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# Quaternary Science Reviews

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## The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives

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### ARTICLE INFO

#### Article history:

Received 1 November 2010  
 Received in revised form  
 13 March 2011  
 Accepted 14 March 2011  
 Available online 29 April 2011

#### Keywords:

South America  
 Open vegetations  
 Seasonally dry tropical forests  
 Cerrado  
 Chaco  
 Caatinga  
 Biogeography  
 Zoogeography

### ABSTRACT

The eastern-central South American open vegetation biomes occur across an extensive range of environmental conditions and are organized diagonally including three complexly interacting tropical/sub-tropical biomes. Seasonally Dry Tropical Forests (SDTFs), Cerrado, and Chaco biomes are seasonally stressed by drought, characterized by significant plant and animal endemism, high levels of diversity, and highly endangered. However, these open biomes have been overlooked in biogeographic studies and conservation projects in South America, especially regarding fauna studies. Here I compile and evaluate the biogeographic hypotheses previously proposed for the diversification of these three major open biomes, specifically their distributions located eastern and southern of Andes. My goal is to generate predictions and provide a background for testable hypotheses. I begin by investigating both continental (inter-biome) and regional (within-biome) levels, and I then provide a biogeographical summary for these regions. I also suggest how novel molecular-based historical biogeographic/phylogeographic approaches could contribute to the resolution of long-standing questions, identify potential target fauna groups for development of these lines of study, and describe fertile future research agendas.

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### 1. Introduction

The open vegetation biomes of South America occur across a great variety of environmental conditions, including large climatic, latitudinal and altitudinal ranges, greater than found elsewhere (Pennington et al., 2006b; Sarmiento, 1975). Eastern South America open biomes are organized diagonally, including three tropical/sub-tropical biomes that interact in very intricate ways: the Seasonally Dry Tropical Forests (with the largest area in northeastern Brazil, Caatinga), the Cerrado savanna (central Brazil), and the Chaco (northeastern Argentina, western Paraguay, and south-eastern Bolivia) (Fig. 1). In many instances, Seasonally Dry Tropical Forests (hereafter: SDTFs) and savannas (Cerrado) occur under the same climatic conditions (Mayle, 2004; Mooney et al., 1995), whereas Chaco is often subject to winter frosts (Pennington et al., 2000). In common, all are seasonally stressed by drought, have vegetations adapted to these climatic conditions, unique biotas, complex mosaic-type distributions, and have received less research attention than tropical wet forests (Furley and Metcalfe, 2007; Mooney et al., 1995). However, in spite of their resemblances these biomes respond differently to climatic and

environmental changes and should be considered separately in biogeographical analyses (Pennington et al., 2000). As a result of highly dynamic and fluctuating savanna and dry forest boundaries (Furley and Metcalfe, 2007), their evolutionary character and extent are complex points of debate, and much study will be needed before consensus views are reached.

Even though the biodiversity of South American open biomes is currently recognized as high, their limits are ill-defined when compared to tropical wet forests (Pennington et al., 2006a; Sarmiento, 1975) and they are still poorly characterized in terms of biogeographical relationships and genetic structure. This occurs for many conceptual and logistic reasons. First, as with most grassy or savanna regions, South American open biomes are often thought to be secondary formations, products of forest clearance by human activity (Bond and Parr, 2010). As critical for the biogeographic study of these biomes is a nomenclatural barrier, characterized by a lack of consensus about names and phytogeographic status of these formations. In fact, SDTFs are known by a plethora of names, in three languages: Spanish, English and Portuguese (Murphy and Lugo, 1986; Pennington et al., 2006b). This happens, in part, due to the elevated structural diversity of Neotropical dry forest types. Concerning the logistic reasons, we can list: paucity of financial resources for conservation and biodiversity studies, scarcity of studies with standard comparable methodologies, and the enormous logistic challenges of implementing comparative studies

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across a huge geographical range, spanning several countries (e.g. field planning and execution, and collections permits). Herein I will focus on the historical biogeography of three open vegetation biomes, specifically their distributions located eastern and southern of Andes: the Seasonally Dry Tropical Forests (SDTFs), the Cerrado, and the Chaco, which are currently well recognized as natural entities sharing close biogeographic affinities (see next sections).

Some of the biogeographic issues addressed in this manuscript might also concern at least partially other biomes, such as the Pantanal and the Andean dry valleys. However, I selected these three open biomes to conduct the review (SDTFs, Cerrado, and Chaco) as a result of practical and, especially, biogeographic considerations. For example, the Pantanal is a large alluvial plain located at the upper Paraguay River depression in southern central Brazil, northwestern Bolivia, and northern Paraguay (Ab'Saber, 1988; Morrone, 2006). It is characterized by extreme multi-annual flooding cycles, with up to 80% of flooding in area during the wet season (Fernandes et al., 2010). Pantanal is considered a temporary wetland and one of the 13 provinces of the Amazonian subregion (Morrone, 2006), with very particular influences from other humid biomes (e.g. Amazon floodplains). To discuss Pantanal biogeographic relations in deep is then beyond the geographic scope of this manuscript, but for a comprehensive review on Pantanal biogeography and conservation see Junk et al. (2006).

Historical biogeography is currently undergoing a 'Renaissance' due to the molecular genetics revolution in systematics and population genetics (Riddle, 2009; Riddle et al., 2008). Emergent methods based on coalescent theory represents great advances in testing for spatial and temporal congruence, including divergence time estimations (reviewed by Rutschmann, 2006), statistical phylogeography (Nielsen and Beaumont, 2009), multi-locus comparative phylogeography (Hickerson and Meyer, 2008; Lapointe and Rissler, 2005), phylogenetics based on ancient DNA (Ramakrishnan and Hadly, 2009), migration rate estimations (Hey and Nielsen, 2004), past

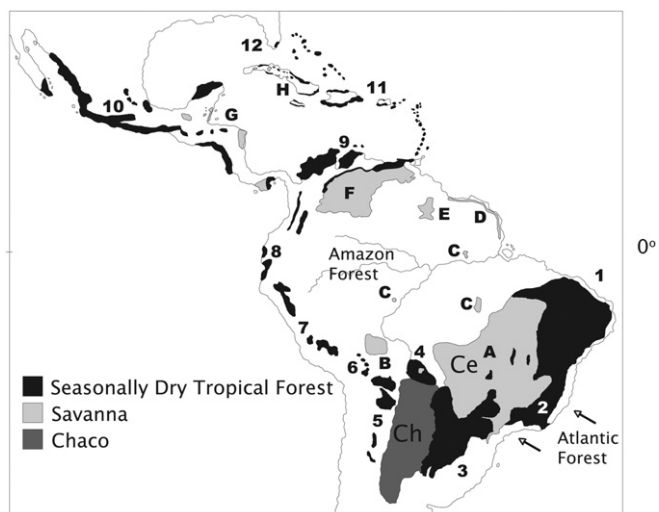
population demography dynamics (Drummond et al., 2005), and phylogeography coupled with GIS-based predictive models, such as distribution modeling (Carstens and Richards, 2007; Hugall et al., 2002; Richards et al., 2007) and landscape genetics (Sork and Waits, 2010). The biogeographic history of Neotropical vegetation is a product of complex interactions between historical and biological processes (Burnham and Graham, 1999), but general flora and fauna patterns are not well established, especially for the open vegetation biomes. Integration of a molecular-based historical biogeographic and phylogeographic perspectives with studies of the South American open biomes diversification will provide some of the data to resolve long-standing and unresolved questions. Such approaches are also likely to reveal previously unknown patterns, including cryptic species and distinct populations of known species, historical refugial areas, concordant range limits, and suture zones (Moritz et al., 2009). These patterns can establish a robust basis for inferring historical processes, species delimitation, and conservation of biodiversity and evolutionary processes of these biomes (Davis et al., 2008; Moritz and Faith, 1998; Riddle et al., 2008).

This paper is part of a major research effort to investigate the evolutionary diversification and to reconstruct the biogeographical relationships among the South American open biomes based on multiple approaches, including: re-evaluation of previously proposed hypotheses, compilation of sparse bibliographic data (including gray literature in different languages), and molecular phylogeographic studies coupled with palaeoclimatic and palaeovegetation modeling. Herein my goals are two-fold. First, to provide future studies with a background of testable hypotheses, I compile and evaluate previously proposed biogeographical hypotheses for the evolution of SDTFs, Cerrado, and Chaco, based on a variety of methods and taxonomic groups (with a main focus on fauna trends). Second, I propose molecular-based biogeographic/phylogeographic approaches that would add strength and robustness in the re-assessment of many previously proposed hypotheses.

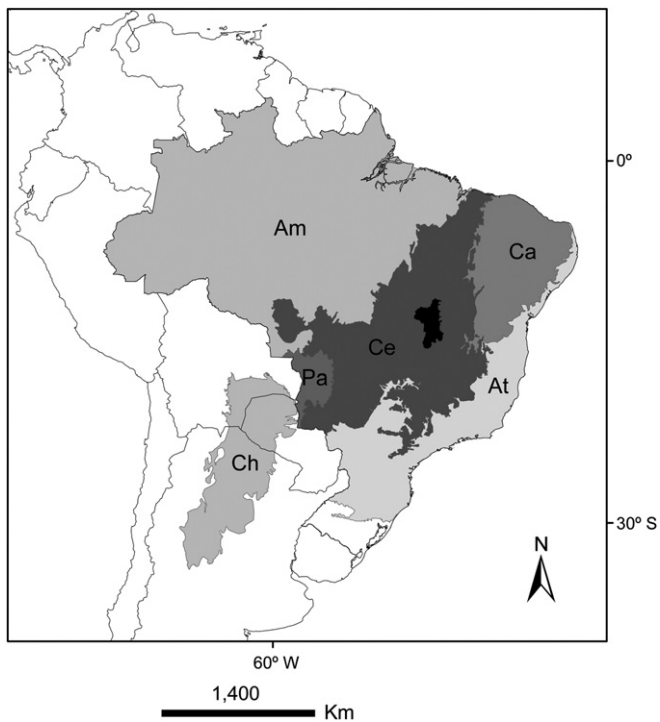
## 2. Regional setting: Tropical/subtropical open biomes of eastern South America general characterization

The Chaco is a open vegetation biome of lowland alluvial plains of central South America located in northern Argentina, western Paraguay, south-eastern Bolivia, and the extreme western edge of Mato Grosso do Sul state in Brazil, covering about 840,000 km<sup>2</sup> (Pennington et al., 2000; Prado, 1993b) (Figs. 1 and 2; Table 1). Like SDTFs and Cerrado, Chaco climate is marked by strong seasonality, but it has more severe summers (maxima up to 48.9° C, the highest temperature recorded for South America) and winter frosts, and is excluded from the definition of SDTFs both floristically and biophysically in terms of climate, soils, and topographic conditions (Pennington et al., 2000; Prado, 1993a). In many instances, the Chaco biome is confounded with the geographical region that contains it, the Gran Chaco that, in fact, includes other kinds of vegetations (as the Paranean semi-deciduous forests and many transitional areas to other biomes; Prado, 1993b). The Gran Chaco extends from tropical latitudes (18° S) to subtropical zones (31° S), and the climate follows gradients that define distinct subregions: Humid Chaco, Dry Chaco, and Montane Chaco (TNC et al., 2005).

Chaco flora is likely a Tertiary (Pliocene) or early Pleistocene relict established over salty soils left after a sea formed by the Andean uplift during the Oligocene withdrew (Iriondo, 1993; Spichiger et al., 2004). Middle–Late Miocene marine incursions covered most of the Chaco-Paraná Basin depression and likely inundated large parts of the Chaco biome, which is evidenced by sedimentology, lithological, and fossil marine animal records in well-documented units, such as the Paranaense Sea in eastern Argentina (Hernández et al., 2005) and Yecua formations in southern Bolivia (Hulka et al., 2006). During



**Fig. 1.** General distribution of rainforests, Seasonally Dry Tropical Forests (SDTFs) and other South American dry vegetation formations. SDTFs: 1. northeast Brazil (Caatinga); 2. southeast Brazilian seasonal forests; 3. Misiones Nucleus; 4. Bolivian Chiquitano region; 5. Piedmont Nucleus; 6. Bolivian inter-Andean valleys; 7. Peruvian and Ecuadorian inter-Andean valleys; 8. Pacific coastal Peru and Ecuador; 9. Caribbean coast of Colombia and Venezuela; 10. Mexico and Central America; 11. Caribbean Islands (small islands colored black are not necessarily covered by SDTFs); 12. Florida. Savannas: (A) Cerrado; (B) Bolivian savannas; (C) Amazonian savannas (smaller areas not represented); (D) coastal (Amapá, Brazil to Guyana); (E) Rio Branco-Rupununi; (F) Llanos; (G) Mexico and Central America; (H) Cuba. Ce: Cerrado, Ch: Chaco. Modified from Pennington et al. (2006b), with permission.



