more extended. This pattern is sustained by four TVEs: *Farrodes texanus* Davis (1987) vs *F. maculatus* (Needham and Murphy 1924), *Callibaetis willineri* Navas (1932) vs *C. pretiosus* Banks (1914), *Callibaetis floridanus* Banks (1900) vs *C. gonzalezi* (Navas 1934) and *Tortopus bellus* Lugo-Ortiz and McCafferty (1996) vs. the rest of the genus.

SVE4 (Fig. 4a-b) separates southern Mexico from Central America + northern South America in the Gulf of Honduras, and is supported by two TVEs: *Farrodes tulija* Domínguez et al. (1996) vs *F. flavipennis* Domínguez et al. (1996), and *F. maya* Domínguez (1999) vs *F. caribbianus* (Traver 1943).

DISCUSSION

Mayflies were shown to be useful in detecting vicariant events in the New World, and particularly in South America, indicating fifty-eight (58) vicariant events. SVE1 (Supported Vicariant Event 1) involves the Tepuis-lowland vicariance. The age of Tepuis rocks has been dated on 1800-1600 Ma (Brewer-Carías and Audy 2011), but the separation of both biotas occurred much recently, after the erosion of the sediments surrounding the actual tepuis or from recent migrations (Rull 2004). Mayflies supporting this vicariant pattern may be indicating two different events (i.e., different time slices), since the taxonomic level of the sisters (i.e., genus) found for Oligoneuriidae (Fig. 1a) may indicate a much older origin of the barrier than that of the two other sister groups involved (*Caenis* and *Spiritiops* Lugo-Ortiz and McCafferty 1998, at species level, Fig. 1b-c). Furthermore, the barrier is more complex in Oligoneuriidae. We hope that future research dating the sister clades could test

