Plant Ecology and Evolution 151 (2): 161–174, 2018
https://doi.org/10.5091/plecevo.2018.1419

REGULAR PAPER

Diversification of *Galianthe* species (Rubiaceae) in the Neotropical seasonally dry forests: a case study of a mainly subshrubby genus

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Aim – To evaluate the current distribution of the species of the genus *Galianthe* by track analysis, and to establish the distributional patterns based on the available tectonic information and the biogeographical regionalization of the Neotropical region.
Methods – A total of 2680 geographical records of 55 species were analysed, representing 100% of the species assigned to *Galianthe*. Individual tracks were obtained for each species by plotting localities and connecting them by minimum-spanning trees. Generalized tracks and nodes were determined from the spatial overlap among individual tracks. Individual and generalized tracks and nodes were geographically located using DIVA-GIS. Generalized tracks and nodes were superimposed on two layers, one of them with the biogeographical provinces of the Neotropical region, and the other with the distribution of Neotropical seasonally dry forests.
Results – Five generalized tracks and four nodes were identified, all located within the Brazilian and Chacoan subregions. These nodes coincide with almost all fragments of Neotropical seasonally dry forests.
Main conclusions – Our results demonstrate the intimate relationship of the ancestral biota of *Galianthe* with the fragments of Neotropical seasonally dry forests, suggesting that they could serve as refugia during unfavourable geological periods and, therefore, actively influence the current distribution of their species. In addition, the early dispersal of the species, along with the various vicariant events such as the rise of the Andes, the cooling and aridification during the Oligocene-Miocene, the formation of the Chacoan subregion, and the alluvial dynamics during the Pliocene-Holocene could favoured adaptive radiation of *Galianthe* species.

Key words – Distribution, *Spermacoce*, biogeography, nodes, track analysis, vicariance.

INTRODUCTION

The knowledge of the distribution of diversity and areas of species co-occurrence is fundamental to understand the evolutionary process in time and space, as the spatial arrangement of living beings is basically the result of the vicariant formation of the taxonomic groups involved (Craw et al. 1999). The vicariant process, which includes the processes of mobility (= dispersal) and vicariance, allows us to understand the biodiversity from a historical perspective, and to generate important information for its conservation (Morrone & Espinosa 1998, Morrone 2000).

In evolutionary biogeography, track analysis emphasizes the importance of the spatial dimension (geographical) of biodiversity, to provide a proper understanding of the patterns and evolutionary processes from geographical distributions. If the distribution of two or more taxa coincides, it can be postulated that they belong to an ancestral biota, i.e. that different taxa, although having different dispersal means, have been spatially-temporally integrated in the same biota (Morrone 2015). In this discipline, nodes are interpreted as zones of tectonic and biotic convergence (Morrone 2004, Loaiza & Morrone 2011).

ISSN: 2032-3913 (print) – 2032-3921 (online)

The Neotropical seasonally dry forests (NSDF) are essentially ecosystems characterized by having a continuous or nearly continuous woody canopy with sparse grasses, with Bromeliaceae, Asteraceae and Malvaceae also represented (Mooney et al. 1995, Pennington et al. 2000), and extending from northern Pacific Mexico to northern Argentina (see distribution map in Linares-Palomino et al. 2011, Banda-R et al. 2016). They have an average rainfall of less than 1600 mm per year and a period of 3–6 months with rainfall practically negligible (Gentry 1995, Graham & Dilcher 1995). In central-north South America these forests spread their distribution across the continent in a horseshoe-shaped fashion, the so called Pleistocenic Arc (Prado & Gibbs 1993, Prado 2000), which allegedly today are the disjunct fragments of once extensive and continuous NSDF during the Pleistocene (Mogni et al. 2015a).

The genus *Galianthe* Griseb. belongs to the family Rubiaceae, tribe Spermacoceae. This tribe has a pantropical distribution with c. 61 genera and 1235 species (Groeninckx et al. 2009). *Galianthe* is one of the 23 genera belonging to the *Spermacoce* clade (Salas et al. 2015), which is a monophyletic group deeply nested among the remaining genera of the tribe Spermacoceae. The genus is considered a monophyletic taxon with well-defined morphological and molecular limits (Salas et al. 2015). It was taxonomically reviewed by Cabral & Bacigalupo (1997) and Cabral (2009), and is morphologically characterized by lax inflorescences, heterostylous flowers, bifid stigma, pollen grains with double reticulum, and 1-seeded carpels (Cabral 2009, Florentín et al. 2017a). *Galianthe* comprises 55 species divided into two subgenera: *Galianthe* subgen. *Galianthe* with 41 South American species, and *Galianthe* subgen. *Ebelia*. This latter subgenus comprises 14 species with two disjunct areas of distribution, one South American, from southeastern and southern Brazil, eastern Paraguay, Uruguay and northeastern and central Argentina; and the other area in Mexico (Chiapas), Belize, Guatemala, Colombia, Ecuador, and Peru (Cabral 2002).

Studies focused on the biogeography of tribe Spermacoceae are scarce, especially in the genus *Galianthe*. Janssens et al. (2016) postulated that in Madagascar, the tribe has its origin in the Oligocene through long-distance dispersal events, with a subsequent radiation in the Miocene. They also mentioned that Africa as well as the Neotropics modelled the current diversity of Spermacoceae in Madagascar, based on two dispersal events from America or Africa. More locally, Iganci et al. (2011) analysed the endemic species of the subtropical altitude grasslands in southern Brazil, finding three species of *Galianthe*, all belonging to the subgenus *Galianthe*. Florentín et al. (2016) performed a track analysis of *Galianthe* subgen. *Ebelia*, and as results a generalized track they called “Parana” was obtained, that represents an ancestral biota connecting the biogeographical provinces of Cerrado and Chaco from Chacoan Dominion, with Atlantic, Parana and Araucaria provinces from Parana Dominion.

The available biogeographic studies in the genus *Galianthe*, even in the tribe Spermacoceae, reveal a remarkable deficit in this area of knowledge, especially in relation with the current regional proposals of biogeographic regionalization. Therefore, the aim of this work is to evaluate the current distribution of the species of the genus *Galianthe* by track analysis, and to establish the distribution patterns based on the available tectonic information and the biogeographical regionalization of the Neotropical region.

MATERIALS AND METHODS

Study area

We employed the biogeographic provinces system proposed by Morrone (2014a, 2017) based on the analysis of distribution patterns of different taxa (fauna and flora). The study areas were the Neotropical region and the South American transition zone. The Neotropical region basically comprises the American tropics, from southern Mexico to central Argentina, and consists of three subregions: Antillean, Brazilian, and Chacoan (Morrone 2014a, 2017). The South American transition zone includes the Andes of South America, from Páramo province in northern Venezuela to Colombia, Ecuador, to Puna, Comechingones and Monte in central Southern Argentina (Martínez et al. 2017, Arana et al. 2017) (fig. 1). This transition zone is formed by the contact between the Neotropical and Andean regions, essentially with taxa belonging to both areas.