**Fig. 2.** Georeferenced location of Cerrado (Ce), Chaco (Ch), and Caatinga SDFT nucleus (Ca) relative to other biomes (Amazon forest [Am], Atlantic forest [At], and Pantanal [Pa]). In black the Paran River Valley, the major SDFT enclave region within the Cerrado biome in central Brazil.

the Quaternary Interglacial periods, the Chaco may have been more humid than today (Nores, 1992), and may have been adversely affected by rises in sea level (Short, 1975). Currently, it corresponds to an alluvial plain with a nearly horizontal topography maintained by the deposition of Quaternary sediments washed down from the Andes (Prado, 1993a). Both the lowest absolute temperatures and annual rainfall show an E-W gradient; eastern Chaco is warmer and has higher annual rainfall (Norman, 1994; Prado, 1993a). At present, Eastern Chaco is a transitional region, where Cerrado, SDFTs and Chaco interdigitate (Prado, 1993b). Considering its extension and occurrence of different environmental gradients, Chaco vegetation shows a pattern of spatial variability including arboreal and savanna-like communities, with few endemic genera but numerous endemic species (Prado, 1993a). Vegetation assemblages have well-developed grass, Cactaceae, and Bromeliaceae components (Cabrera and Willink, 1973). The Chaco vegetation is determined at the regional level by rainfall (higher rainfall increases species richness and basal area of the arboreal community), and at the local level by degree of soil drainage and possibility of flooding (for a comprehensive Chaco forest classification system see Navarro et al., 2006).

The Cerrado is a savanna biome largely confined to the central Brazil Plateau as a result of climatic, topographic, and edaphic interactions (Oliveira and Marquis, 2002). In addition, Bolivian Beni savannas possibly represent a poorly mapped extension of Cerrado distribution (Larrea-Alcazar et al., 2010; Werneck et al., in review). Covering approximately 2 million km<sup>2</sup>, the Cerrado is the second largest biome in South America (exceeded only by the Amazon rainforest) and, because it is distributed across wide latitudinal and altitudinal gradients, it directly contact many other biomes: Amazon forest to the north, Atlantic forest to the south and southeast, Caatinga to the northeast, and Chaco and Pantanal to the southwest (Motta et al., 2002; Ratter et al., 1997; Silva and Santos, 2005) (Fig. 2). Cerrado enclaves occur within other biomes (e.g.

Amazon rainforest) as relicts from an earlier period when the Cerrado was likely more extensive than today (Cole, 1986; Eiten, 1972). Cerrado geomorphology is characterized by younger and older geomorphic surfaces arranged in a landscape dominated by vast plateaus (locally called *chapadas* or *chapades*) representing the end product of an old cycle of erosion, separated by a network of peripheral depressions of younger valleys (Ab'Saber, 1983; Cole, 1986; Silva, 1997). The final uplift of the plateaus to their current altitudes (500–1700 m) and subsidence of peripheral depressions (100–500 m) took place from Late Tertiary to Early Quaternary (Silva, 1997). Subsequently, recent Quaternary cycles of erosion have progressively expanded the depressions with sediments from the plateau's surfaces, and vegetation establishment is correlated with these geomorphological divisions. Savanna-like vegetation (*campos cerrados*; grassy savannas) are dominant in ancient plateaus, whereas more heterogeneous and recently originated plant communities are found in depressions, including a mosaic of wet grasslands, cerrado vegetation, gallery forests, and patches of deciduous and semi-deciduous forests (Cole, 1986; Silva, 1997). Therefore, within Cerrado, open vegetation biomes are supposedly older than forests. Also, higher and more spatially continuous plateaus (e.g. Central Goias and Guimares Plateaus) are hypothesized to have formed a single large Cerrado refugium during the Late Pleistocene (Ab'Saber, 1983). Conversely, lower plateaus and peripheral depressions were much drier than today and dominated by more xeric-adapted vegetation expanded from the Caatinga or from colder/drier biomes in southern South America, as the Pampa and Monte (Ab'Saber, 1983). Amelioration of the climate towards current conditions allowed the Cerrado to spread from this proposed large refugium, while other vegetation types retracted their distributions within Cerrado to isolated patches with favorable edaphic conditions (derived from limestones), mainly in peripheral depressions (Prado and Gibbs, 1993).

Latosols are the most common soil in Cerrado (called Oxisols in the U.S. system), characterized by low concentrations of exchangeable base cations, acidity, infertility, and by offering little resistance to root penetration (Motta et al., 2002). The physiognomy of Cerrado vegetation is extremely variable, ranging from open grassland (*campos cerrados*) to forests (*cerrado*) with a discontinuous grass layer (usually fire-tolerant), including many vegetation types (grasslands, woodlands, and forests) (e.g. Eiten, 1972; Oliveira and Marquis, 2002). Open physiognomies (determined by well-drained, low-fertility soils) predominate, whereas forests physiognomies (including SDFT enclaves) are restricted to sites with increased water availability and/or soil fertility (Oliveira-Filho and Ratter, 2002). In Cerrado, SDFTs enclaves are particularly frequent on peripheral areas of connection with Caatinga and Chaco and probably function as discontinuous bridges between nuclear regions of SDFTs (Oliveira-Filho and Ratter, 2002).

Climatic conditions in Cerrado (Table 1) would favor the establishment of forests if other factors (e.g. soil fertility and drainage, fire regime) were not considered (Oliveira-Filho and Ratter, 2002). In fact, Cerrado is distributed under similar (or slightly wetter) conditions as SDFTs, but tend to be associated with poorer soils (Table 1). Another marked distinction between Cerrado and SDFTs is the grass component: while SDFTs are tree-dominated, with a minor grass element, Cerrado has an important grass layer, usually fire-tolerant (Table 1) (Pennington et al., 2000).

The Seasonally Dry Tropical Forests occur in tropical regions marked by prominent rainfall seasonality, with several months of severe drought (Mooney et al., 1995). SDFTs are biophysically restricted to soils with high nutrient content and moderate to high pH, in frost-free areas where the highly seasonal rainfall is less than 1600 mm/yr, and with a period of at least five months of drought (Gentry, 1995; Murphy and Lugo, 1986; Pennington et al., 2006b).

**Table 1**  
Comparative characterizations of South American dry biomes of Chaco, Cerrado, and SDTFs.

	Chaco	Cerrado	SDTFs
Distribution	Northern Argentina, western Paraguay and south-eastern Bolivia, and the extreme western edge of Mato Grosso do Sul state in Brazil (Pennington et al., 2000; Prado, 1993b).	Mainly central Brazil, plus small areas in eastern Bolivia and northwestern Paraguay (Oliveira and Marquis, 2002).	Disjunct distribution, from the Caatinga in northeastern Brazil to the Uruguay River valley, with three proposed nuclei regions concentration plant taxa distributions (Prado, 2000).
Geology and geomorphology	Alluvial plain formed by Andean sediments (Prado, 1993a); Chaco is likely a Tertiary or early Pleistocene relict (Spichiger et al., 2004).	Associated with the Brazilian Shield a ancient plateaus with both younger (Pleistocene) and older geomorphic surfaces (three main) in the landscape (Motta et al., 2002); Vast plateaus separated by a network of peripheral depressions (Ab'Sáber, 1983; Silva, 1997).	Very variable: at the Caatinga nucleus a large Proterozoic flattened surface predominate (elevation between 300 and 500 m) (Sampaio, 1995); while the Bolivian SDTF are scattered across small and isolated rain-shadowed Andean dry valleys (Herzog and Kessler, 2002).
Climate	Semi-arid climate, strongly seasonal with severe summers (maxima up to 48.9° C) and occurrence of winter frosts (Prado, 1993a).	Two very well established seasons: dry (April–September) and wet (October–March); and mean annual temperature from 20° C to 28° C (Ab'Sáber, 1983; Nimer, 1989).	Several months of severe (even absolute) drought (Mooney et al., 1995). At the Caatinga the monthly temperatures range from 24 to 26 °C (Sarmiento, 1975).
Precipitation	Seasonal with rainy season from October–April and decreasing East–West precipitation gradient (Prado, 1993a).	Rainfall concentrated to the wet season, and average annual rainfall ranges from 800–2000 mm (Ab'Sáber, 1983; Nimer, 1989).	Highly seasonal with pluviosity less than 1600 mm/yr, and a period of at least 5 months of drought (Gentry, 1995; Murphy and Lugo, 1986). At the Caatinga rainfall is highly erratic and ranges from 240 to 1500 mm, with the interior areas receiving less rainfall (Prado, 2003; Sampaio, 1995).
Soils	Fine alluvial Quaternary sediments; saline soils poor in organic matter (Prado, 1993a; Spichiger et al., 2004).	Acid, dystrophic soils, nutrient poor, with low calcium and magnesium availability, and high concentration of aluminum (Mayle, 2004; Oliveira and Marquis, 2002).	High fertility soils (base-rich) in general (Mayle, 2004; Mooney et al., 1995; Ratter, 1992) with a complex mosaic of soil types at the Caatinga (Sampaio, 1995).
Vegetation	Considerable degree of variability, including a mosaic of xerophytic forests and savannic formations (Prado, 1993a,b).	Characterized by the presence of ancient, highly endemic, xeromorphic, fire-adapted flora, abundant grass layer; trees with sclerophyllous, evergreen leaves (Mooney et al., 1995; Oliveira and Marquis, 2002).	Essentially tree-dominated ecosystems with continuous canopy (Mooney et al., 1995); Drought-deciduous forests and dry plant formations (Sarmiento, 1975). At the Caatinga a mosaic of several local vegetation types coexist with shrubs prevailing in opposition to tree-dominated vegetations (Sampaio, 1995). <i>Anadenathera</i> in association with Bromeliaceae and other taxa (Gosling et al., 2009; Mayle et al., 2004).
Pollen signature/indicator taxa	–	Very high abundance of Poaceae (50–90%) (Burbridge et al., 2004; Gosling et al., 2009); <i>Byrsonima</i> , <i>Didymopanax</i> , <i>Curatella</i> , and <i>Vellozia</i> (Ledru, 2002).	
Net/Total carbon storage	From 65 tons C ha <sup>-1</sup> yr <sup>-1</sup> (primary forest) to 24 tons C ha <sup>-1</sup> yr <sup>-1</sup> (shrubby grassland) (Bonino, 2006).	90 tons C ha <sup>-1</sup> yr <sup>-1</sup> (Adams and Faure, 1998).	260 tons C ha <sup>-1</sup> yr <sup>-1</sup> (Adams and Faure, 1998).
Endemism levels	No numeric estimative, but low endemism reported for birds (Short, 1975) and no bat endemic species (López-González, 2004; Myers and Wetzel, 1983). Conversely, substantial endemism of squamates and amphibian (Gallardo, 1979), and rodents (Myers, 1982; Myers and Wetzel, 1983).	Varies from 3.4% (birds) to 44% (plants) (Klink and Machado, 2005), with recently higher levels reported for lizards (45%) (Nogueira, 2006).	Caatinga: ranging from about 3% (birds) and 7% (mammals) to 34% (plants) and 57% (fishes) (Leal et al., 2005).
Protected areas estimative and representativity	1% of the total Paraguayan Chaco preserved at the 90's (Redford et al., 1990); National parks and reserves cover around 3.5% of Paraguay (the main Chaco country), with 75% of the protected land in the Chaco (Yahnke et al., 1998).	Only 2.2% of the Cerrado area is under strictly legal protection (Klink and Machado, 2005).	Caatinga has only 11 strictly protected areas, representing less than 1% of the region; the smallest protected area of any major Brazilian biome (Leal et al., 2005); 8.9% of the total extent of Bolivian SDTFs is protected at this country, with the Noel Kempff Mercado National Park accounting for approximately 72% of this percentage (Portillo-Quintero and Sánchez-Azoifeifa, 2010).
Major threats to biodiversity	Mechanized agriculture, pasture, secondary succession, infrastructure industry, hunting, and altered fire regime (TNC et al., 2005; Zak et al., 2004).	Mechanized agriculture, conversion for human occupation, invasive African grasses, uncontrolled fire (Klink and Machado, 2005)	Human density, intensive agriculture, conversion for human occupation, replacement of gallery and dry forests by open vegetations (Desertification), charcoal production, timber and cattle ranching (Leal et al., 2005; Miles et al., 2006; Pennington et al., 2006a; Sampaio, 1995).
Major conservation initiatives	No major protected areas in the northwestern Argentinean Chaco, which requires urgent conservation initiatives (Ojeda et al., 2003); creation of the El Chaco Biosphere Reserve UNESCO in 2005 (UNESCO, 2008); Gran Chaco Americano Ecoregional Assessment organized by conservationist non-governmental organizations to evaluate Chaco biodiversity and priority areas for conservation (TNC et al., 2005).	Network of governmental, non-governmental organizations (NGOs), researchers, and private sector; establishment and expansion of protection areas and biodiversity corridors (Klink and Machado, 2005); Brazilian government (MMA) conservation workshops to select priority areas and actions for conservation (MMA, 1999); creation of the Cerrado Biosphere Reserve UNESCO in 1993 and extension in 2001(UNESCO, 2008).	Caatinga: Some protected areas (but low representativity) (Leal et al., 2005); Brazilian government (MMA) conservation workshops to select priority areas and actions for conservation (Silva et al., 2004); creation of the Caatinga Biosphere Reserve Unesco in 2001(UNESCO, 2008).

