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Panbiogeographical analysis of passion vines at their southern limit of distribution in the Neotropics

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ABSTRACT: (Panbiogeographical analysis of passion vines at their southern limit of distribution in the Neotropics). The origin of the extant flora of the state of Rio Grande do Sul (RS) in Brazil has long been debated. Spatial distributions of passion vines (Passifloraceae) have been used to support the corresponding hypotheses, subsequent to the pioneer studies of Balduino Rambo. Using a panbiogeographical analysis based on literature data and herbarium material, we mapped the spatial distributions of the 15 species of passion vine that occur naturally in RS, taking into account a broader geographical range (southern South America). None of these passion-vine species has its distribution entirely within the RS political borders. The escarpments of the Serra do Mar (circa -30°S latitude), which coincides with the southern limit of the Paraná biogeographic subregion, was identified as the southern limit for the existence of important diversity of passion vines in the Neotropics. The generalized tracks obtained were associated with different panbiogeographic provinces, indicating a mixed history for the RS passion-vine flora. Two main biotic components were identified: first, species with a northern occurrence, from east of the Andes to the Brazilian Atlantic Forest; second, species typically found in the Brazilian Atlantic Forest. A continuous, U-shaped curve formed by the generalized tracks suggested that the RS area is an extant, southern transition zone, which in conjunction with the Chaco province maintains Amazonian and Atlantic populations of these plants in contact. A node located in the northeast region, roughly on the border between the Pampa province and Paraná subregion, and where three provinces of the latter converge, indicated the existence of greater diversity and endemism of passion-vine species in that part of the state. On a preliminary basis, the consequences of the variation in passion-vine spatial distributions for the herbivores, specifically heliconian butterflies, associated with these plants are also discussed.

Key words: Biogeography, Passifloraceae, Neotropical region, heliconian butterflies.

RESUMO: (Análise panbiogeográfica de passifloráceas no limite sul de distribuição neotropical). A origem da flora existente no estado do Rio Grande do Sul (RS), Brasil, vem sendo debatida há tempo. A distribuição espacial dos maracujás (Passifloraceae) tem sido usada em suporte das hipóteses correspondentes, desde o trabalho pioneiro de Balduino Rambo a respeito. Com base em uma análise panbiogeográfica, calcada em dados da literatura e material depositado em herbários, avaliamos neste estudo a variação na distribuição geográfica das 15 espécies de maracujás com ocorrência natural no RS, levando-se em consideração uma maior área de abrangência (sul da América do Sul). Nenhuma das espécies teve a área de distribuição localizada por completo dentro da área física do estado. As escarpas da Serra do Mar, que coincidem com o limite sul da região biogeográfica do Paraná (cerca de -30°S de latitude), foram identificadas como limite sul para a existência de expressiva diversidade de passifloráceas na região Neotropical. Os traços generalizados obtidos se associaram a diferentes províncias biogeográficas, indicando a natureza mista da composição de espécies de maracujás. Dois componentes bióticos importantes foram identificados: o primeiro, relacionado a espécies com ocorrência ao norte, da parte leste dos Andes à porção norte da Floresta Atlântica brasileira; o segundo, composto por espécies típicas da Floresta Atlântica. Uma curva em forma de “U” formada pelos traços generalizados, sugeriu que o RS se constitui atualmente numa área que, em associação a província do Chaco, representa uma zona de transição que mantém as populações dessas plantas nas florestas Amazônica e Atlântica em contato. A existência de maior diversidade e endemidade foi indicada por um nó localizado na região nordeste, próximo às fronteiras das províncias biogeográficas do Pampa e sub-região do Paraná, para onde os limites das províncias correspondentes convergem, estando, portanto, historicamente relacionadas. Em caráter preliminar, são discutidas algumas das implicações da variação obtida quanto à distribuição das passifloráceas em relação àquela da fauna de herbívoros associada.

Palavras-chave: Biogeografia, Passifloraceae, região Neotropical, borboletas do maracujá.

INTRODUCTION

The panbiogeographical approach stems from a proposal of Croizat (1958, 1964), who postulated that the existence of ancestral biotas that were fragmented by either past vicariant events or climate changes can be revealed by the coincidence of extant taxa distributions or

generalized tracks. He challenged not only the dispersalist explanations for the extant geographical distribution of organisms, but also the relevance of natural selection as a preponderant agent of their evolutionary change (Morrone 2009).

The method consists first in plotting localities of taxa

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on maps and joining them by lines to the minimum spanning trees. It is assumed that these lines represent the geographical area where the evolution of that taxon took place. Then, by finding where two or more individual tracks for different taxa overlap, the generalized tracks are drawn. By determining areas of convergences for two or more generalized tracks, panbiogeographic nodes are identified. By assumption, they represent complex, composite biogeographical areas where ancestral biotic components and geological fragments have interrelated in space and through time (Craw *et al.* 1999, Morrone 2006, 2009). Thus, nodes indirectly represent areas of geobiotic convergence, from which inferences regarding biogeographical features can be made, for example regarding the existence of high diversity and endemism, among others (Heads 2004, Alzate *et al.* 2008). Panbiogeographical studies are simple to implement and do not require previous phylogenetic analyses of the taxa involved. They have been carried out for many groups of organisms, aiming primarily toward the elucidation of the common evolution of areas and biotas (*e.g.*, Morrone *et al.* 2004, Nihei & Carvalho 2005, Hernandez *et al.* 2006, Lopez-Ruf *et al.* 2006, Alzate *et al.* 2008, Arzamendia & Giraudo 2009, Corona *et al.* 2009). Although passion vines (Passifloraceae) exhibit high diversity and have disjunct distributions, to our knowledge this approach has not yet been applied to the Neotropical species.

The geographical distribution of passion vines has been used, for example, to explain the origin of existing forests in the state of Rio Grande Sul (RS), Brazil, since the pioneer work on this subject (Rambo 1951). More recently, with a substantial increase in the area surveyed and consequently better knowledge of their occurrence and diversity (*e.g.*, Sacco 1962, 1980, Mondin 2001), passion vines have been related to RS biogeography in more detail (*e.g.*, Mader *et al.* 2009, Mondin *et al.* 2011). These studies, however, were based upon data collection restricted to within the RS political borders, using physiographic regions as units, and none has been based on the recently available biogeographical method. This is done herein, as part of this special number of the Brazilian Journal of Bioscience on RS passion vines. Using a panbiogeographical analysis based on literature data and information collected from herbarium material, we explored the variations in the spatial distribution of these plants, taking into account a broader geographical range (southern portion of South America). First, maps containing panbiogeographic individual and generalized tracks, and the corresponding nodes, are presented for the 15 species of passion vine that occur naturally in RS. Then, we made biogeographical inferences, using as a reference the subregions and provinces proposed by Morrone (2006). Two main questions guided our work: 1) is there a congruent pattern in passion-vine distributions within the RS borders? 2) are the corresponding geographical distributions associated with any specific biota? On a preliminary basis, the consequences of variation in passion-vine spatial distributions for the distributions

of associated herbivores, the heliconian butterflies, are also discussed.

MATERIALS AND METHODS

Study area

The geographical region covered in the present analysis is circumscribed by a white rectangle in Fig. 1A, and corresponds to a latitudinal range of -7.3 N to -39.11 S in South America. This region was selected arbitrarily, aiming to cover the entire distributional range of most passion-vine species included in the study. The panbiogeographical analysis is restricted to passion-vine species (listed below) that occur naturally within the political borders of Rio Grande do Sul (RS), the southernmost state of Brazil.