Taxa

The primary source is the material of *Galianthe* studied particularly in the revisions of the genus (Cabral & Bacigalupo 1997, Cabral 2002, 2009) and posterior works (Florentín et al. 2017a, 2017b) A total of 2680 geographical records of 55 species from 57 herbaria were analysed, representing 100% of the species assigned to *Galianthe.* Also, the following database were consulted: Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/herbarioVirtual/), speciesLink (1002 data, http://www.splink.cria.org.br) and TROPICOS (120 data, http://www.tropicos.org). The taxonomic identifications were confirmed through available images in the databases (table 1). The full list of records is available under request.

Methods

For each specimen, geographical coordinates were taken from labels; when they were not georeferenced, coordinates from municipalities were registered using Google Earth (2015). Individual tracks were constructed for each species by plotting their localities of occurrence on maps with the minimum distance criterion, called individual tracks (Morrone 2015). These were generated in the DIVA-GIS software Version 7.5 through the Map-Measure commands distance and Data-Draw Shape-lines.

Individual tracks were superimposed to establish the existence of generalized tracks, which in turn can establish the existence of ancestral biotas widely distributed and fragmented by vicariant events and constitute the graphical representation of biotas on a map (Morrone 2009).

The intersection between two or more generalized tracks represents a node, which is interpreted as a zone of tectonic and biotic convergence. The node can present endemism, high diversity, distribution limits, geographical disjunctions, confluence of different ancestral biotas, and anomalous absence of taxa (Heads 2004), denoting a complex area, which is usually the result of geobiotic convergence (Miguel-Talonia & Escalante 2013). The localities of occurrence, individual and generalized tracks, and nodes were plotted using the DIVA-GIS software Version 7.5 (Geographic Information System for Data Analysis Distribution of Species, Hijmans 2015). Tracks and nodes were superimposed with the layers of biogeographic provinces of the Neotropical region (Morrone 2014a, 2017) and of the distribution of Neotropical seasonally dry forests (NSDF) *sensu* Särkinen et al. (2011) (see figs 1 & 2).

RESULTS

In the present analysis, 2680 records belonging to 55 all species of *Galianthe*, distributed in eight countries, were included. The distribution of nine species represents isolated tracks that were not included in the analysis because they do not contribute to any generalized track. These correspond to *G. angulata* (Benth.) Borhidi, *G. chiquitosiana* E.L.Cabral, *G. elegans* E.L.Cabral, *G. hassleriana* (Chodat) E.L.Cabral, *G. macedoi* E.L.Cabral, *G. matogrossiana* E.L.Cabral,

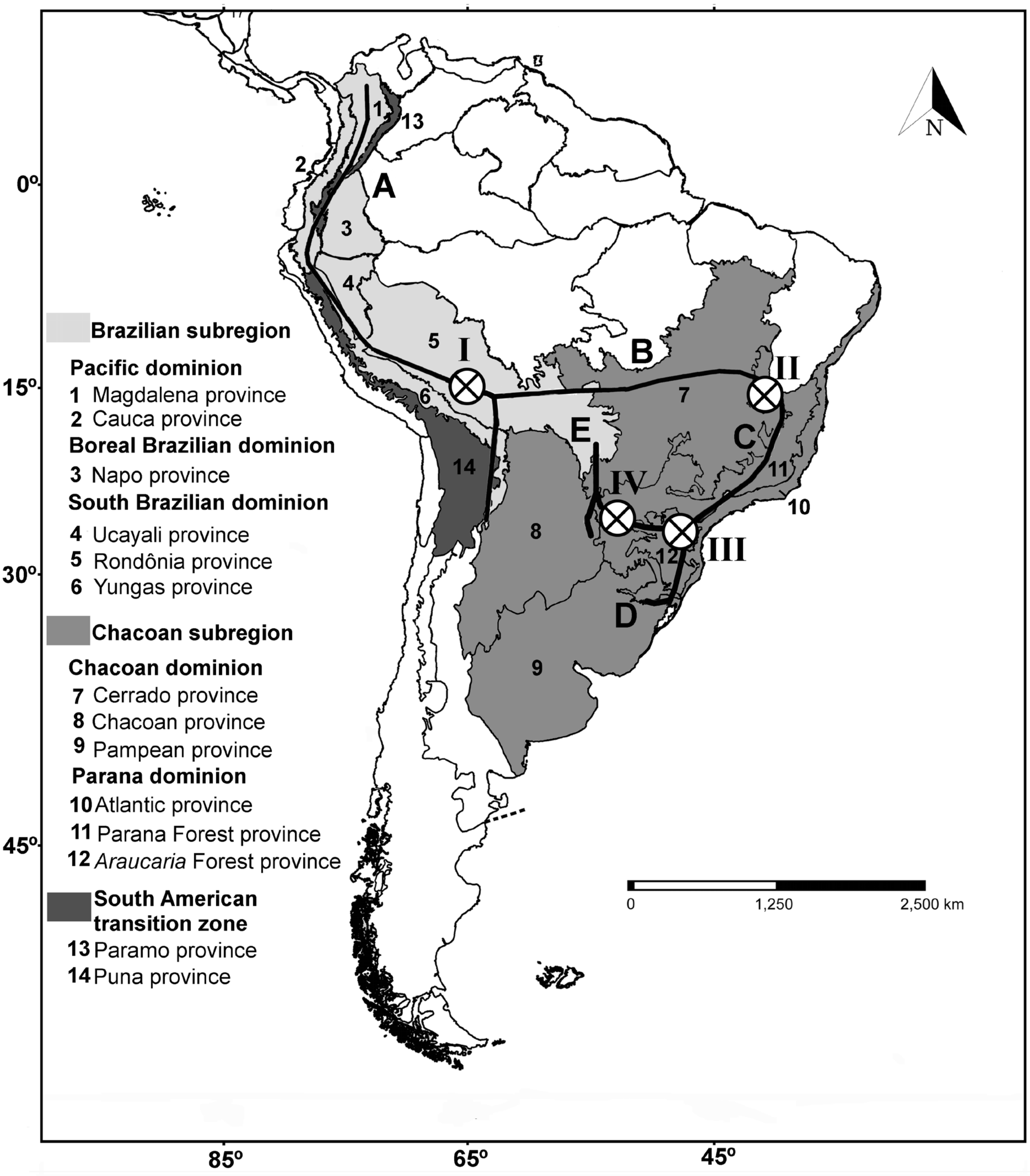

Figure 1 – Superposition of generalized tracks and nodes with the biogeographic provinces of the Neotropical region (modified from Morrone 2014a).

G. linearifolia E.L.Cabral, *G. polygonoides* E.L.Cabral & Bacigalupo, and *G. sudyungensis* E.L.Cabral (figs 3 & 4). Five generalized tracks were obtained (fig. 1), supported by the remaining 46 species. The track supported by the largest number of species was track called here Parana track with 14 species, followed by the so called Chacoan track with 11 species, the Brazilian track with eight species, the Pampean track with seven species, and the Andean track supported by six species. (fig. 5).

