INVITED REVIEW AND META-ANALYSES

Phylogeographical patterns shed light on evolutionary process in South America

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Abstract

The South American continent is composed of several biogeographical regions harbouring the highest biodiversity on the globe, encompassing five of the world's biodiversity 'hot spots'. Nonetheless, the patterns and processes responsible for shaping its astonishing species diversity are largely unknown. Here, we present a review of current South American phylogeographical knowledge based on published articles on this topic. An appraisal of the literature reveals emerging phylogeographical patterns in the biota of South America. The striking phylogeographical divergence observed among organism lineages in South American studies is suggestive of high levels of undocumented species diversity. The interplay between Pleistocene climatic oscillations and Pliocene/Miocene orogenic events has contributed to shaping the current diversity and distribution of modern lineages in both the tropical and temperate regions of South America. Although older divergence times were observed for a range of species, most herpetofauna underwent an intraspecific lineage split much earlier than other organisms. The geographical ranges of species associated with forest habitats were reduced mainly during glacial cycles, whereas species associated with open vegetation domains have shown variable responses to climatic oscillations. The results suggest a highly complex mosaic of phylogeographical patterns in South America. We suggest future research directions to promote a better understanding of the origin and maintenance of the South American biota.

Keywords: biodiversity, microevolution, neotropics, phylogeography, population structure, species diversification

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Introduction

South America is a large continent extending over a wide latitudinal range (between 12°N and 56°S) that includes an extensive variety of climates, closely associated with vegetation formation. The more extensive northern part, located near the equatorial zone, is tropical, whereas the narrower southern part has subtropical and cool temperate climates (Fittkau *et al.* 1969; Sylvestre 2009; Aragon *et al.* 2011). The continent also shows complex geomorphological patterns, such as large river plains (i.e. the Amazon basin) and extensive mountain

chains (i.e. the Andean Cordillera) (Clapperton 1993). South America harbours the greatest biodiversity on Earth, containing five of the world's biodiversity 'hot spots' (Myers *et al.* 2000). Furthermore, South America is a biogeographically diverse continent composed of a variety of different biomes/ecoregions (Morrone 2004, 2006; Aragon *et al.* 2011). The diversification processes on this continent cannot be restricted to a particular time interval or mechanism (Rull 2011). The evolutionary history of South America has been linked to a succession of major geological events that have modified both continents and oceans (Graham 2009; Cavallotto *et al.* 2011; Folguera *et al.* 2011; Lavina & Fauth 2011). Climate changes and associated glaciations, as well as palaeobasins and shifting shorelines due to marine

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transgressions, have impacted this continent, creating complex scenarios for species diversification (Colinvaux *et al.* 1996; Behling 2002; Antonelli & Sanmartin 2011; Aragon *et al.* 2011; Compagnucci 2011).

Much effort has been put into understanding the complex and high levels of biodiversity in South America. Phylogeographical studies of South American taxa may provide valuable insight into the historical processes underlying diversification in this region. Molecular analyses based on DNA sequence variations in living organisms together with advances in statistical phylogeography have shed further light on how geological events and climatic changes have modified the demographic history of populations (Avise 2009). Such phylogeographical studies can provide a better understanding of the biodiversity, dispersal modes, diversification times, extinctions, refugia areas and other species-/population-level processes (microevolutionary processes; reviewed by Diniz-Filho *et al.* 2008). In addition, comparative phylogeography may provide information regarding significant historical events that have a common influence on many species and may indicate common biotic responses to historical climatic and geomorphological processes (Bermingham & Moritz 1998). These studies are able to detect the regional- and landscape-level biodiversity patterns that are important for understanding macroecology, the broad impacts of geological events and areas of high conservation priority (Bermingham & Moritz 1998; Moritz 2002). Thus, phylogeography provides insights into the processes involved in the origin and distribution of biodiversity. Examples of the contributions of phylogeographical studies to the understanding of evolutionary processes on large scales were recently reviewed for Europe (Taberlet *et al.* 1998; Nieto Feliner 2011), North America (Avise 2000; Soltis *et al.* 2006; Shafer *et al.* 2010), New Zealand (Wallis & Trewick 2009), southern Australia (Byrne 2008) and Africa (Lorenzen *et al.* 2012). For instance, in the northern hemisphere, a large number of phylogeographical studies facilitated identification of major Pleistocene refugia, cryptic refugia, demographic expansion and many other species-/population-level aspects (Avise 2000; Cook *et al.* 2001; Lessa *et al.* 2003; Soltis *et al.* 2006; Shafer *et al.* 2010). This includes suture zones–areas containing multiple hybrid and contact zones (Remington 1968; Swenson & Howard 2004). The number of phylogeographical studies of South America is comparatively lower, despite it having one of the highest levels of biodiversity on Earth (Beheregaray 2008; Sérsic *et al.* 2011). Until 2006, only 6.3% of all phylogeographical studies published worldwide were dedicated to organisms from the South American continent (Beheregaray 2008). The field of phylogeography has recently blossomed in South America, and as a result, an increasing number of studies have been published. Nevertheless, comparative phylogeographical studies are still needed. Recent reviews of the phylogeographical patterns within some specific areas in South America have been published (e.g. Brazilian Atlantic Rainforest: Martins 2011; Silva *et al.* 2012; Amazon: Antonelli *et al.* 2010; Aleixo & Rossetti 2007; Pampas grassland: Fregonezi *et al.* 2012; Patagonia: Sérsic *et al.* 2011; Pardiñas *et al.* 2011; Albino 2011). However, no attempt has been made to compare these patterns across the major regions of the continent.

Geological history and climatic changes in South America

The structural framework of the continent was formed by the distribution and interplay of several major geotectonic units, which include the following classes: cratons (Guiana, Central Brazilian and Coastal Brazilian shields), intercratonic basins (Amazonas, Parnaiba, Sao Francisco and Parana), pericratonic basins (Llanos-Iquitos-Acre-Beni-Chaco-Pampas plains), nesocratons (Pampean Ranges, Patagonia and Deseado massifs) and geosynclines (Andean belts) (Harrington 1962).

The geological isolation and long-term climatic stability that have affected the South American continent would have favoured the gradual accumulation of biodiversity over time (Mittelbach *et al.* 2007). Long periods of time marked the separation of the continents, which were associated with episodes of volcanism, uplift and subsidence of large areas. These are important elements of the geological history of South America and continue to occur (Clapperton 1993). The Andean uplift began in the late Oligocene to early Miocene (about 23 Ma), but the most intense peak of Andean mountain building occurred during the late middle Miocene (about 12 Ma) and early Pliocene (about 4.5 Ma) (Hoorn *et al.* 2010; Folguera *et al.* 2011). This mountain range extends for almost 9000 km along the western coast of South America. Elevation, particularly in the Andes, is an important factor for climatic and ecological control in South America (Hoorn *et al.* 1995). Thus, the Andean uplift greatly influenced biodiversity organization in South America (Gentry 1982; Hoorn *et al.* 1995, 2010; Jørgensen & León-Yánez 1999; Antonelli *et al.* 2010). In their northern and central reaches, the Andes are quite wide and contain extensive plateaus, such as the Altiplano, and a number of major valleys (Folguera *et al.* 2011). The southern Andes have been eroded by the Patagonian ice sheet and are much lower and narrower (Garzione *et al.* 2008; Hoorn *et al.* 2010; Lavina & Fauth 2011). The complex and dynamic geological history of South America is of great importance for understanding the origins of the present-day high biodiversity (Clapperton 1993; De

Carvalho & Almeida 2010; Nullo & Combina 2011; Ruzzante & Rabassa 2011).