The vegetation is tree dominated, but can include a variety of formations ranging from tall forests to cactus scrub, and is semi-deciduous or deciduous during the dry season, when more than 50% of the arboreal cover can be completely lost (Murphy and Lugo, 1986; Pennington et al., 2006b) (Tables 1 and 2). It is important to highlight that this broad definition represents an effort to unify the nomenclature and includes many different regional names used in the literature (e.g. tropical and subtropical dry forests, semi-deciduous and deciduous forest, Caatinga, agreste, bosque espinoso, mesophytic forest). Hence, in the definition I adopt here, the Brazilian Caatinga should be interpreted as a SDTF.

The present-day distribution of SDTFs in eastern South America is disjunct, extending from the Caatinga in northeastern Brazil to the Uruguay River valley and with the largest areas [also called Nuclei regions by Prado and Gibbs (1993)] found in northeastern Brazil (the 'Caatingas Nucleus'), along the Paraguay-Paraná rivers system (the 'Misiones Nucleus'), and in southwestern Bolivia and northwestern Argentina (the 'Subandean Piedmont Nucleus') (Prado, 2000) (Fig. 1). Also, significant portions of SDTFs are located along the Caribbean coast of Colombia and Venezuela (Fig. 1; not the primary focus of this paper). Additionally, many smaller isolated areas of SDTFs occur in dry valleys in the Andes in Bolivia, Peru, Ecuador, and Colombia, coastal Ecuador and northern Peru, and scattered throughout the Brazilian Cerrado on areas of favorable edaphic conditions (Ratter et al., 1978; Silva and Bates, 2002) (Fig. 1).

The Caatinga in northeastern Brazil is the largest of the SDTF nuclei. Occurrence of a wetter and cooler climate and an associated humid vegetation had been inferred for the Caatinga region during late Pleistocene and early Holocene, based on a variety of sources: pollen records (De Oliveira et al., 1999), marine pollen content (Behling et al., 2000), paleotemperature record derived from noble gases in ground water (Stute et al., 1995), isotopic composition of carbonate concretions in soil (Dever et al., 1987), palaeobotanical fossils (Wang et al., 2004), and dated fossil bats bones (Czaplewski and Cartelle, 1998). In fact, recurrent pulses of moister climatic regimes with at least 12 pluvial maxima phases were identified in the last 210,000 yr BP (more than the past two glacial cycles), when forests replaced at least partially vegetation similar to present-day Caatinga (Auler et al., 2004; Wang et al., 2004). Conversely, a semi-arid climate similar to current conditions was reported during early Holocene, based on marine core palynological data (Behling et al., 2000). Consequently, although the occurrence of wetter periods and the existence of rainforest migration routes in northeastern Brazil are widely recognized based on independent evidences, the precise timing of forest expansions is still elusive. Present-day rainforest natural enclaves (called *Brejos de altitude*) are supposed to be remnants of this ancient rainforest (likely connecting the Amazon and Atlantic forests) that retracted at the onset of current Caatinga vegetation (Ab'Sáber, 1977; Andrade-Lima, 1982; Bigarella et al., 1975; De Oliveira et al., 1999).

### 3. Open biomes Quaternary climate and vegetation dynamics

South American Quaternary paleoclimates were spatially and temporally complex in both open and forest biomes. Current discussions tend to avoid previous simplistic and dichotomized classifications between arid vs. wet and cold vs. warm climates, and heterogeneous variations in temperature and precipitation/aridity were reported depending on the study region and the time period considered (Werneck et al., 2011). Currently state of knowledge allows summarizing the Quaternary climate at the regions relevant to this review as follows. During the Last Interglacial (LIG, ~130 to 116 thousand years before present, kyr BP) the global surface was warmer than modern climates and any other period within the past 250 kyr BP, apparently about 2 °C warmer globally and up to 5 °C in some Arctic regions (Cape, 2006; Otto-Bliesner et al., 2006). Although the magnitude of cooling is still controversial (from 1 °C to > 5 °C), land surface was in general cooler during the Last Glacial Maximum (LGM; ~21,000 calendar years before present; 21 kyr BP) than modern climates, while precipitation and aridity patterns were more variable across South America (Bush and Silman, 2004; Stute et al., 1995). Independent evidence indicates wetter LGM conditions in portions of Caatinga (Auler et al., 2004; De Oliveira et al., 1999; Wang et al., 2004), in subtropical Botuverá Cave at south-eastern Brazil (Cruz et al., 2005), and in tropical Andes of the Bolivian Altiplano (Baker et al., 2001a, 2001b; but for support for a dry Altiplano during LGM see Placzek et al., 2006), while others report large-scale drying over remaining South America based on palaeodata (Behling and Lichte, 1997; Burbidge et al., 2004; Ledru, 1993) and regional climate modeling (Cook and Vizy, 2006; Vizy and Cook, 2007). Low levels or sedimentation gaps in lakes frequently reported by LGM palaeorecords are thought to reflect such dry climatic conditions and the consequent effects on the vegetation (Ledru et al., 1998). On the other hand, Holocene (~6 kyr BP) evidences are more consistent across studies. Sedimentation rates increased during a humid LGM-Early Holocene transition followed by an extreme dry lower-Holocene/mid-Holocene, when a clear expansion of Cerrado savanna taxa supposedly occurred after 6 kyr BP (Ledru, 2002; Mayle and Beerling, 2004). Drier and more seasonal climatic conditions were also reported during mid-Holocene in Chaco (May et al., 2008). This dry period was followed by increased precipitation towards similar to present-day conditions in Late Holocene, when rainforest taxa expanded to current geographic limits (Mayle and Beerling, 2004; Mayle et al., 2004).

As a consequence of climate and ice volume variations, the Quaternary has been characterized by large-scale changes in sea level, with the LGM identified by the lowest sea level and maximum ice volume (Mix et al., 2001; Sylvestre, 2009). Because of the distinct regional differences in LGM moisture patterns, the extent that these sea levels changes affected continental South

**Table 2**  
Comparative characterization between Seasonally Dry Tropical Forests (SDTFs) and tropical rainforests.

	SDTFs	Amazon	References
Biomass/Net primary productivity	Lower, because growth is restricted to the wet season	Higher	Martínez-Yrizar (1995)
Structure	Lower basal area, smaller stature, and greater abundance of thorny species and vines, with fewer epiphytes and lianas	Higher basal area, higher stature, and more epiphytes	Murphy and Lugo (1986); Gentry (1995)
Plant diversity	Species-rich, but floristically poor when compared with tropical rainforests	Higher	Gentry (1995)
Vertebrate richness	Lower	Higher	Ceballos (1995)
Conservation estimates	Less than 1% of the Caatinga nucleus (northeastern Brazil) in strictly protected areas. 8.9% of Bolivian SDTF areas are protected at Bolivia.	Around 4.9% of Amazon in strictly protected areas and 21% in relatively intact indigenous reserves	Peres (2005); Leal et al. (2005); Portillo-Quintero, and Sánchez-Azoifeifa (2010)

America is not fully described. However, it is expected that the increased continentality (higher thermal variation of continental than marine climates) common during sea level lowstands would have increased seasonal aridity (Carr et al., 2006) and potentially provide feedbacks to climatic variations and their consequences for the biota (Sylvestre, 2009). The same applies for the great marine transgressions that took place at least twice earlier in the Miocene along distinct paleogeographic corridors and covered extensive areas of the South American continent (Hernández et al., 2005).

Vegetation shifts are expected to have occurred as an outcome of these Quaternary climatic and sea-level fluctuations, with some areas experiencing more dramatic changeability than others, even though location and timing of vegetation cycles are not precise. As early as in the 60's, the renowned but controversial 'Neotropical Pleistocene refuge' theory credited the Quaternary cycles as the driving force for speciation (Brown and Ab'Sáber, 1979; Haffer, 1969). Successive expansion and retraction vegetational cycles allegedly occurred, with savannas expanding into the Amazonia region during cold and dry periods, and major Pleistocene connections proposed to occur between savannas blocks located northern and southern of Amazon, by one of the following corridors: (1) Andean corridor, through the eastern Andean slopes; (2) central Amazonian corridor, following a belt of lower precipitation across central Amazon; or (3) the coastal corridor along the eastern Atlantic coast (Sarmiento, 1983; Silva and Bates, 2002; Van der Hammen and Absy, 1994). Some animal disjunct populations inhabiting the northern and central South American savannas have been proposed as evidence for such connections (de Vivo and Carmignotto, 2004; Quijada-Mascareñas et al., 2007). Independent studies indicate that a central Amazonian corridor is unlikely (but for support of this corridor see Quijada-Mascareñas et al., 2007) and the most recent biotic connections between northern Amazon savannas and Cerrado core region were most likely along the Atlantic coast (Ávila-Pires, 1995; Silva and Bates, 2002; Werneck et al., in review). More ancient connections can also be proposed, based on evidence of post-Miocene spread of C<sub>4</sub> grassy biomes world-wide (Edwards et al., 2010) and on Cerrado palaeodistribution modeling results (Werneck et al., in review).

Spatial distribution, species richness, endemism, genetic diversity, and, consequently, biogeography patterns, can be strongly shaped by historical habitat stability (Carnaval and Moritz, 2008; Graham et al., 2006). Palaeodistribution modelling has recently emerged as a methodological alternative capable of producing spatially explicit models of past habitat dynamics of entire landscapes over recent (late Pleistocene) geological time scales (Werneck et al., in review). The occurrence and extent of areas of biome stability (potential refugia) can then be identified by combining current and palaeoclimatic models, which can be cross-validated by independent evidence, as geological, palaeoenvironmental (pollen records), and genetic diversity data (Carnaval et al., 2009; Hugall et al., 2002; Richards et al., 2007). For South American open biomes this 'biodiversity prediction' approach was recently applied for SDTFs (Werneck et al., 2011) and Cerrado (Werneck et al., in review), with refugia predictions that were validated by palaeoenvironmental and will be tested by upcoming genetic studies. Under the 'historic climate' stability model, historically stable areas are expected to have higher persistence of population sizes through climatic fluctuations, which should permit more species to arise and persist in a more stable vegetation cover, resulting in high species diversity and endemism (Graham et al., 2006) and elevate intra-specific genetic diversity (Carnaval et al., 2009; Carnaval and Moritz, 2008; Hewitt, 2004). On the other hand, historically unstable regions are expected to be colonized more recently and, consequently, retain genetic signatures of population expansions, have lower species diversity and endemism, and display

lower levels of intra-specific genetic diversity when compared to stable areas.

