



Species delimitation, phylogeny and evolutionary demography of co-distributed, montane frogs in the southern Brazilian Atlantic Forest



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ABSTRACT

The Brazilian Atlantic Forest (BAF) is recognized as one of the world's biodiversity hotspots, with even more species per unit of area than the Amazon, however the mechanisms that led to such astonishing diversity are yet to be fully understood. In this study, we investigate the diversification of two co-distributed frog genera associated with montane areas of southern BAF: *Melanophryniscus* (Bufonidae) and *Brachycephalus* (Brachycephalidae). Species delimitation methods using mitochondrial and nuclear loci supported the existence of a remarkable number of highly endemic species in each genus, most of which occupy only one or a few adjacent mountaintops. Their timing of diversification was highly congruent, supporting recent speciation events within the past 600 thousand years. Extended Bayesian skyline plots indicate that most populations have remained relatively stable in size across the evolutionary past, with recent growth after 0.15 My, suggesting that the drastic changes found in previous studies on lowland frog species were not shared by these montane taxa. These results are consistent with the existence of a montane refugium in southern BAF, allowing species persistence through the climatic shifts experienced along the BAF during the Quaternary.

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1. Introduction

The Brazilian Atlantic Forest (BAF) is among the world's biodiversity hotspots, featuring exceptional species richness and endemism (Myers et al., 2000). For instance, several estimates indicate that the BAF harbors the equivalent to 50–60% of the species richness of the entire Amazon Forest, despite encompassing less than one fourth of its geographical extent (Silva and Casteleti, 2003; Silva et al., 2005; Ribeiro et al., 2009). Such high diversity was generated over the course of a highly complex and dynamic evolutionary history, which was strongly influenced by a multitude of factors, such as climatic fluctuations during the Pleistocene (e.g. Behling and Lichte, 1997; Behling, 2002), and repeated connections with the Amazon Forest and other neighbouring biomes (Costa, 2003; Batalha-Filho et al., 2013). Understanding the mechanisms that generated such high diversity is not only a considerable challenge (Moritz et al., 2000; Moritz,

2002; Turchetto-Zolet et al., 2013), but also a pressing necessity for the design of efficient conservation efforts, particularly given that the strong pace of deforestation already led to the destruction of nearly 85% of BAF's original distribution (Tabarelli et al., 2005; Ribeiro et al., 2009).

Several studies in recent years investigated the role of climatic fluctuations during the Quaternary in shaping current observed patterns of species distributions in the BAF through the formation of refugia (e.g. Cabanne et al., 2007; Carnaval and Moritz, 2008; Carnaval et al., 2009, 2014), as had been previously suggested for the Amazon Forest (Haffer, 1969; Vanzolini and Williams, 1970, but see Bush and Oliveira, 2006). In particular, three regions of relative climatic stability were identified and hypothesized to be the sources for the later recolonization of the current extent of the biome, as supported by the spatial distribution of genetic variability of several species (Carnaval and Moritz, 2008; Carnaval et al., 2009). An important limitation of the refugia hypothesis as it was originally proposed is that the timescale for the speciation events that gave rise to BAF species often considerably predates the period of Pleistocene glacial cycles (e.g. Lara and Patton, 2000; Fusinato et al., 2013) and therefore cannot be invoked as a mechanism for the origin of the diversity in the biome, even

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though they might have played an important role in its current distribution. Alternative mechanisms to explain the diversity and distribution of species in the BAF such as riverine barriers (Peres et al., 1996; Pellegrino et al., 2005) and adaptation along ecological gradients (Schneider et al., 1999) have received comparatively little attention.

One important caveat for studies on refugia for the BAF to date is that they are mostly based on taxa with low to mid-altitude ranges and broad geographic distributions (Pellegrino et al., 2005; Carnaval et al., 2009; Fitzpatrick et al., 2009; Brunes et al., 2010; Martins, 2011). However, frogs of montane habitats commonly exhibit considerable levels of endemism, not only in high-elevation areas of the BAF, but also in other regions such as the Andes (e.g. Brunes et al., 2010; Thomé et al., 2010; Wollenberg et al., 2011; Amaro et al., 2012; Páez-Moscoso and Guayasamin, 2012; Fusiñatto et al., 2013; Giarla et al., 2014). Indeed, studies on montane species, particularly in the southern BAF, increasingly provide support for a more complex scenario for the evolution of endemism and diversity in the BAF (e.g. Thomé et al., 2010; Amaro et al., 2012; Carnaval et al., 2014). Therefore, uncovering the processes underlying the diversification of the montane BAF fauna is a key component for a broad understanding of the evolution of the biome as a whole.

Here we investigate two co-distributed montane anuran genera *Melanophryniscus* (Bufonidae) and *Brachycephalus* (Brachycephalidae) – as model systems to understand diversification in montane regions along the southern BAF. The genus *Melanophryniscus* has a broad geographic distribution over southeastern South America. Its range includes south and southeastern BAF; the wetlands and grasslands of Brazil to the inter-Andean valleys in Bolivia; and areas across Paraguay and Uruguay down to central Argentina (Frost, 2015). However, along southern BAF, *Melanophryniscus* is characterized by montane endemic species with restricted and isolated distributions in cloud forests, *campos de altitude*, and

