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# The niche and phylogeography of a passerine reveal the history of biological diversification between the Andean and the Atlantic forests

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ABSTRACT

The Atlantic Forest is separated from the Andean tropical forest by dry and open vegetation biomes (Chaco and Cerrado). Despite this isolation, both rainforests share closely related lineages, which suggest a past connection. This connection could have been important for forest taxa evolution. In this study, we used the Saffron-billed Sparrow (*Arremon flavirostris*) as a model to evaluate whether the Andean and the Atlantic forests act as a refugia system, as well as to test for a history of biogeographic connection between them. In addition, we evaluated the molecular systematic of intraspecific lineages of the studied species. We modeled the current and past distribution of *A. flavirostris*, performed phylogeographic analyses based on mitochondrial and nuclear genes, and used Approximate Bayesian Computation (ABC) analyses to test for biogeographic scenarios. The major phylogeographic disjunction within *A. flavirostris* was found between the Andean and the Atlantic forests, with a divergence that occurred during the Mid-Pleistocene. Our paleodistribution models indicated a connection between these forest domains in different periods and through both the Chaco and Cerrado. Additionally, the phylogeographic and ABC analyses supported that the Cerrado was the main route of connection between these rainforests, but without giving decisive evidence against a Chaco connection. Our study with *A. flavirostris* suggest that the biodiversity of the Andean and of the Atlantic forests could have been impacted (and perhaps enriched?) by cycles of connections through the Cerrado and Chaco. This recurrent cycle of connection between the Andean and the Atlantic Forest could have been important for the evolution of Neotropical forest taxa. In addition, we discussed taxonomic implications of the results and proposed to split the studied taxon into two full species.



## 1. Introduction

According to the refugia hypothesis (Haffer, 1969; Haffer and Prance, 2001), Pleistocene climate cycles have driven speciation by promoting contraction, fragmentation and expansion of rainforest ranges, which in turn allowed for vicariance, divergence and secondary contact. Most discussions concerning the refugia hypothesis have been focused on the intra biome level, for example within the Amazon or within the Atlantic Forest (Cabanne et al., 2016; Carnaval et al., 2009; Maldonado-Coelho et al., 2013; Thomé et al., 2010), and less attention has been given to processes occurring among related but fully isolated forest biomes, such as the Andean and Atlantic forests or the Caatinga and Chaco dry forests (Batalha-Filho et al., 2013; Costa, 2003; Pennington et al., 2004; Werneck, 2011).

The Andean and the Atlantic forests (Fig. 1) are among the most diverse forest biomes in the world (Orme et al., 2005). They are currently isolated from each other by dry forests and open-vegetation domains: the Chaco and the Cerrado, respectively. In

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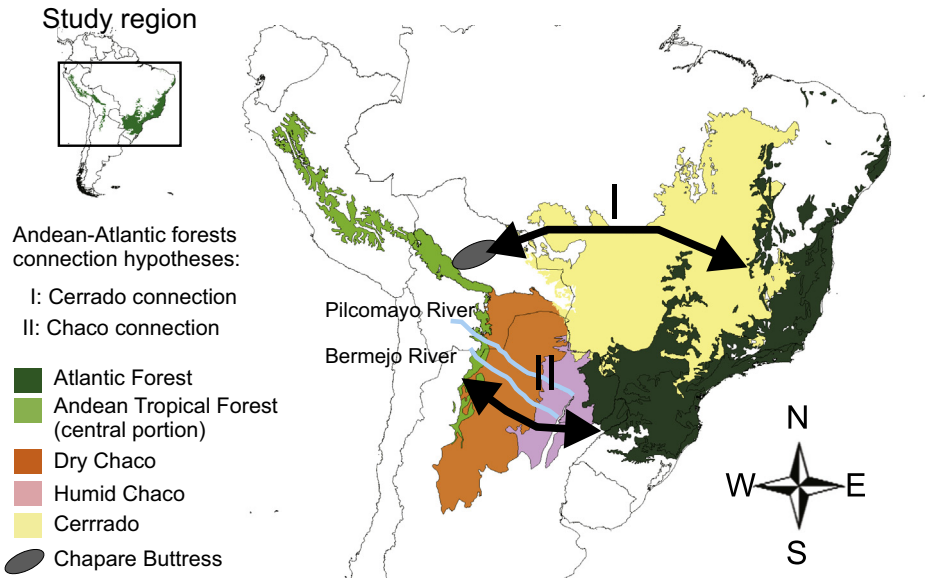