The Andean track is located in Colombia, Ecuador, Peru, and Bolivia, from western Bolívar (Colombia) to south central La Paz (Bolivia), through Ecuador (Sucumbíos, Napo, Tungurahua, Chimborazo, Cañar, Azuay, and Chinchipe), and Peru (Cajamarca, Amazonas, San Martín, Huánuco, Pasco, Junín, Cuzco, and Puno). It is supported by six species: *G. bogotensis* (Kunth) E.L.Cabral & Bacigalupo, *G. boliviana* E.L.Cabral, *G. dichotoma* (Willd. ex Roem. & Schult.) E.L.Cabral & Bacigalupo, *G. peruviana* (Pers.) E.L.Cabral,

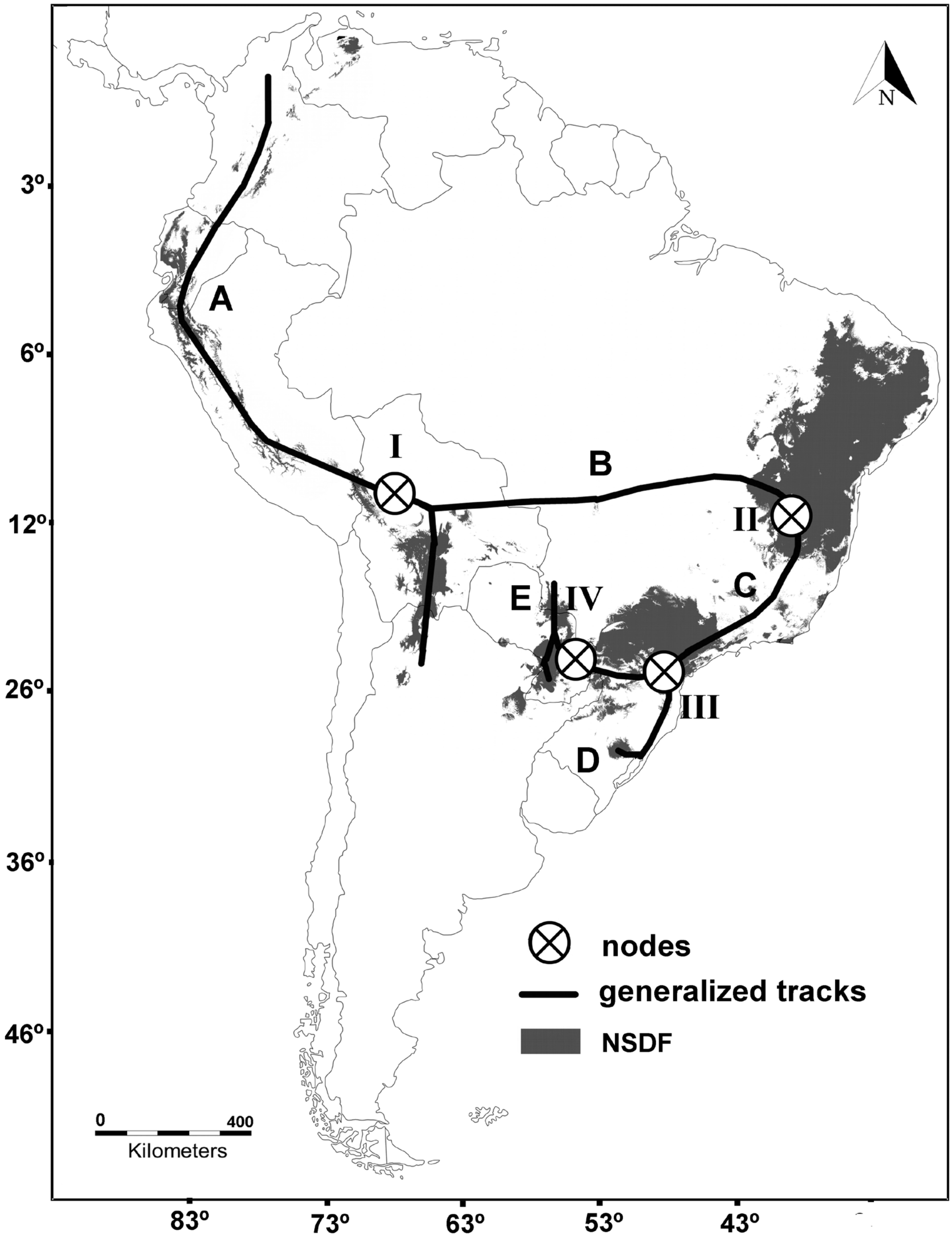

Figure 2 – Generalized tracks: A, Andean; B, Brazilian; C, Parana; D, Pampean; E, Chacoan; Nodes I, II, III and IV and Neotropical seasonally dry forests (NSDF; *sensu* Särkinen et al. 2011).

Table 1 – **Number of records by species.**

Species	Number of records by species
Galianthe andersonii E.L.Cabral	15
G. angustifolia (Cham. & Schltdl.) E.L.Cabral	84
G. aurelii E.L.Cabral	11
G. bisepala E.L.Cabral	14
G. canindeyuensis E.L.Cabral	13
G. centranthoides (Cham. & Schltdl.) E.L.Cabral	145
G. chiquitosiana E.L.Cabral	9
G. chodatiana (Standl.) E.L.Cabral	79
G. cyperoides (Chodat & Hassl.) E.L.Cabral	20
G. elegans E.L.Cabral	16
G. equisetoides (Cham. & Schltdl.) E.L.Cabral	22
G. eupatorioides (Cham. & Schltdl.) E.L.Cabral	201
G. fastigiata Griseb.	214
G. gertii E.L.Cabral	37
G. grandifolia E.L.Cabral	200
G. guaranitica (Chodat & Hassl.) E.L.Cabral	11
G. hassleriana (Chodat) E.L.Cabral	2
G. kempffiana E.L.Cabral	10
G. krausei (Suess.) E.L.Cabral	26
G. lanceifolia E.L.Cabral	20
G. latistipula E.L.Cabral	24
G. laxa (Cham. & Schltdl.) E.L.Cabral	178
G. liliifolia (Standl.) E.L.Cabral	32
G. linearifolia E.L.Cabral	3
G. longifolia (Standl.) E.L.Cabral	20
G. longisepala E.L.Cabral	6
G. macedoi E.L.Cabral	3
G. matogrossiana E.L.Cabral	2
G. montesii E.L.Cabral	3
G. paraguariensis (Chodat & Hassl.) E.L.Cabral	51
G. parvula E.L.Cabral	9
G. peruviana (Pers.) E.L.Cabral	72
G. pseudopeciolata E.L.Cabral	14
G. ramosa E.L.Cabral	70
G. reitzii E.L.Cabral	19
G. riograndensis Florentín & E.L.Cabral	5
G. souzae E.L.Cabral & Bacigalupo	13
G. sudyungensis E.L.Cabral	3
G. thalictroides (K.Schum.) E.L.Cabral	65
G. valerianoides (Cham. & Schltdl.) E.L.Cabral	108
G. verbenoides (Cham. & Schltdl.) Griseb.	48
G. angulata (Benth.) Borhidi	30
G. bogotensis (Kunth) E.L.Cabral & Bacigalupo	33
G. boliviana E.L.Cabral	3

Table 1 (continued) – Number of records by species.

