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Phylogeographic Studies Depict the Role of Space and Time Scales of Plant Speciation in a Highly Diverse Neotropical Region

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ABSTRACT

Phylogeographic studies have merged different disciplines to explain speciation processes at both spatial and time scales. Although the number of phylogeographic extant studies has increased almost exponentially, few have been conducted in tropical countries, especially using plants. Plants are interesting models for such studies because their responses to different habitat conditions are reflected directly in the size and distribution of populations, enabling direct tests of alternative demographic scenarios. Here, we review phylogeographic studies using plant species occurring in different vegetation domains within Brazil, which has the greatest number of plant species in the world. Based on a detailed examination of 41 published articles, we synthesized the current knowledge and discussed the main processes driving the high levels of plant diversity within Brazilian domains. General patterns of diversification could be inferred due to the number of species studied, especially in the Cerrado and Atlantic Forest, the most intensively studied domains (34.1% and 17.1% of the studies, respectively). Distinct vegetation types within both biomes were affected differently by the Pleistocene climatic oscillations. Edaphic conditions and geographical barriers (rivers and mountains) have also influenced the phylogeographical patterns of plants species from Amazonia and the Atlantic Forest. Other Brazilian domains, such as the Caatinga, Pantanal, and Pampas, have been studied to a lesser extent and no common phylogeographic pattern across species could be inferred. Issues regarding past connections between distinct domains also remain unclear, including those affecting the two main forest domains in South America. Future research on plant species will fill these information gaps, improving our understanding of the complex diversification processes affecting the South American biota.

KEYWORDS

biodiversity; microevolution; neotropics; phylogeography; population structure; species diversification

1. Introduction

Species distribution patterns in space and time are critical for understanding speciation processes (Sanmartín, 2012). Major evolutionary forces such as gene flow, genetic drift, and natural selection will be directly influenced by landscape elements, leading to different degrees of divergence among populations and incipient species. For example, geographic barriers would prevent gene exchange among conspecific populations, which in turn may increase their differentiation due to drift and natural selection associated with different environmental conditions. The action of gene flow, drift, and natural selection could be related to historical climatic oscillation events and past geologic processes that changed landscape features and, consequently, the demography of populations and species. For example, glacial cycles dramatically changed the distribution of vegetation domains in South

America (Clapperton, 1993), reducing gene exchange and increasing the effects of drift in fragmented populations. Thus, to find support for speciation models, such as the refugee theory (Haffer, 1969), the associations between past climatic oscillations and both the time and intensity of evolutionary forces involved in lineage diversification must be explored. According to Bennett and Provan (2008), researchers aiming to provide support for the refugee theory need to provide evidence of changes in population sizes; consequently, the time periods in which drift and gene exchange were affected by such demographic changes.

The role of geographic space and time in speciation has been intensively studied within the field of biogeography (Lomolino *et al.*, 2010; Sanmartín, 2012). Scientific expeditions to tropical regions in the eighteenth century have yielded explanations of the evolution of floras in

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different continents, and interest in biogeography again increased in the 1950s, when the theory of continental drift was fully accepted (De Queiroz, 2005). The use of molecular markers to investigate geographical patterns of variation, from populations to higher taxa, enabled the reconstruction of the evolutionary history of various groups, especially those with a poor fossil record (Soltis *et al.*, 2009). At the end of the 1980s, a new discipline emerged aiming to investigate the effects of time and geographic space on speciation events: phylogeography. In his seminal study, Avise *et al.* (1987) coined the term phylogeography in an attempt to provide direction to those interested in the geographic context of speciation events. Later, Avise (2000) provide the basic agenda of phylogeography, guiding population-level studies interested in speciation.

Phylogeographic studies have increasingly merged different disciplines to explain the history and formation of species at geographic and time scales. Initial studies mostly used molecular datasets, using DNA polymorphisms as the primary source of information to infer past demographic events and the existence of multiple lineages in different environments (Olsen and Schaal, 1999; Collevatti *et al.*, 2003). The characterization of highly informative nuclear and plastid regions enabled the testing of alternative demographic scenarios in plant populations (i.e., Palma-Silva *et al.*, 2009; Bonatelli *et al.*, 2014, and others). The role of historical refuges in the diversification of lineages and species has been confirmed for several plant species (Ramos *et al.*, 2007; Ribeiro *et al.*, 2011). The inclusion of species distribution models greatly enhanced the potential to infer past demographic events (Collevatti *et al.*, 2015). By retrieving the potential past distribution area, the results obtained independently from the models could be cross-checked with the molecular evidence of population expansion and/or bottlenecks (Collevatti *et al.*, 2012a; Lima *et al.*, 2014). Natural hybrid zones have also been the subject of phylogeographic studies, which have involved spatial distribution patterns, genetic composition of parental and hybrid plants, and reproductive isolation across species boundaries (Hewitt, 2001; Lorenz-Lemke *et al.*, 2006; Palma-Silva *et al.*, 2011). Because species formation is a population-level process, the study of reproductive isolation within species may shed light on the processes operating during the earliest stages of speciation (Scopece *et al.*, 2010). To achieve this, a detailed phylogeographic picture is crucial to understand how reproductive isolation evolves among lineages, in a geographic context (Pinheiro *et al.*, 2013).

Phylogeography has been growing vigorously as an integrative discipline, bridging different sources of data (Diniz-Filho *et al.*, 2008). The number of extant studies

has increased almost exponentially (Beheregaray, 2008). However, until 2006, most studies were performed in the northern hemisphere, despite the fact that most biodiversity is concentrated in the tropics (Beheregaray, 2008). Indeed, Brazil is the 15th most-productive country in terms of phylogeography studies (Beheregaray, 2008), but has the greatest number of angiosperm species (BFG—The Brazil Flora Group, 2015). Therefore, few phylogeographic studies have been conducted in tropical countries with a rich biota, such as Brazil. There is also an imbalance between the number of studies of plants and animals. Turchetto-Zolet *et al.* (2013) reported that most phylogeographic studies in South America, across all vegetation domains of the continent, involved animals.