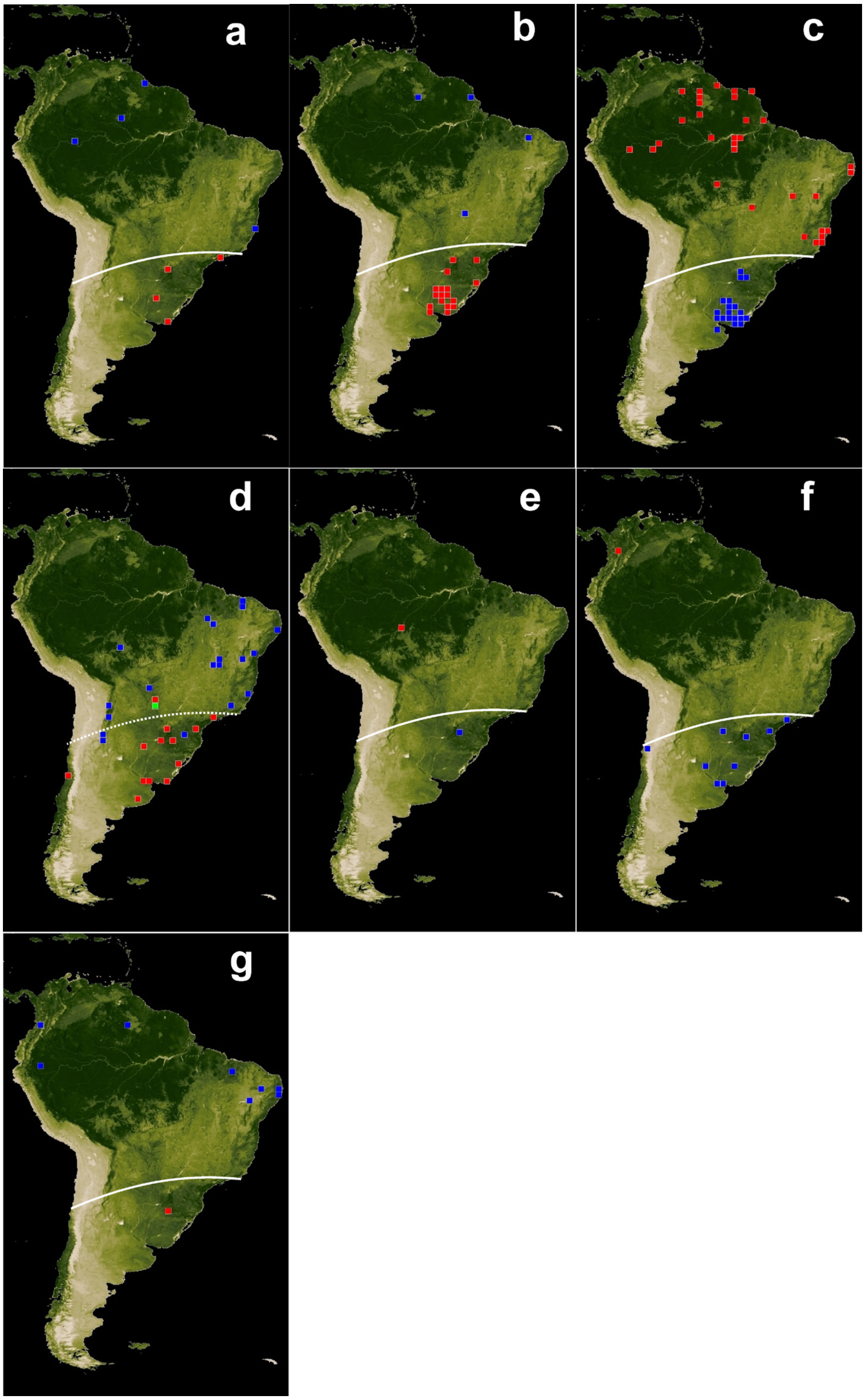

Figure 2 - SVE2 (Supported Vicariant Event 2): **(a)** *Asthenopodes chumuco* (blue) and *A. traverae*+*A. picteti* (red); **(b)** *Campsurus amapaensis* (blue) and *C. major*+*C. argentinus* (red); **(c)** *Homothraulus* (blue) and *Simothraulopsis* (red); **(d)** *Callibaetis sellacki* +C. *fasciatus* (red) and *C. pollens* + *C. dominguezi* + *C. capixaba* + *C. cochlea* (blue); **(e)** *Callibaetis itannae* (red) and *C. calophenigyn* (blue); **(f)** *Callibaetis molinerii* (red) and *C. jocosus* (blue); **(g)** *Caenis gaucha* (red) and *C. chamie* (blue). White lines are for visual reference (they are located in the same place in all the maps).

these hypotheses, nevertheless some studies have estimated divergence in mayfly sister species ranging 3 to 9 Mya (Sekiné et al. 2013, Bisconti et al. 2016). *Zelusia* Lugo-Ortiz and McCafferty (1998), with two described species, presents a similar vicariant pattern (Salles et al. 2016). Two conflicting hypotheses have been proposed to explain patterns of the Pantepui region: the idea of evolution in isolation obtained support from Oligoneuriidae, while the vertical displacement hypothesis (Desamore et al. 2014) would explain the other mayfly vicariants at species level.

SVE2, the south / north separation of subtropical from tropical areas around 22°-23° S latitude, is the most repeated pattern found in the present work. The pattern is not coincident with present river basins, neither with repeated marine introgressions during the Miocene (marine barriers occurred predominantly through Plata-Paraná lowlands) (Rapela et al. 2007). The majority (but not all) of the TVEs supporting this SVE2 present one of the sisters restricted to Uruguay+ Misiones+ south Brazil). The latter pattern roughly coincides with Rio de la Plata craton (Rapela et al. 2007, Gaucher et al. 2011), an ancient Archaean-Palaeoproterozoic craton (1200-2100 Ma), now covered by newer formations (Almeida et al. 2000). Oldest mayflies are much younger (ca. 300 Ma, Staniczek et al. 2011), thus the pattern might be due to other events. Whether the area might have offered continuing suitable habitats (running waters) during part of the evolution of South American mayflies deserves further analysis. This area, now dominated by grasslands mixed with shrubs and forests, is frequently referred to as Brazilian Campos, occupies a transitional zone between tropical and temperate climates, and is characterized by cool winters and hot summers, with an absence of a dry season (Overbeck et al. 2007). Amorim and Pires (1996) recognized this region as an area of endemism (NE Argentina / southern Brazil), Overbeck et al. (2007) for example mention 95 endemic species of plants and animals.