Glacial and interglacial periods associated with past climate changes may also have influenced the dynamics of biodiversity, dramatically altering the landscape and evolution of South America. Glaciations have occurred at different time intervals and are influenced by cyclic variations in the Earth's orbit, known as Milankovitch cycles (Bartlein & Prentice 1989; Berger & Loutre 1989; Zachos et al. 2001). The orbital rhythms act in combination, producing periodic variations in the distribution and intensity of sunlight. An alternating sequence of glacial and interglacial conditions has characterized the second half of the Quaternary. Palaeovegetational reconstructions have recovered drastic past vegetational changes due to glacial–interglacial cycles (e.g. Colinvaux et al. 1996; Rull 1999; Behling 2002; Iglesias et al. 2011; Quattrocchio et al. 2011). It has been argued that Quaternary glaciations may have resulted in the fragmentation of forest land into islands in a sea of savannas and/or deserts (refugia), promoting lineage differentiation (Hooghiemstra & van der Hammen 1998), which may have promoted speciation and diversification. For example, the refuge theory of Amazonian speciation was based on the idea that climatic oscillations occurring during the Pleistocene promoted allopatric/parapatric speciation (Haffer 1969, 2008; Prance 1973) and might have contributed to the high biodiversity in this area. However, this idea has become controversial (Colinvaux et al. 2000; Bush & de Oliveira 2006) because it has been recognized that Tertiary Neogene tectonic and palaeogeographical reorganization have also been important drivers of the origin of Neotropical (Pennington et al. 2004; Hoorn et al. 2010; Rull 2011) and temperate biodiversity (Quiroga & Premoli 2010; Sérsic et al. 2011) in South America.

Here, we review current phylogeographical knowledge of South America based on a detailed examination of published articles, discussing the main results in the light of the current debate concerning the probable agents responsible for the high level of biodiversity and its geographical distribution across the different biogeographical regions in this continent (Hoorn et al. 2010; Antonelli & Sanmartin 2011; Rull 2011; Sérsic et al. 2011). Specifically, we had the following goals: (i) to review the current knowledge of phylogeography in South America; (ii) to verify the occurrence of demographic processes (expansion and contraction) related to glacial/interglacial climatic oscillations; (iii) to assess hypothesized refugia types (multiple or single); and (iv) to discuss the role of geological and climatic changes during the Tertiary and Quaternary in shaping the phylogeographical patterns of South America.

Materials and methods

Literature survey

The database used for this review was compiled by conducting searches in the Web of Science® (Institute of Scientific Information, Thomson Scientific). We first searched articles published from 1987 (date regarded as the birth of phylogeography as discipline: Avise et al. 1987) to 2011 using two key phrases: 'phylogeograph*' and 'South America'. Because many studies did not mention 'South America', we also searched by each South American country individually. We have limited our discussion to organisms that occur mainly in the South American continent. Thus, we did not consider studies in which the range of organisms was largely outside of South America (e.g. Central and North America, New Zealand, Australia and Antarctica). Marine organism was not included when their ranges extended beyond the South American coast. Studies that covered only a small part of a species geographical range were also excluded. Studies of invasive species and Amerindian populations were not considered. Articles with a purely taxonomic or systematic emphasis were also excluded. Additionally, we excluded studies in which the terms 'phylogeography', 'phylogeographical' or 'phylogeographic' appeared only in the keywords or title.

Review of South American phylogeographical patterns

For all of the retrieved articles (Table 1), we recorded the following information: (i) sample taxa, (ii) molecular markers, (iii) main biome/ecoregion, (iv) inferred demographic processes (population expansion or
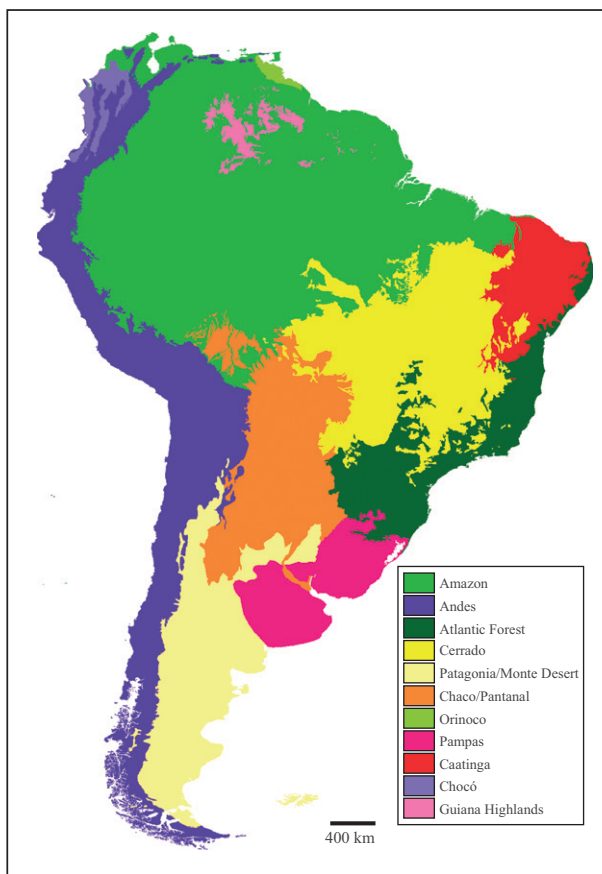
Table 1 Summary of the reviewed studies, including the total number of papers, total number of species encounters and number of studies per taxonomic categories

Category	No of items
Total of studies	214
Total of taxa	476
Total of studies per taxonomic category	
Algae	2
Plant	36
Invertebrate*	29
Fish*	28
Amphibian	20
Reptile	20
Bird	19
Mammal	61

*Note there is one study included in two taxonomic categories, see Table S2 (Supporting information) for details.

contraction), (v) hypothesized refugia types (multiple or single) and (vi) divergence times of the main phylogroups. Categorizing studies by biomes or ecoregions was difficult because many authors have used political divisions (i.e. countries, states, provinces) instead of ecological divisions such as biomes, ecosystems or ecoregions. Because our goal was not to provide a critical biogeographical review of South America, which had previously been done by De Carvalho & Almeida (2010), we used the regionalizations used in each article. The approximate distribution of major terrestrial South American biomes/ecoregions adopted in this review is shown in Fig. 1 (modified from Olson *et al.* 2001; shapefile available at (http://www.worldwildlife.org/science/data/item1875.html). Morrone (2010b) provided a comprehensive review of South American regionalizations and their characteristics.

Given that region, habitat type or latitude may relate to important palaeoclimatic drivers of diversification, we first tested for the relationship between climatic region (temperate vs. tropical/subtropical) and lineage splitting times by analysis of variance (ANOVA) using the software SPSS 11.0 (SPSS, Inc., Chicago, IL, USA). Second, we added organisms (taxonomic groups) as predictor variables of lineage splitting times to refine the analysis and identify additional patterns, also using ANOVA. Third, we used the chi-square test to assess the strength of the association of glacial/interglacial periods with forest-dwelling and open-habitat organisms. We tested the association of population expansion vs. fragmentation during glacial and interglacial periods for forest-dwelling and open-habitat organisms.

Results and discussion

Literature survey

The Web of Science® survey of the literature from 1987 to 2011 identified 323 articles (excluding four reviews) that focused on South American phylogeography. In addition, 678 studies were retrieved using country/territory names. When used as a keyword, Brazil was the most listed country with 219 articles, followed by Argentina with 111, Chile with 79, Peru with 58, Venezuela with 46 and Ecuador with 40; other countries were listed no more than 30 times (Table S1, Supporting information). After excluding duplicates, 640 articles were identified. Focusing on species with a distribution range primarily encompassing South America and after the exclusion of articles that did not meet the requirements described in the Materials and Methods section, 214 relevant studies were retrieved by our literature survey (Table S2, Supporting information). Overall, 476 taxa were studied (Table 1). Plants and vertebrates accounted for 86% of the phylogeographical studies, with other taxonomic groups comprising the remainder, including invertebrates (13%) and algae (<1%). Among plants (a total of 36 articles), angiosperms constituted the majority (34 articles), compared with only two studies of gymnosperms. Fabaceae (17%), Nothofagaceae (12%), Asteraceae (9%), Araucariaceae (6%), Bromeliaceae (6%), Clusiaceae (6%), Meliaceae (6%), Proteaceae (6%) and Solanaceae (6%) were the most represented plant families. Plant-rich families such as Lauraceae, Myrtaceae and Melastomataceae were not considered in these phylogeographical studies. This bias may be related to the lack of specific molecular markers for use in population-level studies (Peakall 2007), mainly for plant families that do not have applied scientific or commercial uses.