**Fig. 1.** Geographic distribution of the central Andean Tropical Forest, the Atlantic Forest, Cerrado and Chaco. The working hypotheses on the historical pathways between the Atlantic and the Andean forests are indicated.

spite of this isolation, they share closely related lineages of rainforest dependent organisms (Faivovich et al., 2004; García-Moreno et al., 1999; Nores, 1992; Olrog, 1963), many of them do not have a continuous range but belong to the same species in both biomes, which indicated that these rainforests have been connected in the past (Chapman, 1926). This connection is also suggested by palynological studies (Ledru, 1993, 1991; Oliveira-Filho and Ratter, 1995), which indicate that wet forest expanded into the Cerrado and towards the Andes during the last glacial maximum, a phenomenon that could have connected forest domains. However, neither the frequency nor the type of connection between regions –i.e., if through continuous or stepping stone forests– have been studied until now.

Thus, the Andean and the Atlantic forests could act as a refugia system, and therefore their past range dynamics could have been important in the process of avian diversification in the Neotropics. Because these forested biomes are currently isolated, they might be at the isolation phase of the cycle of a refugia system. If their connection dynamics (i.e., cycles of connection and isolation) prompt cycles of vicariance and divergence, the species present in both domains should show a deep phylogeographic gap between domains, because major diversification events should have occurred between regions. Alternatively, if the dynamic of the connection allow for high and constant rates of historical gene flow, enough to preclude divergence, the shared organisms should not present a significant population gap between regions.

More specific biogeographic aspects of the connection between the Andean and Atlantic forests are still unknown, such as the geological processes involved, timing and regions that bridged these rainforests. One of the main hypothesis to explain the connection between these forests state that the contact could have occurred in the Chaco region, through gallery forests along main rivers (i.e., Bermejo and Pilcomayo Rivers, Fig. 1) that expanded during interglacial periods (from now on Chaco connection) (Nores, 1992; Olrog, 1963; Smith, 1962). The Chaco connection hypothesis is mostly based on forest bird distribution patterns, and up to now there is not enough evidence from other scientific areas supporting extensive expansions of wet forests in the Chaco (Zurita et al., 2014). Alternatively, Silva (1994) proposed that instead of through the Chaco and its main rivers, the connection occurred during glacial maxima through the southern Amazon forest and through expansions of forests into the Cerrado (from now on Cerrado connection). Forest expansions in the Cerrado are supported by some palinological studies (Ledru, 1993, 1991; Oliveira-Filho and Ratter, 1995), as well as by niche models of the Atlantic Forest biome (Carnaval and Moritz, 2008; Sobral-Souza et al., 2015) and of its organisms (Cabanne et al., 2016; Thomé et al., 2010).

We are not aware of any study specifically oriented to test alternative hypotheses on the Andean-Atlantic forests connection. These hypotheses could be tested by niche models and phylogeographic studies of rainforest species that are present in both regions. For instance, species distribution models would help to test connection routes by estimating potential distributions of forest taxa across different geographic regions and periods (Elith and Leathwick, 2009; Soberon and Peterson, 2005). Also, from the genetic standpoint and a cladistic biogeography paradigm, the phylogenetic position of populations occurring in-between the Andean and the Atlantic forests would shed light onto the biogeographic history of both regions. For instance, if samples of wet forest taxa from gallery forests in the Chaco (e.g., along the Pilcomayo and Bermejo rivers, Fig. 1) are sister groups to populations from the Andes or from the Atlantic Forest, a connection through the Chaco would be supported.

In this paper we studied the Saffron-billed Sparrow (*Arremon flavirostris*) to evaluate the contact between these forest domains. *A. flavirostris* inhabits the understory of moist and semideciduous forests of the base of the central Andes and of the interior Atlantic Forest, as well as gallery forests of the eastern Chaco and of the central and southern Cerrado (Fig. 2a) (Rising, 2011). Although strict categorization of Andean-Atlantic forests core species versus Andean-Atlantic-gallery forests species is simplistic, we view *A. flavirostris* as not strictly Andean-Atlantic forests core species. However, it is a good study model to evaluate the working hypotheses on the Andean-Atlantic forests connection because it inhabits both the moist forest domains and the gallery forests (i.e., at the Bermejo and Pilcomayo Rivers, Figs. 1 and 2) that could have been directly involved in bridging the moist domains. The characterization of the evolutionary relationships of populations from these gallery forests is essential to understand the biogeographic processes that occurred between forest domains. In addition, the species is interesting from the taxonomic standpoint, because (i) it has been suggested to form a superspecies with