SVE3, supported by four TVEs, corresponds to one or more different events of connection and isolation of the South American plate before the formation of the Panama isthmus (3 to 15 Ma BP, Keigwin 1982, Montes et al. 2012, O´Dea et al. 2016). When disjunction patterns are markedly distant (e.g., Fig. 3a-c), an alternative explanation is long distance dispersion (Hovenkamp 1997). Thus, the vicariant explanation for this SVE3 would support the fact that the area of current Central America before the formation of the isthmus served as a corridor (i.e., allowing range expansion) for the ancestor of the four sister pairs supporting this SVE3 (*Farrodes texanus* - *F. maculatus*, *Callibaetis willineri* - *C. pretiosus*, *Callibaetis floridanus* - *C. gonzalezi*, *Tortopus bellus* - remaining *Tortopus* species), but later acted as a barrier that isolated both sisters. *Farrodes*, *Callibaetis* and *Tortopus* are species-rich genera, with much of their diversity in the Neotropics (Domínguez 1999, Molineri 2010, Cruz et al. 2017), which led McCafferty (1998) to hypothesize their South American origin and subsequent dispersal to Central and North America. Our analysis for *Callibaetis* and *Tortopus* shows that all basal clades are distributed in South America, coinciding with its putative southern origin (McCafferty 1998). Domínguez (1999) area cladograms show Central America and Northern South America as ancestral areas for *Farrodes*. Three of the TVEs involve species pairs (*Farrodes* and *Callibaetis*), but one (*Tortopus*) is due to a basal splitting in the genus, thus indicating a likely older occurrence (i.e., different time slices). However, younger events may explain *Farrodes* and *Callibaetis* TVEs: a recent (after the formation of the Panamanian land bridge) S to N dispersion of their ancestral species, followed by the sister's differentiation. An older vicariance between emergent land masses, prior to the final uplift of the isthmus should explain the pattern in *Tortopus*,

