



Pleistocene radiation of coastal species of *Pilosocereus* (Cactaceae) in eastern Brazil



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ABSTRACT

The semiarid region in Northeast Brazil (*Caatinga*) suffered several high moisture periods during the Pleistocene, while neighbouring regions experienced drying events. Effects of this climatic history on the evolution of *Caatinga* xeric flora are poorly understood. Demography and evolutionary relationships between *Pilosocereus arrabidae* and *Pilosocereus catingicola* (Cactaceae) were investigated using two non-coding intergenic spacers of cpDNA (1424 bp) employing distinct statistical methods, such as Bayesian Inference analysis, haplotype network, AMOVA, neutrality tests and Bayesian Skyline Plot. Our data suggests that species formerly arranged as the informal *Pilosocereus arrabidae* group do not form a monophyletic clade. *P. arrabidae* and *P. catingicola* are not reciprocally monophyletic and present very low genetic diversity. The Tajima's D and Fu's Fs statistics provided no significant results. Results suggest a very recent origin for *P. arrabidae* and *P. catingicola*. The beginning of *P. arrabidae* and *P. catingicola* diversification dates back to the Pleistocene. Genetic diversity of *P. catingicola* subsp. *salvadorensis* is geographically structured between major rivers of the region, suggesting a history of isolation in interfluvies during Pleistocene climatic cycles.

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1. Introduction

The astonishing biodiversity found in the Neotropical region includes vast arid and semiarid habitats (Antonelli et al., 2015; Antonelli and Sanmartín, 2011; Hughes et al., 2013). The cacti are among the most iconic of many drought-adapted plant groups that evolved and diversified under the xeric conditions of these ecosystems. According to Hernández-Hernández et al. (2014), the basal lineages of Cactaceae probably originated in the Andean region of Chile and Argentina. Yet, this family has a broad distribution

throughout the New World, where its high diversity, with c. 1450 species (Hunt et al., 2006), is distributed in several diversity centres (Barthlott et al., 2015). Eastern Brazil, with its semiarid *Caatinga* and seasonal *Cerrado* is amongst the three most important areas in terms of cactus diversity, and it concentrates a very large proportion of threatened species of this fascinating family (Goettsch et al., 2015).

In order to endure life in semiarid or arid environments plants need a set of adaptive strategies (e.g. Eggli and Nyffeler, 2009; Mauseth, 2006). Since adaptations to survive drought usually make them less competitive in non-seasonal habitats (Taylor, 2012), they often become isolated and endemic in arid lands. Thus, the environmental changes that occurred during the Quaternary probably affected the distribution and evolution of cacti and other drought enduring plants. The global cooling and drying

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events of the Late Miocene and the lowering of CO₂ levels may have caused expansion of dry habitats (Hughes et al., 2013) and favoured CAM plants (Arakaki et al., 2011), respectively. These events may be responsible for the radiation of xeric species throughout South America (e.g. Hernández-Hernández et al., 2014; Moggi et al., 2015). Further, during the Pleistocene, the recurrent climate changes probably contributed to the allopatric differentiation of populations or species in the Neotropics (Bonatelli et al., 2014; Franco and Manfrin, 2013; Taylor, 2012; Turchetto-Zolet et al., 2013).

Although phylogeographic studies of plants from dry South American ecosystems are relatively few (Turchetto-Zolet et al., 2013), Hughes et al. (2013) postulate that the evolution of plants in Neotropical Seasonally Dry Tropical Forests (SDTF) is marked by high geographical phylogenetic structure, allopatric speciation, niche conservatism and well-supported monophyly of individual species in densely sampled gene trees. For these authors, such patterns suggest a scenario of population fragmentation in arid patches (with dispersal limitation), *in-situ* diversification of species pairs or small clades, and persistence of stable populations of species or lineages over long periods of time.

Bonatelli et al. (2014) studied the phylogeography of *Pilosocereus aurisetus* (Werderm.) Byles & G.D. Rowley and allies in southeast and central Brazil. They were able to find several of the phylogenetic/phylogeographic patterns expected for SDTF taxa according to Hughes et al. (2013). This group of *Pilosocereus* Byles & G.D. Rowley seems to have suffered successive cycles of population fragmentation during wet interglacial periods, followed by demographic explosions during dry glacial periods. According to Bonatelli et al. (2014), the isolation in multiple refuges between successive glaciations would result in the allopatric origin and spread of different haplotypes, explaining the polytomic phylogeny of the genus.

This model of diversification can explain the evolution of several Neotropical plant lineages that exhibit similar phylogenetic patterns, like some Bromeliaceae (Jabaily and Sytsma, 2012) and Lamiaceae (Drew and Sytsma, 2012). However, *Pilosocereus* is widely distributed in tropical America from southeastern USA and Mexico to southeastern Brazil and Paraguay (Zappi, 1994), with representatives in geographic regions that have experienced different climatic histories during the Quaternary. Thus, a more complete phylogeographic analysis of this genus may provide a wider understanding of xeric plant evolution in the Neotropics.