According to Morrone (2006), RS is covered by the Paraná and Chacoan biogeographic subregions. Morrone divided the former subregion into the provinces of the Brazilian Atlantic Forest, Paraná Forest and *Araucaria angustifolia* Forest, all of which include the northern half of RS within their southern limits (province numbers 53, 54 and 55, respectively). The latter subregion is composed of the Caatinga, Cerrado, Chaco and Pampa provinces; only the Pampa (province number 51) covers the southern part, including 63% of the area of RS (IBGE 2004).

A complete description of RS physiognomy is beyond the scope of the present study (for a review, see Rambo 1956, Fortes 1959, Leite 2002, Marchiori 2004). An overview on the main characteristics of the Brazilian Atlantic Forest *sensu lato* was given by Morellato & Haddad (2000). A detailed description for the grasslands of southern Brazil was provided by Overbeck *et al.* (2007). The extant vegetation that covers RS specifically was recently mapped and interpreted from a conservation biology perspective by Cordeiro & Hasenack (2009).

The Paraná and Pampa subregions, which for the purposes of this study were taken as the two broadest divisions for RS, reflect roughly the phytogeographical classifications that were proposed by Cabrera & Willink (1980) for the Neotropical domains (= Paraná and Chacoan, respectively), and by IBGE (2004) for the Brazilian biomes (= Atlantic Forest and Pampa, respectively). In these classifications, however, the natural grassland vegetation that occurs on the plateau in northeastern RS, forming a mosaic with *Araucaria* Forest formations (= province number 55; Figs. 1, 2A-C) was considered as part of the Atlantic Forest. These forest fragments account for 10.63% of RS area, and in conjunction are also known as the Mixed-Umbrophilous Forest (Cordeiro & Hasenack 2009). The Paraná Forest (= province 54) is represented in RS by deciduous and semideciduous forest fragments that range from the upper section of the Uruguay River, from where it continues first southward into the central lowlands, along the Ibicuí and Jacuí river basins; and then eastward as a narrow strip, to the

northeast portion of RS (Figs. 1, 2D). These forests cover the scarpments of Serra do Mar (= slopes of the southern Brazilian plateau), which runs west to east more or less in the center of RS (Fig. 1B), and which demarcates the southern limit of tropical forest distribution in the Neotropics, at circa -30°S (Cabrera & Willink 1980). The corresponding slopes contain the Jacuí River basin in the western part, and increase in elevation and steepness eastward, reaching an altitude of nearly 1,400 m (Pico do Monte Negro, São José dos Ausentes) in the eastern limit, close to the Atlantic Ocean (Fig. 1B). Some semi-deciduous forest fragments occur to the south, covering the eastern slopes of the Southeastern Highlands (for a description, see Jurinitz & Jarenkow 2003).

The Brazilian Atlantic Forest (= province number 53) covers the steep slopes of the South Brazilian plateau in the northeast, in conjunction with a narrow strip of coastal plain located between the plateau and the Atlantic Ocean. Although its forests are relatively well preserved, this province accounts for a small area (less than 0.5%

of RS) that is also known as the Dense-Umbrophilous Forest (Brazilian Atlantic Forest *sensu stricto*) (Cordeiro & Hasenack 2009). Soils in these lowland fragments may receive important sediment input and some are located in poorly drained, swampy areas, associated with the formation of lagoons, and may also be influenced by sand dunes (Figs. 1, 2E-I). According to Nimer (1990), in the Paraná subregion, annual precipitation varies from 1,500 to 2,000 mm, with no dry season; mean annual temperatures range from 16 to 22°C , and are lowest at the highest elevations where frosts occur during the winter.

The Pampean province (Fig. 1A) can be roughly divided into two physiognomic types. The grass-dominated matrix of the northeast part is more or less interwoven with fragments of semideciduous forests, herbaceous and shrub vegetation, forming a mosaic (Figs. 2J-K). This region is also known as the Southeastern Highlands, since it reaches higher elevations than the Pampean areas (Fig. 1B). In the southern and western portions of the Pampa, single-layer grasslands (Fig. 2L) prevail. Teixeira