Most studies of invertebrates (a total of 29 articles) focused on insects (65%), primarily the Culicidae (25%), Reduviidae (25%) and Formicidae (15%). Moreover, these concentrated on vectors of human diseases, such

Fig. 1 Approximate distribution of major terrestrial South American biomes/ecoregions (modified from Olson *et al.* 2001) used in this study. See Morrone (2010b) for detailed revision regarding differences in the resolution and delimitations of such biomes/ecoregions available in the literature.

Legend:
- Amazon
- Andes
- Atlantic Forest
- Cerrado
- Patagonia/Monte Desert
- Chaco/Pantanal
- Orinoco
- Pampas
- Caatinga
- Chocó
- Guiana Highlands

400 km

as Chagas disease (Reduviidae) and malaria (Culicidae). Crustaceans and molluscs were represented by only four studies each. Among vertebrates, mammals were the largest taxonomic group studied, addressed in 61 articles (28%). Of those, 37% were focused on rodents, and most were performed on multiple species using a comparative approach (Da Silva & Patton 1998; Costa 2003; Lessa *et al.* 2010). Among rodents, Cricetidae were analysed in 54% of the studies, followed by Echimyidae (23%). The other well-represented mammal groups included Phyllostomidae (10%), Didelphidae (9%) and Felidae (7%). Fish were addressed in 13% of the studies (a total of 28 articles). Galaxiidae species were examined in 14% of the studies, Characidae (10%), Cichlidae (7%), Percichthyidae (7%), Sciaenidae (7%) and Trichomycteridae (7%). Lizards, snakes, turtles and crocodilians (reptiles) were investigated in 9% of the studies (20 articles), which focused primarily on the Liolaemidae (30%) and Viperidae (25%). Twenty studies were of amphibians (9%), primarily the Hylidae (36%), Bufonidae (23%), Leptodactylidae (14%), Cycloramphidae (9%) and Dendrobatidae (9%). Amphibians were also investigated extensively in comparative phylogeographical studies, providing strong support for the recovered data (Carnaval 2002; Carnaval & Bates 2007; Carnaval *et al.* 2009; Thomé *et al.* 2010). Birds were studied in 9% (total of 19 articles) of the phylogeographical articles; these concentrated on Dendrocolaptidae (26%), Furnariidae (21%) and Psittacidae (15%).

These patterns were generally similar to those in reports from other parts of the globe (Europe: Taberlet *et al.* 1998; North America: Soltis *et al.* 2006; Shafer *et al.* 2010; New Zealand: Wallis & Trewick 2009; southern Australia: Byrne 2008). Some differences between the composition of our literature survey and the review of Beheregaray (2008), which included the entire southern hemisphere, might be attributable to the great increase in phylogeographical studies in South America since 2006, the latest date included in Beheregaray's report

(see Fig. 2). For instance, 67% of the studies recovered in our review were conducted from 2007 to 2011.

One possible reason for the disparity in the number of studies of plants (17%) and animals (82%) is the well-documented lack of polymorphisms in molecular markers available for intraspecific-level studies for plants compared with animals (Schaal & Olsen 2000; Brunsfeld *et al.* 2001; Soltis *et al.* 2006; among others). Therefore, Sanger sequencing of mitochondrial DNA (mtDNA) has predominated in phylogeographical studies in South America (Fig. 3a). Approximately, 78% of all studies used mtDNA to infer phylogeographical patterns: 58% of these used *only* the mtDNA genome, 15% combined mtDNA and nuDNA (including sequencing of low-copy nuclear genes, AFLPs or ISSRs) and 5% combined mtDNA and microsatellite loci. Sanger sequencing of plastidial genome (cpDNA) regions was used in 13% of studies, most of which (59%) used only cpDNA. Four studies combined cpDNA and microsatellites, and another eighth applied a combination of cpDNA and nuDNA. Lastly, a small proportion of articles (3%) referenced other marker combinations. One study used all three genomes (algae: Tellier *et al.* 2009); another used mtDNA, nuDNA and microsatellite loci (Culver *et al.* 2000); four applied mtDNA with karyotypes (Confalonieri *et al.* 1998; Pellegrino *et al.* 2005; Garcia 2006; Bonvicino *et al.* 2009) or morphological measures (Puorto *et al.* 2001; Chaves *et al.* 2007) to determine species-level phylogeographical patterns. Overall, 72% of the studies used *only* one type of molecular marker.

Although it is now common practice for phylogeography studies to use a diverse suite of markers (Toews & Brelsford 2012), studies from South America did not follow this trend (Fig. 4). While the number of studies has increased over the years, the proportion that applied only one molecular marker to those that applied both uniparental (organellar) and biparental (nuclear) inherited markers has not changed accordingly. This is
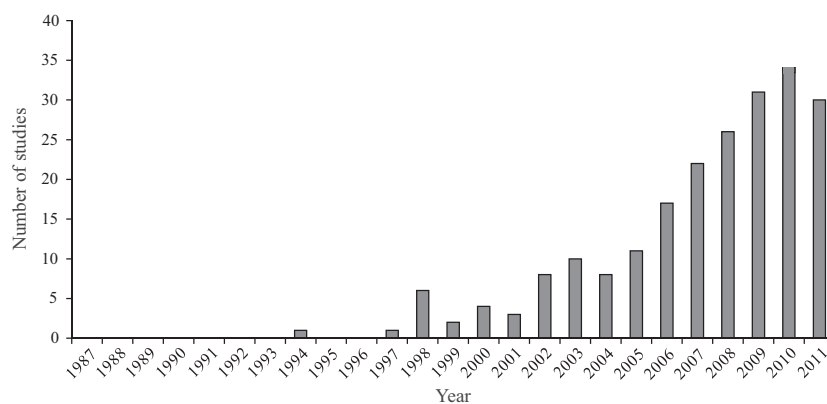
Fig. 2 Number of phylogeographical articles published between 1987 and 2011 in which organism distribution ranges encompass primarily the South American continent.
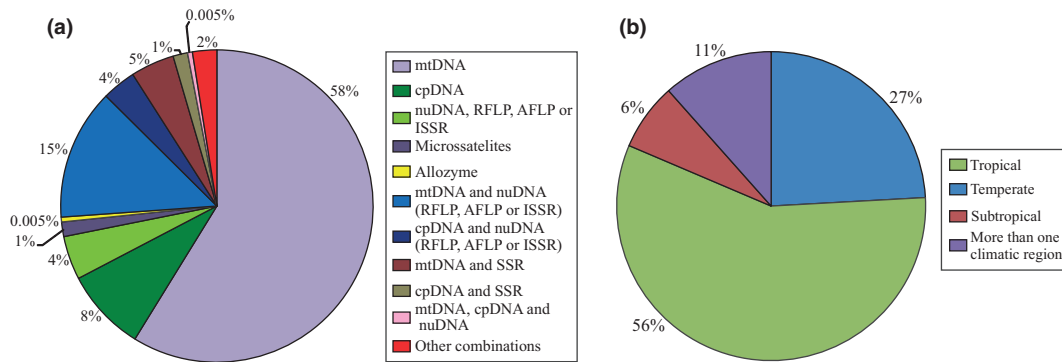
Fig. 3 Percentage of phylogeography articles published between 1987 and 2011 according to (a) classes of genetic marker or marker combinations used (categories are mutually exclusive) and (b) type of environment (see text for details).
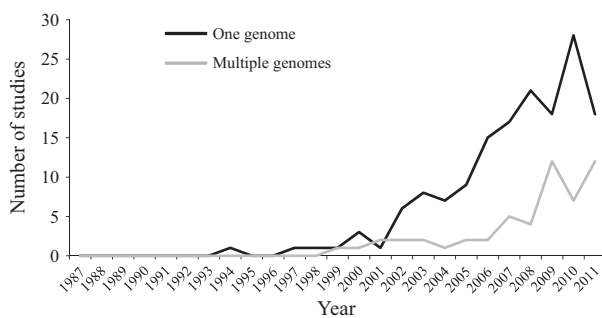
Fig. 4 Phylogeographical studies between 1987 and 2011 showing the proportion per year of those that used a single genome (black line) vs. multiple genomes (grey line).