Various hypotheses regarding the origin of the considerable levels of plant diversity in tropical countries have been formulated (Antonelli and Sanmartin, 2011). Much effort has been devoted to investigating broad patterns of diversification, using plant phylogenies at higher taxonomic levels to determine the mechanisms of plant speciation (Hoorn *et al.*, 2010; Hughes *et al.*, 2013). In contrast, population-level studies have received less attention, and little is known of the microevolutionary mechanisms during the first stages of speciation. Here, we review phylogeographic studies of plant species in Brazil as biological models. Compared to other megadiverse countries, Brazil has the greatest number of angiosperms, with 32,086 species (BFG, 2015). Thus, using plant phylogeographic studies performed in Brazil, we discuss the main processes driving the diversification of lineages and species in this highly biodiverse region. Specifically, we had the following goals: (1) to review the current knowledge of plant phylogeography in Brazil; (2) to verify the occurrence of demographic processes (expansion and contraction) related to glacial/interglacial climatic oscillations; (3) to assess hypothesized refugia types (multiple or single); and (4) to discuss the role of geological and climatic changes during the Tertiary and Quaternary in shaping the phylogeographic patterns of plants in hyperdiverse vegetation domains in South America.

II. Phylogeographic studies in Brazil

This review focuses on the historical distribution and dynamics of Brazilian plant species based on phylogeography and the genetic signatures of vegetation history. For the purpose of this review, we consider all vegetation domains found in Brazilian territory. We review and compare studies on the open and seasonal vegetation domains known as Caatinga, Cerrado, and Pampas, and mesic domains such as the Brazilian Atlantic Forest,

Amazon, and Pantanal. The literature survey was conducted in the Web of Science using the keywords “phylogeograph*” + “plant” and one of the following domains: “Amazon,” “Atlantic Forest,” “Caatinga,” “Cerrado,” “Pampas,” and “Pantanal.” Following this nonexhaustive survey, we selected 41 papers (Table 1) based on an inspection of their title, abstract, and keywords.

The first study using one of the reference phrases was published in 1999, and since then the number of studies has increased (Figure 1), albeit at a different rate than that for South America as a whole (Turcheto-Zolet *et al.*, 2013). The studies involved 20 plant families and 30 genera. The four most studied families were Fabaceae (seven studies), Solanaceae (four), Orchidaceae (three), and Bignoniaceae (three) (Figure 2A). Approximately 78% of the studies focused on only 11 families. Similarly, most genera were studied only once, whereas 30% were investigated twice or more (Table 1, Figure 2B). Most phylogeographic studies used trees (53.7%) and herbs (36.6%) as models (Table 1). Most studies (75.6%) sampled species in only one phylogeographic domain (Figure 3). Cerrado was the most studied domain (34.1% of the studies), followed by the Brazilian Atlantic Forest (17.1%), Amazonia (14.6%), Pampas (7.3%), and Caatinga (2.4%, one study). To the best of our knowledge, no phylogeographic study of plant species from the Pantanal domain has been published. Species occurring in more than one phylogeographic domain were the focus of 11 studies, most of which included populations distributed within the Cerrado domain. Species distributed across Caatinga and Cerrado were the most intensively studied (three studies), followed by the Brazilian Atlantic Forest and Cerrado (two), Amazonia and Cerrado (two), and the Brazilian Atlantic Forest and Amazonia (two). A comparative approach, using two or more co-distributed species, was used in only 17.1% of the studies. Niche models were included in ten studies, and hybridization events were detected in approximately one-third of the studies. Genic/intergenic DNA region sequencing was the most common method used in the phylogeographic studies in this review (Figure 4A). Microsatellite markers were used in nine studies, and in most cases were combined with sequence data. Eighteen studies combined nuclear and plastid regions, and the remaining used only nuclear (6 studies) or plastid markers (13 studies) (Figure 4B).

III. Phylogeographic patterns in tropical forest domains

The Brazilian Atlantic Forest and Amazonia are the two main forest domains in South America (Ab’Saber, 1977). The Brazilian Atlantic Forest is restricted to the Atlantic

Coast. Phylogeographic studies conducted in the Brazilian Atlantic Forest support the idea that this domain was deeply affected by historical climatic oscillation events, such as glacial/interglacial cycles, as well by geographic factors, such as mountains and rivers. The existence of multiple refuges, for example, is reported in almost all plant phylogeographic studies conducted in the Brazilian Atlantic Forest (Table 1). Palma-Silva *et al.* (2009) found multiple lineages along the distribution of *Vriesea gigantea*, an epiphyte bromeliad species distributed across the Brazilian Atlantic Forest. The different demographic signatures of northern and southern populations suggest regions in which the forest was fragmented (in the southern populations) and continuous (in the northern populations) during the Last Glacial Maximum (LGM), following the pattern expected for glacial refuges (Bennett and Provan, 2008). The same pattern has been reported for other plant species, including a tree species, *Dalbergia nigra* (Ribeiro *et al.*, 2011) and a liana, *Passiflora actinia* (Teixeira *et al.*, 2016). Contrasting results were provided by Pinheiro *et al.* (2011) using an herbaceous orchid species that occurs in sand dune vegetation close to the seashore. In this study, increasing levels of genetic diversity and signs of demographic stability were observed in populations distributed in the southern portion of the Brazilian Atlantic Forest. These results are in agreement with the notion that the Brazilian Atlantic Forest is a mosaic of different physiognomies, and each vegetation type was probably differently influenced by past climatic oscillations and geographic barriers (Leite *et al.*, 2016). Considering this heterogeneous scenario, phylogeographic studies using species occurring in different environments may reveal novel and informative patterns.