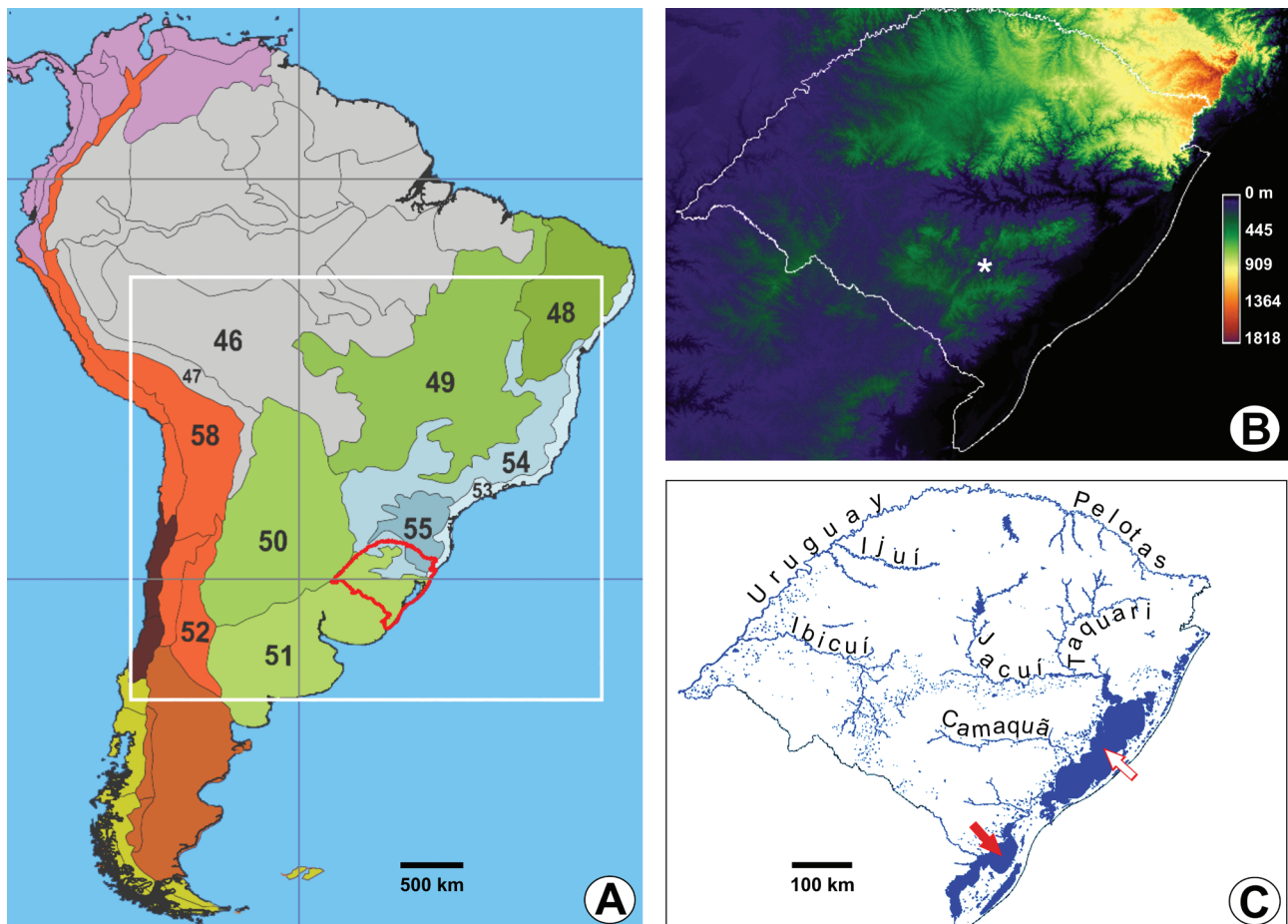


Figure 1. Diagrammatic representation of biogeographic regions, subregions and provinces in South America (A), variation in altitude (B) and locations of main rivers (C) in Rio Grande do Sul state, Brazil (marked with red in A). The broadest area that is covered in the present analysis is circumscribed by a white rectangle in A: South American Transition zone (orange) – Monte (52) and Puna (58) provinces. Neotropical region – Amazonian subregion (pale purple): Pantanal (46) and Yungas (47) provinces; Chacoan subregion (shades of green): Catinga (48), Cerrado (49), Chaco (50) and Pampa (51) provinces. Paraná subregion (shades of blue): Brazilian Atlantic Forest (53), Paraná Forest (54) and *Araucaria angustifolia* Forest (55) provinces. The Southeastern Highlands are indicated by an asterisk in B. Mirim and Patos lagoons are indicated by solid and open arrows, respectively, in C. Sources: A, adapted from Morrone (2006); B and C, modified from Weber & Hasenack (2006).

et al. (1986) and Cordeiro & Hasenack (2009) used the terms steppe and savanna to differentiate the single- and two-layer nature of these grasslands, respectively. In the Pampean province, annual precipitation and mean annual temperatures are lower than in the Paraná subregion, va-

rying from circa 1200 to 1600 mm and from 13 to 17°C, respectively (Overbeck *et al.* 2007).

As described by Cordeiro & Hasenack (2009), any given area in RS has historically suffered from some kind of anthropic influence, mainly related to agricul-

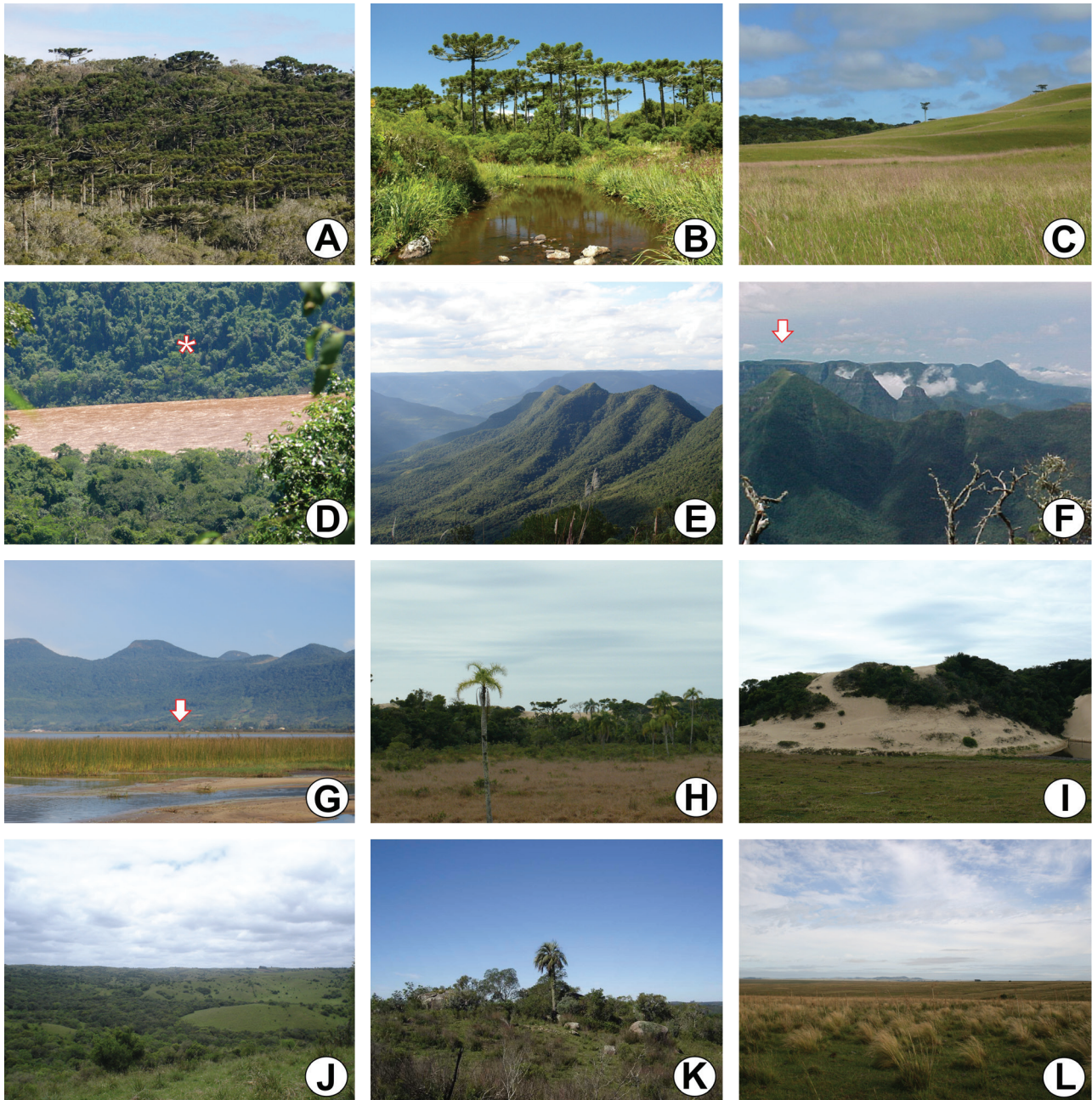


Figure 2. Landscapes in Rio Grande do Sul State, Brazil, according to biogeographic provinces of Morrone (2006): A-C, *Araucaria angustifolia* Forest province; D, Paraná Forest province; E-I, Brazilian Atlantic Forest province; J-L, Pampa province. A, *Araucaria* forest canopy, Aparados da Serra National Park, Cambará do Sul municipality; B, *Araucaria* forest border, Aparados da Serra National Park, Cambará do Sul municipality; C, Steppes (= upper grasslands) in mosaic with *Araucaria* forest, São Francisco de Paula municipality; D, Riparian vegetation (Deciduous Atlantic Forest) on the upper Uruguay River (Argentinian side is indicated by an asterisk) at Turvo State Park, Derrubadas municipality; E, lower portion of the escarpments of Serra do Mar, showing slopes and valleys covered by Atlantic Forest as seen from PROMATA in the Sao Francisco de Paula municipality; F, upper section of the northeast portion of the escarpments of Serra do Mar (at Serra da Rocinha), covered by Atlantic Forest and showing a fragment of *Araucaria* forest (arrow) on the far left horizon, São José dos Ausentes municipality; G, southernmost escarpments of Serra do Mar at Pinguela Lagoon, showing location (arrow) of coastal Dense-Umbrophilous Atlantic Forest, Osorio municipality; H, fragment of lowland Dense-Umbrophilous Atlantic Forest at Itapeva State Park, Torres municipality; I, Sand dunes partially covered by Dense-Umbrophilous Atlantic Forest in Itapeva State Park; J, overview of the Southeastern Highlands, Canguçu municipality; K, close view of Southeastern Highland vegetation, Encruzilhada do Sul municipality; L, Steppes (= lower grasslands), Quaraí municipality.

ture and/or cattle ranching, and lately from widespread expansion of *Eucalyptus*, *Acacia* and *Pinus* plantations. Less than 32% of the total RS area still has a natural or semi-natural appearance, if areas used for cattle grazing are included; more than 80% of the total area formerly covered by natural forests has been removed. The grassland areas are better conserved due to their historical association with livestock raising, a farming activity that has employed traditional land-management practices since the colonization of RS. Overbeck *et al.* (2007) suggested that cattle grazing and the use of fire to clear and improve the quality of grazing lands have been the main factors that impede the expansion of forest within these grasslands, even where climate conditions are favorable. The consequences of these human interferences for the native flora of passion vines remain unknown.