Species	Number of records by species
G. brasiliensis (Spreng.) E.L.Cabral & Bacigalupo	361
G. cymosa (Cham.) E.L.Cabral & Bacigalupo	25
G. dichasia (Sucre & C.G.Costa) E.L.Cabral	51
G. dichotoma (Willd. ex Roem. & Schult.) E.L.Cabral & Bacigalupo	28
G. hispidula (A.Rich. ex DC.) E.L.Cabral & Bacigalupo	114
G. humilis E.L.Cabral & Bacigalupo	2
G. palustris (Cham. & Schltdl.) Cabaña Fader & E.L.Cabral	74
G. polygonoides E.L.Cabral & Bacigalupo	6
G. spicata (Miq.) Cabaña Fader & Dessein	27
G. vaginata E.L.Cabral & Bacigalupo	20
G. vasquezii R.M.Salas & J.Florentín	9
Geographical records	2680

G. spicata (Miq.) Cabaña Fader & Dessein, and *G. vasquezii* R.M.Salas & J.Florentín. (fig. 5A–C). From the biogeographical point of view (Morrone 2014a), it is included in the provinces of Magdalena, Cauca, Napo, Ucayali, Rondônia and Yungas in the Brazilian subregion, and the Paramo and Puna provinces of the South American transition zone (fig. 1). Additionally, this track is intersecting the relicts of NSDF distributed throughout Colombia, Ecuador, Peru, and Bolivia (fig. 2).

The Brazilian track extends from Cochabamba (Bolivia) to southern Bahia (Brazil); in southeastern Cochabamba, this track bifurcates directing one of its branches to northwestern Argentina (Jujuy and Salta provinces), whereas the other goes to Brazil through southern Mato Grosso and northern Goiás, ending in southeastern Bahia. It is supported by eight species: *G. angustifolia* (Cham. & Schltdl.) E.L.Cabral, *G. bisepala* E.L.Cabral, *G. eupatorioides* (Cham. & Schltdl.) E.L.Cabral, *G. kempffiana* E.L.Cabral, *G. lanceifolia* E.L.Cabral, *G. laxa* (Cham. & Schltdl.) E.L.Cabral, *G. longisepala* E.L.Cabral, and *G. ramosa* E.L.Cabral (fig. 5D–G). This track is located in the biogeographic provinces of Rondônia and Yungas, belonging to the Brazilian subregion, also the Cerrado, and Parana Forest provinces belonging to the Chacoan subregion, and the Puna province (fig. 1) belonging to the South American transition zone (Morrone 2014a). As for the NSDF, it relates the piedmont forests in Argentina and Bolivia (seasonally dry forest of the Yungas; Prado 1995), with Inter-Andean dry valleys of northern Bolivia, and the seasonally dry forests of Chiquitanía (fig. 2), recently proposed as a new nucleus of dry forests distribution in South America (Mogni et al. 2015b).

The Parana track is located in Brazil; from southern Bahia and central Minas Gerais, it goes through eastern São Paulo to southwestern Parana state. This track is supported by 14 species, of which the first six correspond to *Galianthe* subgen. *Ebelia* [*G. brasiliensis* (Spreng.) E.L.Cabral & Bacigalupo, *G. cymosa* (Cham.) E.L.Cabral & Bacigalupo, *G. dichasia* (Sucre & C.G.Costa) E.L.Cabral, *G. hispidula* (A. Rich. ex DC.) E.L.Cabral & Bacigalupo, *G. humilis* E.L.Cabral & Bacigalupo, and *G. vaginata* E.L.Cabral & Bacigalupo], and the remaining eight species belong to subgenus *Galianthe* [*G. andersonii* E.L.Cabral, *G. centranthoides* (Cham. & Schltdl.) E.L.Cabral, *G. chodatiana* (Standl.) E.L.Cabral, *G. grandifolia* E.L.Cabral, *G. liliifolia* (Standl.) E.L.Cabral, *G. longifolia* (Standl.) E.L.Cabral, *G. souzae* E.L.Cabral & Bacigalupo, and *G. valerianoides* (Cham. & Schltdl.) E.L.Cabral] (fig. 5H–K). It is entirely located in Brazil, in the Chacoan and Parana dominions, in the first dominion the track is located in the Cerrado province, and in the latter in the Atlantic, Parana Forest and Araucaria Forest provinces, both dominions belonging to the Chacoan subregion (fig. 1) (Morrone 2014a). As for NSDF, Parana track connects the two largest nuclei of South American NSDF (*sensu* Prado 2000), the Misiones nucleus and the southern part of the Caatinga nucleus (fig. 2).

The Pampean track, also exclusively Brazilian, extends from eastern Paraná to northeastern Rio Grande do Sul, going through to eastern Santa Catarina state. This track is supported by seven species: *G. equisetoides* (Cham. & Schltdl.) E.L.Cabral, *G. gertii* E.L.Cabral, *G. latistipula* E.L.Cabral, *G. reitzii* E.L.Cabral, *G. riograndensis* Florentín & E.L.Cabral, *G. palustris* (Cham. & Schltdl.) Cabaña Fader & E.L.Cabral, and *G. pseudopeciolata* E.L.Cabral (fig. 5L–O). It is located in Pampean, Parana Forest, and Araucaria Forest Provinces of the Chacoan Subregion (fig. 1).

The Chacoan Track is located in southwestern Mato Grosso do Sul state (Brazil), Concepción and San Pedro departments (Paraguay); one of its branches goes into Caaguazú and Alto Paraná (Paraguay), and the other branch into Cordillera, Central, and Paraguarí departments. It is supported by 11 taxa: *G. aurelii* E.L.Cabral, *G. canindeyuensis* E.L.Cabral, *G. cyperoides* (Chodat & Hassl.) E.Cabral, *G. fastigiata* Griseb., *G. guaranitica* (Chodat & Hassl.) E.L.Cabral, *G. krausei* (Suess.) E.L.Cabral, *G. montesii* E.L.Cabral, *G. paraguariensis* (Chodat & Hassl.) E.L.Cabral, *G. parvula* E.L.Cabral, *G. thalictroides* (K.Schum.) E.L.Cabral, and *G. verbenoides* (Cham. & Schltdl.) Griseb. (fig. 5P–S). This generalized track is entirely in the Chacoan dominion, in the Cerrado and Chacoan provinces, and in the Paraná forest province of the Paraná dominion, both belonging to the Chacoan subregion (fig. 1). As for NSDF, its entire extension corresponds to fragment of forests by Prado & Gibbs (1993) (fig. 2).