#### 4. South American open vegetation biomes conservation status

Despite often characterized as less rich than tropical rainforests, South America open biomes have high levels of endemism and are very important to understand biogeographic patterns at the continental scale, and are therefore worthy of more focused research and conservation efforts (Mares, 1992; Redford et al., 1990). In fact, higher richness levels reported for the Amazon may be merely an area effect, as this rainforest occupies around twice the area occupied by other open biomes, such as the Cerrado (Colli et al., 2002). When taken as a whole (including other open formations in addition to the three here considered), the South American open biomes collectively occupy a greater area than the Amazon, and harbor the richest mammal fauna of the continent, with the Amazon supporting fewer taxa and endemisms (Mares, 1992). Moreover, other comparisons between SDTFs and rainforest (e.g. plant diversity, structure, and productivity) are extensive in the literature (Table 2). These quantitative comparisons are not extendable to the fauna though, which is usually just referred as having lower richness in SDTFs when compared to Amazon rainforest (Ceballos, 1995).

With distinct proclamation dates, Cerrado, Caatinga, and many Chaco areas in Paraguay, Bolivia and Argentina are all recognized as Biosphere Reserves (UNESCO, 2008) (Table 1). Governmental and non-governmental regional assessments, based mostly on diversity and distributional patterns of plant and animals, showed that the conservation status of these biomes requires awareness (MMA, 1999; Silva et al., 2004; TNC et al., 2005) (See Table 1 for major threats and conservation initiatives). Estimates of strictly protected areas of these biomes vary from less than 1% up to 2.2% (Table 1). All three present high levels of diversity and are highly endangered, due to high rates of deforestation and habitat fragmentation as a result of mechanized agriculture (Klink and Machado, 2005; Leal et al., 2005; TNC et al., 2005). Based on its diversity, high levels of endemism, and elevated human threats, the Cerrado is considered, together with other 34 ecosystems, a global biodiversity 'hotspot' and the most diverse tropical savanna in the world (Myers, 2003). Recent estimates based in satellite images from 2002 showed that approximately 55% of its original vegetation have been already converted by human action, with annual deforestation rates higher than those reported for the Amazon (Machado et al., 2004). Similarly, SDTFs are among the most threatened tropical ecosystems (Prance, 2006), with the greatest annual destruction rate (Whitmore, 1997). From a threatened birds perspective, protected areas were specifically underrepresented in SDTFs (Beissinger et al., 1996). Recently, Portillo-Quintero and Sánchez-Azoifeifa (2010) estimated that Bolivia and Brazil are the South American countries with largest percentage of protected areas of tropical dry forests (using a slightly larger spatial definition than the adopted here), the largest protect area located in the Chiquitano region and protected by a single park (Noel Kempff Mercado National Park; Table 1). On a regional perspective, between 30.4% and 51.7% of the Caatinga has been altered by human activities, which conservatively rank this biome as the third most heavily impacted in Brazil (Leal et al., 2005). Due to elevated deforestation rates and restricted distribution, SDTFs can be considered the most endangered biome in Brazil (Espírito-Santo et al., 2009). On a global basis, Latin American SDTFs experienced the greatest deforestation rates (12% between 1980 and 2000) and virtually all-remaining areas are at risk of disappearance, highlighting their urgent priority for conservation (Miles et al., 2006). Initial estimates revealed roughly

45% of selective or intensive degradation for the Paraguayan Chaco, with protected areas covering only about 1% of the total area (Redford et al., 1990). More recently, satellite images from 1969 to 1999 showed a drastic change in the land cover of the Argentinean Chaco, with 85% of the original vegetation converted to agriculture, pasture, or secondary succession lands (Zak et al., 2004). However, Chaco conservation initiatives are incipient, with a general absence of major protected areas (Ojeda et al., 2003). Regardless of such threats, the biodiversity of these open vegetation biomes has been overlooked in conservation projects in South America, which may explain why all are poorly represented in local protected areas (Klink and Machado, 2005; Ojeda et al., 2003; Prance, 2006) (Table 1). Integrated evaluations for conservation purposes remain to be done, and inter-biome biogeographic patterns have not specifically been addressed on the basis of fauna data.

In the following section I provide a critical review of published studies addressing the biogeography of SDTFs, Cerrado, and Chaco, at both inter- and intra-biome levels. Selection of studies was based on their attempts to address the origin and diversification of these biomes and the associated native biota. Studies with a strictly ecological focus (for example, investigating local associations between diversity and ecological or climatic parameters), human genetics, infective diseases or invasive species were excluded. Further, studies describing only levels of genetic diversity without any historical biogeographic implications were not included. Even though my main focus is on the evolution of open biome faunas, I recognize that zoogeographical subdivisions tend to be coarser than phytogeographical subdivisions, due to higher vagility and lower direct influence of many environmental variables on animals compared to plants. Accordingly, plant biogeographic studies may provide many relevant insights for the evolution of animal communities, and I also considered the most pertinent literature regarding phytogeography. My objective is not an exhaustive survey of all literature, but to provide the reader with a good general picture to guide future studies using novel approaches (such as molecular phylogeography, biogeography, ecological niche modeling, etc) to test those hypotheses. The studies reviewed here implement distinct methodologies and criteria to delimit areas, but all have in common the search for natural historical entities for South American open biomes.

## 5. Biogeography of South American open biomes: status of the field

Information regarding the spatial distribution of any biota and its biogeographical relationships constitutes the base for biodiversity conservation planning (Margules and Pressey, 2000; Whittaker et al., 2005). Regarding South American open biomes biogeography, integrated data are still sparse when compared to tropical forest biomes. In face of this major knowledge gap, a number of studies have previously proposed within-biome biogeographic hypotheses, but fewer have addressed the inter-biome relationships (Appendix I).

The first attempts to study the zoogeography of South American open biomes drew conclusions that many researchers now challenge. An early misleading notion was that Caatinga (usually the only SDTF area considered), Cerrado, and Chaco had low diversity levels and depauperate faunas, lack unique species (endemics), and were all part of a single 'savanna corridor' (Schmidt and Inger, 1951) or a 'diagonal of open formations' (Vanzolini, 1963), extending from southwestern to northeastern South America. This was suggested for several animals groups: lizards (Vanzolini, 1974, 1976; Vitt, 1991), mammals (Mares et al., 1985), birds (Short, 1975; Sick, 1965), and Lepidoptera (Camargo and Becker, 1999). Taking lizards as an example, initial assessments concluded that the Cerrado fauna was

impoverished (Vitt, 1991), whereas more recent studies have confirmed that the Cerrado local diversity is much greater, even comparable to Amazonian levels, with a high proportion of endemics (Colli et al., 2002; Nogueira et al., 2009, in press). Vanzolini et al. (1980) listed 47 species of reptiles in the Caatinga with a single endemic, the lizard *Tropidurus semitaeniatus*, while at least 97 species of reptiles are currently known in Caatinga, with many endemics (even at the generic level), mostly associated with sand formations (e.g. Quaternary sand dunes of the middle Rio São Francisco; Rodrigues, 1996, 2003). Cerrado bird richness estimates have jumped from 245 (Sick, 1965) to 856, with 30 endemic species (Silva and Santos, 2005), representing roughly 50% of the total Brazilian avifauna (Macedo, 2002). Mares et al. (1985) considered that the Caatinga supported one of the poorest mammal faunas in the tropics, an idea not supported by recent studies, which have revealed higher mammal diversities even though endemism levels remain low (Oliveira et al., 2003). Hence, in general, the current levels of faunal richness and endemism are several times higher than those from early assessments, and are potentially even greater because several recently discovered species still await descriptions and large areas of these biomes have never been adequately surveyed (Colli et al., 2002; Leal et al., 2005).

The identity of these biomes was recognized early by phytogeographical assessments on a continental scale (Cabrera and Willink, 1973; Rizzini, 1979), as well as their importance as Neotropical centers of faunal endemism (Muller, 1973), and they started to be treated as single entities in subsequent zoogeographical assessments (Cracraft, 1985; Haffer, 1985; Muller, 1973). Muller (1973) proposed a zoogeographical division of the Neotropical region based on dispersal centers of vertebrates. His assessment of subspecies ranges and lack of comprehensive biodiversity studies at that time likely inflated the suggested endemism levels supporting the centers. Still, he recovered the uniqueness and independence of the three biomes here considered (Caatinga/SDTFs, Cerrado and Chaco), and suggested a close biogeographic relationship between them. A relevant probable scenario also suggested is that climate changes caused fluctuations in the range between the Cerrado and Caatinga centers on one hand, and the Chaco center on the other, contributing to the intermixture of some species ranges that are widely distributed in these biomes (Muller, 1973). This might be a potential challenge for studies dealing with genetic diversity levels, because the multiple evolutionary patterns experienced by these open vegetations may have produced genetic footprints that are particularly hard to detect, especially for species with extensive geographic distributions prone to high levels of migration, gene flow, and secondary contacts among distinct biomes (Manfrin and Sene, 2006; Moraes et al., 2009; Werneck et al., in prep.).

In a comprehensive descriptive historical biogeographic scheme of Latin America and the Caribbean regions, Morrone (2001) grouped the South American open biomes (there called provinces) of Caatinga, Cerrado, Chaco, Pampa, and Monte into the Chacoan subregion of the Neotropical region. According to Morrone (2000), the Chacoan subregion extends from northern and central Argentina, southern Bolivia, through western and central Paraguay, and across central-northeastern central Brazil. Under this definition, the Chacoan subregion corresponds to the 'savanna corridor' of Schmidt and Inger (1951) and the 'diagonal of open formations' of Vanzolini (1963), both revised by Prado and Gibbs (1993). The individual 'tracks' used to define the Chacoan subregion are the plant taxa *Enterolobium contortisiliquum*, *Astronium urundeuva* and *Aramigus* (Morrone, 2001). Panbiogeography is one of the historical biogeography approaches that have received harsher criticism (Myers and Giller, 1988). However, Morrone (2001) study is an elegant summary of the Neartic, Neotropical and Andean biotas and his proposed major groupings for the open biomes can be considered coherent, such as the close

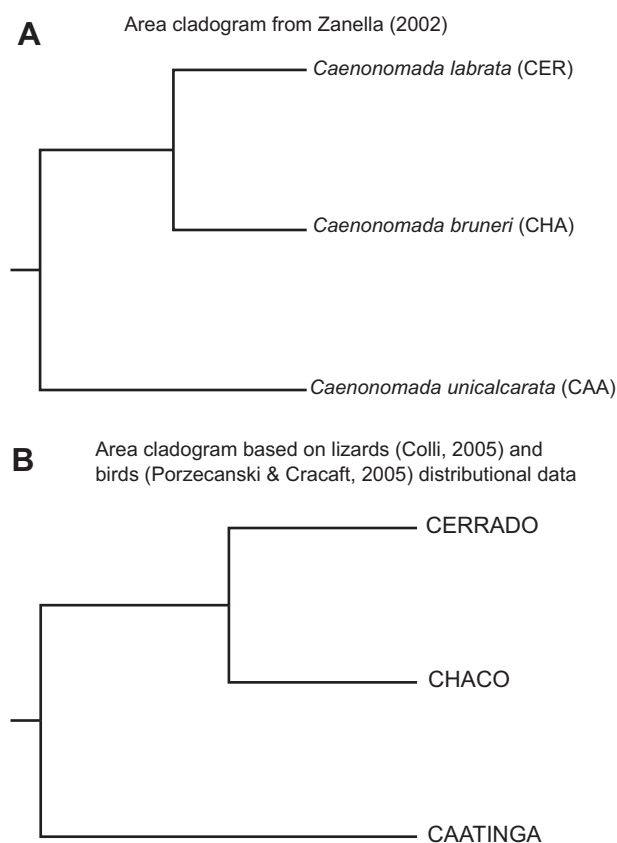


relationships between Caatinga, Cerrado, and Chaco previously recognized (Cabrera and Willink, 1973; Muller, 1973).

After the uniqueness of these biomes became established in the literature, research efforts focused in sampling new areas and describing their levels of diversity, which was still underestimated. Because of the huge knowledge gap and the scarcity of personnel, research groups become established in a disconnected way. Currently the knowledge concerning the high levels of diversity and endemism is well established, but their biogeographic relationships are still open to debate. Even though the ideas that the 'great diagonal' might not be a natural grouping (Colli, 2005), and that a close relationship exists between SDTFs (usually represented by only the Caatinga), Cerrado, and Chaco are widely accepted (Morrone, 2001; Muller, 1973; Prado and Gibbs, 1993), more refined evaluations are still needed.