important because the use of only one type of marker to infer phylogeographical or phylogenetic relationships may not be sufficient to fully investigate certain taxa (Avise & Wollenberg 1997), risking generation of a gene tree that does not represent the true relationships among taxa (Edwards & Bensch 2009; Toews & Brelsford 2012).

Of the 61 studies that used more than one type of molecular marker, 17 showed discordance between the uniparental and biparental inherited markers. A range of South American organisms exhibit stronger phylogeographical structure with uniparental than biparental inherited markers, including algae (Tellier *et al.* 2009), plants (Caetano *et al.* 2008; Collevatti *et al.* 2009; Palma-Silva *et al.* 2009; Tremetsberger *et al.* 2009; Pinheiro *et al.* 2011), birds (Cabanne *et al.* 2008; Caparroz *et al.* 2009; Mila *et al.* 2009), fish (Zemlak *et al.* 2010) and mammals (Culver *et al.* 2000; Eizirik *et al.* 2001; Tchaicka *et al.* 2007; Martins *et al.* 2009; Hollatz *et al.* 2011). Possible reasons for discordant patterns between markers include differences in the dispersal patterns of males and females (Eizirik *et al.* 2001; Tchaicka *et al.* 2007; Caparroz *et al.* 2009; Martins *et al.* 2009; Zemlak *et al.* 2010; Hollatz *et al.* 2011); differences between pollen vs.

seed dispersal rates (Caetano *et al.* 2008; Palma-Silva *et al.* 2009; Tremetsberger *et al.* 2009; Pinheiro *et al.* 2011); differences in the evolution rates and coalescence times of nuclear and cytoplasmic markers (Cabanne *et al.* 2008; Tellier *et al.* 2009); and introgressive hybridization of organellar markers (Dick & Heuertz 2008; Acosta & Premoli 2010; Palma-Silva *et al.* 2011).

The importance of evaluating multiple markers from different genomes in any phylogeographical study is progressively becoming more evident. This idea is particularly applicable in South America, due to its poorly understood and complex historical phylogeography. The shift from single to multiple genome phylogeographical studies will greatly benefit from whole-genome sequencing technologies. As genomic approaches become cheaper and sequencing technologies allow more efficient analysis, surveying different genomes and markers for population samples of non-model species will soon become feasible (Ekblom & Galindo 2010).

The variety of biomes and ecosystems across the continent is a reflection of the remarkable levels of biodiversity observed. The delimitation of regions, subregions, dominions and provinces in a continent with such a complex geological history is a challenging task. Several authors have proposed biogeographical regionalization of the continent based on the identified biotic components (as reviewed by Morrone 2006, 2010a,b). The complexity of the scenario can be identified by the high variation in the number of units and subunits proposed: 98 ecoregions and six bioecoregions (Dinerstein *et al.* 1995); 44 provinces grouped in two subrealms, 10 regions and eight subregions (Rivas-Martínez & Navarro 1994); 46 provinces, divided into seven subregions, further grouped in two regions and one transition zone (Morrone 2006); 26 provinces and six domains (Cabrera & Willink 1973); 20 provinces grouped in two subregions and seven domains (Ringuelet 1975); 33 centres (Müller 1973); 23 domains (Ab'Saber 1977); 13 provinces

(Fittkau *et al.* 1969); and two subregions (Kuschel 1969), among others (for an extensive review, see Morrone 2006, 2010a,b). Despite some differences among the proposed regionalizations, there were certain concordances. For example, most of the proposals recognized a subdivision between tropical and temperate portions of South America, with the Neotropical biota occupying the centre, north and east of South America and the Andean–Patagonic biota in the south and west of the continent (Morrone 2006, 2010a,b).

Using the simplest biogeographical subdivision of the 214 studies in our survey, 120 (56%) were performed in the tropical portion of the continent, 57 (27%) in the temperate region and 14 (6%) within the subtropical domains. Only 23 studies (11%) sampled populations across different climatic regions (Fig. 3b). Overall, our review covered phylogeographical studies in several biomes/ecoregions of South America. Almost half of the studies (47%) sampled only one biome/ecoregion, 39% sampled two or three different biomes/ecoregions and 13% included more than four biomes/ecoregions. Of the latter, only one was based on plant species, an extremely low number compared with those of animals (20 in total). The number of times that a given biome/ecoregion was included in a phylogeographical study is shown in Fig. 5. The most studied biomes/ecoregions were Amazonia and the Andes, which were investigated in 71 and 68 studies, respectively, followed by the Brazilian Atlantic Forest (53 studies), Patagonia and Monte Desert (41 studies), Cerrado (38 studies) and Chaco/Pantanal (27 studies). Gentry (1982) suggested that the evolutionary patterns of the Amazonia and Andes regions would explain much of the richness of the Neotropical domains. In fact, most phylogeographical studies were concentrated in those regions, and the patterns of diversification can now

be detailed (Antonelli & Sanmartin 2011, see also discussion below).

Timing of phylogroup splitting

An appraisal of the literature revealed emerging phylogeographical patterns in the biota of South America. Several studies (125) revealed the presence of deep intraspecific phylogeographical structure with multiple lineages (phylogroups). This led us to believe that many of these could be cryptic species, that is, morphologically indistinguishable (Bickford *et al.* 2007). However, only 13 of these studies discussed possible cases of cryptic speciation (e.g. Dick *et al.* 2003; Camargo *et al.* 2006; Elmer *et al.* 2007; Fouquet *et al.* 2007; Morando *et al.* 2007; Koscinski *et al.* 2008; Mirabello & Conn 2008; Sistrom *et al.* 2009; Tellier *et al.* 2009; Garcia *et al.* 2011; Piggott *et al.* 2011). Because we could not evaluate species' taxonomic status to determine whether they were cryptic, further evaluation of the extent of this phenomenon in South America is necessary.