Based on the intersection of the generalized tracks, four nodes (I–IV) were identified, which represent key areas of high biotic diversity and biotic convergence. Node I represents the intersection of the Andean and Brazilian tracks, and it is geographically located in western Bolivia, in the biogeographic province of Rondônia, belonging to the South Brazilian dominion, Brazilian subregion (fig. 1). Node II corresponds to the intersection of Brazilian and Parana tracks, it is located in Minas Gerais state, in the Cerrado province of the Chacoan dominion, and in the Paraná forest province of the Parana dominion, Chacoan subregion (fig. 1). Node III is located in Paraná state (Brazil), in the Atlantic and Araucaria Forest provinces; it corresponds to the intersection of gener-

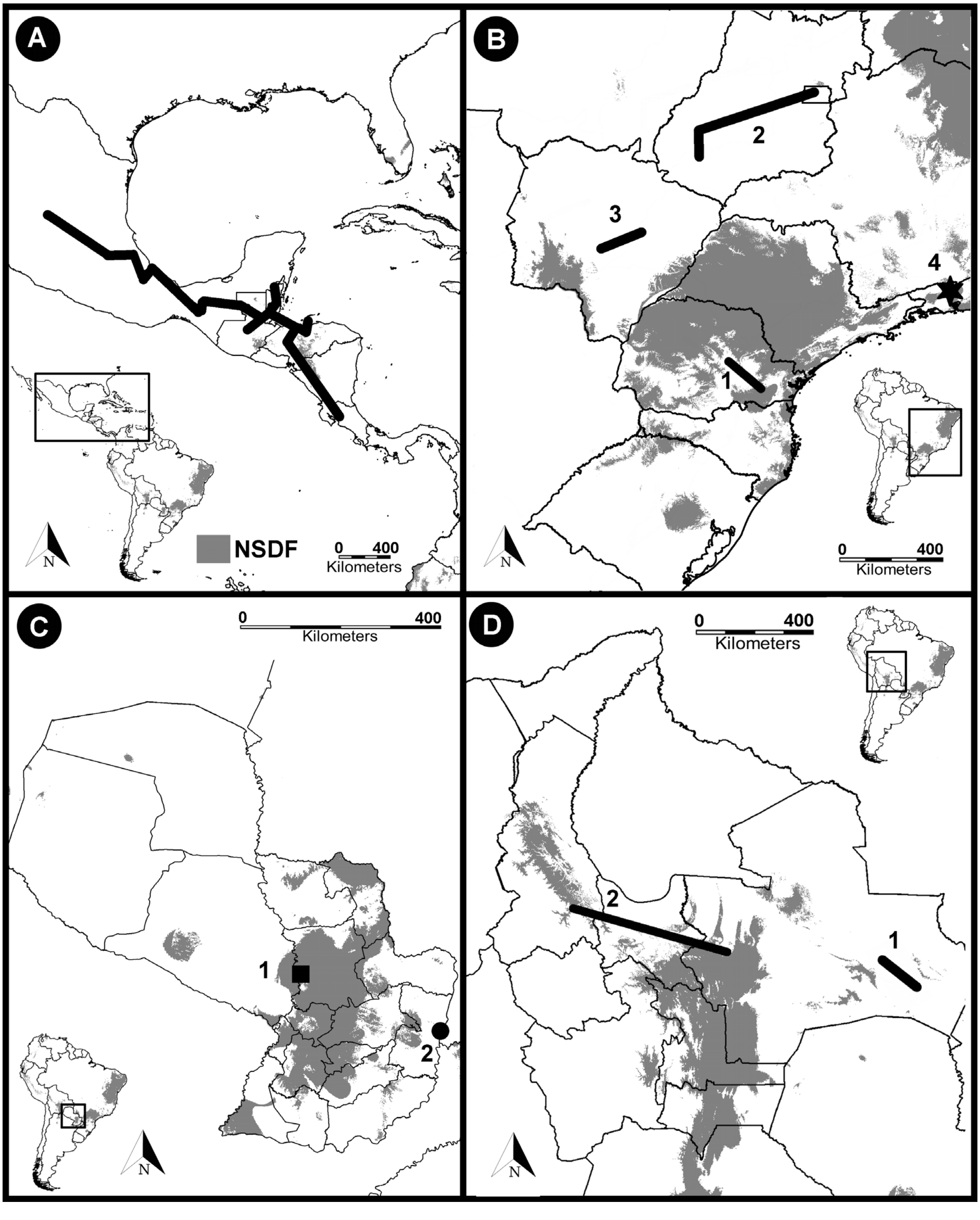

Figure 3 – Individual tracks: A, *Galianthe angulata*; B, 1: *G. elegans*, 2: *G. macedoi*, 3: *G. matogrossiana*, 4: *G. polygonoides*; C, 1: *G. hassleriana*, 2: *G. linearifolia*; D, 1: *G. chiquitosiana*, 2: *G. sudyungensis*.