Following trends from phytogeographic studies (Ab'Sáber, 1977; Andrade-Lima, 1982), faunistic links were proposed between Caatinga and Chaco, the extremes of the 'diagonal of open vegetations' (Haffer, 1985; Vanzolini, 1974). Morphological and plumage trait analyses indicate considerable geographic variation in the bird *Suiriri suiriri*, with some hybridization events between subspecies, and higher shared similarity between Chaco and Caatinga subspecies (Hayes, 2001). However, genetic studies are needed to further elucidate the evolutionary history of this open biome bird species. Nevertheless, these links were later demonstrated to be negligible, and another distributional pattern between the Caatinga and two other disjunct nodal areas of seasonally semi-deciduous and deciduous forests across South America (Misiones and Piedmont Nuclei; see introduction for their distributions) became apparent (Prado and Gibbs, 1993). The current fragmentary distribution of SDTF nuclei supposedly represent vestiges resulting from a former extensive uninterrupted formation present during a dry-cool period in the Late Pleistocene (about 21–18 kyr BP), coincident with the contraction of humid forests (Prado and Gibbs, 1993). This 'Pleistocene Arc of SDTF' hypothesis will be discussed in more detail later, but for now it is enough to say that this hypothesis contradicted the leading biogeographical thinking at the time by suggesting that the Caatinga-Chaco link is wrong. Prado and Gibbs (1993) proposed instead that the Chaco is derived from dry vegetation formations from the southern extreme of South America and that another neglected biogeographical pattern with main consequences for the debate of South America biota evolution should be urgently considered in upcoming studies.

Although sporadic, closer relationships between Cerrado and Chaco were also proposed more recently on the basis of faunal data (Appendix I). Zanella (2002) used morphological phylogeny of *Caenomada* spp. bees, whose species are endemic to the same open vegetations here considered, to derive an area cladogram suggesting that Cerrado is more closely related to Chaco, with Caatinga occupying a more basal position (Fig. 3). A Parsimony Analysis of Endemicity (PAE) based on lizard distributional data for the Cerrado and other South American biomes corroborate a main basal split between mesic forest and open biomes, and also suggested that the Cerrado herpetofauna shared a more recent history with Chaco than with other open biomes (Colli, 2005). Concordantly, based on a similar but modified approach (Cladistic Analysis of Distributions and Endemism, CADE), Porzecanski and Cracraft (2005) predicted that among South American arid land birds, the Cerrado and Chaco species will be more closely related to each other than to Caatinga species (Fig. 3). Humid forest corridors connecting Amazon and Atlantic forests and conversely segregating Caatinga from Cerrado + Chaco (Andrade-Lima, 1982; Bigarella et al., 1975; Costa, 2003; Oliveira-Filho and Ratter, 1995), the uplift of the Brazilian Plateau along the Espinhaço Range, Serra do Mar and Mantiqueira (Late Pliocene-Early Pleistocene, 2–4 millions



**Fig. 3.** Historical biogeography relations between dry biomes proposed based on fauna groups. A) Zanella (2002); B) Colli (2005) and Porzecanski and Cracraft (2005). Other biomes considered by the analyses in B were here omitted.

years ago, MYA), and the subsidence of the Chaco and Pantanal due to the Andean uplift (Colli, 2005; Porzecanski and Cracraft, 2005) can be cited as possible vicariant events accounting for the Cerrado and Chaco grouping. However, simple area cladograms, PAE, and CADE are methods that do not consider important historical events (e.g. extinctions and/or dispersal) and can clearly fail to detect historical complexity. Results of both analyses can reflect just patterns of ecological similarities among localities instead of historical patterns, and should be interpreted with caution (Brooks and van Veller, 2003). Thus, the closer relationships between Cerrado and Chaco faunas should be interpreted as a preliminary hypothesis that needs to be specifically addressed by molecular phylogenetic/phylogeographic methods. In this context, genealogical topologies and coalescent methods that can estimate divergence times and migration rates in widely distributed species (or species complexes), provides an independent test of whether the closer relations between Cerrado and Chaco reflect just a higher number of shared species or actually a shared history.

Indeed, very few studies used molecular approaches to address the tropical/sub-tropical South American open biomes historical biogeography and phylogeography. Complex patterns of genetic diversification at both supra-specific (Almeida et al., 2007) and intra-specific levels (Moraes et al., 2009; Werneck et al., in prep.) have been reported. Almeida et al. (2007) proposed that the vanishing refuge model (Vanzolini and Williams, 1981) explains the diversification of *Calomys* rodents, by parapatric speciation across open vegetation ecotones and consequent shifts from open savanna to dry forest or forest-savanna habitats. Main demographic events reported for *Drosophila gouveai* showed signatures of rapid range

expansion from northeastern (ancestral populations) to southern populations and diversification that pre-date the LGM (Moraes et al., 2009). However, molecular dating credibility intervals were still within Pleistocene (ranging from 24 to 565 ka) and were considered consistent with changes in the distribution of dry vegetation in eastern Brazil during middle Pleistocene (Moraes et al., 2009). Advanced methods of molecular data analysis, including phylogeographic perspectives based on coalescent theory and on multiple, independent molecular markers (not only mitochondrial, but also nuclear, generally lacking in datasets from the Neotropical region) should be able to reveal complex evolutionary histories with high levels of migration, gene flow, and secondary contacts among populations from distinct biomes (Avice, 2009; Werneck et al., in prep.).

### 5.1. Biogeography of Chaco

The Chaco corresponds to a distinct biogeographic unit with a complex biota representing elements from many other biomes (Morrone, 2001; Morrone et al., 2004). Two main assemblages representing well-defined and stable plant compositions frequently characterize the Chaco: the dry (Chaco Seco) and the wet divisions (Chaco Húmedo) (Spichiger et al., 2004, 1995). Recently, an ecoregional assessment led by non-governmental organizations (NGOs) represented the first efforts to propose Chaco areas of significant biodiversity importance, based on a multi-taxa approach (TNC et al., 2005). The results are still too coarse, with 38 priority areas for biodiversity conservation selected, but represent a very important first step, including the first regional scale map of the terrestrial communities of the Gran Chaco (TNC et al., 2005).

Chaco biogeography is often studied in the broader context of the Paraguay-Paraná Basin, mainly located in Paraguay and also including the campos Cerrados and the Paranean semi-deciduous forests of the SDTF Misiones Nucleus (Spichiger et al., 2006, 2004) (Fig. 1). Indeed, much of Paraguay is a huge ecotone region characterized by intermingling open vegetation formations, with climatic and edaphic gradients determining shifts from semi-deciduous forests in the southeast to Chaco vegetation in the northwest, separated by the Paraguay River in the centre (Spichiger et al., 2006, 2004). Mammalian (López-González, 2004; Myers, 1982; Willig et al., 2000) and avian (Short, 1975) zoogeographic studies corroborate this sharp boundary, with western (mesic) and eastern (xeric) distinct faunal compositions coincident with vegetation, geology, and soils patterns delimited by the Paraguay River. In this model, the two regions delimited by the Paraguay River would have very different soil compositions, and the salty and arid Chaco soil could act as a limiting barrier for many organisms, restricting dispersal and maintaining distinct biotas on each side of the river. However, no study has investigated such evolutionary patterns based on evidence other than species occurrence and community composition, and a molecular biogeographic approach is warranted to test these models. An ideal phylogeographic experimental design would consist of comparing conspecific populations in taxonomic groups with different dispersal capacities (such as birds, bats, lizards) occurring on both sides of the river; this design would test for presence of population structure and the extent of gene flow between these populations. Additional support could come from the occurrence of sister-taxa pairs isolated at the two margins of the river.

The character of the Chaco fauna is often described as widely distributed over other South American regions, with moderate diversity and endemism levels, as a consequence of its central location and accessibility (Myers and Wetzel, 1983; Short, 1975; Willig et al., 2000). Avian endemism is considered low in Chaco, with most bird species able to cross extensive unfavorable areas

(Nores, 1992). Moreover, because of its interface between tropical and temperate regions, it is considered a northern extension of a temperate dry formation (Monte) (Pennington et al., 2004), based on some proposed floristic and faunistic links between the Chaco and Monte formations (Cabrera and Willink, 1973; Ojeda et al., 2003; Roig et al., 2009). However, no molecular phylogeographic studies have yet focused on explicitly testing hypotheses of Chaco biogeography.

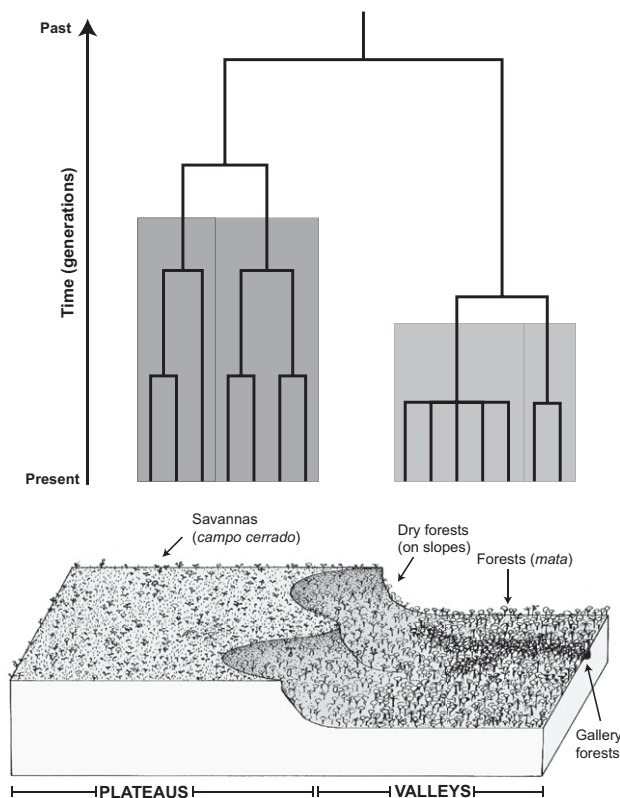
### 5.2. Biogeography of Cerrado

In the last century, studies on Cerrado debated its origin as anthropogenic (formed by human fire regime) or natural (Salgado-Labouriau, 2005). The oldest Cerrado pollen records and charcoal particles (indicative of fire) date to about 32 kyr BP (Ledru, 2002; Salgado-Labouriau, 1997), which is older than the oldest confirmed human presence in South America (Cooke, 1998), and supports the view of a natural origin of Cerrado. In fact, Cerrado may be of great age, possible a Cretaceous formation, primitively present before the final separation of the South American and African continents (Ratter et al., 1997). A more conservative view favors an Eocene origin for Cerrado (Romero, 1993), which would still pre-date human habitation by millions of years. Nonetheless, palaeoenvironmental data resembling present-day Cerrado vegetation occurs only 7 kyr BP in central Brazil and 10 kyr BP in northern Brazil, indicating the highly dynamic nature of this biome in face of Quaternary climatic fluctuations (Ledru et al., 2006; Ledru, 2002).

The complex biogeographic history and high biodiversity levels of the Cerrado are believed to result from a combination of biome age and dynamic Quaternary palaeoclimatic fluctuations (Cole, 1986; Oliveira-Filho and Ratter, 2002). As a consequence, Cerrado's biota has experienced a long and dynamic evolutionary history (Colli, 2005; Silva, 1997), which likely produced marked biodiversity trends and genetic footprints. Some general biogeographic patterns described for the fauna often emphasize the importance of Cerrado's geomorphological surfaces and marked horizontal habitat stratification, responsible for a complex mosaic-like landscape that can promote and maintain diversity despite its vertical simplicity (Colli et al., 2002).

Phylogenetic and phylogeographic assessments taking into account the geomorphological compartmentalization of the Cerrado landscape (described in the general characterization section) are expected to reveal reciprocally monophyletic groups of species associated to savanna-like (*campos cerrados*) and to forest (gallery and dry forests) formations (Fig. 4). At the same time, phylogenetic structure of open vegetation species groups associated with the more ancient plateaus are expected to be characterized by high genealogical structure and genetic diversity, consistent with their older diversification ages. On the other hand, species groups associated with forests located at the younger depressions should have shallower branches and less resolution, many times represented by 'star-like' genealogies and long terminal branches with accumulated mutations, representing more recent expansion scenarios (Excoffier, 2004) (Fig. 4). Other approaches can also investigate signals of recent expansion expected for Cerrado valleys, such as: mismatch distributions (number of mutation differences between pair of genes, expected to be unimodal under this scenario), Hs tests, and Bayesian Skyline Plots (able to estimate posterior distribution of effective population sizes through time) (Drummond et al., 2005; Excoffier, 2004).