The heterogeneous nature of the southern and northern regions of the Brazilian Atlantic Rainforest, as determined by floristic inventories (Oliveira-Filho and Fontes, 2000) and niche models (Carnaval and Moritz, 2008), has been confirmed by phylogeographic studies. Northern Rio de Janeiro, Espírito Santo, and southern Bahia are a transition zone between lineages, which show marked genetic divergences in this region (Ribeiro *et al.*, 2011; Turchetto-Zolet *et al.*, 2012; Pinheiro *et al.*, 2013). The fragmentation of the Brazilian Atlantic Forest during glacial cycles, splitting these large portions of forest is a possible explanation for this pattern (Carnaval and Moritz, 2008). The existence of large river basins that act as geographic barriers for intraspecific gene exchange, such as the Doce River Basin, is an alternative explanation of the marked floristic differences between the northern and southern portions of the Brazilian Atlantic Forest (Bigarella *et al.*, 1975; Prance, 1982). Recently, Cázé *et al.* (2016) provided evidence supporting the



Table 1. Summary of plant phylogeographic studies for different Brazilian vegetation domains.

Reference	Journal	Family	Species	Life-form	Domain(s) ^a	Climate	Markers ^b	Cryptic speciation	Demographic processes ^c	Refugium type	Comparative approach	Niche modelling	Hybridization or introgression
Olsen and Schaal (1999)	PNAS	Euphorbiaceae	<i>Manihot esculenta</i>	Herb	AM; CE	Tropical	One nuDNA: G3pdh	No	NA	NA	No	No	No
Olsen (2002)	Molecular Ecology	Euphorbiaceae	<i>Manihot esculenta</i> ssp. <i>flabellifolia</i> <i>M. pruinosa</i>	Herb	AM; CE	Tropical	One nuDNA: G3pdh	No	NA	NA	No	No	Yes
Collevatti et al. (2003)	Molecular Ecology	Caryocaraceae	<i>Caryocar brasiliense</i>	Tree	CE	Tropical	Two cpDNA: trnT and trnF; 10 cpSSR	No	NA	Multiple	No	No	Yes
Lorenz-Lemke et al. (2005)	Annals of Botany	Passifloraceae	<i>Passiflora actinia</i> <i>P. elegans</i>	Liana	AF	Sub-tropical	Two cpDNA: trnL-trnF and psbA-trnH; nuDNA: ITS	No	Expansion	NA	Yes	No	Yes
Cloutier et al. (2005)	Silvae Genetica	Meliaceae	<i>Carapa guianensis</i>	Tree	AM	Tropical	RFLP	Yes	NA	Multiple	No	No	No
Ramos et al. (2007)	Annals of Botany	Fabaceae	<i>Hymenaea stigonocarpa</i>	Tree	CE	Tropical	One cpDNA: psbC-trnS3	No	Expansion of southern from north after LGM	Multiple	No	No	No
Dick et al. (2007)	Molecular Ecology	Malvaceae	<i>Ceiba pentandra</i>	Tree	AM	Tropical	One cpDNA: psbB-psbF; one nuDNA: ITS	No	NA	NA	No	No	No
Caetano et al. (2008)	Molecular Ecology	Anacardiaceae	<i>Astronitium urundeuva</i>	Tree	CA; CE; CH (SDTF)	Tropical and sub-tropical	Two cpDNA: trnH-psbA and trnS-trnG; 9 nuSSR	No	Expansion	NA	No	No	Yes (secondary contact)
Palma-Silva et al. (2009)	Heredity	Bromeliaceae	<i>Vriesea gigantea</i>	Herb	AF	Tropical and sub-tropical	One cpDNA: rpoB; trnG; 9 nuSSR	No	Spatial expansion toward southern after LGM	Multiple	No	No	No
Collevatti et al. (2009)	Annals of Botany	Asteraceae	<i>Lychnophora ericoides</i>	Shrub	CE	Tropical	Two cpDNA: trnL intron and psbA-trnH; one nuDNA: ITS	No	Expansion during the Kansas Glacial period and retraction in interglacial	multiple	No	No	Yes
Ramos et al. (2009)	Journal of Heredity	Fabaceae	<i>Hymenaea courbaril</i> var. <i>stilbocarpa</i> <i>Hymenaea stigonocarpa</i>	Tree	CE	Tropical	One cpDNA: psbC-trnS3	No	Expansion of southern from north after LGM	multiple	Yes	No	Yes
Lorenz-Lemke et al. (2010)	Molecular Ecology	Solanaceae	<i>Petunia altiplana</i> <i>P. bonjardinensis</i> <i>P. guarapuavensis</i> <i>P. mantiqueirensis</i> <i>P. reitzii</i> <i>P. saxicola</i> <i>P. schiedeana</i>	Herb	AF	Sub-tropical	Two cpDNA: trnH-psbA and trnS-trnG	No	<i>Petunia altiplana</i> : Expansion during LGM	multiple	Yes	No	Yes
Novaes et al. (2010)	Molecular Ecology	Fabaceae	<i>Plathyminia reticulata</i>	Tree	AF; CE	Tropical	Two cpDNA: trnL-trnI-trnF and trnS-trnG	No	Expansion	NA	No	No	No
Lemes et al. (2010)	Tropical Plant Biology	Meliaceae	<i>Swietenia macrophylla</i>	Tree	AM	Tropical	Six cpSSR	No	Refuges in Amazonian basin	multiple	No	No	No
de Oliveira et al. (2010)	Molecular Ecology	Rubiaceae	<i>Carapichea ipecacuanha</i>	Shrub	AF; AM	Tropical		No	Expansion	multiple	No	No	Yes