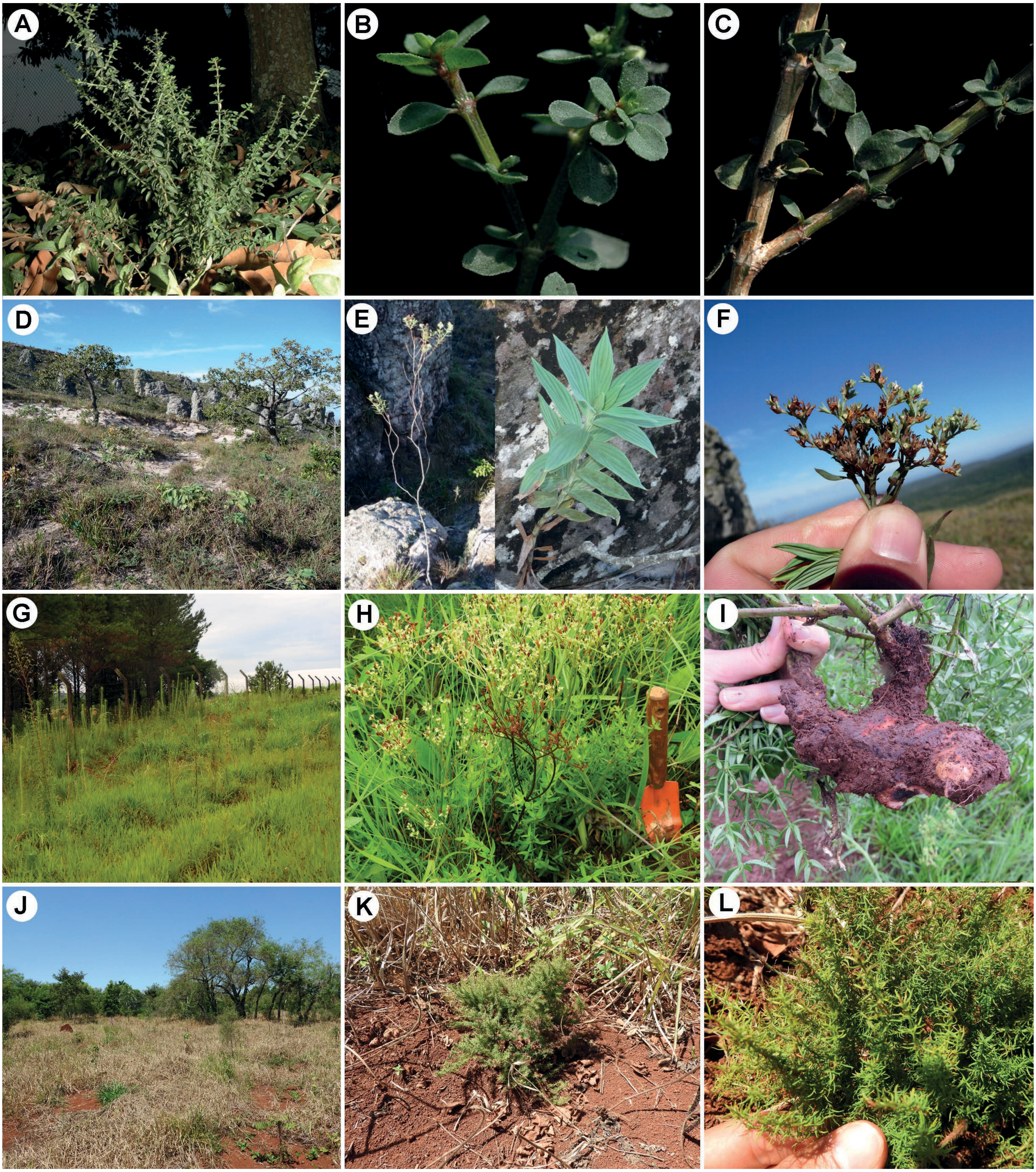

Figure 4 – Species that represent isolated tracks: A–C, *Galianthe angulata*; D–F, *G. chiquitosiana*; G–I, *G. elegans*; J–L, *G. linearifolia*. A, E, H & K, habit; D, G & J, habitat; B & L, leaves; I, xylopodioum; C, portion of a branch; F, inflorescence. A–C photographed by Pedro Tenorio Lezama, plantae mexicanae tenorianae; D–F photographed by R. Salas; G–L photographed by J.E. Florentín.

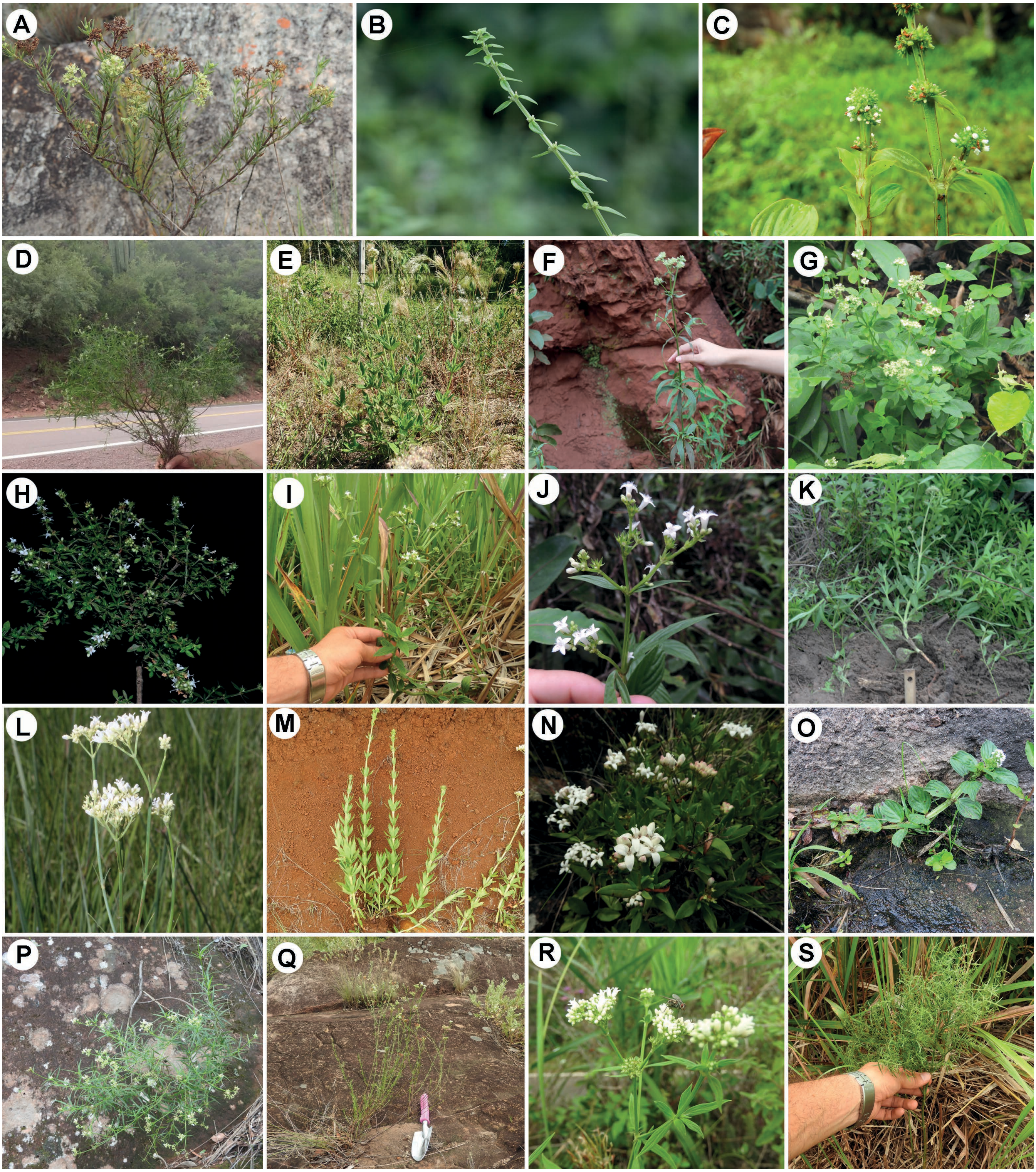

Figure 5 – Species that represent generalized tracks: A–C, Andean tracks; D–G, Brazilian tracks; H–K, Parana tracks; L–O, Pampean tracks; P–O, Chacoan tracks. A, *Galianthe peruviana*; B, *G. spicata*; C, *G. vasquezii*; D, *G. bisepala*; E, *G. eupatorioides*; F, *G. lanceifolia*; G, *G. laxa*; H, *G. brasiliensis*; I, *G. dichasia*; J, *G. vaginata*; K, *G. centranthoides*; L, *G. equisetoides*; M, *G. latistipula*; N, *G. reitzii*; O,*G. palustris*; P, *G. aurelii*; Q, *G. krausei*; R, *G. paraguariensis*; S, *G. thalictroides*. A–C, portion of a branch; D–S, habit. A, C, E, G, I, K & M–S photographed y J.E. Florentín; B photographed by O. Gaubert; D, H & L photographed by R. Salas; F photographed by F. Pastore; J photographed by J. Carmo.

alized Parana and Pampean tracks. Node IV corresponds to the confluence of the Parana and Chacoan tracks, in central Alto Paraná, in Paraguay. It is located in the Paraná Forest province of the Paraná dominion, Chacoan subregion (fig. 1). All nodes are situated at least into one of the nuclei of NSDF, mainly the most extensive forest fragments (e.g. Misiones and Caatinga nuclei) and forest fragments in Bolivia (fig. 2).

