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

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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/subtropical 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.

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), phylochronology 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.

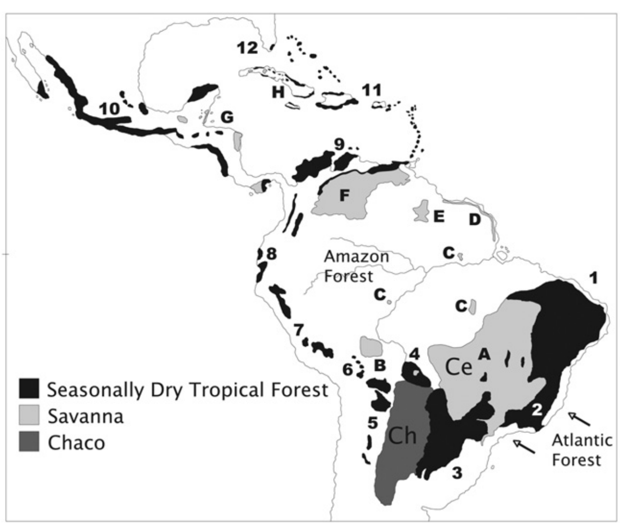

Fig. 1. General distribution of rainforests, Seasonally Dry Tropical Forests (SDTFs) and other South American dry vegetation formations. SDTFs: 1. northeast Brazil (Caatinga); 2. southeast Brazilian seasonal forests; 3. Misiones Nucleus; 4. Bolivian Chiquitano region; 5. Piedmont Nucleus; 6. Bolivian 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.

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^2 (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