The forest formations (e.g. gallery forests, SDTF enclaves) in the Cerrado mosaic landscape are frequently considered especially important for the overall diversity levels and for the community's origin (Redford and Fonseca, 1986; Rodrigues, 2005; Silva, 1996; Werneck and Colli, 2006). In these models, the elevated regional



**Fig. 4.** Diagrammatic representation of the geomorphological compartmentalization of Cerrado landscape between ancient plateaus (dominated by savanna-like vegetation) and younger valleys (dominated by more heterogeneous forests assemblages). On top are displayed the corresponding diversification expectations in terms of phylogenetic and phylogeographic diversity and structure, namely: reciprocal monophyly of plateaus and valleys species groups; older diversification ages, higher genealogical structure and genetic diversity levels of plateaus species groups when compared to groups associated with valleys. Top left: a generic time axis. Geomorphology artwork by Pedro Aquino De Podestà.

diversity and historical formation were mainly determined by an intensive biotic interchange through dispersal corridors from the adjacent major forest regions (Amazon and Atlantic forests) during the Quaternary climatic-vegetational fluctuations (Silva, 1995). Gallery forests are believed to have maintained the connectivity between the central Brazil Plateau and adjacent forests even during the least favorable climatic periods, providing refuge to a stable forest biota (Brown and Gifford, 2002). In opposition, Amazon and Atlantic forests diversity levels have a higher contribution of *in situ* speciation and most (72%) of the Cerrado avifauna is partially or totally dependent upon forests (gallery forests or SDF enclaves) for maintenance of viable populations (Silva and Santos, 2005). This is particularly true for some vertebrate groups with higher mobility and remarkably low endemism levels at Cerrado, as birds (Silva, 1996; Silva and Santos, 2005) and mammals (Johnson et al., 1999; Marinho-Filho et al., 2002; Redford and Fonseca, 1986), with dry forests and gallery forests identified as key habitats, respectively.

Considering data on invertebrate groups, very few Cerrado Lepidoptera species show affinities with Caatinga and Chaco, with the primary links reported to the Atlantic forest to the southeast followed by the Amazonian forests to the northwest (Brown and Gifford, 2002). Again a major role is attributed to gallery forests as refuges to a stable forest biota during the least favorable climatic periods (Brown and Gifford, 2002). Also, bees of the lineage *Paratetrapedia* (with six species endemic to the Cerrado biome) have

closer relationships with Atlantic and Amazon forest species (Aguar and Melo, 2007) in opposition to sister-group relationships with Chaco and Caatinga species as described for other bees species (Zanella, 2002).

Alternatively, Rodrigues (2005) recently proposed a new model for the role of gallery forests in the evolution of Cerrado and Amazon fauna during Quaternary climatic fluctuations (here translated as: Cerrado's Gallery forest modulated speciation). The model is based on the assumption that gallery forests do not constitute an impenetrable barrier for most faunal groups adapted to the open Cerrado formations (but for an alternative view see Nogueira et al., 2009), which can tolerate and frequently visit gallery forests (Rodrigues, 2005). As a result, during humid periods characterized by forest expansion, the expanding humid forests would capture Cerrado open vegetation species. Such capture could be followed by isolation from the Cerrado and subsequent speciation in a way that the gallery forests played an asymmetric role contributing with more species to the rainforests than to the Cerrado (Rodrigues, 2005). In other words, in this model the Cerrado asymmetrically contributes more species to humid forests, enhancing their diversity, rather than the typically assumed reverse scenario. Disjunct distributions of typical open habitat Cerrado species in forested areas in the core of the Amazon forest (some examples: the lizards *Colobosaura modesta* and *Cercosaura* spp.) are cited as evidence supporting this hypothesis (Rodrigues, 2005). Molecular studies addressing deep phylogenetic relations of genera with species distributed in both Cerrado and Amazon could provide tests of this hypothesis. Paraphyletic forest groups indicating multiple and recurring humid forest invasions from Cerrado counterparts would provide additional support for such model, with some lizard groups suggested for such study: *Coleodactylus* geckos, *Mabuya* skinks, *Kentropyx* teiids, *Colobosaura* and *Cercosaura* gymnophthalmids (M.T. Rodrigues, personal communication; Rodrigues, 2005). However, *Kentropyx* phylogeny recovered a monophyletic forest group, which does not corroborate the "asymmetry" hypothesis (Werneck et al., 2009b).

In disagreement with patterns reported for Cerrado mammals and birds (see above), small-bodied, low vagility Cerrado faunal groups (e.g. lizards) could have been less affected by Quaternary climatic fluctuations, presenting higher richness and higher number of endemics associated to open habitats in elevated plateaus in opposition to gallery forests in interplateaus depressions, with few species shared between these major habitats (Nogueira et al., 2009). High extinction rates of habitat specialists previously reported for impoverished peripheral Cerrado isolates (Gainsbury and Colli, 2003) can partially account for lower lizard richness in gallery forests, which are also scattered within a matrix of open habitats. A recent study on the small mammal fauna suggests a concordant pattern with lizards; higher richness and endemism associated with open habitats, challenging the previous trends recorded for the large mammals (Carmignotto, 2004). In summary, despite clearly contributing to the overall levels of fauna diversity, the relative role of gallery forests for the origin and diversification of Cerrado animal communities is not uniform, with higher importance for some groups (birds, large mammals, and possibly some invertebrates) than for others (lizards and small mammals). An interesting comparative molecular phylogeographic study would sample broadly distributed species with occurrence in both Cerrado and other forest biomes (e.g. Amazon and Atlantic Forests) to test for the relative role of gallery forests. If the role as a dispersal corridor from adjacent forest biomes was significant, we would expect populations from Cerrado mosaic-rich areas (with forests in addition to open formations) to have higher gene flow levels and genealogical similarity (e.g. stronger topological associations and similar branching structure) with populations from

other biomes, when compared with populations from more homogeneous Cerrado areas.

Further zoogeographical trends were specifically described for birds, one of the best-known taxonomic groups for the Cerrado (Silva and Santos, 2005). For example, connections between central Brazil Cerrado and northern South America savannas through eastern borders and 'coastal corridors' in opposition to a corridor in the center of the Amazon, have been proposed (Silva, 1995). Preliminary analyses detected low levels of genetic divergence between birds occupying the extremes of the Cerrado range (Amapá savannas and eastern Bolivia), and were interpreted as evidence of a historically limited Cerrado distribution, followed by a recent expansion to the northern Cerrados (Amapá) from the core area at central Brazil through the 'coastal corridor' (Bates et al., 2003). However, this early study was based on limited sampling and used only summary statistics to describe genetic divergence, which lack statistical power and do not incorporate coalescent processes (Kuhner, 2009; Pearse et al., 2004). Analyses specifically developed to detect genetic signatures of population expansion (e.g. Hs tests, Bayesian Skyline Plots) can be employed in future studies aiming to further investigate such expansions through the 'coastal corridor'. To test the hypotheses that within-Cerrado open vegetation formations are older than forests (Cole, 1986), Silva (1997) classified the Cerrado endemic birds in two major groups according to their phylogenetic placement and estimated evolutionary age: *palaeoendemics* (monotypic, taxonomically isolated species or clades, with obscure phylogenetic relationships or basal to a larger radiation including other members occurring in the Cerrado fauna); vs. *neoendemics* (species with sister-taxa in other South American biomes) (Silva, 1997). He concluded that the majority of palaeoendemics species are non-forest, while most of the neoendemics are forest birds, supporting Cole's hypothesis (Cole, 1986). However, the estimated evolutionary age adopted by Silva (1997) to classify the endemic species represented only a relative measure (neoendemics not older than the Plio-Pleistocene transition [2–3 MYA], and palaeoendemics older than this period), without the implementation of any strictly molecular dating approach. As a consequence, the call for a rigorous evaluation of this classification based on molecular and/or paleontological studies recognized by the author is still needed. Multi-locus studies estimating divergence times by preferably adopting methods that incorporate rate heterogeneity (Rutschmann, 2006) would be required to address this hypothesis.

The importance of recent Quaternary events and of the 'Pleistocene Refuge Hypothesis' on the diversification of the South American biota has been clearly overestimated (Colli, 2005; Hoorn et al., 2010). Colli (2005) argues that many older Tertiary historical events may have had more profound influences on the diversification of the Cerrado herpetofauna in particular and on other south American fauna groups in general. Main Tertiary vicariant events listed as promoting herpetofauna diversification include: the formation of a latitudinal temperature gradient (Early Tertiary, ~60 MYA); the vegetation compartmentalization between paleofloras (Paleocene–Eocene transition, ~55 MYA); the great Miocene marine transgression separating Central Brazilian Plateaus from the meridional portion of the continent (Miocene, ~15 MYA); the arrival of immigrants from Central and North America both through marine dispersals and after the closure of the Panama Isthmus (during the Miocene ~15 MYA and Pliocene ~3 MYA, respectively); and the final uplift of the Central Brazilian Plateau (Late Miocene–Early Pliocene transition, ~5 MYA), that promoted additional compartmentalization of the Cerrado landscape between plateaus and peripheral depressions (Colli, 2005). This last stage was a major determinant in the final differentiation of the Cerrado biota in relation to the adjacent open biomes, Caatinga and Chaco Family

(Giugliano et al., 2007), genus (Werneck et al., 2009b), and species group (Maciel et al., 2010) level phylogenies corroborate the importance of such ancient events for the diversification of South American lizard and frog faunas, but the extent that such events might be determinant for the biogeographical diversification of other taxonomic groups is still pending investigation.

There is no complete agreement about main endemism areas for the Cerrado, but some congruent area relationships were proposed based on distributional data of distinct taxonomic groups (Appendix I). Cerrado endemic birds are distributed across four main endemism areas, where they have originated by geographical isolation and afterwards maintained their ranges: Espinhaço Plateau ('campo rupestres' Chapada Diamantina vegetation), Central Goiás Plateau (gallery forests), Araguaia River Valley (gallery forests), and Paranã River Valley (tropical dry forest enclaves) (Silva, 1997; Silva and Bates, 2002). The 'Araguaia endemic center', a region characterized by campo cerrado and forests mosaics within a complex soil matrix with relative geomorphological stability, is also congruently recovered from Lepidoptera distributional patterns (for subspecies of Heliconiini and Ithomiinae Brown and Gifford, 2002). According to a Parsimony Analysis of Endemicity (PAE; see criticisms of this method in previous section) based on lizard occurrence data, Cerrado localities formed at least six major clades, corresponding to main faunistic subdivisions and lizard endemism centers, as follows (with parenthesis representing proposed area relationships): (Espinhaço range (Western Bahia Plateau (Upper La Plata Basin (Tocantins/Araguaia basin and Central interfluves (Paraná River Valley + Western Cerrado)))))) (Nogueira, 2006). This area cladogram is consistent with a major split dividing Cerrado in two large biogeographical regions coincident with the foremost geomorphological divisions (plateaus vs. peripheral depressions; Nogueira, 2006), and with biotic regions proposed for small mammals (Carmignotto, 2004) and woody plants, that basically divide the core Cerrado area into Central-Western, Southern, Central-Southeastern, North-Northeastern regions (Ratter et al., 2003). A succeeding study from the same research group detailed into 10 regions the proposed areas of endemism based on squamate reptiles occurrence records: 1) Cerrados of São Paulo state; 2) Miranda depression; 3) Huanchaca plateau; 4) Parecis plateau; 5) Serra das Araras plateaus and Cáceres region; 6) Chapada dos Guimarães region; 7) Tocantins depression; 8) Jalapão and Serra Geral region; 9) Upper Tocantins drainage and 10) Espinhaço range (Nogueira et al., in press). Distribution patterns of certain plant groups and, more particularly of the legume genus *Mimosa*, suggest that the main Cerrado endemism centers are at highlands (the Chapada dos Veadeiros region in Goiás, the Espinhaço complex in Minas Gerais, the Distrito Federal, and the Chapada dos Guimarães in Mato Grosso; Simon and Proença, 2000). A recent assessment revealed several areas of endemism for Cerrado anuran fauna, including both widely and restricted distributed endemics, but eight out of the 30 Cerrado endemic species are restricted to the Espinhaço mountain range (Valdujo, 2011). In summary, general biotic subdivisions and at least four centers of endemism are supported by concordant distributions of more than one taxonomic group, which are: Paranã River Valley, Araguaia basin, Chapada dos Guimarães and Espinhaço mountain range. These areas were of supposedly singular importance for the evolution of Cerrado fauna and should receive special attention in conservation efforts.