Deep phylogeographical divisions within taxa suggest extensive periods of isolation among some constituent populations of South American species. In instances in which lineage splits have been dated, a mid-Pleistocene divergence was indicated for 57% of species (Fig. 6). Differences in lineage splitting times were not significant with regard to climatic region: temperate, tropical and subtropical ($F = 0.943$, $P = 0.393$, Table 2). There was, however, a significant difference in inferred splitting time according to taxonomic group ($F = 5.480$; $P = 0.000$, Table 2). Overall, mammalian, bird, fish, invertebrate and plant intraspecific phylogroups were structured mostly during the Pleistocene (Table S2, Supporting information). In contrast, most herpetofauna (amphibians and reptiles) underwent an intraspecific
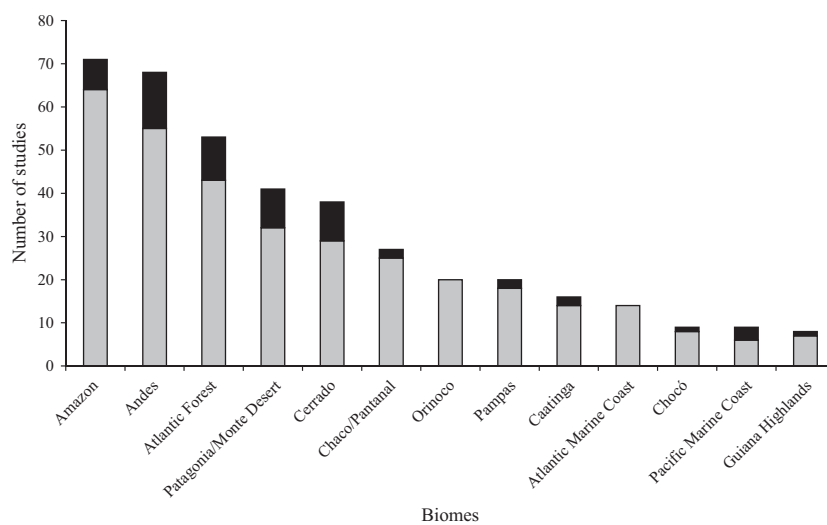
Fig. 5 Number of times that individual biomes/ecoregions were included in a phylogeographical study of South America published between 1987 and 2011 (categories are not exclusive to a certain paper, see the text for details). The corresponding numbers of times that animals (grey) and plants (black) were addressed in each biome/ecoregion are also indicated.
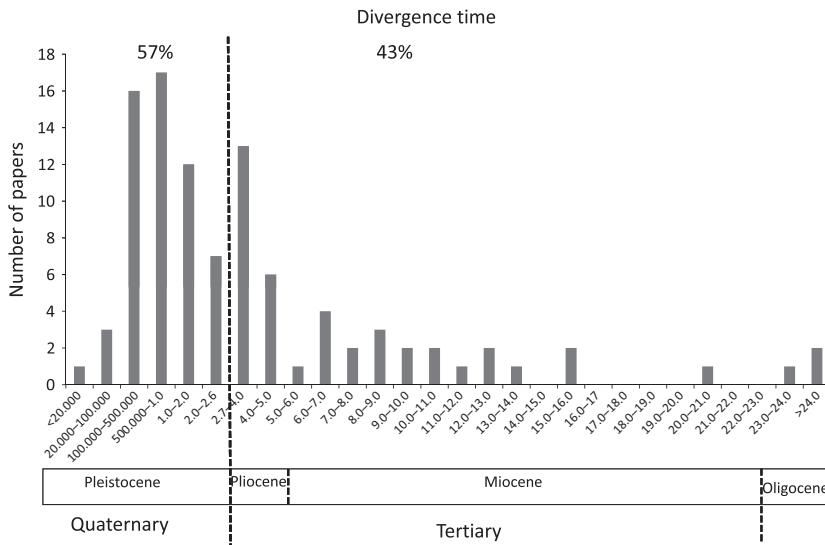
Fig. 6 Timing of lineage divergence of South American taxa based on phylogeographical studies up to 2011. The boundary between the Quaternary and the Tertiary is placed at approximately 2.6 Ma, following Gibbard & Cohen (2008).

Table 2 ANOVA of the effects of taxonomic group and climate region on molecular dating of intraspecific lineage diversification in South America

Source of variation	General linear model				
	d.f.	SS	MS	*F*	*P*-value
Taxonomic group*					
Between groups	6	872.983	145.497	5.480	0.000
Total	96	3262.566			
Climate region†					
Between groups	2	63.655	31.828	0.943	0.393
Total	97	3269.173			

d.f., degrees of freedom; SS, sum of squares; MS, mean square.
*Taxonomic groups: Plants; Invertebrates, Fish, Amphibian, Reptile, Birds. Algae were not included in this analysis.
†Climate region: temperate, tropical, subtropical.

lineage split much earlier, during the Pliocene and/or Miocene (Table S2, Supporting information).

It is important to note that earlier lineage splits have been reported for a substantial amount of studies (43% of the species, Fig. 6), including several taxonomic groups dating back to the Pliocene (*fish*: Ruzzante *et al.* 2008; *herpetofauna*: Morando *et al.* 2008; Avila *et al.* 2006; Thomé *et al.* 2010; Noonan & Gaucher 2005; Grazziotin *et al.* 2006; *birds*: Mila *et al.* 2009; Chaves *et al.* 2007; *mammals*: Eizirik *et al.* 2001; Hoffmann & Baker 2003; and *insects*: Solomon *et al.* 2008), to the Miocene (*herpetofauna*: Chek *et al.* 2001; Souza *et al.* 2003; Pellegrino *et al.* 2005; Yoke *et al.* 2006; Morando *et al.* 2007; Fitzpatrick *et al.* 2009; Guarnizo *et al.* 2009; Brunes *et al.* 2010; Geurgas & Rodrigues 2010; Breitman *et al.* 2011; *fish*: Sistrom *et al.* 2009; *plants*: Cosacov *et al.* 2010; Garcia *et al.* 2011; and *insects*: Solomon *et al.* 2008) and even

earlier (Elmer *et al.* 2007). For instance, Elmer *et al.* (2007), in a study of an Amazonian terrestrial leaflitter frog (*Eleutherodactylus ockendeni*), reported lineage splitting from the mid-Miocene to Oligocene (20–25 Ma).

The chronology of lineage splitting is important for developing a testable hypothesis because it reveals causal mechanisms and forces behind diversification processes (Rull 2011). Within the Quaternary, the main environmental shifts have been linked to climatic changes (temperature and aridity oscillations) and their potential evolutionary impact on adaptability and/or migration, whereas the Tertiary was characterized by significant tectonic and palaeogeographical reorganization leading to the creation/alteration of new pathways and barriers to biotic evolution. The detection of more ancient lineage divergences in almost half of studies analysed indicates that several factors may have contributed to the geographical structure of the population-level diversity of South American species. Therefore, not only Pleistocene Milankovitch cycles but also earlier orogenic events (i.e. volcanic, tectonic, mountain uplift, alteration in drainage systems) occurring during the Miocene and Pliocene likely played an important role in the population divergence of South American species (Rull 2011).

Students of biodiversity have discussed the relative importance of Pleistocene vs. Pliocene/Miocene events in promoting the diversification of extant South American species (*Neotropics*: Moritz *et al.* 2000; Bennett 2004; Hewitt 1996, 2001; Rull 2006, 2008, 2011; Brunes *et al.* 2010; Pennington *et al.* 2004; Werneck *et al.* 2011; *temperate*: Sérsic *et al.* 2011). The idea that climatic oscillations during the Pleistocene promoted allopatric/parapatric speciation was the basis of the refuge theory (Haffer 1969, 2008; Prance 1973) and has been the focus of

much discussion (Bush & de Oliveira 2006). What seems to be evident, however, is that the marked phylogeographical divergence documented in South American studies is suggestive of high levels of undescribed species diversity and a geographical structure of population-level diversity. However, there is no clear overall pattern indicating that in South America, *most* species originated during the Pleistocene, as predicted by the refuge theory. Instead, both Pleistocene climatic oscillations and Pliocene/Miocene orogenic events have contributed to shaping the current diversity and distribution of modern species in both the Neotropical (Bush 1994; Hoorn *et al.* 1995, 2010; Pennington *et al.* 2004; Rull 2006, 2008, 2011; Antonelli & Sanmartin 2011) and temperate regions (Ruzzante *et al.* 2006, 2008; Mathiasen & Premoli 2010; Sérsic *et al.* 2011).