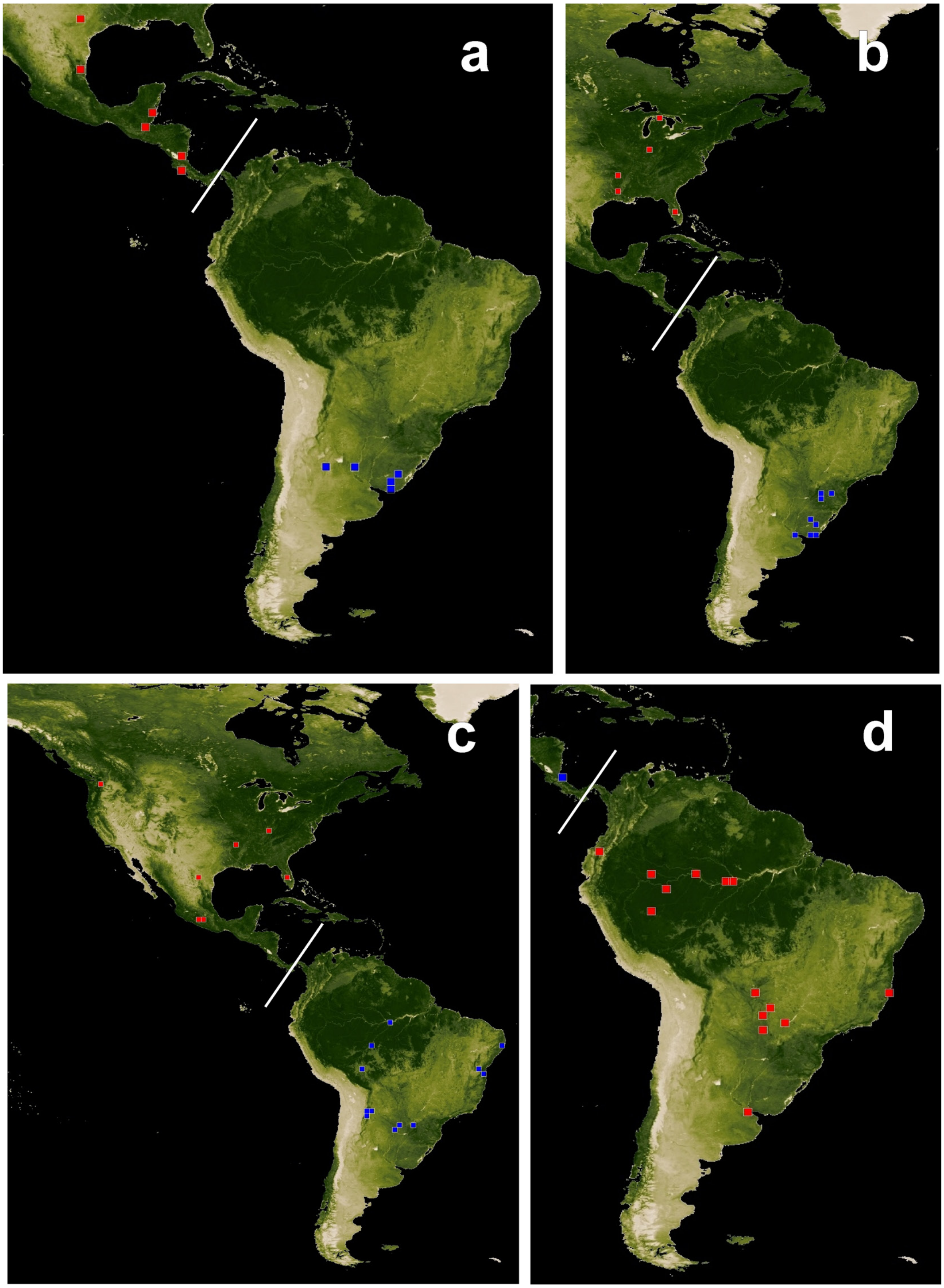

Figure 3 - SVE3 (Supported Vicariant Event 3): **(a)** *Farrodes texanus* (red) vs *F. maculatus* (blue); **(b)** *Callibaetis willineri* (blue) vs *C. pretiosus* (red); **(c)** *Callibaetis floridanus* (red) vs *C. gonzalezi* (blue); **(d)** *Tortopus bellus* (blue) vs rest of the genus (red). White lines are for visual reference (they are located in the same place in all the maps).