Ribeiro et al. (2011)	Hereditry	Fabaceae	<i>Dalbergia nigra</i>	Tree	AF	Tropical	One cpDNA: trnI-trnL; one nuDNA: ITS	No	Weak population expansion	No	No	No	
Pinheiro et al. (2011)	Journal of Biogeography	Orchidaceae	<i>Epidendrum fulgens</i>	Herb	AF	Tropical and sub-tropical	Two cpDNA: trnV-trnM and trnL	No	Expansion after LGM	No	No	No	
Garcia et al. (2011)	Molecular Phylogenetics and Evolution	Meliaceae	<i>Cedrela fissilis</i>	Tree	CA; CE (SDTF)	Tropical	Four cpSSR and nine nuSSR	Yes	Expansion	No	No	Yes	
Turchetto-Zolet et al. (2013)	Molecular Phylogenetics and Evolution	Fabaceae	<i>Schizolobium parathyda</i>	Tree	AF; AM	Tropical	Three cpDNA: trnI-trnL, trnS-trnG, psb8-psbF; nuDNA: ITS	No	Population expansion toward south after LGM	No	No	No	
Barbosa et al. (2012)	American Journal of Botany	Velloziaceae	<i>Yellozia hirsuta</i>	Herb	CE	Tropical	One cpDNA: rpl32-trnL; nuDNA: ITS	No	Expansion during glaciation	No	No	Yes	
Collevatti et al. (2012a)	Natureza & Conservacao	Caryocaraceae	<i>Caryocar brasiliense</i>	Tree	CE	Tropical	Three cpDNA: trnL-intron, psbA-trnH and trnC-ycf6	No	Retraction during LGM	No	Yes	No	
Collevatti et al. (2012b)	Ecology and Evolution	Melastomataceae	<i>Tibouchina papyrus</i>	Tree	CE	Tropical	Three cpDNA: psbA-trnH, trnS-trnG and trnC-ycf6; 10 nuSSR	No	Expansion during Pre-Illinoian glaciation	No	No	No	
Collevatti et al. (2012c)	Molecular Ecology	Bignoniaceae	<i>Tabebuia impetiginosa</i>	Tree	CE; CA (SDTF)	Tropical	Three cpDNA: trnS-trnG, psbA-trnH and ycf6-trnC; one nuDNA: ITS	No	Expansion during LGM	No	Yes	No	
Pinheiro et al. (2013)	Evolution	Orchidaceae	<i>Epidendrum denticulatum</i>	Herb	AF; CE	Tropical	cpDNA: five cpSSR; one SNP; nine nuSSR	No	Expansion after LGM	No	No	No	
Fine et al. (2013)	Journal of Biogeography	Burseraceae	<i>Protium alvarezianum</i>	Tree	AM	Tropical	one nuDNA: PhyC; two nuDNA: ITS and ETS	No	Expansion during Pleistocene or Pliocene Glacial Maxima	Yes	No	Yes	
Scotti-Saintagne et al. (2013)	Journal of Biogeography	Bignoniaceae	<i>Jacaranda copaia</i>	Tree	AM	Tropical	Two cpDNA: trnH-psbA and trnC-ycf6; eight cpSSR; nine nuSSR	No	NA	No	No	Yes	
Novaes et al. (2013)	Plos One	Fabaceae	<i>Dalbergia miscolobium</i>	Tree	CE	Tropical	One cpDNA: trnL-intron; one nuDNA: ITS	No	Spatial and demographic expansion after LGM	No	No	No	
Mader et al. (2013)	BMC Evolutionary Biology	Solanaceae	<i>Calibrachoa heterophylla</i>	Herb	PA	Tropical	Two cpDNA: trnH-psbA and trnS-trnG	No	Expansion after LGM	No	Single (inland)	No	No

(continued on next page)



Table 1. (Continued).

Reference	Journal	Family	Species	Life-form	Domain(s) ^a	Climate	Markers ^b	Cryptic speciation	Demographic processes ^c	Refugium type	Comparative approach	Niche modeling	Hybridization or introgression
Pinheiro et al. (2014)	BMC Evolutionary Biology	Orchidaceae	<i>Epidendrum cinnabarinum</i> <i>E. secundum</i>	Herb	AF; CA	Tropical	One cpDNA: rps16-trnK; six cpSSR; six nuSSR	No	<i>E. secundum</i> —demographic stability <i>E. deniculatum</i> —northern expansion after LGM	multiple	Yes	Yes	No
Bonatelli et al. (2014)	Molecular Ecology	Cactaceae	<i>P. auresetus</i> <i>P. madrisii</i> <i>P. vilboensis</i> <i>P. jauruensis</i> <i>P. aureispinus</i> <i>P. parvus</i> <i>P. bohlei</i>	Herb	CE	Tropical	Two cpDNA: trnT-trnL and trnS-trnG; one nuDNA: PhyC; 10 nuSSR	No	Expansion during LGM and retraction during interglacial periods	multiple	No	Yes	Yes (secondary contact)
Lima et al. (2014)	Journal of Biogeography	Arecaceae	<i>Mauritia flexuosa</i>	Palm	CE	Tropical	Three cpDNA: psbA-trnH, trnS-trnG and trnC-ycf6	No	Retraction during LGM	multiple	No	Yes	No
Longo et al. (2014)	Botanical Journal of the Linnean Society	Solanaceae	<i>Petunia integrifolia</i> <i>P. riograndensis</i> <i>P. littoralis</i> <i>P. inflata</i>	Herb	PA	Sub-tropical	Two cpDNA: trnH-psbA and trnS-trnG; one nuDNA: ITS	No	Expansion earlier than 0.5 Mya	NA	No	No	No
Collevatti et al. (2015)	Frontiers in Plant Science	Bignoniaceae	<i>Tabebuia aurea</i>	Tree	CE	Tropical	Three cpDNA: psbA-trnH, trnC-ycf6 and trnS-trnG; one nuDNA: ITS1+5.8S + ITS2	No	Range retraction during the LGM	single	No	Yes	No
Ramos-Fregonezi et al. (2015)	BMC Evolutionary Biology	Solanaceae	<i>Petunia integrifolia</i> ssp. <i>depauperata</i>	Herb	PA	Sub-tropical	Two cpDNA: trnH-psbA and trnS-trnG	No	Recent range expansion	single	No	No	No
Roncal et al. (2015)	Journal of Biogeography	Arecaceae	<i>Astrocaryum</i> sect. <i>Huicungo</i>	Tree	AM	Tropical	Five cpDNA: psbM-trnD, rps16 intron, rps16-trnQ, trnD-trnT and trnG intron; two nuDNA: WRKY7; PRK	No	Expansion	multiple	No	No	No
Vieira et al. (2015)	Botanical Journal of the Linnean Society	Moraceae	<i>Ficus bonjiesulapensis</i>	Tree	CA	Tropical	One cpDNA: trnQ-5 rps16	No	Southward expansion after LGM	single	No	Yes	No
Goetze et al. (2016)	Botanical Journal of the Linnean Society	Bromeliaceae	<i>Aechmea calyculata</i>	Herb	AF	Sub-tropical	Two cpDNA: rpl32-trnL and rps16-trnK; one nuDNA: PhyC; 12 nuSSR	No	Recent expansion (East distribution)/Stability (West distribution)	NA	No	No	No
Teixera et al. (2016)		Passifloraceae	<i>Passiflora actinia</i>	Herb	AF	Tropical		No	Expansion	multiple	No	Yes	No