Although formerly these explanations were considered mutually exclusive, several phylogeographical studies support the idea that the complex processes of diversification in South America were affected by the interaction of palaeogeographical and palaeoclimatic forces (Bush 1994; Riddle 1996; Rull 2008). Under this hypothesis, many species must have begun diversifying during the Tertiary (Miocene/Pleistocene), perhaps as a consequence of orogenic events (i.e. Andean uplifts), achieving their current biodiversity during the Quaternary when population structuring and young species originated under the influence of climatic oscillations (Rull 2011). For instance, in *Liolaemus bibroni*, a Patagonian lizard, northern and southern phylogroups diverged in the mid-Miocene (11.5 Ma), southern phylogroups during the Pliocene and Pleistocene (5.6–1.4 Ma) and northern phylogroups in the early Pleistocene (1.5–2.3 Ma) (Morando *et al.* 2007). In *Rhinella crucifer*, a frog species from the Brazilian Atlantic Forest, the split between the southern and central/northern clades occurred during the Pliocene (3.97 Ma), whereas splits between the northern and central clades and within the northern clades occurred during the Pleistocene (0.836 and 0.313 Ma, respectively) (Thomé *et al.* 2010). In *Calceolaria polyrhiza*, a herbaceous plant species from the Andean and Patagonia regions, the northern and southern clades diverged during the late Miocene (12.99–10.33 and 6.85–8.55 Ma, respectively). The estimated time of diversification within the northern clade was also late Miocene (8.14–10.17 Ma); however, clades nested within the southern distribution in Patagonia diverged more recently, during the Pleistocene (1.16–1.45 Ma) (Cosacov *et al.* 2010).

It is important to emphasize that the patterns reported for South America were based mostly on timing estimation procedures of a single uniparental marker (i.e. mtDNA or cpDNA; Figs 2a and 3). As discussed above, genealogies based on a single marker do not necessarily correspond to the actual species tree (Pamilo & Nei 1988; Avise & Wollenberg 1997). Moreover, the inference of lineage divergence time from molecular data has been criticized, mainly because dating is prone to many types of error (particularly for those taxa lacking an available fossil record for calibration). Although recent improvements have increased its reliability (Rutschmann 2006; Pulquerio & Nichols 2007), molecular dating inferences are highly influenced by calibration scheme (Sauquet *et al.* 2012). Hence, the patterns we report here must be evaluated carefully. As mentioned previously, further studies of multiple loci or using a whole-genome sequencing approach and increasing the intensity of geographical sampling of a species will provide a more complete picture of the evolution and diversification of South American biota.

Glacial vs. interglacial periods

A range of phylogeographical studies in South America have identified multiple refugia (Table S2, Supporting information),while the contrasting pattern, demographic expansion from a single refuge, was identified mainly in mammals from temperate South America (Palma *et al.* 2005; Rodriguez-Serrano *et al.* 2006; Gonzalez-Ittig *et al.* 2010; Lessa *et al.* 2010). The persistence of some species in multiple refugia localized throughout their distribution indicates that these species might have persisted through multiple climatic cycles in heterogeneous environments. This pattern highlights the importance of dynamic evolutionary processes and a mosaic of habitats in heterogeneous landscapes that allowed species to persist through changing environmental conditions. Accordingly, recent palaeoecological information in the Neotropics indicates that during the Quaternary, spatial reorganization and persistence in suitable microrefugia were more frequent than complete extinctions (Vegas-Vilarrubia *et al.* 2011). Microrefugia are small areas with local favourable environmental features within which small populations can survive outside their main distribution area (the macrorefugium) protected from unfavourable regional environmental conditions (Rull 2009). Pollen records indicate that in the southern Andes, ice-free areas might have facilitated the maintenance of habitat refugia for forest taxa (Markgraf *et al.* 1995; Heusser *et al.* 1999; Heusser 2010). In fact, the persistence of temperate southern populations of several organisms during glacial periods has been reported, principally plants (Muellner *et al.* 2005; Marchelli & Gallo 2006; Allnutt *et al.* 1999; Azpilicueta *et al.* 2009; Jakob *et al.* 2009; Souto & Premoli 2007; Tremetsberger *et al.* 2009; Arana *et al.* 2010; Cosacov *et al.* 2010; Mathiasen & Premoli 2010; Premoli *et al.* 2010; Vidal-Russell *et al.* 2011) and vertebrates

(fish: Zemlak *et al.* 2008; birds: Gonzalez & Wink 2010; mammals: Himes *et al.* 2008). A number of studies show long-term persistence of such species, including even populations close to the ice-sheet coverage limit during the last glacial maximum (LGM) (Jakob *et al.* 2009; Cosacov *et al.* 2010; Vianna *et al.* 2011; references in Sérsic *et al.* 2011). The existence of multiple refugia has also been reported for other parts of the globe, where the effects of climatic oscillations might have been of identical intensities to those in South America (southern Australia: Byrne 2008; southern Europe peninsulas: Nieto Feliner 2011; Africa: Lorenzen *et al.* 2012).

Although South American Pleistocene climate changes have been demonstrated not to be the only driver of speciation (e.g. Hoorn *et al.* 2010; Rull 2011), they have influenced the historical demography and distribution of some species in South America. In fact, demographic changes were identified in 58% of the studies (Table S2, Supporting information). However, only a fraction (35%) of these studies included an estimate of the timing of such demographic oscillations. These studies suggested an important interplay between demographic scenarios and organisms associated with forest and open vegetation habitats. A significant proportion of forest-dwelling species (87%, d.f. = 1, χ^2 = 28.69, P < 0.0001) showed signs of population fragmentation during glacial cycles and/or population expansion during interglacial periods. The geographical ranges of species associated with forest habitats were reduced mainly due to the drier conditions during glacial cycles, which favoured the expansion of grasslands and savannas, following the classical model of tropical refugia (Haffer 1969; Bennett & Provan 2008), as indicated by palaeovegetation reconstructions (Behling 2002; Ledru *et al.* 2005). Forest species associated with dry tropical forests (Caetano *et al.* 2008), temperate forests (Marchelli *et al.* 1998, 2010; Nunez *et al.* 2011; Sallaberry-Pincheira *et al.* 2011), mountain forests (Thomé *et al.* 2010) and riparian forests (Marquez *et al.* 2006) accounted for 13% of studies and also indicated population expansion during interglacial periods and/or fragmentation during glacial cycles.

For species associated with open vegetation, the pattern was unclear (χ^2 = 2.25, d.f. = 1, P = 0.133), as only 68% of the studies showed population expansion during glacial cycles and/or fragmentation during interglacial periods. Species associated with open vegetation domains seemed to show variable responses to climatic oscillations, with a tendency to expand (Marin *et al.* 2008; Jakob *et al.* 2009; Cosacov *et al.* 2010), to maintain (Rodriguez-Serrano *et al.* 2006; Pinheiro *et al.* 2011; Werneck *et al.* 2012) or to shrink (Gonzalez *et al.* 1998; Xu *et al.* 2009; Gonzalez & Wink 2010) their geographical

distribution ranges during glacial cycles. These results highlight the importance of phylogeographical studies with organisms adapted to xeric habitats, which show a more variable response to glacial cycles than do forest-dwelling species. Accordingly, palaeovegetation modelling results indicate that dry tropical seasonal forests in South America were fragmented during the LGM (Werneck *et al.* 2011), as were tropical humid forests (Carnaval & Moritz 2008). Moreover, the role of glacial cycles in generating biotic refugia in nontropical areas of the southern hemisphere has received little attention (Beheregaray 2008; Lessa *et al.* 2010; Sérsic *et al.* 2011). Because only 28% of the studies surveyed focused on species associated with open vegetation habitats, future studies should focus on such organisms to better understand the role of interglacial refuges in the diversification of South American taxa (Antonelli 2008; Bennett & Provan 2008; Werneck 2011; Werneck *et al.* 2011).