At this point, we turn our attention to the informal group proposed by Zappi (1994) to include *Pilosocereus arrabidae* (Lem.) Byles & G.D. Rowley and *Pilosocereus catingicola* (Gürke) Byles & G.D. Rowley, later extended by Hunt et al. (2006) to encompass their presumably close relatives: *Pilosocereus azulensis* N.P. Taylor & Zappi and *P. splendidus* F. Ritter. Together, these species occur over a very large area in eastern Brazil, including both inland and the Atlantic coast (Taylor and Zappi, 2004). Their habitat consists of a semideciduous scrubland or low forest that experienced dry interglacial and wet glacial periods (Auler et al., 2004).

Our aim was to test hypotheses on the phylogeography of *Pilosocereus arrabidae* and allies, as well as the phylogeny of the genus, to increase our understanding of the evolutionary history of the Neotropical xeric flora. Our hypotheses are that: 1) *Pilosocereus arrabidae* and its allies form a basal group in subgenus *Pilosocereus*, based on Zappi (1994); 2) The coastal lineages of *Pilosocereus* recently radiated to northern *Caatinga* from the highland region of the 'Chapada Diamantina' – a putative centre of dispersal for many species from arid environments (Collevatti et al., 2012, 2014; Franco and Manfrin, 2013; Zappi, 1994) through the dry valley of the São Francisco River; 3) Populations of *Pilosocereus* experienced demographic reduction in Northeast Brazil during glacial events, when this region was wetter (Auler et al., 2004); 4) *P. arrabidae* and

allies survived wet periods in a putative dry refuge in the 'Chapada Diamantina' and spread to the coast in the last interglacial period; 5) Unlike *P. aurisetus* group in southeastern Brazil (Bonatelli et al., 2014), populations of *P. arrabidae* and allies should have experienced long-term gene flow due to their almost continuous geographic distribution.

Based on these hypotheses, we predicted that: 1.1) *Pilosocereus arrabidae* and its allies should be part of the most basal lineages in the phylogeny of the genus; 1.2) Taxa of the *P. arrabidae* group should exhibit reciprocal monophyly in cytoplasmic DNA, as is expected in well-established sister species (Avise, 2000; Hubbell, 2001); 1.3) *Pilosocereus arrabidae* and its allies should have an earlier divergence time when compared to the *P. aurisetus* group; 2.1) Inland populations of the *P. arrabidae* group should exhibit a higher number of haplotypes when compared to coastal populations; 2.2) Coastal populations from extremes of its geographic distribution should exhibit lower numbers of haplotypes; 3.1) Demographic analyses should reveal evidence of demographic expansion of *Pilosocereus arrabidae* and allies (that should have happened since the end of the last glacial period); 4.1) *P. arrabidae* and allies should exhibit a high number of haplotypes concentrated in a single place (i.e. 'Chapada Diamantina'); 5.1) Phylogeography of *P. arrabidae* group should not be geographically structured if the habitat occupied by its species can be considered continuous and its representatives experienced predominantly favourable climatic conditions (during interglacial periods, which were longer than the glacial).

2. Materials and methods

2.1. Biological model

Pilosocereus is one of the most diverse genera in tribe Cereeae, with 42 species recognized (Hunt et al., 2006; Zappi and Taylor, 2011) of which most inhabit eastern Brazil (Zappi, 1994). This speciose genus, which is disjunct between Brazil's eastern region and northwestern South America (reaching Mexico and the Caribbean) is in many ways an ideal model to study the diversification of lineages into more seasonal habitats during the Quaternary, as seen by Bonatelli et al. (2014).

According to Hunt et al. (2006), *P. arrabidae* and allies are characterized by the shrubby or tree-like habit, low number of ribs, undifferentiated flower-bearing areoles, acute flower-bud apex and by the robust and wide bat-pollinated flowers (Hunt et al., 2006; Locatelli et al., 1997; Zappi, 1994). *P. arrabidae* occurs along the east coast of Brazil, in the states of Rio de Janeiro, Espírito Santo and southern Bahia (Fig. 1). It inhabits the beach or patches of open shrubby vegetation widespread along sea-level sandy areas, called *Restingas*, which landwards are surrounded by a moister forest matrix (Taylor and Zappi, 2004). According to Taylor and Zappi (2004), *P. catingicola* has two subspecies: subsp. *catingicola*, which inhabits *Caatingas* of the dry valleys of the Brazilian state of Bahia; and subsp. *salvadorensis* (Werderm.) Zappi, which occurs in northern *Restingas* or in the *Caatingas* of the dry valleys, in the states of Bahia, Sergipe, Alagoas, Pernambuco, Paraíba, Rio Grande do Norte and Ceará (Fig. 1). *Pilosocereus azulensis* is known to occur in *Caatingas* of only two adjacent localities in a mountainous region in northeastern Minas Gerais (Hunt et al., 2006). *P. splendidus* provisionally refers to a plant from a unique locality in Northeast Brazil, whose taxonomic status is not yet fully understood (Hunt et al., 2006). Thus, we focused our phylogeographic analyses on *P. arrabidae* and two subspecies of *P. catingicola* (the three original taxa of the group according to Zappi, 1994).

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