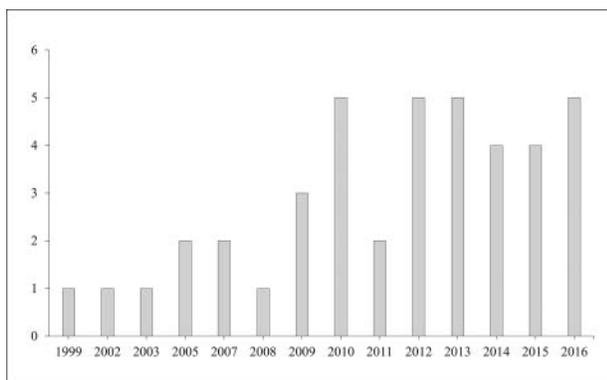


Figure 1. Number of phylogeographic articles published between 1999 and June 2016, referring primarily to plant species occurring in vegetation domains in Brazil.

divergence of lineages of *Passiflora contracta* associated with the major river basins within the Brazilian Atlantic Forest, including the Doce River.

The Brazilian Atlantic Forest is influenced by several mountain chains in its range (Morellato and Haddad, 2000). Severe restrictions in gene exchange may lead to genetic divergence between populations on different mountains, which would explain the high levels of species diversity in this forest domain (Scarano, 2002). This hypothesis has been confirmed by the few studies of species occurring at high elevations within the Brazilian Atlantic Forest. For example, Lorenz-Lemke *et al.* (2010)

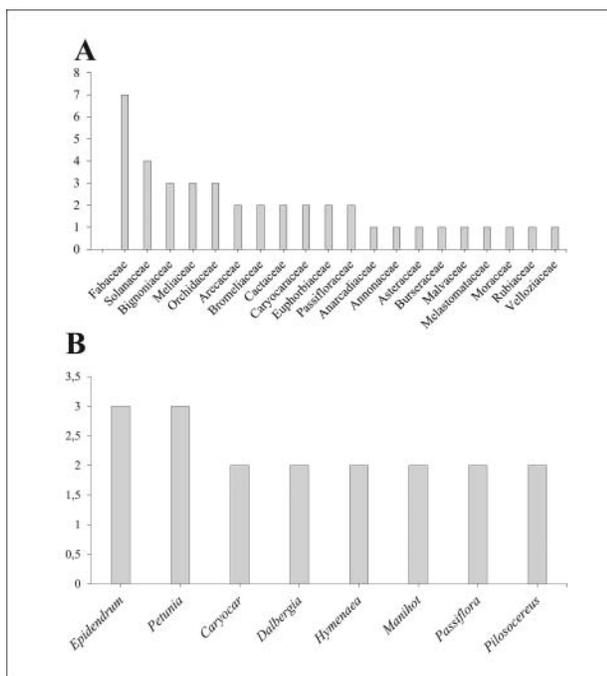


Figure 2. Most frequently investigated plant families (A) and genera that are included more than once (B) in phylogeographic studies of plant species occurring within Brazil.

found multiple lineages of *Petunia* within a species clade restricted to high altitudes. High levels of genetic divergence were found among *Pitcairnia* lineages endemic to rock outcrops separated by a few kilometers (Palma-Silva *et al.*, 2011). These studies support the view that restrictions of gene exchange in these naturally fragmented environments likely contribute to lineage diversification on mountains. The extent to which the restriction of gene exchange increases the reproductive isolation among these incipient lineages and species, and the role of drift, instead of natural selection, in the fragmented environments, should be addressed by future studies using mountain plants as models. Palma-Silva *et al.* (2011) reported the permeability of the reproductive barriers between co-occurring *Pitcairnia* species growing in inselbergs. Extensive levels of haplotype sharing were detected on individual mountains, indicating old hybridization events. Moreover, despite the limited gene flow between conspecific populations, introgression was relatively low and did not affect the cohesion of parental species. In the absence of high levels of gene exchange, selection may play an important role in maintaining species cohesion, particularly in naturally fragmented populations (Palma-Silva *et al.*, 2011; Southcott and Ostevik, 2011).

The Amazonian domain encompasses several countries, but the majority lies in Brazil. Several hypotheses to explain the biogeographical history have been proposed in the Amazon domain (reviewed by Antonelli and Sanmartin, 2011). The effect of soil diversity on levels of plant diversity, tectonic activity, and refuges are considered important drivers of speciation in the Amazonia domain, and were evaluated by phylogeographic studies. However, despite the broad extension and high levels of plant diversity in Amazonia (Forzza *et al.*, 2012), few phylogeographic studies using a lower species level approach have been published (Figure 3A). Fine *et al.* (2013) investigated two *Protium* species with different degrees of edaphic specialization: *P. alvarezianum*, an edaphic specialist of white-sand soils distributed throughout the Amazonia domain; and *P. subserratum*, an edaphic generalist found in different soil types, including white-sand soils. The results confirmed the genetic differentiation of both species, which was partially correlated with the soil types inhabited. The Andean uplift was the most important tectonic event in the recent history of South America. However, a number of other tectonic and geomorphological processes were influenced by the Andean uplift, such as the formation of arches or ridges and changes in the direction and volume of rivers within the Amazon Basin (Marroig and Cerqueira, 1997). Such processes have caused genetic breaks in some species (da Silva and Patton, 1998), and