Taxa and track analysis

A total of 15 species of passion vine that occur naturally in RS were included in the study (Mondin *et al.* 2011): *Passiflora actinia* Hook., *P. amethystina* J. C. Mikan, *P. caerulea* L., *P. capsularis* L., *P. edulis* Sims, *P. eichleriana* Mast., *P. elegans* Mast., *P. foetida* L., *P. misera* Kunth, *P. morifolia* Mast., *P. organensis* Gardner, *P. suberosa* L., *P. tenuifila* Killip, *P. urnifolia* Rusby and *P. urubiciensis* Cervi. Therefore, the results and conclusions from this work are restricted to these taxa within the geographical area described above, and should be taken as preliminary information for future studies that include a larger number of passion-vine species within a broader distributional area. By convention, species known to occur farther north but for which there were no records available are herein indicated by an arbitrary dashed track line.

Mondin *et al.* (2011) pointed out that material previously listed by Sacco (1980), Cervi (1981a) and Mondin (2001) for southern Brazil as *Passiflora tricuspis* Masters was misidentified. In the present study, we treated this material as *P. urnifolia*, as recommended by them. *P. foetida* L. is one of the most variable passion vines, with several named varieties (Ulmer & MacDougal 2004). Although at least two of these varieties occur in southern Brazil (Sacco 1980), in this study they were not considered individually, reserving that for a future study. *P. edulis* f. *flavicarpa* Deg., the yellow passion fruit, has been lately cultivated for production of fruit pulp and juice in several Brazilian states, including RS (Aguiar-Menezes *et al.* 2002, Bianchi & Moreira 2005), which may mask the corresponding geographical distribution if cultivated plants are collected without identification as such. *P. edulis* f. *edulis* occurs spontaneously in the Atlantic Forest and, in particular, in open areas covering sand dunes located in the northeast RS (C.A. Mondin; unpublished data). In addition to cultivation, *Passiflora alata* Curtis is subsponaneous in RS forests (Sacco 1962, Mondin 2001, Mondin *et al.* 2010). Furthermore, Koehler-Santos *et al.* (2006) demonstrated that this passion vine, by unknown mechanisms, has been dispersed

along the edges of many RS roads. For these reasons, *P. alata* was not included in the present study.

Records for each passion-vine species, information on literature and/or herbarium sources, and the associated coordinates are listed in Appendix 1 (available online as a supplementary document at <http://www.ufrgs.br/seerbio/ojs/index.php/rbb/article/view/1817>). Those from localities outside RS were taken from the literature. We benefited from the original work of Cervi (1981b) on the subgenus *Decaloba*, although the list of examined material has not yet been formally published. In other words, the summarized version of the Paraná passion vines published by Cervi (1981a) does not include such a list, which is provided here for the first time; that for the subgenus *Passiflora* was made available by Cervi (1997). Records for RS were complemented by examination of herbarium material, from whose labels collection and identification information was transcribed. Those exsiccatas lacking the passion-vine species name and/or that of the authority who identified them were not included in the survey.

The latitude and longitude of the respective localities were defined according to the following databases: Global Gazetteer (Falling Rain Genomics 2007), Species Link - GeoLoc (CRIA 2007) and GLOSK (2008). By using the software Quantum GIS Geographic Information System (Quantum GIS Development Team 2010), data on latitude and longitude for each species were individually georeferenced on the biogeographic province map of Morrone (2006) (Fig. 1A). Distances among localities were then calculated and the minimum-spanning trees obtained through the use of the software Croizat (Cavalcanti 2010). Generalized tracks were built upon the overlap of three or more individual tracks. Panbiogeographic nodes were identified by the intersection of two or more generalized tracks.

RESULTS AND DISCUSSION

Individual tracks

None of the 15 passion-vine species had a distribution entirely within the RS political borders (Figs. 3-4). They were present in both the Paraná and Chacoan subregions, with the exception of three species (*P. actinia*, *P. organensis* and *P. urubiciensis*), which are restricted to the former subregion. The distributional ranges of nine species extend farther north into the South American transition zone and/or Amazonian subregion, and are discussed below. The individual tracks showed that most species are closely associated with forests located on the escarpments of Serra do Mar (more or less at -30°S) and northwards. Species with southern distributions, extending into the Pampean province, were in general found within Deciduous Atlantic Forest fragments that form the riparian vegetation of the Uruguay River and its tributaries (*e.g.*, the Ijuí and Ibicuí rivers), and also in the Semi-deciduous Atlantic Forest fragments located

on the eastern slopes of the Southeastern Highlands (*P. misera*, *P. elegans*, *P. suberosa* and *P. tenuifila*). Our data do not support the contention that *P. elegans* is restricted in distribution to myrtacean formations located within the Pampean province, as proposed by Rambo (1951) and Sacco (1962). This species occurs primarily within the forest limits of the Paraná and Chaco provinces. Similar results were presented previously by Lorenz-Lemke *et al.* (2005), who, basing their study on molecular markers, demonstrated the existence of a close phylogenetic relationship of this species with *P. actinia*, to which *P. elegans* is parapatric. This phylogenetic proximity is also supported by the existence of similarities between them regarding flower and fruit morphologies (see Mondin *et al.* 2011, for a description), which should be tested through appropriate methodology.