Only few studies have investigated the genetic structure of Cerrado endemic species by studying the phylogeography of typical tree species such as the 'pequi' (*Caryocar brasiliense*; Collevatti et al., 2003) and the 'jatobá-do-cerrado' (*Hymenaea stigonocarpa*; Ramos et al., 2007). The three genetically differentiated groups recovered (eastern, central, and western) are essentially congruent with the area subdivisions previously proposed (see above) and

were associated with climatic and vegetation changes during the Quaternary (Ramos et al., 2007). It was suggested that Cerrado populations became isolated in these three main areas (followed by genetic bottlenecks), and became extinct from the southern portion of the continent by replacement of the expanding subtropical grasslands (Ramos et al., 2007). Extinction of megafauna at the end of the Quaternary (approximately 10,000 YBP) has been implicated as a possible event influencing population structure of those tree species due to loss of ancient dispersers (Collevatti et al., 2003). The phylogeography of the 'vinhático' (*Plathymenia reticulata*), a tree widespread in both Atlantic Forest and Cerrado, was also recently investigated; detecting highest levels of genetic diversity in the central region of Cerrado, in Minas Gerais and Goiás states (Novaes et al., 2010). Further multi-locus molecular studies of other taxonomic groups, especially overlooked fauna groups, within a robust framework for hypothesis testing (e.g. *a priori* generated hypotheses, coalescent theory, statistical phylogeography; Avise, 2009; Knowles, 2004; Nielsen and Beaumont, 2009) will be required to investigate Cerrado evolution and to cross-validate proposed area relationships. In fact, a recent review highlighted the Cerrado as one of the several regions in the world where phylogeographic studies are badly needed (Beheregaray, 2008).

### 5.3. Biogeography of SDTFs

Until the 1990's, SDTFs biogeographic considerations were disjointed between studies focusing on the Caatinga, on one hand, and on other South American dry forests, on the other. Patterns of origin and diversification of SDTFs are complex and most early literature suggested that Caatinga lacked sufficient endemism to characterize a distinct vegetation, and indicated that its flora was derived from Chaco (Andrade-Lima, 1981, 1982) or from both Chaco and Atlantic Forest (Rizzini, 1979). Sarmiento (1975) proposed floristic links with the Caribbean coast and highlighted Caatinga as the only South American open/dry vegetation biome completely isolated from the Andes, being the first to recognize its peculiarity with respect to other formations. Subsequent studies ultimately revealed that Caatinga has significant plant species richness and endemism and is a unique floristic province/biome (Prado and Gibbs, 1993).

SDTFs specifically (and open biomes in general) biogeographic debates were reignited by the proposition that their disjunct distribution should be considered a unique relictual biome including other nuclear regions besides Caatinga (see Introduction). These may have formerly been more extensive and contiguous and reached their maximum extensions during the Last Glacial Maximum (LGM ~21 kyr BP) in the late Pleistocene ('Residual Pleistocene Seasonally Dry Forest model' or 'Pleistocene Arc hypothesis', PAH) (Pennington et al., 2000; Prado, 2000; Prado and Gibbs, 1993). Recent tests of the PAH both corroborated (Caetano et al., 2008; López et al., 2006; Spichiger et al., 2006, 2004; Werneck and Colli, 2006; Zanella, 2000, 2002) and refuted (Mayle, 2004, 2006; Werneck et al., 2011) this hypothesis as an explanation of the biogeographic history of SDTFs (Appendix I).

Disjunct distributions and the occurrence of endemics in the SDTFs (which presumably originated through vicariance after the fragmentation of the Pleistocene Arc) of many plant (Pennington et al., 2000; Prado, 2003; Prado and Gibbs, 1993; Queiroz, 2006; Spichiger et al., 2004), some bee (Zanella, 2000, 2002) and lizard species (Werneck and Colli, 2006; Werneck et al., 2009a) are consistent with the PAH. Some have even proposed a larger extension for the Pleistocene Arc, north to Mexico (López et al., 2006), or including both Cerrado and Chaco into the Arc (Oliveira-Filho et al., 2006) (Appendix I). Some evidence supporting the PAH comes from biogeographic patterns that arise from SDTF

enclaves within Cerrado, with the major area at the Paranã River Valley in central Brazil (Fig. 2). SDTF enclaves are frequently distinguished by their high diversity levels and presence of plants (Oliveira-Filho and Ratter, 1995, 2002), bird (Silva, 1997; Silva and Bates, 2002), drosophilid (Mata et al., 2008), mammal (Moojen et al., 1997), and lizard endemisms (Werneck and Colli, 2006). The Paranã River Valley has been detected as one of Cerrado's center of endemism by several investigators (Nogueira, 2006; Silva, 1997; Silva and Bates, 2002). Alternatively, many of these species were previously either considered endemic to geographical distant Caatinga or to have sister relationships with Caatinga species, and enclaves should be better regarded as displacements of other SDTF nuclear regions (Scariot and Sevilha, 2005; Werneck and Colli, 2006) as proposed by the PAH (Pennington et al., 2000; Prado and Gibbs, 1993). Unfortunately, intense human occupation in the region during the 1980s has extensively fragmented the Paranã River valley SDTFs, and currently these forests are reduced to small isolates in flat, lowland areas or on limestone outcrops, most of them disturbed by human action (Espírito-Santo et al., 2009; Scariot and Sevilha, 2005). In spite of their high biodiversity, biogeographic importance, and highly threatened status, very few preserved areas are located in this region (Espírito-Santo et al., 2009; Scariot and Sevilha, 2005). The single molecular phylogeographic study testing whether the SDTFs of eastern South America were more widespread during the drier glacial periods investigated the genetic structure of *Astronium urundeuva*, a tree restricted to SDTFs, based on two chloroplast intergenic spacers and nine nuclear microsatellite loci (Caetano et al., 2008). Implementing robust data analyses (see Appendix I), a diffuse genetic structure interpreted as consistent with a more continuous SDTF formation under the 'Pleistocene Arc' scenario was found (Caetano et al., 2008).

Studies employing a temporal/historical approach have challenged this hypothesis. Scenarios delineated from preliminary palaeo-ecological data and dynamic vegetation model simulations suggest that dispersal might be a more parsimonious explanation (Mayle, 2004, 2006). Palaeodistribution modeling investigating potential distribution and stability areas of SDTFs during Quaternary climatic fluctuations found no support for the PAH model and proposed an alternative scenario, amenable to further testing, of an earlier SDTF expansion (either at Lower Pleistocene or at the Tertiary), followed by fragmentation in the LGM and secondary expansion in the Holocene (Werneck et al., 2011). In agreement, molecular dated phylogenies suggest that the origin of some SDTF endemic plants in many instances pre-date the Pleistocene (Lavin, 2006; Pennington et al., 2004). However, ancient and recent diversifications are not mutually exclusive, and for SDTF, this scenario is favored (Lavin, 2006; Pennington et al., 2004). Hence, the lack of consensus about SDTFs Quaternary history undoubtedly suggests that more comprehensive tests are needed. Critical appraisals include modeling the past distribution of SDTFs to test for a historically more continuous and widespread distribution at an earlier period (during Tertiary/Lower Pleistocene transition), and molecular phylogenetic/phylogeographic studies dating the divergence times between SDTF endemic species and/or populations and their close relatives, to elucidate if recent demographic histories show evidence of vicariant events, long-distance dispersal, or a combination of both.

In a narrower context, Bolivian SDTFs are scattered across small and isolated northern and southern Andean dry valleys, and eastern lowlands, with the largest natural intact remnant in the Chiquitania region in Santa Cruz. This distributional pattern is often interpreted as consistent with a broader past distribution of SDTFs under the PAH, when colonization of the northern dry valleys by lowland species possibly took place (Herzog and Kessler, 2002).

The composition and biogeographical patterns of Bolivian dry forest bird communities match such historical division, with the dry southern valleys and lowlands concentrating the higher proportion of typical dry forest species (Herzog and Kessler, 2002). Accordingly, bird and mammal communities in northern dry valleys are more heterogeneous and show few affinities with other Bolivian dry forest regions (Anderson, 1997; Herzog and Kessler, 2002). The SDTFs located in the rain-shadowed Bolivian inter-Andean valleys also act as biogeographical island-like systems in terms of species distribution and community composition of distant plant groups (Linares-Palomino and Kessler, 2009). As for the bird and mammal communities, floristic connections show higher remoteness of northern dry valleys and stronger connections between southern valleys and lowland SDTFs in the Chiquitania region and to Chaco, with stronger spatial signal reported for plants with lower dispersal ability (Linares-Palomino and Kessler, 2009). Such interesting biogeographic patterns would comprise an excellent model to understand how Pleistocenic climatic fluctuations shaped current species distribution and their genetic diversification in a naturally fragmented landscape (Soria-Auza, 2009). On the other hand, eastern lowland Chiquitania forests represent a distinctive and complex floristic assemblage, transitional between the humid Amazon forest to the north and the Chaco to the south (Killeen et al., 2006).

The Caatinga represents the largest, most isolated and species-rich nucleus of SDTFs, with a mixed flora of endemic and widely distributed elements (Prado, 2003; Queiroz, 2006). High levels of diversity and endemism are similarly reported for some faunal groups, including lizards (Rodrigues, 1996, 2003) and bees (Zanella and Martins, 2003). Adopting Bailey (1998) methodological approach to delineate ecoregions, Velloso et al. (2002) proposed eight major landscape units (ecoregions), defined by biotic and abiotic factors supposedly relevant for the distribution and diversification of Caatinga biodiversity. These are Borborema plateau, Campo Maior complex, Ibiapaba–Araripe complex, northern Sertaneja depression, southern Sertaneja depression, São Francisco sand dunes, Chapada Diamantina complex, and Raso da Catarina (Fig. 5). Queiroz (2006) recognized seven out of these eight ecoregions (all but the Borborema plateau) as putative regional centers of endemism, based on Leguminosae, the most diverse plant family in Caatinga. In this study, the view that Caatinga comprises two separate biotas, one associated with soils derived from crystalline basement surface and another with sand sedimentary surfaces emerged (Queiroz, 2006). This regional biogeographic pattern is often overlooked because of the large scale adopted by phytogeographical studies that consider the entire Caatinga as a single analytical unity (Queiroz, 2006). According to this model, sand areas harbor most of the endemic Caatinga flora and these areas were partially replaced during the Late Tertiary and early Quaternary, when geological pediplanation exposed the crystalline surfaces, allowing the establishment of species typical of other SDTF nuclei (Queiroz, 2006). In agreement, most of Caatinga herpetofauna endemism is associated with sandy soils, which are assumed to have been much more widespread in the past (e.g. the São Francisco sand dunes covers roughly only 0.8% of the total Caatinga area and 27% of the squamate fauna is restricted to this small region; Rodrigues, 1996, 2003). Despite this, no protected areas are established at the São Francisco sand dunes region (Velloso et al., 2002). This model could straightforwardly be tested using molecular approaches, by estimating the diversification ages of the two major floristic divisions and by using phylogeographic and population genetic methods to estimate timing and routes of expansion of SDTF taxa (Queiroz, 2006). To date, molecular biogeographic/phylogeographic studies including sampling from the Caatinga focus on the existing rainforest natural relicts (so-called 'Brejos'; Cabanne et al., 2008;

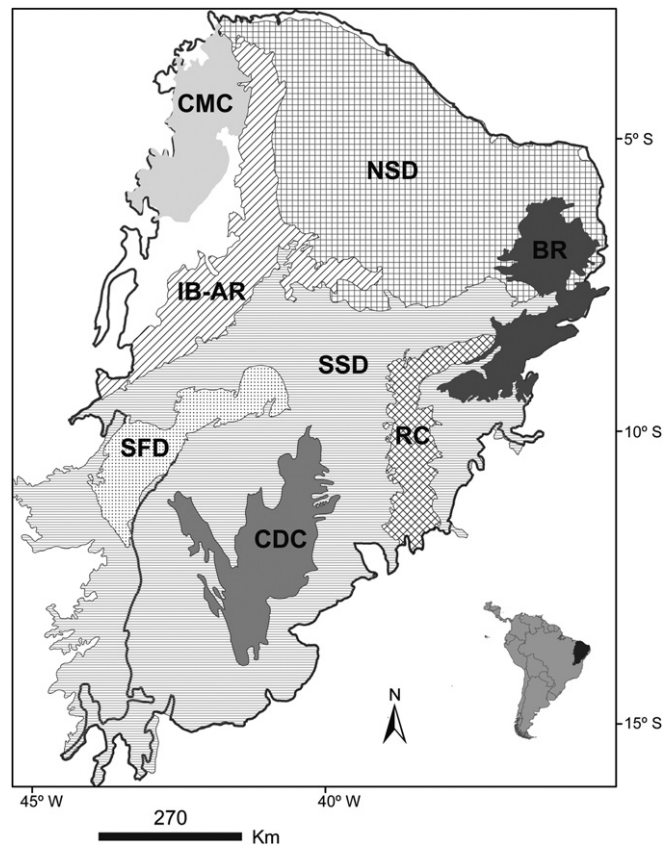


Fig. 5. Caatinga limits and major ecoregions as defined by Velloso et al. (2002). CMC, Campo Maior complex; IB-AR, Ibiapaba–Araripe complex; NSD, northern Sertaneja depression; SSD, southern Sertaneja depression; BR, Borborema plateau; SFD, São Francisco sand dunes; CDC, Chapada Diamantina complex; and RC, Raso da Catarina.