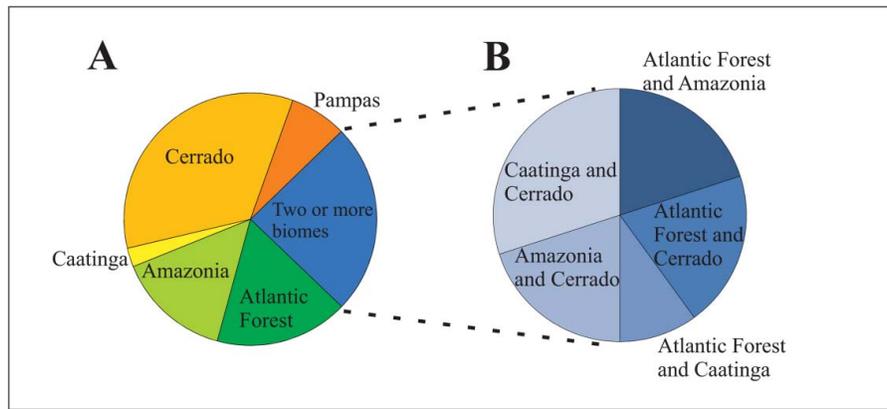


Figure 3. Number of phylogeographic studies using species distributed in single (A) and multiple phylogeographic domains (B).

plant phylogeographic studies have tested some of these hypotheses. For example, Roncal *et al.* (2015) studied *Astrocaryum* species and found evidence of allopatric speciation driven by contrasting geological activity in the Fitzcarrald Arch uplift and subsidence of the northern Amazonian foreland basin.

The Refugia Theory is an influential explanation for the origin of species diversity (Bennett and Provan, 2008), including within the Amazonia domain (Hooghiemstra and van der Hammen, 1998). This theory is controversial due to several inconsistencies (reviewed by Rull, 2011). However, the theory has been abandoned in the absence of population-level studies using plants as models. Phylogeographic studies would enable an evaluation of the role of refuge theory in lineage and species diversification in the Amazonia domain, as in other regions (Petit *et al.*, 2003; Liu *et al.*, 2012; Poncet *et al.*, 2013). According to Bennett and Provan (2008), studies

of refuges should consider both the size and abundance of populations to detect demographic changes due to glacial/interglacial cycles. Unfortunately, only Lemes *et al.* (2010) discussed the role of forest refuges in lineage diversification of the tree *Swietenia macrophylla*. This study detected populations with high levels of differentiation and diversity, which indicates the presence of multiple refuges in the Amazonian basin (Lemes *et al.*, 2010). However, different species may show contrasting patterns of genetic variation due to different pollination and dispersion mechanisms. For example, Dick *et al.* (2007) detected very low levels of genetic differentiation among populations of *Ceiba pentandra*, which did not support any past fragmentation of the Amazonia domain. The high level of diversity detected in populations of *Jacaranda copaia* within the Amazon Basin was interpreted as indicative of a zone of secondary contact between divergent lineages (Scotti-Saintagne *et al.*,

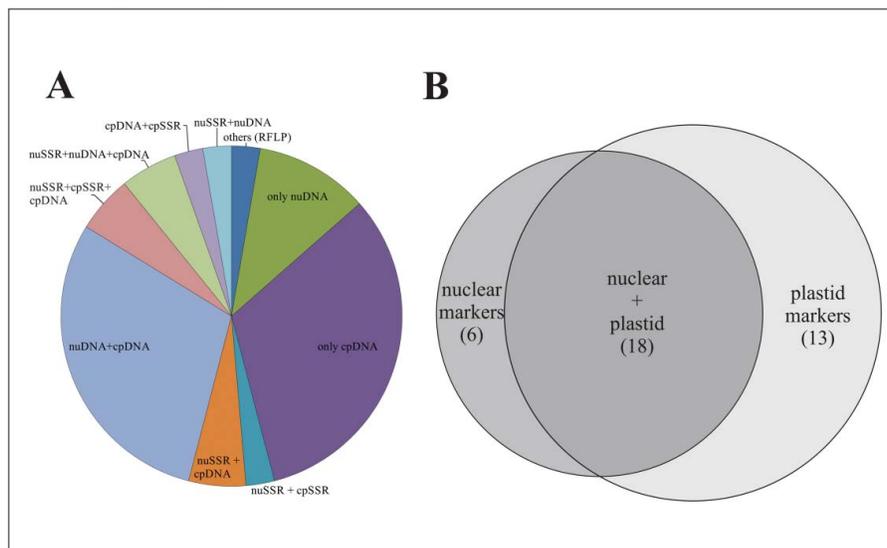


Figure 4. Major molecular markers used in phylogeographic studies of plant species occurring within Brazil (A), and the nuclear and/or organelle origin of markers used in such studies (B). The number of studies is shown in parentheses.

2013). Studies of multiple co-occurring species have been used as natural replicates to support, or not, the persistence of forest refuges during glacial cycles. Consequently, comparative phylogeographic studies would provide important information about the potential effect of past refuges in lineage diversification, as for previous works on tropical forest trees (Poelchau and Hamrick, 2013).

IV. Phylogeography in seasonal vegetation domains

The central Brazilian Cerrado and the Caatinga in northeastern Brazil form, together with the Argentinean, Bolivian, and Paraguayan Chaco, the so-called “dry diagonal of open vegetation” of eastern South America (Sarmiento, 1975; Pennington *et al.*, 2006; Werneck, 2011). The Cerrado is a savanna that covers a huge area of central Brazil and has dystrophic soils, a marked seasonality of precipitation, and experiences frequent fires (Pennington *et al.*, 2006). The Caatinga is the largest nucleus of seasonally dry tropical forest in the country (SDTF; Prado and Gibbs, 1993) and typically harbors fertile soils under the drought-prone climate of northeast Brazil (Prado, 2003; Queiroz, 2006). These open vegetation domains are poorly characterized in terms of biogeographical relationships (see review of Werneck, 2011), and the response patterns of organisms from these domains are unclear (Werneck, 2011; Turchetto-Zolet *et al.*, 2013). Phylogeographic studies of plants from the Brazilian open and seasonal domains are biased toward the Cerrado vegetation. Twelve studies focused on this domain, while three focused on species distributed in SDTFs, including the Caatinga (Figure 3A).