grasslands (Langone et al., 2008; Steinbach-Padilha, 2008; Bornschein et al., 2015a). There are currently 29 described species along the entire genus distribution (Frost, 2015), with only five currently recognized species for the southern BAF: *M. alipioi*, *M. vilavelhensis*, *M. biancae*, *M. milanoi*, and *M. xanthostomus*. These species are also unique in their genus for their association with plants for phytotelm breeding (Langone et al., 2008; Steinbach-Padilha, 2008; Bornschein et al., 2015a). *Brachycephalus* is endemic to the BAF, with its distribution extending nearly 1700 km along the biome, and most of its species occurring in isolated mountaintops from the Brazilian states of Bahia in northeastern Brazil to Santa Catarina in southern Brazil (Pie et al., 2013). Its distribution encompasses the Serra da Mantiqueira and Serra do Mar mountain ranges, including 30 currently recognized species (Frost, 2015), of which 14 correspond to described species of the montane regions of the southern BAF. *Brachycephalus* comprises both cryptic and aposematic toadlets, which live in the forest leaf litter and are commonly active during the day (e.g. Ribeiro et al., 2015). The genus is characterized by miniaturization, which entails severe modifications to their life histories (Izecksohn, 1971; Hanken and Wake, 1993; Yeh, 2002; Ribeiro et al., 2005).

Field efforts by our team over the past five years have uncovered a variety of potentially new species of *Melanophryniscus* and *Brachycephalus* distributed along the BAF in the states of Paraná and Santa Catarina (Fig. 1), of which 11 have been recently described (Pie and Ribeiro, 2015; Ribeiro et al., 2015; Bornschein et al., 2015a). Through extensive field surveys across the vast majority of mountains in the geographical region encompassed by those studies, we observed the restriction of populations to cloud forests and other montane habitats, their effective isolation by valleys, and their absence from lowland habitats. In order to provide a phylogeographic and demographic perspective on their evolutionary history, a fourfold approach has been taken: (1) to establish the validity of the candidate species based on

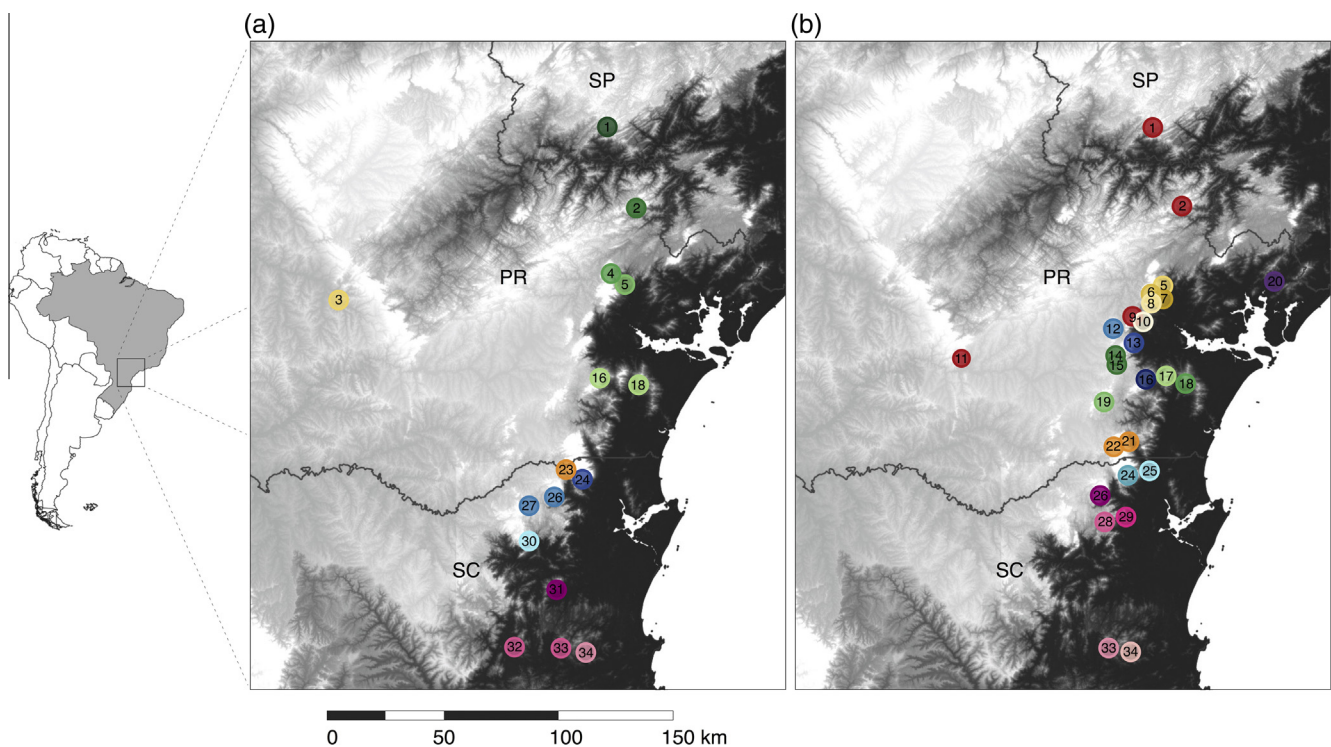


Fig. 1. Locations in the southern Brazilian Atlantic Forest where samples of *Melanophryniscus* (a) and *Brachycephalus* (b) were obtained for the present study. Each locality is enumerated following Table 1, and each species is represented by different shades of colors based on species delimitation (see Section 3 and Fig. 2). Abbreviations are as follows: SP = state of São Paulo, PR = state of Paraná, SC = state of Santa Catarina. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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