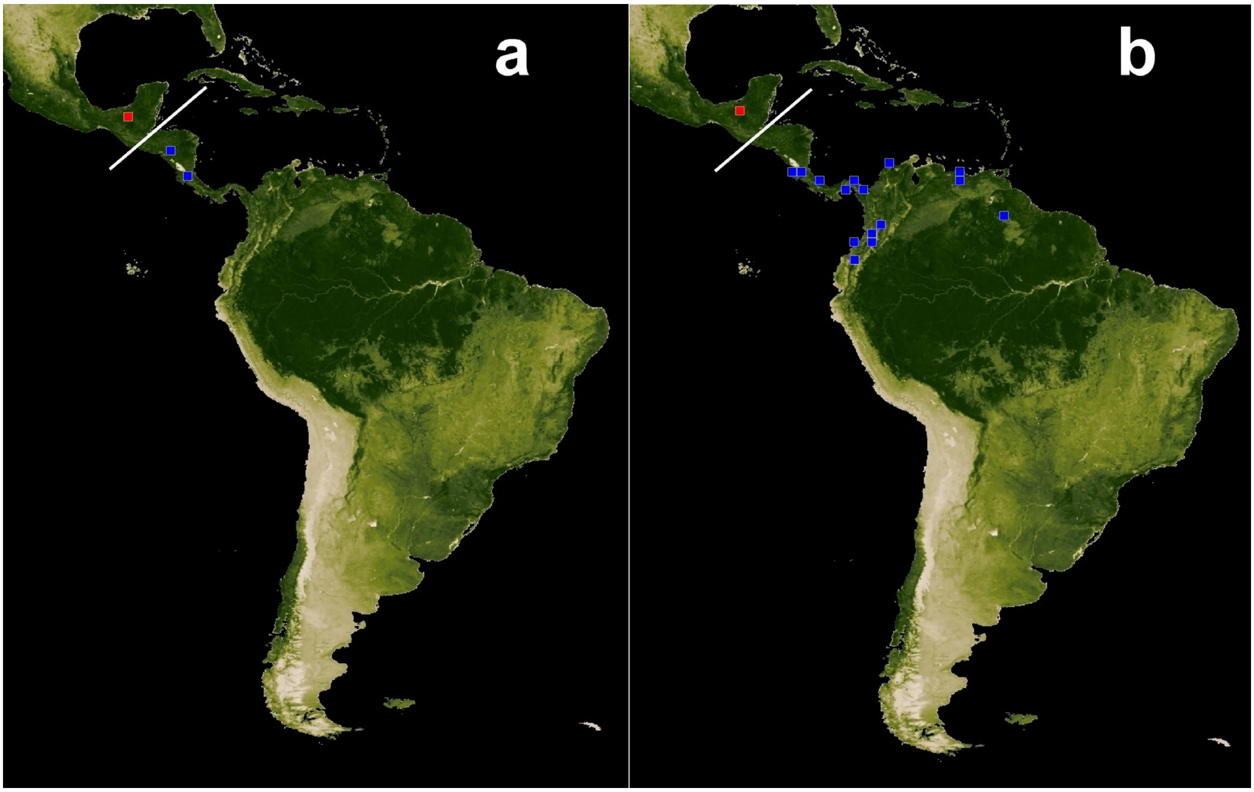

Figure 4 - SVE4 (Supported Vicariant Event 4): **(a)** *Farrodes tulija* (red) and *F. flavipennis* (blue); **(b)** *F. maya* (red) and *F. caribbianus* (blue). White lines are for visual reference (they are located in the same place in all the maps).

by one of these two known processes in the area: 1) the old Cretaceous-Palaeocene proto-Antilles land bridge (72Ma); or 2) the mid-Cenozoic Greater Antilles-Aves Ridge land bridge (GAARlandia, 34Ma) plus the Miocene Middle American land bridge (Říčan et al. 2013). Due to its age, the much older physical connection between North and South America occurring until mid-Jurassic (170 Ma) is excludable.

SVE4 is supported by two TVEs in *Farrodes* (*Farrodes tulija* - *F. flavipennis*, and *F. maya* - *F. caribbianus*), the barrier is located in the area of to the Gulf of Honduras, between the Chortis and Maya blocks (Iturralde-Vinent and MacPhee 1999). In the case vicariance is the underlying process originating these patterns, ancient events are to be invoked (170-148 Ma, Iturralde-Vinent and MacPhee 1999), which is inconsistent with the low taxonomical level of the pattern. Instead, the quaternary fragmentation of forest habitats (Haberle and Maslin 1999), where most species of the genus live, most likely explains this pattern.

We did not find any chronological order for the SVEs. We only found ordered TVEs, but some of them could shed light to the time frame involved. For example in the phylogeny of Asthenopodinae, a basal TVE1 (Fig. S3, available at https://ibn.conicet.gov.ar/recursos/AABC_SFigs) coinciding with the opening of the Atlantic Ocean, results in a minimum age of less than 110 Ma (San Martín and Ronquist 2004) for the other TVEs in the mentioned phylogeny (e.g., TVE27 is similar to SVE2).

Other TVEs (i.e., unique events in our data) are mirrored in other taxa, or match hypothesized geological reconstructions, thus deserving further mention. We are aware that a greater taxa (and phylogeny) sampling would have led to support of these TVEs from other groups, for them to reach the status of SVE. For example, TVE6 and TVE41, occurring in *Tortopsis* (Fig. S9, available at https://ibn.conicet.gov.ar/recursos/AABC_SFigs) partly coincide with vicariants in *Atopophlebia* Flowers, with a first barrier attributable to the Romeral fault (Flowers 2012) and a later barrier separating species in the upper Amazonas or Orinoco. Another pair of interesting TVEs involves *Allenhyphes* Hofmann and Sartori and *Yaurina* Molineri (TVE22 and TVE23). TVE22 (Fig. S6, available at https://ibn.conicet.gov.ar/recursos/AABC_SFigs) separates the Chocó, Caribbean and Central–North American regions (where *Allenhyphes* is found) from the central Andes (Ecuador to Argentina, *Yaurina* distribution). TVE23 (Fig. S6, available at https://ibn.conicet.gov.ar/recursos/ AABC_SFigs) shows the splitting of *Allenhyphes* in a northern (north to Honduras Gulf) and southern species (in Costa Rica, Lesser Antilles, Choco and Maracaibo). These patterns seem to be due to the complex evolution of the area, with many bridges and terrane accretions acting consecutively around current Central America (Meschede and Frisch 1998, Musilová et al. 2015).

CONCLUSIONS

The Ephemeroptera data provided by the phylogenies and distributions available from South and Central America suggests the presence of several barriers that resulted in vicariant events. Many of these events are supported by more than one taxon. Although in some cases there are unique outcomes among the studied taxa, some of them were found also in other mayflies or insect groups. We consider that the information and analyses here provided are valuable for their comparison with other animal and even plant taxa, in pursue of the events that shaped the distribution of the South and Central American biota.

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AUTHOR CONTRIBUTIONS

All authors gathered the data, discussed the results and wrote the manuscript, CM analyzed the data and edited the figures.

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