The Cerrado is not a uniform savanna, but a mosaic of different physiognomies, including savannas, *campos rupestres* (rocky fields) and humid formations, such as *veredas* and gallery forests (Eiten, 1972; Furley and Ratter, 1988). Both geological and paleoclimatic events contributed to the diversification of plant and animal lineages within this domain (Moraes *et al.*, 2009; Prado *et al.*, 2012; Bonatelli *et al.*, 2014). However, studies of plant species from the Cerrado (Table 1) have indicated a preeminent role of the climatic oscillations of the Quaternary on the phylogeographic structure of many species. Although plant community responses to climate are heterogeneous (see above), some diversification patterns have emerged due to the increasing number of species studied, including lineages with distinct ecological requirements.

Tree species in Cerrado show evidence of a recent colonization of the southern Cerrado after a range retraction during the LGM (Collevatti *et al.*, 2003; Ramos

et al., 2007; Novaes *et al.*, 2010, 2013; Collevatti *et al.*, 2015; Ribeiro *et al.*, 2016). This pattern is supported by paleopalynological studies (Behling and Lichte, 1997; Behling, 1998; Behling, 2002) and a recent paleodistribution modeling study (Werneck *et al.*, 2012). Nevertheless, retraction with population subdivision in multiple refugia during the LGM has been recorded for a savanna tree species from central Brazil (Collevatti *et al.*, 2012a) and a palm species restricted to wetlands (Lima *et al.*, 2014). Additionally, a single species presented only a slight range retraction, with a large stable area maintained since the LGM (Souza *et al.*, 2016). Higher genetic diversity in the core distribution of diverse plants has also been reported by these phylogeographic studies (Ramos *et al.*, 2007; Novaes *et al.*, 2010, 2013; Ribeiro *et al.*, 2016; Souza *et al.*, 2016).

Variable genetic effects can be determined by differences in natural-history traits among species, especially those in the contrasting formations of the Cerrado domain. Climate fluctuations have affected plants restricted to the *campos rupestres* formations within the Cerrado in a different manner. Instead of retraction, the evidence suggests range expansion of these plants during glaciations (Collevatti *et al.*, 2009; Barbosa *et al.*, 2012; Collevatti *et al.*, 2012b; Bonatelli *et al.*, 2014). Fossil evidence indicates that the decreasing temperatures and humidity during the glacial period drove a reduction in forest cover and favored the expansion of savanna and grassland vegetation (Salgado-Labouriau *et al.*, 1998; Mayle *et al.*, 2000; Behling and Hooghiemstra, 2001). Such climatic conditions favored range expansion of dry-adapted species to lower altitudes during the LGM. A warmer and wetter climate then resulted in the fragmentation of a broader distribution, which is currently restricted to multiple interglacial microrefugia (see Bonatelli *et al.*, 2014).

Despite these contrasting patterns, studies of the flora of Cerrado have commonly reported a high level of population genetic differentiation (Collevatti *et al.*, 2003; Ramos *et al.*, 2007; Collevatti *et al.*, 2012a, Novaes *et al.*, 2013; Bonatelli *et al.*, 2014). A notable exception is the widely distributed tree species, *Dimorphandra mollis*, which has lower levels of genetic diversity and genetic differentiation (Souza *et al.*, 2016). Additionally, an east-west split in genetic structure was observed in both widely distributed tree species (Collevatti *et al.*, 2003; Ramos *et al.*, 2007, 2009; Novaes *et al.*, 2010, 2013; Ribeiro *et al.*, 2016) and plants from rocky fields (Collevatti *et al.*, 2009; Bonatelli *et al.*, 2014).

SDTFs are scattered throughout other vegetation types, occurring as enclaves within the Cerrado and Chaco domains, and as isolated nuclei—the largest being located in the Caatinga domain (Prado, 2000; Werneck,

2011). In fact, the Caatinga domain is one of the least studied Brazilian vegetation region (Turquetto-Zolet *et al.*, 2013), and vegetation shifts in the SDTF during the Pleistocene are unclear (Thomé *et al.*, 2016). The few extant phylogeographic studies that focused on species from SDTFs (Table 1) reported distinct responses to Quaternary climate changes. Two studies of SDTF plant species (i.e., Caetano *et al.*, 2008; Collevatti *et al.*, 2012c) revealed patterns similar to those predicted by the Pleistocene Arc hypothesis (Prado and Gibbs, 1993). According to this hypothesis, SDTFs were widely and continuously distributed during the dry and cold periods of the Pleistocene, and the present-day range of SDTF nuclei is a relic of a wider distribution (Prado and Gibbs, 1993; Pennington *et al.*, 2000). Phylogeographic analyses of *Ficus bonijesulapensis* (Vieira *et al.*, 2015) and *Cedrela fissilis* (Garcia *et al.*, 2011), however, showed genetic signatures of a recent expansion (during warmer and wetter periods), which is in accordance with the results of paleodistribution modeling (Werneck *et al.*, 2011) and the dispersal scenarios proposed by Mayle *et al.* (2004). According to Werneck *et al.* (2011), the distribution of SDTFs was more fragmented during the LGM than the Holocene, when a southern expansion of this vegetation type occurred. Future research on plant species of these dry and seasonal forests will increase our understanding of the diversification processes of the South American biota.