Only two species (*P. caerulea* and *P. foetida*) were closely associated with the RS steppes and savannas,

occurring throughout both the Pampean and *Araucaria* Forest provinces, as previously pointed out by Rambo (1951) and Sacco (1962). These species, in particular *P. caerulea*, are known to be cold-tolerant (Vanderplank 1991, Ulmer & MacDougal 2004), a requirement to tolerate the winter frosts that are characteristic of these grasslands. *P. caerulea* accounted for the southernmost record of a passion vine in the present study (Sierra La Barrosa, Argentinian part of Pampean province; -37.88°S, -58.26°W). Thus, we are in agreement with Ulmer & MacDougal (2004) in that passion vines can be found south to almost 40° latitude in the Neotropics. However, our data also clearly demonstrated that only a few species reach that latitudinal limit. Diversity drops sharply for localities south of the escarpments of Serra do Mar, which more or less coincides with the southern limit of the Paraná province. We found one record each of only two species, *P. caerulea* and *P. misera*, south of the Plate

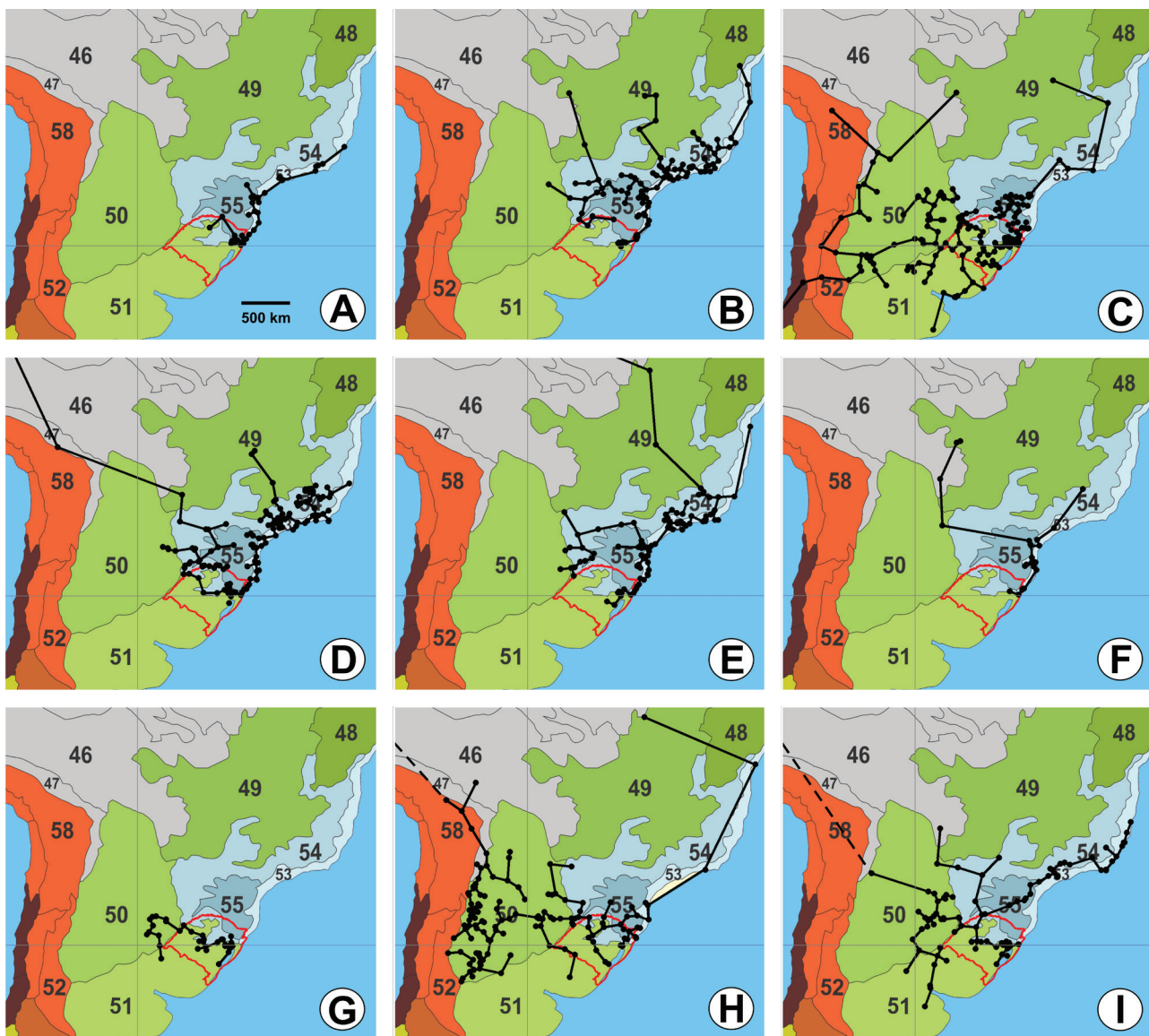


Figure 3. Individual panbiogeographic tracks of *Passiflora* species from Rio Grande do Sul (RS) State, Brazil – A, *P. actinia*; B, *P. amethystina*; C, *P. caerulea*; D, *P. capsularis*; E, *P. edulis*; F, *P. eichleriana*; G, *P. elegans*; H, *P. foetida*; I, *P. misera*. Biogeographic subregions and provinces (Morrone 2006) are represented by different colors and numbers, as listed in Fig. 1. The RS political border is shown in red.

River basin. Such a pattern of decreasing diversity is not unique for passion vines, as this latitude in RS (-30°S) has long been recognized as an important transition zone (from tropical to temperate) for several plant lineages in South America; as mentioned above, in addition to the absence of significant tropical forests at more southern latitudes, the temperature and humidity are also lower (Rambo 1960, Cabrera & Willink 1980, Leite 2002, Waechter 2002, Ritter & Waechter 2004).

Generalized tracks

A total of 35 generalized tracks were identified for the passion vines occurring naturally in RS (Fig. 5A; Table 1). The first one (T1), supported by six species, located at the base of the east side of the Andes, connected the provinces of Yungas (47), Puna (58) and Chaco (50). Its basal portion is similar to those found by Abrahamovich *et al.* (2004), Morrone *et al.* (2004) and López-Ruf *et al.* (2006), and is extended by a series of other tracks (T3, T6, T10-12) into the RS political borders.

The Chaco (50) province was supported by four tracks (T2-3, T5-6). The association between this province with those of the Paraná Forest (54) and the Pampa (51) was supported by tracks T4 and T7, respectively. The northern portion of track T6, and tracks T5 and T10, were congruent to those found by Arzamendia & Giraudo (2009) for snake species of that region.

Two tracks (T24 and T28) were recovered entirely within the limits of the Paraná Forest (54) province, near the Brazilian Atlantic Forest (53) province. However,

several other tracks gave support to the existence of an association of that province with the adjacent ones, for example, tracks T30, T10, and T11 for the Cerrado (49), Chaco (50) and Pampa (51) provinces, respectively.

Five tracks (T21-23, T25-26) coincided with the Brazilian Atlantic Forest (53) province, thus supporting the contention that it is an important area of endemism for the species used in this analysis. Tracks T27 and T31 gave support to the existence of a close association between this province and the Paraná Forest (54). Tracks T22-23 and T25-26 were in agreement with results found by Nihei & Carvalho (2005) for the Brazilian Atlantic Forest in a panbiogeographical analysis carried out with *Polietina* (Diptera, Muscidae). Tracks T25-26 coincided with two sets of endemic areas identified by Sigrist & Carvalho (2008) in a Parsimony Analysis of Endemicity (PAE) carried out with 19 unrelated taxa. The identification of endemic areas at different scales in the Atlantic Forest can be related to a hierarchical pattern of endemism (Espinosa-Organista *et al.* 2001, Silva *et al.* 2004, Sigrist & Carvalho 2008, Ferrari *et al.* 2011).

The *Araucaria angustifolia* Forest (55) province was supported by track T20, and the relationship of this province with the Paraná Forest (54), by tracks T13, T16 and T18.