Phylogeographical breaks, colonization routes and dispersal corridors

Postulating the main phylogeographical breaks, colonization routes and dispersal corridors from the multiple refugia is challenging, especially considering our limited knowledge of the phylogeography of South American organisms. Generally, a complex phylogeographical mosaic of patterns was observed, which was to some extent species specific. As observed in southern European peninsulas (Nieto Feliner 2011), where the history of populations indicates persistence rather than complete extinction (due to drastic events), replicated patterns should be more scarce than in northern hemispheric regions. For instance, several studies have shown how diverse ranges shift directions from the usual latitudinal north–south pattern. Due to the complex patterns resulting from this scenario, proposal of general models is difficult. However, we have attempted to summarize the most common patterns found.

Rivers as phylogeographical barriers

Rivers have been suggested to play an important role in shaping biogeographical patterns in South America (Salo *et al.* 1986; Rasanen *et al.* 1987; Ward *et al.* 2002). The 'riverine' hypothesis of diversification suggests that major rivers act as geographical barriers to dispersal of terrestrial organisms, limiting gene flow and promoting allopatric divergence. For example, rivers within the Amazon basin (Wallace 1852, 1876; Ayres & Clutton-Brock 1992; Capparella 1992; Hayes & Sewlal 2004) and the Doce River in southeastern Brazil (Pellegrino *et al.* 2005; Cabanne *et al.* 2007; Tchaicka *et al.* 2007; Ribeiro

et al. 2011) have been reported to be effective barriers between different species assemblages and populations. Several studies have, indeed, indicated that major rivers might have acted as important phylogeographical barriers. The Amazon River and its tributaries are most frequently reported as representing a historical barrier to gene flow in a range of organisms including mammals (*Leopardus tigrinus*: Johnson *et al.* 1999; *Leopardus pardalis*, *Leopardus wiedii*: Eizirik *et al.* 1998; *Panthera onca*: Eizirik *et al.* 2001; *Callicebus lugens*: Casado *et al.* 2007; *Tapirus terrestris*: De Thoisy *et al.* 2010; *Pteronura brasiliensis*: Pickles *et al.* 2011), birds (*Xiphorhynchus spixii/elegans*: Aleixo 2004; *Lepidothrix coronata*: Cheviron *et al.* 2005), insects (*Charis cleonus*: Hall & Harvey 2002; *Anopheles darling*: Pedro & Sallum 2009; *Anophele triannulatus*: Pedro *et al.* 2010) and frogs (*Dendrobates*: Symula *et al.* 2003). In Bolívia, the Magdalena River Valley was identified as a barrier to dispersal of the western and eastern clades of the bird *Buarremon brunneinucha* (Cadena *et al.* 2007). However, the role of rivers as major drivers of allopatric diversification in South America has been challenged by several studies that do not support the riverine hypothesis (frogs and small mammals: Gascon *et al.* 2000; Lougheed *et al.* 1999; Patton *et al.* 1994, 2000; birds: Cadena *et al.* 2011; insects: Solomon *et al.* 2008; Fairley *et al.* 2002; and reptiles: Vasconcelos *et al.* 2006, 2008). These data indicate that the population structure may be an outcome of barriers that are no longer evident in the landscape (ancient rivers) (Lougheed *et al.* 1999). Others have suggested a significant impact of recent Andean uplift on the lowlands in terms of generating the patterns of diversity along the major rivers in Amazonia (Patton *et al.* 1994; Gascon *et al.* 2000; Turner *et al.* 2004) (for ridge barriers, see discussion below).

In southeastern Brazil, studies have pointed to the Doce River basin as the phylogeographical break for some species (mammals: Costa 2003; lizards: Pellegrino *et al.* 2005; birds: Cabanne *et al.* 2007, 2008; frogs: Thomé *et al.* 2010; and plants: Ribeiro *et al.* 2011). Although this pattern is strongly in agreement with the historical instability involving the coastal areas south of the Doce River, as predicted by Carnaval & Moritz (2008), its role as a real barrier has been debated (Martins 2011) and even refuted (Colombi *et al.* 2010). Because the Doce River basin was severely affected by marine incursions during the Pleistocene, the real barrier might not have been the river itself (Martins 2011). Additionally, contrasting topographies have been evoked to explain the north/south diversity split in the Doce River (Silva *et al.* 2012). The third largest river in South America, the São Francisco River, was reported to be a geographical barrier to populations of the small rodent *Calomys expulsus* (Do Nascimento *et al.* 2011).

In southern South America, other major rivers have also been reported to act as phylogeographical breaks. The Plata River basin is the second largest basin in South America. The Paraguay and Plata River basins were a significant barrier to dispersal and gene flow for the cat *Leopardus colocolo* (Johnson *et al.* 1999). The Paraná River, a tributary of the Plata River basin, separates populations of the marsh deer *Blastocerus dichotomus* (Marquez *et al.* 2006).

Although the largest rivers in South America are in tropical and subtropical regions, the role of several smaller rivers in the temperate region as potential barriers to dispersal was examined, and structured populations were identified. In Chile, the Maipo, Yeso and Aconcagua Rivers represent major barriers to the lizard species *Liolaemus monticola* (Torres-Perez *et al.* 2007). The Maipo River has also been reported to be a geographical barrier to populations of the snake *Philodryas chamissonis* (Sallaberry-Pincheira *et al.* 2011). The Chubut River in Patagonia has affected gene flow among populations of the saxicolous mouse *Phyllotis xanthopygus* (Kim *et al.* 1998). The Chico River in Argentina was considered an ancient barrier to populations of the herbaceous plant *Calceolaria polyrhiza* (Cosacov *et al.* 2010) and for the reptile *Liolaemus lineomaculatus* (Breitman *et al.* 2011). More intensive geographical sampling of an array of taxa across South America is crucial for elucidation of the role of major rivers as historical barriers to gene flow.

Phylogeographical patterns of freshwater organisms

For aquatic organisms, biogeographical studies have indicated the role of geographical isolation across major South American drainage basins in structuring and generating biodiversity (as reviewed by Hubert & Renno 2006). Evidences of population genetic divergence within species occupying the Amazonian River basins were observed in several fish species (*Potamorrhaphis guianensis*: Lovejoy & de Araujo 2000; *Prochilodus magdalene*: Turner *et al.* 2004; *Serrasalmus rhombeus*: Hubert *et al.* 2007; *Nannostomus unifasciatus*: Sistrom *et al.* 2009; *Paracheirodon axelrodi*: Cooke *et al.* 2009); turtles (*Podocnemis expansa*: Pearse *et al.* 2006); and the Amazonian River dolphin, a freshwater mammal (*Inia*: Banguera-Hinestroza *et al.* 2002; Hollatz *et al.* 2011). Hollatz and colleagues argued that the heterogeneity of the water environment may be promoting the genetic differentiation observed between populations on both sides of the Amazon River. Nevertheless, Piggott *et al.* (2011) reported high population genetic differentiation, interpreted as cryptic speciation, of black-wing hatchet fish (*Carnegiella marthae*) in the Rio Negro floodplain in central Amazonia. An interesting finding of this study

is the cryptic speciation within a well-connected system of floodplains with no contemporary barriers that could lead population divergence. These results indicate that the diversity of Amazonian organisms is greatly underestimated.

Rivers can have important role in influencing population structure not only as ecological barriers but also as dispersal corridors. For instance, one study has identified the Casiquiare River as a dispersal corridor from the Amazonian to the Orinoco basins for three peacock cichlid species (*Cichla temensis*, *Cichla monoculus* and *Cichla orinocensis*: Willis *et al.* 2010). However, the role of the geologically recent Casiquiare corridor in promoting gene flow between the Amazonian and Orinoco basins has not been supported for turtle species (*Podocnemis expansa*: Pearse *et al.* 2006; *Podocnemis unifilis*: Escalona *et al.* 2009).