Seasonal formations also occur in the sub-tropical region of Brazil. The Pampas is one of the largest warm grassland areas globally and occurs in east-central Argentina, Uruguay and the extreme south of Brazil (Fregonezi *et al.*, 2013). This sub-tropical domain is characterized by seasonality in precipitation patterns and soil heterogeneity (Overbeck *et al.*, 2007; Roeschet *et al.*, 2009). Few studies have attempted to investigate the phylogeographic structure of the grassland plant species of Southern Brazil (Figure 3A). Diversification of some typical Pampas vegetation species was influenced by ecological factors to a greater degree than historical factors (forest range shifts or ice-sheet advances) (Fregonezi *et al.*, 2013). For example, Longo *et al.* (2014) found that morphological variants within the *Petunia integrifolia* complex may be associated with the variation in soil salinity between mainland and coastal regions. Moreover, an expansion after a size reduction resulted in the establishment of two allopatric groups within this complex, one of them associated with a geologically ancient area and the other in areas under the influence of marine transgressions/regressions. Climatic and sea level changes have also been reported to influence the evolutionary history of *Calibrachoa heterophylla* and *P. integrifolia*, herbaceous species from the South Atlantic

Coastal Region (Mader *et al.*, 2013; Ramos-Fregonezi *et al.*, 2015). Both species exhibited a pattern of recent population expansion associated with colonization of coastal regions. There is a clear need to increase the number of studies of specific grassland formations to assess the impact of climate and ecological barriers on speciation in sub-tropical South America.

V. Phylogeography of species occurring in multiple vegetation domains

The Amazonia and Brazilian Atlantic Forest domains are separated by a broad corridor of open vegetation physiognomies, comprising the Chaco, the Caatinga, and the Cerrado. This corridor of dry vegetation is an important barrier to species interchange and migration between the two tropical forest domains (Rizzini, 1979; Mori *et al.*, 1981). There is much debate in the literature regarding the biogeographic history of both forest domains. Some authors agree with the view that both Amazonia and the Brazilian Atlantic Forest were more connected in the past, before the LGM (Bigarella *et al.*, 1975; Prance, 1982). During drier periods, gallery forests and seasonal forests may have acted as floristic connections between Amazonia and the Brazilian Atlantic Forest (Oliveira-Filho and Ratter, 1995). Alternatively, despite the overall similarities in structure and physiognomy, Amazonia and the Atlantic Forest have a markedly different species composition, which does not support strong biogeographic connections in the past (Oliveira-Filho and Fontes, 2000).

Few plant phylogeographic studies have explored the potential past connection between Amazonia and the Brazilian Atlantic Forest. De Oliveira *et al.* (2010) reported marked differences between lineages of *Carapichea ipecacuanha* in Amazonia and the Brazilian Atlantic Forest, suggesting long periods of isolation, rather than past connections. Turcheto-Zolet *et al.* (2012) reported similar results for the widespread tropical tree species *Schizolobium parahyba*. Intriguingly, the phylogeographic evidence of past connections between these two forest domains came from studies using animals as models (Costa, 2003; Batalha-Filho *et al.*, 2013; Thomé *et al.*, 2016). Future plant phylogeographic studies should explore the potential existence of past connections between Amazonia and the Brazilian Atlantic Forest, because few empirical data are available. Of special interest are species that occur in both forests (Oliveira-Filho and Fontes, 2000), which should be used as models to evaluate the evolution of these tropical forest domains.

Some phylogeographic studies in Brazil have focused on plant species associated with both mesic and seasonal domains (Figure 3B). Advances in understanding the

complex shifts among contrasting biomes have resulted from palynological (Behling and Negrelle, 2001; Pessenda *et al.*, 2009) and phylogeographical (Martins *et al.*, 2009; Franco *et al.*, 2012) evidence, but further work is needed. Studies to date have suggested that forest and grassland expansion/fragmentation and dispersal events explain the differentiation among plant populations. Species from the Cerrado-Atlantic Forest were the focus of the phylogeographic studies by Novaes *et al.* (2010) and Pinheiro *et al.* (2013). The tree *Plathymenia reticulata* shows a pattern of recent expansion from the central Cerrado to northeastern Brazil via eastern (Atlantic coast) and western (inland) colonization routes (Novaes *et al.*, 2010). In contrast, recent population contraction events were detected in populations of *Epidendrum denticulatum*, particularly at the margins of its distribution range (in the Atlantic rainforest), suggesting that it was restricted to multiple refuges during forest expansion events (Pinheiro *et al.*, 2013). Past floristic connections between the Atlantic Forest and Cerrado domains are suggested by this study, because there is no differentiation between *E. denticulatum* populations in such biomes. Such connections are also indicated by the extensive haplotype sharing among populations of *E. cinabarinum*, a species associated with the Atlantic Forest and Caatinga inselbergs (Pinheiro *et al.*, 2014). This orchid species shows signs of expansion from inland toward dry coastal vegetation zones as a result of long-distance dispersal events. Only two studies sampled populations in Amazonia and Cerrado vegetation (Figure 3B). These studies reported the geographical origins of the cassava (*Manihot esculenta*) (Olsen *et al.*, 1999), and inferred fragmentation events consistent with post-Pleistocene habitat shifts in the rainforest–Cerrado ecotone (Olsen *et al.*, 2002). We claim here that the historical connection dynamics among Brazilian biomes should take advantage of the emergence of model-based methods of phylogeographic inference. The evidence mentioned above will be confirmed or refuted using other evolutionary scenarios (Collevatti *et al.*, 2012c; Lima *et al.*, 2014).

VI. Final remarks and conclusions

Plants are long held recognized as models to track climate change over different time scales (Holdridge, 1947). Due to their lack of movement, plant populations show strong changes in distribution and abundance in response to different habitat conditions (Dansereau, 1957; Whitaker, 1975). In this context, plants could be used as models to test the effects of climate change on species distribution under different time scales, from thousands of years to the last century. A detailed record

based on fossilized pollen grains has been used for paleovegetation reconstruction (reviewed by Behling, 2002; Ledru *et al.*, 2015). By studying the genetic architecture and lineage history of plant groups present in the fossilized pollen record, phylogeographic studies using plant species may enable testing of the demographic scenarios inferred by paleovegetation reconstructions and by current patterns of genetic diversity. Plants have also provided important insights into the recent and rapid climate changes (Root *et al.*, 2003), and phylogeographic studies are crucial for understanding the effect of such drastic changes on plant populations.

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