Thus, the generalized tracks were associated with different biogeographic provinces, demonstrating the mixed nature of the RS area. Two important biotic components were identified: one related to species typically associated with the Brazilian Atlantic Forest (*P. actinia*

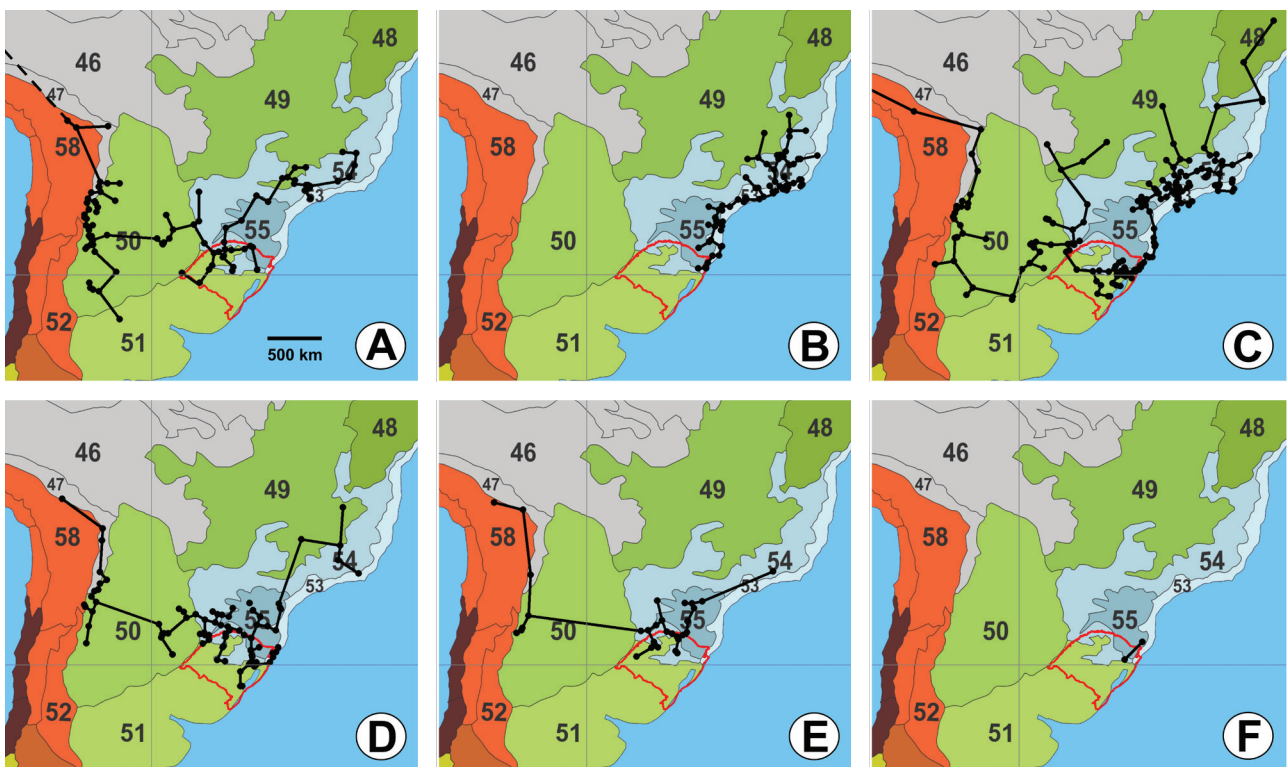


Figure 4. Individual panbiogeographic tracks of *Passiflora* species from Rio Grande do Sul State, Brazil (continuation) - A, *P. morifolia*; B, *P. organensis*; C, *P. suberosa*; D, *P. tenuifila*; E, *P. urnifolia*; F, *P. urubiciensis*. Biogeographic subregions and provinces (Morrone 2006) are represented by different colors and numbers, as listed in Fig. 1. The RS political border is shown in red.

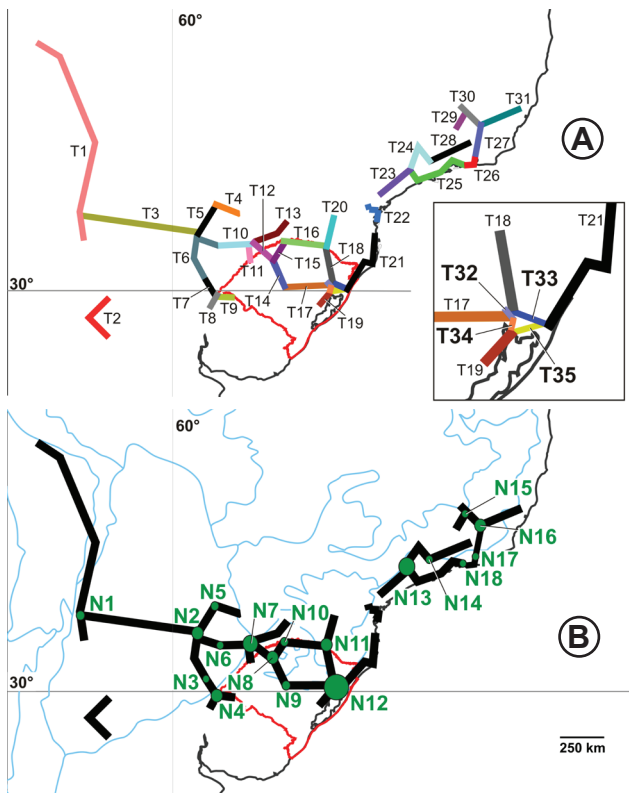


Figure 5. Generalized panbiogeographic tracks of *Passiflora* species from Rio Grande do Sul (RS) state, Brazil (A) and corresponding locations of nodes in relation to Morrone's (2006) biogeographic provinces (B). Track numbers (T) are listed in Table 1. Tracks that form node 12 (N12) are shown in detail in the enlarged inset in A. For identification of biogeographic provinces see Fig. 1. The RS political border is shown in red.

and *P. organensis*), and the other to species that occur from the eastern Andes to the northern portion of the Brazilian Atlantic Forest (*P. caerulea*, *P. capsularis*, *P. foetida*, *P. misera*, *P. morifolia*, *P. suberosa*, *P. tenuiflora*, *P. urnifolia*). This is no surprise, since some of the latter group have long been known to be distributed farther north into Central America (e.g., *P. capsularis* and *P. suberosa*) (Killip 1948, Sacco 1980, Cervi 1997). Also, the northwestern Amazon forests, for example, those located in Colombia and Ecuador, account for a large proportion of passion-vine species diversity existing in the Neotropics (Ulmer & MacDougal 2004, Perez *et al.* 2007). From a dispersalist biogeographical perspective, it has been a tradition to accept that extant RS forests originate from the southward migration of tropical ones located in more northern latitudes, subsequent to the pioneer work of Balduino Rambo (1950) on this subject (e.g., Rambo 1951, 1956, 1961, Mondin & Baptista 1996, Ritter & Waechter 2004, Lorenz-Lenke *et al.* 2005, Mader *et al.* 2009). Whether or not this hypothesis will hold true is open to debate. Recent palynological data presented by Behling *et al.* (2005) gave support to this contention by finding typical tropical elements (genera *Myrsine* and *Cecropia*) far south into the Pampa province (São Francisco de Assis municipality). According to these

authors, this pampean area has been covered by steppes throughout the glacial and postglacial periods, and the corresponding gallery forests were formed later than 5,170 Ma. According to Morrone (2006, 2009), however, there is strong paleontological, paleoclimatological and geological evidence for the prevalence of a temperate climate during the Tertiary ($65.5 \pm 0.3 - 1.806 \pm 0.005$ Ma) in southern South America. This would have allowed the existence of a continuous cloud forest that extended farther south than its present location. After cooling and drying during the Oligocene and Miocene (circa $33.9 \pm 0.1 - 23.03 \pm 0.05$ Ma and $23.03 \pm 0.05 - 5.332 \pm 0.005$ Ma, respectively), this forest fragmented, during a time that coincided with climate changes associated with the uplift of the Andes and expansion of the Chacoan biota. The latter was considered by Zunino (2003) and Morrone (2009) to be an example of dynamic vicariance.