DISCUSSION

The five generalized tracks and the four nodes indicate that the ancestral biotas of *Galianthe* have a spatial pattern closely coincident with the location of the remaining fragments of NSDF (fig. 2). The spatial and historical dynamics (expansion and shrinkage) of these forests may have played an important role in the current distribution of *Galianthe* and its species richness, also these NSDF fragments includes biotas of diverse origin owing to the presence of nodes. Based on the dating of the *Spermacoce* clade, c. 23 Myr, and probably the Middle Miocene diversification, c. 14 Myr (Janssens et al. 2016), it can be assumed that the appearance of most current lineages of the *Spermacoce* clade preceded the probable date of formation of these forest fragments. Therefore, the dynamics of forests both in its expansion and contraction have influenced primarily in the distribution of *Galianthe* species, but not its origin. In that sense, the retraction of the forest fragments allowed the expansion of more open areas, as is the case of Cerrado savannahs. In this biome, a large diversity of *Galianthe* is recognized, with five species strictly endemic to the Cerrado province (*G. andersonii*, *G. macedoi*, *G. matogrossiana*, *G. lanceifolia*, and *G. ramosa*), and 14 species inhabiting also neighbouring provinces besides the Cerrado (*G. angustifolia*, *G. guaranitica*, *G. hispidula*, *G. kempffiana*, *G. laxa*, *G. liliifolia*, *G. longisepala*, *G. peruviana*, *G. thalictroides*, *G. valerianoides*, and *G. verbenoides*). In contrast, a smaller number of species inhabits exclusively within forests (e.g. *Galianthe brasiliensis*, *G. laxa*, *G. palustris*, and *G. vasquezii*), in habitats related to dry forests nuclei, Misiones, Bolivian and Peruvian InterAndean valleys and Caatinga, at the margins of major rivers and their tributaries to the south of South America).

Werneck et al. (2011) have evaluated the NSDF distributions during the last glaciation using species distribution models (57 taxa, only woody species), concluding that the SDFs were more disjunct during the last glacial maximum (LGM) than at present, contrasting the expectations of the Pleistocene arc hypothesis (Prado and Gibbs 1993). Collevati et al. (2013) have evaluated the NSDF hypothesis using 16 species (of the 57 species that support NSDF hypothesis) and concluded that it is necessary to associate them with other tests such as molecular variation and the fossil record. Both studies based their studies on woody species of several families selected following a distributional criterion; in contrast, here we used 55 species covering the total of the known species of a monophyletic genus represented only by non-woody taxa (Florentín et al. 2017a).

All the geographical data shows that the distribution of both subgenera of *Galianthe* lies entirely in the Brazilian and Chacoan subregions (*sensu* Morrone 2014a). Previous studies of the Neotropical flora of northern South America indicate that the South American flora developed throughout the Paleogene and Neogene (van der Hammen 1974, Hooghiemstra & Cleef 1995) and may have reached the greatest diversity of early modern plant genera in the early Miocene (Hoorn et al. 2010). The uplift of the northern Andes beginning in the middle Miocene led to a separation between the Amazonia on one side and the Chocó and Magdalena Valley on the other. In the intercontinental basin formed between the ancient continental shields and the newly formed Andes, when the sea level was low, estuaries leading to coastal environments with mangrove vegetation were established (Hooghiemstra & van der Hammen 1998). These temporal and spatial changes among saline environments and freshwater ecosystems led to a diverse and dynamic history of different geographical areas (Hooghiemstra & van der Hammen 1998). It has been considered that the relative impoverishment of the flora began from the late Miocene, and reached its greatest reduction during the Pliocene and Quaternary (van der Hammen 1974, van der Hammen & Cleef 1986, Hooghiemstra & Cleef 1995). The Pliocene started with a major cold period between 3.2 to c. 2.5 Myr, which caused a significant decrease in global temperature, considered the first of the Quaternary glaciations (Hooghiemstra & Ran 1994). The distributional relationships of the biotas in southern South America also were affected by climatic and geomorphological phenomena that began during the Neogene (Crisci et al. 2001). The uplift of the Andes of central South America along with the development of marine cold currents (especially the Humboldt current), were associated with the diversification of habitats and evolutionary opportunities for biota (Hoorn et al. 2010), particularly during the Miocene, and until the Pliocene, when climate gradually became more arid. The last phase of the Andean orogeny in the late Pliocene also caused the raising of several older mountain systems such as the Pampean and Sub-Andean mountain ranges (Taylor 1991).

The origin of the most recent ancestor of the tribe Spermacoceae has been estimated at about 44 Myr ago (Bremer & Eriksson 2009) during Oligocene, and probably in the Neotropical region (Janssens et al. 2016). Then, during the Eocene the vicariant events mentioned above might have favoured the adaptive radiation of the major lineages within the biogeographic units of the Chacoan dominion (Werneck 2011), for example the *Galianthe* species from the Chacoan and Parana dominions. These species have adaptations to xeric and open environments with sandy, lateritic soils or rock outcrops, such as the presence of xylopodium, thick cuticle, and reduce leaf surface. These features may have allowed them to thrive in open, xeric, and warm Quaternary environments of the Chacoan subregion. According to Rizzini (1976), the presence the xylopodium in the Cerrado savanna, and other organs with the function of water reservoir, was favoured because the porosity soils and constant lixiviation. Furthermore, the great diversity of habitats and microclimates in mountainous areas contributed to the establishment and survival of populations of various groups of plants (Arcand & Ranker 2008). Therefore, the mountainous ranges immersed in the Chacoan subregion would have played the role of biogeographic islands within an area topographically mostly flat. This could have favoured the vicariance and speciation within *Galianthe* and probably the Spermacoceae tribe in the Neotropics. This hypothesis is supported by the presence of several endemic taxa from rocky fields of high plateaus on certain mountain ranges (e.g. *Galianthe polygonoides* and *G. vaginata* from Serra da Mantiqueira, in southeastern Brazil).

Some authors have mentioned that it is not possible to postulate a single hypothesis on the distribution of the Neotropical biota (Costa 2003, Nihei & Carvalho 2007). Instead that, we consider that the biogeographic patterns of *Galianthe* here obtained, combined with the age of onset of the group it belongs to (Janssens et al. 2016), are more consistent with vicariant than the long-distance dispersal events by themselves. However, we cannot dismiss a more complex scenario that combines vicariant events with long-distance mobility, including passive or active dispersal (Morrone & Escalante 2009).