Carnaval and Bates, 2007; Carnaval, 2002; Costa, 2003) (Appendix I). Regardless of identifying consequences of the dynamic nature of the Brazilian northeastern region in the genetic structure of distinct animal taxa (frogs, small mammals and birds), the contributions of these studies for the biogeographic knowledge of the open vegetations biomes are limited, considering that the main spotlight is on rainforest diversification.

Notwithstanding these distinct patterns documented for the diversification and fragmentation of SDTFs, they have been largely ignored in discussions regarding Quaternary vegetation cycles and their consequences (Pennington et al., 2000). More recently though, SDTFs are apparently emerging from this orphaned position and are now inspiring many research groups (some examples: Leal et al., 2003; Miles et al., 2006; Pennington et al., 2006a, 2000; Prado, 2000; Werneck et al., 2011). Despite this 'boom' of studies, only a few have incorporated a molecular perspective (Caetano et al., 2008) or present practical implications for biodiversity conservation (Leal et al., 2003; Werneck et al., 2011). Also, most biogeographical studies that focused on animal communities typically adopted only local or regional perspectives, and have not interpreted patterns in a broader context.

## 6. Summary

Based on the previous sections I can outline some broad trends about current knowledge, and delineate some future research prospects for South American open biomes biogeography in general, and zoogeography in particular. First, the view that these biomes are

species-poor and harbor few endemics is a misleading myth for the Cerrado and SDTF biotas and, to a less extent, for the Chaco. The last is probably more recently formed biome than the first two, and the degree that current composition of Chaco biota is influenced by external sources is higher. Also, it is possible that low elevation Chaco regions were more affected by Quaternary climatic fluctuations than other open biomes located at higher elevations. For example, interglacial rises in sea level could be enough to inundate many Chaco areas (Short, 1975). Among the South American open biomes here considered, the Chaco has probably undergone the greatest boundary shifts, and its ecologically generalist fauna could easily find refuge in higher elevation open vegetation formations (e.g. surrounding Cerrado and SDTF remnants). As an outcome, these supposedly less stable Chaco areas across climatic fluctuations are predicted to shelter a less differentiated fauna, with lower levels of intra-specific genetic diversity, when compared to populations from the other two open biomes. In fact, a preliminary phylogeographic assessment of the lizard *Phyllorhynchus pollicaris*, which is extensively distributed across the 'diagonal of open formations', reveals lower mtDNA and nuclear haplotype diversity from Chaco populations (Werneck et al., in prep.). It is critical to emphasize that this prediction does not diminish the significance of the Chaco as an important center for the evolution of the 'open/dry biota', as already proposed in the literature. Iriondo (1993) said: "In my opinion, from an evolutionary point of view, the Chaco Dominion can be interpreted as a secondary environment, evolutioned (sic) by the interaction of the Neotropical poles: Patagonia and Amazonia". On the contrary, the Chaco's central location places it strategically in a very active ecotonal region where many different vegetation types meet, and it may represent a region of 'current evolutionary history' crucial to the dynamics of many species. Ecotonal areas are potentially important regions of differentiation and speciation, and so have great evolutionary potential (Schilthuizen, 2000; Smith et al., 1997). In addition, if we rank these three open biomes with respect to the amount of research focused on each, we realize that the Chaco occupies an extreme position marked by a general lack of zoogeography studies (Cerrado > SDTF/Caatinga > Chaco) and most references date to the 1970's and 1980's. As a consequence, Chaco lower diversity and endemism may simply reflect a research bias artifact. Paraguay biota (the main country comprising the Chaco) is certainly one of the least known among Latin American countries, with only preliminary biodiversity inventories available (Rios and Zardini, 1989; Yahnke et al., 1998). As more intensive studies are taken, including new species description and reconstruction of historical relationships, new knowledge will be attained, with potential major impacts for the comprehension of Chaco biogeography.

In contrast, in terms of zoogeographical studies Cerrado is the best-known open biome, but many points still need further clarification. For example, forest formations (Amazon and Atlantic forests, gallery forests and SDTF enclaves within Cerrado) appear to play a more relevant role to overall diversity levels and biogeographical patterns in Cerrado than in other open biomes. However, this contribution does not seem uniform across different taxonomic groups, being more relevant for some (birds, large mammals, and possibly some invertebrates) than for others (lizards and small mammals). Moreover, a still open question is whether molecular evidence agrees with hypothesized Cerrado endemism areas based on plant and animal occurrence data (Appendix I). Cerrado's high species richness and endemism, and elevated spatial heterogeneity are decisive for the complex biogeographic patterns reported for this biome, and comparative molecular approaches are especially needed to address these questions.

Most area relations already proposed both at the continental (between open biomes) and regional levels (within each biome) are derived from phylogeographic studies, with a few exceptions

regarding bees, Cerrado herpetofauna and avifauna. More inclusive biotic relationships initially suggested Chaco-Caatinga connections during the LGM. However, these connections are probably in error, while the more recently proposed Cerrado-Chaco biotic relationships need further investigation. Regarding centers of endemism, which are more specifically delineated for the Cerrado and for the Caatinga SDTF nucleus, refinement of relationships and number of areas of endemism are likely to increase with addition of studies on other taxonomic groups, such as invertebrates and amphibians.

The study of South American open biomes biogeography is generally marked by a lack of integrated appraisals, especially using phylogeographic approaches (Appendix I). More studies and hypotheses have been proposed for within-biomes than between-biome level, and general scenarios are still controversial (Appendix I). However, the historical relationships and endemism areas proposed to date (mostly based on phylogeographical assessments, species lists, multivariate and ordination methods) are sufficient to suggest hypotheses and to stimulate the development of new research; this alone represents an initial step towards an integrated historical biogeographic approach. Fertile areas of research include: (1) a better comprehension of the enclaves' role for the evolution of open biota diversity (both open enclaves within humid vegetation formation [e.g. pockets of Cerrado in Amazon] and vice-versa [SDTF enclaves and gallery forest within Cerrado and Atlantic forest *brejos* within SDTF/Caatinga]); (2) investigation of the importance of the open biomes highly dynamic ecotonal nature for speciation processes; (3) estimating divergence times for monophyletic phylogenetic and phylogeographic groups that can be associated with major geological events shaping open biota evolution; and (4) understanding the genetic diversity levels and diversification of distinct biomes. Accomplishment of these research goals depends on resolving a number of logistic issues, including: (1) completing inventories of unsampled areas; (2) increasing financial support for basic research, including the still markedly expensive molecular techniques (especially for developing countries); (3) facilitating inter-institutional collaborative research that includes multiple samples and perspectives in the study of the highly complex and dynamic Neotropical ecosystems for broader scales questions (for example, instead of developing studies for the rainforest including few samples for the open biomes, one could benefit from a more comprehensive study by achieving inter-institutional collaborations and perspectives); and (4) fostering government and international support for scientific partnerships to facilitate development of research in several countries covering the range of distribution of the open biomes, despite national boundaries (including processing of collection permits, planning of joint field expeditions, etc).

Historical and ecological biogeography knowledge of South American open biomes would benefit from the integration of multi-species phylogeographic perspectives, with more traditional "deep" phylogenetic perspectives, palynological studies, syntheses of geological data to generate *a priori* predictions, and further integration of niche modeling and GIS technologies. Even more critically needed, refined molecular phylogeographic perspectives based on the use of coalescent theory and statistical methods, coupled with the use of multi-locus data sets should be able reconstruction of complex evolutionary histories, identification of stable refugial areas, recent population expansions, and secondary contacts among populations from the distinct biomes expected for highly dynamic biotas (Avise, 2009; Hewitt, 2004; Nielsen and Beaumont, 2009; Riddle, 2009; Riddle et al., 2008). Importantly, such studies should be prioritized on the short term, before molecular "signatures" of phylogeographic histories are overwritten by human occupation and habitat loss (for examples in the Cerrado see Soares et al., 2008; Telles et al., 2007).

Finally, several studies associated patterns of diversity, assemblage composition, genetic diversity, and historical biogeography of species distributed at the eastern South America open biomes with influences of Quaternary climatic fluctuations. Still, various taxa have older divergence dates (Almeida et al., 2007; Maciel et al., 2010; Pennington et al., 2004; Werneck et al., 2009b), which implies a combination of both Tertiary and Quaternary influences in their diversification histories. Tertiary events respond for deep splits in the evolutionary history and broad biodiversity patterns (Hoorn et al., 2010), while Quaternary climatic fluctuations were likely strong enough to influence population sizes and, consequently, affect genetic diversification at shallow time scales and community dynamics at smaller scales (Jansson, 2003). Analytical methods and multi-locus data sets now available will permit temporal resolution between very shallow (Quaternary) and very ancient (Tertiary) splits, with sufficiently narrow error terms to distinguish between times of speciation. Examples of model taxonomic groups broadly distributed across the open biomes that are attractive for the development of phylogeography investigations are abundant in the literature and I will list some here to illustrate: the co-distributed lizards *Phyllopezus pollicaris*, *Vanzosaura rubricauda*, *Micrablepharus maximiliani*, and *Lygodactylus* genus (Werneck and Colli, 2006; Werneck et al., in prep.); species of the *Drosophila buzzatii* cluster that utilize decaying cacti distributed across the open biomes as an exclusive larval food resource (Manfrin and Sene, 2006; Moraes et al., 2009); bees of the genus *Caenonomada* (Zanella, 2000, 2002) and *Parapsaenythia* (Ramos and Melo, 2010); the bird *Suiriri suiriri* (Hayes, 2001); and the rodent *Kerodon* (Bezerra et al., 2010; Lessa et al., 2005). Population genetic studies should ultimately be able to contribute to long-standing taxonomic questions within these groups and biogeographic patterns issues among the open biomes, with possible positive contributions to species delimitation and identification of evolutionary significant units for conservation.

## Acknowledgments

FPW was supported by a fellowship from CAPES/Fulbright and by a graduate research assistantship from the Brigham Young University (BYU) Department of Biology. FPW PhD research received additional funding from the National Geographic Society (NGS), Society of Systematic Biologists (SSB), Neotropical Grassland Conservancy (NGC), Society for the Study of Amphibians and Reptiles (SSAR), and Idea Wild. I thank G. C. Costa, G. R. Colli, B. Adams, J. B. Johnson, C. Nogueira, B. P. Noonan, J. W. Sites, R. N. Leite for reviewing previous versions of the manuscript; three anonymous reviewers for constructive suggestions and comments on the manuscript; F. Zanella, and A. Bezerra for assistance with questions related to their taxonomic groups of expertise (bees and small mammals, respectively); M. M. Espírito-Santo, S. K. Herzog, M. Kessler, D. E. Prado, and M. T. Rodrigues for suggestions and helpful bibliography exchange; P. Podestà for designing the artwork of Fig. 4.

## Appendix. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.quascirev.2011.03.009.

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