The northwestern Amazon region supported a high biodiversity prior to the Quaternary Period (earlier than 2.6 Ma), and might have had an important role in the evolution of Amazonian biodiversity in general, after the Andean uplift (Hoorn *et al.* 2010, Wesselingh *et al.* 2010). Before the Late Miocene (circa 10 Ma), the area known today as the Amazon was part of a larger "pan-Amazonian" region, which extended south on occasion, reaching the Paraná province *sensu lato* (Lundberg *et al.* 1998, Hoorn *et al.* 2010). The continuous, U-shaped curve formed by the generalized tracks (Fig. 5) gives support to this scenario. It indicates that the RS area is an extant, southern transition zone, which in conjunction with the Chaco province maintains contact between Amazonian and Atlantic populations of these plants. The existence of gene exchange among these passion-vine populations and the possible consequences for the herbivores associated with them should be explored. The function of gallery and deciduous forests located in the Chacoan subregion as past and present bridges between the Amazonian and Paraná subregions was previously demonstrated by Costa (2003) for small forest mammals.

Nodes

A total of 18 panbiogeographic nodes were identified (Fig. 5B). The interpretation of the nodes located far from the RS borders is beyond the scope of the present work. Node N7 connected species that occur in the Chaco (50), Pampa (51), Paraná Forest (54) and *Araucaria angustifolia* Forest (55) provinces, and was closely associated with the borders of these provinces. This is in agreement with the patterns found by Morrone *et al.* (2004) for water bugs (Heteroptera) in the same area. Nodes N8-10 were located near the limits of the Paraná Forest and Pampa provinces, and therefore provide support for the corresponding classification of Morrone (2006). Recovery of these nodes is related to the association of passion-vine distributions with the riparian vegetation of the Uruguay River in the north, and with the forests that cover the slopes of the South Brazilian plateau in the center, and with which the Ibicuí and Jacuí river basins are associa-

Table 1. Generalized tracks of *Passiflora* species occurring in Rio Grande do Sul State, arranged in biogeographic subregions and provinces according to Morrone (2006), with the species defining them.

Track (T)	Subregion	Province	Species
1	Amazonian, Chacoan, South American transition zone	47, 58, 50	<i>P. morifolia</i> , <i>P. caerulea</i> , <i>P. suberosa</i> , <i>P. foetida</i> , <i>P. tenuifila</i> , <i>P. urnifolia</i>
2	Chacoan	50	<i>P. foetida</i> , <i>P. morifolia</i> , <i>P. caerulea</i> , <i>P. suberosa</i>
3	Chacoan	50	<i>P. urnifolia</i> , <i>P. morifolia</i> , <i>P. tenuifila</i>
4	Chacoan	50	<i>P. tenuifila</i> , <i>P. suberosa</i> , <i>P. foetida</i> , <i>P. capsularis</i> , <i>P. caerulea</i> , <i>P. misera</i>
5	Chacoan	50	<i>P. morifolia</i> , <i>P. misera</i> , <i>P. tenuifila</i> , <i>P. caerulea</i>
6	Chacoan	50	<i>P. caerulea</i> , <i>P. foetida</i> , <i>P. tenuifila</i> , <i>P. elegans</i> , <i>P. suberosa</i>
7	Chacoan	50	<i>P. caerulea</i> , <i>P. foetida</i> , <i>P. elegans</i>
8	Chacoan	51	<i>P. caerulea</i> , <i>P. misera</i> , <i>P. elegans</i>
9	Chacoan	51	<i>P. morifolia</i> , <i>P. foetida</i> , <i>P. caerulea</i>
10	Chacoan	50	<i>P. misera</i> , <i>P. foetida</i> , <i>P. suberosa</i>
11	Chacoan	51	<i>P. misera</i> , <i>P. suberosa</i> , <i>P. edulis</i>
12	Paraná	54	<i>P. caerulea</i> , <i>P. morifolia</i> , <i>P. capsularis</i> , <i>P. amethystina</i>
13	Paraná	55, 54	<i>P. edulis</i> , <i>P. urnifolia</i> , <i>P. caerulea</i>
14	Chacoan, Paraná	51, 54	<i>P. foetida</i> , <i>P. capsularis</i> , <i>P. misera</i> , <i>P. tenuifila</i>
15	Paraná	54	<i>P. amethystina</i> , <i>P. misera</i> , <i>P. tenuifila</i> , <i>P. foetida</i>
16	Paraná	54, 55	<i>P. amethystina</i> , <i>P. capsularis</i> , <i>P. misera</i> , <i>P. urnifolia</i> , <i>P. tenuifila</i> ;
17	Paraná	54	<i>P. elegans</i> , <i>P. suberosa</i> , <i>P. capsularis</i> , <i>P. misera</i> ;
18	Paraná	54, 55	<i>P. morifolia</i> , <i>P. tenuifila</i> , <i>P. actinia</i>
19	Chacoan	51	<i>P. misera</i> , <i>P. elegans</i> , <i>P. edulis</i>
20	Paraná	55	<i>P. urnifolia</i> , <i>P. tenuifila</i> , <i>P. caerulea</i>
21	Paraná	53	<i>P. capsularis</i> , <i>P. eichleriana</i> , <i>P. actinia</i> , <i>P. edulis</i> , <i>P. suberosa</i> , <i>P. amethystina</i>
22	Paraná	53, 55	<i>P. amethystina</i> , <i>P. edulis</i> , <i>P. capsularis</i> , <i>P. actinia</i>
23	Paraná	53	<i>P. eichleriana</i> , <i>P. amethystina</i> , <i>P. organensis</i>
24	Paraná	53, 54	<i>P. edulis</i> , <i>P. caerulea</i> , <i>P. amethystina</i> , <i>P. suberosa</i> ;
25	Paraná	53	<i>P. edulis</i> , <i>P. capsularis</i> , <i>P. actinia</i> , <i>P. amethystina</i>
26	Paraná	53	<i>P. actinia</i> , <i>P. suberosa</i> , <i>P. amethystina</i> , <i>P. caerulea</i> , <i>P. edulis</i> , <i>P. foetida</i>
27	Paraná	53, 54	<i>P. caerulea</i> , <i>P. foetida</i> , <i>P. suberosa</i>
28	Paraná	54	<i>P. morifolia</i> , <i>P. misera</i> , <i>P. urnifolia</i>
29	Paraná	54	<i>P. organensis</i> , <i>P. tenuifila</i> , <i>P. capsularis</i>
30	Chacoan, Paraná	49, 54	<i>P. capsularis</i> , <i>P. suberosa</i> , <i>P. organensis</i>
31	Paraná	53, 54	<i>P. organensis</i> , <i>P. capsularis</i> , <i>P. suberosa</i>
32	Paraná	54	<i>P. edulis</i> , <i>P. suberosa</i> , <i>P. caerulea</i>
33	Paraná	53, 54	<i>P. capsularis</i> , <i>P. caerulea</i> , <i>P. eichleriana</i>
34	Chacoan, Paraná	51, 54	<i>P. edulis</i> , <i>P. suberosa</i> , <i>P. elegans</i>
35	Chacoan, Paraná	51, 53	<i>P. suberosa</i> , <i>P. tenuifila</i> , <i>P. misera</i>

ted, thus dividing the positions of the generalized tracks into two routes. The analysis of Arzamendia & Giraudo (2009) suggested that the Paraná, Paraguay and Uruguay rivers, which form the Plata River Basin, have individually influenced, in different ways, faunal and floristic tropical elements with their origins in the Amazon and Atlantic regions *sensu lato*. These relationships should be also explored for passion vines.