The Andean track is located in the Inter-Andean Valleys of northwestern South America, where it is estimated that occurred the final uplift of the Eastern Andes Cordillera to its current state, in the Pliocene and early Pleistocene, mainly between 6 and 3 Myr. This uprising was documented based on palynological, paleobotanical and geological studies (van der Hammen et al. 1973, Wijninga 1996). Alzate et al. (2008), studying the genus *Bomarea* Mirb. (Alstroemeriaceae), described four generalized tracks and three nodes which have a spatial pattern closely coincident with Andean Track here obtained almost in the whole extension. They described a fifth track that coincides with the distribution of the individual track of *Galianthe angulata*. However, *Bomarea* has a very different evolutionary history with almost all species restricted in this area (98 of 101 analysed species), while *Galianthe* is represented by only one generalized track supported by six species. Similar pattern of ancestral biotas were found using different lineages of plants as lycophytes (Arana et al. 2011), ferns (Arana et al. 2016) or even mammals (Ferro & Morrone 2014).

According to van der Hammen et al. (1973), at the beginning of the Pliocene the primitive Páramo vegetation continues being very poor in species. Based on pollen fossil records, they described the vegetation as dominated by grasses and accompanied by *Polylepis* Ruiz & Pav., *Aragoa* Kunth, *Hypericum* L., *Miconia* Ruiz & Pav., *Borreria* G.Mey., *Jussiaea* L., *Polygonum* L., *Valeriana* L., *Plantago* L., Ranunculaceae, *Myriophyllum* L., and *Jamesonia* Hook. & Grev. The authors also considered that some of these elements were derived from the local flora, whereas others must have been derived from founder species that arrived at the newly created Páramo "islands" by long-distance dispersal. From these pollinic types, cited by them, those assigned to *Borreria* are relevant for this study, because they are morphological similar and practically indistinguishable from *Galianthe* pollen grains. This perhaps could reflect the contribution and presence of *Galianthe* species in the primitive vegetation of the Páramo.

The Andean and Brazilian tracks are located in the Brazilian subregion, connecting the Inter-Andean Valleys of Ecuador and Peru with the dry valleys of Bolivia, which are connected to the piedmont forest in northwestern Argentina and southeastern Bolivia (Prado 1995). This forest covers a narrow strip of woodlands that constitute the lowest floor of the Yungas (Cabrera & Willink 1973, Mogni et al. 2015a). In addition, the Brazilian track also connects with the seasonally dry forests of Bolivian Chiquitanía, along the foothills of Santiago de Chiquitos to Santa Cruz de la Sierra department. It also extends through some isolated patches in the plains of the Paraguayan Chaco, such as the seasonal forest vegetation on the slopes of the Cerro León (Ramella & Spichiger 1989), and Cerro Chovoreca (Navarro 2005) to the Cerrado, area where it converges with the Parana generalized track. This connection of the generalized tracks strongly corroborates the proposal of Prado & Gibbs (1993), who postulated that there were formations of seasonally dry forests much more extensive than in the present day, which would have facilitated the exchange and connection between the biotas corresponding to the Brazilian and Parana generalized tracks. Both tracks connect the aforementioned NSDF fragments, that according to Pennington et al. (2004), the biotic exchanges between them may have taken place apparently since the Pliocene (between 5.3 and 2.5 Myr). It must be pointed out as well, that there is a strong resemblance between our present results plus the *Galianthe* generalized tracks (fig. 2), with the NSDF maps in Banda-R et al. (2016) and particularly the Neotropical dry forest floristic groups based on woody plants inventories (their fig. 2). All the areas of NSDF indicated in this present contribution as relevant for the distribution of *Galianthe* (e.g. Piedmont, Chiquitanía, Caatinga, Misiones nucleus, calcareous outcrops within the Cerrado biome, etc.) are also relevant for the recent analysis of dry forests in Latin America (Banda-R et al. 2016).

Regarding the Cerrado vegetation, a recent study estimates that its formation dates from the late Miocene or early Pliocene, about 10 Myr ago (Simon et al. 2009), accompanied by a large diversification of C4 grasses. During the late Miocene to early Pliocene, the Cerrado exceeded the current limits because it was strongly favoured by the prevailing dry environment and reduced CO_2, retracting to its current situation in the mid-Holocene (Vieira-Zanella 2011). In other floristic analysis using phylogenetic approaches, the authors concluded that the biota that inhabits the Cerrado is the result of a mixture of components of the surrounding biotas, and its geographical location played an important role in increasing species richness (Simon et al. 2009). While the Cerrado province does not belong to the NSDF, it is possible to observe that the seasonally dry forests constitute true "islands" of deciduous forests on limestone outcrops (Prado & Gibbs 1993). These outcrops with wooded vegetation cover act as 'stepping stones' connecting the Cerrado with the Caatinga nucleus (Prado 2003, Banda-R et al. 2016). Future phylogenetic and biogeographic studies based on molecular data on *Galianthe* will allow us reveal the role played by the Cerrado vegetation in the origin and diversification of its species.

The Parana track appears mostly included in the Parana Forest biogeographic province, with small areas in the Cerrado province (Chacoan dominion), Atlantic Forest, and Araucaria forest provinces (Parana dominion). Regarding NSDF, this generalized track joins the Caatinga at Northeast Brazil with Misiones nucleus in South Brazil, Paraguay and Northeast Argentina. Parana Track was discussed by Florentín et al. (2016), contrasting with the biogeographical model of the Neotropical region postulated by Morrone (2014b). They only included species belonging to subgen *Ebelia* and have postulated that the same vicariant events acting in the origin of the Chacoan subregion have influenced in its adaptive radiation, i.e. aridification of South America originated by Andean orogeny and marine introgression.

Our findings represent the first study of non-woody species that support the current distribution the NSDF and the refuge hypothesis during unfavourable periods owing to the generalized tracks (= ancestral biotas) obtained here. Also, the NSDF nuclei represent areas of biotic convergence, including ancestral biotas of Galianthe from different geobiotic origin represented by the nodes. New collections, especially in areas of nodes, and the analysis of specimens from more herbaria will bring new records for both endemic and widely distributed species, which will lead to a better understanding of the evolutionary history of the genus.

ACKNOWLEDGEMENTS

This work is dedicated to Elsa L. Cabral, whose taxonomic work has become fundamental to understand the diversity of the genus *Galianthe*. We thank the anonymous referees for critical reading and suggestions that improved previous version of the manuscript and Tiina Särkinen for sending us the shape files of the NSDF maps. M.D. Arana thanks Universidad Nacional de Río Cuarto, for the facilities given to perform the study. D. Prado thanks the Universidad Nacional de Rosario and CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas).

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Manuscript received 21 Nov. 2017; accepted in revised version 25 May 2018.

Communicating Editor: André Simões.