In the Guyanas coastal rivers, a divergent lineage of a freshwater fish *Pseudancistrus brevispinis* (Cardoso & Montoya-Burgos 2009) was identified, and the authors believe that sea level fluctuation during the Pleistocene could have been responsible for this diversification. For the catfish *Pimelodus albicans* (Vergara *et al.* 2008), genetic structuring was detected among different sites of the Plata River basin. The populations of the freshwater catfish *Trichomycterus areolatus* (Unmack *et al.* 2009) were highly isolated among drainage systems in Chile. For the Patagonian fish *Galaxias platei* (Zemlak *et al.* 2008), the strong phylogeographical structure observed was influenced by both the orogeny of the southern Andes and the glacial cycles of the Pleistocene. A deep phylogenetic structure was reported for the Patagonian freshwater crab *Aegla alacalufi* (Xu *et al.* 2009). The authors believed that Pleistocene glaciations, drainage isolation, habitat fragmentation and poor dispersal ability have influenced the patterns of the population genetic structure of this aquatic species. In contrast, there was little evidence of population structure within the Paraná River in the fish *Prochilodus lineatus* (Sivasundar *et al.* 2001). Additionally, no phylogeographical structure was observed by Ruzzante *et al.* (2011) for the Patagonian fish *Percichthys trucha*. This species appears to have dispersed and mixed across diverse Patagonian drainages, most likely as a result of changes in sea level and the extension of the Patagonian landscape that occurred during the Quaternary.

Ridges as phylogeographical barriers

Ridges and mountain uplifts are well-known mechanisms of geneflow interruption and promote divergence among populations. Accordingly, evidence of this effect in a range of taxa from regions around the world is available (Soltis *et al.* 2006). Andean uplift was one of the major drivers of biodiversity organization in South America (Gentry 1982; Jørgensen & León-Yánez 1999; Antonelli *et al.* 2010; Hoorn *et al.* 2010). The Andean Cordillera is a continuous strip that divides South America east and west, serving as an effective moisture barrier (Aragon *et al.* 2011). Cross-Andean disjoint distributions have been reported for several organisms (Brower 1994; Zamudio & Greene 1997; Jørgensen & León-Yánez 1999; Dick *et al.* 2003; Weigt *et al.* 2005; Trenel *et al.* 2007; Turchetto-Zolet *et al.* 2012). These patterns suggest that under the vicariance hypothesis, lowland biota might have evolved due to Andean uplift (Gentry 1982; Raven 1999). High genetic divergence between populations on either side of the Andes Cordillera, which suggests that differentiation is a result of long-term geographical isolation, has been reported for several taxa including plants (*Symphonia globulifera*: Dick *et al.* 2003; Dick & Heuertz 2008; *Cyathostegia mathewsii*: Pennington *et al.* 2010), birds (*Lepidothrix coronata*: Cheviron *et al.* 2005; *Adelomyia melanogenys*: Chaves *et al.* 2007; *Glyphorynchus spirurus*: Mila *et al.* 2009), frogs (*Rinella marina*: Slade & Moritz 1998; *Hypsiboas andinus*: Koscinski *et al.* 2008), fish (*Percichthys* and *Percilia*: Ruzzante *et al.* 2006), butterflies (*Heliconious erato*: Brower 1994) and mammals (*Glossophaga soricina*: Ditchfield 2000; *Corollia* sps: Hoffmann & Baker 2003; *Oreailurus jacobita*: Johnson *et al.* 1998). These studies found genetic population divergence across the Andes Mountains during a period of major Andean uplift in the Miocene, in agreement with the orogeny-driven vicariance hypothesis. In the wax palm plant (*Ceroxylon echinulatum*), however, an eastern–western population split occurred more recently, during the Quaternary (Trenel *et al.* 2008). Hence, these authors propose cross-Andean dispersal to be a more plausible explanation of the observed disjunction than orogeny-driven vicariance.

The cross-Andean dispersal hypothesis is supported by several other studies of aquatic and terrestrial species, including fish (*Galaxias platei*: Zemlak *et al.* 2008), small mammals (*Oligoryzomys longicaudatus*: Palma *et al.* 2005; *Abrothrix olivaceus*: Smith *et al.* 2001; Rodriguez-Serrano *et al.* 2006; *Dromiciops gliroides*: Himes *et al.* 2008; *Loxodontomys micropus*: Canon *et al.* 2010; *Abrothrix longipilis*: Lessa *et al.* 2010), birds (*Cyanoliseus patagonus*: Masello *et al.* 2011; *Adelomyia melanogenys*: Chaves & Smith 2011), insects (Euglossini: Dick *et al.* 2004) and plants (*Tristerix corymbosus* and *Tristerix aphyllus*: Amico & Nickrent 2009). Migration across the Andean divide was possible in regions where mountains were not very high, as well as through continuous forests (Zemlak *et al.* 2008; Amico & Nickrent 2009; Masello *et al.* 2011). For aquatic organisms, drainages that currently or previously traversed the Andes from the east side have been sug-

gested as dispersal corridors (Zemlak *et al.* 2008). A study of the fish *Galaxias maculatus* (Zemlak *et al.* 2010) also indicated that the Chilean Coastal Cordillera might represent an eastern–western dispersal barrier.

South America is a topographically complex continent, and although Andean uplift is one of the major events that contributed to biota organization, other mountain uplifts have also been reported to have acted as phylogeographical barriers to South American species. For example, the Serra do Mar and Mantiqueira mountain uplifts in southeastern Brazil for a freshwater turtle during the Pliocene and Miocene (*Hydromedusa maximiliani*: Souza *et al.* 2003), for rats (*Trinomys*: Lara & Patton 2000) and freshwater fish (*Mimagoniates microlepis*: Torres & Ribeiro 2009). The Mitaraka archipelago inselbergs, in French Guiana, represent a strong barrier to gene flow among *Pitcairnia geyskesii* populations (Boisselier-Dubayle *et al.* 2010).

Conclusions and future perspectives

An increasing number of studies of South American phylogeography have recently been published. Nonetheless, the number remains insufficient, pointing to an urgent need for more investigations of historical biogeography and phylogeography to assess how species responded to past changes and to predict how they might cope with current changes. Comparative studies of phylogeography on a smaller scale (i.e. a specific biome/ecoregion) would facilitate the identification of refugia and contact zones such as those available for vertebrates and plants from the Patagonian region (Sérsic *et al.* 2011), rodents from the Patagonian and Tierra del Fuego regions (Pardiñas *et al.* 2011), squamates from Patagonia (Albino 2011), vertebrates from the Brazilian Atlantic Forest (Martins 2011; Porto *et al.* 2012; Silva *et al.* 2012), plants from Pampas grassland (Fregonezi *et al.* 2012) and tetrapods from the Amazonia region (Aleixo & Rossetti 2007; Antonelli *et al.* 2010). It is important to highlight the fact that most of these recent reviews discuss mainly vertebrate patterns, likely because this taxonomic category is the most studied in South America (89% of phylogeographcial studies). In addition, a greater number of plant (trees and herbs) and invertebrate species, which show contrasting dispersal abilities, should be included to generate a nonbiased picture of biota evolution in South America. We predict that in the next few years, next-generation sequencing techniques will solve most of the problems encountered in plant groups due to the low diversity of molecular markers, thus facilitating phylogeographical studies of a broader range of organisms. Phylogeographical studies of the xeric regions of Cerrado, Chaco/Pantanal, Caatinga, Pampas and Orinoco could provide important information on the demographic responses of populations adapted to drought stress during climatic oscillations because a large amount of the published data relates to forest-dwelling species. Hence, there is an urgent need to compile phylogeographical studies of a wider range of taxonomic groups into a more regionalized review of comparative phylogeography of important South American regions. This will facilitate more accurate elucidation of phylogeographical patterns and promote a better understanding of the origin and maintenance of South American biota.

Acknowledgements

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The authors share interest in phylogeography, population genetics, plant speciation and evolutionary biology of South American organisms.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Number of articles retrieved in this review.

Table S2 Summary of phylogeographic studies for South America.