Seven generalized tracks (T17-19, T21 and T32-35; detail in Fig. 5A) gave support to the node N12, located at the southernmost limits of the Paraná subregion (provinces 53, 54 and 55) and the Pampa (51) province, thus associating this area with the highest biogeographical complexity found in this study. In fact, forests located in northeastern RS have long been recognized for their great plant specific diversity (Ritter & Waechter 2004). Contributing to this scenario is the unique physiognomy in this region, where for example near the Torres Municipality within a distance of few kilometers, the altitude varies more than 1,000 m, and the forest changes from an *Araucaria* formation at the top of the South Brazilian

plateau to a continuous longitudinal variation of Semi-deciduous forests on the slopes, to Dense-Umbrophilous forest fragments interspersed with steppes on the lowlands; all in association with high temperature and condensed moisture coming from the nearby Atlantic Ocean (Leite 2002). Alluding to these peculiarities in geography, Rambo (1950) termed that region the Torres "door", through which elements of the Atlantic Forest *sensu stricto* would have migrated south. However, as discussed above, there is also evidence to the contrary. The data presented herein, in conjunction with information available in the literature, lead to a more general interpretation than that for passion vines. We suggest that the biogeographically and historically related northeast RS region is highly likely to be part of a broader endemism area for these plants, which should be explored in the future. In addition to the three species shown in this study to be closely associated with northeastern RS (*P. actinia*, *P. organensis* and *P. urubiciensis*), several others have distributions restricted to the southern part of the Atlantic Forest *sensu lato* (e.g., *P. catharinensis* Sacco,

P. lepidota Mast., *P. mendocaei* Harms, *P. reitzii* Sacco and *P. truncata* Regel) (Sacco 1980, Cervi 1997).

Consequences for herbivores

The results found in this study lead to several questions regarding the consequences of this variation in passion-vine spatial distributions for the herbivores that are associated with them, which should be further explored. For example, the heliconians (= Heliconiini, *sensu* Penz & Peggie 2003), a well-known tropical butterfly group (biology reviewed by Benson *et al.* 1976, Brown 1981, Gilbert 1991) with larvae that in most cases feed only on passion vines (Beccaloni *et al.* 2008) should have southern distributional limits similar to those of these plants. In fact, in Rio Grande do Sul are located the southernmost areas of the Neotropical region, which harbor a highly diverse fauna of heliconian butterflies (Brown & Mielke 1972, Brown 1979). It is reasonable to assume that the limit for this richness in diversity, as for passion vines, coincides with the southern border of the Brazilian Atlantic Forest itself (roughly at latitude -30°S, as mentioned above). Thus, moving south in RS, one expects to find large numbers of heliconian butterflies in the forests located on the escarpments of the Serra do Mar, compared to those existing in the nearby southern Pampa areas, where their diversity would drop out. In accordance with this pattern, a total of 13 heliconian species have been reported up to now in RS (Teston *et al.* 2006, Iserhard *et al.* 2010), some of them with distributions restricted to the northern portion covered by the Brazilian Atlantic Forest *sensu lato* (Morellato & Haddad 2000). Only eight heliconian species have been recorded in neighboring Uruguay (Biezanko *et al.* 1978, Bentancur-Viglione 2009), within the Pampa biome and where four naturally occurring species of passion vine (*P. caerulea*, *P. elegans*, *P. foetida* and *P. misera*) were recorded herein. Only four heliconian species were reported by Canals (2000) and Bustos (2008) for the Argentinian province of Buenos Aires, where only two of the passion vines (*P. caerulea* and *P. misera*) treated in the present study were recorded.

This variation in distribution results primarily from selection of host plants during oviposition, which in general is positively associated with larval feeding preferences and better life-history performance (regarding survivorship, development time, and size attained in the adult stage) in heliconian butterflies (*e.g.*, Rodrigues & Moreira 2002, 2004, Kerpel & Moreira 2005). Species of *Heliconius* in particular may have small home ranges: the adults show roosting behavior, and an individual may use the same roost throughout its life (Di Mare 1984). As a consequence, spatial distributions in these cases are potentially influenced by those of host plants on a very small scale for a given locality. For example, Cerveira *et al.* (2003) demonstrated for a population of *Heliconius erato phyllis* (Fabricius) that was distributed within a 21.5-ha area located in the Barra do Ribeiro municipality, first, that the adults are spatially aggregated; and second,

that their spatial distributions are highly correlated, not only with those of the flower resources but also with *P. misera*, one of the most used and preferred larval host plant for this heliconian in RS. Thus, although *H. erato phyllis* is widespread, since the larvae accept a broader range of lower-ranked passion vine species for feeding, it should be found in greater frequencies in the forest fragments located in the northwestern, central and northeastern areas. That is, it should be more common within the distribution ranges of *P. misera*, *P. suberosa* and *P. capsularis*, the three most preferred and used host plants (Menna-Barreto & Araujo 1985, Perico 1995, Kerpel & Moreira 2005). The same pattern could be inferred for *Dryas iulia alcionea* (Cramer), a heliconian species that uses similar host plants as *H. erato phyllis* (Perico & Araujo 1981), but that feeds on older leaves, in contrast to the meristem feeding habit of the former (Rodrigues & Moreira 1999, Borges 2005). On the other hand, *Heliconius ethilla narcaea* Godart, which shows a preference for and achieves the best performance on *P. actinia*, should be more commonly found in the northeast region of RS, where this passion vine is abundant. In this case, however, such a pattern may be somewhat masked by that of *P. alata*, a species recently introduced into RS, and that is also successfully used as a host plant by the larva of *H. ethilla narcaea* (Silva 2008). Similarly, *Dione junio junio* (Cramer) populations are expected to be largely determined by the existence of cultivated fields of *P. edulis*. This species is nowadays widely grown for commercial production of passion-fruit juice, mainly in the northeast region, and is the preferred and most-suitable larval-feeding resource for this heliconian species in RS (Bianchi & Moreira 2005). Populations of *Dione moneta moneta* Hubner, apparently a monophagous feeder on *P. morifolia* in southern Brazil (Brown & Mielke 1972), should be more frequently found in the northwestern areas of RS, where this passion-vine species is more or less restricted in distribution. In contrast, *Agraulis vanillae maculosa* (Stichel) should be widespread, and should also be the predominant heliconian butterfly in the relatively vast extension of the more open areas existing in the Pampa. Unpublished data (G.R.P. Moreira, UFRGS) show that it successfully uses *P. caerulea*, the only common and widespread passion vine species in that province. We are now carrying out a survey of passion vines and heliconian butterflies existing in herbarium and museum collections in order to evaluate records from a broader geographical area, to further test not only these hypotheses related to their covariation in spatial distribution, but also the corresponding roles in co-speciation.

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